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A phylogenetic classification of Leptodirini (Coleoptera, Leiodidae, Cholevinae)

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Abstract: The tribe Leptodirini of the beetle family Leiodidae is one of the most diverse radiations of subterranean animals, with a distribution centered north of the Mediterranean basin from the Iberian Peninsula to Iran. It currently comprises some 1340 species and subspecies in around 250 genera and subgenera. We present a molecular phylogeny of the tribe, and subsequently a revision of their taxonomy taking into account our phylogenetic results. We investigated and established the phylogenetic relationships of 558 species using a combination of fragments of four mitochondrial (two fragments of COI, 16s and cytochrome b) as well as two nuclear (18s and 28s) genes, analysed using maximum likelihood methods. In agreement with the results of the phylogenetic analysis we establish the following synonymies: Leptodirini Lacordaire, 1854 [1849] = Bathysciae Horn, 1880 **syn. nov.** = Pholeuones Reitter, 1886 **syn. nov.** = Anthroherpona Jeannel, 1910 **syn. nov.** = Bathysciotina V.B. Guéorguiev, 1974 **syn. nov.** = Spelaeobatina V.B. Guéorguiev, 1974 **syn. nov.** We divided the tribe Leptodirini into three subtribes, two of them monogeneric, Platycholeina and Adelopsellina **subtr. nov.**, and a third one including all of the other Leptodirini, the Leptodirina **sensu novo**. We further informally divide Leptodirina **sensu novo** into several monophyletic «series», the most of them strongly supported by the phylogeny, as well as geographically well-defined and morphologically coherent.

20 new genera and one subgenera are established: *Ariejasia* **gen. nov.** (type species *Speonomus carrerei* Fourès, 1954), *Casalella* **gen. nov.** (type species *Adelops meridionalis* Jacquelin du Val, 1854), *Catalaniana* **gen. nov.** (type species *Bathysciola zariquieyi* Bolívar, 1919), *Dupreia* **gen. nov.** (type species *Euryspeonomus beruetei* Dupré, 1991), *Galliana* **gen. nov.** (type species *Adelops linderi* Abeille de Perrin, 1875), *Georgiana* **gen. nov.** (type species *Bathysciola suramensis* Jeannel, 1930), *Hypogesia* **gen. nov.** (type species *Speocharis minos* Jeannel, 1909), *Lakedemoniana* **gen. nov.** (type species *Lakedemoniana mizerakisi* **sp. nov.**), *Luquesia* **gen. nov.** (type species *Quaestus pasensis* Salgado, Labrada & Luque, 2010), *Latellana* **gen. nov.** (type species *Bathysciola fortesculpta* Jeannel, 1914), *Nanobathysciola* **gen. nov.** (type species *Bathyscia ovata* Kiesenwetter, 1850), *Perreauia* **gen. nov.** (type species *Perreauia dalmatica* **sp. nov.**), *Pyrenaeola* **gen. nov.** (type species *Adelops lapidicola* Saulcy, 1872), *Pyrenaeola* (*Garunnia*) **subgen. nov.** (type species *Bathyscia larcennei* Abeille de Perrin, 1883), *Schaufussia* **gen. nov.** (type species *Speocharis pachecoi* Bolívar, 1915), *Serbiana* **gen. nov.** (type species *Serbiana latitarsis* **sp. nov.**), *Uhagoniella* **gen. nov.** (type species *Speocharis zariquieyi* Jeannel, 1924), *Valdesiella* **gen. nov.** (type species *Dellabeffaella olmii* Casale, 1980), *Vallespirana* **gen. nov.** (type species *Adelops grenieri* Saulcy, 1872), *Vanderberghia* **gen. nov.** (type species *Adelops speluncarum* Delarouzée, 1857) and *Zoiana* **gen. nov.** (type species *Phaneropella* (*Hittitia*) *kociani* Švec, 2016).

We describe 29 new species: *Aphaobius gorenjskanus* **sp. nov.**, *Aphaobius luckae* **sp. nov.**, *Archeoboldoria martinottii* **sp. nov.**, *Bathyscidius crnagorensis* **sp. nov.**, *Bathysciola balestrae* **sp. nov.**, *Bathysciola chestai* **sp. nov.**, *Bathysciola lanai* **sp. nov.**, *Bathysciola oliveroi* **sp. nov.**, *Batinoscelis degiovannii* **sp. nov.**, *Batinoscelis onnisi* **sp. nov.**, *Catopsinus rudoyi* **sp. nov.**, *Lakedemoniana mizerakisi* **sp. nov.**, *Latellana benellii* **sp. nov.**, *Latellana degiovannii* **sp. nov.**, *Latellana magrinii* **sp. nov.**, *Latellana petruzziellana* **sp. nov.**, *Latellana petruzzielloi* **sp. nov.**, *Nafarroa ericduprei* **sp. nov.,** *Paratroglophyes juberthiei* **sp. nov.**, *Perreauia dalmatica* **sp. nov.**, *Proleonhardella epimikes* **sp. nov.**, *Salfia angelinii* **sp. nov.**, *Salfia laudis* **sp. nov.**, *Schaufussia sinuatipenis* **sp. nov.**, *Serbiana latitarsis* **sp. nov.**, *Tamaniniella pivai* **sp. nov.**, *Troglocharinus bellesi* **sp. nov.**, *Troglocharinus rizzoae* **sp. nov.** and *Vanderberghia corbazi* **sp. nov.**

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We establish the generic synonymies: *Espanoliella* V.B. Guéorguiev, 1976 = *Samanolla* Salgado, 2000 **syn. nov.** (type species *Speocharis oxypterus* Bolívar, 1917); *Ovobathysciola* Jeannel, 1924 = *Patriziella* Jeannel, 1956 **syn. nov.** (type species *Patriziella sardoa* Jeannel, 1956) = *Sardostygia* Casale, 2019 **syn. nov.** (type species *Sardostygia cogonii* Casale, 2019); *Quaestus* Schaufuss, 1861 = *Oresigenus* Jeannel, 1948 **syn. nov.** (type species *Oresigenus jaspei* Jeannel, 1948) = *Speogeus* Salgado, 1985 **syn. nov.** (type species *Speocharis avicularis* Salgado, 1985) = *Asturianella* Salgado & Fresneda, 2004 **syn. nov.** (type species *Quaestus incognitus* Salgado & Fresneda, 2004); *Speonomus* Jeannel, 1908 = *Metaspeonomus* Coiffait, 1959 **syn. nov.** (type species *Speonomus monticola* Coiffait, 1959); *Bathysciella* Jeannel, 1906 = *Phacomorphus* Jeannel, 1908 **syn. nov.** (type species *Bathyscia Mascarauxi* Sainte Claire Deville, 1905) = *Phacomorphoides* Dupré, 1996 **syn. nov.** (type species *Bathyscia alexinae* Jeannel, 1906); *Magdelainella* Jeannel, 1924 = *Kosaniniella* S. Ćurčić, Brajković & B. Ćurčić, 2004 **syn. nov.** (type species *Kosaniniella javorensis* S. Ćurčić, Brajković & B. Ćurčić in S. Ćurčić *et al.*, 2004); *Proleonhardella* Jeannel, 1910 = *Bozidaria* S. Ćurčić & Pavićević in S. Ćurčić *et al*., 2021 **syn. nov.** (type species *Bozidaria serboocidentalis* S. Ćurčić & Pavićević in S. Ćurčić *et al*., 2021), = *Serboleonhardella* S. Ćurčić & Schönmann in S. Ćurčić *et al*., 2008 **syn. nov.** (type species *Proleonhardella remyi* Jeannel, 1934); *Rozajella* S. Ćurčić, Brajković & B. Ćurčić, 2007 in S. Ćurčić *et al*., 2007 = *Nonveilleriella* Perreau & Pavićević, 2008 **syn. nov.** (type species *Nonveilleriella ognjenovici* Perreau & Pavićević, 2008).

Six subgenera are elevated to the rank of genus: *Amphogeus* Salgado, 2000 **stat. nov.** (type species *Bathyscia cantabrica* Uhagón, 1881); *Hittitia* Casale, Giachino, Vailati & Rampini, 1991 **stat. nov.** (type species *Bathyscia* (*Bathyscia*) *turcica* Reitter, 1885); *Ochsiella* Jeannel, 1947 **stat. nov.** (type species *Bathyscia Bucheti* Abeille de Perrin, 1905); *Salfia* Tamanini, 1955 **stat. nov.** (type species *Bathysciola* (*Salfia*) *ruffoi* Tamanini, 1955); *Uludagites* Casale, Giachino, Vailati & Rampini, 1991 **stat. nov.** (type species *Phaneropella* (*Uludagites*) *minuta* Casale, Giachino, Vailati & Rampini, 1991) and *Cernella* Jeannel, 1930 **stat. nov.** (type species *Bathyscia* (*Sophrochaeta*) *reitteri* Frivaldsky, 1884).

Bathyscia schiodtei Kiesenwetter, 1850 = *Hoffmannia biokovensis* Knirsch, 1928 **syn. nov.** *Zariquieyella* Jeannel, 1929 is substitute name for *Hoffmannia* Knirsch, 1928 *nom. praeocc*. The name *Zariquieyella* applies to the genus for the species of the *Bathysciola schiodtei* group.

A lectotype is designated for *Adelops lapidicola* Saulcy, 1872.

164 new combinations for species and subspecies are proposed.

Close relationships between *Coreobathyscia* and *Proleptodirina* with Leptodirini are refuted, with the former genus appearing more closely related to Cholevini and the latter to Ptomaphagini.

Key words: Coleoptera, Leiodidae, Cholevinae, Leptodirini, molecular phylogeny, taxonomic classification, new genera, new species, new combinations.

Riassunto: *Una classificazione filogenetica dei Leptodirini (Coleoptera, Leiodidae, Cholevinae)*

La tribù dei Leptodirini, della famiglia dei Coleotteri Leiodidae, presenta una delle maggiori radiazioni degli animali sotterranei, con una distribuzione centrata a nord del bacino del Mediterraneo, dalla penisola iberica all'Iran. Attualmente comprende circa 1340 specie e sottospecie raggruppate in circa 250 generi e sottogeneri. In questo contributo presentiamo una filogenesi molecolare della tribù e, successivamente, una revisione tassonomica che tiene in considerazione i risultati filogenetici ottenuti. Abbiamo studiato e stabilito le relazioni filogenetiche di 558 specie utilizzando una combinazione di frammenti di quattro geni mitocondriali (due frammenti di COI, 16s e citocromo b) e due geni nucleari (18s e 28s), analizzati utilizzando metodi di massima verosimiglianza. In accordo con i risultati delle analisi filogenetiche stabiliamo le seguenti sinonimie: Leptodirini Lacordaire, 1854 [1849] = Bathysciae Horn, 1880 **syn. nov.**= Pholeuones Reitter, 1886 **syn. nov.** = Anthroherpona Jeannel, 1910 **syn. nov.** = Bathysciotina V.B. Guéorguiev, 1974 **syn. nov.** = Spelaeobatina V.B. Guéorguiev, 1974 **syn. nov.** Abbiamo diviso la tribù Leptodirini in tre sottotribù, due delle quali monogeneriche, Platycholeina e Adelopsellina **subtr. nov.**, e una terza, Leptodirina sensu novo, comprendente tutti gli altri Leptodirini. Dividiamo inoltre in modo informale Leptodirina sensu novo in diverse «serie» monofiletiche, la maggior parte delle quali fortemente supportate dalla filogenesi, oltre che geograficamente ben definite e morfologicamente coerenti.

Vengono istituiti 20 nuovi generi e un sottogenere: *Ariejasia* **gen. nov.** (specie tipo *Speonomus carrerei* Fourès, 1954), *Casalella* **gen. nov.** (specie tipo *Adelops meridionalis* Jacquelin du Val, 1854), *Catalaniana* **gen. nov.** (specie tipo *Bathysciola zariquieyi* Bolívar, 1919), *Dupreia* **gen. nov.** (specie tipo *Euryspeonomus beruetei* Dupré, 1991), *Galliana* **gen. nov.** (specie tipo *Adelops linderi* Abeille de Perrin, 1875), *Georgiana* **gen. nov.** (specie tipo *Bathysciola suramensis* Jeannel, 1930), *Hypogesia* **gen. nov.** (specie tipo *Speocharis minos* Jeannel, 1909), *Lakedemoniana* **gen. nov.** (specie tipo *Lakedemoniana mizerakisi* **sp. nov.**), *Luquesia* **gen. nov.** (specie tipo *Quaestus pasensis* Salgado, Labrada & Luque, 2010), *Latellana* **gen. nov.** (specie tipo *Bathysciola fortesculpta* Jeannel, 1914), *Nanobathysciola* **gen. nov.** (specie tipo *Bathyscia ovata* Kiesenwetter, 1850), *Perreauia* **gen. nov.** (specie tipo *Perreauia dalmatica* **sp. nov.**), *Pyrenaeola* **gen. nov.** (specie tipo *Adelops lapidicola* Saulcy, 1872), *Pyrenaeola* (*Garunnia*) **subgen. nov.** (specie tipo *Bathyscia larcennei* Abeille de Perrin, 1883), *Schaufussia* **gen. nov.** (specie tipo *Speocharis pachecoi* Bolívar, 1915), *Serbiana* **gen. nov.** (specie tipo *Serbiana latitarsis* **sp. nov.**), *Uhagoniella* **gen. nov.** (specie tipo *Speocharis zariquieyi* Jeannel, 1924), *Valdesiella* **gen. nov.** (specie tipo *Dellabeffaella olmii* Casale, 1980), *Vallespirana* **gen. nov.** (specie tipo *Adelops grenieri* Saulcy, 1872), *Vanderberghia* **gen. nov.** (specie tipo *Adelops speluncarum* Delarouzée, 1857) and *Zoiana* **gen. nov.** (specie tipo *Phaneropella* (*Hittitia*) *kociani* Švec, 2016).

Vengono descritte 29 nuove specie: *Aphaobius gorenjskanus* **sp. nov.**, *Aphaobius luckae* **sp. nov.**, *Archeoboldoria martinottii* **sp. nov.**, *Bathyscidius crnagorensis* **sp. nov.**, *Bathysciola balestrae* **sp. nov.**, *Bathysciola chestai* **sp. nov.**, *Bathysciola lanai* **sp. nov.**, *Bathysciola oliveroi* **sp. nov.**, *Batinoscelis degiovannii* **sp. nov.**, *Batinoscelis onnisi* **sp. nov.**, *Catopsinus rudoyi* **sp. nov.**, *Lakedemoniana mizerakisi* **sp. nov.**, *Latellana benellii* **sp. nov.**, *Latellana degiovannii* **sp. nov.**, *Latellana magrinii* **sp. nov.**, *Latellana petruzziellana* **sp. nov.**, *Latellana petruzzielloi* **sp. nov.**, *Nafarroa ericduprei* **sp. nov.**, *Paratroglophyes juberthiei* **sp. nov.**, *Perreauia dalmatica* **sp. nov.**, *Proleonhardella epimikes* **sp. nov.**, *Salfia angelinii* **sp. nov.**, *Salfia laudis* **sp. nov.**, *Schaufussia sinuatipenis* **sp. nov.**, *Serbiana latitarsis* **sp. nov.**, *Tamaniniella pivai* **sp. nov.**, *Troglocharinus bellesi* **sp. nov.**, *Troglocharinus rizzoae* **sp. nov.** e *Vanderberghia corbazi* **sp. nov.**

Stabiliamo le seguenti sinonimie di generi: *Espanoliella* V.B. Guéorguiev, 1976 = *Samanolla* Salgado, 2000 **syn. nov.** (specie tipo *Speocharis oxypterus* Bolívar, 1917); *Ovobathysciola* Jeannel, 1924 = *Patriziella* Jeannel, 1956 **syn. nov.** (specie tipo *Patriziella sardoa* Jeannel, 1956) = *Sardostygia* Casale, 2019 **syn. nov.** (specie tipo *Sardostygia cogonii* Casale, 2019); *Quaestus* Schaufuss, 1861 = *Oresigenus* Jeannel, 1948 **syn. nov.** (specie tipo *Oresigenus jaspei* Jeannel, 1948) = *Speogeus* Salgado, 1985 **syn. nov.** (specie tipo *Speocharis avicularis* Salgado, 1985) = *Asturianella* Salgado & Fresneda, 2004 **syn. nov.** (specie tipo *Quaestus incognitus* Salgado & Fresneda, 2004); *Speonomus* Jeannel, 1908 = *Metaspeonomus* Coiffait, 1959 **syn. nov.** (specie tipo *Speonomus monticola* Coiffait, 1959); *Bathysciella* Jeannel, 1906 = *Phacomorphus* Jeannel, 1908 **syn. nov.** (specie tipo *Bathyscia Mascarauxi* Sainte Claire Deville, 1905) = *Phacomorphoides* Dupré, 1996 **syn. nov.** (specie tipo *Bathyscia*

alexinae Jeannel, 1906); *Magdelainella* Jeannel, 1924 = *Kosaniniella* S. Ćurčić, Brajković & B. Ćurčić, 2004 **syn. nov.** (specie tipo *Kosaniniella javorensis* S. Ćurčić, Brajković & B. Ćurčić in S. Ćurčić et al., 2004); *Proleonhardella* Jeannel, 1910 = *Bozidaria* S. Ćurčić & Pavićević in S. Ćurčić et al., 2021 **syn. nov.** (specie tipo *Bozidaria serboocidentalis* S. Ćurčić & Pavićević in S. Ćurčić et al., 2021), = *Serboleonhardella* S. Ćurčić & Schönmann in S. Ćurčić et al., 2008 **syn. nov.** (specie tipo *Proleonhardella remyi* Jeannel, 1934); *Rozajella* S. Ćurčić, Brajković & B. Ćurčić, 2007 in S. Ćurčić et al., 2007 = *Nonveilleriella* Perreau & Pavićević, 2008 **syn. nov.** (specie tipo *Nonveilleriella ognjenovici* Perreau & Pavićević, 2008).

Sei sottogeneri sono elevati al rango di generi: *Amphogeus* Salgado, 2000 stat. nov. (specie tipo *Bathyscia cantabrica* Uhagón, 1881); *Hittitia* Casale, Giachino, Vailati & Rampini, 1991 stat. nov. (specie tipo *Bathyscia* (*Bathyscia*) *turcica* Reitter, 1885); *Ochsiella* Jeannel, 1947 stat. nov. (specie tipo *Bathyscia Bucheti* Abeille de Perrin, 1905); *Salfia* Tamanini, 1955 **stat. nov.** (specie tipo *Bathysciola* (*Salfia*) *ruffoi* Tamanini, 1955); *Uludagites* Casale, Giachino, Vailati & Rampini, 1991 **stat. nov.** (specie tipo *Phaneropella* (*Uludagites*) *minuta* Casale, Giachino, Vailati & Rampini, 1991) e *Cernella* Jeannel, 1930 **stat. nov.** (specie tipo *Bathyscia* (*Sophrochaeta*) *reitteri* Frivaldsky, 1884).

Bathyscia schiodtei Kiesenwetter, 1850 = *Hoffmannia biokovensis* Knirsch, 1928 **syn. nov.** *Zariquieyella* Jeannel, 1929 è nomen novum per *Hoffmannia* Knirsch, 1928 nom. praeocc. Il nome *Zariquieyella* si applica al genere per le specie del gruppo di *Bathysciola schiodtei*.

Viene designato il lectotypus di *Adelops lapidicola* Saulcy, 1872.

Sono proposte 164 nuove combinazioni per specie e sottospecie.

Sono confutate le strette relazioni tra *Coreobathyscia* e *Proleptodirina* con i Leptodirini, con il primo genere che appare più strettamente imparentato con i Cholevini e il secondo con i Ptomaphagini.

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Exactly 100 years after the publication of the fundamental «Monographie des Bathysciinae» by René Jeannel, we dedicate this contribution to this giant of the entomology

Introduction

Leptodirini is a tribe of Leiodidae within subfamily Cholevinae. Currently it has approximately 1000 described species in around 235 genera. It´s geographic distribution stretches from the mountain massifs of the Mediterranean region in the Northern hemisphere, hence from the northwest of the Iberian Peninsula to Northern Iran. However, some isolated species are found in the Far East around Shanghai in China, and in the West in California in the USA (Fresneda *et al.* 2011b: Fig. 1). Most species of Leptodirini are strictly subterranean, many with highly modified morphologies that are traditionally interpreted as adaptations to the subterranean environment. This so-called troglobiont phenotype is characterised for instance by depigmentation, loss of eyes and wings, slender body and appendages and hypertrophy of the non-optic sensory organs. They also have many other physiological and ecological modifications associated to the subterranean habitat (e.g. fat metabolism, reduced endocrine activity, temperature and humidity regulation, absent circadian rhythms, etc.) Nevertheless their origin, adaptive value and taxonomic prevalence are still poorly understood. Notably among those adaptations is a change of reproductive strategy towards a K-strategy, including changes such as production of fewer eggs larger and with a long developmental times, the reduction of the number of larval instars and longer postembryonic development. Also sexual maturity reached much later than expected for small animals like cave beetles as is the extremely long life expectancy.

These adaptations were studied in great detail by the researchers in the Moulis subterranean laboratory mainly in the sixties and seventies of the last century (Jeannel 1943; Glaçon 1955a, 1956; Glaçon-Deleurance 1958, 1961; Deleurance-Glaçon 1963; Juberthie & Decu 1970; Juberthie-Jupeau & Cazals 1988; Adamcyk *et al*. 2011). Thus, from species with the ancestral life cycle of three instar active campodeiform larvae, different lineages independently developed a two instar life cycle, and finally a fully «contracted» life cycle where the larval development is reduced to a single instar with an immobile and non-feeding larvae which is immediately after hatching building a cocoon and stays immobile absorbing only water through the cuticle until it pupates and metamorphoses into an adult (Cieslak *et al*. 2014a, 2014b).

The Leptodirini have attracted the attention of subterranean biologists and entomologists ever since the description of the first species, *Leptodirus hochenwartii* F.J. Schmidt, 1832, which was also the first troglobiomorphic invertebrate to be described. The general resemblance of troglobiomorphic species, with a similar phenotype in species of very different origin, poses an additional difficulty when trying to recognise true phylogenetic relationships among species or lineages using morphological approaches. The total lack of fossils further hampered the efforts to establish the phylogenetic relationship as there is no knowledge on the ancestral characters from fossils or a temporal framework for the evolution of the tribe.

The first classification proposed for Leptodirini was that of Reitter (1885a, 1886a, 1889a, 1908c), who, based on external characters, grouped the species in three morphological types, bathyscioid, pholeuonoid and leptodiroid. Ganglbauer (1899a: 76) introduced a more evolutionary view, subsequently adopted by Jeannel (1924a): «Es ist sehr bemerkenswerth, dass die ganz eigenthümlich differenzirte Gestalt eines *Leptoderus* durch eine fast continuirliche Reihe von Zwischenformen mit der wenig differenzirten, geschlossen ovalen Gestalt einer *Bathyscia* verbunden ist.» [«It is noteworthy that the peculiarly differentiated shape of a *Leptoderus* is connected by an almost continuous series of intermediate forms with the less differentiated, compact oval shape of a *Bathyscia*»]. In this work, the author also provided excellent descriptions of the genera and species, and described a large number of characters.

The structure of the male genitalia was used for the first time in the classification of Leptodirini by Jeannel (1910a, 1911a), who recognised that each species has a particular conformation that according to Jeannel (1914a, 1922a) corresponds «en quelque sorte à la signature d'une série phylétique» [«in some way to the signature of a phyletic series»]. Jeannel (1910a, 1911a) proposed the use of the genital structures of the male to hypothesise on the evolutionary history of the species, establishing the main models of the internal sac of the aedeagus (the endophallus) and largely obviating the aedeagus itself in his revisions of the group

(Jeannel, 1911a, 1922a). Later, Jeannel (1924a) coined the term «section» to organize the «phyletic series» of *Bathysciola*, and later, the term «group of species» (Jeannel, 1947a). His classification was based on the following characters: (i) insertion of antennae, and relative length of the first two antennomeres; (ii) shape and size of the claws; (iii) number of male protarsomeres; (iv) structure of the apex of tibiae (presence of a comb of setae, presence of spurs or of an excavation). Subsequently, Jeannel (1947a) proposed a classification of the large Pyrenean genus *Speonomus* based on the structure of the apex of the lateral stylus of the tegmen (the parameres), and Jeannel (1955a) established what he considered the fundamental division of Leptodirini (by then called Bathysciinae), the «Supraflagellates» and «Infraflagellates», based on the presence or absence and the position (dorsal or ventral) of a sclerotized «Y»-like shaped structure (the «pièce en Y») at the base of the endophallus.

Reitter (1910) rejected Jeannel's (1910a) classification, essentially on the grounds that he had fragmented the genus *Bathyscia*, which he considered «homogeneous». Breit (1913a) attempted to reconcile the two views by maintaining Reitter's arrangement but incorporating Jeannel's subgenera of *Bathyscia*.

G. Müller (1917) made an interesting contribution in which he grouped the bathyscioid genera according to new characters: the structure of the male protarsus and the armor of the protibiae (presence/absence of the pectinated series of small spines on the outer face).

Laneyrie (1967, 1970, 1978) used the structures of the basal region of the endophallus to divide Bathysciinae into four groups, one of them further subdivided into subgroups. Laneyrie (1978) acknowledged Jeannel (1955a) as the original work in which these structures were recognized, ignoring previous papers by the same author (Jeannel, 1910a, 1924a) and the characters described in them. He also explicitly stated that his classification did not pretend to reflect the phylogeny of the group.

V.B. Guéorguiev (1974a, 1974b, 1976) basically rejected Laneyrie (1967) grouping and returned to the original classification of Jeannel (1910a), using the same characters and upgrading Jeannel's groups at subfamilial rank.

Casale *et al*. (1991a) proposed a new systematic model for the highest phyletic lines of the subfamily Leptodirinae and established two dendrograms, taking into account the arrangements and generic distribution in genera proposed by Jeannel (1924a), Laneyrie (1967) and V.B. Guéorguiev (1976).

Newton (1998) established a subtribal key of the tribe Leptodirini, including Platycholeina in Leptodirini, and excluded *Neotropospeonella* Pace, 1983 considering it as a group *incertae sedis*.

Giachino *et al*. (1998) maped characters but did not introduce formal changes. They proposed a hypothesis and origin for the different subfamilies, and zoogeographical history of the Cholevidae as a whole. Among the subfamilies, Leptodirinae present the most specialised and impressive adaptations to the subterranean environment. For this reason, convergent adaptive features are present in different genera and/or phyletic lineages which are not directly related to each other. They combined the classification of Jeannel (1910a, 1955a) with new data in a phylogenetic tree.

Perreau (1989, 2000), in the first of his works, build the foundations for the phylogeny of the Cholevidae subfamilies and pointed out tetramery in females of all Leptodirini and a study on the uroventrite VIII and spermathecal complex of females as the basis of that classification. For that reason, in his second work he excluded *Sciaphyes* from Leptodirini and placed it in his own tribe Sciaphyini.

Fresneda *et al*. (2007) questioned what has been considered the most primitive division of the Leptodirinae, according to Jeannel (1955a), «Supraflagellates» and «Infraflagellates». Fresneda *et al*. (2011b) using molecular data confirmed that *Platycholeus* is sister to all old world Leptodirini, and confirmed the exclusion of *Sciaphyes* Jeannel, 1910. They also excluded the Eastern Palaearctic genus *Fusi* Perkovsky, 1989 from Leptodirini, being more related to Cholevini.

Antunes-Carvalho & Gnaspini (2016) added completely new morphological elements of Leptodirini to the morphological analysis, such as the sensilla that are projected onto the apical maxillary palpomere or the pore plates of the terminal tarsomere. Although the scarce material studied did not allow them to obtain a high resolution inside the Leptodirini clade they were able to point out the very important issue, that the modern subtribal classification is obsolete, this is in accordance with what is supported by the presented molecular phylogeny. Antunes-Carvalho *et al*. (2019) and Gnaspini *et al*. (2017a, 2017b, 2020) highlighted the importance of the arrangement, insertion part and shape of the spurs and spines at the apex of all the tibiae, as well as the claws and setae brushes on the ventral side of the tarsomeres, to establish phylogenetic relationships between the tribes and subtribes of Leiodidae. They suggested that these morphological characters might bear phylogenetic signal. Antunes-Carvalho *et al*. (2019) made a cladistic hypothesis based on putative synapomorphies or molecular studies,

based on an extensive set of morphological characters, which allowed an evaluation of relationships between tribes and/or subtribes of Cholevinae. They concluded the monophyletic origin of Cholevinae, and precised the position of various tribes and their relationships. The fundamental role of the male genital structures and the relevant importance of the female abdominal terminalia were also pointed out, and in the list of characters they showed the great value of the morphological characteres of the ventral side in taxonomic descriptions, in contrast to the common practice which usually only focuses on dorsal characters.

The current classification thus basically follows that of Jeannel (1910a) and V.B. Guéorguiev (1974a, 1974b, 1976) based on a combination of characters, not in a formal phylogenetic analysis. With some modifications this is the classification currently in use (e.g. Perreau 2000, 2004):

Tribe Bathysciini (changed to Leptodirini by Newton 1998)

1 (10) Insertion of the antennae in the basal third of the head. Claws slender, long and thin.

2 (5) Male protarsi with four tarsomeres, «Théléomorphes» of Jeannel (1910a, 1924a).

3 (4) Protibia without series of spines in the external apical margin, with 2-3 well-developed external spurs. Meso and metatibia without excavations or apical expansions, with well-developed external spurs: Subtribe Bathysciina (corresponding to the Division II of Jeannel, 1910a, 1924a).

4 (3) Protibia with a series of spines on the external apical margin, without external spurs. Meso and metatibia with a cavity flanked by an expansion: Subtribe Bathysciotina (corresponding to the Division III of Jeannel, 1910a, 1924a).

5 (2) Male protarsi with five tarsomeres, «Euryscapes» and «Brachyscapes» of Jeannel (1910a, 1924a).

6 (9) Protibia with at least one well-developed external spur, but without series of spines in the external apical margin. Meso- and metatibia with well-developed external spurs.

7 (8) Protibia with 2–3 well-developed apical spurs, without series of spines and without excavation flanked by an apical expansion: Subtribe Pholeuonina (Pholeuina in Newton, 1998) (corresponding to the Divisions I and IV in pars of Jeannel, 1910a, 1924a).

8 (7) Protibia with a single well-developed external apical spur, with an excavation flanked by apical expansions but without series of spines at the external apical margin. Meso- and metatibia with an excavation flanked by apical expansions: Subtribe Ghidiniina – a synonymy of Pholeuina Newton (1998) – (corresponding *in pars* to the Division IV of Jeannel 1910a, 1924a).

9 (6) Protibia without well-developed external apical spurs, usually with series of spines. Meso- and metatibia without external spurs, usually with an apical excavation flanked by an expansion: Subtribe Leptodirina (corresponding to the Division V of Jeannel 1924a).

10 (1) Antenna inserted in the posterior part of the head. Claws very long, concave, curved and spoon shaped: Tribe Anthroherponini (subtribe Anthroherponina by Perreau 2000).

11 (12) Mesoventrite with a more or less developed keel, male protarsi with four tarsomeres: Subtribe Speleaobatina.

12 (11) Mesoventrite without carina, male protarsi with five tarsomeres: Subtribe Anthroherponina.

As shown below, all these characters show some degree of homoplasy, rendering the currently recognised subtribes para- or polyphyletic.

Material and methods

Taxon sampling and morphological study

Specimens used in the study (Appendix 2) were collected by the authors, obtained from private collaborators or loans from institutional collections. For the study of material preserved dry and glued on cardboard labels we first unglued the specimen and rehydrated the specimens before their genitalia whenever were dissected if required. After this procedure they were re-mounted on the same card or on a new one. Newly obtained specimens were collected by hand or in pitfall traps, usually containing salt-saturated water (following the technique proposed by Giachino & Vailati, 2010) or contained propylene glycol (known to preserve DNA, Rubink *et al.* 2003; López & Oromí 2010). After collection specimens were transferred to vials containing either 70% (for morphological studies) or 96% ethanol (for DNA extraction and sequencing). Specimens preserved in 70% ethanol and specimens after DNA extraction were mounted on cards for subsequent morphological studies and served as voucher specimens in the collections. We dissected their genitalia and either mounted them directly in water-soluble dimethyl hydantoin formaldehyde resin (DMHF) on a transparent card or treated it with an aqueous solution of KOH 10% for six hours. After this treatment, genitalia were dehydrated in a series of increased ethanol concentrations (60º–96º) for ca. 15', and finally xylene for ca. 12h. Genitalia were then

mounted in Canada balsam on a transparent acetate card, and pinned with the same specimen. To allow the study of the aedeagus in dorsal view, the median lobes were mounted with the base and the apex resting on the transparent card and photographed in a view perpendicular to the card. Photographs of the habitus and other external structures were done with an Olympus SZX16 stereomicroscope (Olympus, Tokyo, Japan); photographs of the aedeagus, spermathecal complex and female uroventrite VIII were done with an Olympus CH transmission microscope. In both cases we used an Olympus C5060WZ digital camera to obtain serial photographs, which were subsequently stacked with CombineZP (Informer Technologies Inc., Dominica) and processed with Adobe Photoshop CS (Adobe, San José, California); SEM photographs have been made with a Hitachi S3500N scanning electron microscope (Hitachi High-Technologies Co., Ltd., Tokyo, Japan) at the Institute of Marine Sciences, Barcelona (ICM) of the Spanish Consejo Superior de Investigaciones Científicas (CSIC). The figures obtained from other sources are acknowledged in the respective figure legends. Body length was measured between the anterior margin of the labrum and the apex of the elytra.

We focussed the morphological study on the structures as described in detail below: body appearance, structure of the antennae, shape of the pronotum, elytra, legs, structure and position of tibial spurs and setae; tarsal setae; empodial seta (Jeannel 1924a; Newton 1998; Antunes-Carvalho & Gnaspini 2016; Gnaspini *et al*. 2017a, 2017b, 2020); mesoventral keel; metaventral sutures (sutures of the metaventrite); metatergal structures (Friedrich & Beutel 2006); metendosternite; spermathecal complex – Bellés, 1984; Perreau 1989; Fresneda 1998; Salgado *et al*. 2008 –; median lobe of aedeagus, endophallus, or internal sac of the aedeagus – many of the structures of the endophallus have been described by Jeannel (1924a, 1955a), Bellés (1984), Dupré (1989, 1990) and Fresneda (1998) –, we only include those with taxonomic relevance in the studied species, the «Y»-piece («pièce en Y» of Jeannel 1924a), dorsal and ventral phanerae («faneras» *sensu* Bellés, 1984), nodules of the phanerae and floating pieces (Fresneda 1998), apical reinforcement stripes («bandelette de renforcement apical» of Jeannel 1924a), and sclerotized nodules (Dupré 1989, 1990); lateral stylus of the tegmen (parameres); female uroventrite VIII.

The order in the description of the series in the text is given according to their placement in the phylogenetic tree (Figs 1A–1K) – it is arranged in the order of the cladogenesis, from the most basal to the most derived.

The genera and subgenera in the different series are arranged alphabetically, as well as the groups and subgroups if present. Those series for which no molecular data is available have been placed after the series that seemed closest by morphological characteristics and distribution area. In the lists of names of the species of each genus, only synonyms and changes in genus or subgenus are incorporated. The list of species is updated until 30 September 2024.

DNA extraction and sequencing

For DNA extraction and sequencing we used the same methods as given in detail e.g. in Ribera *et al*. (2010), Faille *et al*. (2010a, 2010b) or Fresneda *et al*. (2011b, 2019, 2021). Extractions of single specimens were non-destructive, using a standard phenol chloroform extraction or commercial kits following manufacturer's indications (usually the DNeasy Tissue Kit or Qiagen GmbH, Hilden, Germany). Specimen vouchers and DNA samples are kept in the collection of the Museo Nacional de Ciencias Naturales (MNCN, Madrid) and the authors collections (see Appendix 2).

We amplified fragments of four mitochondrial and two nuclear genes in six PCR reactions. Mitochondrial genes were 5' and 3' ends of cytochrome c oxidase subunit (cox1 5', the barcode, and cox1 3' respectively); a single fragment including the 3' end of the large ribosomal unit (rrnL), the whole tRNA-Leu gene (trnL) and the 5' end of the NADH dehydrogenase 1 (nad1); and an internal fragment of the cytochrome b gene (cob). Nuclear genes were internal fragments of the large and small ribosomal units (LSU and SSU respectively) (see Table 1 for details on the primers used). Sequences were assembled and edited using Sequencher TM 4.8 (Gene Codes, Inc., Ann Arbor, Michigan) or Geneious R10 (https://www.geneious.com). In total 1249 new sequences were submitted to database (https://www.ncbi.nlm.nih.gov/genbank/).

Electronic Supplement Files
at https://doi.org/10.4081/memoriesei.2024.3

File 1: Fresneda_et_al_2024_Leptodirini_phylogeny_matrix.nex. Concatenated alignment as used in phylogenetic analysis.

File 2: Fresneda_et_al_2024_Leptodirini_phylogeny_Appendix_2.xlsx. Material used in the molecular phylogeny, with code voucher, locality, date, collector and GenBank accession numbers. (In progress: 27.XI.2024).

TABLE I. Primers used in the PCR amplification and sequencing

Gene	Name	Sense	Sequence	Reference
cox1-3'	Jerry (M202)	F	CAACATTTATTTTGATTTTTTGG	Simon *et al.* (1994)
	Pat (M70)	R	TCCA(A)TGCACTAATCTGCCATATTA	Simon *et al.* (1994)
	Chy	F	T(A/T)GTAGCCCA(T/C)TTTCATTA(T/C)GT	Ribera *et al.* (2010)
	Tom	R	AC(A/G)TAATGAAA(A/G)TGGGCTAC(T/A)A	Ribera *et al.* (2010)
	Tom-2	R	A(A/G)GGGAATCATTGAATAAA(A/T)CC	Ribera *et al.* (2010)
cox1-5'	LCO1490	F	GGTCAACAAATCATAAAGATATTGG	Folmer *et al.* (1994)
	HCO 2198	R	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al.* (1994)
	Uni LepF1b	F	TAATACGACTCACTATAGGGATTCAACCAATCATAAA GATATTGGAAC	Hebert *et al.* (2004)
	Uni LepR1	R	ATTAACCCTCACTAAAGTAAACTTCTGGATGTCCAAA AAATCA	Hebert *et al.* (2004)
cob	CB3	F	GAGGAGCAACTGTAATTACTAA	Barraclough *et al*. (1999)
	CB4	R	AAAAGAAA(AG)TATCATTCAGGTTGAAT	Barraclough *et al*. (1999)
rrnL-nad1	16saR (M14)	F	CGCCTGTTTA(A/T)CAAAAACAT	Simon *et al.* (1994)
	16Sa	R	ATGTTTTTGTTAAACAGGCG	Simon *et al.* (1994)
	16Sb	R	CCGGTCTGAACTCAGATCATGT	Simon *et al.* (1994)
	16SAlf1	R	GCATCACAAAAAGGCTGAGG	Vogler *et al.* (1993)
	ND1A (M223)	R	GGTCCCTTACGAATTTGAATATATCCT	Simon *et al.* (1994)
SSU	5'	F	GACAACCTGGTTGATCCTGCCAGT	Shull *et al.* (2001)
	b5.0	R	TAACCGCAACAACTTTAAT	Shull *et al.* (2001)
LSU	Ka	F	ACACGGACCAAGGAGTCTAGCATG	Ribera *et al.* (2010)
	Kb	R	CGTCCTGCTGTCTTAAGTTAC	Ribera *et al.* (2010)

Phylogenetic analysis

We included in the analysis a selection of sequences from previous works (mostly Ribera *et al.* 2010; Fresneda *et al.* 2011b; Rizzo *et al.* 2013; Cieslak *et al.* 2014a; Njunjić 2016; Fresneda *et al.* 2019, 2021, 2022), plus sequences downloaded from Genbank and the newly obtained sequences (Appendix 2). As outgroups we included a wide representation of different subfamilies and tribes of Leiodidae. We rooted the tree with a selection of Staphylinidae species (Appendix 2), known to belong to the same superfamily Staphylinoidea but clearly outside Leiodidae (Lawrence & Newton 1982, 1995; Newton 2005).

The sequences of the genes that show variation in length have been aligned using the MAFFT online v 7.520 program applying the strategy Auto: FFT-NS-i = 16s, 18s, 28s, bar, cob; FFT-NS-2 = COI. The matrix with the concatenated sequences has been analyzed using maximum likelihood algorithms with IQ TREE v1.6 (Nguyen *et al*. 2015), using three partitions corresponding to the mitochondrial protein coding genes (bar+cob+COI), the 16s, mitochondrial ribosomal (rrnL+trnL) + mitochondrial protein coding gene (nad1) and the nuclear ribosomal (18s+28s). ModelFinder (Kalyaanamoorthy *et al.* 2017) plus the Akaike Information Criterion (AIC) were applied to select the most appropriate evolutionary model for every partition. Three trees obtained with different evolutionary models for each partition are provided:

– Tree-1 is shown complete, with all species and support values for all nodes, plus a summarized version with support values only for the large clades; par-

tition models = GTR+F+R8: 16s, SYM+I+G4: 18s+28s, GTR+F+R5: barcobCOI.

– Tree-2 is offered in the condensed version, also with the support values only for the large clades; an alternative position of some clades is shown that does not affect the general topology and is very similar to Tree-1; partition models = GTR+F+R8: 16s, SYM+I+G4: 18s+28s, GTR+F+R10: bar+cob+COI.

– From Tree-3 only one alternative position of the *Halbherria-Neobathyscia* clade is shown; partition models = GTR+F+R10: 16s, SYM+I+G4: 18s+28s, GTR+F+R6: bar+cob+COI.

Topological stability and node support were assessed with 1000 bootstraps (UFBoot) (Minh *et al.* 2013; Hoang *et al.* 2018) and 1000 SH-aLRT replicates (Nguyen *et al.* 2015).

Acronyms

The following acronyms for institutions and private collections are used in the text:

CAC: coll. A. Casale (Torino, Italy)
CAF: coll. A. Faille (Stuttgart, Germany)
CCB: coll. C. Bourdeau (Rebigue, France)
CDB: coll. D. Bianco (Vicenza, Italy)
CDV: coll. D. Vailati (Brescia, Italy)
CEP: coll. E. Piva (Vicenza, Italy)
CFL: coll. Fresneda-Lagar (Llesp, Spain).
CLP: coll. L. Petruzziello (Brescia, Italy)
CPM: coll. P. Magrini (Firenze, Italy)
CPMG: coll. P.M. Giachino (Torino, Italy)
CMB: coll. M. Bastianini (Firenze, Italy)
CMNH: Croatian Museum of Natural History (Zagreb, Croatia)
CZULE: Colecciones Zoológicas de la Universidad de León (León, Spain)
IBE: Institut de Biologia Evolutiva (Barcelona, Spain)
MNCN: Museo Nacional de Ciencias Naturales (Madrid, Spain)
MNHNP: Museum National d'Histoire Naturelle (Paris, France)
MZB: Museu de Ciències Naturals (Zoologia) (Barcelona, Spain)
SMNS: State Museum of Natural History (Stuttgart, Germany)
ZSM: Zoologische Staatssammlung München (Munich, Germany).

In the literal transcription of the labels the following abbreviations are used: hw = handwritten, pr = printed, rl = red label.

Results and discussion

A molecular phylogeny of Leptodirini

The phylogram obtained is shown in figures 1A–1K. We report the results with 558 terminals (species and subspecies). In IQ-TREE analysis the monophyly of the tribe Leptodirini, with the inclusion of *Platycholeus* and the exclusion of *Sciaphyes* and *Fusi*, was strongly supported in all molecular analysis (Fig. 2: Tree-1: 99.5/100; Tree-2: 99.9/100). Also in all analysis the first split in Leptodirini was between *Platycholeus* and the rest (in agreement with current classification, Newton 1998; Fresneda *et al.* 2011b), and the second between *Adelopsella* and the rest of genera, always with strong support (Fig. 2: Tree-1: 92.6/98: Tree-2: 91.7/98). The sister group of Leptodirini is *Prionochaeta* Horn, 1880 (Cholevini, Cholevina) with extremely low support among them 0/14 (Fig. 1J). The subtribes in the sense of Perreau (2000, 2004), Anthroherponina, Bathysciina, Bathysciotina, Leptodirina and Pholeuina are para- or polyphyletics:

– Anthroherponina: *Croatodirus*, currently included in this subtribe actually situates in the *Leptodirus* clade, is the sister genus to *Parapropus*, *Charonites* and *Apholeuonus* with strong support (99.6/100); but they also form part of the *Anthroherpon* clade, *Remyella*, *Rozajella* and *Pholeuonella* (in Leptodirina sec. Perreau 2000, 2004) with 100/99 support, *Pholeuonopsis*, *Proleonhardella*, and *Leonhardella* (in Bathysciina sec. Perreau 2000, 2004), and *Speonesiotes* (*Kulzeria*) (in Bathysciotina sec. Perreau 2000, 2004) with support 88.1/89. The *Anthroherpon* clade is thus composed of elements from four of the subtribes (Fig. 3). To convert Anthroherponina in a monophyletic group, one genus would have to be excluded and genera from other subtribes incorporated, but there are no morphological elements supporting a transfer of this kind.

– Bathysciina, sec. Perreau (2000, 2004), incorporates genera from the *Anthroherpon* clade (*Pholeuonopsis*, *Proleonhardella* and *Leonhardella*), from the *Oryotus* clade (*Aphaobius*, *Lotharia*, *Oryotus*, *Cansiliella* and *Orostygia*), from the *Cytodromus* clade (*Speophyes*), and from the *Hittitia* clade (*Hittitia* stat. nov. and *Uludagites* stat. nov.) although the latter is listed as a sister group to the *Drimeotus* clade with very low support, 21.7/66. Again this subtribe was identified as being an artificial group united by effects of homoplasys; it is made up of elements that molecular study indicates should be placed in four clades distributed along the phylogenetic tree (Fig. 3). There are no morphological

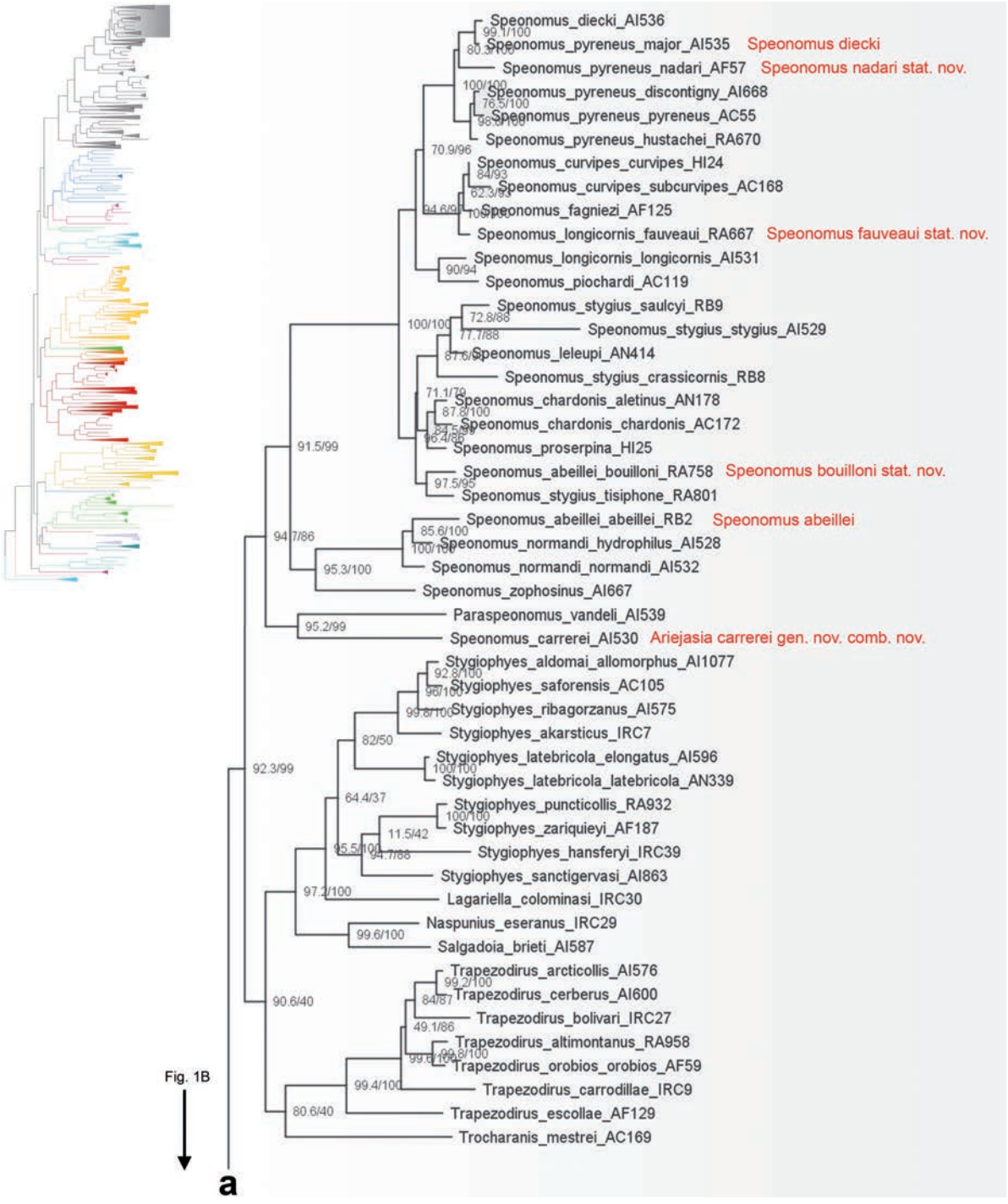


FIGURE 1A: Tree-1: Majority rule consensus tree obtained in IQ TREE v1.6 using the combined data matrix with the reconstructed Leptodirini phylogeny (analysis data in the Material and Methods section). Maximum likelihood supports of the Ultrafast Bootstrap and SH-aLRT (UFBoot/SH-aLRT) tests are shown above the nodes. See Appendix 2 for details on specimens. In red new taxa (gen. nov., subgen. nov., sp. nov.) and taxonomic changes (comb. nov., stat. nov.)

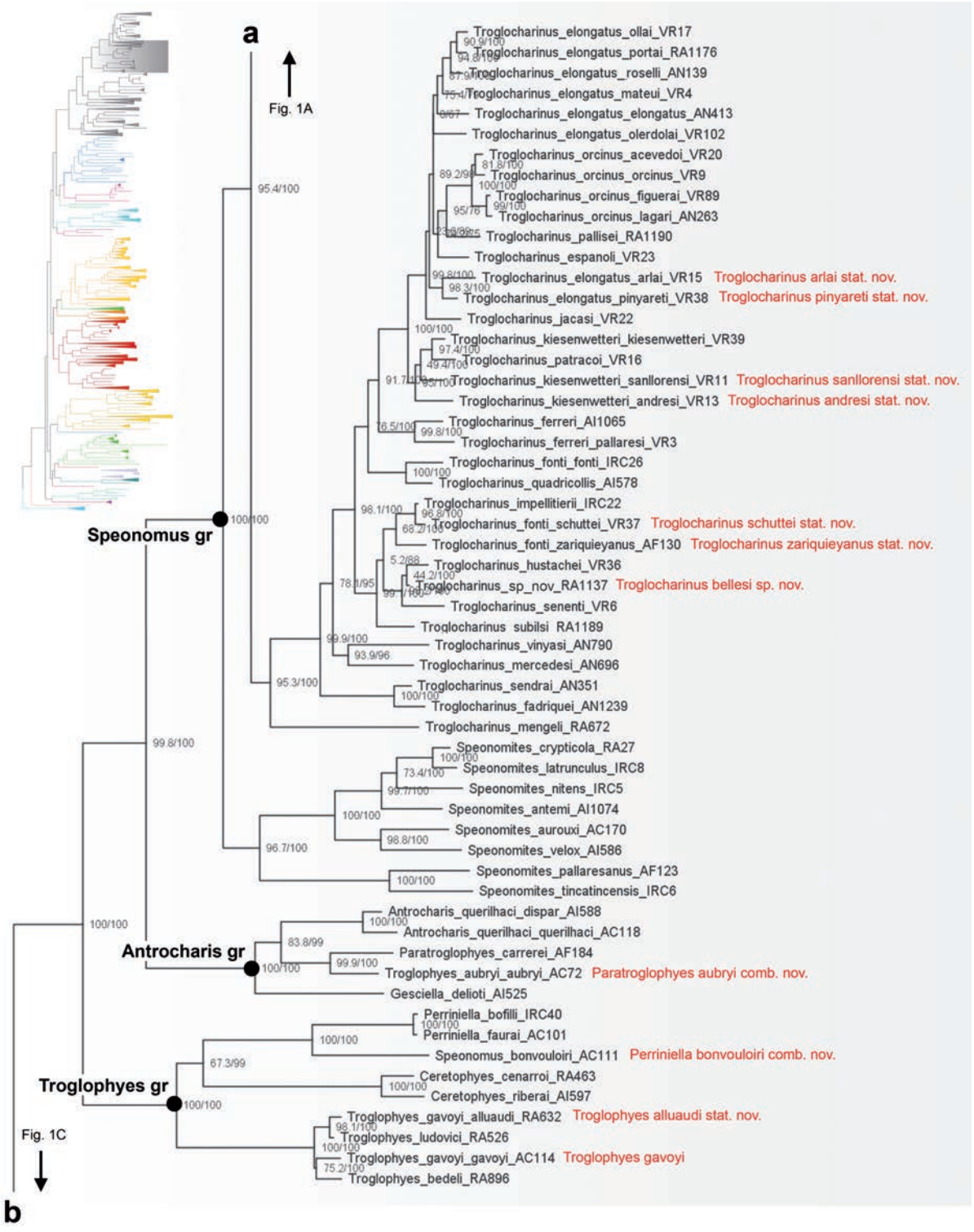


FIGURE 1B: (continued)

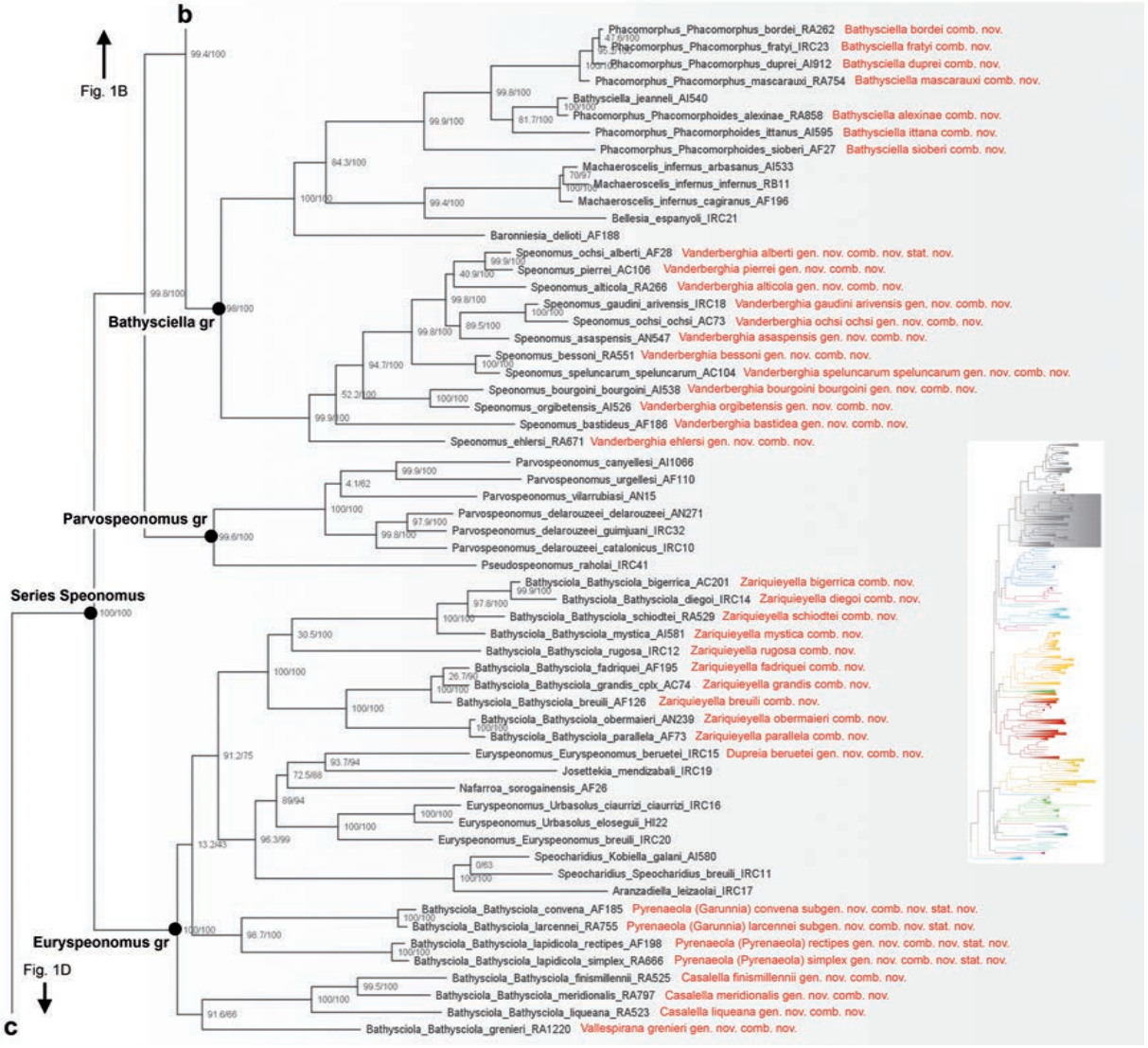


FIGURE 1C: (continued)

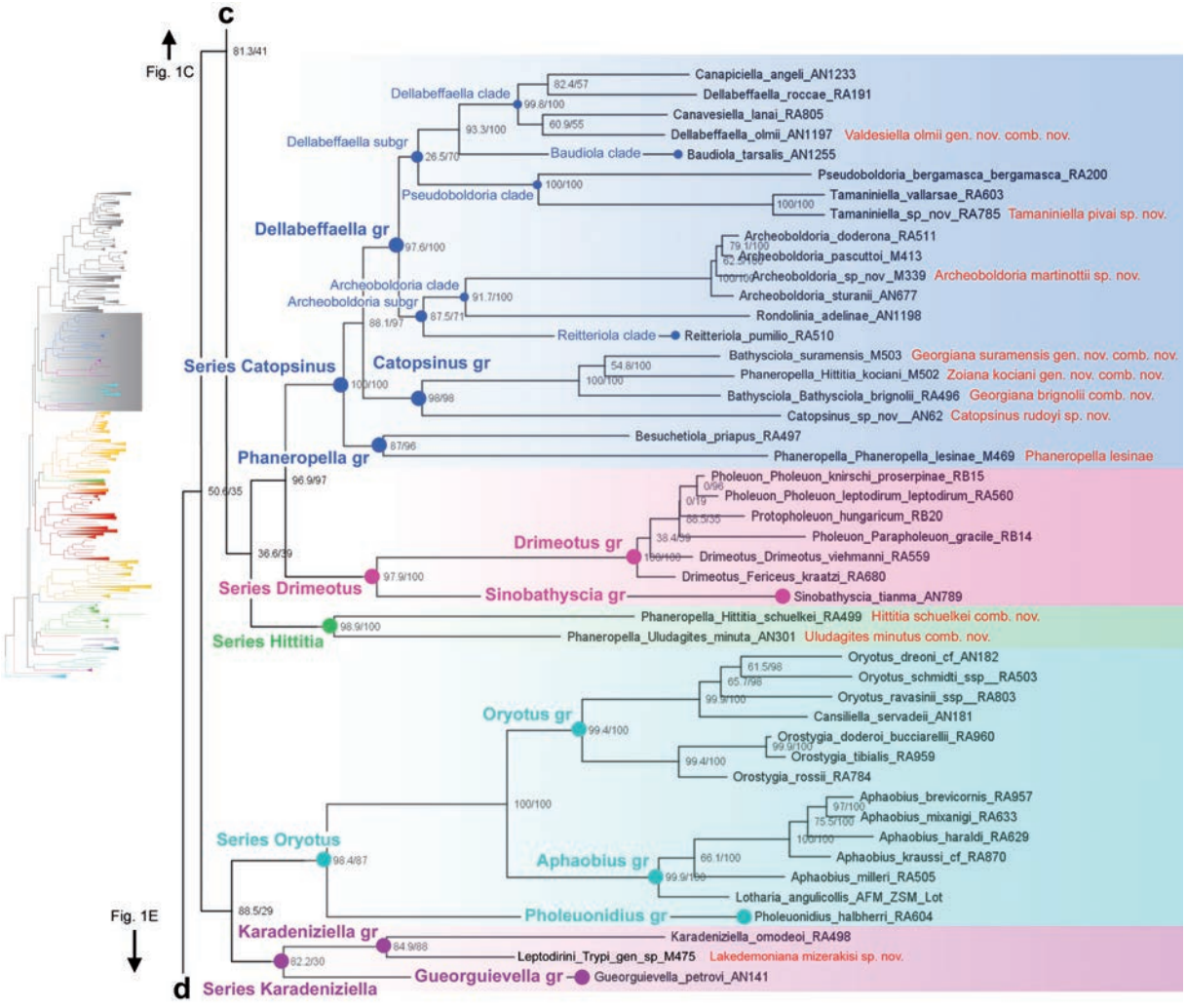


FIGURE 1D: (continued)

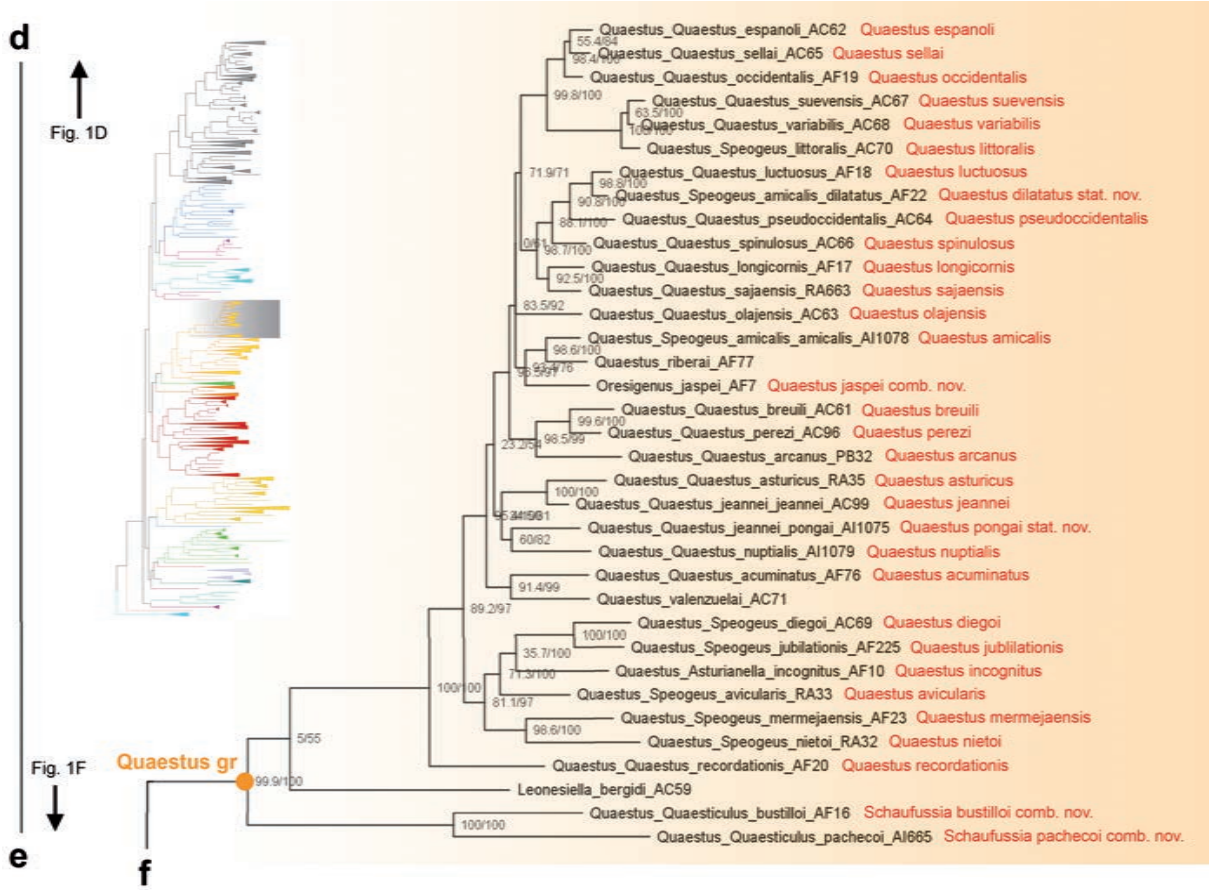


FIGURE 1E: (continued)

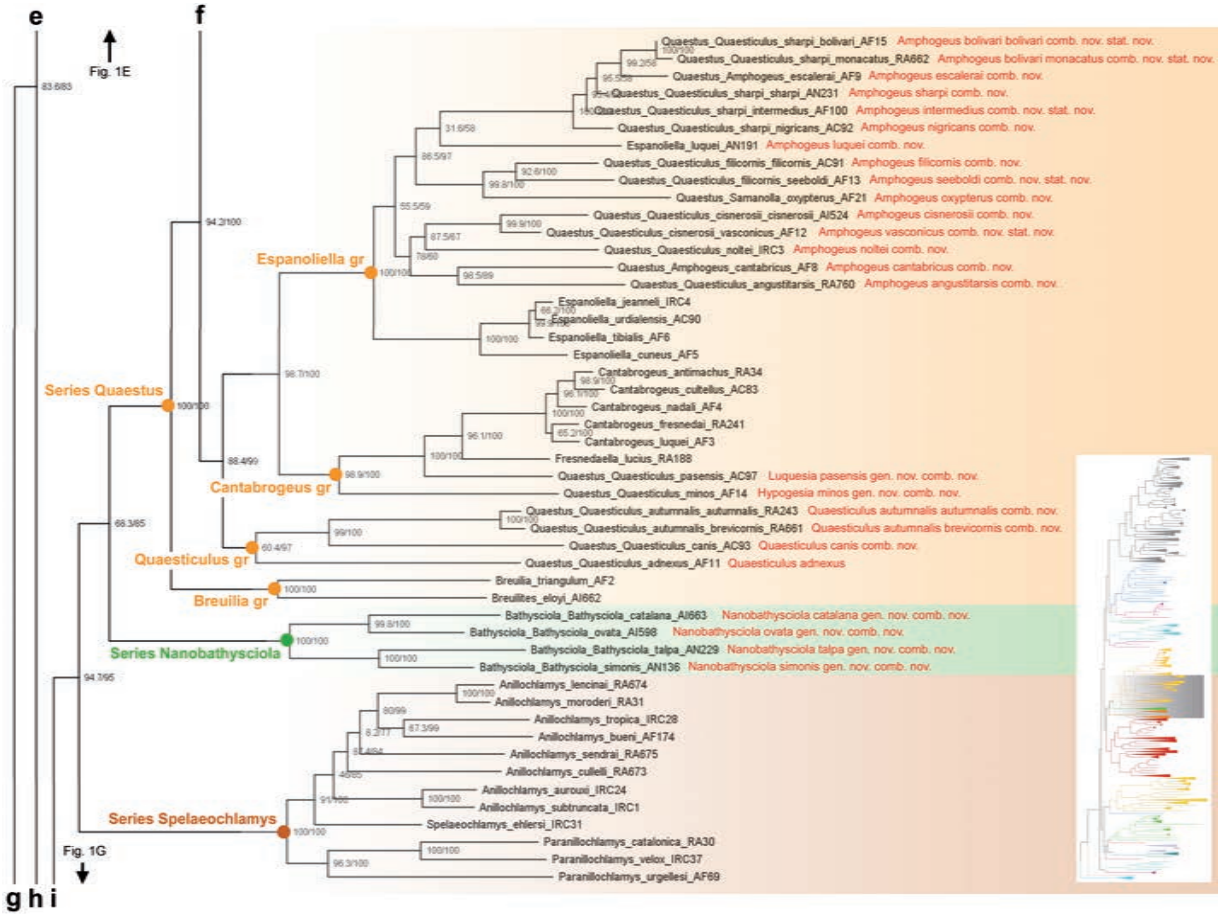


FIGURE 1F: (continued)

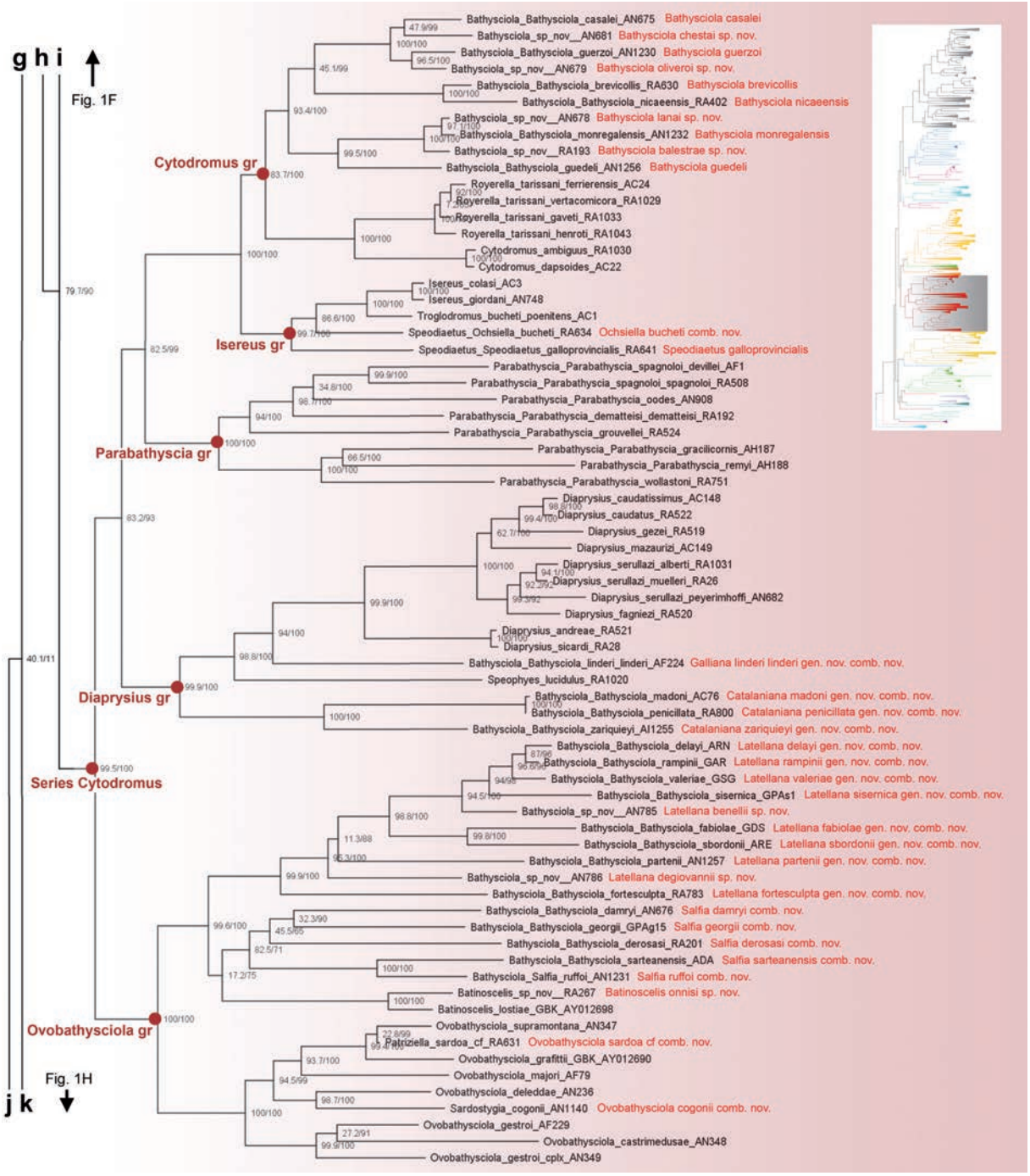


FIGURE 1G: (continued)

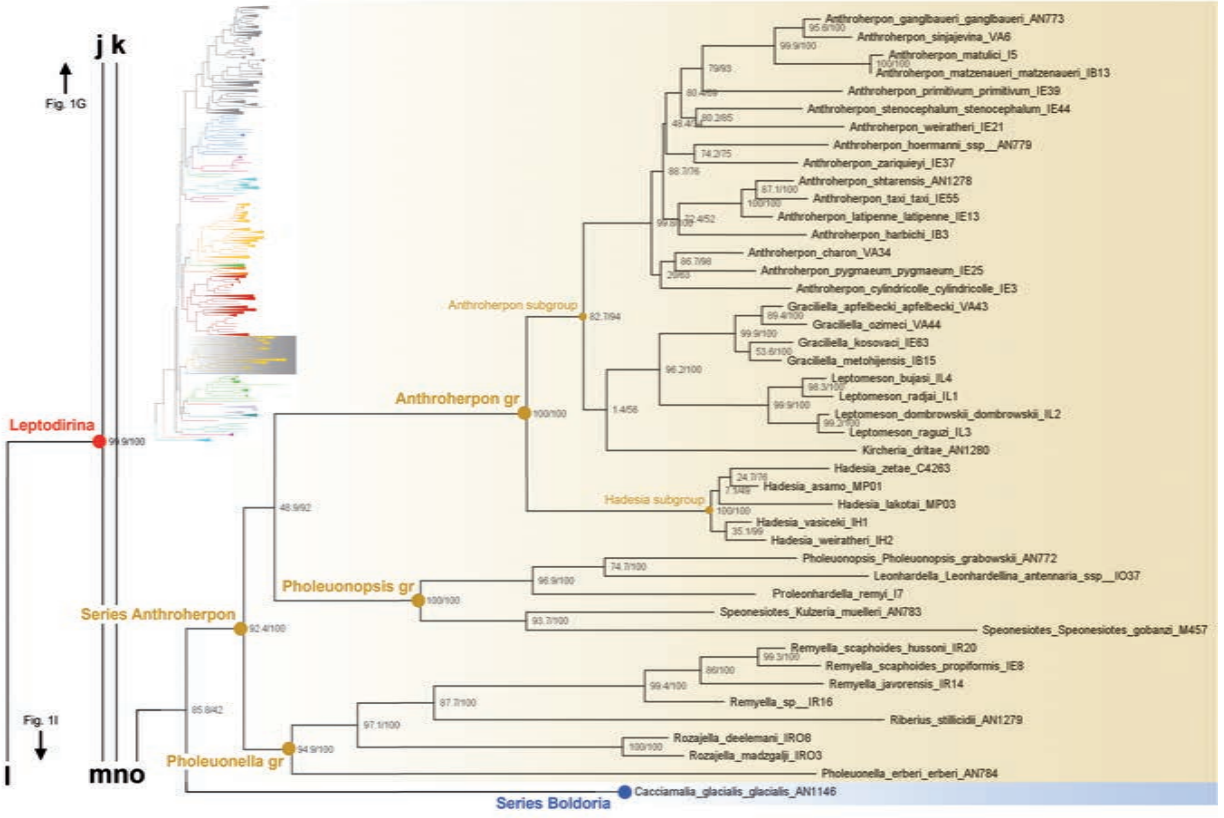


FIGURE 1H: (continued)

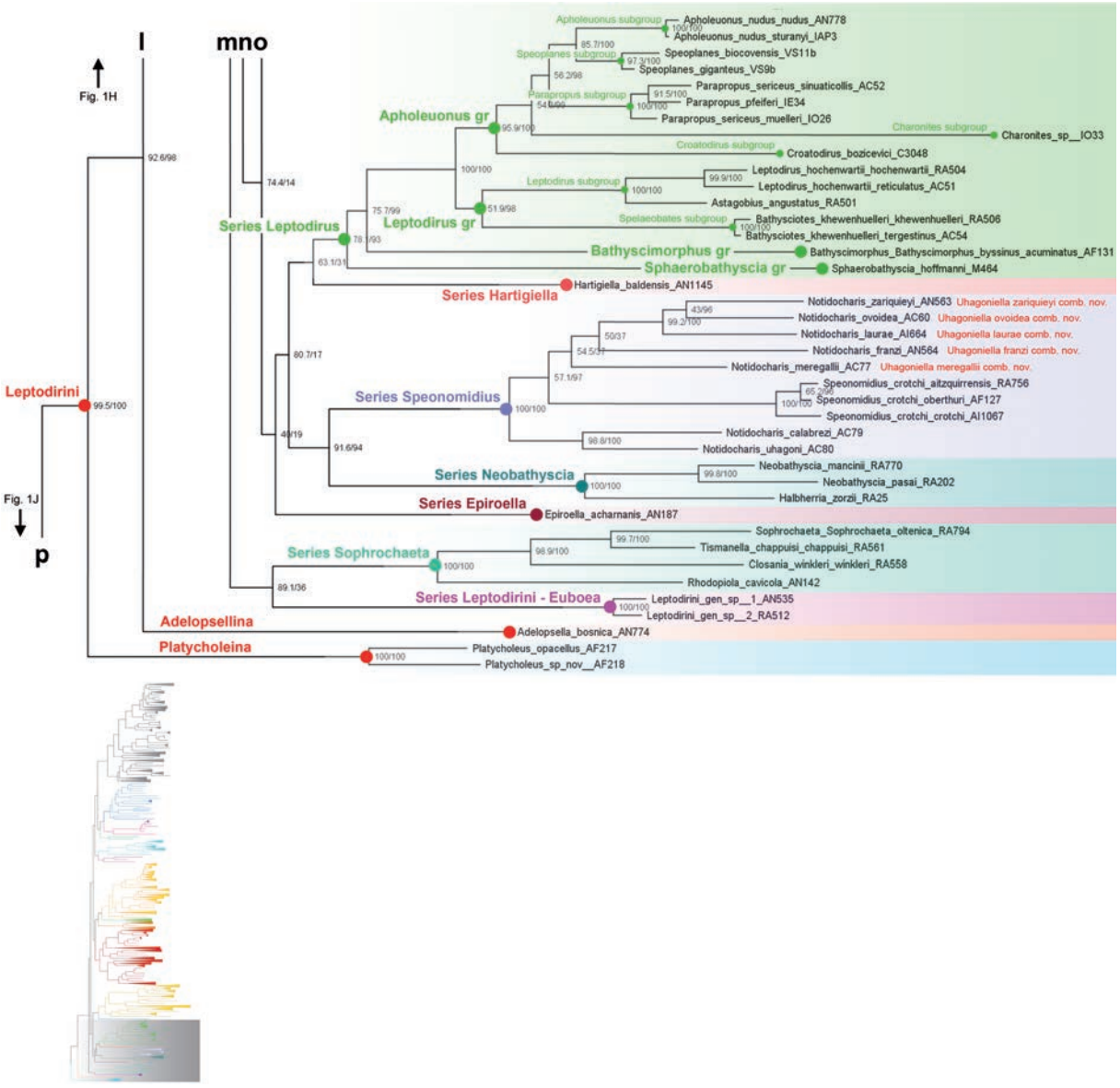


FIGURE 1I: (continued)

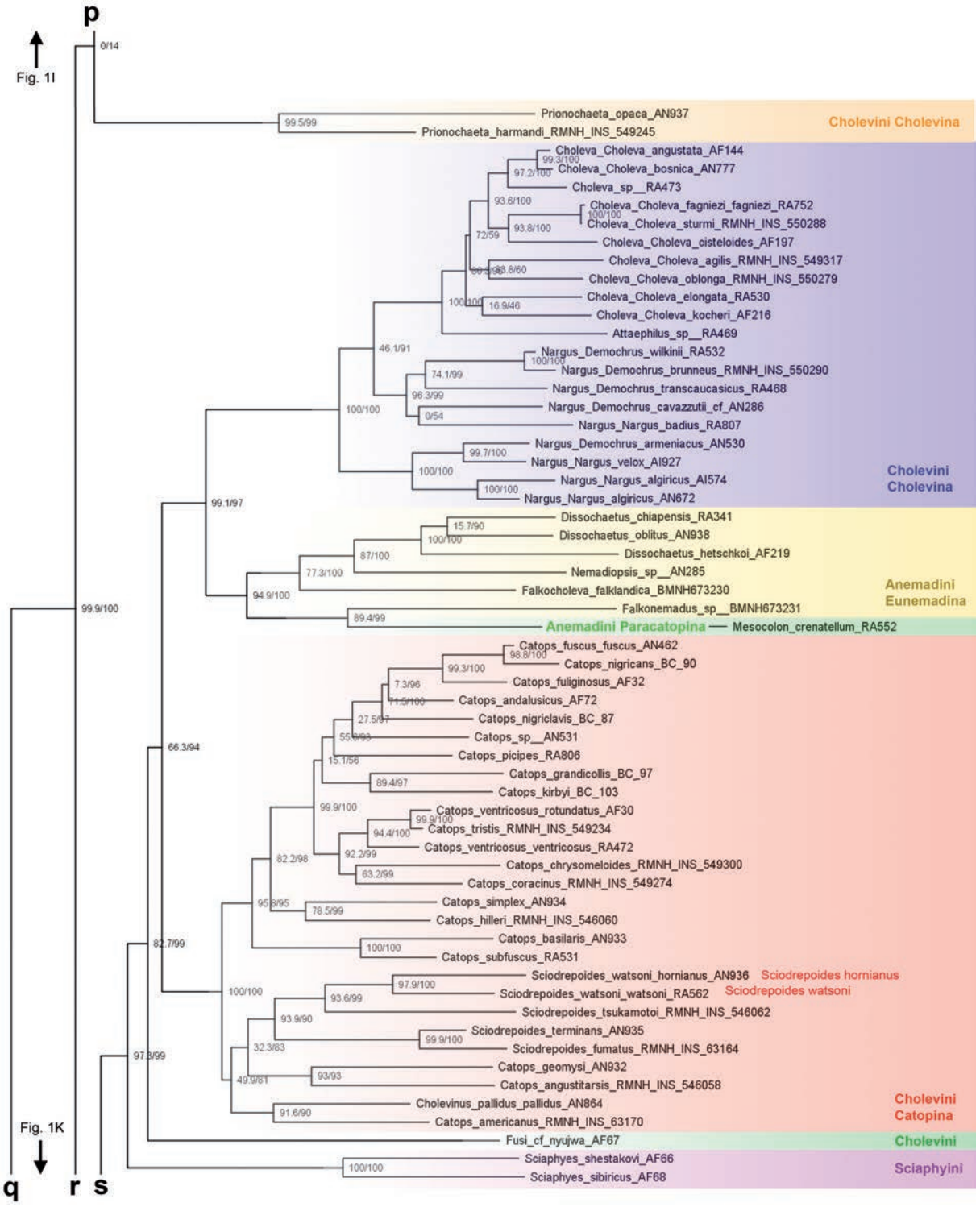


FIGURE 1J: (continued)

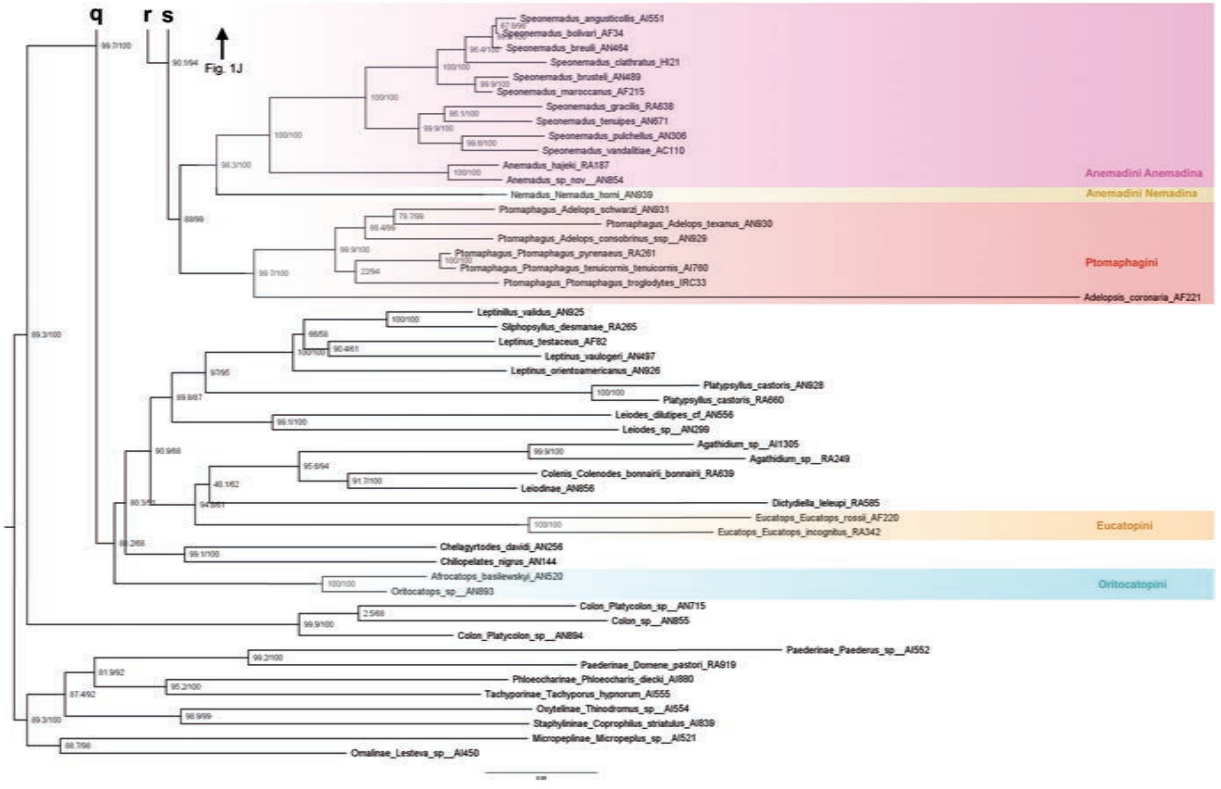


FIGURE 1K: (continued)

characters that allow Bathysciina to be converted into a monophyletic group.

– Bathysciotina, sec. Perreau (2000, 2004), incorporates genera from the *Anthroherpon* clade (*Speonesiotes*), from the *Neobathyscia* series clade (*Halbherria* and *Neobathyscia*), these link to their clades with good support, 95.3/86, as well as those from the *Leptodirus* clade (*Bathysciotes*). Bathysciotina is therefore composed of elements that the molecular study places in three different clades located in different places of the phylogenetic tree (Fig. 3); revealed them as a para- or polyphyletic group.

– Leptodirina: From the configuration of Perreau (2000, 2004), should be excluded *Pholeuonidius* belonging to the *Oryotus* clade with support 85.3/99, should also be excluded, *Remyella*, *Rozajella* and *Pholeuonella* belonging to the *Anthroherpon* clade with strong support 100/99. It would be necessary to incorporate *Croatodirus* (in the description considered an Anthroherponina).

– Pholeuina: This subtribe presents the most widespread characters among the Leptodirini, they are well defined and of considerable phylogenetic value, established by classical authors (Jeannel 1910a, 1924a; G. Müller 1917). Thus, it is the most numerous subtribe and distributed along the phylogenetic tree (Fig. 3), from the most basal cladogenesis (*Adelopsella*) to the most terminal (*Troglocharinus*). In a way this seems to indicate that this set of characters is the «plesiomorphic set». If it could be considered as such, which has been transmitted along most of the branches; then the other subtribes could be «derived sets» that have appeared at various points and constituted by an undoubtedly smaller contingent of taxa. In any case Pholeuina is also a para- or polyphyletic subtribe. *Adelopsella* (Adelopsellina subtrib. nov.), is sister species to all Leptodirina with good support 97.3/100, up to members of the *Sophrochaeta*, *Cytodromus*, *Speonomidius*, *Bathysciola* clade of the *ovata* group (*Nanobathysciola* gen. nov.), *Quaestus*, *Drimeotus*, *Dellabeffaella* and *Speonomus*. Pholeuina brings together elements that molecular phylogeny places in nine different clades (Fig. 3), which shows a structure based on homoplasys.

It seems that the Spelaeobatina subtribe, composed of a single genus, should be the only monophyletic subtribe, but by establishing the synonymy of all the others, their conservation loses meaning; furthermore, there are no molecular data on *Spelaeobates*. Thus, according to Antunes-Carvalho & Gnaspini (2016), everything indicates that the subtribal classification in use is obsolete. Consequently, the following synonymies are established: Leptodirini Lacordaire, 1854 [1849] = Bathysciae Horn, 1880 syn. nov. = Pholeuones Reitter, 1886 syn. nov. = Anthroherpona Jeannel, 1910 syn. nov.= Bathysciotina V.B. Guéorguiev, 1974 syn. nov. = Spelaeobatina V.B. Guéorguiev, 1974 syn. nov.

General criteria used for the classification. Our proposed classification is based on two general criteria, (i) all formal or informal named lineages should be monophyletic according to our best phylogenetic estimate, and (ii) these lineages should be as stable as possible. Under these criteria we divide tribe Leptodirini into three subtribes, two of them monogeneric (Platycholeina and Adelopsellina subtr. nov.) and a third including most of the diversity of the extant Leptodirina sensu novo (235 genera). The division of Leptodirini in these three clades is strongly supported in all our phylogenetic analysis (see below) and two of them are already named (Perreau 2000, 2004).

We further informally divide Leptodirina sensu novo into several monophyletic «series», the majority of them strongly supported in the phylogeny, geographically well defined and morphologically coherent. In turn, the most diverse and/or heterogeneous series are divided into groups of genera, according to their morphology, geographic distribution and phylogenetic support. Both series and groups of genera are informally defined, so that future changes in the phylogenetic placement of some genera do not introduce nomenclatural instability.

For the recognition of genera we mostly rely on morphological characters, provided that they have strong support in the phylogeny. We have tried to maintain as many currently recognised genera as possible, limiting the new genera or new synonymies to a minimum necessary when the current genera were found to be non-monophyletic with strong support. Characters used to delimitate genera varied depending on the series, but usually include male and female genitalia and some ventral structures (see below the section on Morphological Characters). Only in a limited number of cases we introduce changes in infrageneric taxa (subgenera, species or subspecies).

Genera have been placed according to morphological data if molecular data were not available. In some cases the degree of uncertainty made advisable to refrain from too speculative hypotheses of relationships; these genera were considered «*incertae sedis*» within subtribe Leptodirina sensu novo, or within a group or series if these could be assigned with confidence.

The examination of the phyletic series obtained by molecular analysis and synthesized in the phylograms

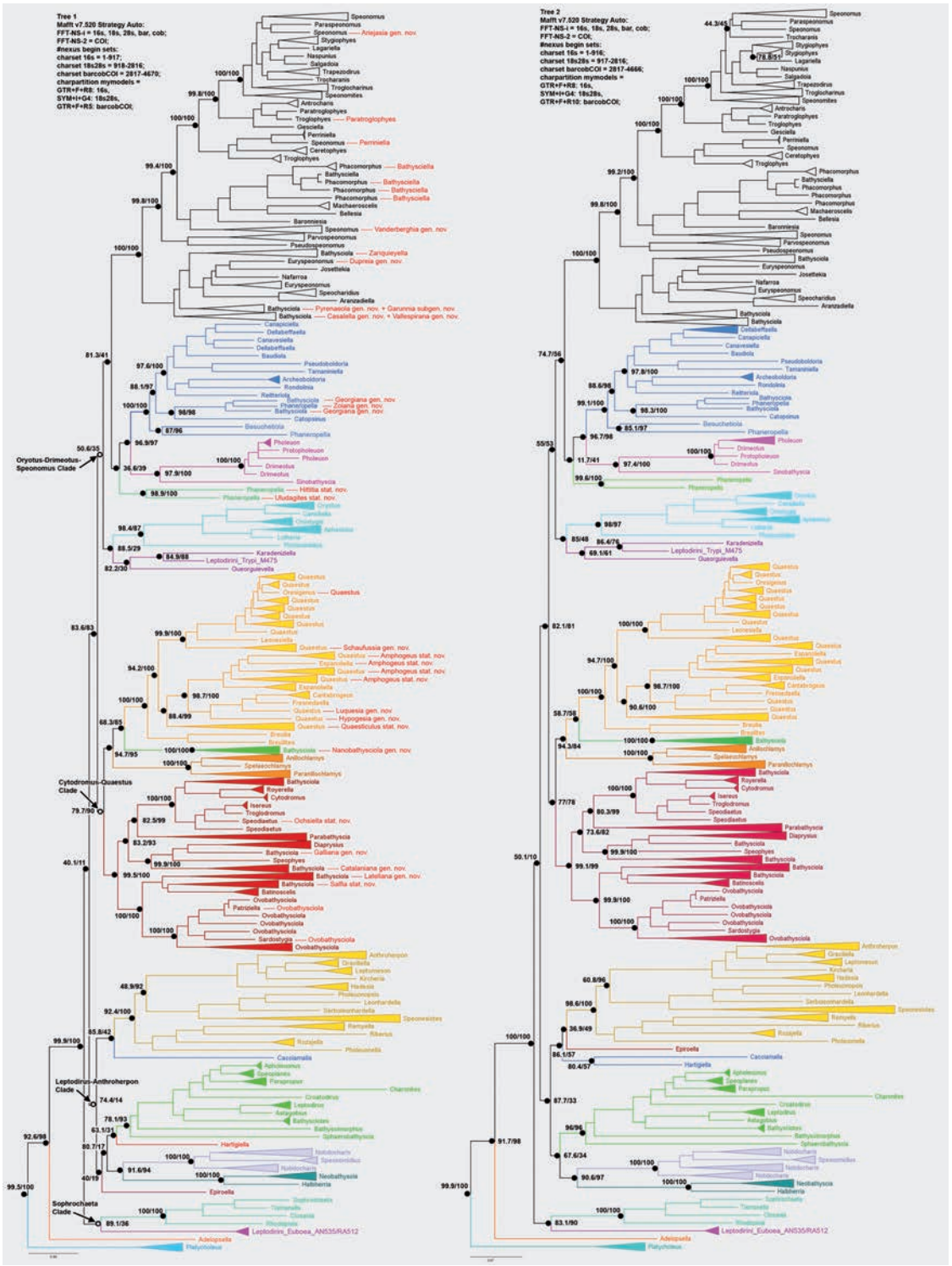


FIGURE 2: Condensed version of Tree-1; condensed version of Tree-2 with an alternative position for some clades. Support values only for large clades.

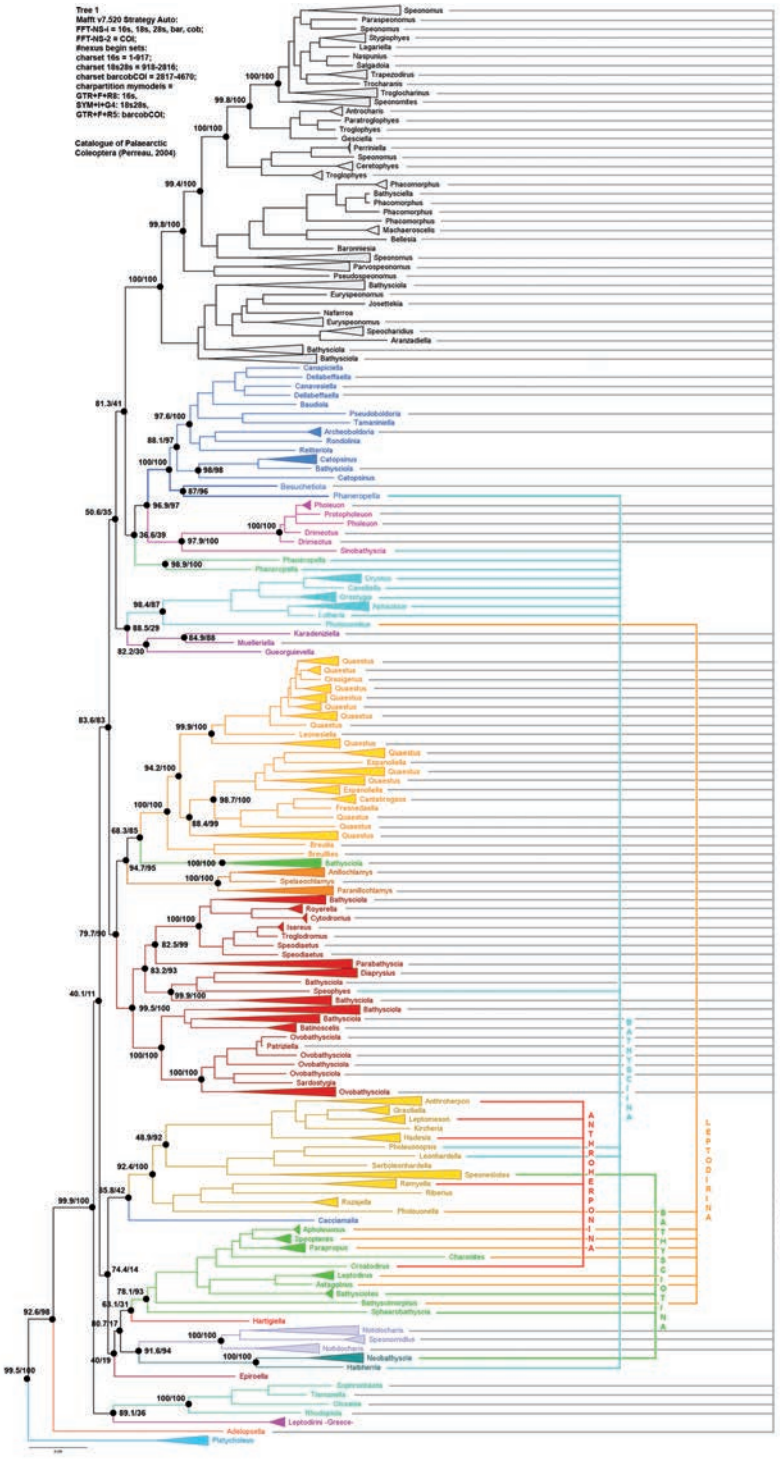


FIGURE 3: Comparison between the currently accepted classification of the Leptodirini (Perreau 2004) and the results obtained in this study. The topology of Tree-1 shows that none of the subtribes into which Leptodirini are currently divided constitute a monophyletic group.

of figures 1A–1K, is preparatory to some general considerations on the meaning and use of some morphological characters normally functional to cladistic analysis on a traditional morphological basis. Examining the set of all phyletic series, we notice that, in general, we do not have synapomorphies that characterize series or groups. Rather, combinations of characters specific to each clade characterize series or groups, but each of these characters is also found in other clades along the entire phylogenetic tree. This fact is probably due to the phenomena of morphological specialization towards the subterranean environment, particularly pushed in this tribe. Specialization masks the traits that can be used in a classical cladistic analysis, conducted on a morphological basis. This means that all the attempts to construct a «natural» system of Leptodirini made by previous authors (Jeannel 1924a; Laneyrie 1967; V.B. Guéorguiev 1976; Giachino *et al*. 1998) fall in front of this reconstruction of ours. The attempt, which we have made several times, to assign synapomorphies to series or groups, has always been shattered by the impossibility of identifying them. Each of these attempts has invariably led us to «pieces» of classical systematics and, of course, not at all compatible with molecular results. This objective situation leads us to some considerations. First, that synapomorphies in certain animal groups may not be evident and that this cannot and must not invalidate the validity of phyletic reconstruction. In addition, conversely, that phylogenetic reconstruction must consider all the components and types of analysis. Morphology, rather than molecular analysis, ecology or biogeography, are just some of the components that must be taken into account by those conducting a study. A specialist in the group can of course, only successfully conduct this multidisciplinary analysis.

Morphological characters

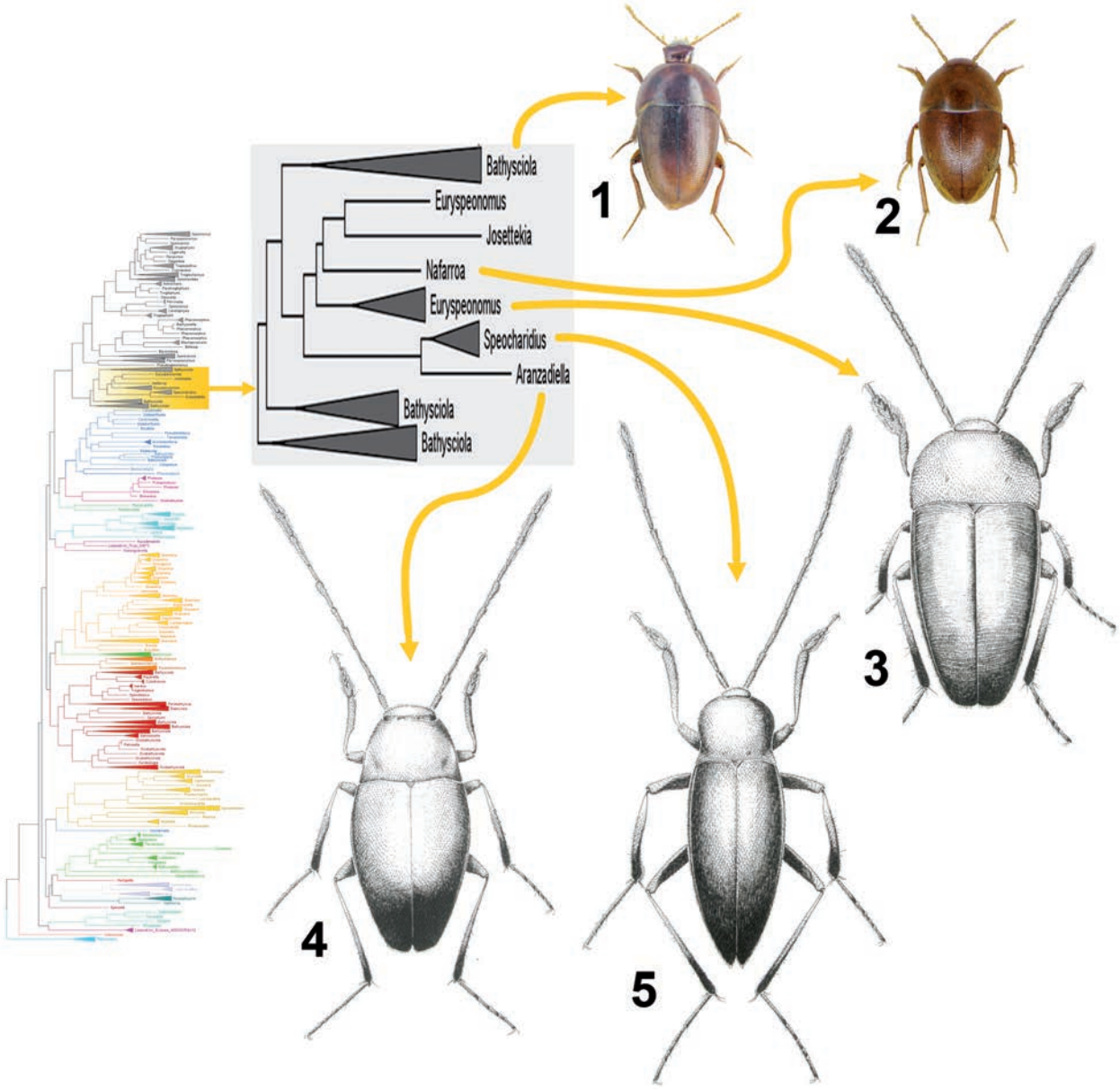
Particular attention was paid to the preventive choice of the characters to be used for the evaluation of the affinities. In this sense, the contributions published by various authors have been of considerable help: Reitter (1885a, 1886a, 1889a, 1908c), Ganglbauer (1887, 1899a), G. Müller (1917), Laneyrie (1967), Jeannel (1910a, 1911a, 1924a, 1947a, 1955a), Perreau (1989, 2000), Giachino *et al.* (1998), Newton (1998, 2015), Fresneda (1998), Fresneda *et al*. (2007), Salgado *et al*. (2008), Antunes-Carvalho & Gnaspini (2016), Antunes-Carvalho *et al*. (2019) and Gnaspini *et al.* (2017a, 2017b, 2020). The characters used in this contribution are as follows.

Habitus

The first classification of what are now the species of Leptodirini was that of Reitter (1885a, 1886a, 1889a, 1908c), who based on external characters grouped the species in three morphological types, bathyscioid, pholeuonoid and leptodiroid, with the only purpose of easing the classification of species. Later Laneyrie (1967) adds the scaphoid type, which is still a certain variation of the leptodiroid type. This characterization of the forms is useful to describe and to differentiate the genera from each other. The plesiomorphic stage seems to be the bathyscioid form, existing in the most basal cladogenesis of the Leptodirini phylogeny. This form is transmitted by being present in at least the base of each of the clades and, in some of them, any of the other forms is also found, with the pholeuonoid predominating. It is thus verified that the elongated derived state (pholeuonoid, leptodiroid and scaphoid) has appeared several times in the evolutionary history of the group. See for example the clade of the *Euryspeonomus* group of the *Speonomus* series (Figs 4.1 to 4.5), where both forms are found, bathyscioid (*Zariquieyella*, *Casalella* gen. nov., *Pyrenaeola* gen. nov. and *Nafarroa*) and pholeuonoid (*Speocharidius*), as well as other intermediate forms, elongated bathyscioid (*Euryspeonomus*) or the elongated bathyscioid with the bell-like pronotum of *Aranzadiella* (with a certain tendency to the pholeuonoid). A paradigmatic example is that of *Bathysciotes* (bathyscioid), which is the sister genus of *Leptodirus* + *Astagobius* (both leptodiroids). All these forms could be summarized in two basic ones:

– The oval, rounded, tending to the hemisphere (Figs 4.1, 4.2), generally present in the animals most typical of the superficial compartments of the underground environment (soil, litter, MSS, etc.); there are exceptions: the elements of the *Quaestus* series, all of them round-oval, are universal in deep subterranean environments in their distribution area. These forms usually have short legs and antennae, as well as a high, well-developed, more or less long mesoventral keel.

– The oblong, elongated (Fig. 4.5), present in general, in the animals most typical of the deep subterranean environment. These forms tend to have long legs and antennae, as well as a reduced or absent mesoventral keel. In the genus *Troglocharinus* there are both elongated bathyscioid forms with a developed mesoventral keel (*T. fadriquei*) and markedly pholeuonoid forms with a reduced mesoventral keel (*T. hustachei* or *T. ferreri*), as well as various intermediate



FIGURES 4.1–4.5: Habitus. Phylogenetic tree of the Leptodirini with genera grouped together (Fig. 2: Tree-1). Habitus of: (**1**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* comb. nov., (**2**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**3**) *Euryspeonomus* (*Euryspeonomus*) *breuili*, (**4**) *Aranzadiella leizaolai*, (**5**) *Speocharidius* (*Speocharidius*) *breuili*. Figs **3**–**5** modified from Salgado *et al*. (2008).

forms (*T. kiesenwetteri*); although all of them have elongated legs and antennae (Fresneda *et al.* 2021).

Pronotum. With lateral margins regularly arched (Figs 4.1 to 4.3) or sinuate or rectilinear (Figs 4.4, 4.5). Thus expressed, if a pronotum is considered to be regularly arched, any other case will belong to the second group, which can be more or less sinuous or more or less rectilinear.

Dorsal sculpture

Dorsal sculpture pronotum: Surface with transverse striolae only in Ptomaphagini (Fig. 5–9). Pronotum covered with an irregular punctation all the Leptodirini (Figs 5.6–5.8); this is the plesiomorphic state of the character in Leptodirini, the transverse striolae in pronotum is a derivated state in Ptomaphagini. The integument can be absolutely smooth (Fig. 5.8) or marked by a more or less microreticle (Figs 5.6, 5.7).

Dorsal sculpture elytra: Surface of elytra with transverse striolae (Figs 5.1, 5.2), which could disappear towards the apex or elytra covered with an irregular punctation or entirely marked by irregular stippling (Figs 5.3, 5.4). Several authors consider the presence of transverse striolae in the elytra to be a plesiomorphy of the subfamily Cholevinae (e.g. Blas 1981; Giachino & Vailati 1993). From an hypothetical striolated ancestor, the elytral sculpture would have derived towards two states: i) a reduction in the striolae, as observed in Cholevini and some Leptodirini; ii) a further development of the striolae, with a more complex design (i.e. longitudinal striae), as in e.g. the genera *Anemadus* or *Speonemadus* (Anemadini); Fresneda *et al*. (2011b) observed a secondary striolation in *Anemadus* (Fig. 5.5). The ancestral condition of the character in Leptodirini, as reconstructed in the phylogenetic tree (Figs 1A–1K), is that of elytra covered with transverse striolae, as in *Speonemadus* (Fig. 5.10). The irregular punctation of the elytra is independently developed in *Catops* and in the origin of the clade grouping the series «*Spelaeochlamys*» and «*Quaestus*». In the serie «*Speonomus*», *Speonomus* group, *Speonomites velox* with irregular stippling is the sister species of *Speonomites aurouxi* with transverse striolae; in fact *S. velox* is the single species of the genus *Speonomites* with irregular stippling. Other cases occur in the *Euryspeonomus* group of the «*Speonomus*» series with irregularly punctation in *Nafarroa sorogainensis*, the sister species of *Dupreia* gen. nov. + *Josettekia* with transverse striolation; or the entire basal subclade with *Pyrenaeola* gen. nov., *Garunnia* subgen. nov. and *Casalella* gen. nov. with irregular stippling and *Vallespirana* gen. nov. with transverse striolation. The existence of the two possibilities distributed throughout the clade, even within a genus, invalidates the character to establish phylogenetic relationships. At least in some Anemadini (e.g. *Speonemadus*) there may be longitudinal striae on the elytra (Fig. 5.10), a feature not found in any Leptodirini, but it is possible to find in these longitudinal ridges (*Drimeotus*).

Other dorsal features

Elytral parasutural stria: Marked in most or all of the elytra (Fig. 5.11) (*Bathysciola*, *Catalaniana* gen. nov. *Dellabeffaella*, etc.) the character is found in various clades throughout the phylogenetic tree; or absent, blurred or marked by only a few points in the basal area of the elytra (all the genera of series *Speonomus* except *Troglophyes* group, *Bathysciotes*, *Redensekia*, *Sphaerobathyscia*, etc.); the character is distributed throughout the phylogenetic tree.

Elytral apex: Rounded, pointed or truncated.

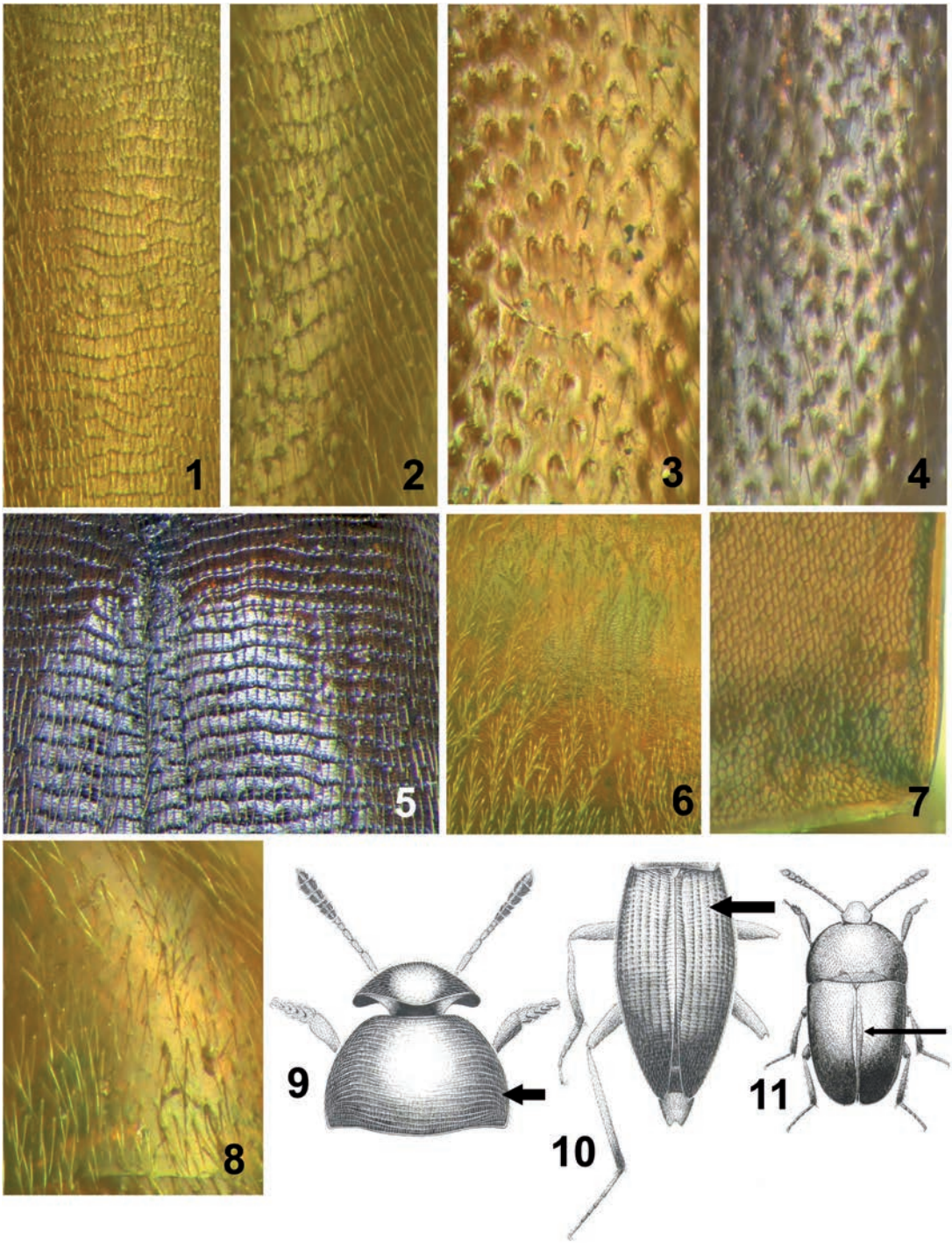
Pigmentation

Pigmented or depigmented animals. Among other peculiar adaptations to the subterranean environment that characterize the Leptodirini is the absence of pigments (except *Adelopsella bosnica* and *Platycholeus*). the yellowish colour common to all taxa comes from The colour of chitin itself, but they do not synthesize pigments. Depigmentation also occurs in Nearctic Ptomaphagini and *Ptomaphagus troglodytes* Blas & Vives, 1983; also *Catops arifensis* Giachino & Vailati, 2000 (Cholevini) is depigmented. But this is a troglobiomorphic trait, typical of the inhabitants of aphotic environments that is found in numerous families of Coleoptera: Dytiscidae, Carabidae, Histeridae or Curculionidae.

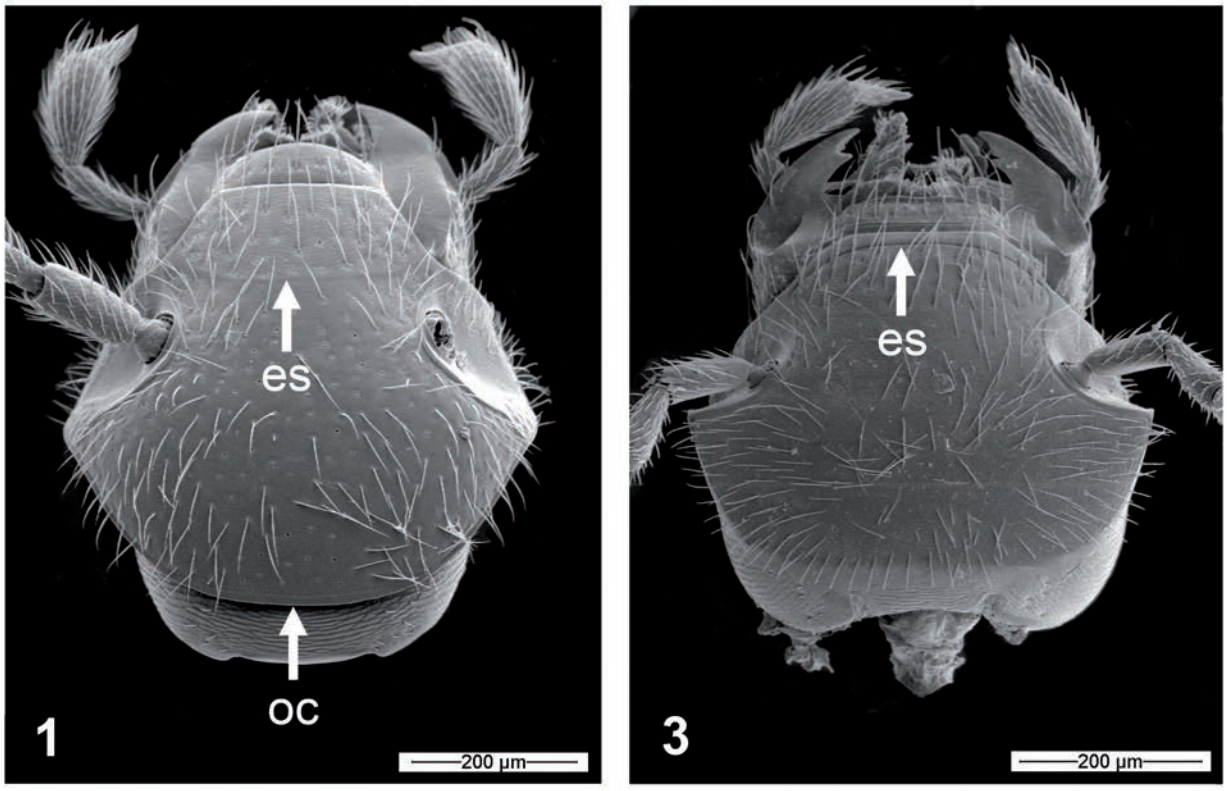
Head

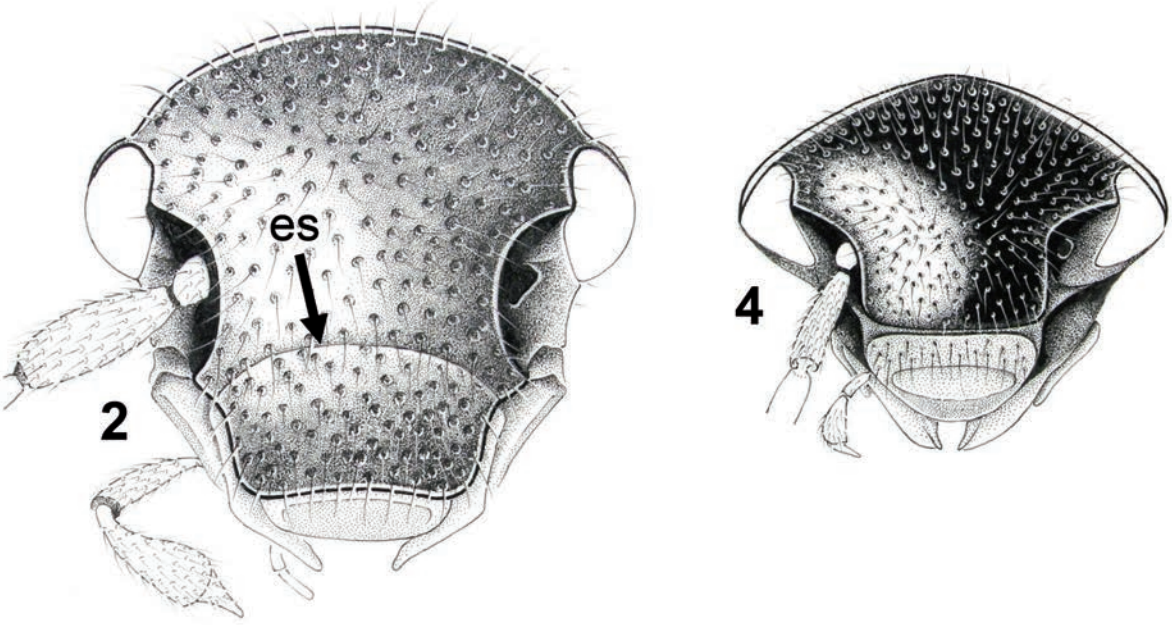
The cephalic morphology has been studied in depth by Luo *et al*. (2019a) in *Troglocharinus ferreri*. The head is almost always retractile and is provided with a well-developed occipital carina or carina in Anemadini (Fig. 6.1: oc), Cholevini, Eucatopini and Ptomaphagini. It is somewhat reduced in Oritocatopini and is very little prominent, blurred or absent in Leptodirini (Fig. 6.3). The epistoma is transverse and the anterior margin is truncated or, exceptionally, curved in some Anemadini (Paracatopina). Most of the Cholevinae, including Leptodirini, have an epistomal suture (Figs 6.1, 6.2, 6.3: es) that separates the forehead from the epistoma. This suture is lacking in all the Ptomaphagini (Fig. 6.4), in the Catopina (Cholevini), in Eucatopini, in Oritocatopini, and in some groups of Anemadini. In *Anemadus hajeki* Růžička & Perreau, 2017 it is very inconspicuous (Fig. 6.1: es), the same as in *Sciaphyes* (Sciaphyini) (Fig. 7.3: es).

Maxillary palps: They are made up of three segments, the last of which is narrow, conical and notice-

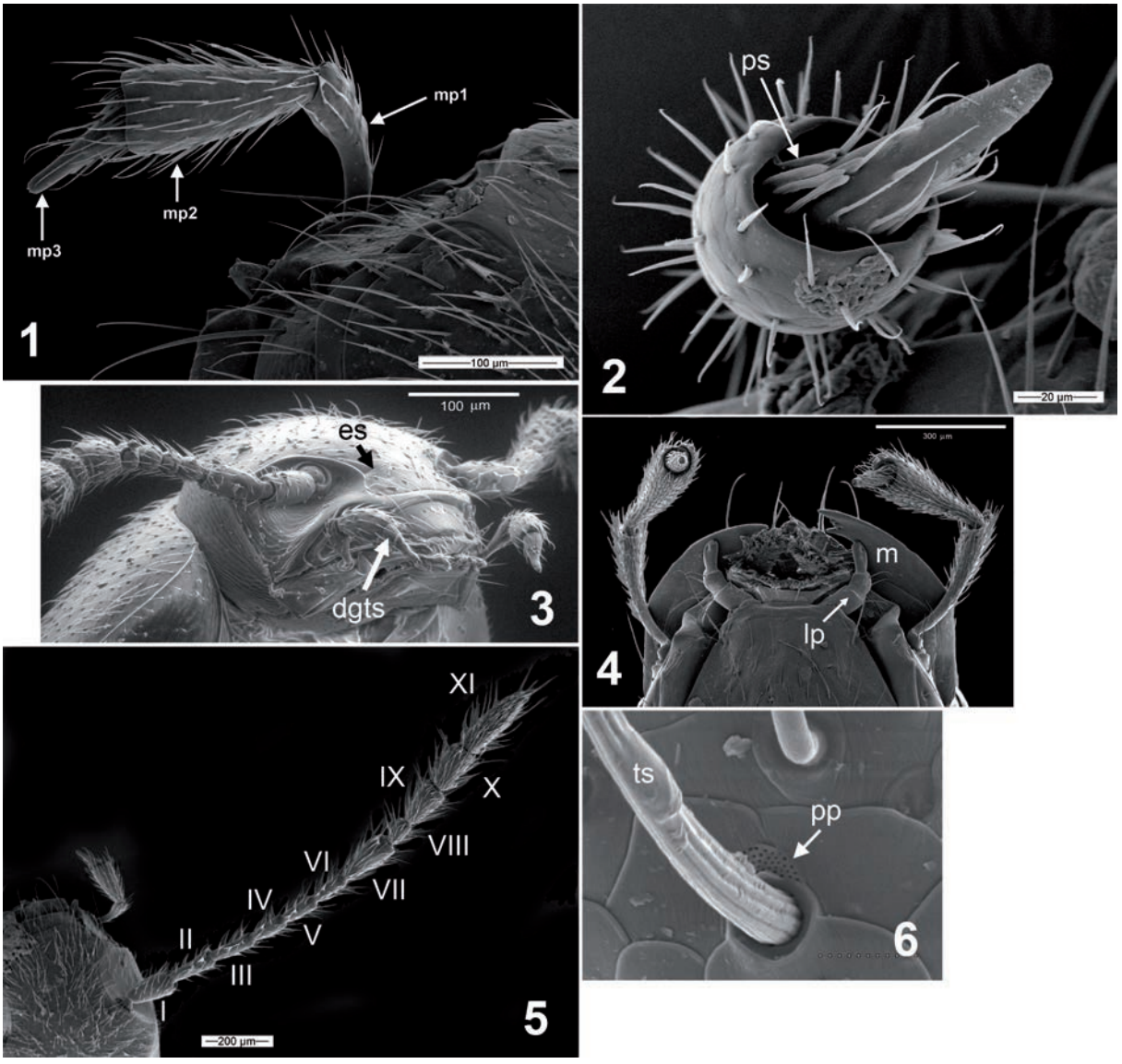


FIGURES 5.1–5.11: Habitus. Elytral sculpture of: (**1**) *Valdesiella olmii* **comb. nov.**, (**2**) *Speonomites nitens*, (**3**) *Blattochaeta matchai*, (**4**) *Protopholeuon hungaricum*, (**5**) *Anemadus* sp. Pronotal sculpture of: (**6**) *Josettekia angelinae*, (**7**) *Apholeuonus nudus nudus*, (**8**) *Speonomites velox*, (**9**) *Ptomaphagus tenuicornis* ssp. (black arrow pointing to transverse striolae). Elytra of: (**10**) *Speonemadus angusticollis* (Kraatz, 1870) (black arrow pointing to longitudinal striolae). Habitus of: (**11**) *Catalaniana zariquieyi* comb. nov. (black arrow pointing to parasutural stria). Figs **9–11** modified from Salgado *et al*. (2008).





FIGURES 6.1–6.4: Head. Dorsal view of the head of: (**1**) *Anemadus hajeki* Růžička & Perreau, 2017, (**2**) *Speonemadus angusticollis* (Kraatz, 1870), (**3**) *Zariquieyella grandis* comb. nov., (**4**) *Ptomaphagus tenuicornis* ssp. Abbreviations: **es**, epistomal suture; **oc**, occipital carina. Figs **2**, **4**, modified from Salgado *et al*. (2008).



FIGURES 7.1–7.6: Head. Maxillary palps of: (**1**) *Aphaobius haraldi*, (**2**) *Speophyes lucidulus*, (**3**) *Sciaphyes shestakovi* Fresneda *et al*., 2011 (modified from Fresneda *et al*. 2011). Mouth parts of: (**4**) *Pholeuon* (*Pholeuon*) *leptodirum leptodirum*. Antenna of: (**5**) *Aphaobius haraldi*. Sensilla of: (**6**) *Quaestus longicornis*. Abbreviations: **dgts**, digitiform sensilla; **es**, epistomal suture; **lp**, labial palp; **m**, mandible; **mp1/2/3**, maxillary palpomeres; **pp**, porus plate; **ps**, projected sensillae; **ts**, trichoidea sensilla; **I-XI**, antennomeres.

ably shorter than the penultimate one (except in *Catopodes* Portevin, 1914) in Anemadini, Leptodirini (Fig. 7.1: mp1–3), Ptomaphagini and Sciaphyini (Fig. 7.3), while in the Cholevini, Eucatopini and Oritocatopini the last two articles are subequal or the last is only slightly shorter than the second. The distal maxillary palpomere has a conical shape in most of the Cholevinae (Figs 7.1–7.3), although in most of the Ptomaphagini, it is subcylindrical and thinnest just after its base; a slender apical palpomere is also found in *Spelaeobates* (Leptodirini). It is not clear which of the two forms is the plesiomorphic state of the character. Apical maxillary palpomeres are pubescent in all Cholevinae excluding Ptomaphagini; in these it is

practically glabrous with only a few minute setae. Antunes-Carvalho *et al*. (2019) found pores plates on the maxillary palp of *Catops* (Catopina), an unusual feature apparently restricted to Cholevinae: they have been found in all tribes except Eucatopini and Oritocatopini; the Sciaphyini are unknown. Again, Antunes-Carvalho *et al*. (2019), phylogenetically interpret the presence of a set of sensilla projecting on the apical maxillary palpomere in Leptodirini (Fig. 7.2: ps), in contrast to the digitiform sensilla of the palpomere integument in the remaining Cholevinae (Fig. 7.3: dgts). Projected sensilla are an apomorphy almost unique to Leptodirini, except for their existence in *Nargomorphus* Jeannel, 1936 (Anemadini), and a possible reversal in *Spelaeobates*. This feature was already observed, but not phylogenetically interpreted, by Moldovan *et al*. (2004) in *Closania*, *Sophrochaeta* and *Tismanella*, and by Njunjić *et al*. (2016) in *Anthroherpon*, *Leptomeson* and *Graciliella*. Antunes-Carvalho *et al*. (2019) describe this structure also in *Hadesia vasiceki*.

Mandibles (Fig. 7.4: m): In general they are triangular, robust and highly sclerotized; the shape of the apex is variable according to the groups and the chewing edge is concave and may be covered with hairs. Only in some genera of Leptodirini specialized to the hygropetric environment, such as *Hadesia* or *Radziella*, the mandibles are modified, like the other mouthparts, for filtration (Giachino *et al*. 1998b; Dorigo *et al*. 2017). The base of the mandible is articulated by two condyles.

Antennae: They consist of 11 segments or antennomeres of variable length, with a club that is more or less differentiated and of an interrupted type, in which the 8th segment is the smallest, generally globose or quadrangular, or at least narrower than the 7th and 9th segments (Fig. 7.5); *Baronniesia* is an exception as the 8th antennomere is not reduced (Figs 9.4–9.5). The 7th, 9th and 10th antennomeres carry olfactory organs housed in the dilated apical part, their development and complexity is related to the degree of adaptation to the subterranean environment (Corbière-Tichane 1977).

Antennae insertion point: Is located in the medial lateral part of the head (Fig. 8.6), although in the New Zealand Paracatopina the anterior part of the head is reduced while in some Leptodirini said cephalic region is very elongated (Fig. 8.7), which shows the prognathism of the head. Jeannel (1924a) used this character to define the tribe Antroherpona (= subtribe Anthroherponina auct.), emphasizing the insertion in the hind quarter of the head instead of the middle third. Subsequent authors have usually understood this statement as a «shift to the back» of the insertion point. Observing the relative position of the antennae with respect to the progressive specialization of the body, proceeding from less specialized ones (bathyscioids) to the more specialized ones (leptodiroids or scaphoids), what is noticeable is not a backward displacement of the antennae, but an elongation, probably due to different ways of specialization, of the mouth apparatus, of the front part of the head (Giachino & Vailati 1993; Perreau & Pavićević 2008b). Different types of specialization of mouth pieces would probably deserve careful evaluation, aimed so far only to the apparatus of hygropetricolous taxa (as i.e. *Riberius* and *Kircheria*), where mouth pieces taking long setae, i.e. adapted to filtering water and organic matter (see Jeannel 1924a; Casale & Jalžić 1988; Nonveiller & Pavićević 1999; Casale *et al.* 2000a, 2000b; Moravec & Mlejnek 2002; Mlejnek & Moravec 2003; Moldovan *et al.* 2004; Casale *et al.* 2004; Giachino & Vailati 2006; Giachino *et al.* 2021). We recall that a similar phenomenon, although of opposite polarity, can be found in the Paracatopini (Leiodidae, Cholevinae) of New Zealand, where the pre-antennal part of the head is shortened (Giachino & Vailati 1993). Consequently, in our opinion, the insertion position of antennae, as shown also by molecular data (Fig. 2: Tree-1, Tree-2), is a character, at least in part linked to the specialization degree of the mouth apparatus which may appears as autoapomorphy in different lineages. For this reason, it would be better not to use it for phylogenetic reconstructions. A practical example is provided by the genus *Hygrodromus*, which present all typical characters of the phyletic lineage of *Anthroherpon-Hadesia*, but has the antennae inserted in the middle third of the head, as in *Riberius* (Giachino & Casale 2022).

Antennae structure: Understood as the relative length of the antennomeres, it appears significantly different in the different species and does not always seem to be correlated to the degree of morphological specialization of the different taxa. Thus, for example, the overall length of the antennae in *Canapiciella*, comparable in degree of specialization to *Doderiola* and *Rondolinia*, is considerably shorter, while in *Doderiola* the relative length of the second antennomere is considerably greater than in all the other taxa treated. The 8th antennomere instead appears transverse in *Reitteriola*, *Tamaniniella* and *Muelleriola*, subsquared in *Baudiola* and *Canapiciella*, elongated in *Doderiola* and *Rondolinia*. In general, in the bathyscioid species the antennae tend to be short–with

exceptions, *Troglocharinus mercedesi*, *T. mengeli* or *T. fadriquei*–, and in the pholeuonoid, leptodiroid and scaphoid species tend to be long. But the total length of the antennae is hardly measurable; by comparison, *Troglocharinus ferreri* has long ones and *T. fonti* short ones, although the latter are proportionally considerably longer than in any species of the genus *Bathysciola*. So the character is only of some use for making comparisons between species or perhaps between genera, but no more. Also to quantify the length of antennae, the length of the body has been used as a unit of measurement: short antennae are those that do not reach half the length of the body and long antennae are those that exceed half the length of the body. Following this criterion, a *Troglocharinus fonti* and an *Anthroherpon* would have the same character status. although in the latter the antennae far exceed the length of the body.

Antennae sensilla: pore plates similar to those described by Antunes-Carvalho *et al*. (2019) on the maxillary palps of *Catops* Paykull, 1798 are present on the 8th, 9th and 10th antennomeres (Fig. 7.6). It has been observed in Leptodirini, *Quaestus longicornis* (*Quaestus* series clade), *Speonomus longicornis* or *Troglocharinus orcinus* (*Speonomus* series clade), but has not been studied in other Cholevinae tribes. The sensilla trichoidea are striated (Fig. 7.6: ts) and hollow. As in the last maxillary palpomere, projecting sensilla are also found on the 8th, 9th and 10th antennomeres (Figs 8.1–8.5: ps) in both males and females; they are hollow and there is probably some fluid inside them: they frequently collapse when the specimen is metallized for SEM photographs. This has been observed in *Aphaobius haraldi* (Fig. 8.1: ps) (*Oryotus* series clade), *Machaeroscelis infernus* (Fig. 8.2: ps), *Parvospeonomus delarouzeei catalonicus* (Fig. 8.3: ps) or *Quaestus longicornis* (Fig. 8.4: ps) (*Quaestus* series clade). Since it has been found in distinct clades, it is possible that those sensilla are present in all Leptodirini. It is also recorded in Ptomaphagini (Fig. 8.5: ps), but it is not known in the other tribes of Cholevinae.

Relative length of the first and second antennomeres: The second article is shorter or as long as the first or is clearly longer (Figs 9.1–9.3). Discussed by Jeannel (1924a), Laneyrie (1967) and V.B. Guéorguiev (1976), the molecular data seems to confirm a significant phylogenetic importance to this character. Various genera of the *Anthroherpon* phyletic lineage (*Anthroherpon*, *Graciliella*, *Leptomeson*, *Hadesia*, *Kircheria*, *Nauticiella* and *Riberius*) or in *Leptodirus* series (*Velebitodromus*, *Hygrodromus*), have the first antennomere much longer than the second one and, often, also the third much longer. We observed that the second article can be similar in length to the 3rd or clearly longer, that the 8th can be transverse or oblong, as same than the 9th and 10th, which may or may not be transverse, or that the antennomeres of the club – 9th to 11th –, if it is differentiated, can be either of similar or very different lenght. In some *Quaestus* – e. g. *Q. mermejaensis* – the 11th antennomere is very long (Fig. 197.8); in a few cases: *Baronniesia delioti* (Figs 9.4, 9.5), *Josettekia angelinae* and *Paraspeonomus vandeli* (Fig. 9.6), males harbour some strongly dilated antennomeres.

Eyes: Reduction, microphthalmy, or even anophthalmy (i.e. complete lack of eyes), is a phenomenon commonly observed in Coleoptera, particularly in groups inhabiting leaf litter, soil or caves (Carabidae, Staphylinidae, etc.). The beetle family Leiodidae appears to be particularly prone to eye reduction, which is even more striking considering that this is not a very large family with just over 3,000 species (Newton 1998; Perreau 2000). As presently known, complete loss of eyes in adults occurred independently not less than eleven times in the following Leiodidae lineages:

– All members of the subfamily Catopocerinae: leaf litter and caves from most of the formerly unglaciated Nearctic, *Perkovskius* Lafer, 1989 – **Note**: Newton (1998) includes *Perkovskius* in the subfamily Leiodinae, Pseudoliodini – from the Russian Far East and an undescribed genus from South America (Fresneda *et al*. 2011b).

– At least one species of the genus *Anemadus* Reitter, 1885 *(Anemadus kabaki* Perreau, 2009 from China, Sichuan), while some other congeners are microphthalmic (Perreau 2009).

– The monotypic *Fusi* Perkovsky, 1989 from the Russian Far East (Cholevinae Cholevini *sec.* Fresneda *et al*. 2011b).

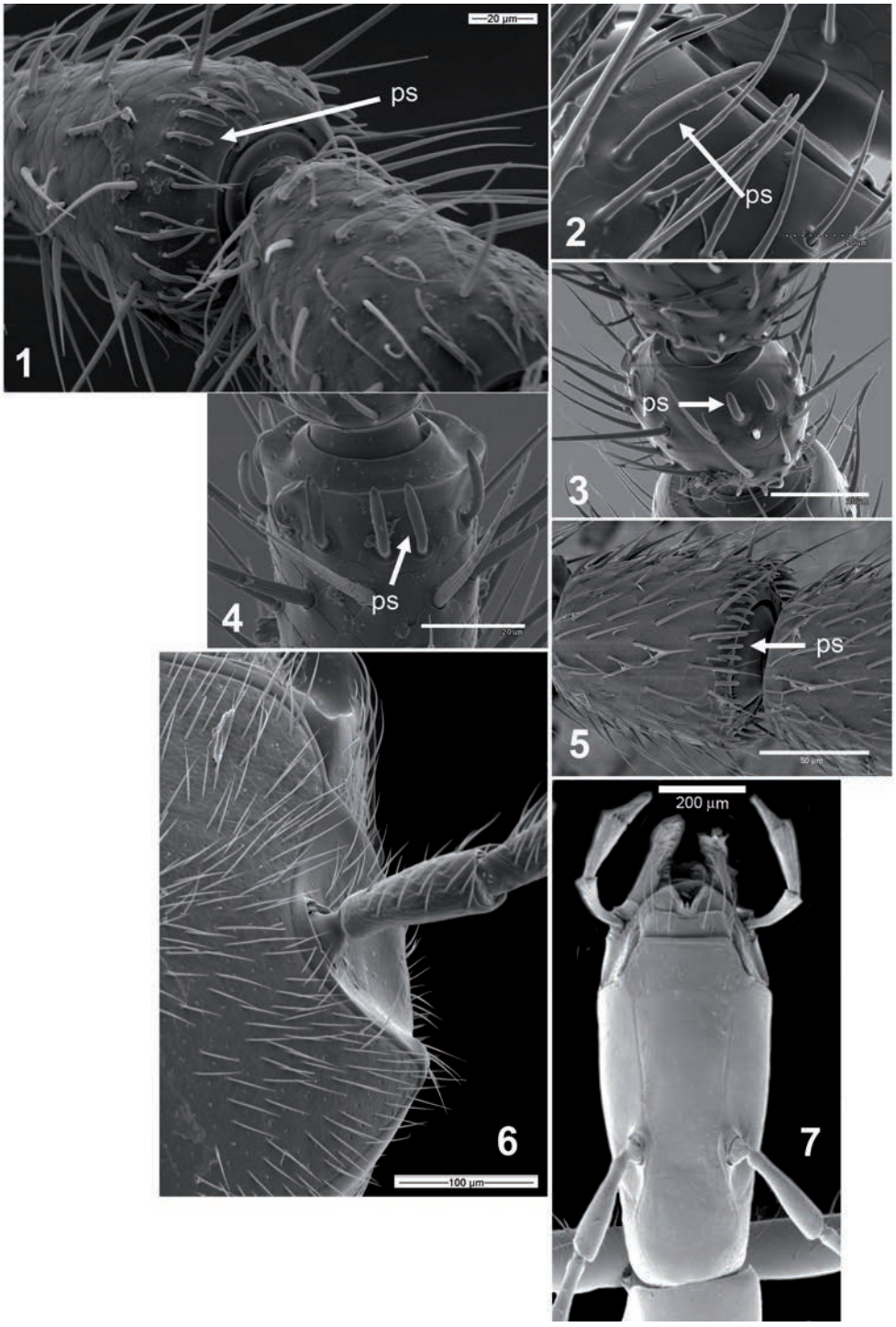
– All species of *Sciaphyes* Jeannel, 1910 (Cholevinae, Sciaphyini: Fresneda *et al*. 2011b).

– All species of mammal-associated Holarctic Platypsyllinae, except *Leptinillus validus* Horn, 1872 with an unfaceted eye remnant (Fresneda *et al*. 2011b).

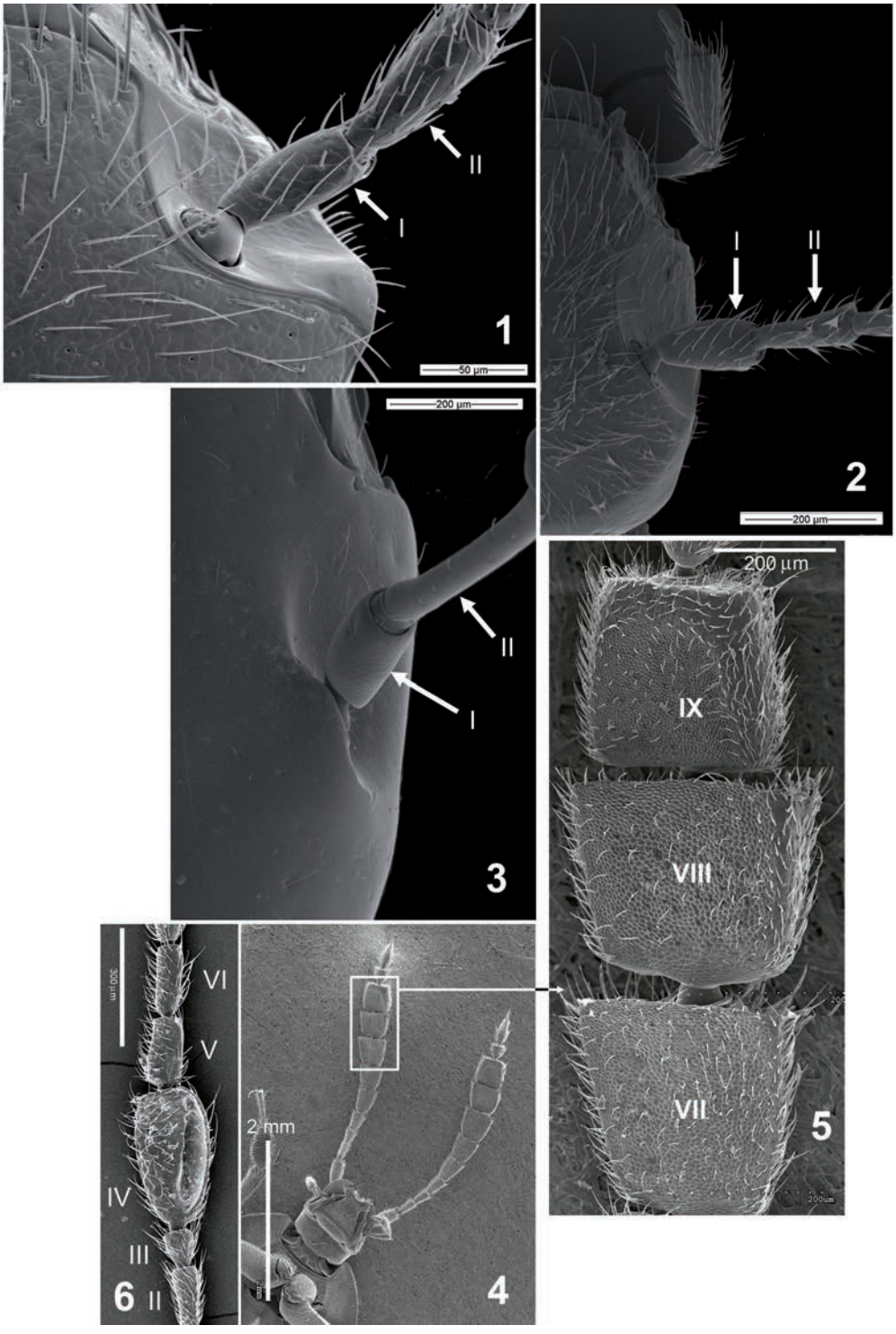
– The two species of *Zelodes* Leschen, 2000 from New Zealand (Leiodinae: Pseudoliodini) collected from litter or rotten potatoes (Leschen 2000).

– The three species of *Typhlocolenis* Hoshina, 2008 from caves in Japan (Leiodinae: Pseudoliodini; Hoshina 2008).

– Various, and some possibly not most closely interrelated, members of Leiodinae, Scotocryptini (Newton, 1998), including those associated with bee



FIGURES 8.1–8.7: Head. Projected sensillae in antennomeres of: (**1**) *Aphaobius haraldi* (IX), (**2**) *Machaeroscelis infernus cagiranus* **comb. nov.** (IX), (**3**) *Parvospeonomus delarouzeei catalonicus* (VIII), (**4**) *Quaestus longicornis* (VIII), (**5**) *Ptomaphagus troglodytes* Blas & Vives, 1983 (IX). Dorsal view of the head of: (**6**) *Speonomidius crotchi* ssp., (**7**) *Leptomeson radjai* (modified from Njunjić 2016). Abbreviations: **ps**, projected sensilla.



FIGURES 9.1–9.6: Head. First and second antennomeres of: (**1**) *Besuchetiola priapus*, (**2**) *Aphaobius haraldi*, (**3**) *Leptodirus hochenwarti hochenwarti*. Antennae of: (**4**) *Baronniesia delioti*, (**5**) magnification of the VII, VIII and IX antennomeres of the same species, (**6**) *Paraspeonomus vandeli*. **I-IX**, antennomeres.

nests such as *Parabystus* Portevin, 1907 and *Scotocryptus* Girard, 1874 (Peck 2003).

– *Agathidium* (*Agathidium*) *anophthalmousum* Angelini & De Marzo, 1984 from India: Darjeeling – Leiodinae: Agathidiini – (Angelini & De Marzo 1984).

– *Ptomaphagus troglodytes* Blas & Vives, 1983, from caves in south Spain. Although apparently none among the numerous cave- and soil-inhabiting *Ptomaphagus* Hellwig, 1795 species is truly anophthalmous in North America (Peck 1973), some cave species with an unfaceted eye spot were thought to be certainly blind with the optic nerves being lost (Peck 1973).

– All members of the tribe Leptodirini (Cholevinae) (Fig. 10), except *Platycholeus* (Platycholeina) (Fig. 10.4) and *Adelopsella* (Adelopsellina subtrib. nov.), the Leptodirina sensu novo: *Bathyscia* (some species), *Baudiola*, *Besuchetiola* (Fig. 10.1), *Capraiola*, *Catopsinus*, *Hittitia* stat. nov., *Iranobathyscia*, *Karadeniziella* (Fig. 10.2), *Notidocharis* (Fig. 10.3), *Pholeuonopsis zlatiborensis* (some ommatidia), *Sbordoniola*, *Georgiana* gen. nov., *Uhagoniella* gen. nov., *Zoiana* gen. nov. and *Uludagites* stat. nov. with a variable number of ommatidia. The eyeless *Coreobathyscia solivaga* Szymczakowski, 1975, described from a South Korean cave and known only from the type specimens, remains dubiously associated with Leptodirini – Fresneda *et al*. 2011b; see the section Genera *Coreobathyscia* and *Proleptodirina*–.

The presence of eyes is plesiomorphic as it occurs in the two most basal cladogenesis, *Platycholeus* and *Adelopsella*, and also in sister groups and outgroups (except *Ptomaphagus troglodytes*).

Anophthalmia, is derived and, based on the taxa of the phylogenetic tree, it is seen that the loss of eyes occurred not less than a twelve times (Fig. 10.1). It is a convergent character state of low for phylogenetic value, only useful in characterizing and differentiating genera.

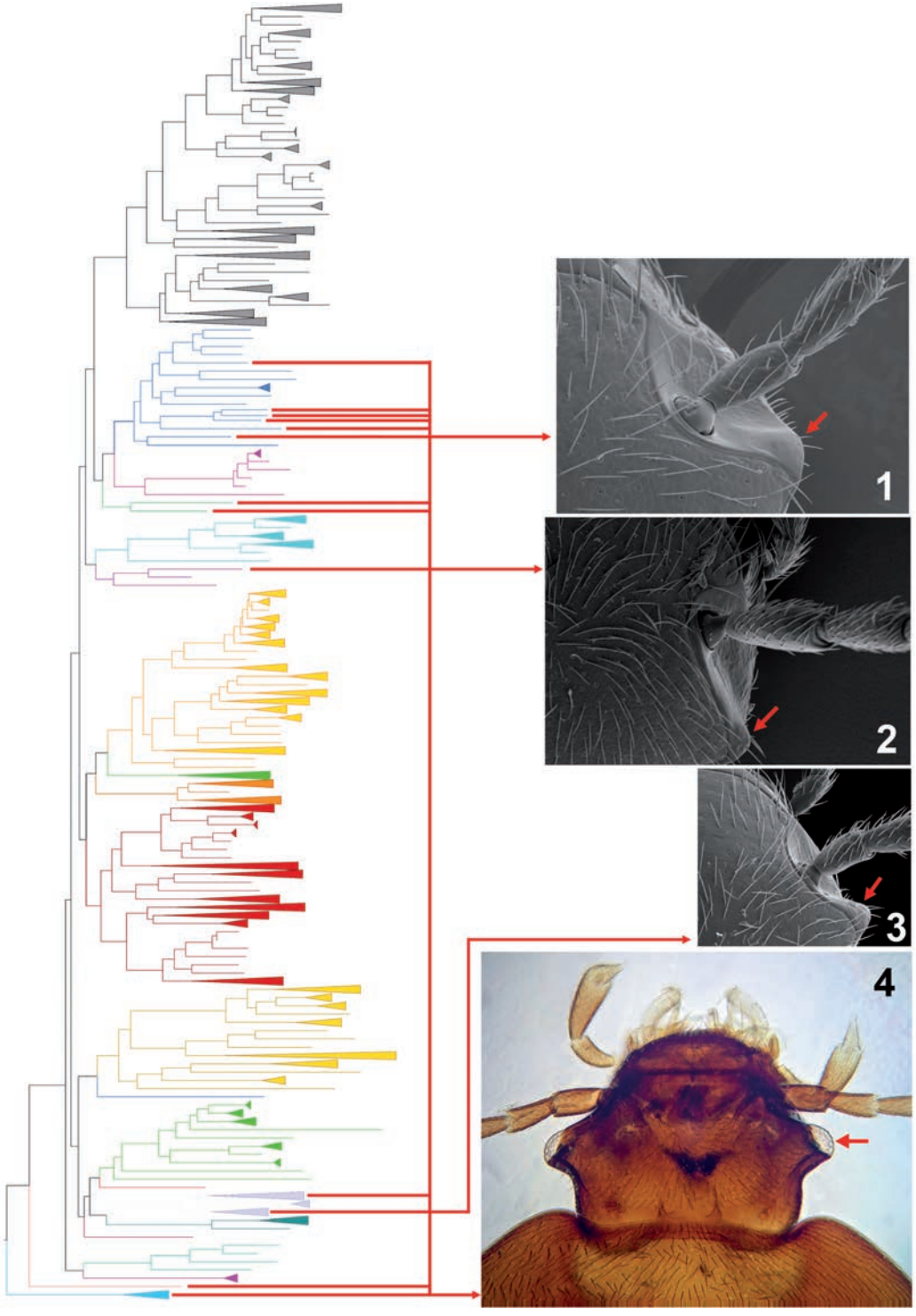
Legs

Various leg structures are important in both the systematics and phylogeny of different families, groups, and genera. Among them:

Tarsal formula: It is diverse in the different families of Coleoptera, four segments on all tarsi (tetrameres 4-4-4), such as Cerambycidae, Curculionidae, Chrysomelidae, etc., three segments on all tarsi (trimeres 3-3-3), such as Coccinellidae, Staphylinidae (with a very variable tarsal formula, most of the time non-trimers…), etc., or the most frequent, the pentameres with 5-5-5 tarsomeres, such as Carabidae, Elateridae, Scarabaeidae or all tribes of Cholevinae in both sexes, except a few groups of Leptodirini. This is the case of the Leptodirini males that Jeannel (1924a) designated as «Théléomorphes», with 4-5-5, which could be described as heteromers, although not in the sense normally applied to the term, 5-5-4, as in the Tenebrionidae. The «Théléomorphes» of R. Jeannel are scattered across different clades of the phylogenetic tree (Figs 11, 15). All females of the Leptodirini have four protarsomeres (Casale *et al.* 1991a; Giachino *et al.* 1998) and therefore present 4-5-5, the same as the males of the «Théléomorphes»; *Baryodirus* also has tetrameric and dilated protarsi in both sexes. Since both sister groups of Leptodirini or the outgroups also belonging to Cholevinae (Fig. 13.3) present the formula 5-5-5, this is the plesiomorphic state of the character; the tetramery of the females protarsi is a derived state that appears with Leptodirini, already in the first cladogenesis *Platycholeus*, thus the reduction in the number of protarsomeres (from five to four) in females (Fig. 13.4) (Jeannel 1936; Giachino *et al*. 1998; Newton 1998) is a synapomorphy of the Leptodirini. Respect to males, the 4-5-5 formula is a derived state that appears on various occasions (in several genera, such as: *Anillocharis*, *Hexaurus*, *Oryotus*, etc.) independently throughout the evolutionary history of the group (Fig. 15.1). This peculiarity was used as a phylogenetic character that characterised the Bathysciotina subtribe (V.B. Guéorguiev 1974a, 1974b, 1976), which has been revealed as a polyphyletic group.

Pretarsal morphology (sec. Antunes-Carvalho & Gnaspini, 2016): The median projection is notched in the centre (Fig. 12.1: mp); as a result, two triangular projections are found on the ventral distal margin of the terminal tarsomere (Fig. 12.1: mpp). In *Anthroherpon hoermanni* (*Anthroherpon* series), the two triangular projections are quite far apart compared to other Leptodirini and, in *Leptodirus hochenwarti*, *Astagobius angustatus* or *Speoplanes biocovensis*, all three in the *Leptodirus* series, the two projections are slightly inclined to each other, resulting in a deeper notch between them. In the margin between these two triangular projections of some species some tiny teeth can be seen.

The lateral seta (Fig. 12.1: ls) is inserted on the ventrolateral margin of the lateral lobe, while the ventrolateral seta (Fig. 12.1: vs) is inserted on the inner surface of the lateral lobe. There are pores or small depressions at the base of the inner face of the lateral



FIGURES 10.1–10.4: Head. Phylogenetic tree of Leptodirini (Fig. 2: Tree-1) with the distribution of oculate species. Head of: (**1**) *Besuchetiola priapus*, (**2**) *Karadeniziella omodeoi*, (**3**) *Notidocharis calabrezi*, (**4**) *Platycholeus opacellus*. The red arrow points to the eyes.

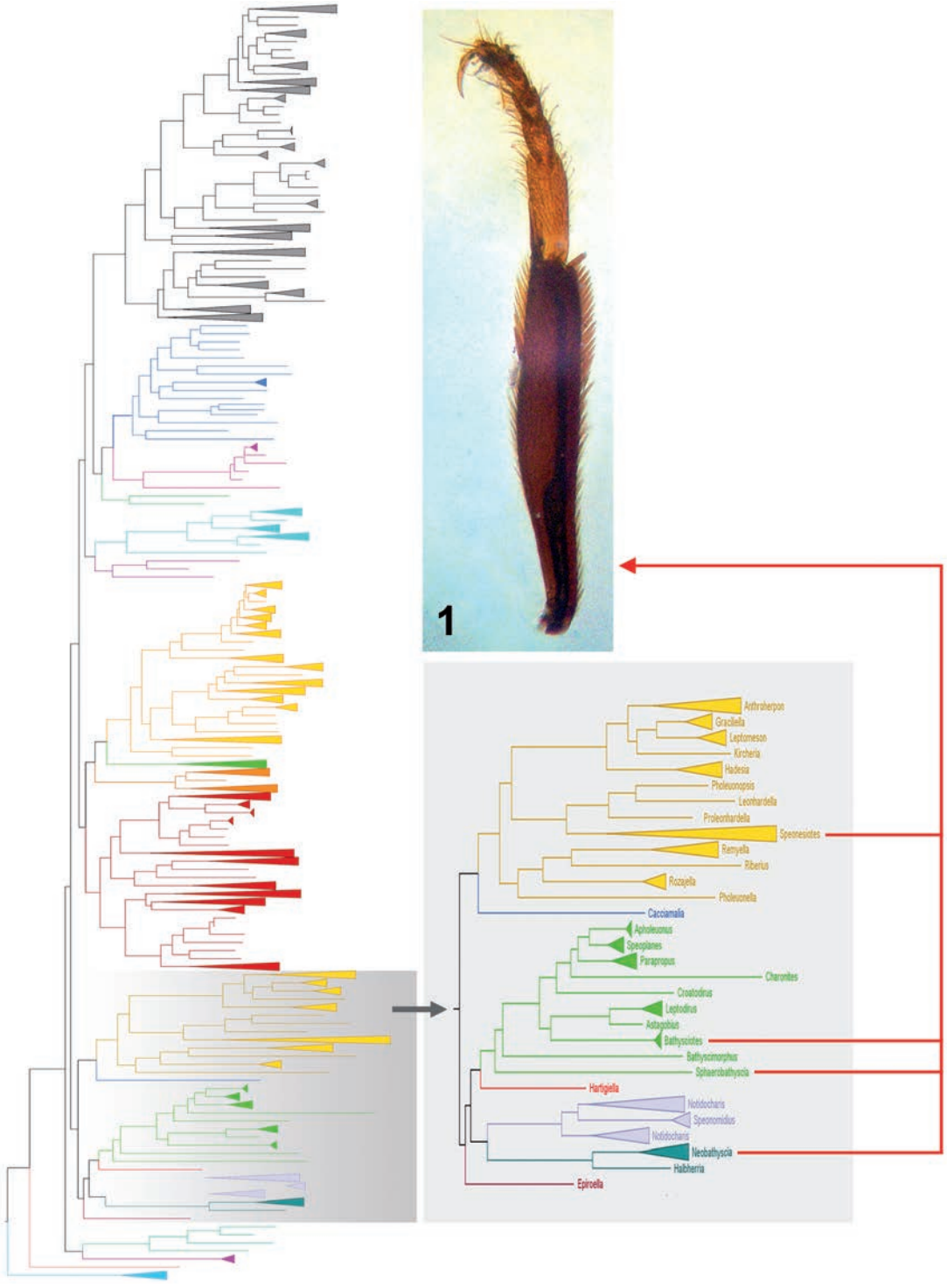


FIGURE 11: Legs. Phylogenetic tree of the Leptodirini with collapsed clades (Fig. 2: Tree-1) and distribution of species with tetramerous protarsi and protibiae with external comb, «Théléomorphes Division III» of Jeannel (1924a). Protibia of: (**1**) *Speonesiotes* (*Kulzeria*) *muelleri*.

lobes in some species such as *Aphaobius milleri* belonging to the *Oryotus* series.

The lateral lamellae of the unguitractor (Fig. 12.1: up) of *Baronniesia*, of *Bathysciotes khevenhuelleri* or *Astagobius angustatus* (*Leptodirus* series), touch in the midline, which is not the case in *Anthroherpon hoermanni* or *Remyella scaphoides* (*Anthroherpon* series), or in *Oryotus schmidti* and *Orostygia doderoi doderoi* (series *Oryotus*), species in which an additional median row of lamellae is found on the axis of symmetry of the unguitractor.

There are no cuticular protrusions around the unguitractor in *Aphaobius milleri* and *Oryotus schmidti* (*Oryotus* series), nor in *Ghidinia vailatii* of the *Dellabeffaella* series, but there are some microtrichia in *Bathysciotes khevenhuelleri tergestinus* (*Leptodirus* series), in *Machaeroscelis infernus* and *Troglocharinus ferreri* (*Speonomus* series); these microtrichia are often arranged in rows as in *Astagobius angustatus* (*Leptodirus* series) and *Anthroherpon hoermanni* (*Anthroherpon* series).

The middle sclerite is fused with the empodial sclerites (Figs 12.3, 12.6: esc); in general, the empodial sclerites are not clearly recognized and appear to be completely fused together, in such a way that the two empodial setae are fused at the base as can be seen in *Pholeuon leptodirum* (Fig. 12.3: esc) or *Sinobathyscia tianma* (Fig. 12.6: esc); it also occurs in *Speoplanes biocovensis* of the *Leptodirus* series (Antunes-Carvalho & Gnaspini 2016).

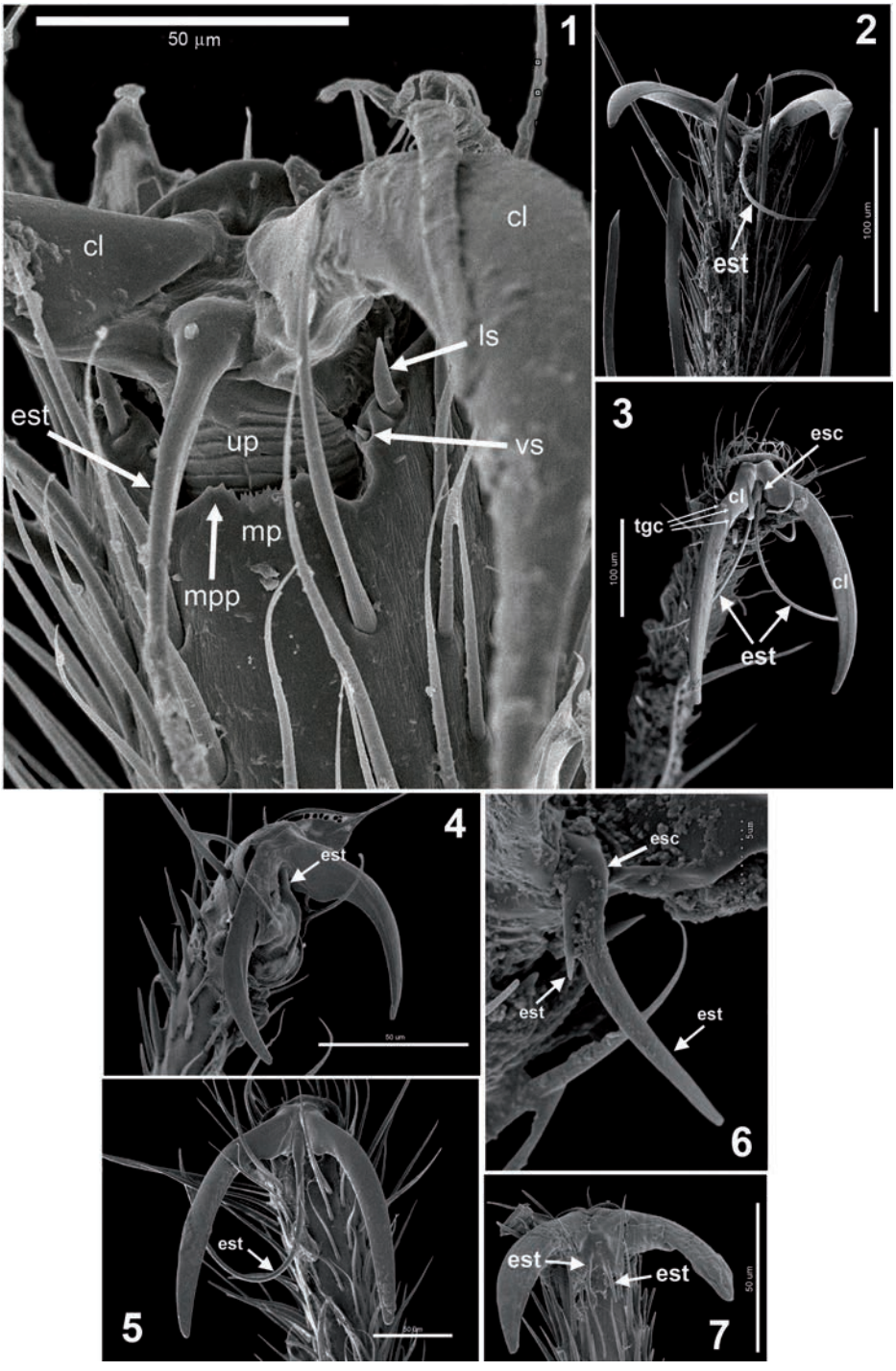
The tarsomeres, in general, are covered with fine and dense pubescence, although in some genera some other type of sensilia trichoidea can be found; long, flattened, ribbon-like setae are found on the protarsi of *Drimeotus* (Fig. 13.1). The distribution of this feature among the Leptodirini is unknown.

Male protarsa dilatation: The presence or absence of dilatation of the male protarsomeres often represents in Leptodirini an important diacritic character, usable at a supraspecific level in the definition of single genera (Jeannel, 1924a; Vailati, 1988, 2017a). There are taxa which have pentamerous male protarsi, in some cases without dilatation (e. g. *Reitteriola*, *Doderiola* and *Tamaniniella*), in others slightly dilated (e.g. *Rondolinia*, *Canapiciella* and *Muelleriola*), in others still very dilated (*Baudiola*, *Nanobathysciola talpa* comb. nov.). In general, the first three protarsomeres of the male are dilated (Figs 13.2, 13.5), only the males of *Aphaobius*, *Aphaotus* or *Hexaurus*, among others, have filiform ones, the same as those of the females (Fig. 13.4). *Speodiaetus* and *Knirschiella* females have the first three protarsomeres slightly dilated.

Tarsal empodium: Newton (1998) added the presence of a non-articulated empodial seta as a synapomorphy of the tribe Leptodirini, in contrast to all other Leiodidae that would have two articulated setae. In Leptodirini there are frequently two empodial sclerites but they cannot be recognized as individual structures (Antunes-Carvalho & Gnaspini 2016); when these two setae exist they appear to be basally fused unlike all other Cholevinae in which the empodial setae are positioned side by side with independent insertions. The two empodial setae of the Leptodirini are arranged diagonally in *Speoplanes biocovensis*, *Astagobius angustatus*, *Ghidinia vailatii* and *Oryotus schmidti*, in *Pretneria latitarsis* and *Bathysciotes khevenhuelleri tergestinus* being almost vertically, or vertically to each other in *Aphaobius milleri springeri* and *Orostygia doderoi doderoi*; this characteristic had already been observed by Vailati (1998) in *Orostygia*, or by Polak & Jalžić (2009) in *Blattochaeta*.

The only exceptions to this pattern are *Anthroherpon* and *Pholeuon*, whose empodial setae are laterally aligned with each other (Fig. 12.3); in *Anthroherpon* they do not appear to have the same degree of basal fusion as in other Leptodirini. However, these are derived states that have appeared in different clades; *Anthroherpon* does not derive from a basal cladogenesis as suggested by Giachino & M. Etonti (1995), where other representatives such as *Remyella* fit perfectly into the structural pattern of the remaining Leptodirini. Perreau & Pavićević (2008b) excluded *Remyella* from Anthroherponina to place it in Leptodirina (a position maintained by Antunes-Carvalho & Gnaspini 2016); but molecular study (Fig. 1H) shows that it has to be maintained in the *Anthroherpon* series within the *Pholeuonella* group of genera. In this context, the basal fusion of the setae and the rotation of the empodial sclerites can be considered apomorphies of the clade formed by Old World Leptodirini, excluding *Anthroherpon* and *Pholeuon* (Fig. 12.3). The two setae that share the insertion point at their base may be of equal length – *Pholeuon* (Fig. 12.3), *Hadesia vasiceki*, *Canavesiella lanai* or *Aphaobius milleri* –, or one of them may be reduced: *Sinobathyscia* (Fig. 12.6) or very reduced – *Notidocharis ovoidea*, *Antrocharis querilhaci*, *Paratroglophyes jeanneli*, *Paraspeonomus vandeli* or *Parabathyscia ligurica* (Antunes-Carvalho *et al*. 2019) –.

In *Speonomus* and *Troglocharinus*, only a single long, well-developed empodial seta is seen, but there is an extremely reduced outer seta welded to the base of the other; this particularity is also found in *Sinobathyscia* although the outer seta is not as reduced and



FIGURES 12.1–12.7: Legs. Protarsi of: (**1**) *Baronniesia delioti*, (**2**) *Drimeotus* (*Drimeotus*) *viehmanni* ssp., (**3**) *Pholeuon* (*Pholeuon*) *leptodirum leptodirum*, (**4**) *Adelopsella bosnica*, (**5**) *Trocharanis mestrei*, (**6**) *Sinobathyscia tianma*, (7) *Ptomaphagus tenuicornis* ssp. Abbreviations: **cl**, claws; **esc**, empodial sclerites; **est**, empodial seta; **ls**, lateral seta; **mp**, median projection of ventral edge of terminal tarsomere; **mpp**, paired median projections of edge of terminal tarsomere; **tgc**, transverse groove in claw; **up**, unguitractor; **vs**, ventrolateral seta.

is clearly visible (Fig. 12.6). A single empodial seta has been observed in other species of the genus *Speonomus* (Juberthie *et al*. 1981; Gers 1983, 1989; Gers & Dupuy 1988; Perreau 2000), or in *Trapezodirus* (Fresneda *et al*. 2011a) and *Pholeuon* (Moldovan *et al*. 2007); also in *Adelopsella* (Fig. 12.4), *Baronniesia* (Fig. 12.1), *Drimeotus* (Fig. 12.2) or *Trocharanis* (Fig. 12.5); but it is possible that the extremely reduced outer seta welded to the base of the other exists. It seems that the base of the two setae has fused and rotated, arranging itself obliquely or vertically, it may be a synapomorphy of Leptodirini; the plesiomorphic state would be that of two setae with independent insertion arranged in the plane of the claws as occurs in the remaining Cholevinae (e.g. *Ptomaphagus*, Fig. 12.7) with two articulated setae or small lobes each with its own point of insertion although in some species one of them is greatly reduced.

Torsion of the empodial setae is a synapomorphy of the Leptodirini if *Platycholeus* and *Notidocharis* are excluded, the latter representing a derivative reversal. The proximal portion of the empodial setae is round in section and slightly crenellated, while the rest up to the apex is somewhat flattened. The apex of the two setae often appear to touch (as in *Aphaobius milleri*), but they do not appear to be fused. In *Machaeroscelis infernus* and *Troglocharinus ferreri* only a long (internal) empodial seta can be seen, round in cross section, and the external seta is greatly reduced. Antunes-Carvalho & Gnaspini (2016) provide other characters, including the existence of a set of pore plates on the cuticular surface of the terminal tarsomere; they also indicated that this structure was identified in members of five of the seven subtribes; these plates do not exist in *Platycholeus* and *Spelaeobates*.

Claws: The absence of longitudinal grooves and the presence of a transverse groove seems to be a synapomorphy of the Leptodirini; the remaining Cholevinae have striated claws and no transverse groove (Antunes-Carvalho & Gnaspini 2016). In general, the claws are elongated with a rounded apex. At the distance of one-fifth to one-third of their length from the base, there is a convex transverse groove on the dorsal surface of the claws (Fig. 14.3), from which and to the apex they are somewhat flattened (Fig. 12.3: tgc) as in *Aphaobius milleri*, *Orostygia doderoi doderoi*, *Oryotus schmidti* and *Pretneria latitarsis* (*Oryotus* series), as well as *Ghidinia vailatii* (*Dellabeffaella* series). Jeannel (1924a) establishes two groups based on the shape of the claws, Bathysciae with thin, long and narrow claws and Anthroherpona with robust, wide and usually recurved spoon-shaped claws, a character that occurs in all genera of the *Anthroherpon* group, *Anthroherpon* series, except in *Nauticiella* with thin claws on the metatarsals and broadened on the pro- and mesotarsals.

Mesotarse: All studied species of Leptodirini and Ptomaphagini have non-dilated male first mesotarsomere (Fig. 14.2), except *Adelopsella* and *Platycholeus*. In other Cholevinae tribes it is common for males to have a dilated first mesotarsomere (Fig. 14.1). In *Perriniella* (*P. faurai* and *P. bofilli*) the first tarsomere of the mesotarsa has a tuft of very long setae on its underside (Fig. 293.7). No other species in its clade, nor in the *Quaestus* clade, have this tuft but its existence in other Leptodirini is unknown.

Male metafemora: The presence of a tooth on the posterior edge of the male metafemora (Fig. 197.9) is an infrequent feature in Leptodirini (Vailati 1988, 2017a) and often of high taxonomic significance. In the Italian Leptodirini, for example, a metafemoral tooth is present in males of the species of the genera *Stoppaniola* and *Rondolinia*; it is also found in males of *Speonomus leleupi*, *Zariquieyella grandis* comb. nov., *Z. schiodtei* comb. nov. or in many of the species of *Vanderberghia* gen. nov., *Schaufussia* gen. nov. and some species of *Quaestus*; most often there is no spine on the posterior part of the metafemur although it is possible that the entire femur may have a characteristic shape – e.g. *Paratroglophyes* –.

Protibial apical armature: The analysis of the set of spines and protibial spurs in the taxa considered appears quite complex, and highly diverse among the different species. The armor of the protibiae on the outer margin bears a pectinated series of numerous small spines or is only provided with apical spurs. So it seems that there are basically two types of configuration:

– The protibiae are not attenuated at their apex; they have an internal pectinated spur, one ventral and two or three external spurs; between the internal and external spurs, the dorsal edge presents some unequal spines; the meso- and metatibia are armed with three pairs of spines along the outer edge and four apical spurs, of which the inner and dorsal spurs are generally longer and pectinate or polydentate (*multifide* of Jeannel 1924a); the spines on the external face can be very small, hidden between the pubescence of the tibia, or be very robust, as large as the spurs.

– The armor of the protibiae is composed of a pectinate or bifid internal spur and a regular series of small spines, a comb that extends all along the apical edge and a variable extension of the external margin;

there is no external apical angle of the tibia so the tibia appears to have a narrowed apex; on the other hand, the meso- and metatibiae are barely spiny on their external face and their apical extremity does not have external spurs, although it is decorated with an apical crown of small and regularly aligned spines.

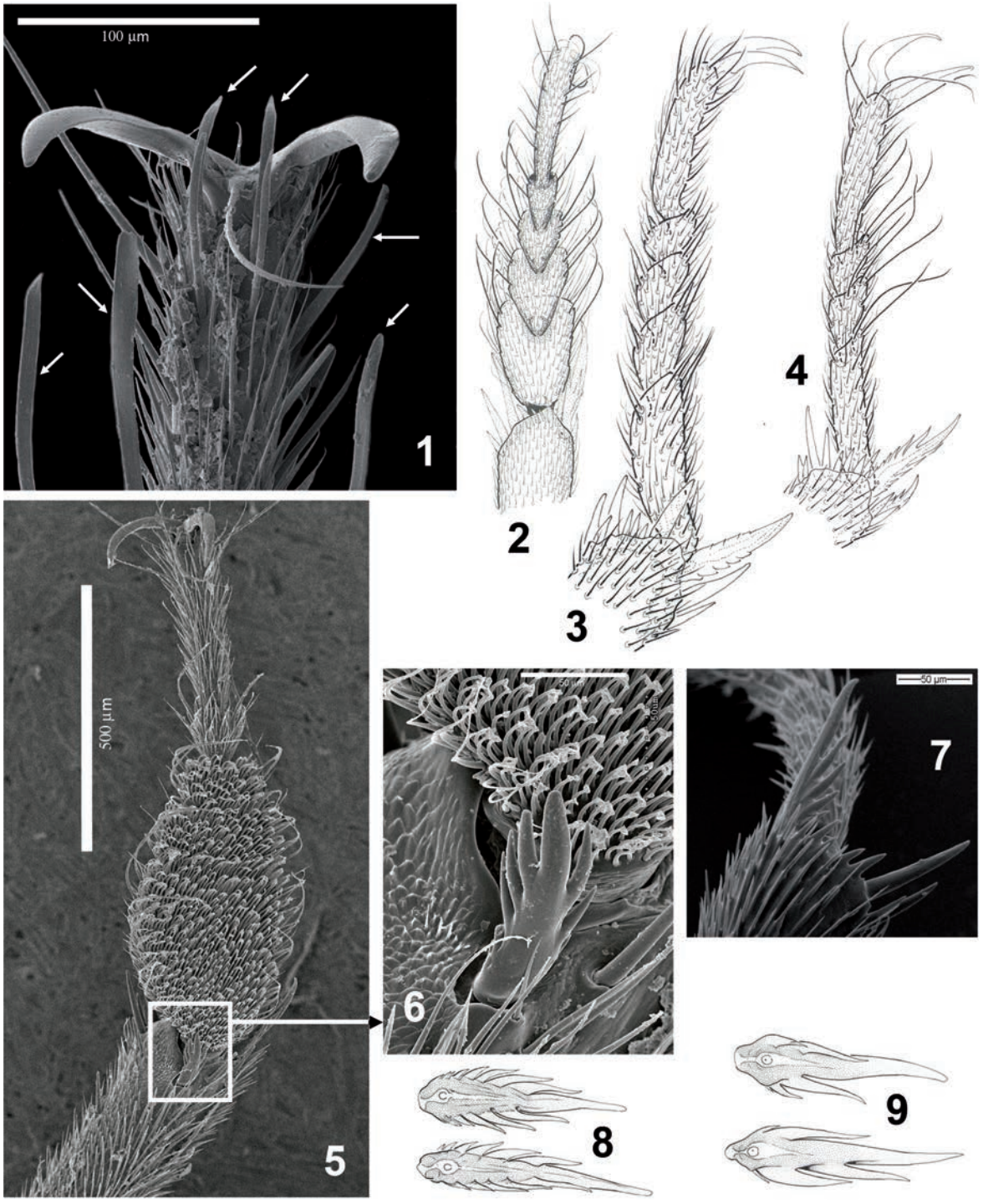
The existence of a lateral series of spines on the outer face of the protibiae and a crown of spines on the apex of the meso- and metatibiae in certain series (Bathysciotina or Leptodirina) is one of the characters used for the classical division into subtribes (Fig. 11.1). Similar structures are found in Ptomaphagini or Eucatopini. Various authors (sic Perreau 2000) consider the existence of this character as a derived state that has appeared independently on various occasions (Fig. 11). Perreau (2000) discovered that some genera that do not have this structure actually harbour a short or reduced protibial comb, masked by the setae that cover the terminal sector of the apex of the tibiae (e.g. *Speonomus diecki*); it is unknown in how many taxa something similar happens, or if it is a universal conformation in the Leptodirini.

In two species (*Reitteriola pumilio* and *Rondolinia adelinae*) a series of 3-4 spines on the external protibial margin placed in a clearly preapical position is present, a character that is not found in other taxa. Other genera like *Canapiciella*, *Doderiola*, *Baudiola*, *Tamaniniella* or *Muelleriola* have a more or less complete crown of apical spines and two apical spurs of the polydentate type (*sensu* Vailati 1988, 2017a; Giachino 1993), one on the internal apical margin and one, smaller, on the ventral margin.

If it is confirmed that there are taxa without a comb of spines on the external face of the protibia (*sensu* Jeannel, 1924a), then these would be a derived state, since the presence of this series in the sister group of Leptodirini evidences that this is the plesiomorphic state; considering the loss as a derived state is more parsimonious.

Tibial spurs: All studied species of Leptodirini have internal tibial spurs with secondary dentition, polydentate (Fig. 13.9) or pectinate (Figs 13.4, 13.6–13.8). The phyletic importance of the shape, polydentate (with few secondary spines) or pectinate (with many secondary spines), of the pro-, meso- and metatibial internal spurs in the Leptodirini of the phyletic lines of *Boldoria* and *Dellabeffaella* was first highlighted by Vailati (1988, 2017a), followed by Giachino (1993a) who used this trait to hypothesize that several species do not belong to the genus *Bathysciola*. In fact, in *Reitteriola*, *Canapiciella*, *Rondolinia*, *Baudiola*, *Tamaniniella* and *Muelleriola*, the tibial spurs are always more or less «polydentate». In the genus *Doderiola* there is a high number of secondary teeth, bringing it closer to the «pectinate» type. All the representatives of the *Quaestus* series are polydentate and those of the *Speonomus* series (except *Gesciella*) are pectinated. The bifid (*Gesciella*, *Pholeuon*, *Leptodirus* or *Speoplanes*), polydentate (*Quaestus* or *Espanoliella*) or pectinate (*Speonomus* or *Troglocharinus*) internal spur is characteristic of Leptodirini with the exception of *Platycholeus* and *Anthroherpon* whose spurs are simple as in Catopina (Fig. 13.3).

Relative length of the legs: The relative length of the legs is of special interest, although expressing this type of characters is somewhat difficult: «longer than», «as long as» or «more or less than»… Legs tend to be proportionally longer and more slender in pholeuonoid, leptodiroid or scaphoid taxa and relatively shorter and more robust in the bathyscioid. However there are exceptions. The disproportionate length of the legs of *Troglocharinus vinyasi*, originally described as *Speonomus* in part because of its bathyscioid shape, corresponds to the *Troglocharinus* model; in the same way it happens in the bathyscioid species *Troglocharinus mengeli* or *T. mercedesi* (Fresneda *et al*. 2021); all of them derive from the most basal cladogenesis of the genus *Troglocharinus*. At least in this clade, it seems that the first character to change is the length of the legs and antennae; then the whole insect acquires its elongated shape. Indeed, in *Troglocharinus* or *Pholeuon* the legs are long, but where this characteristic reaches the extreme is in the *Anthroherpon* and *Leptodirus* clades; *Anthroherpon* or *Leptodirus* are paradigmatic examples, but also *Leptomeson*, *Remyella* or *Kircheria*, just to name a few; the considerable elongation also affects the antennae of all these genera. The relative lengths of each of the legs would also have to be considered. In general the profemurs are shorter than the meso- or metafemurs, even in genera with very elongated appendages such as *Albanodirus*. But this is not always the case; in *Croatodirus bozicevici* the three femurs appear to be of equal length and in *Leptomeson soltensis* the profemurs are the longest of the three pairs. The thickness of the femurs also shows variations, in *Kircheria dritae* the three femurs have a similar thickness while in *Anthroherpon charon* the profemurs are much thicker than the meso- and metafemurs. The distribution of these peculiarities in the phylogenetic tree has not been studied and is unknown, thus in *Leptomeson* and *Anthroherpon* it seems variable among species; neither has it been found so far how to unambiguously assess these characters.



FIGURES 13.1–13.9: Legs. Protarsi of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni* ssp. (white arrow pointing to ribbon-like setae), (**2**) male of *Quaestus incognitus*, (**3**) female of *Catops fuliginosus* Erichson, 1837, (**4**) female of *Trapezodirus gimenezi*, (**5**) male of *Baronniesia delioti*. Magnification of the tibial spur of: (**6**) *Baronniesia delioti*, (**7**) *Paraspeonomus vandeli*. Pectinate spur of (**8**) *Stygiophyes akarsticus* and polydentate spur of (**9**) *Espanoliella jeanneli*. Figs **8**–**9** modified from Salgado *et al*. (2008).

Pterothorax

In the morphological study the terms mesoventrite, mesoventral keel and metaventrite have been used. Mesosternum, mesosternal keel, and metasternum had traditionally been used in the Leptodirini literature. Lawrence (1999) recovered the observations of Campau (1940), Ferris (1940) and Baehr (1975) (ignored by the vast majority of later authors) in which an observation error is evident: «*… the terms mesosternum and metasternum, as used in Coleoptera, are misapplied to regions which consist of paired subcoxal elements (preepisterna), sometimes combined with paired katepisterna, the true sternum having been invaginated along the midline where the discrimen usually lies*.» (Lawrence, 1999). This author proposes the neutral terms mesoventrite and metaventrite to replace mesosternum and metasternum respectively. The new names have been incorporated into basic morphology manuals (Beutel & Lawrence, 2005; Lawrence *et al.* 2010) and their use is becoming more widespread (Lawrence *et al.* 1999, 2011; Beutel & Haas, 2000).

The thoracic morphology has been studied in depth by Luo *et al*. (2019b) in *Troglocharinus ferreri*.

Metathoracic wings: Only *Platycholeus* are winged, the other Leptodirini are apterous.

Mesoventrite: With a well-defined suture between mesoventrite and anteromedian process of metaventrite, the meso-metaventral suture (i.e. «metasternal suture» of authors, cf. Beutel & Lawrence, 2005) (Fig. 16.3: mms), or totally fused with the metaventrite (Fig. 16.2). Most species of Leptodirini have a well-defined lateral suture between the extension of the mesoventrite and the anteromedian process of the metaventrite (the «metasternal process»). In the genera of the series *Spelaeochlamys* (except *Anillochlamys*) or *Patriziella* (*Ovobathysciola* sensu novo, *Cytodromus* series) the mesoventrite is fused with the anteromedian process of the metaventrite, so there is no visible suture on the ventral side (Fig. 16.4). Viewed laterally, there are indications of a suture starting from the mesocoxal cavities, but not reaching the ventral surface. This character was mentioned by Laneyrie (1967) for some eastern Mediterranean species of Leptodirini.

Mesoventral keel: On the midline it has a raised and thin crest that forms two wings on its sides that overlap the episternum and form part of the internal edge of the mesocoxal cavities: the mesoventral keel. It is present in most of the species of Leptodirini, in Ptomaphagini, but not in Cholevini; however, some Leptodirini do not have it. Schaufuss (1861b) described the structure in *Quaesticulus adnexus*: «*Mesosterno et metasterno subtiliter carinatis*». This keel was used by Reitter (1885a) to establish a dichotomy in a key: «*Carina mesosternali simplicia, antrorsum haud magis elevata*» versus «*Carina mesosternali antrorsum magis elevata et subdentata*». Jeannel (1911) achieved a detailed study and identified some of the main models:

– Elevated and rounded in *Speonesiotes*.

– Coarse and toothed in *Speonomus* and close genera.

– Prolonged over the metaventrite in *Breuilia* and *Speocharis*.

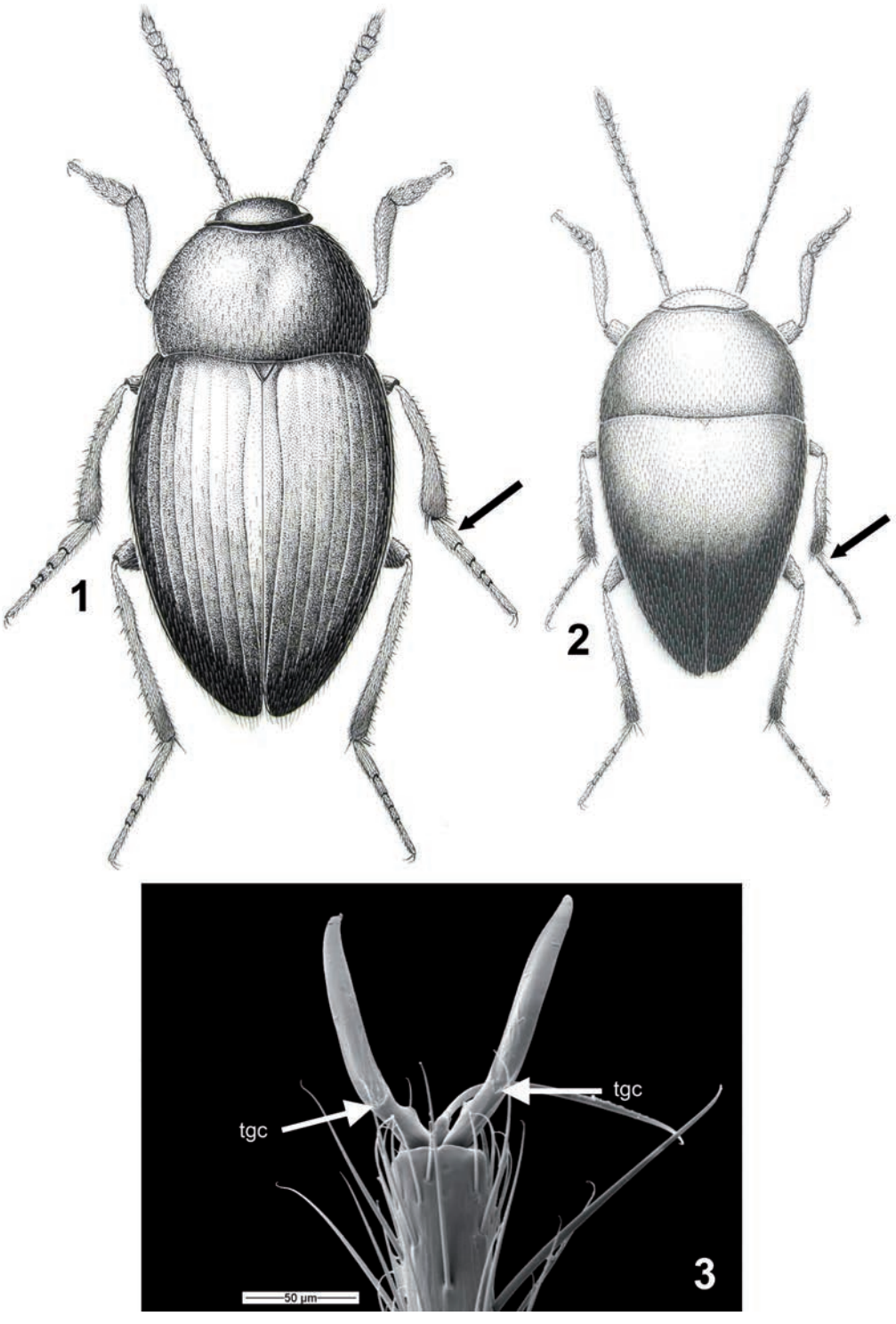
– In the elongated species it tends to reduce and does not exist in some genera like *Parapropus*, *Leptodirus* or *Anthroherpon*. To Jeannel (1911) list we must add *Astagobius*, *Remyella*, *Genestiella* and *Cansiliella*.

The great variety of forms has led to the fact that this structure has been given great taxonomic value by Jeannel (1911, 1914, 1924a), Laneyrie (1967, 1969), V.B. Guéorguiev (1974a, 1974b, 1976), Bellés *et al*. (1978), Salgado (1996a) and practically all the taxonomists who have dealt with this zoological group. V.B. Guéorguiev (1974a) separates Spelaeobatina with a keel from Anthroherponina without a keel. Or in Leptodirina the genera *Pholeuonella*, *Laneyriella* and *Pholeuonidius* with long keel were separated from *Bathyscimorphus*, *Bathysciopsis* and *Rectipenis* with short keel.

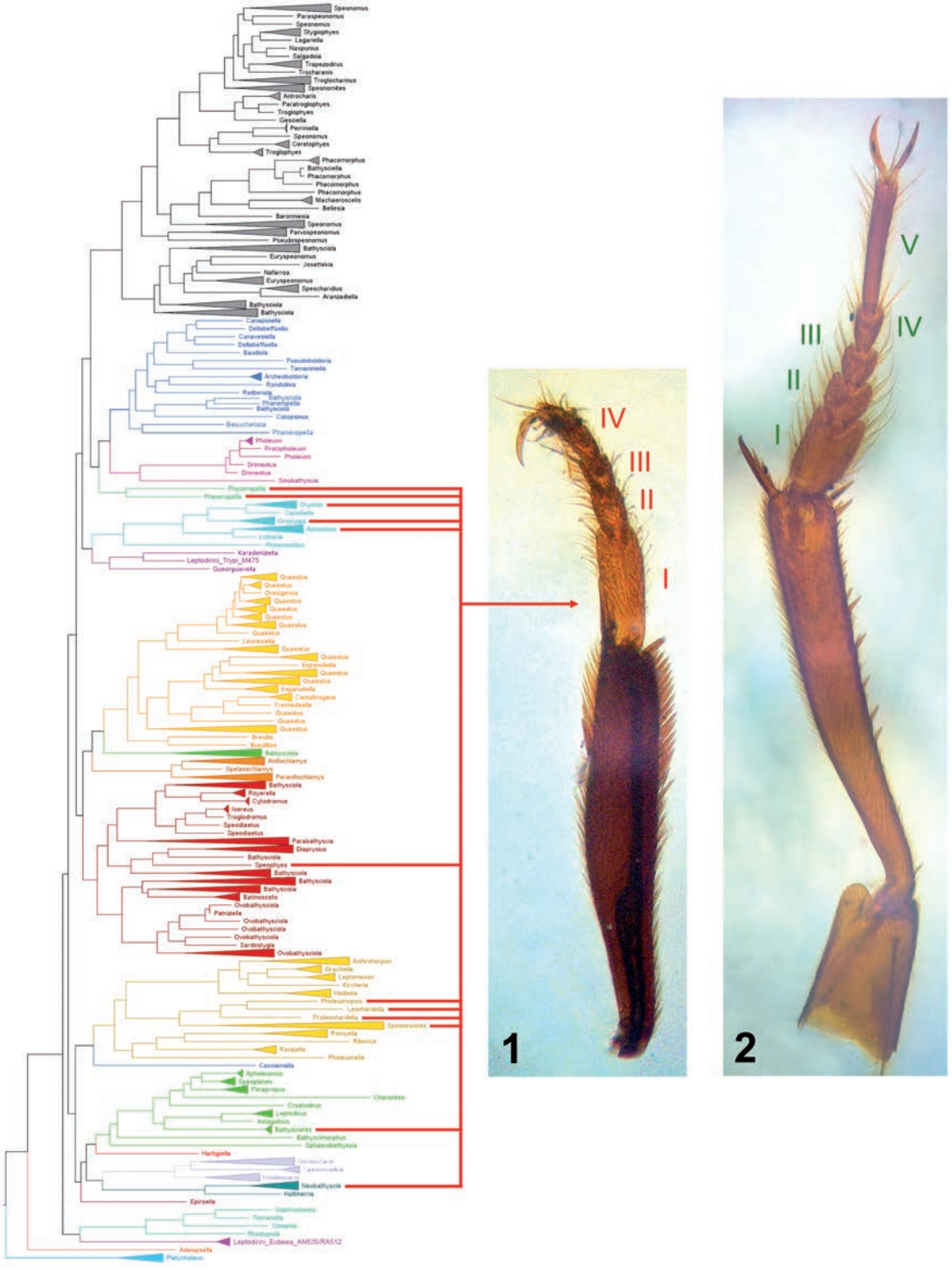
Its presence or absence is not characteristic of each clade but can be found even within the same genus. In general, a reduction or even complete atrophy is observed in the pholeuonoid forms. Since these are, in general, a derived morphologies in the clades in which it exists, consequently the reduction or loss seems to also be a derived state. The existence of a keel in Ptomaphagini supports that the presence of this structure is the plesiomorphic state of the character. Generally in clades that contain species with a well-developed keel and the species without keel, the genera or species with a well-developed keel are found in the early splits of the cladogenesis:

– In *Trocharanis* in which the keel is absolutely absent (Fig. 304.10) whereas it is well-developed in its sister clade – *Trapezodirus* – (Fig. 304.9). Nor does it exist in *Antrocharis* (Fig. 297.4), *Parapropus* (Fig. 82.3), *Isereus* (Fig. 173.3) and others.

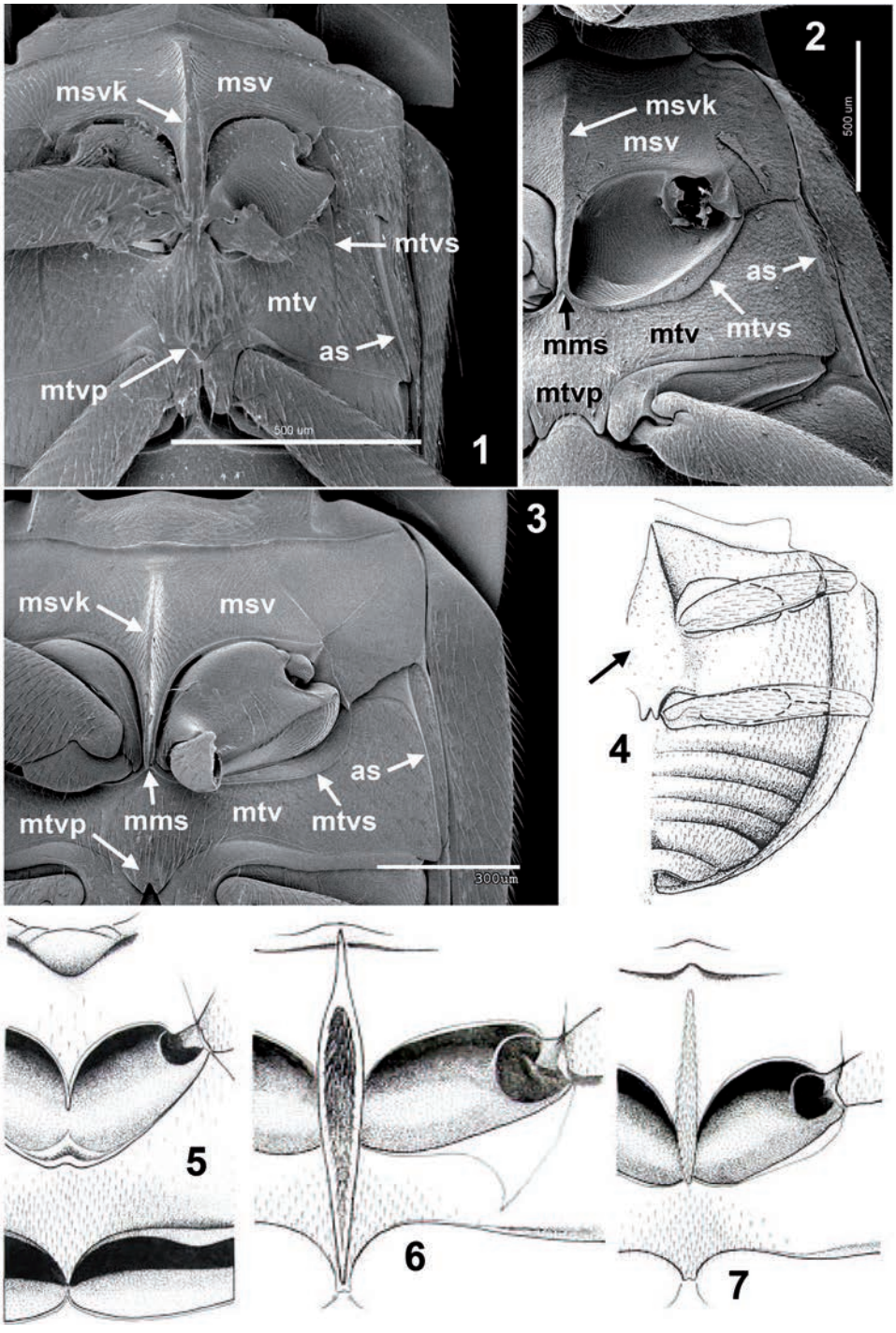
– In the genus *Troglocharinus*, in which there is a whole series of development from fully absent (*T. espanoli*) to a well-developed keel with a denticulated vertex – *T. mengeli*, *T. mercedesi*, *T. vinyasi*, *T. fadriquei* (Fig. 17.8) or *T. rizzoae* sp. nov. –.



FIGURES 14.1–14.2: Legs. Habitus of: (**1**) *Catops nigricans* (Spence, 1813), (**2**) *Quaestus incognitus*. Claws of: (**3**) *Antrocharis querilhaci querilhaci* (Black arrow pointing to first mesotarsomere; white arrow pointing to transverse groove). Figs **1–2** modified from Salgado *et al*. (2008). Abbreviations: **tgc**, transverse groove of the claw.



FIGURES 15.1–15.2: Legs. Distribution of the species with tetramerous and pentamerous male protarsi. Protarsomeres of: (**1**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**2**) *Trapezodirus escollae*. **I–V**, Protarsomeres.



FIGURES 16.1–16.7: Pterothorax. Ventral view of: (**1**) *Ptomaphagus troglodytes* Blas & Vives, 1983, (**2**) *Pholeuon* (*Pholeuon*) *leptodirum leptodirum,* (**3**) *Adelopsella bosnica,* (**4**) *Paranillochlamys urgellesi,* (**5**) *Catops fuliginosus* Erichson, 1837, (**6**) *Espanoliella noltei* **comb. nov.**, (**7**) *Stygiophyes puncticollis*. Abbreviations: **as**, anapleural suture; **mms**, meso-metaventral suture; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvp**, metaventral process; **mtvs**, metaventral suture. Black arrow indicating the mesoventrite completely fused with the metaventrite without suture. Figs **5**–**7** modified from Salgado *et al*. (2008).

– In *Tismanella* it is summed up in an eyelashy circle bristling with setae (Fig. 40.7).

When there is a mesoventral keel it can be:

– Tall, triangular in shape, rounded, prolonged towards the front, with or without a hooked vertex – with rounded or pointed form: *Quaestus*, *Cantabrogeus*, *Espanoliella*, *Closania* or *Neobathyscia* (Figs 17.5, 17.6, 18.2, 18.4); with hooked vertex: *Speonomidius, Ovobathysciola*, *Spelaeochlamys, Sophrochaeta* or *Protopholeuon* – (Figs 18.1, 18.3, 18.7).

– Low, with a rounded profile – *Perriniella*, *Catalaniana* gen. nov. – (Fig. 167.1).

– It may not reach the mesocoxal cavities, therefore these are in contact (Figs 17.2, 17.3). At the same time *Prospelaeobates* presents, unlike *Spelaeobates* (where this character has never been previously reported), the mesocoxal cavities which are not confluent, but separated by the intercoxal apophysis which reaches the anterior edge of the metathorax, a character of significant importance in the reconstruction of phyletic relationships in Leptodirini and Cholevinae in general (Giachino & Vailati 1993). The presence of respectively separate and confluent mesocoxal cavities in two genera of the same phyletic line leads us to some considerations about the state of this character in the Leptodirini, which present separate mesocoxal cavities in almost all genera, with exceptions, in the state of our current knowledge, only in the genera *Anthroherpon*, *Remyella* and *Spelaeobates* (Giachino & M. Etonti 1995) or in *Oryotus*, *Isereus*, *Parapropus*, *Platycholeus* and *Adelopsella*. This fact has led to consider the character «separate mesocoxal cavities» as synapomorphic in the Leptodirini and the situation with confluent cavities as plesiomorphic in the genera *Anthroherpon* and *Remyella* (Giachino & M. Etonti 1995), also in consideration of other plesiomorphies detectable in the two aforementioned genera (non-curved aedeagus, non-reduced male genital segment). This hypothesis contrasts with what was supposed by Jeannel (1924a), who attributed this state to a reduction of the mesoventral keel in taxa highly specialized in the subterranean environment. It is evident that the interpretation provided by Giachino & M. Etonti (1995) cannot be applied to the phyletic series of *Spelaeobates* (series pertaining to the grouping of «Théléomorphes» and therefore, as such, derived from the «Infraflagellates» *sensu* Casale *et al*. 1991), where just the least specialized genus (*Prospelaeobates*) has separate mesocoxal cavities. In this case, the hypothesis of Jeannel (1924a) of a reduction of the intercoxal apophysis linked to the reduction/disappearance of the mesoventral carina and to the degree of general specialization of the body appears much more likely. The existence of a keel in Ptomaphagini or in the basal clades of Leptodirini, *Platycholeus* and *Adelopsella* seems to indicate that this is the plesiomorphic state of the character and its disappearance or reduction even with retraction of the intercoxal process is the derived state. The analysis of this character, and of its transformation, must therefore lead to prudence in the evaluation of its state, especially when examining groups with very ancient origins, in which phenomena of very strong specialization and adaptive convergence tend to mask phylogenetically significant characters. The Ptomaphagini also has separate mesocoxal cavities (Fig. 16.1). However, other subfamilies or Leiodidae not included as outgroups have also non-confluent mesocoxal cavities (Newton 1998).

The mesoventral keel can be prolonged until it comes into contact with the anterior edge of the metaventrite so that it separates the mesocoxal cavities – *Aphaobius*, *Speophyes*, *Sophrochaeta, Speonesiotes, Anillochlamys* – (Figs 17.4, 17.7); or may extend partially – *Quaestus* – (Fig. 17.5), totally – *Espanoliella* – (Fig. 17.6) over the metaventrite or even exceed the posterior edge of the metaventrite (Figs 217.3, 217.4); the mesoventral keel is well-developed, extending over the metaventrite, in the series *Quaestus*, in *Nanobathysciola ovata* comb. nov., *Neobathyscia* or *Bathysciotes*. The mesoventral keel was studied by Salgado (1996a), in where the different types occurring in the series *Quaestus* and the genus *Notidocharis* were described:

– Model 1: Short and narrow keel, in which the process does not extend over the metaventrite or does not reach the distance of one third of its width.

– Model 2: Keel long, narrow or wide, and the process extends widely over the metaventrite.

– Model 2A: With a wide middle area and no groove (with various shapes).

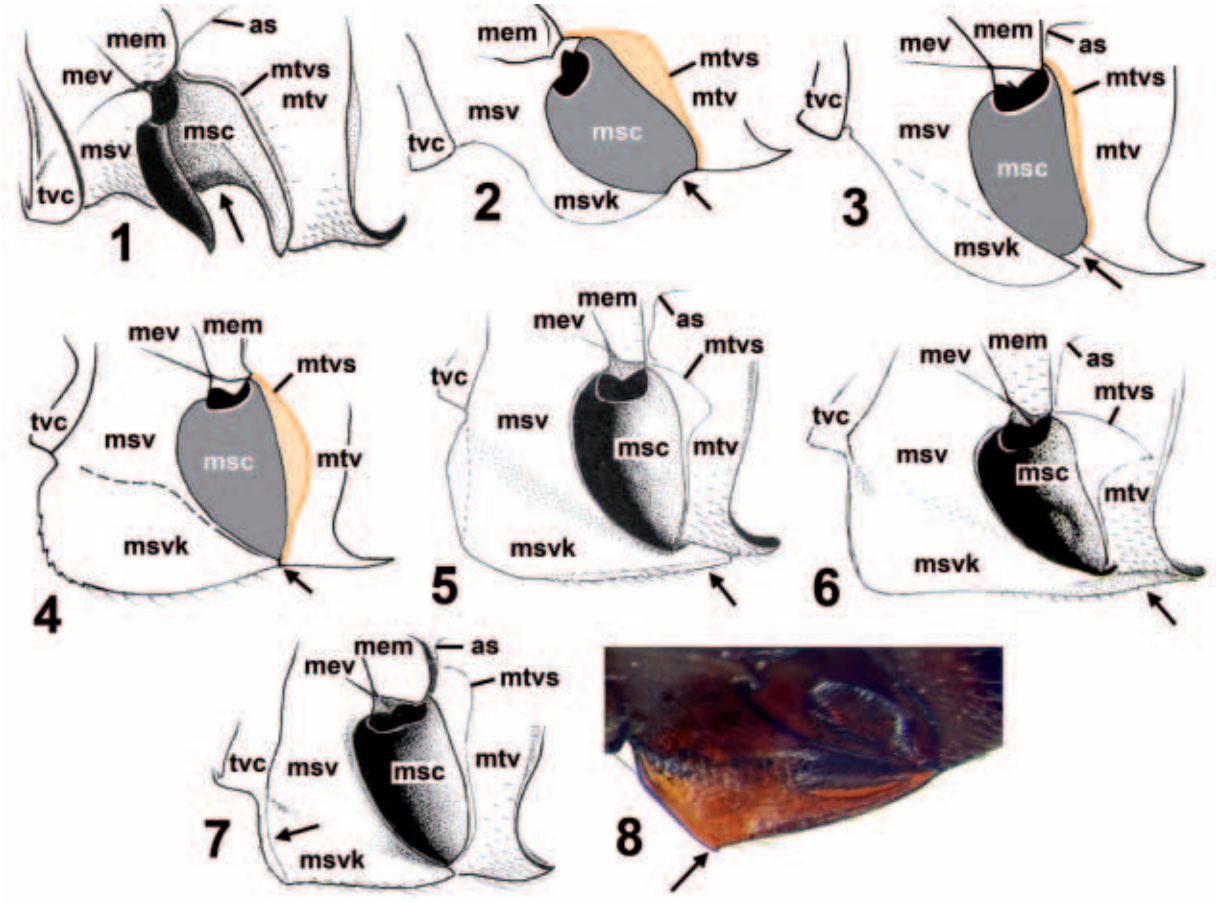
– Model 2B: With a wide middle area and groove (with various shapes).

– Model 2C: With a narrow or slightly wide middle area, always without groove (with various shapes).

It can be fused with the metaventrite, finding a simple suture – *Speonesiotes* (Fig. 17.4), *Bathyscimorphus byssinus* – or without a suture – *Paranillochlamys* in *Spelaeochlamys* clade (Fig. 16.4) –.

The ventral margin of the keel is ciliated and can be:

– Smooth, rounded, as in all the *Speonomus* series when there is a mesoventral keel – *Stygiophyes*, *Trapezodirus*, etc. – (Figs 16.7).



FIGURES 17.1–17.8: Pterothorax. Lateral view of: (**1**) *Catops fuliginosus* Erichson, 1837 (black arrow pointing to mesocoxal cavities in contact), (**2**) *Platycholeus opacellus* (black arrow pointing to mesocoxal cavities in contact), (**3**) *Adelopsella bosnica* (black arrow pointing to mesocoxal cavities in contact), (**4**) *Speonesiotes* (*Kulzeria*) *dorotkanus* (black arrow pointing to mesoventral keel extended until it contacts the anterior margin of the metaventrite), (**5**) *Quaestus sajaensis* (black arrow pointing to the mesoventral keel partially extending over the metaventrite), (**6**) *Espanoliella oxyptera* **comb. nov.** (black arrow pointing to the mesoventral keel extending completely over the metaventrite), (**7**) *Anillochlamys tropica* (black arrow pointing to the lateral groove parallel to the anterior edge of the mesoventral keel, continuation of the suture between the mesoventrite and the transverse collar); (**8**) *Troglocharinus fadriquei* (black arrow pointing to the hooked vertex) (modified from Fresneda *et al*. 2021). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral sutures; **tvc**, transverse collar. Figs **1**, **5**–**7** modified from Salgado *et al*. (2008).

– Plan – *Paranillochlamys* – (Figs 16.4).

– It can have a longitudinal groove or cavity, only when this border is wide, as in the genera *Breuilia*, *Espanoliella* (Fig. 16.6), *Amphogeus* stat. nov. and *Hypogesia* gen. nov. (*Quaestus* series). In the other genera of the *Quaestus* series there is no groove. A groove is also present in *Zoiana* gen. nov. (*Catopsinus* series) or in the genera *Atticiella* and *Maroniella* (*Sophrochaeta* series), and *Speophyes* (*Cytodromus* series).

There may be a lateral groove almost parallel to the anterior margin of the mesoventral keel, continuation of the suture between the mesoventrite and the transverse collar (Luo *et al*. 2019b): *Anillochlamys*, *Paranillochlamys* and *Spelaeochlamys* (apparently an apomorphy of the clade) (Figs 17.7). The anterior margin of the keel without a groove seems to be universal in the remaining Leptodirini.

By transparency it can be seen that some –

Speocharidius breuili or *Speonomites pallaresanus* (Fig. 18.6) and others – present a kind of hole or a strongly thinned cuticle on the back of the keel.

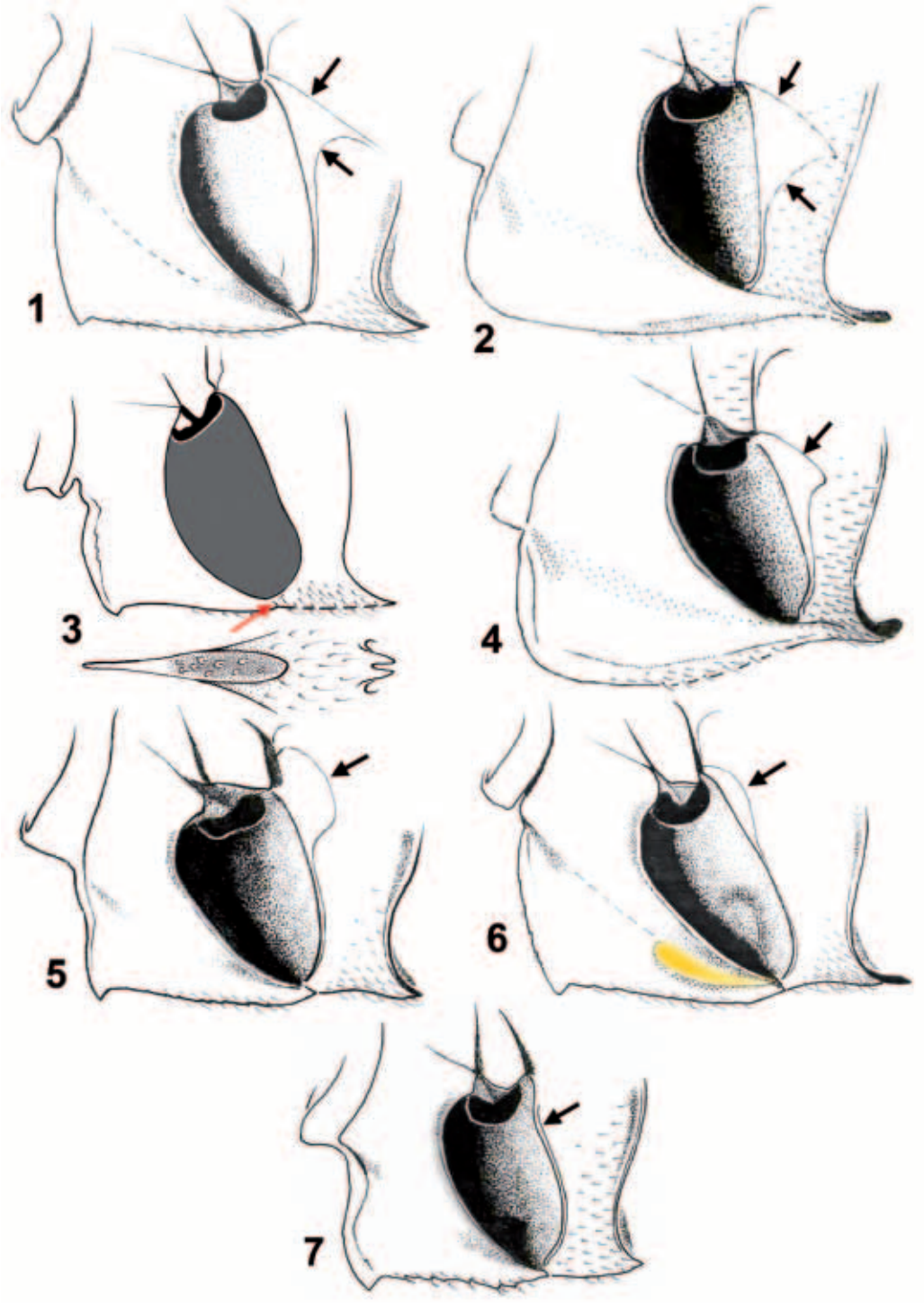
The importance of the mesoventral keel must be studied in great detail. The molecular study includes the *Quaestus* series in the same clade with the *Nanobathysciola* gen. nov. The latter has, like *Quaestus*, the prolonged mesoventral keel on the metaventrite, although it does not have a stylet in the endophallus, nor any of the pieces that characterize this series, but rather a unique «Y»-shaped piece. Also both *Platycholeus* and *Adelopsella*, with a short keel, have the endophallus with a stylet, which could be homologous with the twisted tube typical of the Ptomaphagini endophallus; it therefore seems that the «Y»-shaped piece with its flagellum is the derived state of the structure. Everything points to a certain phylogenetic weight of the keel extension on the metaventrite. Another case to comment on is that of *Neobathyscia*, with an unexpected situation as a sister group to *Notidocharis* + *Speonomidius* with 95.3/86 support; this support is on the border of what is acceptable but there are morphological elements that support its position at some point in this clade: it coincides with *Nanobathysciola* gen. nov. – sister genus of the whole group with support 88/81 – in having the prolonged mesoventral keel on the metaventrite.

Metaventrite: It is prolonged into a generally bifid point or bulge that separates the metacoxal cavities; these cavities may be contiguous (e. g. Cholevini, (Figs. 16.5, 17.1) or separated by a bifid metaventrite apophysis (Figs 16.2, 16.3). All studied Leptodirini have an apophysis in the metaventrite separating the metacoxa, while the Cholevini and Anemadini do not have any (Giachino *et al*. 1998). Thus, the bifid process that separates the metacoxae seems to be a synapomorphy of Leptodirini. The metaventrite has a smooth axial area, although there is a high keel in male *Speocharidius* of the *Speocharidius* subgenus, whereas much lower in both sexes of *Speonesiotes* and *Bathyscimorphus*. In these cases it seems to be attached to the posterior part of the mesoventral keel, although a suture is observed at the point of union. In *Paranillochlamys* the mesoventral keel is completely welded to the metaventrite, in this case there is no keel on the metaventrite since the surface is flat.

Sutures of the metaventrite: Some Leptodirini have two well-developed metaventral sutures – *Notidocharis*, *Speonomidius* –, as also present in *Sciaphyes sibiricus* (Sciaphyini) (Perreau 2000; Fresneda *et al*. 2011b); in other cases the suture is unique and runs from one end of the mesocoxal cavity to the other. In the species with the sutures clearly visible, the external suture starts in the posterior part of the contact area between the mesepimeron and the mesocoxal cavity, and extends to the posterior margin of the metaventrite, at the edge of the metacoxal cavity. The internal suture starts on the other side of the mesocoxal cavity, in contact with the mesoventral keel, and runs parallel to the mesocoxal cavity first and then goes towards the metacoxal cavity, joining the external suture. The two sutures and the margin of the coxal cavity form a triangular area, similar to that described for *Sciaphyes* by Perreau (2000), for *Anemadus aciculatus* by Antunes *et al*. (2019) or for *Breuilia triangulum* by Salgado *et al*. (2008). Alternatively, the two sutures may run together crossing the mesocoxal cavity. There are different degrees of differentiation of these sutures, likely to influence the overall flexibility and resistance of the ventral structures, and thus likely to be of adaptive value in subterranean or endogeous species in close contact with a hard substratum, like those of many species of Leptodirini. The character described above ranges from the extreme reduction of the two sutures, with an almost complete obliteration of the triangular internal area (e.g. the genera of the *Speonomus* series and the genus *Spelaeochlamys* to a fusion of the sutures with a strong reduction of the internal area (e.g. *Leonesiella*, *Anillochlamys*) and the presence of typical sutures with a well defined triangular internal area (e.g. *Breuilites, Fresnedaella* and more *Quaestus*). We can therefore intuitively regard it as a recurrent process of morphological evolution, from well defined sutures to extreme reduction. This character has never been systematically studied in Leptodirini. In Fresneda *et al*. (2007) this character was simplified: «*Suture between mesoventrite and anteromedian process of metaventrite (i.e. «metasternal suture»): a single suture between mesoventrite and anteromedian process of metaventrite (likely to be the fusion of two), running parallel and close to the coxal cavities, delimiting an extremely reduced area (0) (Fig. 5B); two well defined sutures between mesoventrite and anteromedian process of metaventrite, delimiting an internal area (usually triangular, but could be reduced forming a more or less narrow string) (1) (Fig. 5A). The two sutures are well defined, delimiting a triangular area in all supraflagellates with the only exception of Spelaeochlamys*».

Different models are identified:

– Model 1 (Fig. 18.1): The metaventral sutures originate from both ends of the coxal cavity, extending towards the metacoxal cavities, converging but not joining.



FIGURES 18.1–18.7: Pterothorax. Lateral view of: (**1**) *Speonomidius crotchi* ssp., (**2**) *Espanoliella cantabrica* **comb. nov**., (**3**) *Ovobathysciola majori,* (**4**) *Quaestus incognitus,* (**5**) *Paranillochlamys velox,* (**6**) *Speonomites pallaresanus* (in orange, hole or strongly thinned cuticle), (**7**) *Spelaeochlamys ehlersi.* Black arrow pointing to the metaventral sutures; red arrow pointing to the suture between meso- and metaventrite. Figs **1**, **2**, **4**–**7** modified from Salgado *et al*. (2008).

– Model 2 (Fig. 18.2): The metaventral sutures have their origin at both ends of the coxal cavity, extending towards the metacoxal cavities, converging at a point, more or less away from them and delimiting a triangular interior area.

– Model 3 (Fig. 18.3): The metaventral sutures have their origin at both ends of the coxal cavity, extend towards the metacoxal cavities, converging at a point, more or less away from them, delimiting an interior triangular area and extending together until reaching the metacoxal cavities. It occurs only in *Ovobathysciola* and looks like a prominent suture, a ridge.

– Model 4 (Figs 18.4, 18.5): The metaventral suture is unique and originates at the upper end of the coxa, describes a more or less complex curvature and ends at the lower end of the coxa; presumably this suture would derive from the union of the two sutures described above; the resulting interior area can be of various shapes and sizes and probably different «submodels» could be pointed out.

– Model 5 (Fig. 18.6): The single metaventral suture runs a short distance from the coxal cavity, being practically parallel to it and delimiting a reduced area. Almost all genera of the *Speonomus* series

– Model 6 (Fig. 18.7): Extremely reduced or absent: apparently forms a rim of the mesocoxal cavity as in *Spelaeochlamys*, *Sophrochaeta* or *Tismanella*.

Metanotum and axillaria

Metatergal apparatus: This structure serves for the insertion of the wing musculature and is therefore fully developed in the winged species of all tribes; as a practically universal model, one could take that of *Catops* (Fig. 19.1) or that of *Nargus* (Fig. 19.2). Consequently, in wingless taxa, *Ptomaphagus troglodytes* Blas & Vives, 1983, or all Leptodirini excluding *Platycholeus*, there is a reduction in structure, sometimes severe. The nomenclature of the different parts proposed for Scirtoidea (Coleoptera, Polyphaga) after Friedrich & Beutel (2006) has been adopted.

In ventral view of metanotum and axillaria, endoskeleton, of *Platycholeus* (Fig. 20.1) you can see the structures of a winged species: alacrista with its apophysis (alc), anterior notal process (anp), anterolateral scutal suture (ass), first, second and third axillary sclerite (ax1/2/3), median membranous area (mma), mesoscutum (sc2), metascutum (sc3), mesoscutellum (scl2), metascutellum (scl3) and wings (w). In the remaining Leptodirini the metatergal apparatus is reduced and only the alacrista (alc), metascutum (sc3) and mesoscutellum (scl2) are found (Figs 20.2, 20.3). The alacrista and metascutum processes can be extremely reduced (Fig. 306.2) in general in elongated species (pholeuonoids or leptodiroids/scaphoids) although in some bathyscioids they can also be very short (Fig. 20.3), without reaching the extreme of disappearing completely as it happens in *Antrocharis* group (Fig. 298.3), in *Astagobius* (Fig. 99.1) or *Pholeuon* (*Parapholeuon*) (Fig. 238.2); in these a well-developed metascutum is preserved. The alacrista apophysis can extend along the lower part of the elytral suture and the metascutum is preserved in many bathyscioid species (*Sinobathyscia*, *Breuilia*, *Breuilites*, *Espanoliella*, *Schaufussia* gen. nov., etc.) (Fig. 20.2), a conformation that never occurs in markedly oblong species. In the clades with bathyscioid and pholeuonoid-leptodiroid species, there are all cases of development of this structure, which invalidates the character for internal classification at of Leptodirini.

The shape of the metatergal apparatus was used by Vailati (1988) and Giachino (1993a) as a discriminating character of a supraspecific level. In particular, Giachino (1993a), similarly to what was highlighted in relation to Crowson's organ, underlines how the morphology of this apparatus is, in *Reitteriola*, *Canapiciella*, *Doderiola*, *Rondolinia*, *Baudiola* and *Tamaniniella* (Fig. 259.7), much more similar to that of *Dellabeffaella* than to that of *Bathysciola – aubei* group (Fig. 183.1) –, while its morphology differs slightly from this model in *Muelleriola*.

Metendosternite

The metendosternite or Crowson's organ has been described and its parts named by Crowson (1938, 1944, 1955, 1981), Balfour-Browne (1961) – Coleoptera –, Iablokoff-Khnzorian (1977), Pretorius (2000) – Scarabaeoidea –, Konstantinov & Lopatin (1987), Konstantinov (1994) – Chrysomelidae –, Kolivac (1987) – Cleridae –, Naomi (1989) – Staphylinidae –, Morimoto (1962), Velázquez de Castro (1998), Franz (2010a, 2010b) and Franz & O'Brien (2001a, 2001b) – Curculionoidea –. Velázquez de Castro (2002) unifies the terminology for Coleoptera Polyphaga.

In the Leiodidae Cholevinae the furca is made up of two united sheets forming like the two eaves of a roof by the median furcal keel in a variable length according to clades and even genera, which is joined to the two sutures that follow the anterior edge of the arms and thus form the three branches of a Y, the two upper ones corresponding to the arms and the lower

one to the trunk. Thus, various pieces of this structure present in Leiodidae Cholevinae are designated to facilitate their description and identification: the presence or absence of any of these pieces as well as their length and relative size characterize various clades. In the metendosternite of the genera *Catops* (Fig. 21.3), *Ptomaphagus* (Fig. 21.4), *Nargus* (Fig. 21.1) and *Speonemadus* (Fig. 21.5) there is a well-developed «anterior lamina of the furca» (afp) probably related to the insertion of the alar muscles; this is absent in the genera of Leptodirini (Figs 21.2, 21.6–21.9), the furca is reduced, and this lack is a synapomorphy of the tribe.

Several models can be defined:

– With «Y»-shape, when the length of the furcal arm is less than or equal to the length of the furcal trunk, in this case if the trunk is longer than wide (Figs 21.3–21.7), or «V»-shape, when the length of the furcal arm is greater than or is equal to the length of the furcal trunk, in this case if the trunk is wider than it is long (Figs 21.8, 21.9).

– Short, with the furcal arms (fa) regularly waning (Fig. 21.6) or with the furcal arms wide over their entire length (Fig. 21.2).

– Long, with arms outstretched without furcal plate (fp) (Fig. 21.7)

– With a short furcal trunk (ft), shorter than the furcal arms (fa), these long and thin, without a furcal plate (fp) (Fig. 21.8) or with a furcal plate (Fig. 21.9).

– With long furcal trunk (ft), longer or as long as the arms (Figs 21.3–21.7)

– With (Figs 21.2, 21.7) or without arm apophysis (aa) (Figs 21.6, 21.8, 21.9).

In Leptodirini, Vailati (1988), pioneered the use of metendosternite as a significant character in the taxonomic analysis of the supraspecific level in the phyletic lines of *Boldoria* and *Dellabeffaella*. Giachino (1993a) highlighted how the shape of the metendosternite in *Reitteriola*, *Canapiciella*, *Doderiola*, *Rondolinia*, *Baudiola* and *Tamaniniella* (Fig. 261.4), is much more similar to that of *Dellabeffaella* than to *Bathysciola – aubei* group (Fig. 184.1) –. Once again Giachino (1993a) underlines how some questions remain, with respect to *Muelleriola*, which presents a metendosternite with a morphology that differs slightly from the model that characterizes the previous species, approaching that of *Bathysciola* (Figs 184.1, 105.4).

The nomenclature of the different parts of the furca (Figs 21.1, 21.2) are as follows: aa, arm apophysis; aff, anterior furcal flange; afp, anterior furcal plate (Opitz 2019); fs, anterior furcal suture; fa, furcal arm (Crowson 1944); fp, furcal plate (Kolivac 1987); fps, furcal plate suture; ft, furcal trunk (Franz 2010a–b); lff, lateral furcal flange; mfk, median furcal keel (Franz 2010a–b).

Aedeagus

The male copulatory organ, or aedeagus, is trilobed (Figs 22.3–22.6, 23.5). In the Cholevinae it does not appear uniform and its characteristics allow to clearly define the tribes (Jeannel 1922b, 1955; Iablokov-Khnzorian 1976). It is generally symmetrical and is usually highly sclerotized and, in most cases, curved towards the ventral side. It is made up of a central piece, the median lobe, inside which is the endophallus or inner sac, which is connected to the ejaculatory canal and the tegmen; the tegmen ring divides the median lobe into two parts and may be located closer or further from the base, which determines the ratio between the lobe or basal lamina and the rest of the median lobe. Such an aedeagus is what Jeannel & Paulian (1944) call a «primitive» copulatory organ, as opposed to those that are asymmetrical and in which the lateral styles of the tegmen or parameres may not be present. The arrangement of the aedeagus at rest (Fig. 22.1) exposes its convex part towards the upper part of the abdomen, the lower part of the elytra, and its concave part towards the abdominal uroventrites. From now on the convex face will be called dorsal (Fig. 22.2: dp) and the concave one ventral (Fig. 22.2: vp).

The structure of the aedeagus is very constant at a specific level, which makes it an excellent character in the taxonomy of each genus. The diversity in aedeagus models is unusual and it seems that it is one of the first structures to change during the speciation process, since these changes may imply a mechanical isolation or the impossibility of copulation between sister species in the process of divergence (Jeannel, 1924c). However, despite this high diversity that occurs in the Leptodirini, the aedeagus can be grouped by «models» that generally correspond to genera Fresneda (1998, 1999) and Fresneda & Salgado (2000) based on the structures of the endophallus, complemented with other structures of the aedeagus, distributed the Leptodirini in genera from the Iberian slope of the Pyrenees; subsequently Ribera *et al*. (2010) confirm this arrangement with a molecular study of the same group of species, which confirmed the use of the endophallus to establish phylogenetic relationships.

Median lobe: This structure is formed by a conical tube, more (Fig. 23.6) or less (Fig. 23.7) bent, open throughout its entire section at the basal end (Fig.

22.2: pb) and by a pore, or perhaps more exactly by a «trapdoor» at the apical end (Fig. 22.2: ap); the apical foramen is ventrally located. Median lobe has a ventral extension called the basal lamina (Fig. 22.2: bl), which in some groups surrounds the base of the endophallus; the latter is the continuation of the ejaculatory canal and is formed by an elongated membranous bag that can be inermous or bears spines, phanerae or other parts or complex structures more or less sclerotized (Figs 22.2: is; 23.6). The function of the median lobe is to hold and transport the endophallus during copulation. It also houses and protects the resting endophallus.

In Anemadini the median lobe is symmetrical (Figs 22.3, 22.4) and slightly curved towards the ventral side; the apical orifice is located ventrally, it lacks ligules and the basal lamina, quadrangular in shape, is well-developed and very long, while the ventral lamina of the tegmen appears to be formed by a narrow sclerotized band. The aedeagus of Paracatopina, considered by Jeannel (1936) to be similar to that of the Anemadini, is very different in structure, with the basal lamina elongated, but not widened, and the ventral lamina much reduced (Giachino & Vailati 1993). Sciaphyini follows the model described for Anemadini (Fig. 22.5).

In Cholevini it is generally symmetrical (Fig. 22.6), it can be strongly curved towards the ventral face and has a very variable shape; in general it is tubular and in many cases laterally compressed; the apex of the lobe is usually entire, although sometimes it can be bifid and even trifid due to the development of lateral lobes; the apical orifice is located ventrally, the ligules may or may not be pubescent, the basal lamina is short.

In Ptomaphagini, the aedeagus is highly modified and always responds to the same model (Fig. 23.1), although the median lobe presents different shapes for each genus and species. In most species it is symmetrical and in some of the most primitive genera, the apical orifice is in a ventral position, while in the more specialized ones this orifice has become dorsal, moving to the right side – Ptomaphaginini – or to the left – Ptomaphagini –; this displacement causes important modifications of the aedeagus, including a certain asymmetry, which in certain cases is very marked – (Fig. 23.2) some *Adelopsis* Portevin, 1907 –. In the Baryodirini tribe the structure of the aedeagus is not known since the males are unknown. The median lobe in Ptomaphagini is provided with sensory hairs on the lateral margins of the apical part and lacks a basal lamina. The ventral lamina of the tegmen is atrophied, and the parameres are attached laterally exactly at the base of the median lobe.

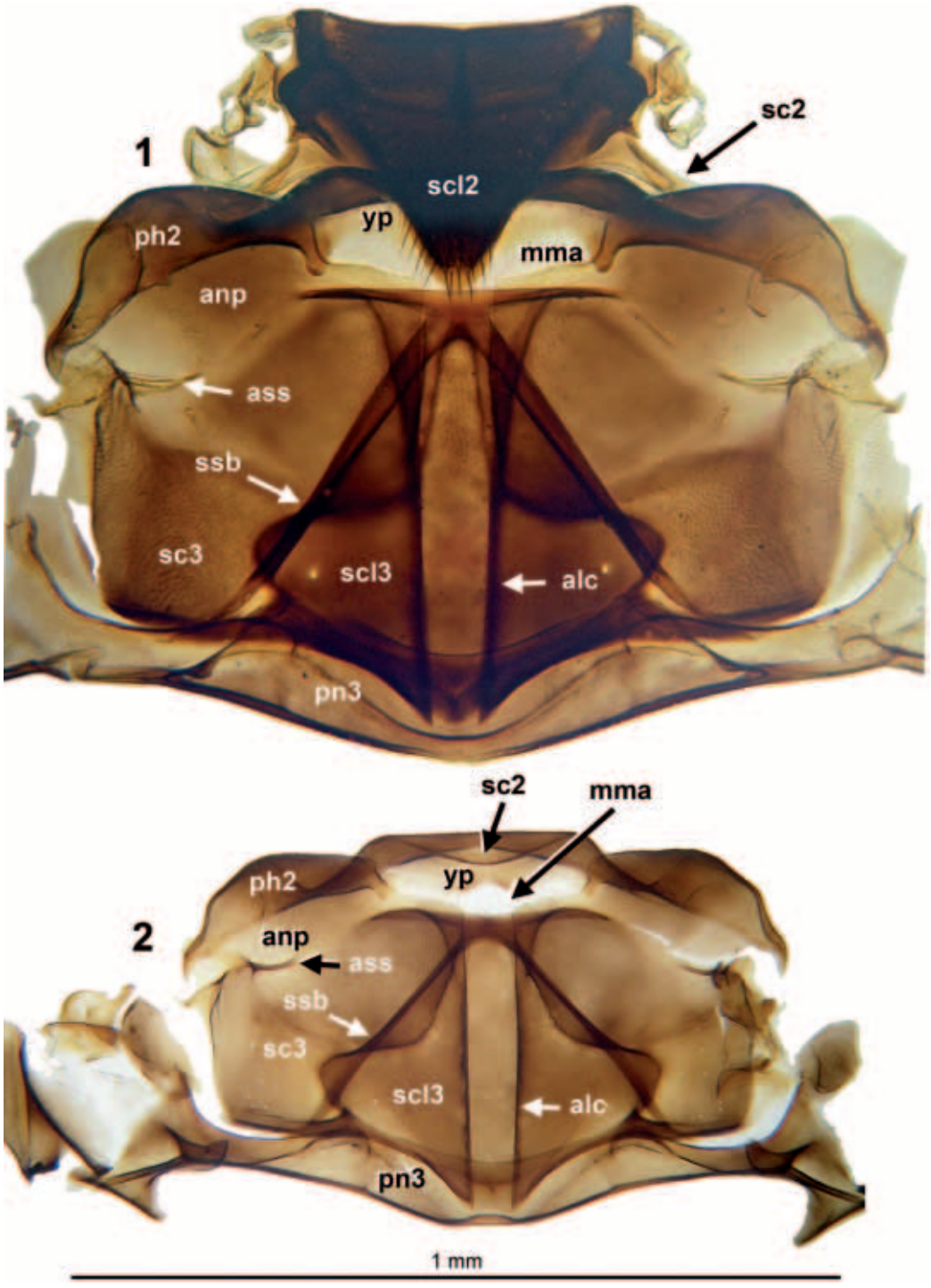
In Eucatopini the basal lamina is much more developed than the apical one and the parameres are very short although they exceed the apex of the median lobe (Fig. 23.3). The Oritocatopini have an aedeagus very similar to the Anemadini although the parameres are inserted on the sides of the median lobe, not on the dorsal part as in the others (Fig. 23.4).

In Leptodirini it is always symmetrical (Fig. 23.5); generally a conical tube with a thick base and tapering to the apex; but it can have very different forms, such as being very curved towards the ventral side at a more or less central point (Fig. 23.6), being slightly and gently curved from one end to the other (Fig. 23.7), with a strong dorsal invagination in *Pholeuon* – «nid de pigeon», Jeannel, 1924a – or even twisted in «S» in the sagittal plane as in *Ceuthmonocharis* (Fig. 101.3); the apex is usually entire and can be pointed, ogival or oval, more or less rounded or broadly or slightly truncated; be arranged horizontally or facing dorsally or ventrally, and very rarely may be notched; sometimes it can be trifid by the development of lateral lobes like *Aphaotus* (Fig. 68.6); the apical foramen is located ventrally and the basal lamina is one quarter of the total length.

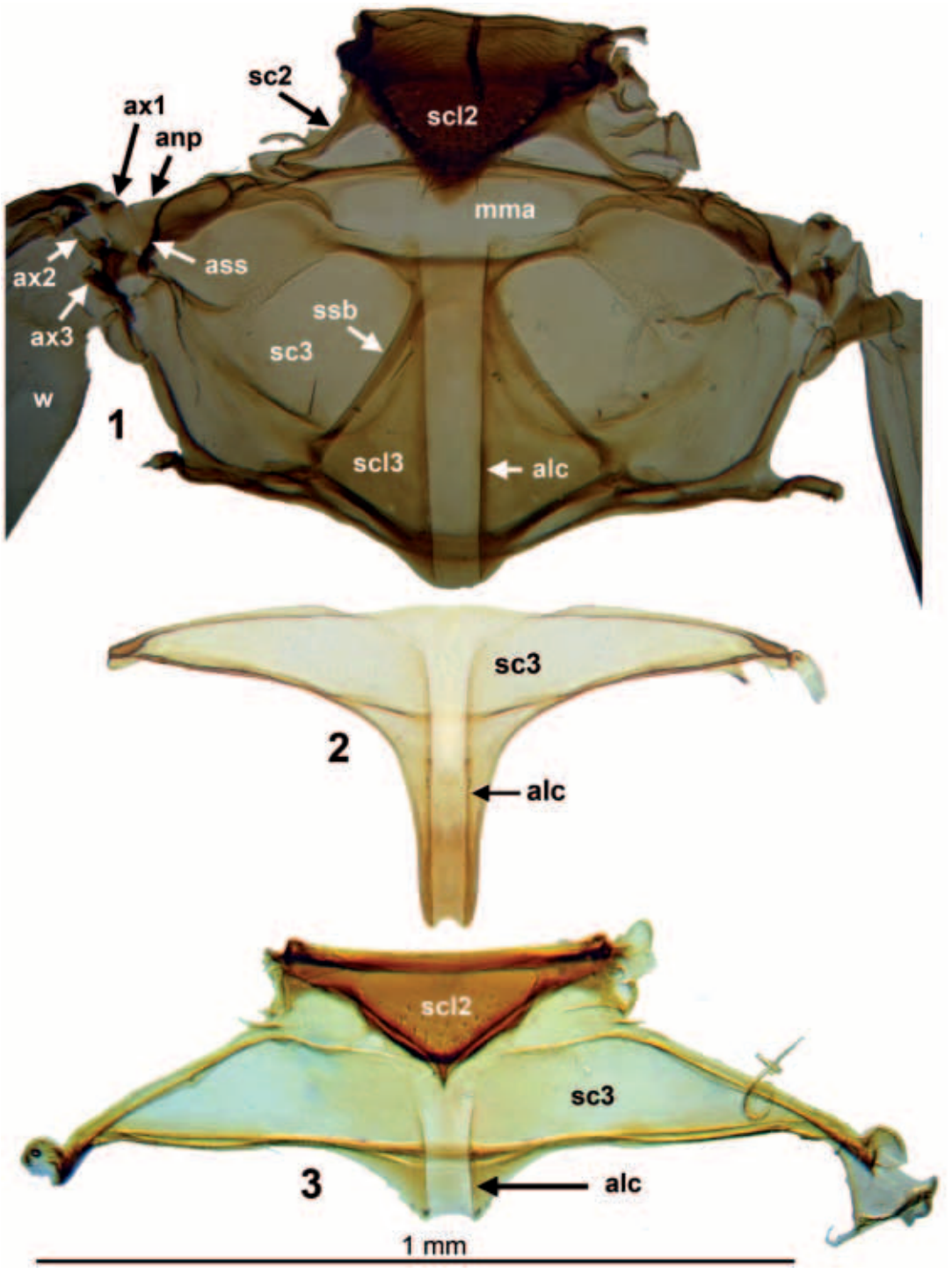
Tegmen and parameres: Tegmen is composed of a ventral lamina with a posterior semiring that surrounds the median lobe, of uneven development in the Cholevinae as a whole, and by the lateral styles or parameres, which in some cases are articulated with the median lobe in its basal part (Figs 24.1, 24.2); the parameres are the main sensory elements of the aedeagus; it seems that they do not penetrate at the time of copulation and presumably serve to locate and even recognize the female genital orifice.

In the Anemadini (Figs 22.3, 22.4) the parameres are robust, longer than the median lobe, and are inserted in their dorsal part; they are armed with several setae and spines at the apex, the number and location of which are characteristic of each species; the ring of the tegmen is situated almost half the length of the median lobe, making the two parts of the median lobe similar in length; idem in Sciaphyini (Fig. 22.5).

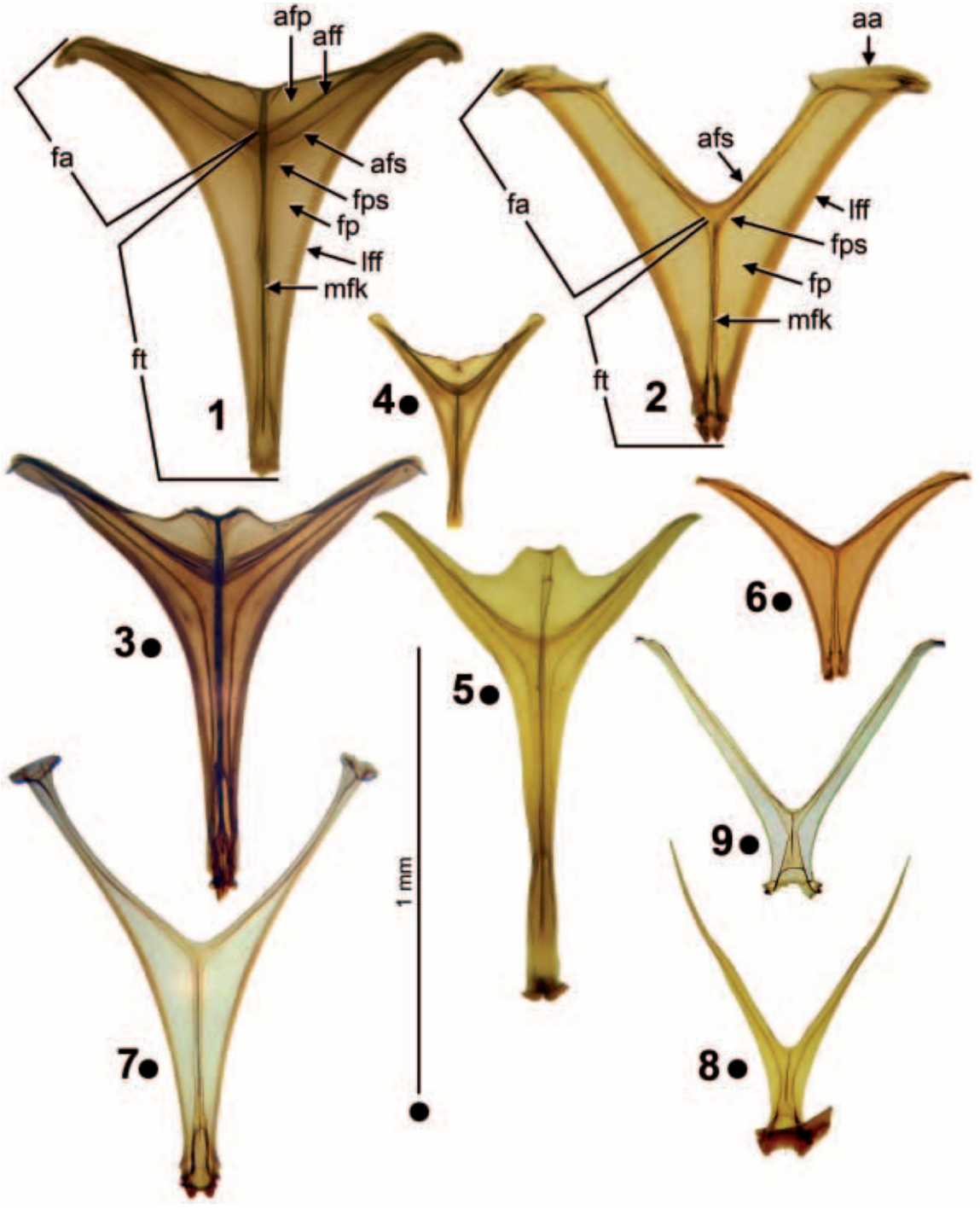
In Cholevini (Fig. 22.6) the tegmen is constituted by a well-developed ventral ring or lamina that is located near the base of the median lobe and by the parameres that are variably shaped: robust, not sharp at the apex and armed with several setae, the number and location of which is characteristic for each species (Cholevina) or less developed, gracile and generally sharp at the apex (exceptionally thickened in *Drepos-*



FIGURES 19.1–19.2: Metanotum. Ventral view of metanotum and axillaria, endoskeleton of: (**1**) *Catops tristis* (Panzer, 1794), (**2**) *Nargus algiricus* Portevin, 1903. Abbreviations: **alc**, alacrista; **anp**, anterior notal process; **ass**, anterolateral scutal suture; **mma**, median membranous area; **ph2**, mesophragma; **pn3**, metapostnotum; **sc2**, mesoscutum; **sc3**, metascutum; **scl2**, mesoscutellum; **scl3**, metascutellum; **ssb**, scuto-scutellar border; **yp**, yoke plate.



FIGURES 20.1–20.3: Metanotum. Ventral view of metanotum and axillaria, endoskeleton of: (**1**) *Platycholeus opacellus*, (**2**) *Espanoliella cisnerosii* **comb. nov.**, (**3**) *Pyrenaeola* (*Pyrenaeola*) *aranensis* **comb. nov**. Abbreviations: **alc**, alacrista; **anp**, anterior notal process; **ass**, anterolateral scutal suture; **ax1/2/3**, first, second, third axillary sclerite; **mma**, median membranous area; **sc2**, mesoscutum; **sc3**, metascutum; **scl2**, mesoscutellum; **scl3**, metascutellum; **ssb**, scuto-scutellar border; **w**, wing.



FIGURES 21.1–21.9: Metendosternite of: (**1**) *Nargus algiricus* Portevin, 1903, (**2**) *Zariquieyella diegoi* **comb. nov.**, (**3**) *Catops tristis* (Panzer, 1794), (**4**) *Ptomaphagus tenuicornis* ssp., (**5**) *Speonemadus angusticollis* (Kraatz, 1870), (**6**) *Uhagoniella laurae* **comb. nov.**, (**7**) *Troglocharinus senenti*, (**8**) *Spelaeochlamys ehlersi*, (**9**) *Pseudospeonomus raholai*. Abbreviations: **aa**, arm apophysis; **aff**, anterior furcal flange; **afp**, anterior furcal plate; **afs**, anterior furcal suture; **fa**, furcal arm; **fp**, furcal plate; **fps**, furcal plate suture; **ft**, furcal trunk; **lff**, lateral furcal flange; **mfk**, median furcal keel.

cia Jeannel, 1924 and *Catops* Paykull, 1798 of the «*morio*» group); in general, in the Catopina the parameres are provided with two apical setae.

In Ptomaphagini (Figs 23.1, 23.2) the tegmen lamina is very reduced and is situated almost exactly at the base of the median lobe so that it is practically non-existent. The parameres are usually thin and shorter than the median lobe, and the apex is armed with three setae.

In Leptodirini (Figs 23.5, 23.7) the lamina of the tegmen, always present, with its posterior semiring is at a distance of a quarter of the total length of the median lobe from the tip of the basal lamina. The two paramerescan have different lengths and thickness; the apex may be ogival, rounded, broadened into a club or spoon-shaped, funnel-shaped, prolonged into a pseudo-lamina, or have a cavity. Different inserted parts can be found: membranous sheet, penicillum, differentiated setae (trichoid sensilla) in diverse number and arrangements, and placoid sensilla. These structures can be present together or not. Both Ptomaphagini (Fig. 24.6) and *Platycholeus* have three setae and no other structures at the apex of the parameres, which suggests a plesiomorphic configuration. In the next cladogenesis, *Adelopsella* (Fig. 25.1), there is only one seta and later the variations increase and are distributed among all the clades of the tribe. Parameres can have one or more of the following characteristics:

– Parameres thickness: They can be thick (Fig. 24.2) or thin throughout their length (Fig. 24.1).

– Cross section: They can be cylindrical or compressed.

– Length: They can be as long as the median lobe (Fig. 23.5), slightly shorter (Fig. 24.1) or longer (Fig. 24.2).

– Insertion of the parameres in the tegmen: On both sides of the median lobe (Figs 3.1, 3.2, 23.6, 23.7). In contrast to the Anemadini (Figs 22.3, 22.4) and Sciaphyini (Fig. 22.5) whose insertion is always dorsal.

– Parameral apex: May be dilated (Figs 24.4, 25.10, 25.14) or not (Figs 24.5, 24.6, 25.2, 25.7), sharp (Fig. 25.1), thickened and club-shaped (Fig. 25.5), widened by the existence of a translucent lateral sheet (Fig. 179.5), widened and spoon-shaped (Fig. 223.7), funnel-shaped (Fig. 290.5) or with a depression or cavity (Fig. 25.17). Some genera within the *Speonomus* series have a well-defined, spoon-shaped lateral excavation in the apex of the paramere. The genus *Bellesia* has a funnel-shape cavity, which Fresneda (1998) did not considered to be homologous with this structure. However, according to molecular results, the funnel-shaped apex of the parameres of *Bellesia* should be homologous to the depression/cavity of the others.

– Membranous lamina: the apex of the paramere has a well-defined contour (Fig. 25.8) or is extended forming a membranous lamina (Fig. 25.6). While species have the apex of the paramere modified, with an extension forming a lamina; in one case the origin is a (presumably) modified sensilla forming a membranous lamina with a clear insertion suture (Fig. 25.6); the second case is an extension of the apex of the paramere (Fig. 191.7). The two conditions are not considered to be homologous. The apex of the paramere is extended in a membranous lamina in two genera of the series *Spelaeochlamys* (*Anillochlamys* and *Paranillochlamys*) and in the *Speocharidius* group of genera. The membranous lamina may be highly developed (Fig. 25.6) or reduced (Fig. 25.15), entire (Fig. 25.6) or divided into two—(Fig. 312.1) e. g. *Ariejasia* gen. nov.—, with a simple margin (Fig. 25.6) or anastomosed with peduncular extensions—(Fig. 312.1) e. g. *Ariejasia* gen. nov.—. Either be glabrous (Fig. 25.15) or with the penicillum inserted into it (Fig. 25.6).

– Penicillum: The apex of the parameres may have a penicillum (Figs 25.6, 25.17) or not (Figs 25.2–25.5, 25.7–25.11). If present,the penicillum may be dense (Figs 25.6, 25.17) or scarce (Fig. 25.16), and made up of long (Fig. 25.6) or short setae (Fig. 25.16), inserted on the side of the apex of the paramere (Fig. 25.16), inside a cavity or depression (Fig. 25.17), or on the membranous lamina (Fig. 25.6). Some genera within the series *Speonomus* have a more or less developed tuff of setae (the «penicillum», Fresneda 1998) on the apex of the paramere.

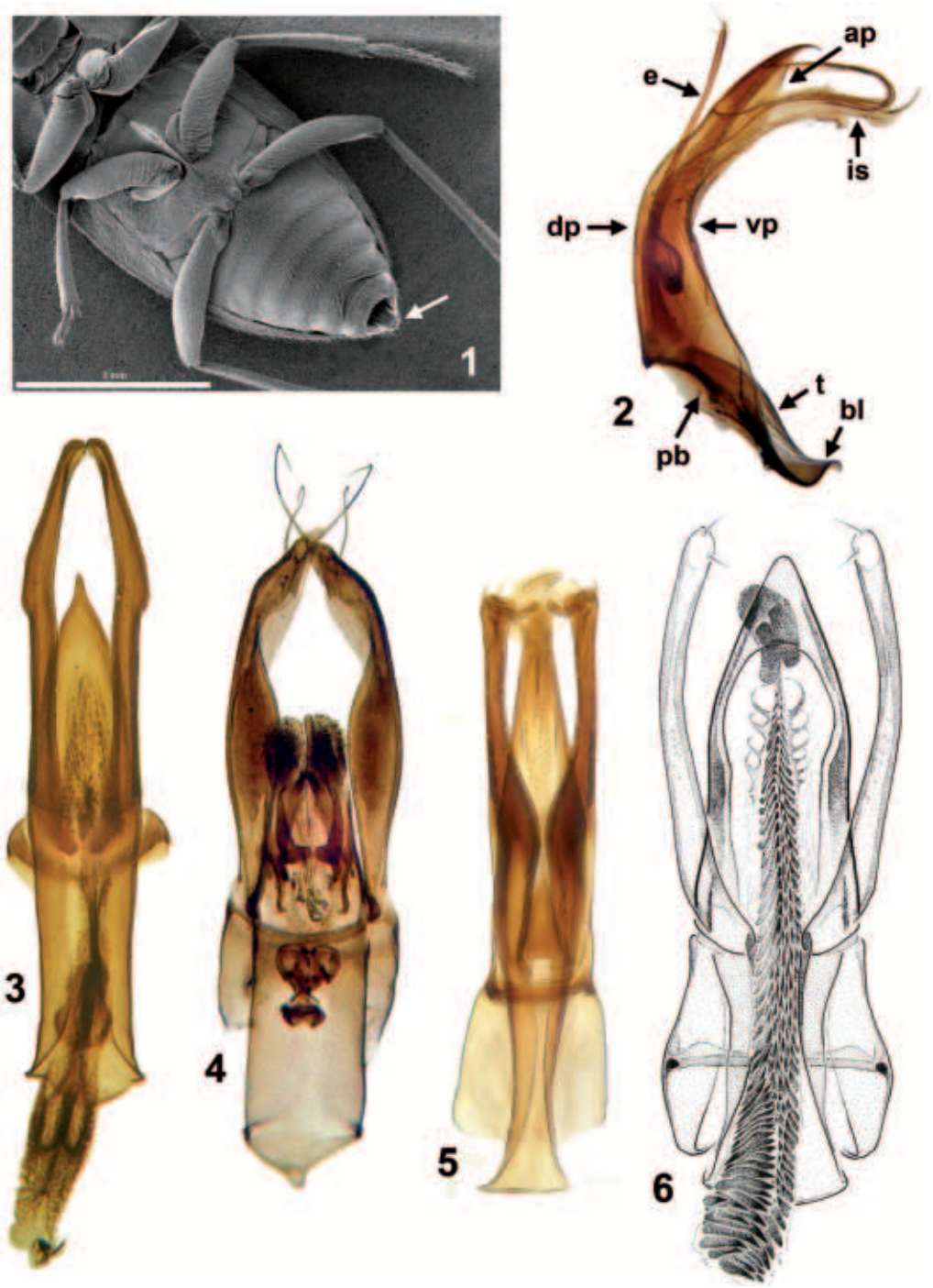
– Main setae: When there is more than one, they can be of similar length, all short or long, of different lengths; with same or different thickness; inserted between the penicillum or separate from it. The following configurations have been observed:

1. Apex armed of a single seta (Fig. 25.1): *Adelopsella*.

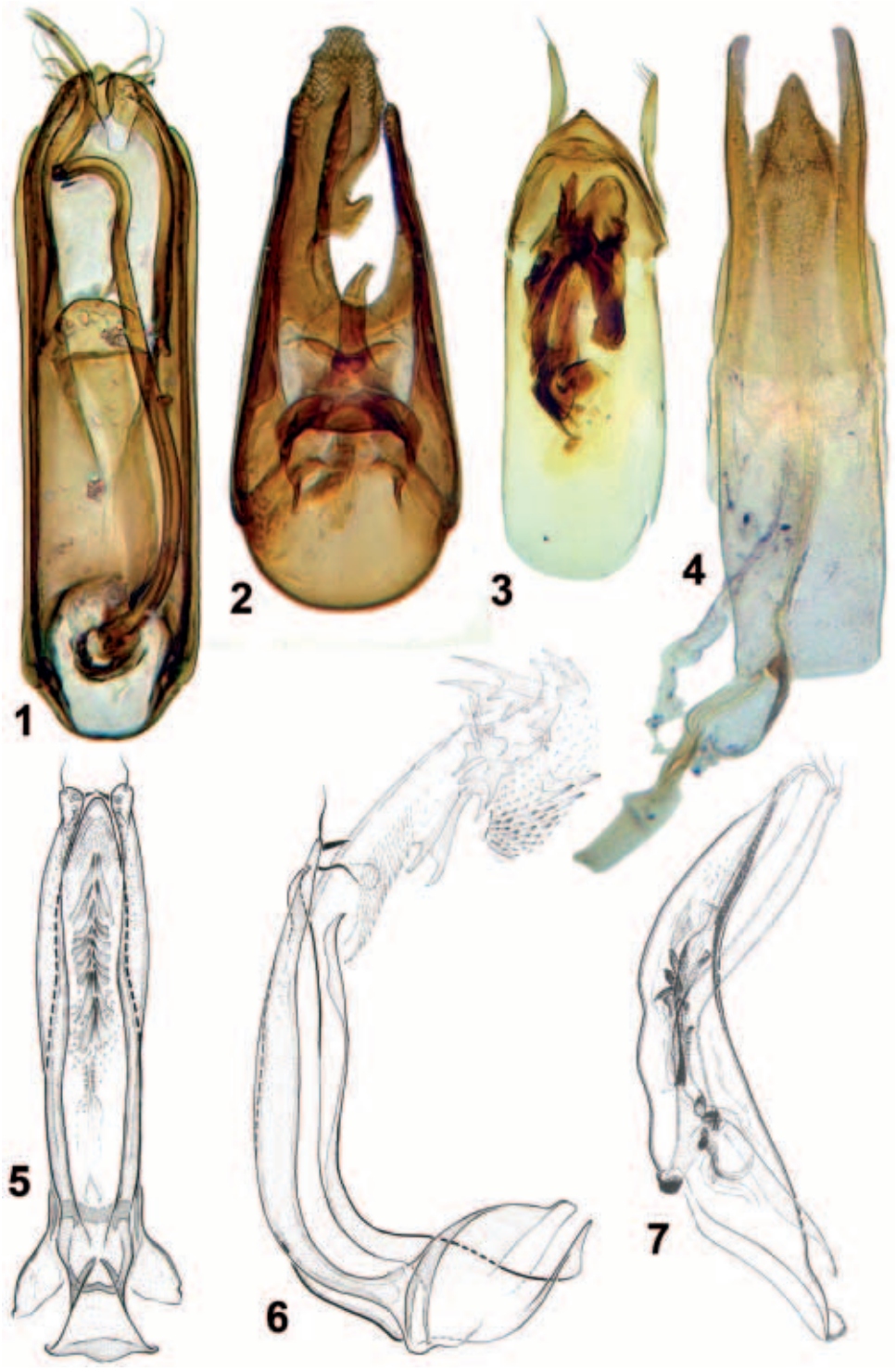
2. Apex armed of two setae: *Catops* Paykull, 1798 and *Attumbra* Des Gozis, 1886 (Figs 24.5, 24.7), *Sinuicollia* (Fig. 69.4),

3. Apex armed with three differentiated setae. In most of the taxa of the series *Quaestus*, *Spelaeochlamys* and *Speonomus* the apex of the paramere has three setae, or a multiple of three (Figs 25.3, 25.4, 25.12); as in the Ptomaphagini (Fig. 24.6).

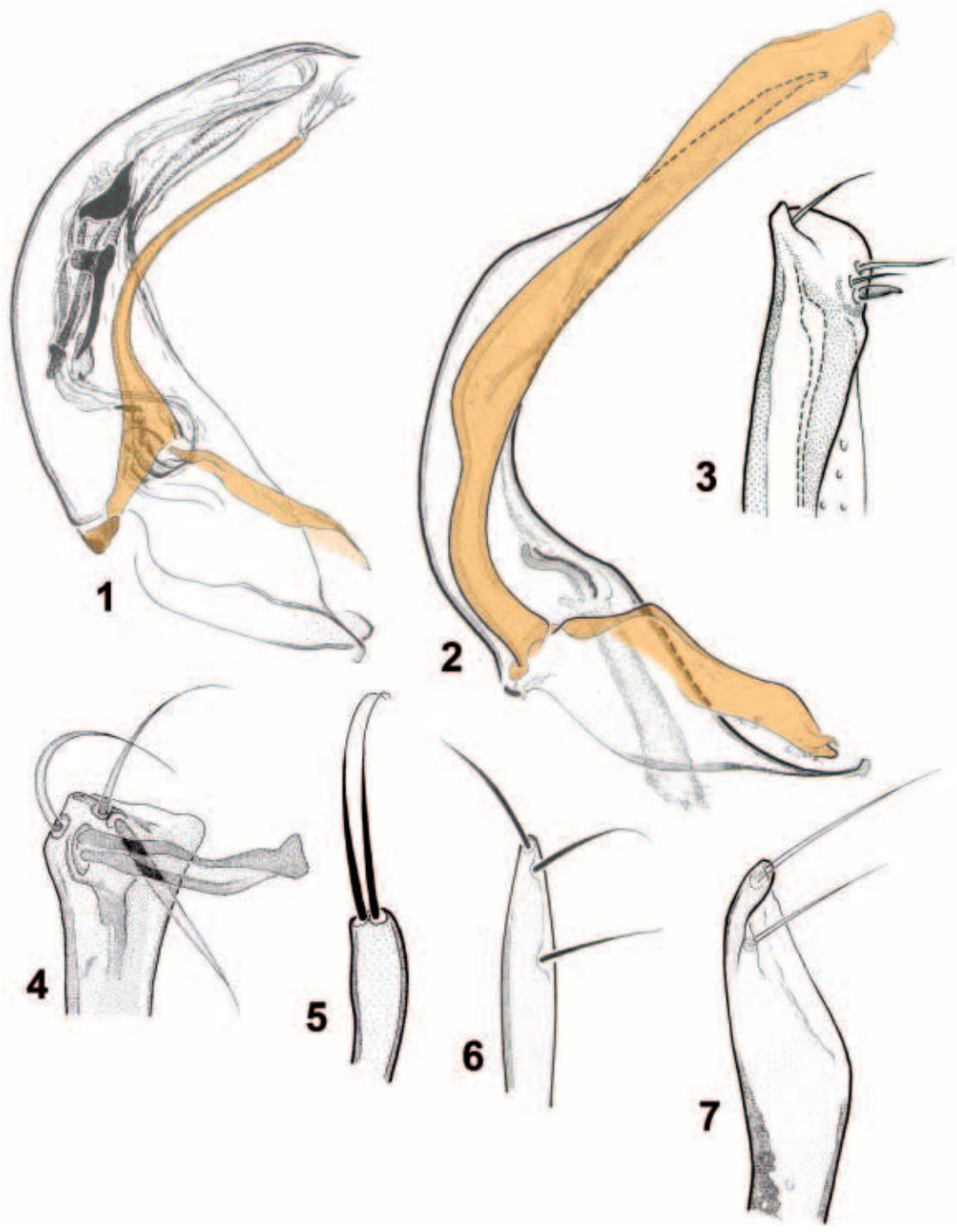
3.1. Setae similar in thickness and length and attached at the apex (Fig. 25.3).



FIGURES 22.1–22.6: Aedeagus. Ventral view of (**1**) *Baronniesia delioti* (white arrow pointing to aedeagus in resting position). (**2**) Lateral view of the aedeagus with the partially evaginated endophallus of *Quaestus jeannei*. Dorsal view of the aedeagus of: (**3**) *Anemadus graecus* (Kraatz, 1870), (**4**) *Dissochaetus confusus* Salgado, 2010, (**5**) *Sciaphyes sibiricus* (Reitter, 1887) (modified from Fresneda *et al*. 2011b), (**6**) *Choleva vandeli* Coiffait, 1954 (modified from Salgado *et al*. 2008). Abbreviations: **ap**, apical porus; **bl**, basal lamina; **e**, paramere (lateral stylus of tegmen); **dp**, dorsal part; **is**, endophallus (internal sac); **pb**, basal porus; **t**, ring of tegmen; **vp**, ventral part.



FIGURES 23.1–23.7: Aedeagus. Dorsal view of: (**1**) *Paulipalpina baenai* Fresneda & Salgado, 2017, (**2**) *Adelopsis bruchi* Pic, 1926, (**3**) *Eucatops rossii* Salgado, 2008, (**4**) *Oritocatops* sp., (**5**) *Espanoliella luquei* and (**6**) with the endophallus evaginated. Aedeagus in lateral view of: (**7**) *Zariquieyella rugosa* **comb. nov.** Figs **5**–**7** modified from Salgado *et al*. (2008).



FIGURES 24.1–24.7: Aedeagus. Lateral view of: (**1**) *Troglocharinus jacasi* (in orange: thin paramere), (**2**) *Josettekia angelinae* (in orange: broad paramere). Apex of the paramere of: (**3**) *Speonemadus clathratus* (Perris, 1864), (**4**) *Sciaphyes sibiricus* (Reitter, 1887), (**5**) *Catops fuliginosus* Erichson, 1837, (**6**) *Ptomaphagus troglodytes* Blas & Vives, 1983, (**7**) *Attumbra josephinae* (Saulcy, 1862). Figs **1**, **2**, **5**–**7** modified from Salgado *et al*. (2008); Fig. **3** from Fresneda *et al*. (2019); Fig. **4** from Fresneda *et al*. (2011b).

3.2. One of the setae extremely reduced so that it looks like a placoid sensilla: *Karadeniziella* (Fig. 25.2).

3.3. Two setae attached to the apex and one proximal (Fig. 25.4).

3.4. Two simple setae, similar to each other, while the third is modified, thicker like a thorn (Fig. 25.5).

3.5. Apex armed with two large, long and thick sinuous setae inserted on one side of the apex and a shorter, straight and thin seta inserted on the other side of the apex (Fig. 25.6).

3.6. One seta modified in the form of a sheet, the other two thin and similar to each other (Fig. 179.4).

4. Apex armed with four differentiated setae.

4.1. Setae similar to each other (Fig. 25.7), thick, long, sinuous or strongly twisted.

4.2. Four identical minute setae (Fig. 25.8).

4.3. The four setae inserted at the apex (Fig. 25.7).

4.5. The four setae inserted along the terminal third of the paramere (Fig. 25.9).

4.6. Three setae attached to the apex, one proximal (Fig. 25.10).

4.7. Four apical setae, three short and one more robust, spiny-shaped. (Fig. 24.3).

5. Apex armed with five setae (Fig. 25.11).

6. Apex armed with six setae (Fig. 170.3).

7. Nine-armed apex (Fig. 25.12); or between eight to fourteen setae.

8. Apex armed with more than fifteen differentiated setae, up to thirty, thick and ordered (Fig. 25.14).

9. Apex armed with more than fifteen thick, tight, disorderly and hard to count setae (Fig. 25.13).

Examples:

– Developed penicillum, no excavation, three setae and a membranous lamina with a clearly defined insertion suture: *Speonomites pallaresanus* (Fig. 312.6).

– Presence of a membranous lamina with a clearly defined insertion suture, without penicillum: *Troglocharinus orcinus* (Fig. 25.15).

– A well-defined lateral excavation and penicillum: *Parvospeonomus urgellesi* (Fig. 25.17).

– A membranous lamina without a clearly defined insertion suture, apex of the paramere extended in a membranous lamina: *Anillochlamys subtruncatus* (Fig. 191.7).

– Three setae without penicillum: *Cantabrogeus nadali* (Fig. 208.8).

– Four setae of similar length without penicillum or lamina: *Speocharinus llosesi* (Fig. 208.13).

– Five setae of variable length without penicillum or lamina: *Breuilia triangulum* (Fig. 25.11).

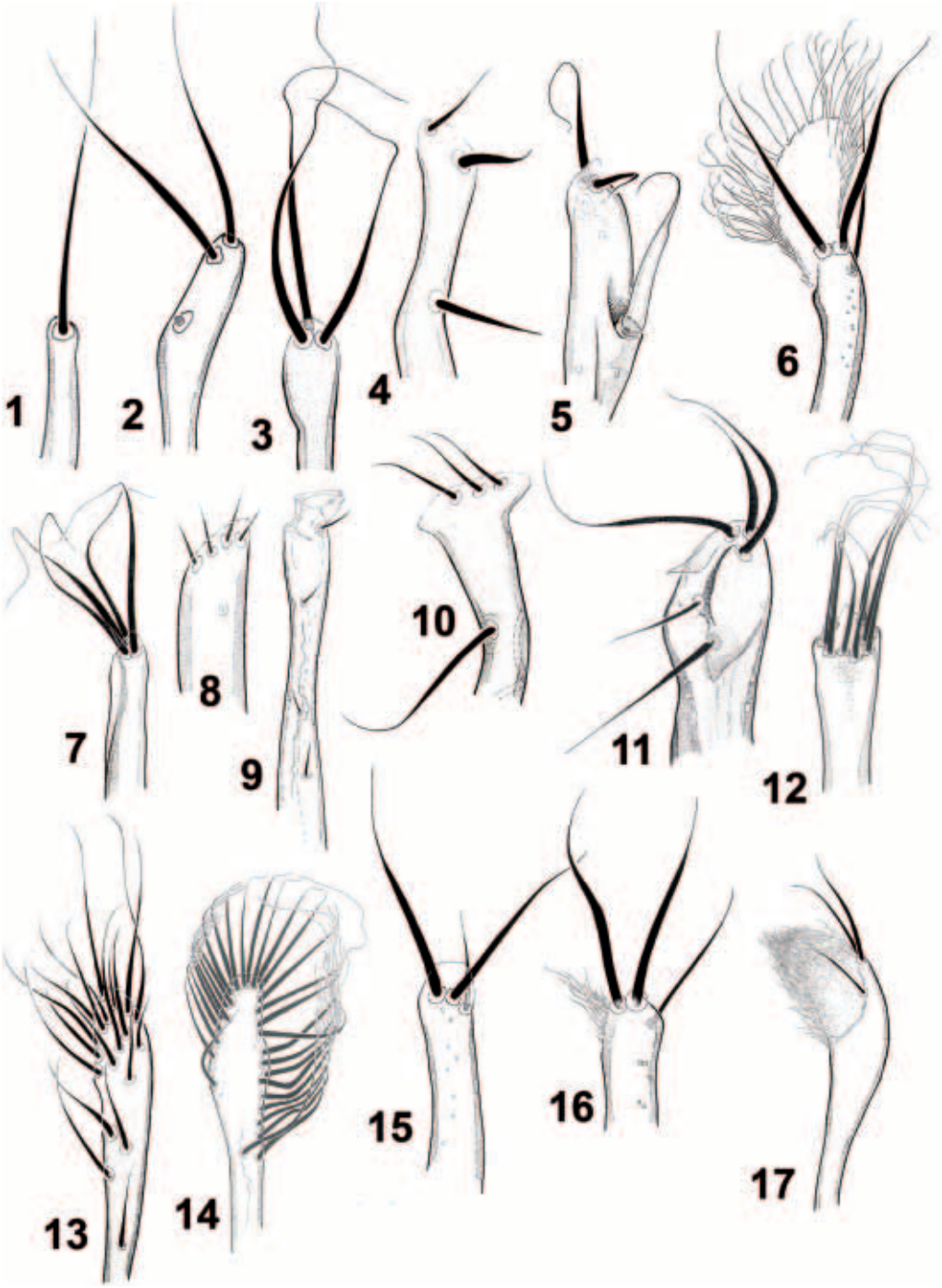
Endophallus: In Anemadini (Fig. 26.1) the armor of the endophallus is variable, but in general there are several long chains of sclerotized teeth, interlocking at the base, which seem to support the sac when it evaginates during copulation; in addition, some species have a more or less developed apical tooth formed by imbricated spines; there are no unarmed endophallus.

In Sciaphyini there can be two chains of teeth – *Sciaphyes sibiricus* (Fresneda *et al*. 2011b: Fig. 10) – or an inermous endophallus – *Sciaphyes shestakovi* (Fresneda *et al*. 2011b: Fig. 8) –.

In Cholevini the armor of the endophallus is very variable throughout the group and sometimes presents very complex sclerotized structures, as for example in the genera *Choleva*, *Nargus* or *Sciodrepoides*, among others; there are also simpler endophallus, a membranous sac lined with spicules, as found in some *Catops* (Fig. 26.2). There are no unarmed endophallus.

In Ptomaphagini (Fig. 26.3) the endophallus has, as the most evident structures, a generally spherical ampulla in the basal part and a more or less developed evaginable stylet that is characteristic of the group. There are no unarmed endophallus.

In Leptodirini there is a great diversity in the endophallus structure (Figs 26.4, 27.1–27.4). An attempt has been made to systematize this structure by naming the identified pieces (Jeannel 1924a; Bellés 1984; Bellés & Comas 1986; Dupré 1989, 1992; Fresneda 1998; Salgado *et al*. 2008) but the work has been largely useless. The great diversity of pieces existing in some groups makes their nomination unnecessary if these pieces are not also found in other groups, as a consequence they are only useful to establish comparisons within the group where they are found. The homologies of that pieces are also hard to track, it is therefore possible that they have received different names even though they are the same piece. Only the name of a few existing structures in a large majority of Leptodirini seems to be useful. There are unarmed endophalli (Fig. 107.8) and with two (Fig. 26.4) or three (Fig. 28) differentiated regions. In some endophalli there are large, highly developed spines that form groups characterised by their shape and location within the sac (Fig. 27.1). In the two basal thirds of the endophallus there can be a bag formed by a tissue covered with scales of various shapes, rounded, pointed, etc. (Fig. 27.2: mb). There may also be some more modified scales, large, complex in shape and sclerotized (Fig. 27.4). For example, for the *Speonomus* series from the Pyrenees, three regions where identified in the endophallus, and numerous names have been proposed for the pieces that make up the internal armor of the endophallus (Fig. 28).



FIGURES 25.1-25.17: Aedeagus. Apex of the paramere of: (**1**) *Adelopsella bosnica*, (**2**) *Karadeniziella omodeoi*, (**3**) *Quaestus canis*, (**4**) *Q. sharpi*, (**5**) *Espanoliella jeanneli*, (**6**) *Troglocharinus jacasi*, (**7**) *Zariquieyella parallela* **comb. nov.**, (**8**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* **comb. nov.**, (**9**) *Euryspeonomus* (*Euryspeonomus*) *breuili*, (**10**) *Q. incognitus*, (**11**) *Breuilia triangulum*, (**12**) *Casalella finismillennii* **comb. nov.**, (**13**) *Uhagoniella ovoidea* **comb. nov.**, (**14**) *Aranzadiella leizaolai*, (**15**) *Troglocharinus orcinus*, (**16**) *Lagariella porroiensis*, (**17**) *Parvospeonomus urgellesi*. Figs, **3**–**6**, **9**–**11**, **13**–**17** modified from Salgado *et al*. (2008); Figs **7**, **8**, **12** from Fresneda & Salgado (2006).

Basal region («rb» of Bellés 1984) (Fig. 28: rb): In general, taxa have been differentiated either by the presence of a «Y»-piece and flagellum, or a stylet; it is possible that the flagellum and the stylet are two homologous pieces. In the basal region of the endophalli with «Y»-piece, two complex structures are present, made up of different pieces apparently articulated with each other:

– Dorsal basal complex («cdb» of Dupré 1989) (Fig. 28: cdb): The dorsal complex is included in the tergal side of the sac and is made up of a very sclerotized «Y»-shaped piece («pièce en Y» by Jeannel 1924a or «py» by Bellés, 1984) (Fig. 28: py). All infraflagellates of Jeannel (1944, 1955a) have a piece with a «Y»-piece in the endophallus. The symmetrical arms of the «Y»-piece advance along the sides of the sac in direction of the median region (Jeannel 1924a, or «rm» of Bellés 1984); by means of a tubule («nodule de liaison» or «nl» from Dupré 1992) (Fig. 28: nl) they connect with some hyaline funnels, or apical fibres of the py («fibras apicales de la PY» from Fresneda 1998, or «fm4» from Dupré 1992) (Fig. 28: fapy); these apical fibres connect, or extend into apparently floating pieces («piezas flotantes» of Fresneda 1998) (Fig. 28: pf), and through these the connection with the dorsal phanerae («faneras dorsales» of Bellés 1984) (Fig. 28: fdm) of the median region is established. In some models of endophallus there are phanerae attached to the «Y»-piece («faneras anexas a la PY» of Bellés 1984) (Fig: 289.9) that extend in the direction of the median region («fm1» and «fm3» of Dupré 1992; «scm» of Bellés 1984) until reaching the ventral phanerae of the median region («faneras ventrales» of Bellés 1984) (Fig. 28: fvm). The unpaired branch of the «Y»-piece (the «manubrium» of Jeannel 1924a) curves at the base of the sac and passes freely through the central canal in the direction of the median region; its thickness decreases until it becomes a filament or flagellum (the «flagellum of the py» or «fy» of Bellés 1984) (Fig. 28: fy). The flagellum of the «Y»-piece may be long and thin or short and thick, similar to a stylet (Fig. 289.8). Each of the basal dorsal complex pieces is also made up of other sclerotized structures and conjunctive and muscular fibres, which have been identified by Dupré (1989, 1992) for some models of endophallus. At the junction of the three arms of the «Y»-piece, on the «manubrium», opens the ejaculatory duct («conducto eyaculador» of Bellés 1984). In the original description of the genera *Bellesia* and *Josettekia* (Fresneda & Hernando 1994 and Bellés & Déliot 1983 respectively) an «atypical» «Y»-piece was described for both of them, which was subsequently considered to be non-homologous to the standard «Y»-piece by Fresneda (1998) and Salgado (2000), in where the «section *Josettekia*» was defined as including species otherwise close to the *Speonomus* section but without typical «Y»-piece. The re-examination of the aedeagus of these genera in a wider comparative study shows that there is no reason to consider their «atypical» «Y»-piece as non-homologous to the «Y»-piece of the rest of the species of the series *Speonomus* (see Figs. 1 and 3 in Fresneda & Hernando 1994 and Figs. 5 and 1 in Dupré 1991 and Fresneda 1999 respectively).

– Basal ventral complex («cvb» of Bellés 1984) (Fig. 28: cvb): The cvb is included in the sternal side of the sac and is formed by a basal lamina («lámina basal»lb of Bellés & Comas 1986) (Fig. 28: lb) that shows two revolute and symmetrical lateral wings; an axial canal or tube is articulated with this basal lamina («gm» of Dupré 1992). It is topped by an apical crown («ca» of Dupré 1992). Through the interior of the ventral complex runs the flagellum of the «Y»-piece and emerges to the outside in the direction of the rm through a pore. In the species with ventral complex, a flagellum originates in the union of the two branches of the «Y»-piece, surrounding the base of the sac, and extending to the apex; the basal part of this flagellum could be enlarged, and it is inserted in a sclerotized tube. All infraflagellates of Jeannel (1944, 1955a) have ventral complex, except *Pseudospeonomus* and *Bellesia*.

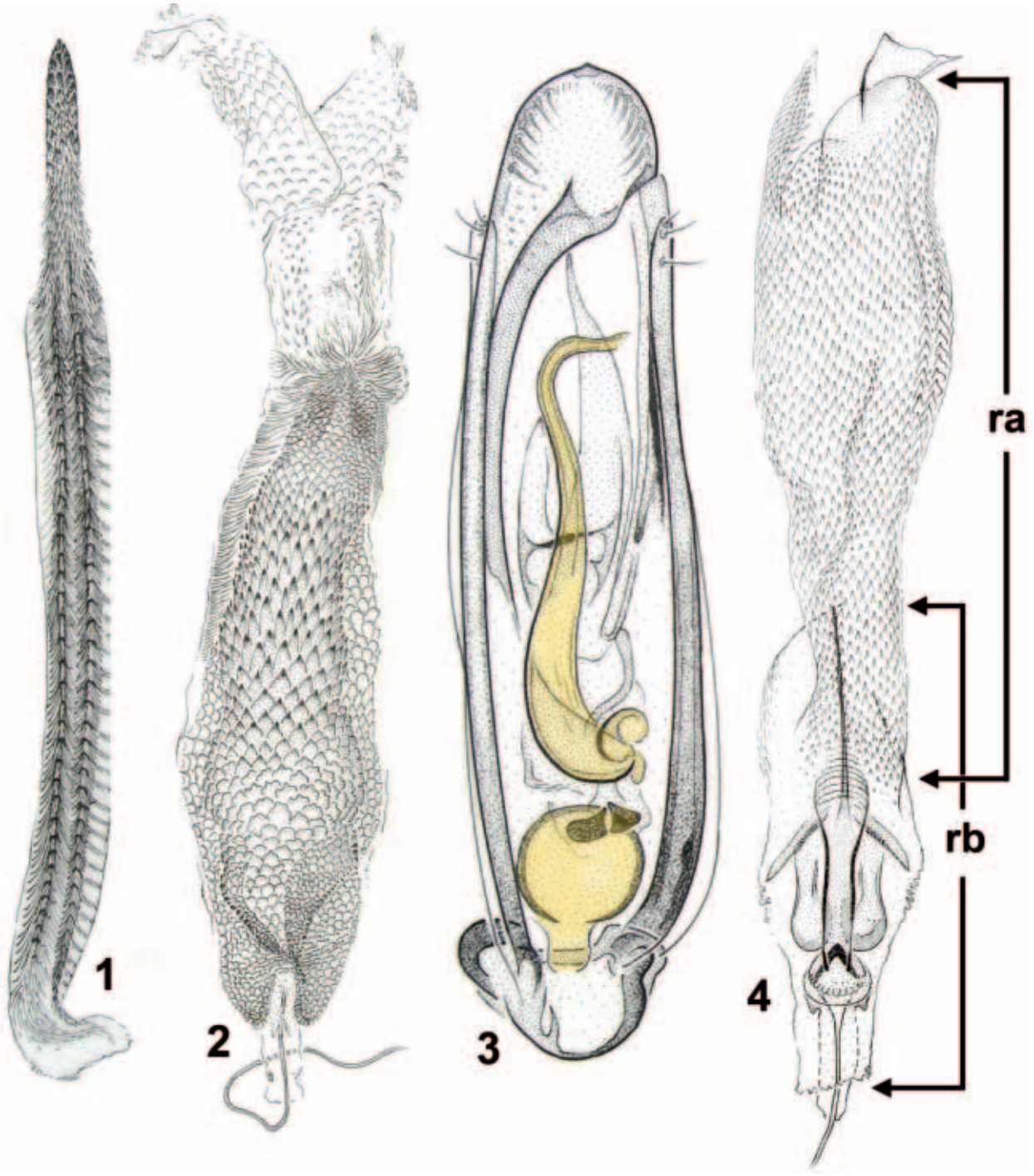
In endophallus without dorsal and ventral complex there may be a stylet originating in the basal region that extends in some cases to the other end of the sac.

Stylet of the endophallus: In all species of supraflagellates of Jeannel (1944, 1955a) with the exception of *Breuilia, Espanoliella* and *Breuilites,* the endophallus has a stylet of variable length, from a small dent with a complex shape, to a straight stylus as long as the entire sac. However it is not unlikely that the flagellum of the infraflagellates (Jeannel 1944, 1955a) is homologous to the stylet of the supraflagellates (Jeannel 1944, 1955a). The stylet may be:

– Well developed, long (Fig. 27.4) or very long (Fig. 27.2: s).

– Reduced to a small tooth (Fig. 27.3: s). The stylet of the endophallus is reduced to a small tooth in the series *Spelaeochlamys*, with the exception of *Paranillochlamys*; this tooth may have a complex shape.

– In the *Quaestus* series, the stylet can have a simple base (Fig. 27.4), or when it is well-developed it can have a basal plate or cup of various shapes, rounded or rectangular (Fig. 27.2: bp).



FIGURES 26.1–26.4: Aedeagus. Endophallus of: (**1**) *Speonemadus maroccanus* (Jeannel, 1936), (**2**) *Catops fuliginosus* Erichson, 1837, (**3**) *Ptomaphagus subvillosus* (Goeze, 1777) (in orange, basal vesicle and evaginable stylet), (**4**) *Speonomidius crotchi aitzquirrensis*. Abbreviations: **ra**, apical region; **rb**, basal region. Figs **1**–**4** modified from Salgado *et al*. (2008).

– In some of the species the stylet in the endophallus is placed inside a membranous conduct, sometimes with different kinds of sclerotized structures in the surface (scales, spicules, spines). All species of the series *Quaestus* with stylet have a membranous conduct covered with scales or spicules, including the stylet with the exception of *Quaestus jaspei* comb. nov. The genus *Breuilites*, without stylet, has also the same character.

– The stylet is simple, without associated phanerae (Fig. 27.2) or has associated phanerae (e. g. some populations of *Quaestus nuptialis*).

– The basal half is thickened, or is simple throughout its length.

– The base of the stylet bears a ring with the upper part more sclerotized so that the base of the stylet appears to be bifurcated and resembles an inverted «Y»-piece.

Middle region (Fig. 28: rm): Two dorsal phanerae (Fig. 28: fdm) are observed with one end included in the wall of the sac and the upper end in the interior space; they are elongated and vary in shape: thin and sinuous, or widened, or with two processes at their lower end. Apparently these fdm are the continuation of the cdb because, by means of some pieces that apparently float inside the tissue («floating pieces or pf» from Fresneda 1998) (Fig. 28: pf) they connect with the annexes phanerae of the «Y»-piece of the dorsal complex. The two dorsal phanerae tend to approach each other until a tubule appears at its upper end (the «axial piece or pa» of Bellés 1984) (Fig. 28: pa) which at its end presents a differentiated armor (the «armadura de la pieza axial» or «apa» of Bellés 1984) (Fig. 28: apa); the axial piece is normally covered by striated muscle tissue. The flagellum of the «Y»-piece continues to the axial piece armor. There are also two ventral phanerae («fvm» of Bellés 1984) (Fig. 28: fvm) attached by connective tissue to the inner wall of the sac. Its shape is variable: from wide plates with revolute processes, to narrow and regularly curved. There may also be a dorsal plate («superior dorsal plate of the middle region or pdsm» of Fresneda 1998) (Fig. 28: pdsm) associated with the ventral phanerae; this is translucent, although it can present one or two of its strongly sclerotized margins («phanera of the upper dorsal plate of the middle region, fpdsm1–2» from Fresneda 1998) or the entire plate is reduced to a simple and weakly sclerotized phanera. In the apical part of the median region there are two phanerae highly sclerotized arranged in the shape of an inverted «V», localized below the dorsal and ventral phanerae (Fig. 299.4; «pvi» of Fresneda *et al*. 2009).

Apical region (Jeannel 1924a; «ra» of Bellés 1984) (Figs 27.4, 28: ra): It measures approximately one third of the total length of the endophallus. There are two long and robust phanerae included in the wall of the bag, on both sides of it («bandelettes de renforcement» by Jeannel 1924a; «bra» of Bellés 1984) (Fig. 28: bra). In some models of endophallus, these reinforcement bands articulate with parts across the middle and apical regions; these have the appearance of a pouch («apical dorsal pouches of the middle region or bdam» of Fresneda 1998; «nc» of Dupré 1992) (Fig. 28: bdam) and may show a sclerotized nodule inside (the «phanera of the bdam or fbdam» of Fresneda 1998) (Fig. 28: fbdam) or an appendix also more sclerotized («appendix of the bdam or abdam» of Fresneda 1998) (Fig. 28: abdam). Between the reinforcement bands, in the interior canal of the sac, a bag can be observed (the «apical bag or ba» of Fresneda 1998) (Fig. 28: ba) whose integument can be smooth, or covered with scales or spicules; in some cases, there may also be a plate included inside the sternal lining of the sac («la» of Bellés & Comas 1986; «px» of Dupré 1992). All Leptodirini, with the exception of the series *Speonomidius* and some species of *Espanoliella*, have reinforcement bands in the endophallus. In an endophallus that presents bands of apical reinforcement, these may have different configurations:

– Two simple reinforcing bands (Fig. 27.2: bra; 28: bra).

– Four pubescent reinforcing bands (Fig. 289.8).

– Short reinforcing bands, with size of one third or less of the length of the sac. In the *Speonomus* series (Fig. 310.3) it is always about 1/3 the length of the bag or even less; it might be homologous withthe upper part of the reinforcing bands of some *Quaestus*.

– Reinforcing bands almost as long as the entire sac. In *Quaestus nietoi* and other *Quaestus* the bra are very long, about 4/5 or even 5/6 of the total length of the sac (Fig. 27.2: bra); they also seem to be made up of two regions with different degrees of sclerotization.

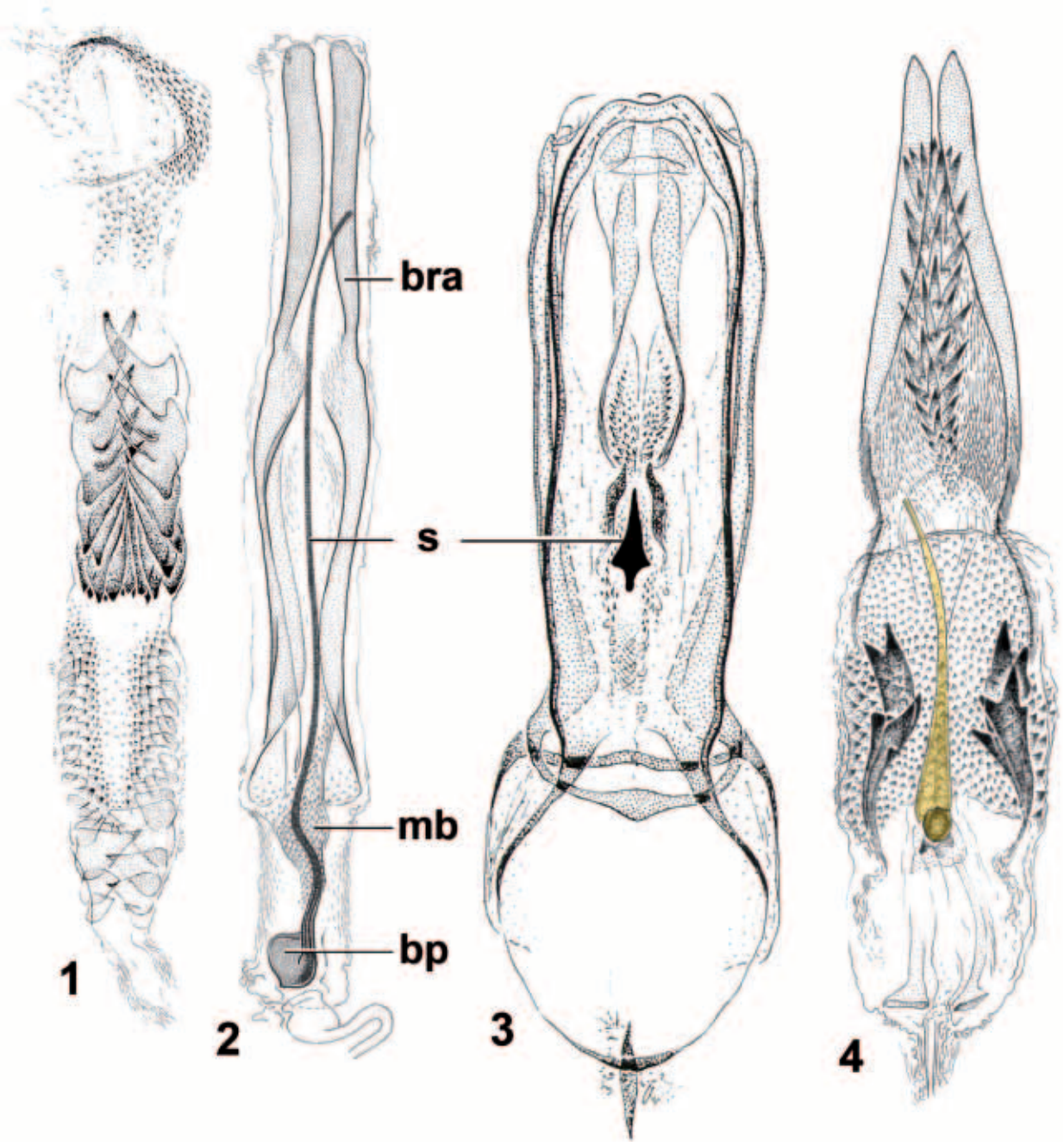
– Reinforcing bands on sclerotized nodules (Fig. 28: fbdam) or on membranous ligules (Fig. 289.9).

– Reinforcing bands on ligules of smooth tissue (Fig. 289.9), of slightly sclerotized and strongly striated tissue (Fig. 311.5), or of squamous tissue.

– Reinforcing bands welded to the basal structure forming a single piece with it.

– Between the reinforcing bands there can be one or two bags whose integument is covered with scales, spicules or spines, there can be a tubule or a pubescent drumstick (Fig. 276.11).

– Presence of a large or underdeveloped px (Fig. 311.1).



FIGURES 27.1–27.4: Aedeagus. Endophallus of: (**1**) *Espanoliella jeanneli*, (**2**) *Quaestus nietoi*, (**3**) *Anillochlamys cullelli*, (**4**) *Cantabrogeus luquei* (stylet in orange). Abbreviations: **bp**, basal plate of the stylet; **bra**, apical reinforcement bands; **mb**, membranous sac; **s**, stylet. Figs **1**–**4** modified from Salgado *et al*. (2008).

Male urite IX

This structure is reduced, either partially, forming an open receptacle for the reception of the apex of the aedeagus (Figs 29.3–29.7), or completely, forming a chitinous ring (Figs 29.1, 29.2) or is fully developed, forming a closed receptacle for the aedeagus (Fig. 29.4). The IX urite of males is fully developed only in *Speonemadus* Jeannel, 1922 (Anemadini) (Fig. 29.4), it is partially reduced in *Catops* Paykull, 1798, *Choleva* Latreille, 1796 and *Nargus* Thomson, 1867 (Cholevini) (Figs 29.5–29.7) or *Ptomaphagus* Hellwig, 1795 (Ptomaphagini) (Fig. 29.3), and fully reduced in Leptodirini (Figs 29.1, 29.2).

– In the Anemadini it is well-developed and formed by a tergite, two pleurites and a very modified sternum in the form of a manubrium in which the pleurites articulate (Fig. 29.4). It is a complete segment, closed, similar to Sciaphyini own.

– In Cholevini the male genital segment is reduced to a flat ring, largely membranous, formed by a tergite and a pleurite. Although the segment is reduced, there is a marked bowl at its distal end. Two submodels could be distinguished: Cholevina and Catopina. Note the differences between *Catops fuliginosus* Erichson, 1837 and *Sciodrepoides fumatus* (Spence, 1815) (with that finely sclerotized manubrium on top) (Fig. 29.5), and *Nargus wilkini* (Spence, 1815) and *Choleva fagniezi* Jeannel, 1922 (with the equivalent of that upper manubrium which is shaped as a less sclerotized broad sheet) (Figs 29.6, 29.7).

– In Ptomaphagini, the genital segment is also reduced to a more or less membranous ring, with lamellar pleurites, and the sternite transformed into a kind of narrow, elongated manubrium surrounded by the genital segment. The segment (Fig. 29.3) is reduced but there is a marked cup split in two halves at its distal end. There is a prominent manubrium on the upper part that is not found in the Leptodirini.

– In Leptodirini it is reduced to a poorly sclerotized ring in which two manifest peduncles are inserted (Fig. 29.1), sometimes reduced (Fig. 29.2); only some genera, such as *Anthroherpon* or *Remyella*, have the genital segment complete or only partially reduced (Giachino *et al*. 1998). The extreme reduction, complemented by the existence of two peduncles of the segment seems to be a synapomorphy of the Leptodirini, only absent in *Anthroherpon* and *Remyella*.

Spermathecal complex

It consists mainly of spermatheca, annexed or basal gland, ejaculatory duct and bursa copulatrix. Some of these structures have been described and figured for some Leptodirini (Bellés 1984; Zoia & Rampini 1985; Giachino 1988; Perreau 1989; Salgado 1989b, 1991, 1992, 1993b, 1994a; Giachino & V.B. Guéorguiev 1989, Rampini & Latella 1993; Latella & Rampini 1994; Fresneda 1998, 1999; Fresneda *et al*. 1998; Latella 2002; Giachino & Vailati 2019). Perreau (1989) established the basic models of spermatheca:

– Fully membranous, without any particular structure in the insertion of the sperm duct («atypical spermatheca» of Perreau, 1989); the «atypical» spermatheca, globose and hyaline is present in *Catops* Paykull, 1798, *Fusi* Perkovsky, 1989 (Fig. 30.1), *Choleva* Latreille, 1797 (Fig. 30.2) or *Sciodrepoides* Hatch, 1933 (Cholevini); also in *Speonemadus* Jeannel, 1922 (Fig. 30.6) (Anemadini).

– Uniformly sclerotized spermatheca («type 2», according to Perreau 1989) in highly variable forms exists, for example, in *Adelopsis* Portevin, 1907 (Fig. 30.3) *Ptomaphagus* Hellwig, 1795 (Fig. 30.4), *Paulipalpina* Gnaspini & Peck, 1996 (Fig. 30.5) and *Ptomaphaginus* Portevin, 1914 (Ptomaphagini), or in *Eucatops* Portevin, 1903 (Fig. 30.8) (Eucatopini) (Salgado, 2011).

– With basal and apical lobes sclerotized to some degree and the medial part or union duct membranous, with a well-defined insertion point of the sperm duct («type 1» spermatheca according to Perreau 1989) (Figs 31.1–31.6). All studied species of Leptodirini have a spermatheca of the «type 1»; also found in some Anemadini such as *Dissochaetus* Reitter, 1885 (Fig. 30.7).

A different case figurated but not described is that of *Baryodirus* Perreau, 2000 (Ptomaphagini, Baryodirina) which has a ringed spermatheca, with an attached gland and a short spermatic duct (Perreau 2000: Fig. 41); a similar conformation is found in *Coreobathyscia* Szymczakowski, 1975.

The spermatheca consists of a slightly sclerotized tube closed at one end and in which three regions can be identified: the basal (Fig. 31.2: bl), the apical (Fig. 31.2: al) and both lobes joined by the middle region or union duct (Fig. 31.2: mr), a tube with a regular or constricted section and a generally hyaline appearance; both lobes may be thickened and sclerotized; the sperm duct opens in the basal lobe (Fig. 31.2: s) directly into the interior of the spermatheca or through a thickened section (nodule) (Fig. 31.2: als); the annexed gland or

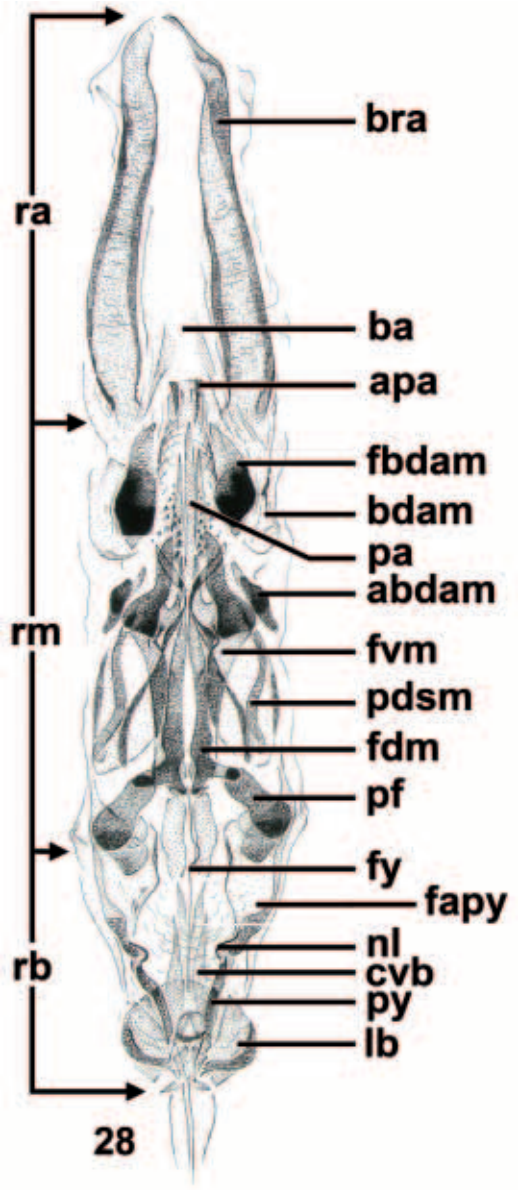


FIGURE 28: Aedeagus. Endophallus of *Speonomites antemi* (modified from Salgado *et al*. 2008). Abbreviations: **abdam**, appendix of the dorsal sac of the apex of the median region; **apa**, armature of the axial piece; **ba**, apical sac; **bdam**, dorsal sac of the median region of the apex; **bra**, apical reinforcement bands; **cvb**, ventral basal complex; **fapy**, apical fibres of the «Y»-shaped piece; **fbdam**, phanera of the dorsal sac of the median region of the apex; **fdm**, dorsal phanera of the median region; **fvm**, ventral phanera of the median region; **fy**, flagellum of the «Y»-shaped piece; **lb**, basal lamina; **nl**, junction nodule; **pa**, axial piece; **pdsm**, upper back plate of the median region; **pf**, floating piece; **py**, «Y»-shaped piece; **ra**, apical region; **rb**, basal region; **rm**, median region.

spermathecal gland also opens into the basal lobe (Fig. 31.2: sg); the spermatic duct can be extraordinarily long, of the same thickness throughout its entire length (Fig. 31.2: s) or have the basal half thickened (Fig. 313.7); it can also be short (Fig. 31.3); the unit of measurement is the spermatheca itself, how many times is the duct the length of the spermatheca; the insertion of the conduit in the copulatory bag can be direct or through a sclerotized piece that can be shaped like a sheet, disc or funnel (Fig. 31.2: bp). The spermatheca can have different shapes and sizes, even within the same genus, but several characteristics can be defined that can have a specific generic distribution:

– Spermatheca short, with a reduced medial region (Fig. 31.3) or without middle region (Fig. 31.5), the two lobes being united.

– Spermatheca long, with a well-developed medial region (Figs 31.2, 31.6). All studied species of «infraflagellates» (*sensu* Jeannel 1955a) have a long spermatheca, with a well-developed medial region.

– Degree of development of the lobules of the spermatheca (size of the lobes): both equally developed (Figs 31.2, 31.3), the basal more developed (Fig. 31.4) or the apical more developed (Fig. 31.5).

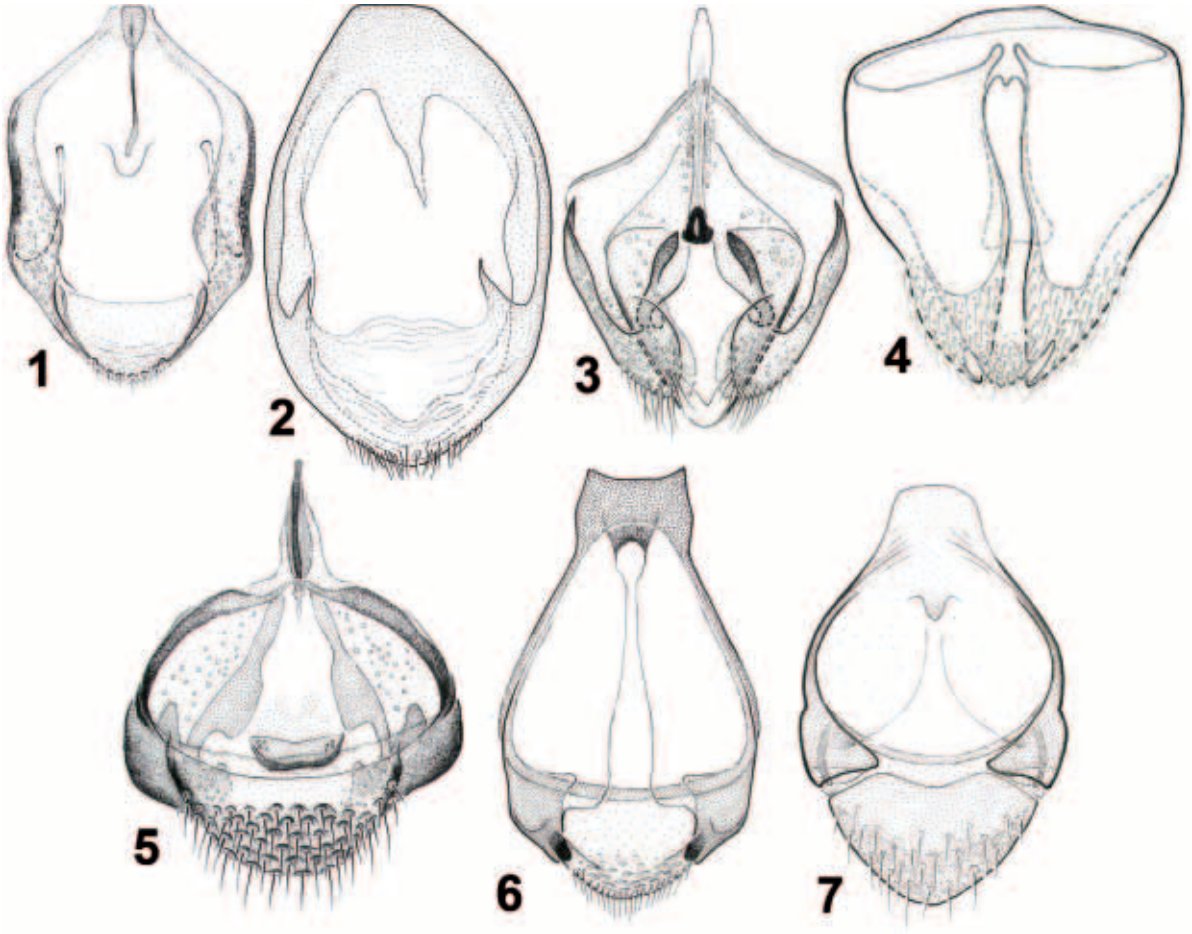
– Connection between the bursa copulatrix and the sperm duct: direct, without any defined structure (Figs 31.3, 31.4), with the sector near the insertion somewhat thickened and sclerotized or through a sclerotized piece (Figs 31.2, 31.6: bp). Several groups of the studied Leptodirini have a sclerotized piece connecting the bursa copulatrix and the spermatic duct: the series *Speonomidius*, the Sardinian genus *Ovobathysciola*, *Zariquieyella*, *Lagariella*, *Naspunius*, *Speocharidius*, *Speonomites*, *Stygiophyes*, etc. This character was described by Giachino & V.B. Guéorguiev (1989) in *Gesciella*, but never studied in other genera of Leptodirini before.

– Connection between the spermatheca and the sperm duct: Inserted into the spermatheca directly (Figs 31.3, 31.5) or thickened to form a lobe (or nodule) at the point of insertion (Figs 31.4, 31.6: als).

– Length of the spermiduct: Long (Fig. 31.1) or short (Fig. 31.3).

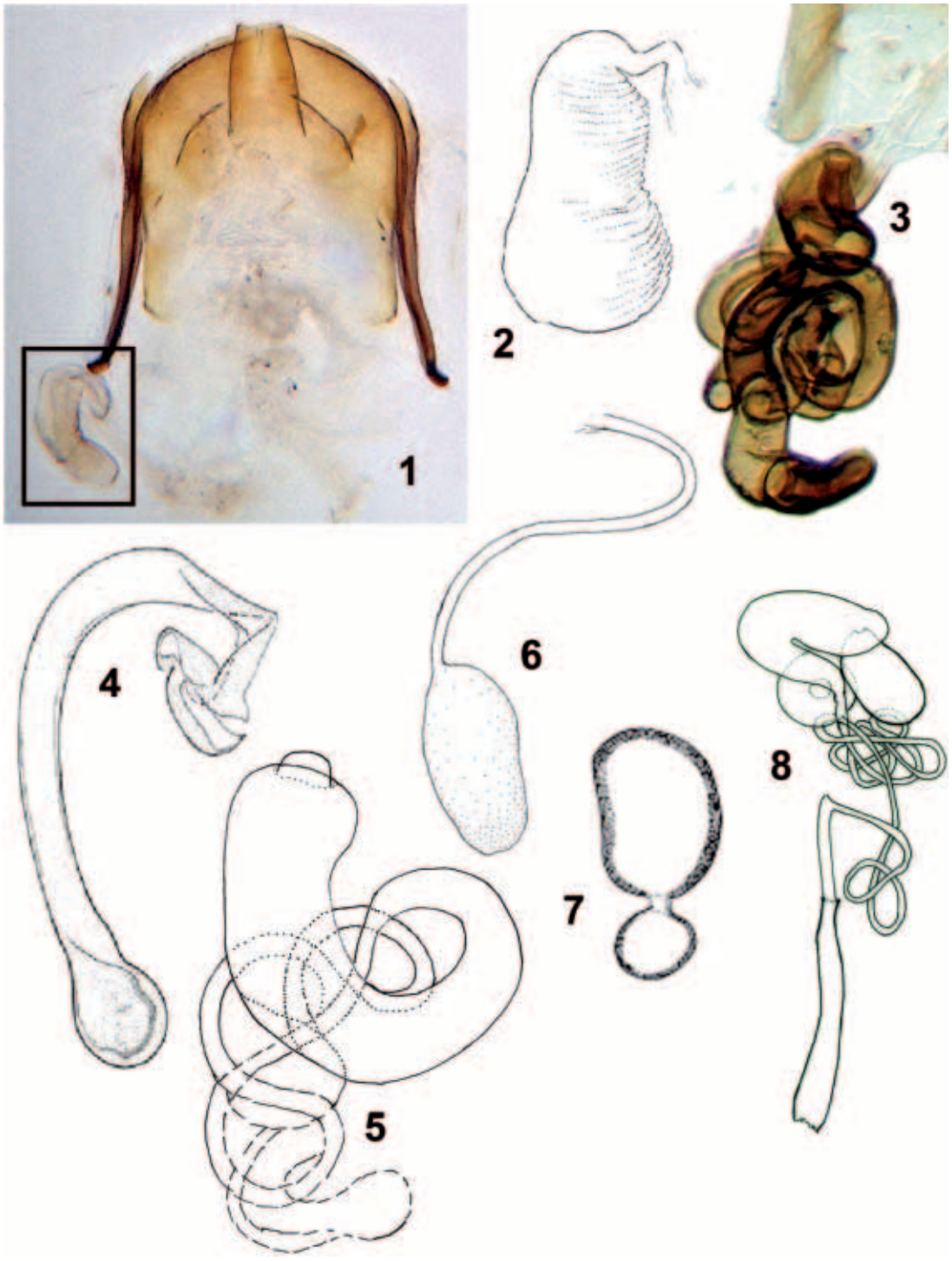
– Thickness of the sperm duct: Of uniform thickness throughout its length (Figs 31.3, 31.4) or with the apical half thin and the basal half of greater caliber clearly differentiated (Figs. 31.2, 313.7).

Significant, in the taxa of the genus *Bathysciola*, is the morphology of some traits of the female genital system referable in particular to the spermathecal complex (spermatheca + spermathecal duct + annexed gland). These characters, well represented, but not em-

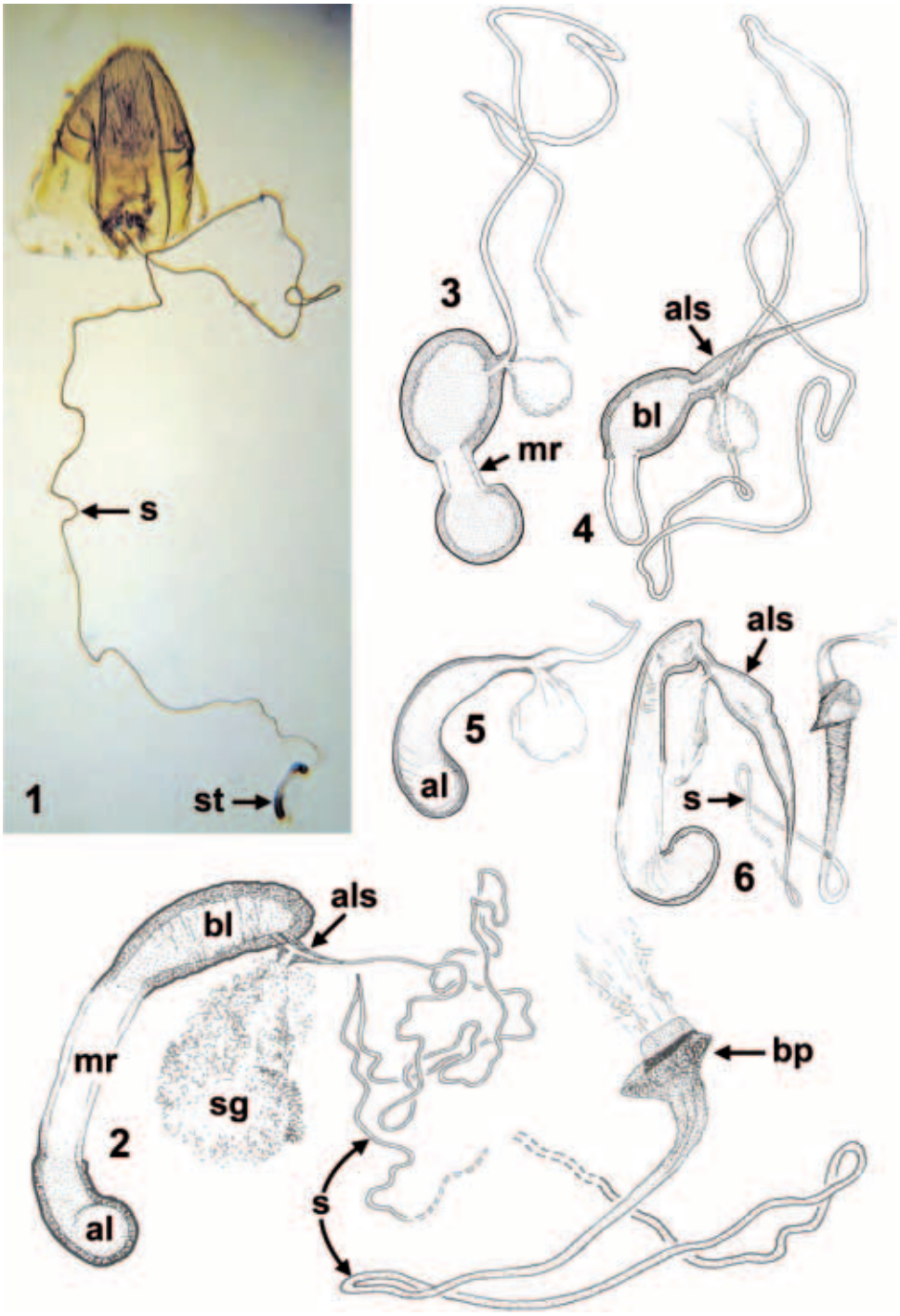


FIGURES 29.1–29.7: Male, 9th uroventrite of: (**1**) *Zariquieyella rugosa* **comb. nov.**, (**2**) *Kircheria beroni*, (**3**) *Ptomaphagus medius* (Rey, 1889), (**4**) *Speonemadus vandalitiae* (Heyden, 1870), (**5**) *Catops fuliginosus* Erichson, 1837, (**6**) *Choleva fagniezi* Jeannel, 1922, (**7**) *Nargus wilkinii* (Spence, 1813). Figs **1**, **3**–**7** modified from Salgado *et al*. (2008); Fig. **2** from Giachino & Vailati (2006).

phasized, in the contributions of Zoia & Rampini (1985), Rampini & Latella (1993), Latella & Rampini (1994) and Latella (2002), appear instead of great phylogenetic importance and might be considered as synapomorphies of some groups of species/genera that are well characterised both taxonomically and zoogeographically. In particular, the shape of the spermathecal duct and the presence/absence of dilatations along the duct appear taxonomically significant. The preliminary study conducted by Giachino (1988) on some species of *Bathysciola* showed that in this genus, the spermathecal duct is long and without significant dilatations, the spermatheca is simple and reniform and the annexed gland hyaline, bag-shaped. The study of the spermathecal complex of *Reitteriola* (Fig. 266.7), *Canapiciella* (Fig. 266.3), *Doderiola* (Fig. 266.5), *Rondolinia* (Fig. 266.8), *Baudiola* (Fig. 266.2), *Tamaniniella* (Fig. 266.10) and *Muelleriola* (Fig. 105.8) allowed us to highlight, in the different taxa, the presence of significant morphological differences in the shape of the spermatheca compared to the classic kidney-shaped model, as well as significant dimensional differences in *Baudiola* compared to all the other species. Several taxa also present a clear dilatation of the duct at the insertion point in the spermatheca, particularly evident in *Baudiola*, *Reitteriola* and *Muelleriola*. However, the spermathecae of these genera are morphologically very different from each other and difficult to refer to a structure that can be interpreted on a generic basis.



FIGURES 30.1–30.8: Spermathecal complex of: (**1**) *Fusi nyujwa* Perkovsky, 1989, (**2**) *Choleva fagniezi* Jeannel, 1922, (**3**) *Adelopsis bruchi* Pic, 1926, (**4**) *Ptomaphagus subvillosus* (Goeze, 1777), (**5**) *Paulipalpina arcuata* Salgado, 2013, (**6**) *Speonemadus vandalitiae* (Heyden, 1870), (**7**) *Dissochaetus costaricensis* Salgado, 2010, (**8**) *Eucatops rufescens* Portevin, 1903. Figs **2**, **4**, **6** modified from Salgado *et al*. (2008); Fig. **5** from Salgado (2013); Fig. **7** from Salgado (2010a); Fig. **8** from Salgado (2010b).



FIGURES 31.1–31.8: Spermathecal complex of: (**1**) *Troglocharinus mercedesi*, (**2**) *T. fadriquei*, (**3**) *Quaesticulus adnexus*, (**4**) *Quaestus jeannei,* (**5**) *Breuilia triangulum*, (**6**) *Euryspeonomus* (*Euryspeonomus*) *breuili.* Abbreviations: **al**, apical lobe; **als**, apical lobe of the spermatic duct; **bl**, basal lobe; **bp**, basal piece of the spermatic duct; **mr**, median region or union duct; **s**, spermatic duct; **sg**, spermathecal gland; **st**, spermatheca. Fig. **1** modified from Fresneda *et al*. (2021); Figs **2**–**6** modified from Salgado *et al*. (2008).

Female uroventrite VIII

This structure was first studied by Zwick (1979) in *Catoposchema tasmaniae* Jeannel, 1936 (Anemadini) but it was Perreau (1989) who described a «spiculum ventrale» («ventral spine» of Salgado *et al*. 2008) prolongation of the eighth segment in numerous Coleoptera Polyphaga, though absent in some. Among the Cholevinae this structure is found in Leptodirini, Cholevini (Figs 32.1–32.3: s), Anemadini (Fig. 32.4: s), Agyrtodini and Nemadini. It is absent in *Eocatops* Peyerimhoff, 1924, Oritocatopini, Ptomaphagini (Figs 32.5, 32.6) and Eucatopini. It is found in other Leiodidae such as *Neocamiarus* Jeannel, 1957, *Neopelatops edwardsi* Jeannel, 1936, *Agathidium* (*Neoceble*) *varians* Beck, 1817, *Leiodes* Latreille, 1796 or *Colon* Herbst, 1797. In Catopina there is a depression («fossette» of Perreau 1989) (Fig. 32.1: f) along the spiculum, or at the base of this, with one exception: *Catoptrichus frankenhauseri* Mannerheim, 1852 and *Fusi nyujwa* Perkovsky, 1989 (Fig. 32.3), sister species of all Catopina.

The long or short spiculum of the Leptodirini is a character that is difficult to measure, since between extreme cases it is possible to find numerous intermediate states. It can be seen that although the spiculum of *Parvospeonomus urgellesi* (Fig. 283.10) is considered short, that of *Cantabrogeus luquei* (Fig. 210.4) or *Euryspeonomus* (*Urbasolus*) *eloseguii* (Fig. 279.5) is long, however in the latter it is as long or longer than that of *P. urgellesi*. The spiculum instead assumes forms from small (*Canapiciella* and *Tamaniniella*) to very prominent (*Rondolinia*, *Baudiola*, *Doderiola* and *Reitteriola*). The forms that present in these taxa the VIII uroventrite + spiculum complex are, however, morphologically very different from each other and difficult to refer to a unique form that can be interpreted generically. Therefore, it must be interpreted that in general the assessment is made by comparison with other representatives of the same series.

Among the Leptodirini the following models are found:

– Spiculum ventrale long and thin (Figs 33.1, 33.2: s): in general most of the representatives of the *Quaestus*, *Speonomidius* and *Speonomus* series.

– Spiculum ventrale short (Figs 33.3–33.5: s): *Quaestus avicularis* or *Q. arcanus* from the *Quaestus* series or *Aranzadiella*, *Ceretophyes*, *Stygiophyes*, *Parvospeonomus*, *Phacomorphus, Speocharidius* or *Troglocharinus orcinus* from the *Speonomus* series.

– Spiculum ventrale into forked spine (Figs 33.4, 33.5: s) – *Salgadoia*, some *Troglocharinus* or *Speonomites*, of the *Speonomus* series –, or with two membranous extensions (Fig. 33.6) – *Perriniella*, *Lagariella* or some *Speonomites* –.

– Spiculum ventrale totally atrophied (Fig. 33.7).

The apical end of the uroventrite is generally regularly rounded, although peculiar conformation can be found in some species. *Amphogeus oxypterus* comb. nov., for example, has the apex formed by two lobes with a notch between them (Fig. 210.2) or in *Tamaniniella* where the anterior edges are clearly convergent (Fig. 267.11), in the shape of a semicircle with the anterior margin largely straight, and the anterior edges not convergent; both cases seem to be unique among all the Leptodirini.

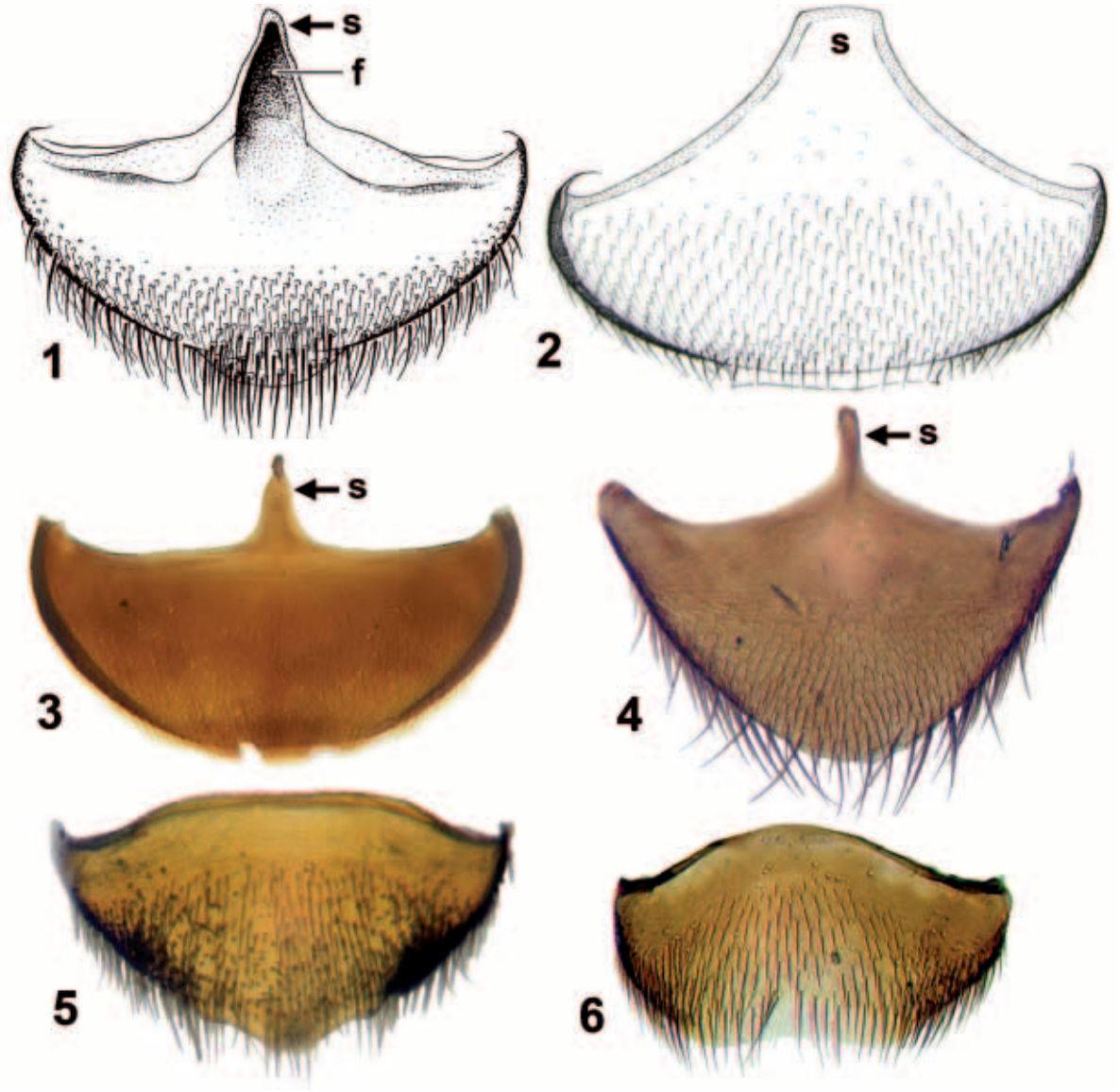
A new taxonomic classification of the tribe Leptodirini

Leptodirini Lacordaire, 1854 [1849]

Stagobiinae Schiødte, 1849: 16
Leptodérides Lacordaire, 1854: 195
Leptodirites Abeille de Perrin, 1878: 145
Bathysciae Horn, 1880: 251 syn. nov.
Pholeuones Reitter, 1886a: 314 syn. nov.
Oriotini Reitter, 1889a: 296.
Antroherpona Jeannel, 1910a: 25 syn. nov.
Euryscapiti Jeannel, 1910a: 7
Gynomorphi Jeannel, 1910a: 14
Brachiscapiti Jeannel, 1910a: 19
Hadesiini Absolon, 1913b: 108
Théléomorphes Jeannel, 1914a: 71
Leptodiridae Hatch, 1933: 188
Bathysciotina V.B. Guéorguiev, 1974a: 841 syn. nov.
Ghidiniina V.B. Guéorguiev, 1974a: 841
Leptodirina V.B. Guéorguiev, 1974a: 841
Spelaeobatina V.B. Guéorguiev, 1974a: 841 syn. nov.

Type genus. *Leptodirus* F.J. Schmidt, 1832.

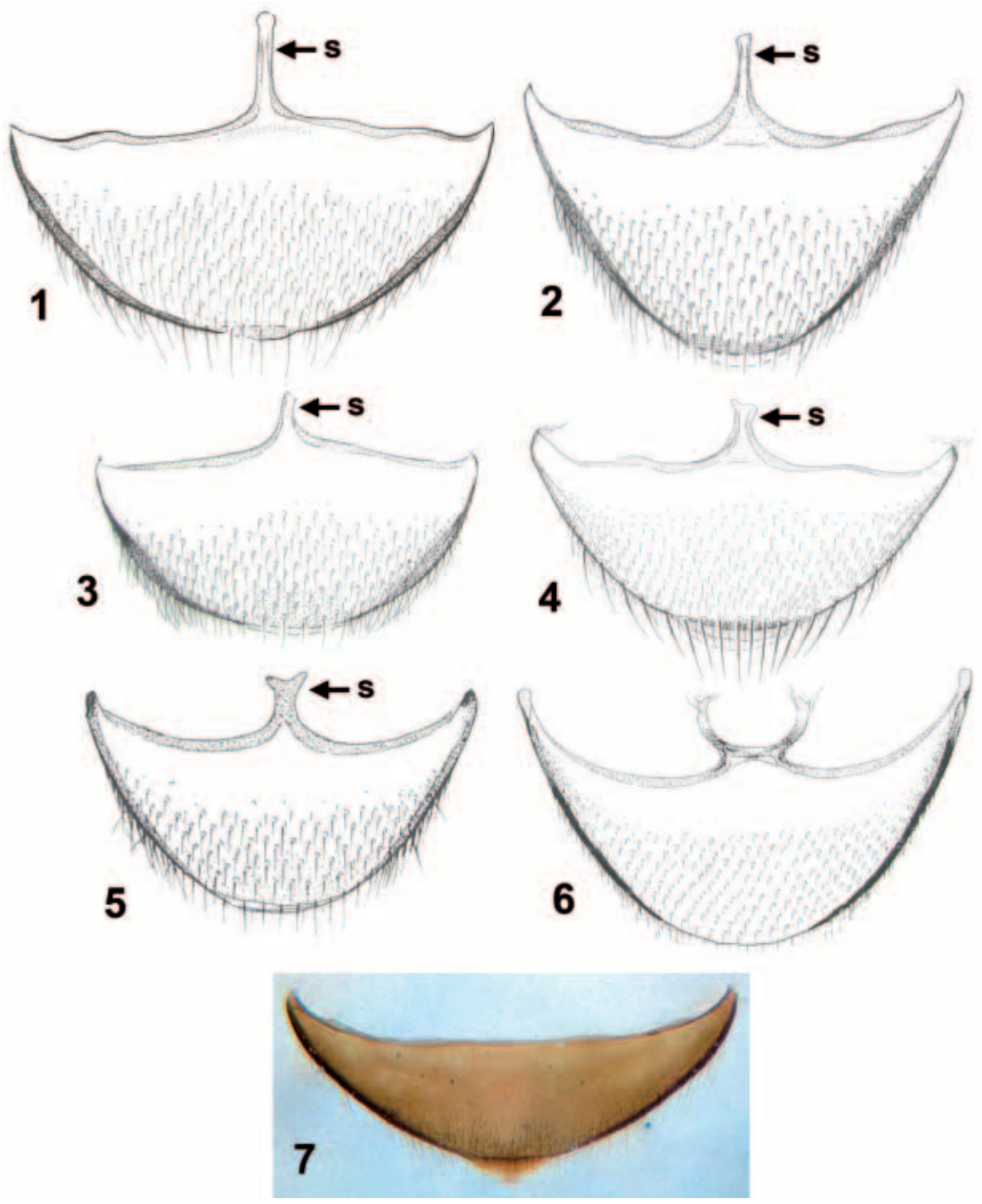
Diagnosis. Epistomal suture present (Fig. 6.3); female protarsi tetrameres (Fig. 13.4); mesocoxal cavities narrowly separated in prolonged mesoventral process with posterior edge widened (Figs 16.2–16.4, 16.6, 16.7); metaventral process generally bifid (or simple) resulting in more or less separated metacoxa (Fig. 16.2: mtvp); presence of a set of projecting sensilla on the apical maxillary palpomere (Fig. 7.2: ps) – digitiform sensilla adpressed to the surface of the palpomere in Cholevinae non leptodirines (Fig. 7.3: dgts) –; base of two setae of tarsal empodium fused (Fig. 12.3, 12.6); claws without longitudinal grooves



FIGURES 32.1-32.6: Female, uroventrite VIII of: (**1**) *Catops fuliginosus* Erichson, 1837, (**2**) *Choleva oblonga* Latreille, 1807 (**3**) *Fusi nyujwa* Perkovsky, 1989, (**2**) *Dissochaetus confusus* Salgado, 2010, (**5**) *Ptomaphagus troglodytes* Blas & Vives, 1983, (**6**) *Paulipalpina baenai* Fresneda & Salgado, 2017. Figs **1**, **2** modified from Salgado *et al*. (2008). Abbreviations: **f**, «fossette»; **s**, spiculum ventrale.

and with a transverse groove (Fig. 14.3: tgc); metendosternite reduced, without anterior lamina of the furca (Fig. 21.2) – in the other Cholevinae tribes there is a lamina on the inside of the two symmetrical arms (Fig. 21.1: afp) –; genital segment of the male reduced to a ring without a manubrium, with two lateral inserted peduncles (Fig. 29.1, 29.2).

Discussion. Jeannel (1924a) defineds division I, the «Euryscapes». The characters are valid both for Adelopsellina subtribe nov. and Platycholeina, but also for what he calls the phyletic series of *Sciaphyes*, *Dalmatiola*, *Muelleriella*, *Ceutophyes*, *Anillochlamys*, *Hoffmanella*, *Quaestus*, *Magdelainella*, *Bathysciola*, *Parabathyscia*, *Speonomus*, *Diaprysius*



FIGURES 33.1-33.7: Female, uroventrite VIII of: (**1**) *Espanoliella escalerai*, (**2**) *Quaestus incognitus*, (**3**) *Q. avicularis*, (**4**) *Troglocharinus orcinus*, (**5**) *Speonomites pallaresanus*, (**6**) *Perriniella faurai*, (**7**) *Aphaobius* sp. Abbreviations: **s**, spiculum ventrale. Figs **1–6** modified from Salgado *et al*. (2008).

and *Cytodromus*, that is, for all the Leptodirini except the clade formed by *Anthroherpon*, *Graciliella*, *Hadesia* and *Leptomeson*. The characters he described for the «Euryscapes» are: Antennae inserted in the middle third of the length of the head; first article of the antennae as long as the second; male protarsi pentamerous whereas tetramerous in females; protibiae without comb but with two or three well-developed external spurs; meso- and metatibiae with the apex not widened forming a hole surrounded by rigid spines («corbeilles» = baskets); claws slender, long and thin.

In the phylogenetic tree (Fig. 1I) the subtribes Platycholeina, Adelopsellina subtribe nov. and Leptodirina sensu novo within the Leptodirini tribe are highly supported (99.5/100). Since these series are scattered throughout different clades of the tree it is shown that the set of characters has no phylogenetic value. The two subtribes, Adelopsellina subtribe nov. and Platycholeina present exclusive characteristics among the Leptodirini and in the case of Platycholeina it shares some with other Cholevinae tribes: pigment, simple or complexes spurs, metatergal apparatus and metendosternite to insert the alar muscles. In fact, Platycholeina seems to be situated at a point of «morphological transition» between the epigean Cholevinae and the subterranean Leptodirini in the broad sense. The «morphological jump» between the epigean morphology and the morphology of pre-adaptation to the subterranean environment occurs between Platycholeina and Adelopsellina subtribe nov. Although the morphology separates them somewhat from the Leptodirini, since they come from the most basal cladogenesis of this great clade and the nodes have a high support, they are considered to belong to this tribe.

Both *Platycholeus* and *Adelopsella*, which derive from the more basal cladogenesis of Leptodirini, have an armed endophallus made up of sclerotized pieces in the same way as the Ptomaphagini. *Adelopsella* even exhibits the basal stylet frequent in clades derived from the tribe, a structure that could be homologous to the evaginable stylet of the Ptomaphagini endophallus. Thus, an armed endophallus seems to be the plesiomorphic state and the unarmed one the derivative, resulting in a more parsimonious single appearance from the latter during the evolutionary history of Leptodirini. It should be noted that the general appearance of the aedeagus of *Platycholeus* is very similar to that of *Ptomaphagus*.

KEY TO SUBTRIBES
(modified from Newton 1998 and Perreau 2000)

1. Presence of wings and eyes. Elytra with longitudinal striolae. Short but free tergite of the male genital segment, well sclerotized and with a wide median pit (Fig. 34.7). Furca of the metendosternite with anterior and posterior lamina (Fig. 34.3). Median lobe of aedeagus with the basal lamina reduced and the ventral lamina of the tegmen in the form of a narrow ribbon (Figs 34.4, 34.5). Non-sclerotized spermatheca.. .....Platycholeina
– Lack of wings, anophthalmous or with atrophied or very small eyes, with a reduced number of ommatidia. Elytra without longitudinal striae. Tergite of the male genital segment, short and fused to the pleurites, forming a thin, slightly sclerotized ring without a median pit. Furca of metendosternite only with more or less developed posterior lamina, very rarely a reduced anterior lamina (Fig. 35.4). Median lobe of aedeagus normally with well-developed basal and ventral lamina (Fig. 35.5, 35.6). Spermatheca sclerotized at least at one end (membranous in *Adelopsella*).....2

2. Dark brown pigmentation. First mesotarsomere of males dilated. Parameres with a single apical seta (Fig. 35.7). Spermatheca without differentiated lobes (Fig. 35.8) ..... Adelopsellina subtrib. nov.
– In general more or less intense orange pigmentation. First mesotarsomere of males not dilated. Parameres with more than one apical seta. Spermatheca with at least one differentiated lobe ....Leptodirina sensu novo

1. Subtribe ***Platycholeina*** Horn, 1880

Platycholei Horn, 1880: 251.
Platycholeini Jeannel, 1911a: 193.
Platycholeina Horn, 1880: Newton, 1998: 112.

TYPE GENUS. *Platycholeus* Horn, 1880 by original designation.

DIAGNOSIS. Pigmented animal, with pigmented eyes presumably functional. Winged. Longitudinal striae are hinted at the elytra; these are limited to a slight depression and alignment of the pubescence along the interstriae; there is no transverse striolation.

Pronotum: Has the flanged base.

Metatergal apparatus and metendosternite: Complex.

Metaventrite: With a wide and truncated projecting process that separates the metacoxal cavities.

Legs: First male mesotarsomere dilated; spurs at tibial apex of all legs simple; metatibiae with a thick curved hook-shaped spur and comb of subequal spines; no series of spines along external side of the tibia.

Last male uroventrite: Deeply notched.

Male genital segment: Complex, forms a capsule closed at the apical end and with a middle pit.

Mesoventral keel: Rounded and very short so that the mesocoxal cavities are in contact.

Metendosternite: Furca with anterior and posterior laminae.

Median lobe of aedeagus: With the tegmen anchored exactly at the base as in Ptomaphagini; ventral lamina of tegmen reduced, resembling a strip.

Spermatheca: Non-sclerotized, completely hyaline.

Discussion. It derives from the most basal part in the Leptodirini clade whose node has a robust support, 99.5/100, which also separates it from the rest by a long genetic distance (Fig. 1I).

Genus ***Platycholeus*** Horn, 1880
Platycholeus Horn, 1880: 254.

Type species. *Ptomaphagus leptinoides* Crotch, 1874 by monotypy (for the habitus see that of the similar species *Platycholeus* sp. in Fig. 34.1).

Diagnosis. Size: 3.0 mm. Bathyscioid appearance, oval and depressed shape (Fig. 34.1). Pigmented, dark brown in colour and the integument entirely covered by thin, short, lying down, yellowish and dense pubescence. Integument of the pronotum marked by minute, simple and irregular points and on the elytra by vaguely transversely aligned granular points.

Head: With the occipital carina obliterated in its middle part; epistomal suture (clypeus-frontal) well marked and practically straight; along the line the integument is black. Last article of the maxillary palps very short and conical, and the second globulous; eyes pigmented, presumably functional, located at the end of a stem (Fig. 10.4)

Antennae: With 11 antennomeres. Much shorter than the body – two thirds of the length of the elytral suture –; club somewhat differentiated since the articles are slightly thickened from the 7th element, with the 8th being the smallest.

Pronotum: Very transverse with lateral margins regularly arched from the base to the apex; very sinuous base with a flange; somewhat wider than the elytra taken together and the greatest width is before the base.

Elytra: Short, wide. Regularly arched from one end to the other. Longitudinal striae are insinuated; without parasutural stria.

Wings: Posterior wings present, well-developed.

Metaventrite: With a extensión broad and truncated that separates the metacoxal cavities.

Legs: Protarsi pentamerous in males and tetramerous in females; in the males the first three protarsomeres dilated and being the first narrower than the apex of the protibia; protibiae short and triangular, with simple tibial apex spurs, not pectinate, with a comb of sub-equal spines and without a series of spines on the external face. Mesofemora thickened in the middle part of the posterior margin; mesotibiae strongly curved with several simple spurs, a comb of subequal spines and without a series of spines on the external side; first mesotarsomere dilated. Metafemora widened with notched posterior margin; metatibiae strongly notched on their inner face with a thick curved spur in the shape of a hook and a comb of subequal spines; without a series of spines along outer face of the tibia.

Last male uroventrite: Deeply notched.

Male genital segment: Complex, forms a capsule closed at one end; the urotergite with a deep median impression (Fig. 34.7).

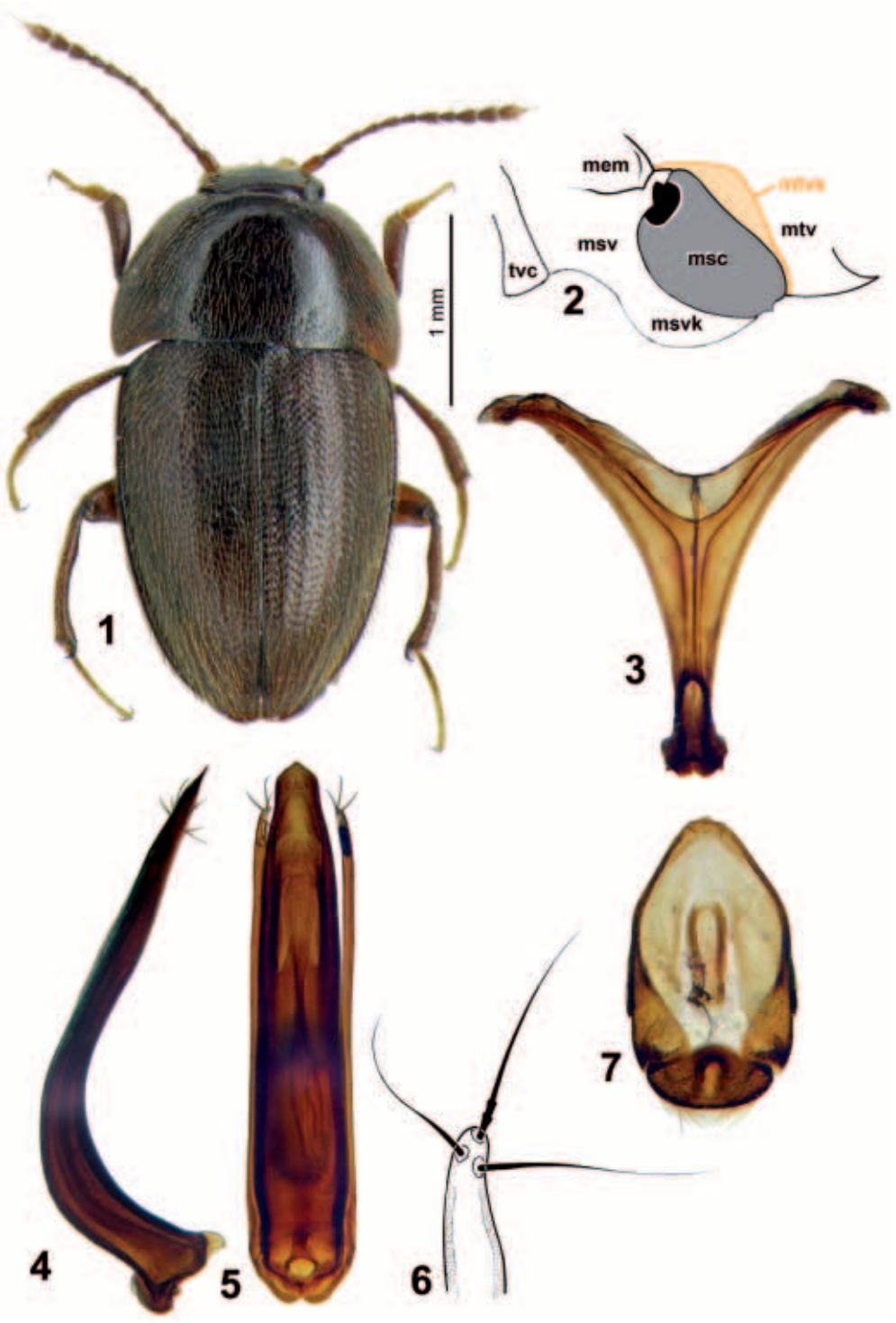
Mesoventral keel (Fig. 34.2): With the anterior part not prominent and the posterior part high, strongly rounded and very short so that it does not reach the metaventrite, therefore the mesocoxal cavities are in contact.

Suture of the metaventrite (Fig. 34.2: mtvs): Separated from the edge of the mesocoxal cavity, it defines a triangular area with a slightly projecting vertex.

Metatergal apparatus (Fig. 20.1): Large and complex as as expected in a winged animal; the metascutum exhibit laminae of great dimensions and the alacrista are very long and fused to other structures.

Metendosternite (Fig. 34.3): «Y»-shaped. Furcal arms somewhat shorter than the furcal trunk, with arched apical area; there is a highly developed anterior lamina that disappears in the apical area of the arm and is wide at the base, and a posterior lamina that progressively narrows towards the apical area of the arm, with an arched edge; inconspicuous terminal apophysis. Furcal trunk longer than the part of greatest width and the median keel with the posterior divergence long and well evident.

Median lobe of aedeagus: In lateral view (Fig. 34.4), long, very narrow, curved at the basal quarter,



FIGURES 34.1–34.7: *Platycholeus* sp.: (**1**) habitus (modified from Fresneda *et al*. 2011b). *Platycholeus opacellus*: (**2**) Pterothorax, (**3**) Metendosternite, (**4**) Aedeagus in lateral view, (**5**) Aedeagus in dorsal view, (**6**) Apex of the paramere, (**7**) Genital segment of the male. Abbreviations: **mem**, mesoepimere (mesothoracic epimere); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

the apex sharp. In dorsal view (Fig. 34.5), the margins of the apical area are slightly concave and the apex has a triangular appearance with an angle of almost 90º. Basal and ventral laminae greatly reduced.

Endophallus (Fig. 34.5): Without divisions, with two elongated bands that join towards the middle of their path and with spinules more developed in the union area of the bands.

Parameres (Fig. 34.6): Very fine, shorter than the median lobe, with four apical setae, three at apex and the fourth more distant. The tegmen, ribbon-shaped, anchored exactly at the base of the median lobe.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. *Platycholeus* was hypothesized by Jeannel (1910a, 1924a) to be related to the Old World Leptodirini, who remarked its similarities with *Sciaphyes* in head shape and mesoventral keel. Recent molecular phylogenetic studies on the Leptodirini tribe (Fresneda *et al*. 2011b; Cieslak *et al*. 2014a) have placed *Platycholeus*, the only New World representative of this tribe, as a sister group to the Palearctic Leptodirini. Also the detailed study of the larvae of *Platycholeus* (Kilian & Newton 2017) confirms the great similarities that exist with larvae of other Leptodirini, for example with those of *Quaestus* (Adamczyk *et al*. 2011).

Distribution. Western North America from British Columbia to California. Currently, the genus includes termitophilous *P. leptinoides*, myrmecophilous *P. opacellus*, plus an undescribed species, all of them found under bark of decayed conifer logs (Newton 1998; Fresneda *et al*. 2011b).

Species

Platycholeus leptinoides (Crotch, 1874)
Ptomaphagus leptinoides Crotch, 1874: 77.
Platycholeus leptinoides (Crotch): Horn, 1880: 254.

Platycholeus opacellus Fall, 1909
Platycholeus opacellus Fall, 1909: 133.

Platycholeus sp.
«named tentatively by A. Newton as "*hamatus*" ms» (Kilian 2012: p. 33) (*Nomen nudum*)
Platycholeus hamatus Kilian & Madra 2015: 62 (*Nomen nudum*).

2. Subtribe ***Adelopsellina*** nov.

Type genus. *Adelopsella* Jeannel, 1908 by present designation.

Diagnosis. Pigmented, dark brown colour; eyes somewhat reduced with pigmented ommatidia, apparently functional. Posterior wings absent.

Pronotum: With the base flanged.

Mesocoxal cavities: Separated by a mesoventral keel; the end of that keel does not touch the metaventrite so that at that point the two mesocoxal cavities are in contact inferiorly.

Metacoxae: Separated by a bifid projection of the metaventrite.

Mesoventrite: Has a ridge at the line of contact with the mesocoxal cavity.

Suture of the metaventrite: Outlines a very narrow and elongated area.

Legs: First mesotarsomere dilated in males and spurs of mesotibiae simple.

Median lobe of aedeagus: Basal portion reduced, reminiscent of the appearance of this structure in *Catops*.

Parameres: With a single apical seta.

Spermatheca: Without differentiated lobes.

Female uroventrite VIII: Base has two large laminar lobes located on either side of the spiculum.

Discussion. It emerges from the second most basal arm of the Leptodirini clade and clusters with clade of the entire Leptodirina sensu novo subtribe with a node support of92.6/98, and also separates it from the rest by a long genetic distance (Fig. 1I).

Genus ***Adelopsella*** Jeannel, 1908
Adelopsella Jeannel, 1908c: 182.

Type species. *Bathyscia (Bathyscia) bosnica* Reitter, 1885 by monotypy (habitus in Fig. 35.1).

Diagnosis. Size ranging between 2.0–2.5 mm. Bathyscioid appearance (Fig. 35.1); broad, depressed body shape; elytra regularly arched from one end to the other. Pigmented and the integument entirely covered by thin, short, recumbent, yellowish and sparse pubescence. Integument of the pronotum marked by small simple irregular punctation and that of the elytra by granular points vaguely aligned transversely.

Head: Small and retractable, with the occipital carina visible and entire; epistomal suture (clypeal-frontal) indicated by a curved line of darker coloura-

tion; eyes reduced, pigmented and functional, with a dozen of ommatidia. Last article of the maxillary palps short and conical.

Antennae: With 11 segments, much shorter than the body—two thirds of the length of the elytral suture—, somewhat thickened towards the 7th antennomere while the 8th is reduced; first antennomere slightly shorter than the second.

Pronotum: Very transverse almost twice as wide as long and somewhat wider than the elytra; regularly arched sides that widen towards the base, with the greatest width a little in front of the posterior angles which are acute; base sinuous with ridge.

Elytra: Short and a little longer than wide (1.25 times), with the maximum width located in the basal part; posterior lateral margins decrease in regular curve to the apex; fine and rough punctation, with a diffuse transverse striation as the points irregularly aligned; blurred parasutural stria along the posterior area.

Metaventrite: With a bifid protruding process that separates the metacoxal cavities (Fig. 16.3: mtvp).

Legs: Short and quite robust; protarsi pentamerous in males and tetramerous in females; in those the first three protarsomeres subequal, short and dilated, and slightly narrower than the distal end of the protibia; protibiae straight, not attenuated at their distal end with two internal spurs pectinate dorsal and ventral, one simple external one and a series of unequal spines between them; there is a regular series of spines, decreasing in size on the external face, without apical comb; mesotibiae slightly arched with a simple spur on the inside and three or four smaller simple spurs on the outside; there is a double series of five or six spines decreasing in size on the external face; first mesotarsomere dilated in males; metatibiae slightly arched with a long inner spur, two or three smaller outer spurs, and a series of spines along the external face of the tibia.

Male genital segment: Reduced, forms a ring with the fused urotergite, urosternite, and uropleurites.

Mesoventral keel (Fig. 35.2): Quite elevated towards the posterior third, being rounded from one end to the other, without rim, with a sharp and very short ventral ridge, it does not reach the metaventrite so that the two mesocoxal cavities are in contact inferiorly.

Suture of the metaventrite (Fig. 35.2: mtvs): With the suture very close to the edge of the mesocoxal cavity so that it delimits a very narrow arched area.

Metatergal apparatus (Fig. 35.3): With the metascutum long and quite wide, one wing almost twice the length of the alacrista; the apophysis of the alacrista little prolonged with sharp apices.

Metendosternite (Fig. 35.4): Furcal arms somewhat longer than the trunk, they narrow sharply in the apical area with a highly developed terminal apophysis; very marked furcal sutures, also in the posterior lamina which is regularly arched and narrows in trunk and arms, in these it does not reach the apex. Trunk distinctly longer than the width of the basal part; the middle keel on the trunk with reduced divergence in the posterior area.

Median lobe of aedeagus: Short and quite thick. In lateral view (Fig. 35.5), bent at an obtuse angle in its basal third, the apex presents a small apical thickening and is slightly curved towards the dorsal face. In dorsal view (Fig. 35.6), widened in the basal part, then somewhat narrowed towards the apical quarter and the apical part narrows to a blunt arc. Basal lamina robust and longer than the ventral lamina of tegmen.

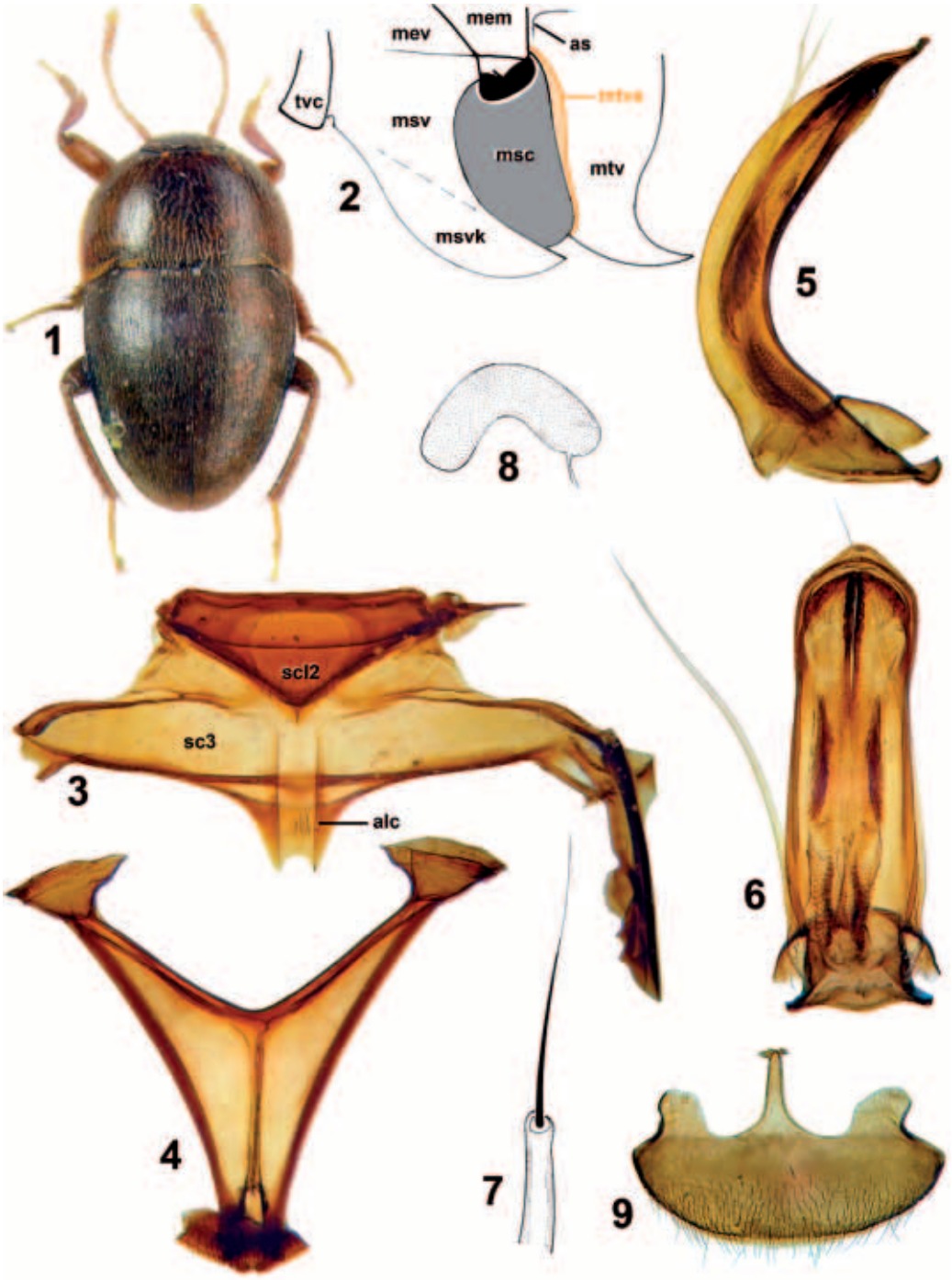
Endophallus (Fig. 35.6): Formed by three regions and with the external membrane densely covered with thick scales. In the basal region there are two bands of parallel spines that meet at the bottom and a stylet between them in an axial position. In the middle region there are two bands of spines and scales in lateral position. In the apical region there are two elongated strongly sclerotized structures closely spaced arranged on both sides of the axis, which extend to the middle region.

Parameres: Extremely fine, shorter than the median lobe and with a single seta attached to the apex (Fig. 35.7).

Spermathecal complex: Spermatheca (Fig. 35.8) short and hyaline, no part sclerotized, without differentiated lobes and uniform thickness; spermatic duct very fine and very short.

Female uroventrite VIII (Fig. 35.9): Apical margin in wide arc; basal margin with two large laminar lobes on either side of the spiculum, which is very long, broad at the base and slightly ogival at the apex.

Discussion. The multiple plesiomorphic characters of *Adelopsella* were recognised by Jeannel (1908c, 1911a, 1924a) who included it in the Division I of Pholeuina together with *Sciaphyes* and *Platycholeus* (Jeannel 1924a). *Platycholeus* and *Adelopsella* are the only Leptodirini with the first male mesotarsomere dilated, as in Cholevinae (Jeannel 1924a; Newton 1998). Other plesiomorphic characters are: weak pigmentation; eyes reduced, but with pigmented ommatidia; base of the pronotum bordered; mesotibial spurs simple; mesocoxal cavities bordered; basal part of the aedeagus reduced; parameres with only one apical seta; Female uroventrite VIII with two lateral lam-



FIGURES 35.1–35.4: *Adelopsella bosnica*: (**1**) Habitus, (**2**) Pterothorax, (**3**) Metatergal apparatus, ventral view of the metanotum and axillaria, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere, (**8**) Spermatheca, (**9**) female, uroventrite VIII. Abbreviations. Metatergal apparatus: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum. Pterothorax: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

inar lobes; membranous spermatheca. Synapomorphy of *Adelopsella* plus Leptodirina sensu novo are: male IX abdominal segment reduced, with tergum, pleurites and sternum fused, forming a closed ring surrounding the male genitalia (Newton 1998; Fresneda *et al*. 2011b).

Genus included in the subtribe Pholeuonina (V.B. Guéorguiev 1974a) or Pholeuina (Perreau 2000) with some morphological characteristics that approximate it to genera of the *Ceuthophyes* series, although it should be excluded from that subtribe as it presents two unique characters that do not exist in Leptodirina sensu novo, the first tarsomere of the mesotarsi dilated in males (also in Platycholeina) and a single apical seta at the apex of the aedeagus parameres, in addition to the hyaline spermatheca (also in Platycholeina) without differentiated lobes.

Distribution. Muscicolous species that has colonized the region of Dalmatia in Croatia and with a wide dispersion in Bosnia-Herzegovina (Jeannel 1908c, 1924a; Perreau 2000).

Species

Adelopsella bosnica (Reitter, 1885)
Adelopsella bosnica bosnica (Reitter, 1885)
Bathyscia (Bathyscia) bosnica Reitter, 1885a [1884]: 20.
Adelopsella bosnica (Reitter): Jeannel, 1908c: 183.
Leptodirus robicii Joseph, 1867: 170.
Adelopsella bosnica jezerensis Jeannel, 1911
Adelopsella bosnica jezerensis Jeannel, 1911a: 206.

Subtribe **Leptodirina** Lacordaire, 1854 [1849] *sensu novo*

Diagnosis. They present exactly the same characters that define Leptodirini with the exclusion of those that have the first dilated mesotarsomere (Platycholeina and Adelopsellina subtrib. nov.), are winged (Platycholeina) or only have a single seta at the apex of the parameres (Adelopsellina subtrib. nov.).

Discussion. It derives from the second most basal node of the Leptodirini clade and joins Adelopsellina subtrib. nov. (the sister subtribe) with a node that has a support, 92.6/98. Leptodirina sensu novo includes, in addition to the Leptodirina *sensu* V.B. Guéorguiev (1974a), to the remaining subtribes (*sensu* Perreau 2004): Leptodirina Lacordaire, 1854 [1849] = Bathysciae Horn, 1880 syn. nov., Pholeuones Reitter, 1886 syn. nov., Antroherpona Jeannel, 1910 syn. nov., Bathysciotina V.B. Guéorguiev, 1974 syn. nov. and Spelaeobatina V.B. Guéorguiev, 1974 syn. nov.

3.1 Clade ***Sophrochaeta***

This clade includes the Leptodirini inhabiting the Carpathian mountain range in the broad sense, i.e. the Carpathians (specifically southern Romania), its extension to the Black Sea, the Stara Planina (Balkan, Bulgaria), and its derivation to Bulgaria-Greece (Rhodopes-Pirin mountains range). Based on morphological and biogeographic criteria, the genera *Hexaurus* and *Netolitzkya* are included as a sister series of the clade *Sophrochaeta* group. Genera *Balcanobius*, *Beronia*, *Beroniella*, *Beskovia*, *Bulgariella*, *Genestiellina*, *Hanusia* and *Radevia* are also added, without specifying their position within the basal clade, grouped in series based on morphological similarities and biogeographic criteria. It was sugested that several species of *Bathyscia* and several species of *Albaniola*, two polyphyletic genera with representatives in the Rhodopes mountains, could also belong to this clade.

3.1.1 Series ***Sophrochaeta*** V.B. Guéorguiev, 1963 *sensu novo*

Diagnosis. Body shape mostly bathysciod, although it is pholeunoid in *Closania* and intermediate in *Tismanella*. Depigmented.

Head: Anophthalmous.

Antennae: Variables in length, without a defined club and always the first antennomere much shorter than the second one.

Elytra: With more or less well defined transverse striolae, only absent in *Closania*; parasutural stria absent.

Legs: Male protarsi pentameres more or less dilated, always narrower than the width of the apical part of the protibiae. Protibiae without comb on the external side. Meso- and metatibiae armed with long and robust spines on the outer margins.

Mesoventral keel: Variable in shape, but if present it is high and short.

Median lobe of aedeagus: Robust or very thin and long; without marked depression or dorsal pit.

Endophallus: Without basal armor or present in *Rhodopiola*, *Bureschiana* and *Maroniella*.

Parameres: Thin, shorter than the median lobe, without a defined club and in this are inserted three setae of similar length, and generally short.

Discussion. To the genera defined, on a molecular base, as belonging to the series of *Sophrochaeta* (Fig. 1I), must be added to certain genera from Romania (*Mehadiella*, *Cernella* stat. nov. and *Banatiola*), Bulgaria (*Bureschiana*) and Greece (*Maroniella* and *Bureschiana*) which most likely belong to the same series, but for which, in the absence of molecular data, we can only assume that they belong together on the base of morphological information.

About the real taxonomic rank to be assigned to the taxon *Cernella* stat. nov., hitherto considered a subgenus of *Sophrochaeta*, to which we will return later, here it is reclassified and is now considered a genus (see Discussion section of genus *Cernella* stat. nov.).

For the Greek genera was defined on a morphological basis by Giachino (1995) and confirmed as such by Giachino & B.V. Guéorguiev (2008) a phyletic lineage of *Atticiella*. Doubts remain about the validity of this lineage, especially regarding the genus *Atticiella*, on the basis of the original description by Coiffait (1955c), which was rather preliminary and incomplete.

The *Sophrochaeta* series is going to be divided into two groups:

– *Rhodopiola* group: with robust aedeagus and more or less complex armed endophallus (with «Y»-piece and a curved transverse phanera in the middle region of the sac) distributed to the south, Rhodopes mountain range (Bulgaria-Greece border): genera *Bureschiana*, *Maroniella* and *Rhodopiola*.

– *Sophrochaeta* group: with slender aedeagus and unarmed endophallus distributed throughout Oltenia in Southern Romania: genera *Banatiola*, *Closania*, *Mehadiella*, *Sophrochaeta* and *Tismanella*. Genus *Cernella* stat. nov. of this area, it has a robust aedeagus although the endophallus is practically unarmed: it is a membranous sac with a kind of diffuse apical reinforcement bands in the upper region. Due to the peculiarities of the aedeagus, it could be included in the *Sophrochaeta* group as well as in the *Rhodopiola* group. Due to its distribution coinciding with *Sophrochaeta*, it will be provisionally included in this group. Only molecular data can show its definitive position. Genus *Cernella* stat. nov. it is possible that is actually a derived form within the *Sophrochaeta* group or perhaps it could derive from an early cladogenesis: since the unarmed endophallus is considered a derived character and appears in different clades of Leptodirini independently, as seen in the phylogenetic tree (Fig. 2: Tree-1, Tree-2), therefore it would come to no surprise when at the base of the *Sophrochaeta* series there is a robust aedeagus present, inherited from a common ancestor also of the *Rhodopiola* group clade.

Given the geographic distance, it may be surprising that *Rhodopiola* (and consequently the other genera in its group) is part of the *Sophrochaeta* clade, but support is 100/100 in both Tree-1 and Tree-2 (Fig. 2). If the case is studied, there is an apparent gap between the Rhodopes mountains and the Southern Carpathians which indeed may not be real. In Stara Planina in Bulgaria (a territory located between the southern Carpathians and the Rhodopes mountains) there are Leptodirini of which some, have an unarmed endophallus like the elements found in the *Sophrochaeta* group: *Hexaurus* and *Netolitzkya*, a group which appears morphologically related to *Sophrochaeta*. The other Leptodirini of Stara Planina, with armed endophallus, seem morphologically related to the clade of the *Rhodopiola* group: genera *Beronia*, *Beroniella Beskovia*, *Bulgariella*, *Radevia*, *Balcanobius* or *Genestiellina*. The hypothesis that the space between the *Sophrochaeta* group (southern Romania) and *Rhodopiola* (Greek-Bulgarian border) is occupied by related taxa that link both distribution areas is biogeographically coherent. The Carpathians begin in Slovakia-Poland and form an inverted «S» that extends without interruption to the Black Sea across Bulgaria. When it crosses Bulgaria it is called Stara Planina but it is the same mountain range. All of these animals are found on the Carpathian-Balkan, and Rhodopes mountains are a branch of the massif to the south. Thus, at Stara Planina, an intermediate place belonging to the massif, the two groups of the *Sophrochaeta* series overlap.

There is still not enough data, but it is already clear that the biogeographic issue in Greece *sensu lato* is very interesting. The Carpathian-Balkan-Rhodopes fauna is distributed through the eastern offshots and the Dinarides including the fauna (*Leptodirus-Anthroherpon* clade) that is distributed through its western offshots, both overlapping with elements of a third southern parts belonging to the Anatolian distribution part (genus *Karadeniziella*) which includes, at least, one Bulgarian genus from the Rhodopes massif (genus *Gueorguievella*). This means that the confirmation of the species of *Henrotiella eubeensis* belongs to the *Pholeuonopsis* group of the *Anthroherpon* series by molecular data the area of overlap with the *Sophrochaeta* clade reaches the eastern borders of Greece.

With the current molecular data (Fig. 1I), we have information on only four genera—*Sophrochaeta*, *Tismanella*, *Closania* and *Rhodopiola*—that belong to the *Sophrochaeta* clade and are linked, as shown by support values of 100/100; in turn this clade is related

to the unnamed sister clade from Euboea Island (Greece) with a support 89.1/36 in Tree-1 and 83.1/90 in Tree-2 (Fig. 2). These two clades are the most basal of the Leptodirina sensu novo.

Groups key

1. Endophallus (Figs 36.15–36.17) armed with «Y»-piece and a curved transverse phanera in the middle region.....*Rhodopiola* group
- Unarmed endophallus (Figs 42.6, 42.8–42.11) that may have diffuse reinforcement bands in the apical region (Fig. 42.7) .....*Sophrochaeta* group

3.1.1.1 ***Rhodopiola*** group

Bathysciod appearance, with pronotum sides rounded in the basal area. Antennae short or very short, not reaching the middle of the elytra; antennomere 8 transverse or slightly longer than wide; robust aedeagus and armed endophallus.

Distributed at the Rhodopes and Pirin massifs, on both sides of the Greek-Bulgarian border.

Key to Genera

1. Antennae with the 8th antennomere being as long as or slightly longer than wide and the 9th–10th somewhat longer than wide. Mesoventral keel with slightly widened ventral margin (Fig. 36.6) .....*Rhodopiola*
- Antennae with the antennomeres 8 to10 markedly transverse. Mesoventral keel with very broadened ventral edge, mainly in the posterior region (Figs 36.4, 36.5).....2

2. Mesoventral keel with ventral margin sub-rectilinear, more or less widened, flat and without sulcus. Median lobe of aedeagus, in dorsal view (Fig. 36.15), broadened and stout apex, from slightly sub-triangular to sub-truncated, or slightly concave. Endophallus (Fig. 36.15) with «Y»-piece, with sinuous and variously dilated dorsal branches, in addition to a very long and very sharp flagellum; median area with one or two pairs of rods and very fine and small spines... .....*Bureschiana*
- Mesoventral keel with ventral margin rectilinear, widened and depressed, provided with a superficial furrow posteriorly open. Median lobe of aedeagus, in dorsal view (Fig. 36.16), rounded and provided with a narrow, sharp and salient apical blade. Endophallus (Fig. 36.16) with «Y»-piece and a complex structure formed by three lateral branches for each side and by a dorsal, semicircular and advanced, sclerotized band; median area occupied by a complex and slightly sclerotized «H»-shaped structure.....*Maroniella*

Genus ***Bureschiana*** V.B. Guéorguiev, 1963
Bureschiana V.B. Guéorguiev, 1963: 391.

Type species. *Bureschiana drenskii* V.B. Guéorguiev, 1963 by original designation (habitus in Fig. 36.1).

Diagnosis. Small size, 1.4–2.0 mm; body shape bathyscioid (Fig. 36.1), convex and wide. Brownish colour. Pubescence very short, fine and procumbent.

Head: Retractile, with complete occipital carina.

Antennae: Short, just reaching the base of the pronotum, with the tips of the club dilated and flattened; first antennomere shorter or longer than the second one and shorter than the 11th; the 8th, 9th and 10th antennomeres transverse.

Pronotum: Very transverse, at least twice as wide as long, with regularly arcuated sides, and maximum width at the basal fourth, before the base. Larger than the elytral base; punctation very fine so that the integuments are granulated; posterior vertex not sharp, more or less rounded, with the angles about right.

Elytra: Short, very ovoidal and very convex, almost as wide as long, largely rounded at apex, with maximum width at the anterior fifth; punctation very diffuse, with very thin transverse striolae than are more visible in the basal area. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres, slightly dilated and narrower than the apex of the protibia. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae without apical basket, with long and robust spines on the outer margins; metatibiae not sinuated but compressed, flattened.

Mesoventral keel (Fig. 36.4): High, with an evident tooth. Anterior edge curved, ventral margin sub-rectilinear, more or less widened, flat and without sulcus. Not prolonged on the metaventrite.

Metaventrite: Without keel, with intercoxal apophysis very wide and projected backward by a couple of spines, separated by a deep groove.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Small and short, stout. In lateral view (Fig. 36.12) slightly arched and preapically slightly sinuous, or not, dorsally. In dorsal view (Fig. 36.15), broadened and stout apex, from slightly sub-triangular to sub-truncated, or slightly concave. Basal blade very developed, more than 1/3 of the median lobe long.

Endophallus (Fig. 36.15): Characterised by three well-differentiated areas. Basal region with a not very developed «Y»-piece with sinuous and variously dilated dorsal branches, in addition to a very long and very sharp flagellum. Median area with one or two pairs of rods, sometimes hooked in lateral view and very fine and small thorns. Distal area equipped with a pair of narrow and long rods, sometimes hooked in lateral view, sometimes absent, and a pair of reinforcing bands facing inward.

Parameres (Fig. 37.1): Thin, shorter than the median lobe, carrying three apical setae of similar length.

Spermathecal complex: Spermatheca (Fig. 37.4) well sclerotized, of elongated ovoid shape, narrowed in central part, with proximal lobe more developed than distal one. Ductus briefly enlarged and strongly sclerotized at the point of insertion into the spermatheca; small and hyaline spermathecal gland.

Female uroventrite VIII (Fig. 37.8): Spiculum short, subrectangular and truncated; anterior edges subrectilinear and sightly converging. Apical part showing a slightly, not regularly, concave lateral margins; base of this part without macula.

Discussion. The section above on the *Atticiella* genus the possibility not to fromalise the inclusion of *Bureschiana* into an «*Atticiella* group» on gorunds ofmorphological data only.. On a purely morphological basis, the phyletic lineage of *Atticiella*, as pointed out by V.B. Guéorguiev (1963), and confirmed by Giachino & B.V. Guéorguiev (2008), appears sustainable and based on characters such as the general shape of body, characterised by a peculiar widening of the pronotum, the shape of the mesoventral keel and the intercoxal apophysis of the metaventrite, the poorly dilated male protarsi, as well as the morphology of median lobe of aedeagus and endophallus. However, the clear gap in the distribution areas of the genera belonging to this non-formalised group is interesting: with three genera (*Rhodopiola*, *Bureschiana* and *Maroniella*) to the North (in the Rhodopes mountains in the broad sense) and a genus, *Atticiella*, to the South of Greece, on Attica.

Distribution. NE-Greece and S-Bulgaria. Rhodopes mountains.

Species

Bureschiana drenskii V.B. Guéorguiev, 1963
Bureschiana drenskii V.B. Guéorguiev, 1963: 393.

Bureschiana raitchevi Giachino, 1995
Bureschiana raitchevi Giachino, 1995: 305.

Bureschiana thracica Giachino, 1989
Bureschiana thracica Giachino, 1989: 43.

Genus ***Maroniella*** Casale & Giachino, 1985
Maroniella Casale & Giachino, 1985: 226.

Type species. *Maroniella beroni* Casale & Giachino, 1985 by original designation (habitus in Fig. 36.2).

Diagnosis. Small size, 1.7–2.1 mm; body shape bathyscioid (Fig. 36.2), convex and wide, with pronotum larger than the elytral base. Brown-reddish colour. Pubescence very short, dense and procumbent.

Head: Retractile, with complete occipital carina.

Antennae: Short, not reaching the base of the pronotum, with the tips of the club dilated and flattened; first antennomere just shorter than the second one and shorter than the 11th; 8th, 9th and 10th antennomeres transverse.

Pronotum: Very transverse, at least twice as wide as long, with regularly arcuated sides and maximum width at the basal fourth, before the base. Larger than the elytral base. Posterior vertex moderately sharp, more or less rounded, with the angles less of 90º. Punctation very fine so that the integuments are shiny.

Elytra: Short and very ovoidal, almost as wide as long, largely rounded at apex, with maximum width at the anterior fifth; punctation very diffuse, with very thin transverse striolae,hardly visible and restricted tothe basal area. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres, slightly dilated and narrower than the apex of the protibia. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae without apical basket, with long and robust spines on the outer margins; metatibiae not sinuated but compressed, flattened.

Mesoventral keel (Fig. 36.5): High, angular and toothed. Ventral margin rectilinear, widened and depressed, provided with a superficial furrow posteriorly open. Not prolonged on the metaventrite.

Metaventrite: Without keel with intercoxal apophysis very wide and projected backward by a couple of spines, separated by a deep groove.

Suture of the metaventrite (Fig. 36.6): Delimits a well-developed arcuate area, narrowing towards the basal one quarter.

Metatergal apparatus (Fig. 36.8): Wings of metascutum elongate, rather broad and arched; apophysis of alacrista null.

Metendosternite (Fig. 36.10): «V»-shaped; furcal arms long more than twice the length of the trunk, with the posterior plate very narrow in the apical part, then progressively widening until it ends in an apophysis (deformed in one of the arms in Fig. 36.10); furcal trunk short, as long as wide in the widest area; with anterior furcal plate.

Median lobe of aedeagus: Large, longly and regularly arched. Apex, in lateral view (Fig. 36.13), progressively attenuated and sharpened. In dorsal view (Fig. 36.16), is rounded and provided with a narrow, sharp and salient apical blade. Basal blade large and well chitinised.

Endophallus (Fig. 36.16): Clearly distinct in three areas. Basal part with a «Y»-piece, complex and formed by three lateral branches for each side and by a dorsal, semicircular and advanced, sclerotized band. Median area occupied by a complex, slightly sclerotized «H»-shaped structure. Distal area equipped with an omega-shaped structure with thin and sclerotized reinforcing bands.

Parameres (Fig. 37.2): Thin, shorter than the median lobe of aedeagus. Apex slightly dilated, carrying three sub-equal setae, one apical and two subapical internal. Basal blade of the tegmen, hyaline, slightly sclerotized and hardly visible.

Spermathecal complex: Spermatheca (Fig. 37.5) well sclerotized, kidney-shaped, elongated and narrowed in center. Ductus briefly enlarged and sclerotized at the point of insertion into the spermatheca, differentiating a small nodule.

Female uroventrite VIII (Fig. 37.9): Apical area narrowed, with arcuate anterior edges and spiculum of regular length, triangular shape and tapering apex.

Discussion. The discussion on the *Atticiella* and *Bureschiana* genera is contributing to the considerations on fomalisation of the inclusion of *Maroniella* into the «*Atticiella* group» on the morphological basis only. Geographical position of *Maroniella*, known from the Greek Rhodopes, is congruent with the morphological affinities shown towards the genera *Rhodopiola* and *Bureschiana*.

Distribution. NE-Greece. Rhodopes mountains, Maronia Cave.

Species

Maroniella beroni Casale & Giachino, 1985
Maroniella beroni Casale & Giachino, 1985: 228.

Genus ***Rhodopiola*** V.B. Guéorguiev, 1960
Rhodopiola V.B. Guéorguiev, 1960b: 721.

Type species. *Rhodopiola cavicola* V.B. Guéorguiev, 1960 by original designation (habitus in Fig. 36.3).
Diagnosis. Small size, 1.7–2.1 mm, body shape bathyscioid, hemispherical, convex and very wide (Fig. 36.3). Brownish colour. Pubescence very short and procumbent.

Head: Retractile, with complete occipital carina; punctation very fine and very spaced.

Antennae: Short, although clearly exceeding the length of the pronotum, with the tips of the club somewhat dilated; first antennomere strongly shorter than the second one and as long as the 11th; 8th, 9th and 10th antennomeres being longer than wide.

Pronotum: Very transverse, at least twice as wide as long, with regularly arcuated sides, and maximum width at the base than is equal to that of the base of elytra; posterior vertex not sharp and the angles about right; punctation very fine and scattered so that the integuments are shiny.

Elytra: Short and very ovoidal, altogether wider than long, largely rounded at apex, with maximum width at the middle; punctation forms very diffuse transverse striolae only visible in the shoulder area, in the rest of the elytra the points are very fine and scattered, the surface being shiny. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres, slightly dilated. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae without apical basket, with long and robust spines on the outer margins; mesotibia being slightly arched.

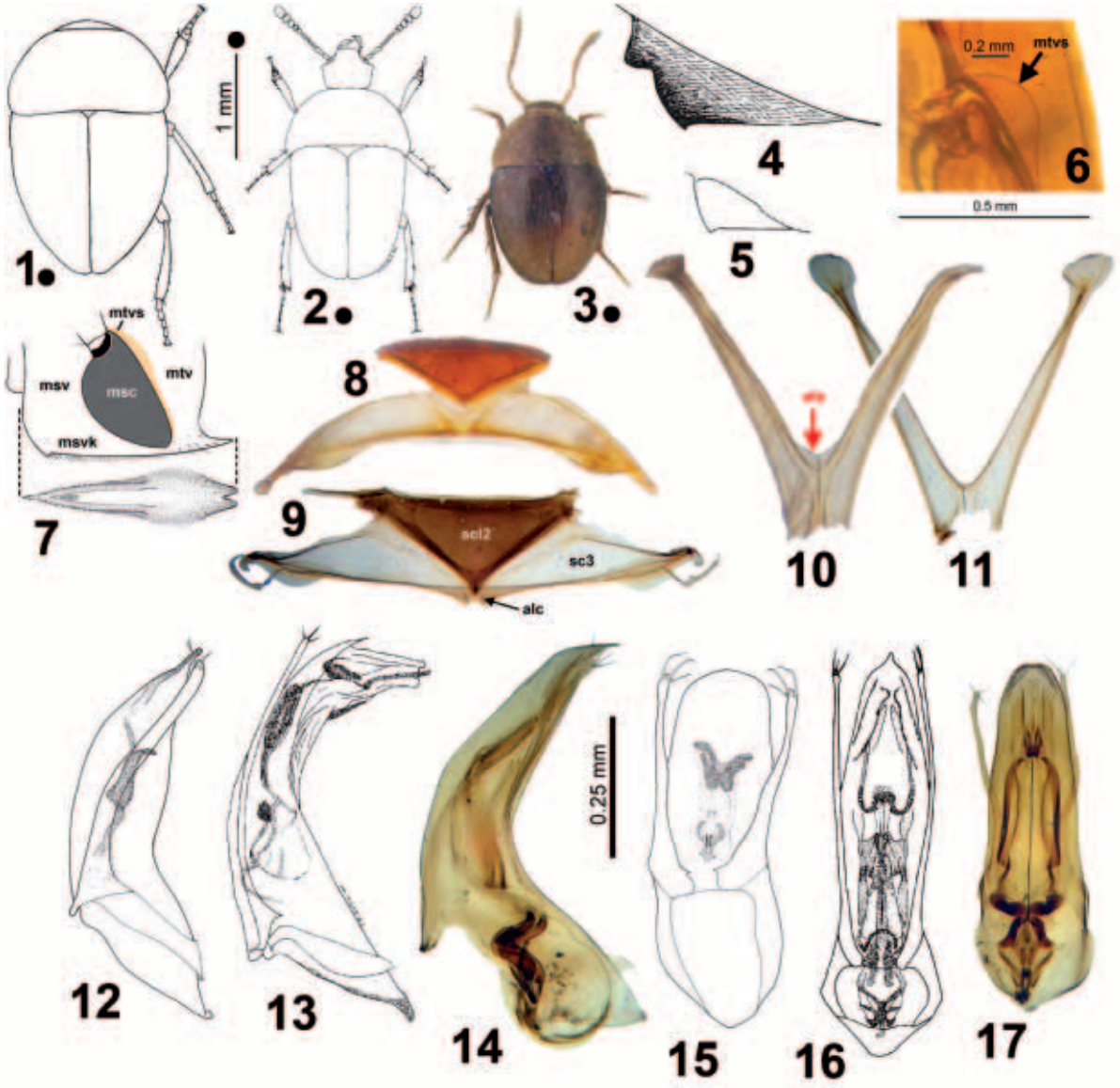
Mesoventral keel (Fig. 36.7): High, with rounded front edge, and toothed vertex. Ventral edge widens towards the posterior area and shows an elongated groove. Keel fused to the metaventrite.

Suture of the metaventrite (Fig. 36.7): Proximal to the coxal cavity and delimits a reduced arched area in the apical half.

Metatergal apparatus (Fig. 36.9): Wings of the metascutum short and broad define a triangular structure; apophyses of the alacrista very reduced, forming two small sharp lobes.

Metendosternite (Fig. 36.11): «V»-shaped, with furcal arms long, about two and a half times longer than the trunk, and very narrowed in the apical part where a globose apophysis is found; posterior lamina progressively narrowing to the apical part. Furcal trunk short as wide as long.

Median lobe of aedeagus: Not very long and clearly robust. In lateral view (Fig. 36.14), stout in the



FIGURES 36.1–36.17: *Sophrochaeta* series, *Rhodopiola* group. Habitus of: (**1**) *Bureschiana drenskii,* (**2**) *Maroniella beroni,* (**3**) *Rhodopiola cavicola*. Pterothorax in lateral view of: (**4**) *B. drenskii*, (**5**) *M. beroni* with (**6**) metaventral suture, (**7**) *R. cavicola,* (lateral and ventral views). Metatergal apparatus, ventral view of the metanotum and axillaria of: (**8**) *M. beroni*, (**9**) *R. cavicola*. Metendosternite of: (**10**) *M. beroni*, (**11**) *R. cavicola*. Aedeagus in lateral view of: (**12**) *B. drenskii*, (**13**) *M. beroni*, (**14**) *R. cavicola.* Aedeagus in dorsal view of: (**15**) *B. drenskii*, (**16**) *M. beroni*, (**17**) *R. cavicola*. Figs **1**, **4** modified from V.B. Guéorguiev 1963; Figs **2**, **5**, **13**, **16** from Casale & Giachino 1985; Figs **12**, **15** from Giachino 1995. Abbreviations: **afp**, anterior furcal plate; **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral sutures.

basal part; it forms a regular obtuse angle; dorsal edge in a wide arc with a slight depression in the apical third; apical area being flattened and which extends into a slender, pointed, straight or slightly oriented towards the ventral apex. In dorsal view (Fig. 36.17), lateral margins slightly sinuous, with the greatest width at the base and apex slightly narrowed and arcuated.

Endophallus (Fig. (Fig. 36.17): Complex, with three regions well differentiated. Basal region shows,

at the bottom, a sclerotized structure similar to an «Y»-piece that is surrounded by two pairs of arcuated phanerae to these are fixed two robust apical phanerae in a very open «U». The middle region has two pairs of phanerae, thin internal ones and other robust and long external ones that curve inwards in the apical part and join a sclerotized structure in the shape of an inverted saddle; also a long flagellum with a bifid base runs along the axis of symmetry from the basal region to the distal end of the middle part. In the apical region, on both sides, are the reinforcing bands that are short.

Parameres (Fig. 37.3): Thin, wavy and shorter than the median lobe; apical part does not form a distinct club carrying three setae of similar length.

Spermathecal complex: The spermatheca (Figs 37.6, 37.7), in the two microscopic preparations that we have been able to observe (Giachino & B.V.Guéorguiev 2008) seems morphogically variable. In reality, the appearance of the spermatheca could simply be an artifact due to a different angle of observation, combined with a spermatheca folded on itself at the level of the central area, not very sclerotized. We therefore prefer to provide both figures, but we proceed to the description on the basis of the figure provided by Giachino & B.V. Guéorguiev (2008). Spermatheca very elongated, with proximal and distal parts sclerotized, with the proximal lobe slightly wider than the distal lobe, which is more elongated; hyaline junction duct as wide as the distal lobe and somewhat longer. Ductus long, conspicuously sclerotized, enlarged, and «U»-bent before insertion into the spermatheca.

Female uroventrite VIII (Fig. 37.10): Spiculum short, narrow and sharp; apical part showing a slightly concave lateral margin and at the base of this part, an elongated and transverse macula.

Discussion. While the Leptodirini of Bulgaria, for which we were able to generate molecular data only from *Rhodopiola cavicola* and *Gueorguievella petrovi*, have been fairly recently revised (Giachino & B.V. Guéorguiev 2008), and on this basis we will treat them in the present paper, the same thing cannot be said for those of Greece and Turkey. Furthermore, in all molecular analysis, the genus *Rhodopiola* is related to the *Sophrochaeta* series. In the phylogenetic tree (Fig. 1I) *Rhodopiola* appears at the base of the *Sophrochaeta* series and joins in the clade with the highest possible support (100/100) defining the *Sophrochaeta* + *Tismanella* + *Closania* clade. There is some morphological evidence that separate *Rhodopiola* from the other genera, such as the body shape or the arrangement and development of the transverse striolae, although the most relevant diacritic characters of separation is observed in the complexity of the sclerotized structures of the endophallus, especially the presence of basal sclerotized structure.

Distribution. Bulgaria. Western Rhodopes, Plovdiv district, «Sipeja» cave, and Lâki district «Sepran dupka» cave.

Species

Rhodopiola cavicola V.B. Guéorguiev, 1960
Rhodopiola cavicola V.B. Guéorguiev, 1960b: 721.

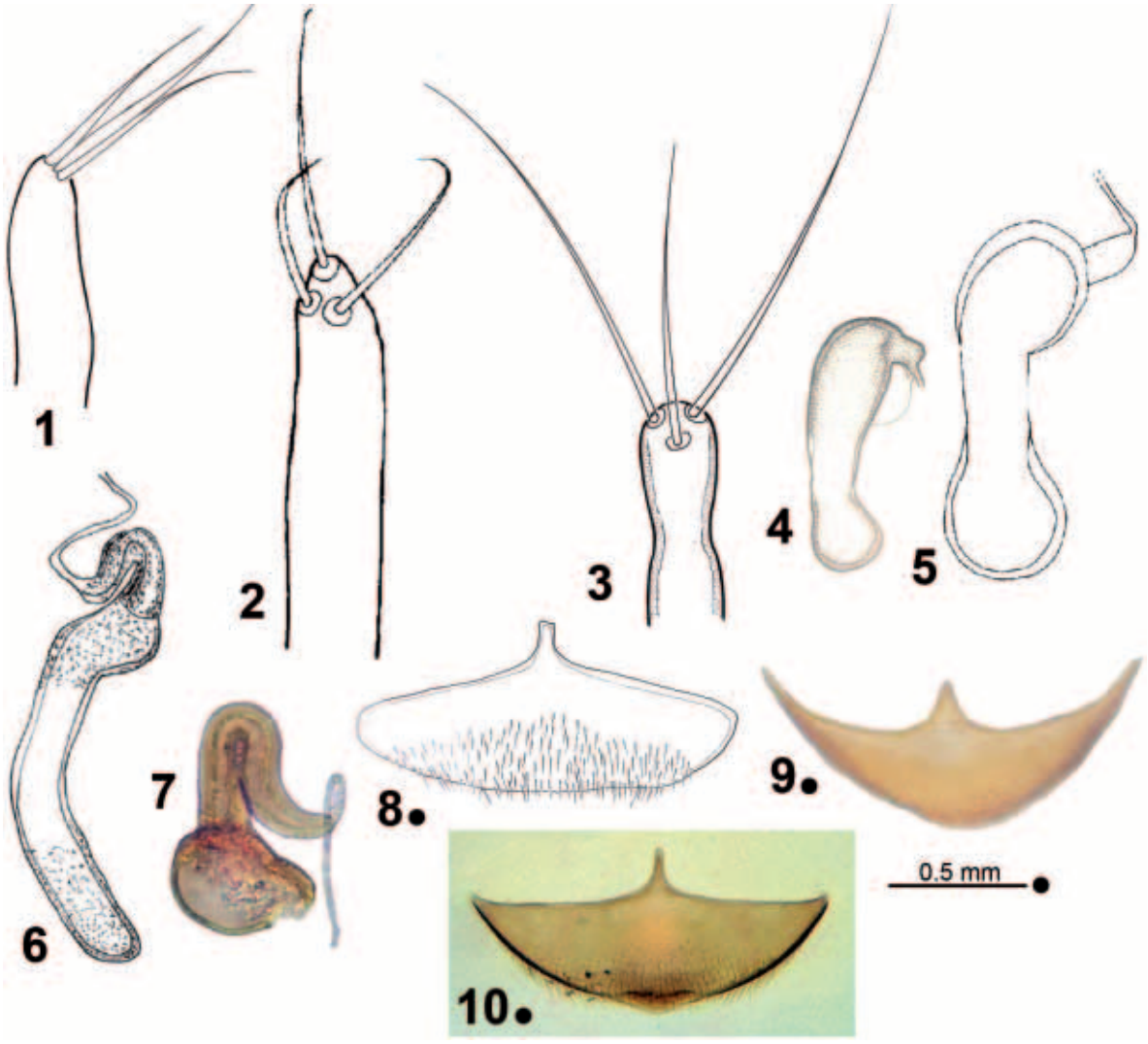
3.1.1.2 ***Sophrochaeta*** group

Group characterised by slender aedeagus with unarmed endophallus. In general, the apical lobe of the spermatheca is not sclerotized or is very poorly differentiated. Genus *Cernella* stat. nov. presents «intermediate» characters between the *Sophrochaeta* and *Rhodopiola* groups: a robust median lobe of aedeagus and an endophallus with poorly defined apical reinforcement bands in its apical region. Its distribution coincident with genus *Sophrochaeta* justifies its provisional inclusion in this group.
Group of genera distributed by Oltenia, Carpathians mountains range, in southern Romania.

Key to genera

1. Sub-pholeuonoid or pholeuonoid appearance, with pronotum sides more or less concave in the basal third. Antennae very long, almost as long or as long as the body length; antennomere 8th at least five times longer than wide 2
- Bathysciod facies, with pronotum sides rounded in the basal area. Antennae short or very short, not reaching the middle of the elytra; antennomere 8 transverse or slightly longer than wide 3

2. Pholeuonoid appearance. Elytra without transverse striolae. Mesoventral keel high, slightly prolonged on the metaventrite (Fig. 40.3). Metendosternite almost «Y»-shaped, with furcal trunk longer than wide (Fig. 41.5) .....*Closania*
- Sub-pholeuonoid facies. Elytra with transverse striolae poorly marked in the basal half. Mesoventral keel reduced to a small membranous prominence with setae in the posterior area of the mesoventrite (Fig. 40.6). Metendosternite in «V», with furcal trunk short, as long as wide (Fig. 41.6) .....*Tismanella*



FIGURES 37.1–37.10: *Sophrochaeta* series, *Rhodopiola* group. Apex of the paramere of: (**1**) *Bureschiana drenskii* (redrawn from V.B. Guéorguiev 1963), (**2**) *Maroniella beroni*, (**3**) *Rhodopiola cavicola.* Spermatheca of: (**4**) *B. thracica* (modified from Giachino 1989), (**5**) *M. beroni*, (**6**) *R. cavicola* (modified from Giachino & B.V. Guéorguiev 2008), (**7**) *R. cavicola*. Female uroventrite VIII of: (**8**) *B. raitchevi* (modified from Giachino 1995), (**9**) *M. beroni,* (**10**) *R. cavicola.* Figs **2**, **5** modified from Casale & Giachino 1985.

3. Body oval, moderately elongated, with elytra clearly longer than wide. Antennae with the 8th antennomere slightly longer than wide and 9th–10th at least twice as long as wide and not flattened. Mesoventral keel high, not thick and ventral edge narrow (Figs 40.5, 40.6) 4
- Body hemispherical, with elytra as long as or slightly longer than wide. Antennae with antennomeres 7th to 11th flattened and from 8th to 10th more transverse. Mesoventral keel high and very thick, ventral edge wide and flattened in a sort of triangular ventral facet (Fig. 40.1, 40.4) 5

4. Smaller size, 1.6–3.8 mm. Base of the pronotum wider than the elytra. Elytra with oblique transverse striolae towards the middle and in the apical area. Endophallus without sclerotized structures (Fig. 42.10). Parameres without membranous prolongation in the

apical part (Fig. 43.5) .....*Sophrochaeta*
- Larger size, 4.2–4.8 mm. Base of the pronotum narrower than the elytra. Elytra without defined transverse striolae. Endophallus unarmed, except two apical reinforcing bands of filamentous appearance (Fig. 42.7). Parameres with a short membranous prolongation in the apical part (Fig. 43.2) .....*Cernella* stat. nov.

5. Very small size, 1.6–1.8 mm. Intercoxal process of the metaventrite very wide. Male protarsi slightly dilated. Basal blade of the median lobe triangular (Fig. 42.9). Parameres with three very short apical setae (Fig. 43.4).....*Mehadiella*
- Large size, 2.5 mm. Intercoxal process of the metaventrite narrow. Male protarsi very dilated. Basal blade of the median lobe strongly narrowed in the median part (Fig. 42.6). Parameres with two rather long apical setae (Fig. 43.1).....*Banatiola*

Genus ***Banatiola*** Decu, 1967
Banatiola Decu, 1967: 434.

Type species. *Banatiola vandeli* Decu, 1967 by original designation (habitus in Fig. 38.1).

Diagnosis. Small size, 2.5 mm, with short, very convex and hemispheric body; bathysciod appearance (Fig. 38.1). Brown-reddish colour.

Head: Retractile, with complete occipital carina.

Antennae: Thin, relatively short, not reaching the middle of the body, with the first antennomere strongly shorter than the second one; the 3rd shorter than the 2nd one, the 8th subsquared; antennomeres 7 to 11 flattened.

Pronotum: Very convex, transverse, with maximum width in the base, as wide as the elytra, with sides regularly, but slightly, arched and not sinuated in front of the base. Posterior vertices blunt and slightly protruding backwards. Disc very convex and punctation of small size. Pubescence short and procumbent.

Elytra: Very short, slightly longer than wide, and very convex, largely rounded at apex, with maximum width in the anterior third; pubescence short and procumbentprocumbent; punctation slightly aligned in transversal striolae, hardly visible only in the basal part along the elytral suture. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres and very dilated. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae straight, without apical basket, with long and robust spines on the outer margins.

Mesoventral keel (Fig. 40.1): High, with slightly curved, non-pubescent, front edge and slightly toothed angle. Ventral edge pubescent, wide and flattened, in a sort of triangular ventral facet, which gradually widens from the edge of the keel to the posterior edge of the mesoventrite. Not prolonged on the metaventrite.

Metaventrite: Intercoxal apophysis bifid, as wide as the metaventrite along its midline.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Thin and very elongated, long almost half of the body. In lateral view (Fig. 42.1), slightly and regularly arched, thinned in a long hook apically. Sides, in dorsal view (Fig. 42.6), subparallel with rounded apex. Basal blade strongly narrowed in the median part.

Endophallus: Completely devoid of chitinised structures.

Parameres (Fig. 43.1): Thin and shorter than the median lobe; carrying two short and robust apical setae. Basal blade of the tegmen with dorsal piece chitinised.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Genus of which we do not have molecular data, attributed by Decu (1967) to the phyletic series of *Sophrochaeta*. Is maintained by us in this position on the basis of the shape of the aedeagus and numerous external characters: shape of antennae and mesoventral keel, absence of parasutural stria and structure of legs.

Distribution. Romania. Western Carpathians, Banat Mountains, Gaura Porcariului cave in Nera Gorge.

Species

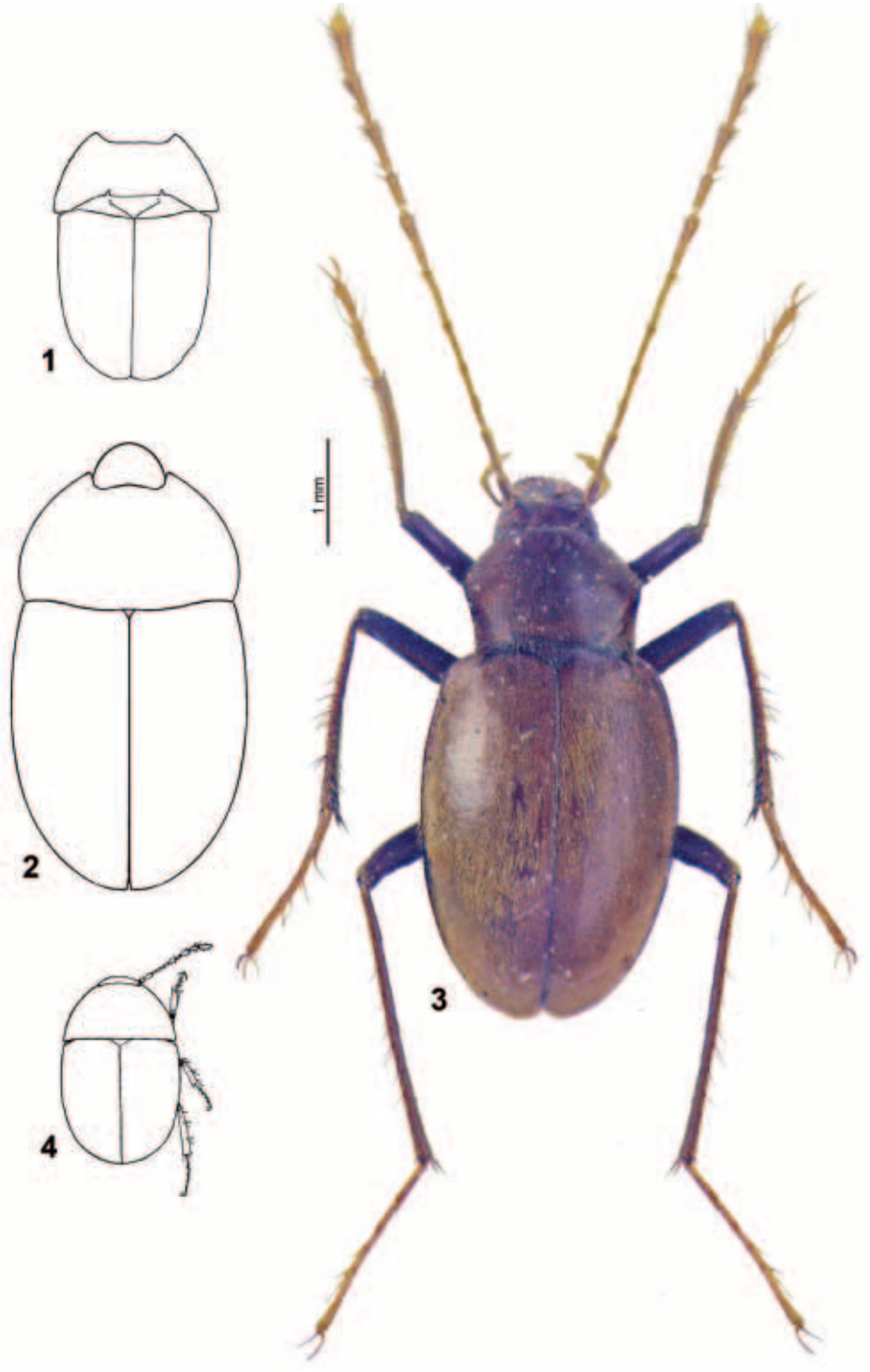
Banatiola vandeli Decu, 1967
Banatiola vandeli Decu, 1967: 436.

Genus ***Cernella*** Jeannel, 1930 stat. nov.
Sophrochaeta (*Cernella*) Jeannel, 1930d: 28.

Type species. *Bathyscia reitteri* J. Frivaldszky, 1884 by monotypy (for the habitus see that of the similar subspecies *Cernella reitteri mallaszi* comb. nov. in Fig. 38.2).

Diagnosis. Medium-large size, 4.2–4.8 mm, with bathyscioid, but elongated, body (Fig. 38.2).

Pronotum: The base is narrower than the elytra.



FIGURES 38.1–38.4: *Sophrochaeta* series, *Sophrochaeta* group. Habitus of: (**1**) *Banatiola vandeli* (modified from Decu 1967), (**2**) *Cernella reitteri mallaszi* **comb. nov.**, (**3**) *Closania winkleri winkleri,* (**4**) *Mehadiella paveli* (modified from Jeannel 1924a).

Elytra: Elongated and little convex, with the maximum width towards the middle; the punctation is dense and confused, without defined transverse striolae.

Legs: Males pentamerous and females tetramerous. Females have a long hair coat on the protarsomeres.

Mesoventral keel (Fig. 40.2): With almost straight anterior and posterior edges, vertex always strongly toothed, with a sharp and forward protruding like a ship spur. Not prolonged on the metaventrite.

Suture of the metaventrite (Fig. 40.2): Very close throughout its entire length to the coxal cavity, no area is observed between the cavity and the suture.

Metatergal apparatus (Fig. 41.1): With narrow and elongated wings of the metascutum; apophysis of the alacrista almost null, reduced to a stump.

Metendosternite (Fig. 41.5): «V»-shaped, with furcal arms long, twice as long as the furcal trunk; posterior lamina narrows towards the apical area of the arm and wider in the short area of the trunk, with a straight edge; apophysis well-developed, subtriangular. Furcal trunk short, somewhat longer than wide, median keel with a well marked posterior divergence.

Median lobe of aedeagus: Shorter and sturdy. The apex, in lateral view (Fig. 42.2), in the shape of a hook. In dorsal vision (Fig. 42.7) ogivete and subtruncate; also the apical part bears only two bands of thorny scales.

Endophallus (Fig. 42.7): Unarmed, except for two apical reinforcing bands (bra) of filamentous appearance and sinuous.

Parameres (Fig. 43.2): Very thin, shorter than the median lobe without apical club. There is a membranous prolongation at the apex and three equal and contiguous curved setae.

Spermathecal complex: The spermatheca is «C»-shaped; the one in the picture (Fig. 43.7) has been deformed during the drying process of the inclusion medium. Proximal lobe well sclerotized and rough in appearance; apical lobe rounded and sclerotized on the outer surface, between the two lobes a long hyaline part. The spermatic duct, without nodule, and the spermathecal gland flow together into the proximal lobe.

Female uroventrite VIII (Fig. 43.11): Middle area of the slightly concave posterior margin with an elongated, darkened notch; anterior margin with straight sides and short, broad spiculum with rounded apex.

Discussion. No molecular data are available on *Cernella* stat. nov., so its systematic position is based only on the morphological and biogeographical data. As already mentioned in the Discussion section concerning the genus *Sophrochaeta*, the real taxonomic rank of *Cernella* stat. nov., considered a simple subgenus of *Sophrochaeta*, seems somewhat underestimated. Numerous important morphological characters, highlighted in the descriptive part, seem to suggest a generic rank for this taxon.

Comparative examination *Cernella*-*Sophrochaeta*: In *Cernella* the elytra are more elongate and less convex than *Sophrochaeta*; base of the pronotum narrower than the elytra of *Sophrochaeta*; the median lobe of aedeagus is shorter and sturdy, it is more elongate and gracile in *Sophrochaeta*; the endophallus has apical reinforcement bands, not in *Sophrochaeta*; parameres with a small apical membranous lobe, not in *Sophrochaeta*.

Distribution. Romania. Southern Carpathians. The four subspecies colonize a wide area on the Oltenian slope of the Southern Carpathians.

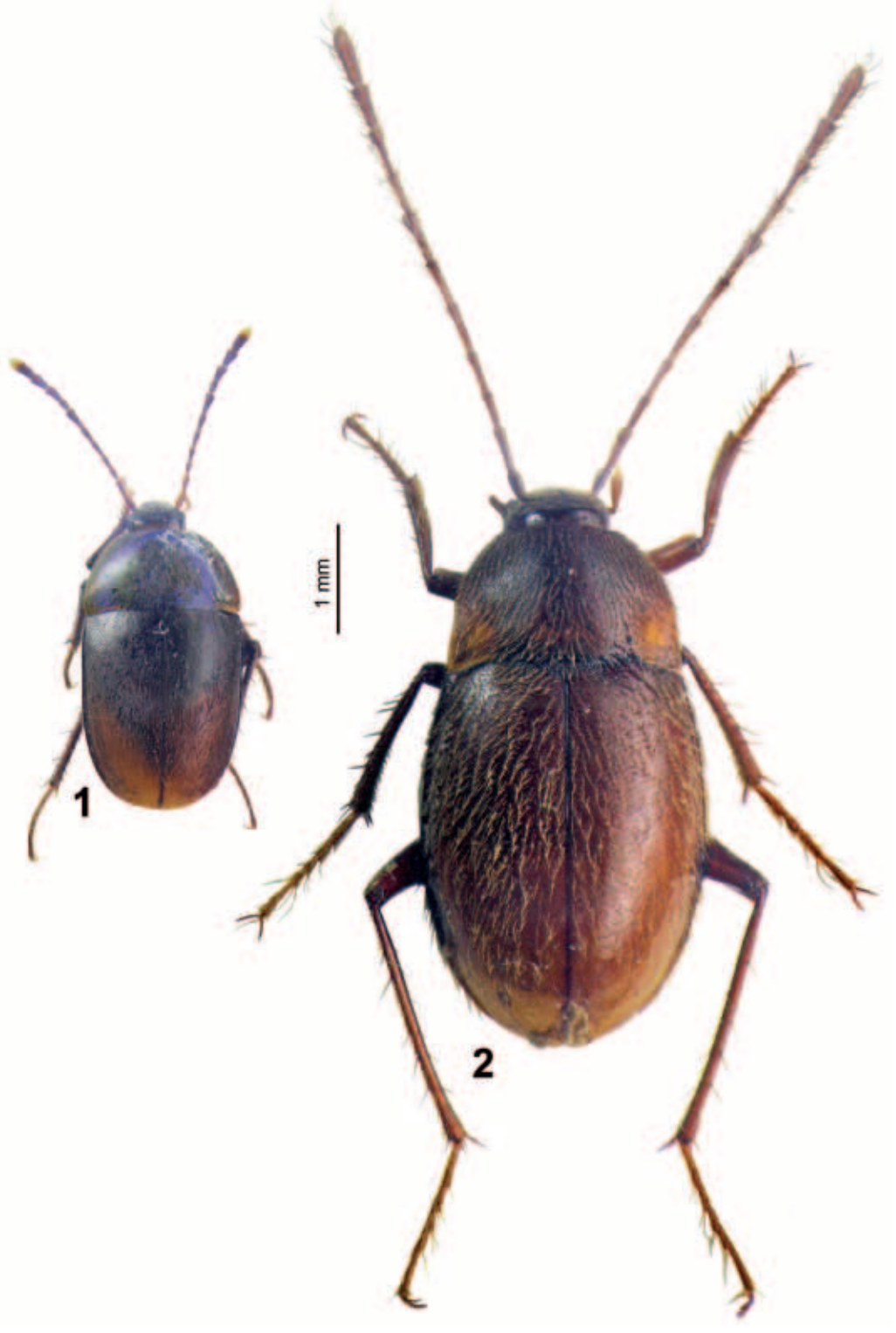
Species

Cernella reitteri (J. Frivaldszky, 1884) comb. nov.
Cernella reitteri mallaszi (Bokor, 1928) comb. nov.
Sophrochaeta Mallászi Bokor, 1928: 118.
Sophrochaeta (*Cernella*) *Reitteri* subsp. *Mallászi* Bok.: Jeannel, 1930d: 40.
Sophrochaeta (*Cernella*) *reitteri mallaszi* Bokor: Perreau, 2000: 295.

Cernella reitteri parallela (Jeannel, 1928) comb. nov.
Sophrochaeta Reitteri parallela Jeannel, 1928: 270.
Sophrochaeta (*Cernella*) *Reitteri* subsp. *parallela* Jeann.: Jeannel, 1930d: 40.
Sophrochaeta (*Cernella*) *reitteri parallela* Jeannel: Perreau, 2000: 295.

Cernella reitteri reitteri (J. Frivaldszky, 1884) comb. nov.
Bathyscia (*Sophrochaeta*) *Reitteri* J. Frivaldszky, 1884: 280.
Sophrochaeta Reitteri J. Frivaldszky: Jeannel, 1910a: 41.
Sophrochaeta (*Cernella*) *reitteri reitteri* (J. Frivaldszky, 1884): Perreau, 2000: 295.

Cernella reitteri retezati (Mallász, 1928) comb. nov.
Sophrochaeta Mallászi Retezati Mallász, 1928: 135.
Sophrochaeta (*Cernella*) *Reitteri* subsp. *Retezati* Mall.: Jeannel, 1930d: 40.
Sophrochaeta (*Cernella*) *reitteri retezati* Mallász: Perreau, 2000: 295.



FIGURES 39.1–39.2: *Sophrochaeta* series, *Sophrochaeta* group. Habitus of: (**1**) *Sophrochaeta oltenica oltenica,* (**2**) *Tismanella chappuisi chappuisi*.

Genus ***Closania*** Jeannel, 1928
Closania Jeannel, 1928: 272.

Type species. *Closania winkleri* Jeannel, 1928 by monotypy (habitus in Fig. 38.3).

Diagnosis. Large size, 5.0–6.0 mm, with elongated and convex, pholeuonoid body (Fig. 38.3). Brownish colour. Short, dense and lying pubescence.

Head: Retractile, with complete occipital carina.

Antennae: Thin, elongated, reaching the tip of the elytra, with the first antennomere strongly shorter than the second one; the 3rd short, half the length of 4th, seventh being the longest of all.

Pronotum: Little transverse with maximum width in the anterior third, narrower than the elytra, cordiform, with sides arched forward, projecting towards the middle and more or less sinuated in front of the base. Posterior vertices sharp and protruding backwards, expanded on the humeral surface of the elytra; posterior angles acute. Disc regularly convex; punctation of small size. Pubescence short and procumbent.

Elytra: Ovoidal, very convex and elongate, largely rounded at apex, with maximum width at the middle; pubescence short and procumbent; punctation not aligned in transversal striolae. Parasutural stria absent.

Legs: Very elongate, fine and straight. Males protarsi pentameres slightly dilated. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae straight, without apical basket; with long and robust spines on the outer margins.

Mesoventral keel (Fig. 40.3): High, with rounded front edge and not toothed vertex. Slightly prolonged on the metaventrite.

Suture of the metaventrite (Fig. 40.3): Parallel to the mesocoxal cavity, it delimits a small area between the upper apical border of the mesocoxal cavity.

Metatergal apparatus (Fig. 41.2): With the metascutum wings short, triangular-looking, narrow and elongated; apophysis of the alacrista reduced to a small lobes.

Metendosternite (Fig. 41.6): Furca almost «Y»-shaped, long arms one and a half times longer than the furcal trunk; in the arms, the posterior lateral ridge slightly arcuated; posterior lamina narrows towards the apical area; a reduced anterior lamina is observed in the most membranous apical area, as a possible prolongation of the structure or apophysis that is well-developed and globose. Furcal trunk is somewhat longer than wide, and the median keel clearly diverges posteriorly.

Median lobe of aedeagus: Long, thin, strongly «S»-bent in lateral view (Fig. 42.3), with the apical area curved towards the ventral face. In dorsal view (Fig. 42.8), deeply depressed, with narrow basal part and ogive-shaped, rounded apex.

Endophallus (Fig. 42.8): Completely devoid of sclerotized structures.

Parameres (Fig. 43.3): Thin, curved, shorter than the median lobe; ending in a small club carrying three apical setae quite long and facing inwards.

Spermathecal complex: Spermatheca small (Fig. 43.8), with a spherical apical lobe very small; long and hyaline union duct, somewhat wider than the apical lobe and narrower than the proximal or basal lobe; the proximal lobe is well sclerotized and is the thickest area; the spermatic duct is attached to this area by a small nodule.

Female uroventrite VIII (Fig. 43.12): The entire uroventrite has a subtriangular appearance because the lateral margins in its final part are straight; there is a small macula in the apical part; wide and very short spiculum.

Discussion. In the phylogenetic tree (Fig. 1I) *Closania* appears as sister group of the clade *Sophrochaeta* + *Tismanella* with very high support, 98.9/100. Equally high, 100/100, is the support that separates the complex *Sophrochaeta* + *Tismanella* + *Closania* from *Rhodopiola*.

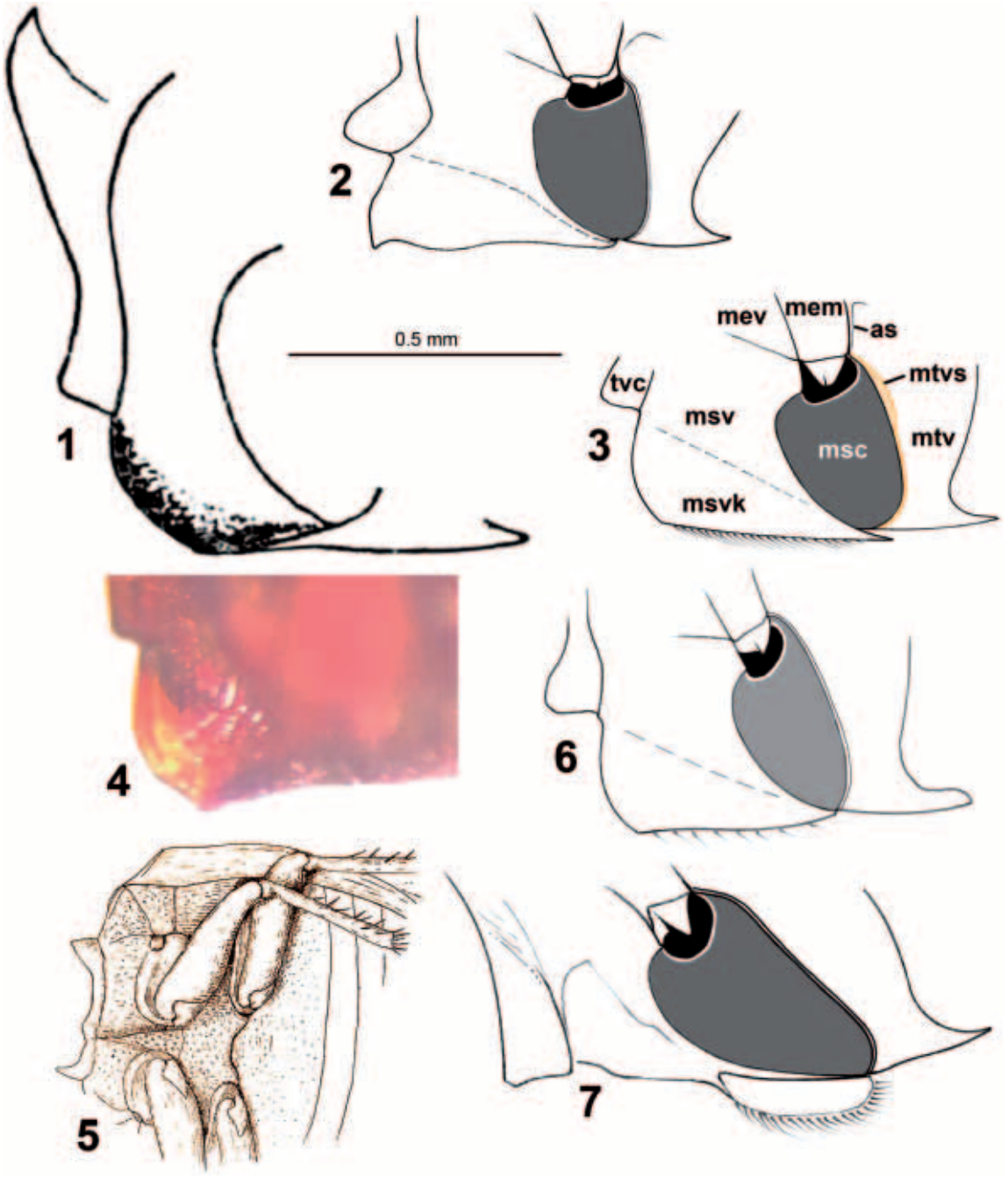
Distribution. Romania. Present in caves in the Oltenia region of the South Carpathians.

Species

Closania orghidani Decu, 1959
Closania orghidani Decu, 1959a: 186.

Genus ***Mehadiella*** Csiki, 1899
Bathyscia (*Frivaldszkya*) Ganglbauer, 1899: 98.
Mehadiella Csiki, 1899: 247 (unjustified new replacement name).

Note. From 1899 to the present *Frivaldszkya* Ganglbauer, 1899 has been considered a homonymy with *Frivaldskia* Schiner, 1861, *nomen novum* pro *Fallenia* Meigen, 838 – Diptera –. However, *Frivaldszkya* Ganglbauer and *Frivaldskia* Schiner differ by two letters and according to article 56.2 of the International Code of Zoological Nomenclature (ICZN 1999), there is no homonymy and the name of Ganglbauer (1899a) can be retained. To apply the article 23.9 (ICZN 1999), reversal of precedence, the evidence of article 23.9.1.2 must be provided; the article 23.9.1 of the code must



FIGURES 40.1–40.7: *Sophrochaeta* series, *Sophrochaeta* group. Pterothorax in lateral view of: (**1**) *Banatiola vandeli* (modified from Decu 1967), (**2**) *Cernella reitteri mallaszi* **comb. nov.**, (**3**) *Closania winkleri winkleri,* (**4**) *Mehadiella paveli* and (**5**) ventral view (modified from Jeannel 1911a), (**6**) *Sophrochaeta oltenica oltenica,* (**7**) *Tismanella chappuisi chappuisi.* Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **mtvs**, metaventral suture; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **tvc**, transverse collar.

be applied and declared *Frivaldszkya nomen oblitum* and *Mehadiella nomen protectum*. The conditions of article 23.9.1.2 are not met and the case has been referred to the Nomenclature Commission; until the case is resolved, the name *Mehadiella* can continue to be used in accordance with article 23.9.3.

Type species. *Adelops Paveli* J. Frivaldszky, 1880 by monotypy (habitus in Fig. 38.4).

Diagnosis. Small size, 1.6–1.8 mm, with short, very convex and hemispheric body; bathyscioid appearance (Fig. 38.4). Brownish colour. Pubescence few, short and lying down.

Head: Retractile, with complete occipital carina.

Antennae: Thin, short, just reaching the base of the pronotum, with the first antennomere strongly shorter than the second one; the 3rd shorter than the second, the 8th very small; antennomeres 7th to 11th flattened.

Pronotum: Very convex and very transverse with maximum width in the base; as wide as the elytra, with sides regularly arched and not sinuated in front of the base. Posterior vertices blunt and not protruding backwards. Disc very convex; punctation of small size. Pubescence short and procumbent.

Elytra: Very short, as long as wide, and very convex, largely rounded at apex, with maximum width just before the middle; pubescence short and procumbent; punctation very fine not aligned in transversal striolae. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres very slightly dilated. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae straight, without apical basket; with long and robust spines on the outer margins.

Mesoventral keel (Fig. 40.4): High and very thick; front edge straight, with a slightly toothed angle. Ventral edge (Fig. 40.5) wide and flattened in a sort of triangular ventral facet, strongly punctate, which gradually widens from the edge of the keel to the posterior edge of the mesoventrite. Not prolonged on the metaventrite. In the image of Jeannel (1911a) (Fig. 40.5), the bifid prolongation of the metaventrite is not visible.

Metaventrite: Intercoxal apophysis as wide as the metaventrite along its midline.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Small, thin and slightly chitinised, in dorsal view (Fig. 42.9) with flattened and rounded apex. Basal blade triangular.

Endophallus (Fig. 42.9): Completely devoid of chitinised structures.

Parameres (Fig. 43.4): Thin, shorter than the median lobe, carrying three axial, short and apical setae. Basal blade of the tegmen rolled at the base and dorsal piece chitinised.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Genus of which we do not have molecular data, attributed by Jeannel (1911a) to the phyletic series of *Drimeotus* and then, again by Jeannel (1924a), moved to the series *Sophrochaeta*. Is maintained by us in this position on the basis of the numerous external characters, shape of antennae and mesoventral keel, absence of parasutural stria, structure of legs and for the shape of the aedeagus.

Distribution. Romania. South Carpathians, Cerna Valley, north of Băile Herculane.

Species

Mehadiella paveli (J. Frivaldszky, 1880)
Adelops Paveli J. Frivaldszky, 1880: 183.
Bathyscia (*Sophrochaeta*) *Paveli* Friv.: Reitter, 1885a [1884]: 18.
Bathyscia (*Frivaldszkya*) *paveli* Frivaldszky: Ganglbauer, 1899: 100.
Mehadiella Paveli Frivaldszky: Csiki, 1899: 247.
Mehadiella paveli (J. Frivaldszky): Perreau, 2000: 294.

Genus ***Sophrochaeta*** Reitter, 1885
Bathyscia (*Sophrochaeta*) Reitter, 1885a [1884]: 17.
Sophrochaeta Reitter, 1885 [1884]: Jeannel, 1911a: 486.

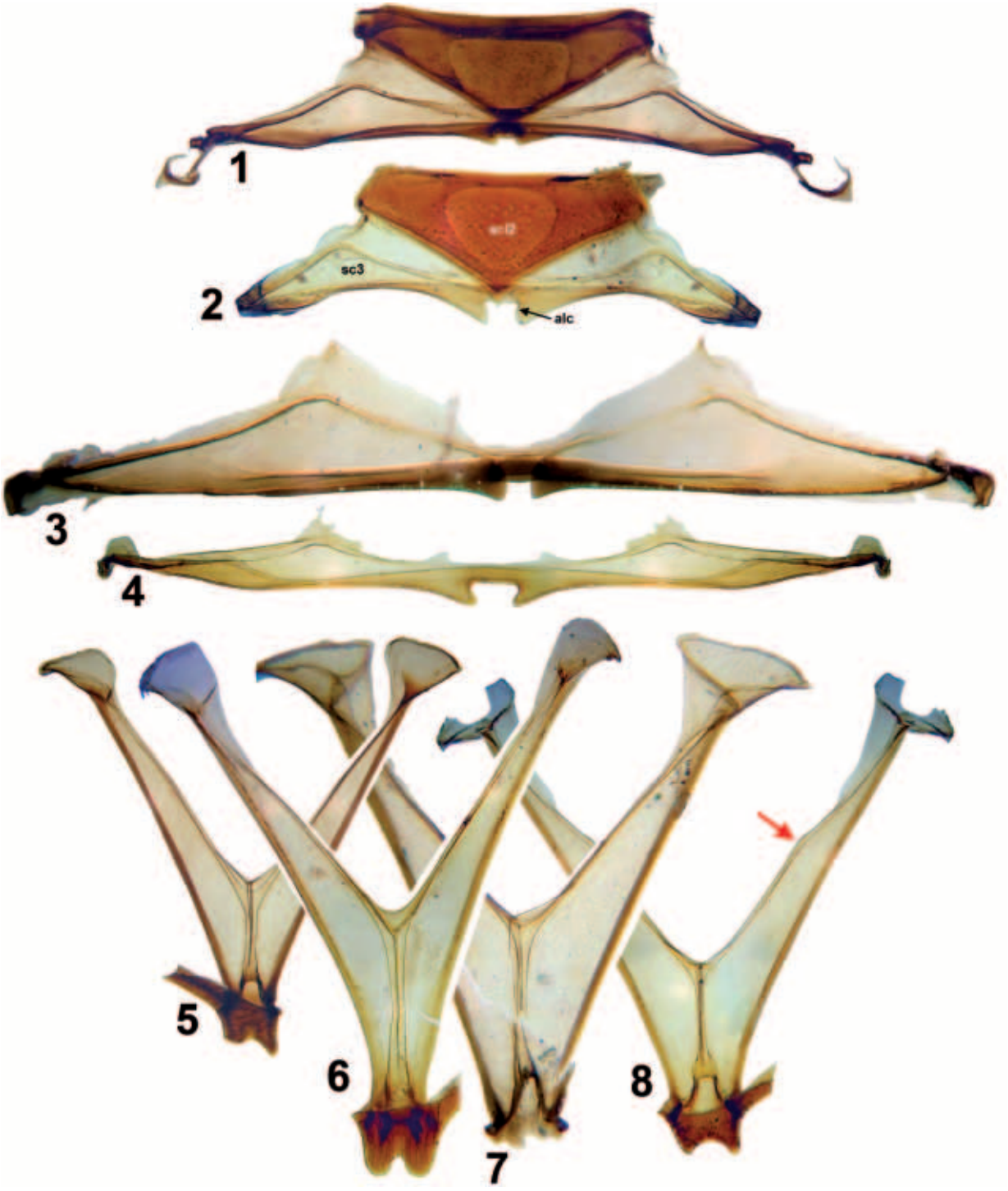
Type species. *Adelops insignis* J. Frivaldszky, 1880 by subsequent designation (for the habitus see that of the similar species *Sophrochaeta oltenica oltenica* in Fig. 39.1).

Diagnosis. Small-medium size, 1.6–3.8 mm, with bathyscioid and moderately elongated body (Fig. 39.1).

Head: Retractile, with complete occipital carina.

Antennae: Thin, elongated, but not reaching the middle of the elytra, with the first antennomere significantly shorter than the second one; the 8th always longer than wide; without a differentiated club.

Pronotum: With the base wider than the elytra, but always transverse, with sides regularly rounded, not sinuate before the base; basal vertices not very sharp



FIGURES 41.1–41.8: *Sophrochaeta* series, *Sophrochaeta* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Cernella reitteri mallaszi* **comb. nov.**, (**2**) *Closania winkleri winkleri,* (**3**) *Sophrochaeta oltenica oltenica*, (**4**) *Tismanella chappuisi chappuisi.* Metendosternite of: (**5**) *C. r. mallaszi* **comb. nov.**, (**6**) *Closania winkleri winkleri*, (**7**) *S. o. oltenica*, (**8**) *T. c. chappuisi.* Red arrow pointing to an internal protuberance. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

with the angles acute; convex in the area of the disc and the stippling formed by small and numerous points. Disc regularly convex. Punctation of small size and dense. Pubescence short and recumbent.

Elytra: Ovoid, slightly elongate and largely rounded at apex, with maximum width at the anterior third; pubescence short and recumbent, with transversal striae. Parasutural stria absent.

Legs: Robust. Males protarsi pentameres, weakly dilated and do not usually exceed the width of the apical end of the protibia, that is without comb on the external side. Straight meso- and metatibiae without apical basket; armed with long and robust spines; first metatarsomere short, slightly longer than the second one. In female protarsi are filiform.

Mesoventral keel (Fig. 40.6): Hight, with the anterior border convex and a slightly widened and more or less wavy ventral edge, rounded vertex or obviously hooked towards the ventral face and with angle right. Not prolonged on the metaventrite.

Suture of the metaventrite (Fig. 40.6): Parallel and very close to the mesocoxal cavity, without delimiting an area.

Metatergal apparatus (Fig. 41.3): With the wings of the metascutum narrow and elongated, in the form of triangles, and the alacrista reduced to two small lobes.

Metendosternite (Fig. 41.7): In «V», with long furcal arms, a little more than twice the length of the trunk, tapering progressively towards the apical area, where a large terminal apophysis can be seen. Furcal trunk short, as wide as long at the widest area.

Median lobe of aedeagus: Long and slender. The apex, in lateral view (Fig. 42.4), not hook-shaped. In dorsal view (Fig. 42.10) ogivete and more or less pointed.

Endophallus (Fig. 42.10): Completely without sclerotized structures.

Parameres (Fig. 43.5): Thin, shorter than the median lobe and carrying three apical setae, with a small, more or less defined club and a rounded or sharp apex.

Spermathecal complex: Spermatheca (Fig. 43.9) with junction duct and apical lobe undifferentiated and the whole area hyaline, with the apical area curved upwards; basal lobe sclerotized and somewhat depressed in the middle area, with the spermatic duct leading into this area somewhat more anteriorly widened.

Female uroventrite VIII (Fig. 43.13): With a regular arched posterior margin and an arched macula close to the apical area; straight anterior margin throughout the middle area and the spiculum reduced to a broad prominence with a bevelled apex.

Discussion. The phylogenetic tree (Fig. 1I), albeit based on a single *Sophrochaeta* species, shows a close affinity of this genus with its sister group *Tismanella* with high support, 99.7/100. No molecular data are available for the genus *Cernella* stat. nov.

Distribution. Romania. Southern Carpathians between Turan to Parâng and further south to the Cernei Massif.

Species

Sophrochaeta chappuisi Jeannel, 1930
Sophrochaeta (s. str.) *Chappuisi* Jeannel, 1930d: 31.
Sophrochaeta (s. str.) *chappuisi* Jeannel: Perreau, 2000: 295.

Sophrochaeta dacica Ienistea, 1955
Sophrochaeta (s. str.) *dacica* Ienistea, 1955: 411, 424.

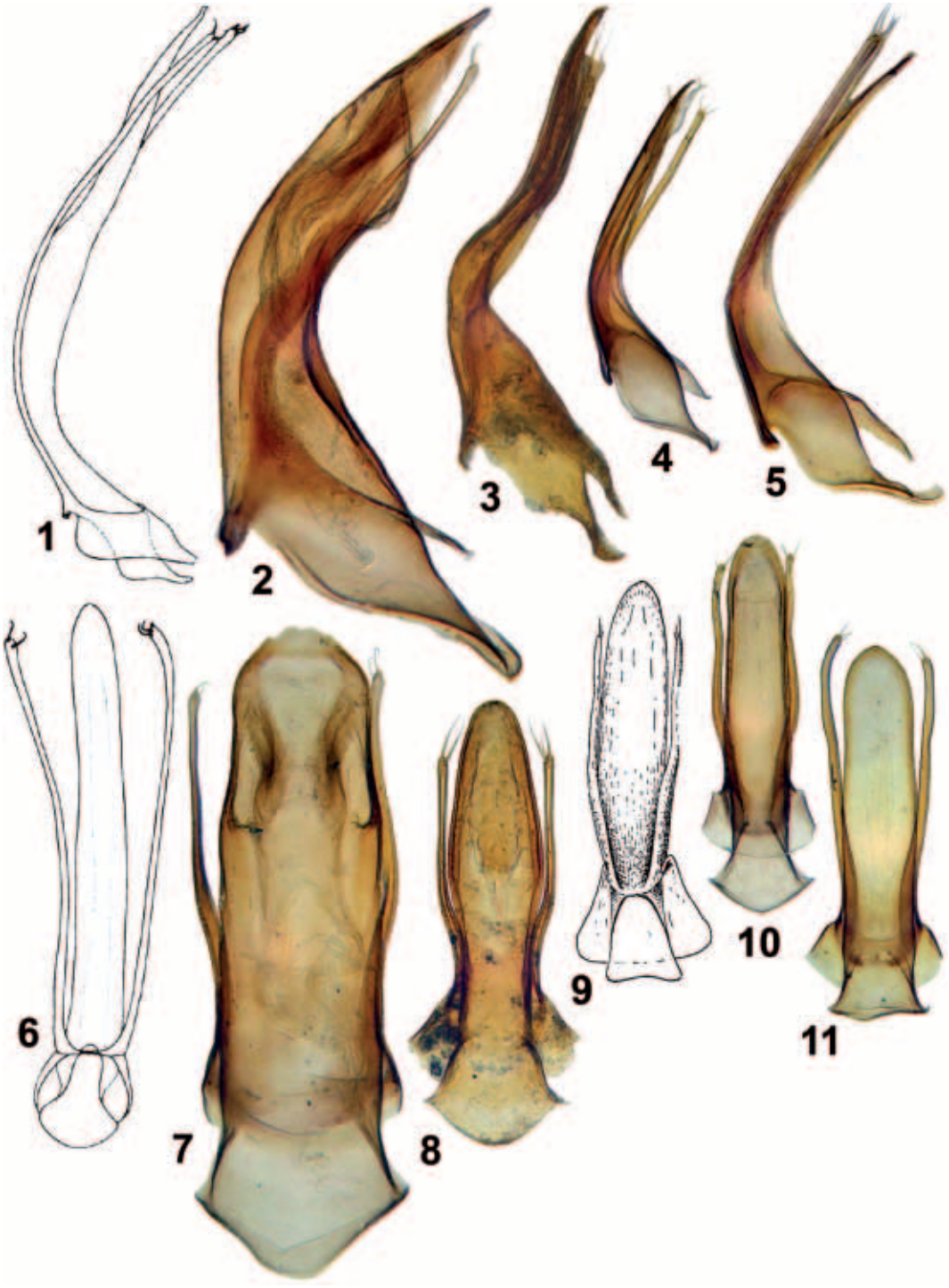
Sophrochaeta globosa Jeannel, 1928
Sophrochaeta globosa Jeannel, 1928: 271.
Sophrochaeta (s. str.) *globosa* Jeannel: Jeannel, 1930d: 30.

Sophrochaeta insignis (J. Frivaldszky, 1880)
Sophrochaeta insignis insignis (J. Frivaldszky, 1880)
Adelops insignis J. Frivaldszky, 1880: 181.
Bathyscia (*Sophrochaeta*) *insignis* Friv.: Reitter, 1885a [1884]: 18.
Sophrochaeta insignis Frivaldszky: Jeannel, 1910a: 41.
Sophrochaeta insignis Subsp. *insignis* J. Frivaldszky, 1880: Jeannel, 1924a: 297.
Sophrochaeta (s. str.) *insignis* J. Frivaldszky: Jeannel, 1930d: 35.
Bathyscia (*Sophrochaeta*) *Fodori* Csiki, 1913: 386.
Sophrochaeta Fodori Csiki: Jeannel, 1914b: 19.

Sophrochaeta insignis zoltani (Csiki, 1913)
Bathyscia (*Sophrochaeta*) *Zoltáni* Csiki, 1913: 387.
Sophrochaeta Zoltani Csiki: Jeannel, 1914b: 20.
Sophrochaeta insignis Subsp. *Zoltáni* Csiki, 1913: Jeannel, 1924a: 297.
Sophrochaeta (s. str.) *insignis zoltani* (Csiki): Perreau, 2000: 296.

Sophrochaeta jeanneli Decu, 1959
Sophrochaeta (s. str.) *Jeanneli* Decu, 1959b: 355.
Sophrochaeta (s. str.) *jeanneli* Decu: Perreau, 2000: 296.

Sophrochaeta kovalitzkyi Knirsch, 1913
Sophrochaeta Kovalitzkyi Knirsch, 1913a: 109.



FIGURES 42.1–42.11: *Sophrochaeta* series, *Sophrochaeta* group. Aedeagus in lateral view of: (**1**) *Banatiola vandeli*, (**2**) *Cernella reitteri mallaszi* **comb. nov.**, (**3**) *Closania winkleri winkleri,* (**4**) *Sophrochaeta oltenica oltenica,* (**5**) *Tismanella chappuisi chappuisi.* Aedeagus in dorsal view of: (**6**) *B. vandeli,* (**7**) *C. r. mallaszi* **comb. nov.**, (**8**) *Closania winkleri winkleri,* (**9**) *Mehadiella paveli* (modified from Jeannel 1924a), (**10**) *S. o. oltenica,* (**11**) *T. c. chappuisi.* Figs **1**, **6** modified from Decu 1967.

Sophrochaeta (s. str.) *Kovalitzkyi* Knirsch: Jeannel, 1930d: 34.
Sophrochaeta (s. str.) *kovalitzkyi* Knirsch: Perreau, 2000: 296.

Sophrochaeta longicornis Jeannel, 1931
Sophrochaeta (s. str.) *longicornis* Jeannel, 1931a: 137.

Sophrochaeta merkli (J. Frivaldszky, 1883)
Bathyscia Merklii J. Frivaldszky, 1883: 12.
Bathyscia (*Sophrochaeta*) *Merklii* Friv.: Reitter, 1885a [1884]: 18.
Sophrochaeta Merklii Frivaldszky: Jeannel, 1910a: 41.
Sophrochaeta (s. str.) *Merklii* Frivaldszky: Jeannel, 1930d: 34.
Sophrochaeta (s. str.) *merklii* Frivaldszky: Perreau, 2000: 296.

Sophrochaeta mihoki Bokor, 1921
Sophrochaeta Mihóki Bokor, 1921: 110.
Sophrochaeta (s. str.) *Mihoki* Bokor, 1921: Jeannel, 1930d: 35.
Sophrochaeta (s. str.) *mihoki* Bokor: Perreau, 2000: 297.

Sophrochaeta motasi Decu, 1959
Sophrochaeta Motasi Decu, 1959a: 192.
Sophrochaeta (s. str.) *motasi* Decu: Perreau, 2000: 297.

Sophrochaeta obtusa Jeannel, 1931
Sophrochaeta (s. str.) *obtusa* Jeannel, 1931a: 138.

Sophrochaeta oltenica Jeannel & Mallász, 1930
Sophrochaeta oltenica densepunctata Jeannel, 1931
Sophrochaeta (s. str.) *oltenica* subsp. *densepunctata* Jeannel, 1931a: 140.
Sophrochaeta oltenica oltenica Jeannel & Mallász, 1930
Sophrochaeta oltenica Jeannel & Mallász, 1930: 3.
Sophrochaeta (s. str.) *oltenica* Jeannel & Mallász: Jeannel, 1930d: 35.
Sophrochaeta (s. str.) *oltenica oltenica*: Perreau, 2000: 297.

Sophrochaeta orghidani Ienistea, 1955
Sophrochaeta (s. str.) *orghidani* Ienistea, 1955: 410, 423.

Sophrochaeta racovitzai Decu, 1959
Sophrochaeta (s. str.) *Racovitzai* Decu, 1959b: 352.
Sophrochaeta (s. str.) *racovitzai* Decu: Perreau, 2000: 297.

Sophrochaeta rothi Jeannel, 1924
Sophrochaeta Rothi Jeannel, 1924a: 298.
Sophrochaeta (s. str.) *Rothi* Jeannel: Jeannel, 1930d: 32.
Sophrochaeta (s. str.) *rothi* Jeannel: Perreau, 2000: 297.

Sophrochaeta subaspera Jeannel, 1928
Sophrochaeta subaspera arcticollis Jeannel, 1931
Sophrochaeta (s. str.) *subaspera* subsp. *arcticollis* Jeannel, 1931a: 139.
Sophrochaeta subaspera subaspera Jeannel, 1928
Sophrochaeta subaspera Jeannel, 1928: 270.
Sophrochaeta (s. str.) *subaspera* Jeannel: Jeannel, 1930d: 36.
Sophrochaeta (s. str.) *subaspera subaspera* Jeannel: Perreau, 2000: 298.

Genus ***Tismanella*** Jeannel, 1928
Tismanella Jeannel, 1928: 271.

Type species. *Tismanella chappuisi* Jeannel, 1928 by monotypy (habitus in Fig. 39.2).

Diagnosis. Medium-large size, 4.5–5.2 mm, with elongated and convex, body; sub-pholeuonoid facies (Fig. 39.2). Colour reddish-brown. Long and raised pubescence.

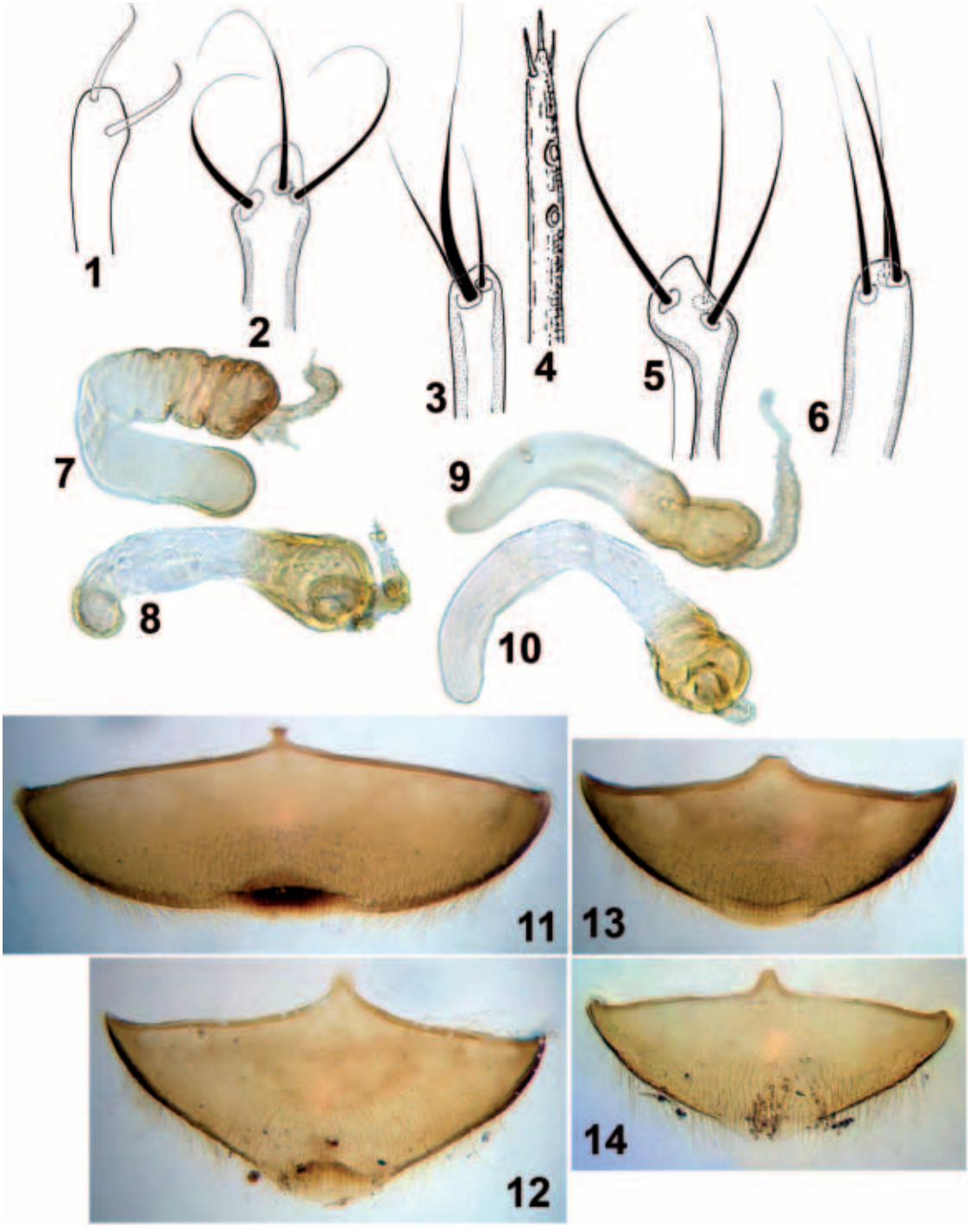
Head: Retractile, with complete occipital carina.

Antennae: Thin, elongated, exceeding the middle of the elytra, with the first antennomere strongly shorter than the second one; 8th very elongated about five times as long as wide, as long as 9th; club's antennomeres elongated and undelated.

Pronotum: With the maximum width at the base which is narrower than the elytra, always very transverse, almost twice as wide as long, with sides regularly rounded in the anterior part, not sinuate before the base. Disc regularly convex; punctation of small size and very dense; pubescence long and erect.

Elytra: Pear-shaped, very elongate and largely rounded at apex, with maximum width at the posterior third; pubescence long and erect, punctation aligned in transversal fine striolae, superficial and oblique to the suture in the basal half; punctation being weaker and widely dispersed in the apical half with a smooth and shiny surface. Parasutural stria absent.

Legs: Males protarsi pentameres not dilated. Protibiae not dilated apically, without comb on the ex-



FIGURES 43.1–43.14: *Sophrochaeta* series, *Sophrochaeta* group. Apex of the paramere of: (**1**) *Banatiola vandeli* (redrawn from Decu 1967), (**2**) *Cernella reitteri mallaszi* **comb. nov.**, (**3**) *Closania winkleri winkleri,* (**4**) *Mehadiella paveli* (modified from Jeannel 1924a), (**5**) *Sophrochaeta oltenica oltenica,* (**6**) *Tismanella chappuisi chappuisi.* Spermatheca of: (**7**) *C. r. mallaszi* **comb. nov.,** (**8**) *Closania winkleri winkleri,* (**9**) *S. o. oltenica,* (**10**) *T. c. chappuisi.* Female uroventrite VIII of: (**11**) *C. r. mallaszi* **comb. nov.**, (**12**) *Closania winkleri winkleri,* (**13**) *S. o. oltenica,* (**14**) *T. c. chappuisi.*

ternal side. Meso- and metatibiae straight and wounded with long thorns, without apical basket.

Mesoventral keel (Fig. 40.7): Reduced to a small membranous prominence with setae in the posterior area of the mesoventrite.

Suture of the metaventrite (Fig. 40.7): Parallel to the mesocoxal cavity, without delimiting an area.

Metatergal apparatus (Fig. 41.4): With wings of the metascutum very narrow and very elongated; alacrista apophysis null, reduced to two small lobes.

Metendosternite (Fig. 41.8): In «V» with furcal arms long, twice as long as the furcal trunk; arms keel sags towards the apical area, for this reason the posterior lamina narrows and the anterior lamina is observed in that area; apophysis or terminal process widened, rhomboid in shape; there is a slight protuberance on the inner face of the furcal arms. Furcal trunk short, as long as wide; median keel with a well marked posterior divergence.

Median lobe of aedeagus: Long and slender. The apex, in lateral view (Fig. 42.5), with straight and sharp apical area. In dorsal vision (Fig. 42.11) ogivete and slightly pointed.

Endophallus (Fig. 42.11): Completely without sclerotized structures.

Parameres (Fig. 42.6): Slender, long and straight, as long or almost as long as the middle lobe, with a blunt apical area and at the apex three rather long and divergent setae.

Spermathecal complex: Spermatheca (Fig. 43.10) elongated in the shape of an inverted «C». The distal lobe and the union duct are not differentiated, all this hyaline part; only the short proximal lobe is sclerotized, which is somewhat wider.

Female uroventrite VIII (Fig. 43.14): Equipped with a short and stout spiculum.

Discussion. In the phylogenetic tree (Fig. 1I) *Tismanella* appears as sister group of *Sophrochaeta* with very high support, 99.7/100. Equally high is the support of the clade that separates *Sophrochaeta* + *Tismanella* from *Closania*, 98.9/100.

Distribution. Romania. The two species and the four geographic races colonizes several caves in the eastern Carpathians, around Tismana, Gorj district in the Oltenia region.

Species

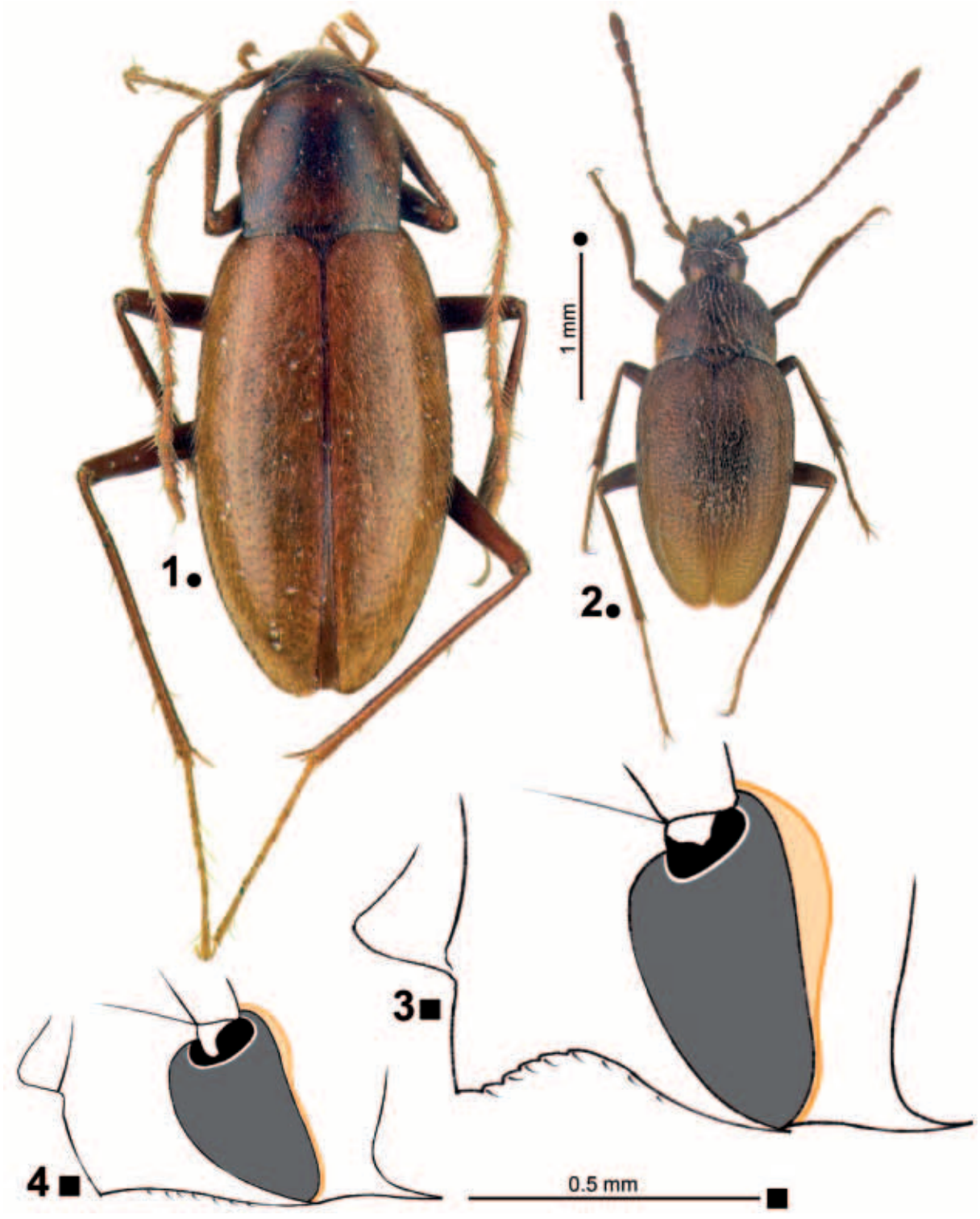
Tismanella chappuisi Jeannel, 1928
Tismanella chappuisi arcuata Jeannel, 1930
Tismanella Chappuisi subsp. *arcuata* Jeannel, 1930d: 43.
Tismanella chappuisi arcuata Jeannel: Perreau, 2000: 298.
Tismanella chappuisi chappuisi Jeannel, 1928
Tismanella Chappuisi Jeannel, 1928: 271.
Tismanella Chappuisi subsp. *Chappuisi* Jeannel: Jeannel, 1930d: 43.
Tismanella chappuisi chappuisi Jeannel: Perreau, 2000: 298.
Tismanella chappuisi convexipennis Jeannel, 1930
Tismanella Chappuisi subsp. *convexipennis* Jeannel, 1930d: 43.
Tismanella chappuisi convexipennis Jeannel: Perreau, 2000: 298.
Tismanella chappuisi diversa Decu, 1961
Tismanella Chappuisi diversa Decu, 1961: 212.
Tismanella chappuisi diversa Decu: Perreau, 2000: 298.

Tismanella winkleriana Jeannel, 1931
Tismanella Winkleriana Jeannel, 1931a: 141.
Tismanella winkleriana Jeannel: Perreau, 2000: 298.

3.1.2 Series ***Hexaurus*** Jeannel, 1924

Protibiae without comb and with 2–3 external spurs; meso- and metatibiae without apical basket and little aedeagus with unarmed endophallus. On a morphological basis Casale *et al*. (1991a), confirmed as such by Giachino & B.V. Guéorguiev (2008) included in the same group the genera *Bathyscia*, *Hexaurus* and *Netolitzkya*. However, both morphological data (simple aedeagus with unarmed endophallus) and biogeographic data suggest that their relationships must be found among their neighboring inhabitants of the same mountain massif, also with simple aedeagus and unarmed endophallus (see Discussion section of series Sophrochaeta).

The Greco-Bulgarian *Bathyscia* from Rhodopes-Pirin mountains, also with simple aedeagus and unarmed endophallus, must also belong to the *Hexaurus* series clade. The distribution of *Bathyscia* is implausible and will probably have to be fragmented into two or three genera if molecular data are one day available and consistent morphological characters are found (see comments in genus *Bathyscia* section). Furthermore, it is hypothesized that *Bathyscia hungarica*



FIGURES 44.1–44.4: *Hexaurus* series. Habitus of: (**1**) *Hexaurus merklii,* (**2**) *Netolitzkya jeanneli matroffi*. Pterothorax in lateral view of: (**3**) *H. merklii,* (**4**) *N. j. matroffi*.

from the northern reaches of the Carpathians is phylogenetically related to the south Carphatians clade *Sophrochaeta* group of the homonymous series. The postulated phylogenetic relationship of this Carpathian-Balkan-Rhodopean fauna with that of the Dinarides is highly unlikely. These two territories are separated by a tertiary basin (Pannonian basin) (Popov *et al*. 2004) from the Langian (15.97–13.82 My) which also suggests a close phylogenetic relationship between *Bathyscia* from Rhodopes and the Balkan *Hexaurus* series (the two genera with unarmed endophallus) but not with *Bathyscia montana* from Dinarides, the type species of the genus.

KEY TO GENERA

1. Size 3.7–5.1 mm. Subpholeuonoid or pholeuonoid body (Fig. 44.1). Pronotum sinuate in the basal third, with a very narrow base and the posterior vertices not raised (Fig. 44.1). Elytra without transverse striolae. Eighth antennomere much shorter than the ninth. Median lobe of aedeagus not narrowed towards the middle (Fig. 45.5) ..... *Hexaurus*
- Size 2.5–2.8 mm. Elliptical body (Fig. 44.2). Pronotum not sinuate in the basal third, with a slightly narrowed base and more or less raised posterior vertices (Fig. 44.2). Elytra with transverse striolae. Eighth antennomere as long or almost as long as the ninth. Median lobe of aedeagus narrowed towards the middle (Fig. 45.6) .....*Netolitzkya*

Genus ***Hexaurus*** Reitter, 1885
Hexaurus Reitter, 1885a [1884]: 11.

TYPE SPECIES. *Pholeuon Merklii* Frivaldszky, 1879 by monotypy (habitus in Fig. 44.1).

DIAGNOSIS. A medium-large size, 3.7–5.1 mm, convex and elongated body with pholeuonoid facies (Fig. 44.1). Shiny integuments, covered with sparse, golden, long and erect pubescence.

Head: Elongate, without occipital carina; anophthalmous.

Antennae: Very long, slight, almost reaching the apex of the elytra, with cylindrical or conical articles, not flattened; second antennomere as long as the first one; the 8th elongated, much shorter than the 9th one.

Pronotum: From transverse to sub-square, narrower than elytra, with maximum width at the anterior third; sides subretilinear or distinctly sinuated posteriorly, before the basal angles, which are well marked, straight or slightly obtuse.

Elytra: Oval, elongated, very convex, not transversally striolate and without parasutural stria.

Legs: Long and frail. Protarsomeri tetrameres and not dilated in male. Protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 44.3): High but short, with subrectilinear or slightly curved anterior edge. Ventral edge slightly serrated, from subrectilinear to more or less curved or with a deep concavity, but not prolonged into the metaventrite. Vertex widely rounded, pointed or hooked.

Suture of the metaventrite (Fig. 44.3): In the upper half it delimits an elongated arched area and the lower half runs parallel to the edge of the mesocoxal cavity.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Slight and elongated, regularly curved. Apex, in lateral view (Fig. 45.3), in the shape of a squat and rounded hook. In dorsal view (Fig. 45.5) very thin, with a more or less narrow and blunt apex. Basal blade of the median lobe short, about 1/5 of the median lobe long.

Endophallus: Completely hyaline, without any internal structure.

Parameres: Relatively robust, just shorter to slightly longer than the median lobe. Apical part without club, sometimes with a small membranous tongue and equipped with a number of setae ranging from three (Fig. 46.1) to five (Fig. 46.2).

Spermathecal complex: Unknown.

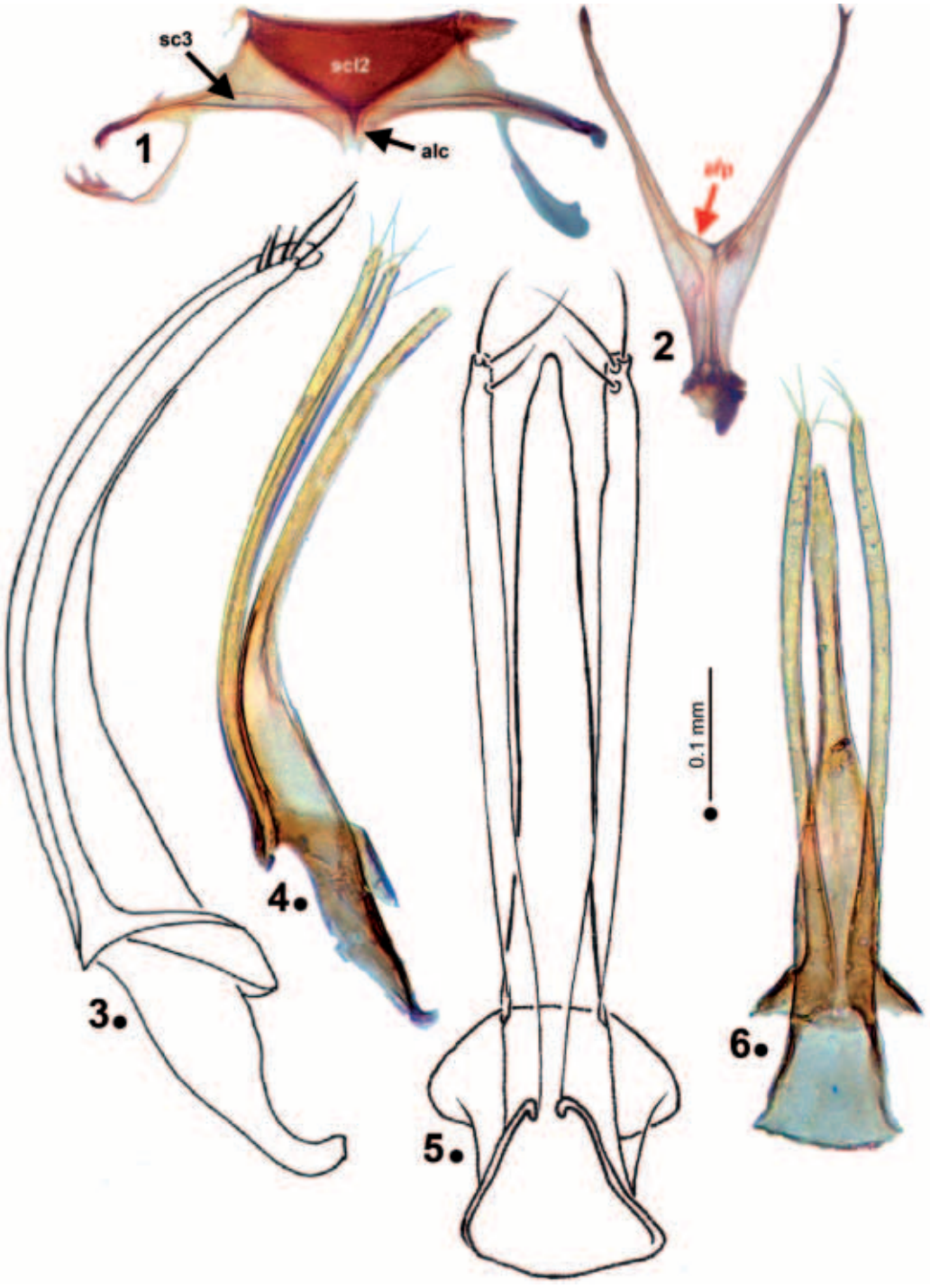
Female uroventrite VIII (Fig. 46.5): The apical margin in ample arc with numerous short setae and some very long setae with almost regular insertion; the spiculum short, rather broad and with truncate apex.

DISCUSSION. No molecular data are available on this genus. Jeannel (1924a) approaches *Hexaurus* to the genus *Netolitzkya* considering them to belong to a single phyletic lineage. While Zerche (1990), in the context of his revision of the genus, raises doubts by not noting the presence of synapomorphic characters between these two genera.

DISTRIBUTION. Bulgaria, Central Stara planina.

Species

Hexaurus beroni Giachino & B.V. Guéorguiev, 2008
Hexaurus beroni Giachino & B.V.Guéorguiev, 2008: 106.



FIGURES 45.1–45.6: *Hexaurus* series. *Netolitzkya jeanneli matroffi*: (**1**) Metatergal apparatus, ventral view of metanotum and axillaria, (**2**) Metendosternite. Aedeagus in lateral view of: (**3**) *Hexaurus beroni* (modified from Giachino & B.V. Guéorguiev 2008), (**4**) *N. j. matroffi*. Aedeagus in dorsal view of: (**5**) *H. merklii* (redrawn from Zerche 1990), (**6**) *N. j. matroffi*. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Hexaurus merklii (J. Frivaldszky, 1879)
Pholeuon Merklii J. Frivaldszky, 1879: 232.
Pholeuon Merklii var. *affine* J. Frivaldszky, 1879: 232.
Hexaurus Merkli J. Frivaldszky: Reitter, 1885a [1884]: 15.
Hexaurus merklii var. *affinis* (J. Frivaldszky): Zerche, 1990: 6.

Hexaurus paradisi Zerche, 1990
Hexaurus paradisi Zerche, 1990: 9.

Hexaurus schipkaensis Zerche, 1990
Hexaurus schipkaensis Zerche, 1990: 7.

Hexaurus simile (J. Frivaldszky, 1879)
Pholeuon Merklii var. *simile* J. Frivaldszky, 1879: 232.
Hexaurus Merkli subsp. *similis* Frivaldszky: Jeannel, 1910a: 37.
Hexaurus similis Frivaldszky, 1879: Jeannel, 1924a: 226.

Genus ***Netolitzkya*** G. Müller, 1913
Netolitzkya G. Müller, 1913a: 2.

Type species. *Aphaobius Maneki* G. Müller, 1909 by monotypy (for the habitus see that of the similar species *Netolitzkya jeanneli matroffi* Jeannel, 1930 in Fig. 44.2).

Diagnosis. Medium size, 2.5–2.8 mm, with elliptic or slightly pholeuonoid facies (Fig. 44.2).

Head: Elongate, without occipital carina; anophthalmous.

Antennae: Long, almost reaching half of the elytra; first antennomere as long as the second one; the 8th elongated, as long as the 9th one.

Pronotum: Transverse, narrower than the elytra, with marked and raised basal angles.

Elytra: Transversely striolated, without parasutural stria.

Legs: Thin and relatively elongated. Protarsi tetrameres and not dilated in male; protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 44.4): High, complete, but not prolonged on the metaventrite. Front edge more or less curved, with toothed vertex; ventral edge smooth, with the anterior half slightly concave and the posterior half convex.

Suture of the metaventrite (Fig. 44.4): It delimits a very narrow and small area in the upper third, then runs very close to the coxal cavity in the lower two thirds.

Metatergal apparatus (Fig. 45.1): With the wings of the metascutum elongated, in their proximal half triangular and in their distal half very narrow and the alacrista reduced, very short with apex pointed.

Metendosternite (Fig. 45.2): «V»-shaped; furcal arms very narrow one and a half times longer than trunk, only posterior lamina distinct at base of the arm and continued on trunk, without terminal apophysis. Furcal trunk somewhat longer than the area of greatest basal width and the median keel with posterior divergence.

Median lobe of aedeagus: Small, frail. In lateral view (Fig. 45.4), very narrow, arched basal half and subrectilinear apical half, with rounded, not sharp apex. In dorsal view (Fig. 45.6) very narrow, lozenge-shaped in the apical third.

Endophallus: Completely hyaline, without any internal structure.

Parameres (Fig. 46.3): Thin, as long as or shorter than the median lobe. Carrying three apical setae.

Spermathecal complex: Although the illustration is not very clear (Fig. 46.4), the spermatheca appears to be membranous in the form of a sacciform arc, without differentiated regions and much more dilated in its apical half.

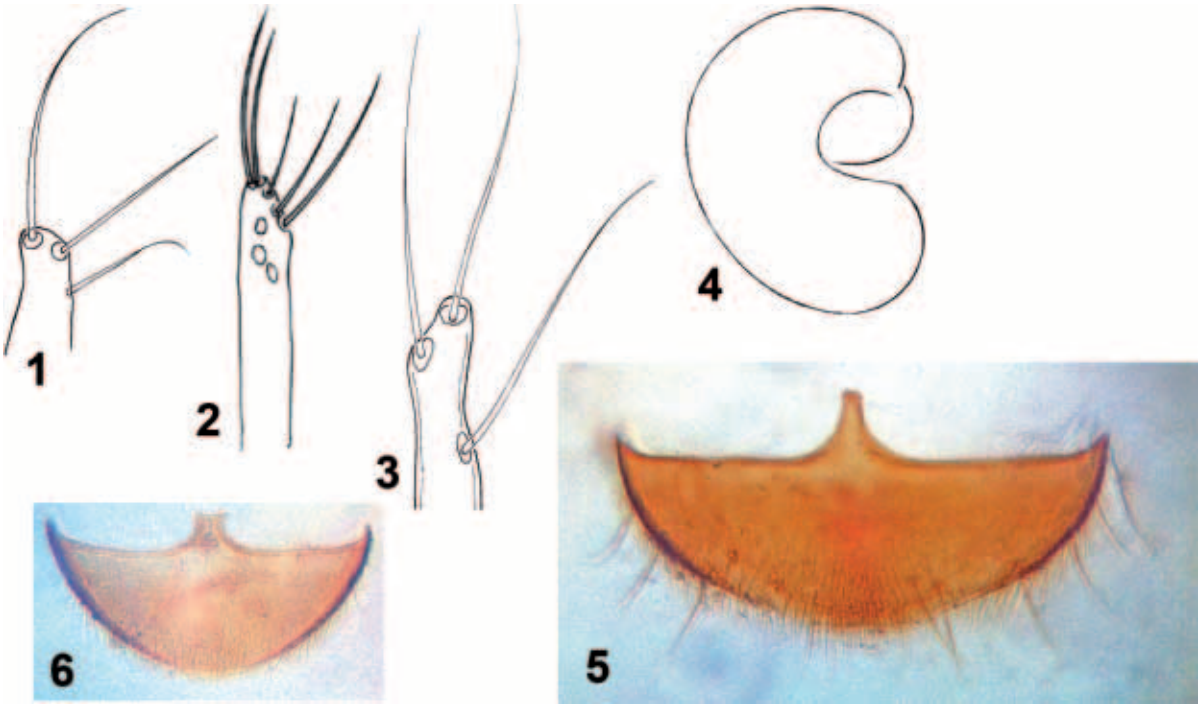
Female uroventrite VIII (Fig. 46.6): With the posterior edge in a uniform, slightly pointed arch; spiculum short, broad and the apex truncate, straight or slightly concave.

Discussion. The belonging of the genus *Netolitzkya* to the *Sophrochaeta* lineage is hypothesized on a purely morphological basis. The biogeographic evidences support this hypothesis (see Discussion section of the *Sophrochaeta* clade).

Distribution. Bulgaria, Central Balkan Ridge.

Species

Netolitzkya jeanneli Buresch, 1924
Netolitzkya jeanneli jeanneli Buresch, 1924
Netolitzkya Maneki Jeanneli Buresch, 1924: 160.
Netolitzkya Jeanneli Buresch: Jeannel, 1930b: 227.
Netolitzkya jeanneli jeanneli Buresch: Perreau, 2000: 173.
Netolitzkya jeanneli matroffi Jeannel, 1930
Netolitzkya Jeanneli subsp. *Matroffi* Jeannel, 1930b: 228.
Netolitzkya jeanneli matroffi Jeannel: Perreau, 2000: 173.



FIGURES 46.1–46.5: *Hexaurus* series. Apex of the paramere of: (**1**) *Hexaurus merklii,* (redrawn from Zerche 1990), (**2**) *H. beroni* (modified from Giachino & B.V. Guéorguiev 2008), (**3**) *Netolitzkya jeanneli matroffi.* Spermatheca of: (**4**) *N. j. matroffi.* Female uroventrite VIII of: (**5**) *H. merklii,* (**6**) *N. j. matroffi.*

Netolitzkya maneki (G. Müller, 1909)
Netolitzkya maneki iltschewi Jeannel, 1924
Netolitzkya Maneki subsp. *Iltschewi* Jeannel, 1924a: 224.
Netolitzkya maneki iltschewi Jeannel: Perreau, 2000: 173.
Netolitzkya maneki maneki (G. Müller, 1909)
Aphaobius Maneki G. Müller, 1909: 281.
Netolitzkya Maneki Müller: Jeannel, 1914b: 36.
Netolitzkya maneki maneki (Müller, 1909): Perreau, 2000: 173.

3.1.3 Unnamed series from Euboea Island, Greece

There is a number of unnnamend series from Greece which are extremely difficult to name, e.g. contextualise their origin and taxonomic position. So it appears to be impossible to carry out an analysis based on morphology only to identify the position of the Leptodirini around the Hellenic Trench. Currently there are 11 genera and around 30 spcies described from Greece, however out samples show that there are at least 50 genera and approximally 140 species present in Greece, of which at least 110 are not described yet. A similar picture arises when focussing on Turkey, for which 12 genera and 24 species were known. Taken together it is a complex taxonomic group and so far we only were able to generate molecular data for two taxa from the island of Euboea, This is concerning a single species of a *Epiroella* and an yet undescribed species from the Taygetos Mountain. These genera from Greece and adjacent regions were used by taxonomists during the last century as containers to grouping taxa showing certain similarities. This issue is not part of this study as the group will be reviewed with due care by Giachino & Vailati (in prep.). Their

current systematic classification is not available to us and cannot be used here.

These problems required a change in the approach to the contribution for this section of the tribe. This mean in detail that morphological redescriptions of the single genera will not be provided with regard to the genera present in Greece. Only the list of species, where necessary, will be added and considerations in the form of notes will supplement the here. In the case of genera, present in Greece, with species also found in Albania, Republic of North Macedonia and Bulgaria will also be treated on this occasion. Single cases of phyletic lineages already previously defined in the literature, also involving the Bulgarian fauna, is treated in more detail.Several of the genera have been considered as separate series and sometimes they are the only representatives of these. Here we follow the approach of of Giachino & B.V. Guéorguiev (2008) and it is also known that each of these series will be enriched with various genera in the future (Giachino & Vailati *in prep*., personal communication).

In all these territories mentioned above the distribution areas of different series overlap; thus, for example, it is observed that the few representatives of the Hellenic fauna that have been available belong to different clades:

– Leptodirini_Trypi_M475 from Taygetos mountain, sister genus of *Karadeniziella* and *Gueorguievella*, hence sister of the *Oryotus* series.

– Two unnamed genera as sister of the *Sophrochaeta* series from Euboea Island, a cavern in the Dirfi mountain (Specimens AN535 and RA512).

Henrotiella eubeensis was already known from another locality on the same island (Perreau, 1999); morphological evidence suggests that this genus belongs to the *Pholeuonopsis* group of the *Anthroherpon* series. The small clade formed by the two taxa of Euboea is sister to the *Sophrochaeta* series with fairly low support 89.1/36 in Tree-1 and wit higher support of 83.1/90 in Tree-2 (Fig. 2). Given the genetic distance (Fig. 1I) and the geographical location, we have chosen to consider these taxa (Spcimen ID: AN535, RA512) as an indication of the existence of a series that may be complex, given the number of new taxa from Greece currently being about to be described (Giachino & Vailati *in prep*.). Therefore these specimens will not be described here, as they are part of an extensive work on the Greek fauna by the authors mentioned above.

3.1.4 Series ***Atticiella*** V.B. Guéorguiev, 1963 sensu novo

The characters are described in the diagnosis of the genus.

Genus ***Atticiella*** Coiffait, 1955
Atticiella Coiffait, 1955c: 208.

Type species. *Atticiella lindbergi* Coiffait, 1955 by original designation (habitus in Fig. 47.1).

Diagnosis. Small size, 1.4–2.1 mm; body shape bathyscioid (Fig. 47.1), poorly convex and very wide, with pronotum much larger than the elytral base. Brownish colour. Pubescence very short, stitched and procumbent.

Head: Retractile, with complete occipital carina; punctation very fine and very spaced.

Antennae: Short, although clearly exceeding the length of the pronotum, with the tips of the club not dilated but flattened; first antennomere shorter than the second one and shorter than the 8th, 9th, 10th and 11th;antennomeres slightly transverse.

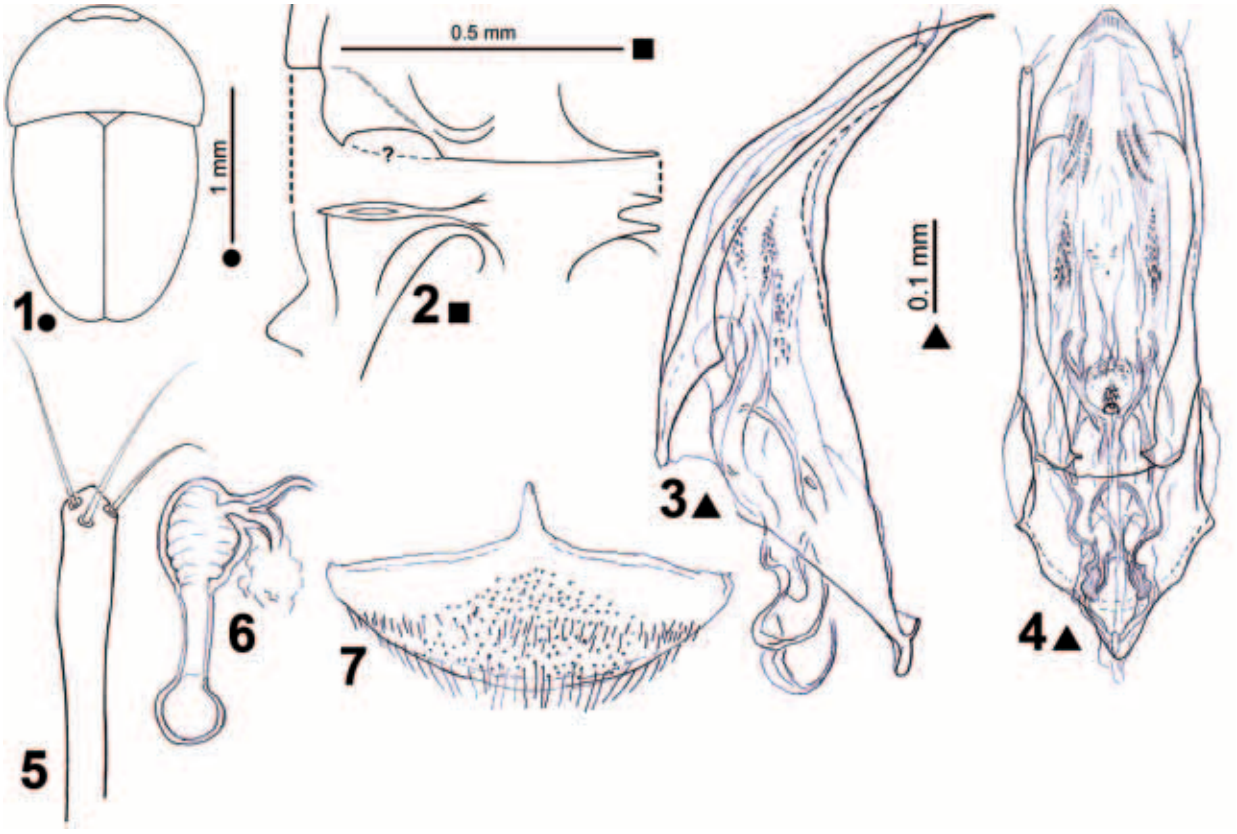
Pronotum: Very transverse, at least twice as wide as long, with regularly arcuated sides, and maximum width at the basal fourth; much larger than the elytral base; posterior vertex not sharp, rounded, with an almost right angle. Punctation very fine so that the integuments appears granulated.

Elytra: Short and very ovoidal, almost as wide as long, largely rounded at apex, with maximum width at the anterior fifth; punctation very diffuse, practically without transverse striolae than are hardly visible in the basal area, in the rest of the elytra the points are very fine and the surface appears granulated. Parasutural stria absent.

Legs: Short and robust. Males protarsi pentameres, slightly dilated but narrower than, or as wide as, the apex of the protibia. Protibiae not dilated apically, without comb on the external side. Meso- and metatibiae without apical basket, with long and robust spines on the outer margins; metatibia being hardly sinuated on the inner edge of the apical third.

Mesoventral keel (Fig. 47.2): High, with rounded front edge and toothed vertex. Ventral border thick, marked by a deep, finely dotted median furrow, not prolonged on the metaventrite. Keel fused to the metaventrite.

Metaventrite: Not carinated with intercoxal apophysis very wide and projected backward by a couple of spines, separated by a deep furrow.



FIGURES 47.1–47.7: *Atticiella lindbergi*: (**1**) Habitus, (**2**) Pterothorax in lateral and ventral views, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of the paramere, (**6**) Spermatheca, (**7**) Female uroventrite VIII.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and stout. In lateral view (Fig. 47.3), stout in the basal part, it forms a regular obtuse angle; dorsal edge in a wide arc with a slight depression in the apical third; apical area being flattened and extending into a fine pointed point, slightly downward. In dorsal view (Fig. 47.4), with lateral margins slightly sinuous in the basal part, with the greatest width at the base and apex narrowed and slightly arcuated, subtriangular.

Endophallus (Fig. 47.4): Complex, with three regions well differentiated. Basal region shows, at the bottom, a sclerotized structure similar to an «Y»-piece that is anteriorly surmounted by two pairs of thin and arcuated phanerae surrounding the ejaculatory duct. The middle region show a complex phanera, in a vague shape of «H», with an addional posterior central arm; the front arms of this «H» are clearly bifid and this upper and anterior part of this phanera assumes a not well-defined «cup» shape. In the apical region, on both sides, are two long reinforcing bands, anteriorly denticulated.

Parameres (Fig. 47.5): Thin, slightly wavy and shorter than the median lobe; apical part does not form a distinct club carrying three setae of similar length.

Spermathecal complex: Spermatheca (Fig. 47.6) very elongated, with proximal and distal lobes sclerotized, the distal one spherical and the proximal one globular and wider; hyaline junction duct, longer than the distal lobe but narrower. Ductus long, conspicuously sclerotized, enlarged, and «S»-shaped before the inserting into the spermatheca. Ductus and spermathecal gland converge to end at the same point in the spermatheca. There is a spermathecal gland.

Female uroventrite VIII (Fig. 47.7): Spiculum short, triangular and sharp; anterior edges subrectilinear and sightly converging. Apical part showing a

slightly concave lateral margins; base of this part without macula.

Discussion. V.B. Guéorguiev (1960b) describes the genus *Rhodopiola* bringing it systematically closer to *Sophrochaeta*. Subsequently, always V.B. Guéorguiev (1963), describing the genus *Bureschiana*, approaches it to *Atticiella* and establishes for this two genera the «*Atticiella* phyletic series», distinct from a «*Sophrochaeta* phyletic series», albeit closely related to each other. Casale & Giachino (1985) described the genus *Maroniella* assigning it to «*Atticiella* phyletic lineage», which includes three genera: *Atticiella*, *Bureschiana* and *Maroniella*. Giachino (1989) described *Bureschiana thracica* from the Greek Rhodopes and, subsequently, always Giachino (1995), in the context of description of *Bureschiana raitchevi*, confirms, on a strictly morphological basis, the monophyly of «*Atticiella* phyletic lineage» also assigning it to the genus *Rhodopiola*. Finally, Giachino & B.V. Guéorguiev (2008) confirmed,the»*Atticiella* phyletic lineage» using the approach suggested by Giachino (1995). Keel fused with metaventrite as in *Rhodopiola*, which could reveal a closer relationship than with the other genera of its series.

Now, with regard to *Atticiella* phyletic lineage (*sensu* Giachino, 1995), we have available molecular data only for the genus *Rhodopiola* which in the phylogenetic tree (Fig. 1I) is included in *Sophrochaeta* phyletic series and closely related (with a support of 100/100) to the complex of genera *Sophrochaeta* + *Tismanella* + *Closania*. Since the molecular data relating it to *Atticiella*, *Bureschiana* and *Maroniella* are not available, it is impossible for us to confirm the validity of the supposed *Atticiella* lineage. Furthermore, it seems more correct in this moment, not to formalise the taxonomic classification on morphological characters only. There establishingan *Atticiella* as an isolated genus and sister of the Leptodirini from Euboea Island in basal *Sophrochaeta* clade seems not justified. Nevertheless the position of *Atticiella* seems to be isolated and it occurs in a geographically defined area that is also populated by an other phyletic lines, of which all of them undescribed and unpublished (Giachino & Vailati *in prep*.). What appears, at this preliminary stage, is that the species of the northerncentral part of Euboea have links with those of the eastern Greek coastal chain, where *Atticiella* occurs.

Distribution. Greece. Attica, caves of Mount Hymettos, on the suburbs of Athens.

Species

Atticiella lindbergi Coiffait, 1955
Atticiella Lindbergi Coiffait, 1955c: 209.
Atticiella lindbergi Coiffait: Perreau, 2000: 223.

3.1.5 *Incertae sedis* in Clade ***Sophrochaeta***

3.1.5.1 Series ***Radevia*** Giachino & V.B. Guéorguiev, 1996

Diagnosis. A medium sized genus of Leptodirini with bathyscioid facies and body convex or completely flattened. Depigmented.

Head: With an evident and complete occipital carina; anophthalmous.

Antennae: Slender or short or medium length, with the first antennomere shorter than the second one. Club's articles, 7th–11th, not or very enlarged and flattened or not.

Pronotum: Transverse, with maximum width at the base, or just before it. Sides not sinuated posteriorly, but more or less regularly curved.

Elytra: Ovoid, short or slightly elongated. Disc with microsculpture not transversely or only slightly aligned; without parasutural stria.

Legs: Short. Males protarsi pentameres and slightly dilated. Protibiae equipped with a comb on the external edge and an external apical spur. Meso- and metatibiae with or without complete apical basket.

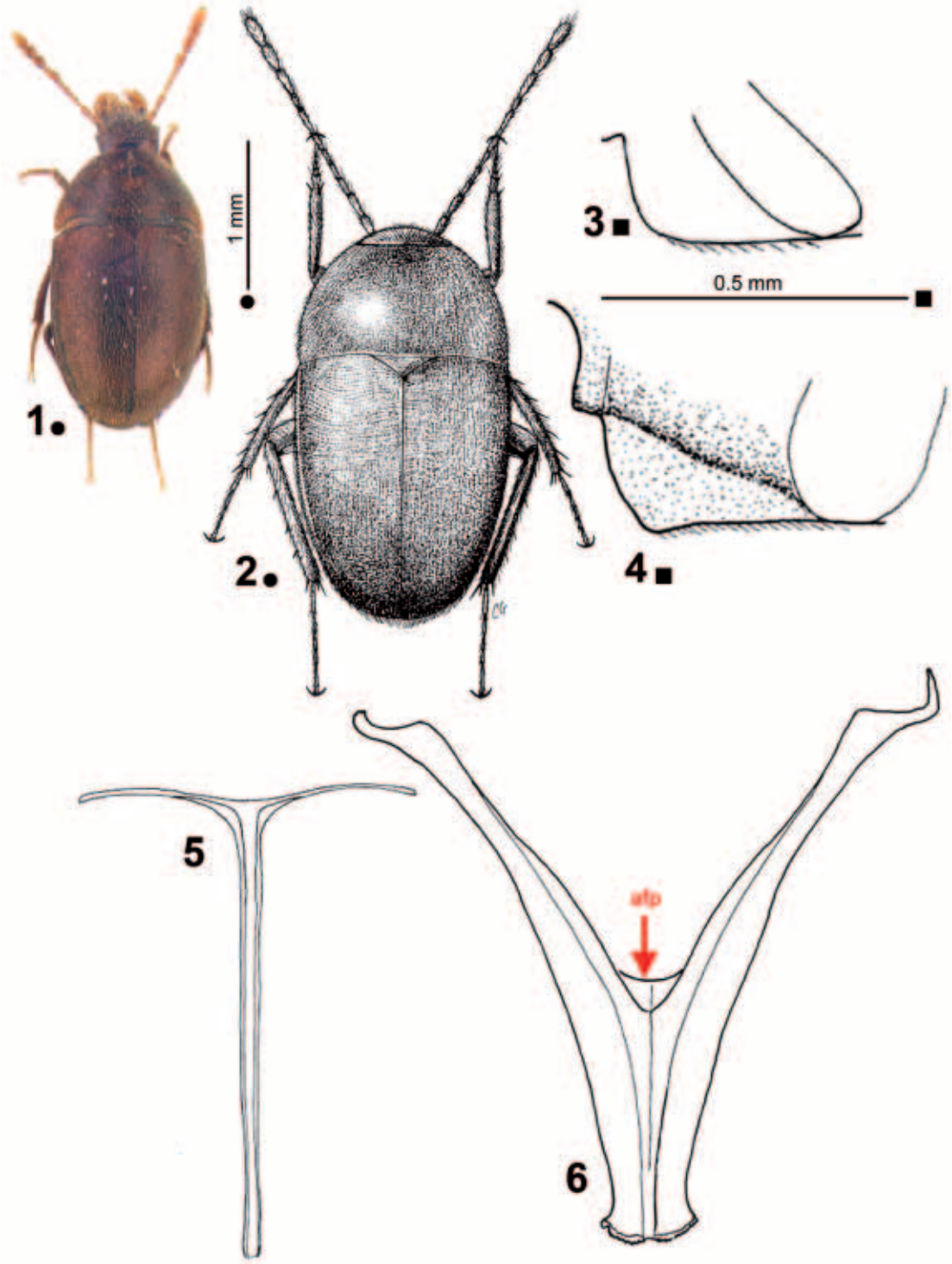
Mesoventral keel (Figs 48.3–48.4): High. Anterior edge subrettilinear or slightly curved, with widely rounded or obtuse and not toothed angle. Not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 48.5): Very developed. Very slender wings of the metascutum. Apophysis of the alacrista very elongated, as long as the elytra and probably involved into the elytral coaptation system. Known only in *Radevia*.

Metendosternite (Fig. 48.6): «V»-shaped, with normally developed furcal trunk and furcal arms very thin. Arms apophysis hooked. Known only in *Radevia*.

Median lobe of aedeagus: Strong, elongated. In lateral view (Figs 49.1–49.2) clearly and more or less sharply arched in the distal half, with apex in shape of an acute hook clearly hooked towards the ventral side. In dorsal view (Figs 49.3–49.4) with sub-trapezoidal, or sub-triangular apex, more or less truncated or weakly bi-lobed. Basal blade short and stout, ¼ long of the median lobe.



FIGURES 48.1–48.6: *Radevia* series. Habitus of: (**1**) *Beskovia bulgarica,* (**2**) *Radevia hanusi*. Pterothorax in lateral view of: (**3**) *B. tranteevi* (modified from Giachino & B.V. Guéorguiev 2008), (**4**) *R. hanusi*. Metatergal apparatus, ventral view of the metanotum and axillaria of (**5**) *R. hanusi.* Metendosternite of (**6**) *R. hanusi*. Figs **2**, **4–6** modified from Giachino & V.B. Guéorguiev (1996). Abbreviations: **afp**, anterior furcal plate (Opitz 2019).

Endophallus (Figs 49.3–49.4): Basal area with two sclerotized branches, sometimes simple, sometimes equipped with paired, dentiform, structures, or simply joined together by a semicircular, moderately sclerotized, posterior band. Median area with two long silky or toothed phanerae.

Parameres (Figs 49.5–49.6): Shorter than the median lobe. Carrying three sub-equal setae in apical and subapical position.

Spermathecal complex (Figs 50.1–50.3): Spematheca kidney-shape, very elongated and completely sclerotized. Very long to long ductus without dilation. Spermathecal gland small in size.

Female uroventrite VIII (Figs 50.4, 50.5): Transverse, with short and sturdy spiculum.

Discussion. The phyletic series of *Radevia* was defined by Giachino & V.B. Guéorguiev (1996) on a purely morphological basis: on the genital characters (both male and female) and on the characters of the protibial armature characterised by the presence of a comb and an external apical spur, usually absent in genera exhibiting a protibial comb (Jeannel, 1924a; V.B. Guéorguiev, 1976). The peculiar shape of the metatergal apparatus, with apophysis of the alacrista very elongated, as long as the elytra, is identical to the model of the *Balcanobius* series; despite the different external morphology, a closed relationship of these two series is postulated, *Radevia* and *Balcanobius*; this hypothesis was confirmed by Giachino & B.V. Guéorguiev (2008). On the other hand, the anterior furcal plate of the metendosternite found in *Radevia* (the *Beskovia* metendosternite is not known) is also found in *Netolitzkya* and is unknown in *Hexaurus*. This peculiarity of the metendosternite is not frequent among the Leptodirini. However, it has been described as an element found in the *Leptodirus* series such as *Astagobius*, *Bathyscimorphus*, *Bathysciotes* or *Leptodirus*. It is considered a plesiomorphy as it is the norm in the other tribes of Cholevinae and is therefore not useful for establishing parentage relationships.

The presence of a protibial comb in the phyletic line of *Radevia* represents the character that separates it from the lineage of *Sophrochaeta* (Giachino & V.B. Guéorguiev, 1996). No molecular data are available.

Key to genera

1. Body length, 1.8–2.2 mm. Elytra without transverse striolae. Meso- and metatibiae with complete apical basket. Median lobe of aedeagus in dorsal view (Fig. 49.3), with sub-trapezoidal or sub-triangular and asymmetric apex more or less truncated and more or less emarginated. Endophallus (Fig. 49.3) with two sclerotized branches in the basal region, sometimes equipped with paired and dentiform structures; in the median region with two long silky phanerae, which surround a ventral tubular structure .....*Beskovia*
- Body length, 2.6–2.9 mm. Elytra with transverse striolation not very evident in the basal part. Meso- and metatibiae without apical basket. Median lobe of aedeagus in dorsal view (Fig. 49.4), with abrupt curvature of the apical part makes the apex appear as weakly bi-lobed. Endophallus (Fig. 49.4) with two sclerotized branches in the basal region that join to form an inverted «Y» structure; in the median region with two rows of toothed phanerae, larger the apical ones.....*Radevia*

Genus ***Beskovia*** V.B. Guéorguiev, 1960
Beskovia V.B. Guéorguiev, 1960b: 723.

Type species. *Beskovia bulgarica* V.B. Guéorguiev, 1960 by original designation (habitus in Fig. 48.1).

Diagnosis. Medium size, 1.8–2.2 mm; bathyscioid shape (Fig. 48.1).

Head: With elongated and evident occipital carina.

Antennae: Short, slender, with the first antennomere shorter than the second one; the club's articles, 7th–11th, very enlarged and flattened; the 8th small and sub-square.

Pronotum: Transverse, with the maximum width just before the base. Sides not sinuated posteriorly, but more or less regularly curved; subrectilinear base.

Elytra: Ovoid, slightly elongated, with the maximum width around the forequarter. Disc with microsculpture not transversely aligned; without parasutural stria.

Legs: Short and slender. Males protarsi pentameres and slightly dilated. Protibiae equipped with a promiment comb on the external edge and a simple external apical spur. Meso- and metatibiae with complete apical basket.

Mesoventral keel (Fig. 48.3): High. Anterior edge subrectilinear with widely rounded, fuzzy angle and nontoothed vertex. Not prolonged on the metaventrite

Suture of the metaventrite. *Metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Strong, elongated. In lateral view (Fig. 49.1) clearly and more or less sharply arched in the distal half, with the apex delimited by an indentation and ending with a hook oriented

towards the ventral face. In dorsal view (Fig. 49.3) with sub-trapezoidal or sub-triangular and asymmetric apex more or less truncated and more or less emarginated. Basal blade short and stout, ¼ long of the median lobe.

Endophallus (Fig. 49.3): Basal area with two sclerotized branches, sometimes equipped with paired and dentiform structures; sometimes simply joined together by a semicircular and moderately sclerotized, posterior band. Median area with two long silky phanerae, which surround a ventral tubular structure.

Parameres (Fig. 49.5): Thin and shorter than the median lobe. Carrying three setae: one, long, apical and two, short, subapical internal.

Spermathecal complex (Figs 50.1, 50.2): Spematheca kidney-shape, very elongated and completely sclerotized, with distal and basal lobes of similar thickness. Very long ductus without dilatation. Spermathecal gland small in size. In *Beskovia bulgarica* the area of the joining duct is hyaline. (Fig. 50.2).

Female uroventrite VIII (Fig. 50.4): Very transverse, with short and sturdy spiculum; middle part of the apical margin slightly concave, with darkened edge.

Discussion. Several morphological characters suggest that the genus *Beskovia* is phylogenetically close to *Radevia*, it seems to constitute a monophyletic unit well characterised by: Median lobe of aedeagus, in lateral view, abruptly flexed at the apex (Figs 49.1, 49.2); a similar morphology of the endophallus (Figs 49.3, 49.4); a particularly elongated spermatheca (Figs 50.1–50.3); the presence of a comb to the protibiae (there is only a sketch in *Radevia*). Due to the lack of molecular data this is so far good evidence for this postulated relationship.

Distribution. Bulgaria. Stara Planina.

Species

Beskovia beroni Giachino & B.V.Guéorguiev, 2008
Beskovia beroni Giachino & B.V. Guéorguiev, 2008: 86.

Beskovia bulgarica V.B. Guéorguiev, 1960
Beskovia bulgarica V.B. Guéorguiev, 1960b: 723.

Beskovia tranteevi Giachino & B.V. Guéorguiev, 2008
Beskovia tranteevi Giachino & B.V. Guéorguiev, 2008: 88.

Genus ***Radevia*** Knirsch, 1925
Radevia Knirsch, 1925b: 60.
Vratzaniola Dupré, 2000: 158 (Type species. *Vratzaniola pandurskii* Dupré, 2000).

Type species. *Radevia Hanuši* Knirsch, 1925 by monotypy (habitus in Fig. 48.2).

Diagnosis. Medium size, 2.6–2.9 mm, with bathyscioid facies but with a flattened body (Fig. 48.2).

Head: Sub-square, slightly longer than wide; complete occipital carina.

Antennae: Medium length, slight exceeding the half of the elytra. First antennomere shorter than the second one; the 8th non-transverse, elongated; antennomeres of the antennal club, 7th–11th, not enlarged or flattened; the 11th the longest of all.

Pronotum: Transverse, with the maximum width at the base, which is as wide as the base of the elytra, and sides not sinuate posteriorly.

Elytra: Short oval, with the maximum width at the base; regularly rounded and narrowed from the base to the apex. Disc with weakly transversely aligned punctation and absent parasutural stria. Lateral furrow particularly evident in the apical half.

Legs: Short. Male protarsi pentamerous and slightly dilated. Protibiae provided with only one, stout, apical spur on the external side, and with a short external, ventro-lateral, preapical comb. Meso- and metatibiae without apical basket.

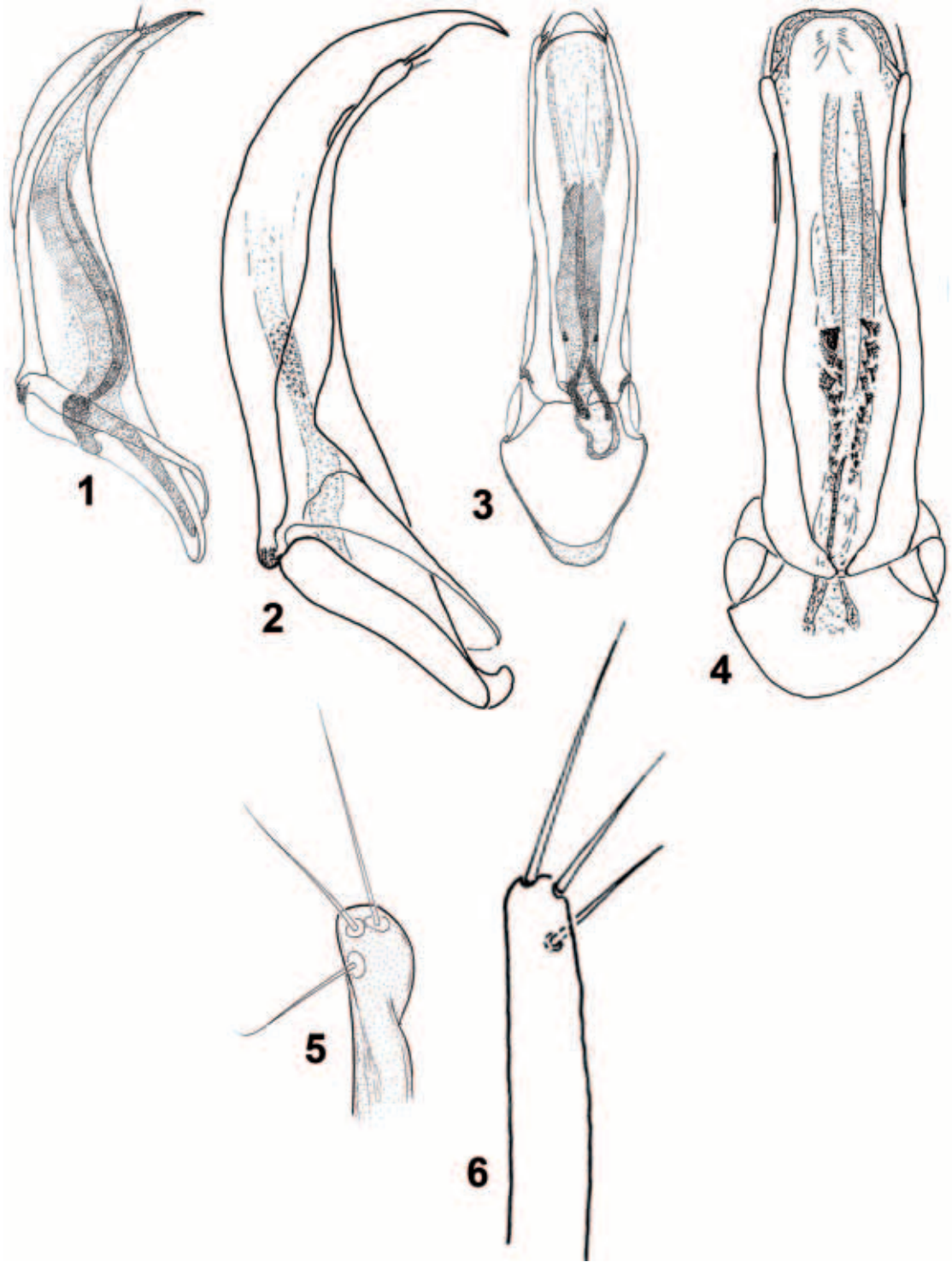
Mesoventral keel (Fig. 48.4): High, with slightly curved front edge forming an obtuse angle, not toothed, and margin ventrally slightly sinuous and pubescent. Not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 48.5): Very slender wings of the metascutum. The apophysis of the alacrista very elongated, as long as the elytra and probably involved into the elytral co-aptation system.

Metendosternite (Fig. 48.6): «V»-shaped, with normally developed furcal trunk and furcal arms very thin. Arms a little more than one and a half times longer than the trunk. Arms with apophysis hooked. With anterior furcal plate. Furcal trunk almost twice as long as the maximum width at the base.

Median lobe of aedeagus: In lateral view (Fig. 49.2), strongly and sharply arched starting from the apical third, with a stout and clearly hooked apex towards the ventral side. In dorsal view (Fig. 49.4), the abrupt curvature of the apical part makes the apex appear weakly bi-lobed.



FIGURES 49.1–49.6: *Radevia* series. Aedeagus in lateral view of: (**1**) *Beskovia tranteevi*, (**2**) *Radevia hanusi*. Aedeagus in dorsal view of: (**3**) *B. tranteevi*, (**4**) *R. hanusi*. Apex of the paramere of: (**5**) *B. tranteevi,* (**6**) *R. hanusi*. Figs **1**, **3** modified from Giachino & B.V. Guéorguiev (2008); Figs **2**, **4**, **6** modified from Giachino & V.B. Guéorguiev (1996).

Endophallus (Fig. 49.4): With two sclerotized branches that join to form an inverted «Y» structure in the basal region and two rows of toothed phanerae in the median region; apical region with two narrow and long reinforcing bands.

Parameres (Fig. 49.6): In dorsal view, sinuous and normal thickness, shorter than the median lobe. Equipped with three sub equal setae: one apical, another one internal, subapical, and a third one ventral, slightly set back from the second one.

Spermathecal complex (Fig. 50.3): Spermatheca elongated, completely sclerotized, clearly lobed at the distal end, no difference between the union part and the basal lobe. Duct moderately long, slightly dilated in the area of attachment to the spermatheca and in the anterior part; spermathecal gland hyaline and shapeless.

Female uroventrite VIII (Fig. 50.5): With the anterior edge slightly curved and spiculum short, subtriangular.

Discussion. Several characters bring the *Radevia* genus close to *Beskovia*, with which, in the absence of molecular data, it seems to constitute a monophyletic unit. See the Discussion section of *Beskovia*.
Distribution. Bulgaria. Stara Planina.

Species

Radevia hanusi Knirsch, 1925
Radevia Hanuši Knirsch, 1925b: 61.
Vratzaniola pandurskii Duprè, 2000: 162.
Radevia hanuši Knirsch: Perreau, 2000: 293.

3.1.5.2 Series ***Balcanobius*** V.B. Guéorguiev, 1965

Diagnosis. Large sized Leptodirini, with scaphoid facies, clearly elongated. Depigmented.

Head: Elongated, without occipital carina; anophthalmous.

Antennae: Inserted in the middle third of the head. Very elongated, much longer than the apex of the elytra; first antennomere shorter than the second one.

Pronotum: Longer than wide; lateral sides sinuate posteriorly.

Elytra: Scaphoid, without parasutural stria and transverse striolae.

Legs: Very elongated. Males protarsi pentameres and not dilated. Protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (Figs 52.1): Just outlined as a thin crest, not at all elevated, or completely absent. Not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Figs 52.2, 52.3): With very small, thin, wings of the metascutum. Apophysis of the alacrista very long, reaching the apex of the elytra, but thin and narrow from the basal region.

Metendosternite (Figs 52.4, 52.5): «V»-shaped, with normally developed furcal trunk and furcal arms very thin. Arms apophysis hooked. *Balcanobius* with anterior furcal plate.

Median lobe of aedeagus: Short and sturdy. In lateral view (Figs 53.1, 53.2), sharply bent in the distal third. Apex, subtriangular or largely rounded in dorsal view (Figs 53.3, 53.4). Basal blade of «normal» size.

Endophallus (Figs 53.4, 53.5): Basal «Y»-piece small, with dorsal branches terminating in a flagellum; the «Y»-piece is surrounded by two chitinised phanerae. The median region is characterised by the presence of two dorsal phanerae, of different shape, formed by aggregated bundles of spines.

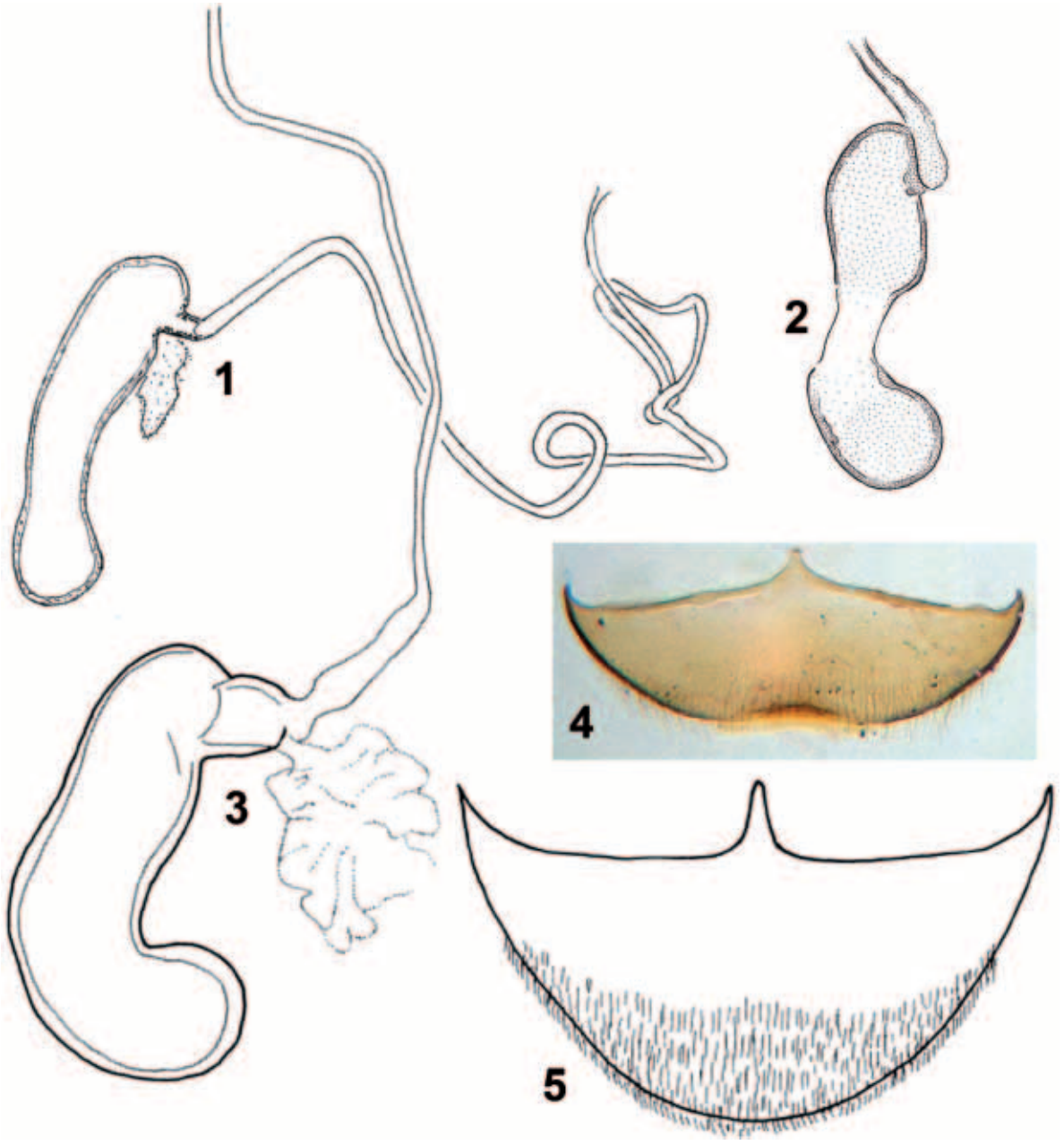
Parameres (Figs 53.6, 53.7): Thin, clearly shorter than the median lobe. Carrying three setae, two apical and one sub-apical.

Spermathecal complex (Fig. 54.1, 54.2): Spermatheca elongated, with moderately prominent lobes. Ductus of medium length, sturdy, more or less dilated and sclerotized at the insertion into the spermatheca. Spermathecal gland shapeless, hyaline.

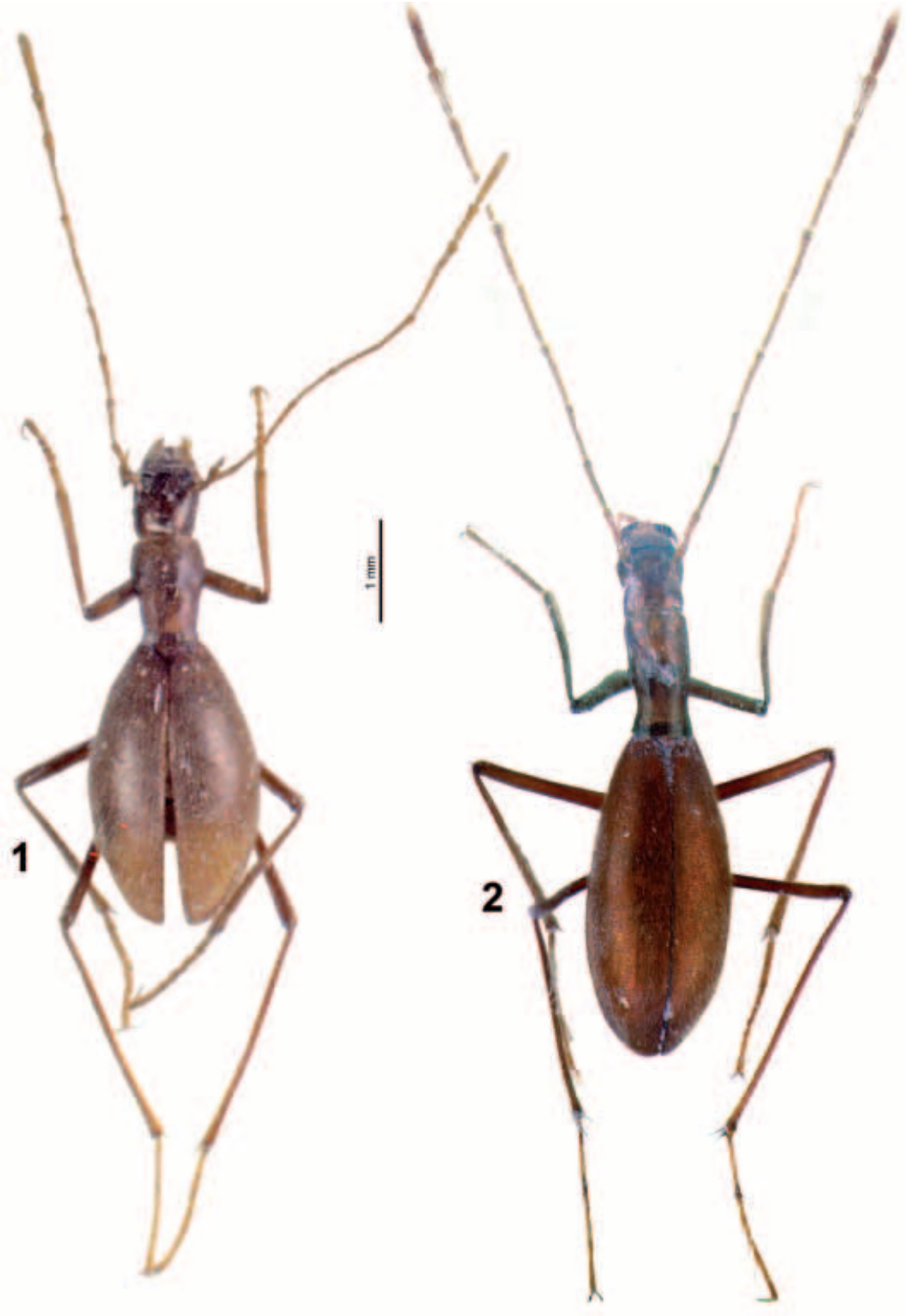
Female uroventrite VIII (Fig. 54.3, 54.4): Crescent-shaped or not, with ventro-anterior edge from very curved to subrectilinear and spiculum slender or stout.

Discussion. This series was defined on a morphological basis by V.B. Guéorguiev (1965a) and confirmed by Giachino (1992) and Giachino & B.V. Guéorguiev (2008). No molecular data are available.

The shape of the metatergal apparatus, with a very narrow and very elongated apophysis of the alacrista, and the metendosternite, with the furcal arms hook-shaped. these characters allow to place the *Balcanobius* lineage closer to that of *Radevia*, which are considered to be part of the *Sophrochaeta* phyletic series. However, in the moment these seem to bethe only apparent similarities between morphologically very different genera. The diffierences also concerncharacters considered relevant forphyletically placement, such as the shape of the aedeagus. In this sense, these two phyletic lineages taken into account here, even though it became clear that resolving the relationship will only succeed once molecular data of these taxa will be available.



FIGURES 50.1–50.5: *Radevia* series. Spermathecal complex of: (**1**) *Beskovia tranteevi* (modified from Giachino & B.V. Guéorguiev 2008), (**2**) *B. bulgarica*, (**3**) *Radevia hanusi*. Female uroventrite VIII of: (**4**) *B. bulgarica*, (**5**) *R. hanusi*. Figs **3**, **5** modified from Giachino & V.B. Guéorguiev (1996).



FIGURES 51.1–51.2: *Balcanobius* series. Habitus of: (**1**) *Balcanobius etropolensis* modified from [https://www.nmnhs.com/e-natura/types-bulgaria/type_id_en-NMNHSINV0081.html], Types in the natural history collections in Bulgaria, *Balcanobius etropolensis* V.B. Gueorguiev, 1965, specimen NMNHSINV0081, (**2**) *Genestiellina gueorguievi*.

KEY TO GENERA

1. Body length, 4.4–4.8 mm. Mesoventral keel formed by a thin crest, not at all elevated. Median lobe of aedeagus in dorsal view (Fig. 53.3) with apex broadly rounded and an elongated fossette in the apical middle part. Endophallus (Fig. 53.5) with «Y»-shaped piece in the basal region surrounded by two long chitinised phanerae; median region with two long, lateral, chitinised phanerae, which in the median part exhibit two additional arched dorsal phanerae forming an in inverted «V», these carryingcarrying on the inner face spiny scales. FEMALE UROVENTRITE VIII (Fig. 54.3) crescent-shaped, with very curved ventro-anterior edge and spiculum small and slender .....*Balcanobius*
- Body length, 4.8–5.9 mm. Mesoventral keel non-existent (Fig. 52.1). Median lobe of aedeagus in dorsal view (Fig. 53.4) with subtriangular apex. Endophallus (Fig. 53.4) with «Y»-piece in the basal region surrounded by two short chitinised phanerae; median region with two short, not arched, dorsal phanerae formed by aggregated bundles of spines. FEMALE UROVENTRITE VIII (Fig. 54.4) not crescent-shaped, with subrectilinear ventro-anterior edge and spiculum large and stout .....*Genestiellina*

Genus ***Balcanobius*** V.B. Guéorguiev, 1965
Balcanobius V.B. Guéorguiev, 1965a: 393.

TYPE SPECIES. *Balcanobius etropolensis* V.B. Guéorguiev, 1965 by original designation (habitus in Fig. 51.1).

DIAGNOSIS. Large size, 4.4–4.8 mm, with scaphoid facies, clearlyclearly elongated (Fig. 51.1).

Head: Elongated, without occipital carina.

Antennae: Very elongated, much longer than the apex of the elytra; first antennomere shorter than the second one; the 11th being the longest of all.

Pronotum: Longer than wide, narrower at the base than anteriorly and the maximum width at the anterior third. Lateral sides narrow and sinuate posteriorly.

Elytra: Scaphoid, without transverse striolae and without parasutural stria.

Legs: Very elongated. Male protarsi pentameres and not dilated. Protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (V.B. Guéorguiev 1965a): Just outlined as a thin crest, not at all elevated. Not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 52.2): With very small, thin, wings of the metascutum. Apophysis of the alacrista very long, reaching the apex of the elytra, but thin and narrow from the basal region.

Metendosternite (Fig. 52.4): «V»-shaped, with normally developed furcal trunk and furcal arms very thin, slightly longer than the trunk; arms apophysis hooked. With a reduced anterior furcal plate.

Median lobe of aedeagus: Short and sturdy. In lateral view (Fig. 53.1) sharply bent in the distal third; apical part similar to a duck's hook. Apex broadly rounded in dorsal view (Fig. 53.3) and an elongated fossette in the apical middle part. Basal blade of «normal» size.

Endophallus (Fig. 53.5): Basal «Y»-piece small with dorsal branches terminating in a flagellum, nearly as long as the median lobe; the «Y»-piece is surrounded by two long chitinised phanerae. The median and distal region is characterised by the presence of two long, lateral and chitinised phanerae, with the addition, in the median area, of two dorsal phanerae, arched, in inverted «V», and carrying on the inner face, spiny scales.

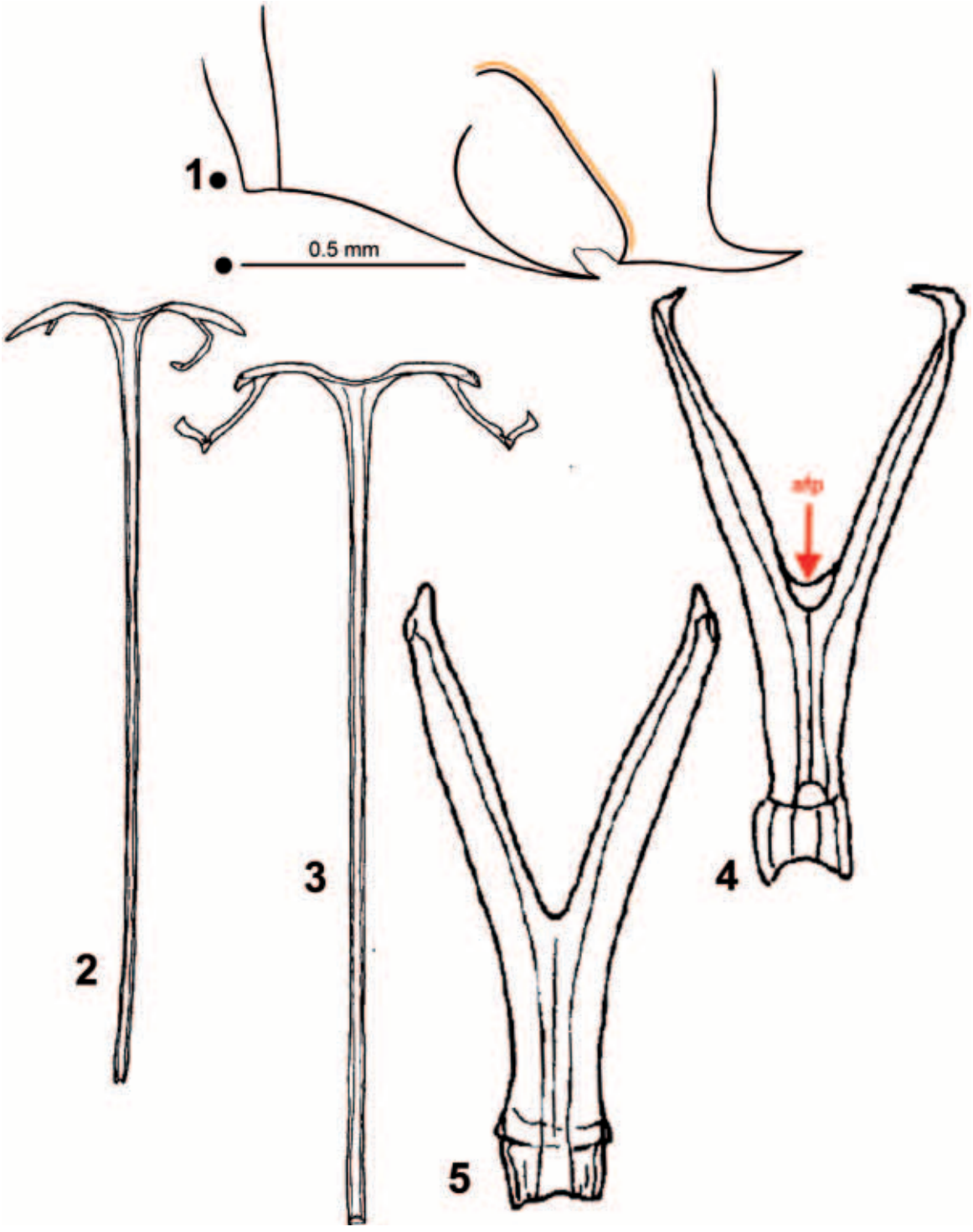
Parameres (Fig. 53.6): Thin, clearly shorter than the median lobe. Carrying three setae, two apical and one sub-apical, clearly distant. Spermatheca (Fig. 54.1) elongated and well sclerotized, with moderately evident lobes; union duct long, somewhat narrower than the lobes.

Spermathecal complex: Spermatheca (Fig. 54.1) with ductus of medium length, sturdy, dilated and well sclerotized at the insertion into the spermatheca. Spermathecal gland shapeless, hyaline.

Female uroventrite VIII (Fig. 54.3): Crescent-shaped, with very curved ventro-anterior edge and spiculum small and slender.

DISCUSSION. At the time of the description V.B. Guéorguiev (1965a) compares *Balcanobius* to the genera *Spelaeodromus* and *Speoplanes* based on the scaphoid shape of the body. This hypothesis was then deepened by Giachino (1992) when describing the genus *Genestiellina*, who discussed in detail some characters and established a separate phyletic lineage including *Balcanobius* and *Genestiellina*. Wioth this refraining from phyletic considerations apparently premature and invalid. This approach was then confirmed by Giachino & B.V. Guéorguiev (2008). In the absence of molecular data and the complex situation by placing the genus by morphology alone this genus was not part of thephylogenetic hypotheses.

DISTRIBUTION. Bulgaria. Central Stara Planina



FIGURES 52.1–52.4: *Balcanobius* series. Pterothorax of: (**1**) *Genestiellina gueorguievi*. Metatergal apparatus of: (**2**) *Balcanobius etropolensis,* (**3**) *G. gueorguievi*. Metendosternite of: (**4**) *B. etropolensis,* (**5**) *G. gueorguievi.* Figs **2**–**4** modified from Giachino (1992). Abbreviations: **afp**, anterior furcal plate.

Species

Balcanobius etropolensis V.B. Guéorguiev, 1965
Balcanobius etropolensis V.B. Guéorguiev, 1965a: 395.

Genus ***Genestiellina*** Giachino, 1997
Genestiella Giachino, 1992: 316 (*Nom. praeocc*. Homonymy with *Genestiella* Fennah, 1969 – Hemiptera –).
Genestiellina Giachino, 1997 [1996]: 167 (*Nomen novum*).

Type species. *Genestiella gueorguievi* Giachino, 1992 by original designation (habitus in Fig. 51.2).

Diagnosis. Large size, 4.8–5.9 mm, with scaphoid facies, clearly elongated (Fig. 51.2).

Head: Elongated, without occipital carina.

Antennae: Very elongated, much longer than the apex of the elytra; first antennomere shorter than the second one.

Pronotum: Longer than wide, larger at the base than in the anterior part and with a maximum width near the base. Lateral sides sinuate posteriorly.

Elytra: Scaphoid, without transverse striolae and parasutural stria.

Legs: Very elongated. Males protarsi pentameres and not dilated. Protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 52.1): Completely absent.

Suture of the metaventrite (Fig. 52.1): Parallel to the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 52.3): With very small, thin wings of the metascutum. Apophysis of the alacrista very long, reaching the apex of the elytra, but thin and narrow from the basal region.

Metendosternite (Fig. 52.5): «V»-shaped, with the furcal arms slender and somewhat longer than the trunk, the furcal posterior plate almost of similar width on arms and trunk; arms apophysis little hooked. Long furcal trunk, almost three times longer than wide.

Median lobe of aedeagus: Short and sturdy. In lateral view (Fig. 53.2) sharply bent in the distal third. Apex subtriangular in dorsal view (Fig. 53.4). Basal blade of «normal» size.

Endophallus (Fig. 53.4): Basal «Y»-piece small with dorsal branches terminating in a flagellum, nearly as long as the middle of the median lobe; the «Y»-piece is surrounded by two short chitinised phanerae. The median region is characterised by the presence of two short and not arched dorsal phanerae formed by aggregated bundles of spines.

Parameres (Fig. 53.7): Thin, clearly shorter than the median lobe. Carrying three setae, two apical and one sub-apical.

Spermathecal complex (Fig. 54.2): Spermatheca elongated and well sclerotized, with moderately evident lobes; union duct long, somewhat narrower than the lobes. Ductus of medium length, sturdy, poorly dilated and poorly sclerotized at the insertion into the spermatheca. Spermathecal gland shapeless, hyaline.

Female uroventrite VIII (Fig. 54.4): Not crescent-shaped, with subrectilinear ventro-anterior edge and short, wide, rounded and robust spiculum.

Discussion. Giachino (1992) when describing the genus *Genestiellina* discussed in detail some characters and established a separate phyletic lineage including *Balcanobius* and *Genestiellina*. This meant withdrawal of early and apparently premature phyletic placement deemed premature. This finding was later confirmed by Giachino & B.V. Guéorguiev (2008). In the absence of molecular data, the group was not included in the general approach described here.

Distribution. Bulgaria: Central Stara Planina.

Species

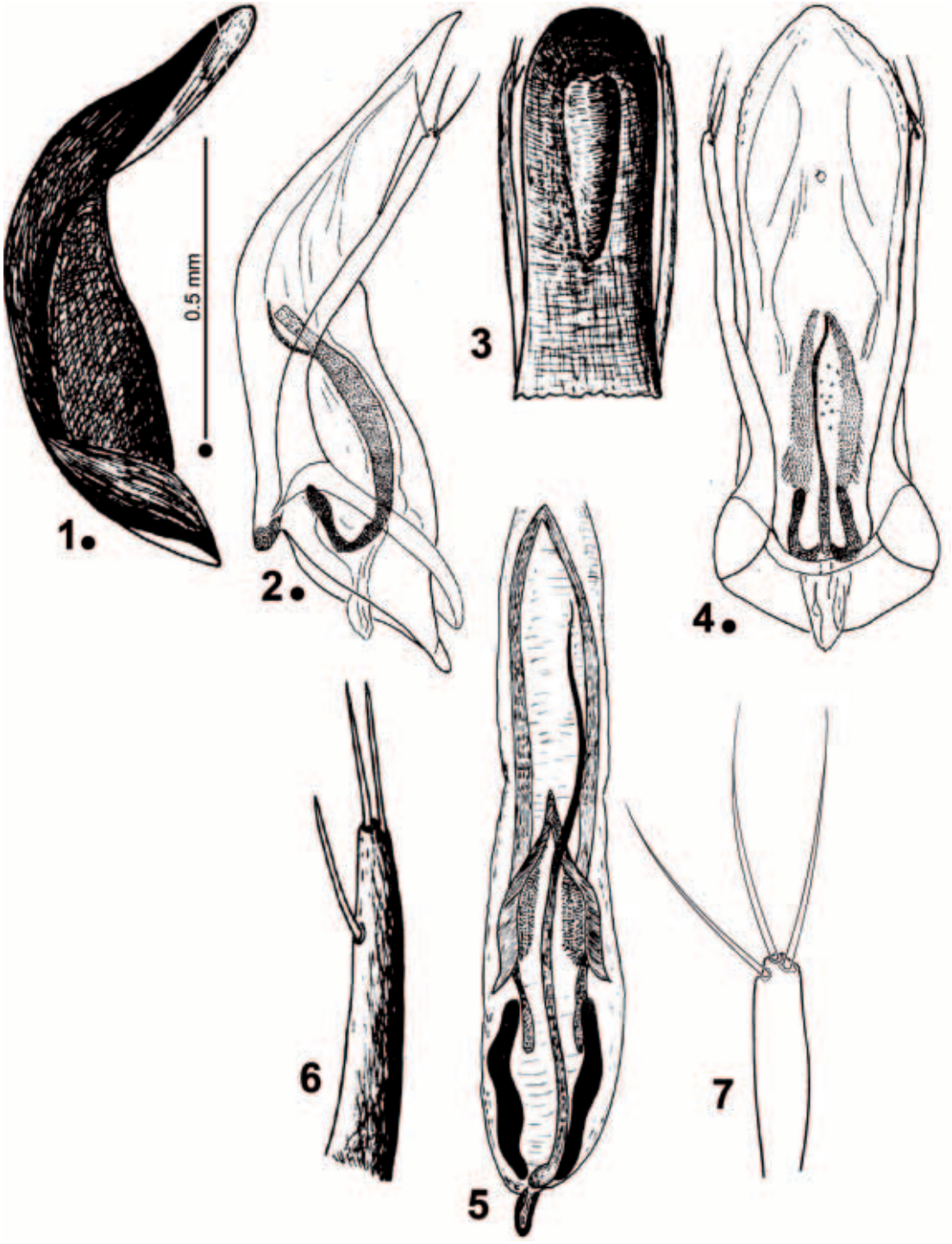
Genestiellina gueorguievi (Giachino, 1992)
Genestiella gueorguievi Giachino, 1992: 320.
Genestiellina gueorguievi Giachino: Giachino, 1997: 167.

3.1.5.3 Series ***Beronia*** Giachino & B.V. Guéorguiev, 2008

This series was defined on morphology by Giachino & B.V. Guéorguiev (2008). No molecular data are available. As a monogeneric series the characters of the series were used for the classification. See genus discussion

Genus ***Beronia*** V.B. Guéorguiev, 1960
Beronia V.B. Guéorguiev, 1960a: 607.

Type species. *Beronia micevi* V.B. Guéorguiev, 1960 by original designation (habitus in Fig. 55.1).
Diagnosis. Medium sized Leptodirini, 2.2–3.0 mm. Bathyscioid facies (Fig. 55.1); body oval, more or less elongated, convex and with pronotum not, or much narrower than the elytra. Semi-shiny integuments, uniformly covered by golden pubescence, of medium length and lying down.



FIGURES 53.1–53.7: *Balcanobius* series. Aedeagus in lateral view of: (**1**) *Balcanobius etropolensis*, (**2**) *Genestiellina gueorguievi*. Aedeagus in dorsal view of: (**3**) *B. etropolensis*, (**4**) *G. gueorguievi*. Endophallus of: (**5**) *B. etropolensis*. Apex of the paramere of: (**6**) *B. etropolensis*, (**7**) *G. gueorguievi* (redrawn from Giachino 1992). Figs **1**, **3**, **5**, **6** modified from V.B. Guéorguiev (1965); Figs **2**, **4** modified from Giachino (1992).

Head: Elongated, with evident occipital carina; anophthalmous.

Elytra: Ovoid, sturdy or very elongated, with maximum width approximately at the anterior third, or at half length, separately and regularly rounded distally. Convex disc, with microsculpture aligned in transverse striolae. Parasutural stria absent.

Antennae: Short or long segements, slender, just reaching or exceeding half of the elytra stretched backwards; with slightly flattened club; second antennomere much longer than the first one.

Pronotum: More or less transverse, with maximum width at the base or just ahead of it. Base about as wide as the elytral base or significantly narrower than the same. Sides not sinuated posteriorly.

Legs: Short or long segements andslim. Protarsi pentameres, only very few dilated in the male; protibiae without comb, slightly club-like and provided with three external spurs; meso- and metatibiae straight and devoid of apical basket.

Mesoventral keel (Fig. 55.2): High and not prolonged on the metaventrite; anterior edge more or less regularly arched, with a more or less widely toothed vertex.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Robust, very elongated and regularly arched. In lateral view (Fig. 55.3) regularly arched ventrally; apex in the form of a sharp hook, slightly emarginated or deeply saddle-like dorsally. In dorsal view (Fig. 55.4) stout with a truncated or rounded subtriangular apex, and with sides regularly converging at the apex. Basal blade elongated in a narrow apophysis almost as long as the median lobe.

Endophallus (Fig. 55.4): Peculiarly shaped, with a large basal bulb, characterised by a long prolonged ejection of the seminal duct (partially sclerotized), well beyond the base of the median lobe and up to about the middle of the basal blade of the median lobe. From the basal bulb to the apex, the entire length of the endophallus is k´lined by a long phanera carrying an uneven median row of dorsal teeth. There is a flagelliform structure inserts ventrally and coiled in the distal part.

Parameres (Fig. 55.5): Clearly shorter than the median lobe, relatively robust and carrying two setae: one, very long, apical and another one shorter, subapical, internal.

S*permathecal complex* (Fig. 55.6): Spermatheca, elongated, slightly sclerotized, distally enlarged, with undifferentiated junction duct and basal lobe; very long and thin spermiduct which has a small nodule at the attachment to the spermatheca and a small hyaline spermathecal gland.

Female uroventrite VIII: Unknown.

Discussion. Giachino & B.V. Guéorguiev (2008) assigned on a strictly morphological basis, the genus *Beronia* to a distinct phyletic lineage. No molecular data are available. The peculiar basal blade morphology of the median lobe and the presence of a dorsal flagellum in the endophallus suggests a possible relationship with *Albaniola* (*Ceuthophyes* series) currently undergoing taxonomic revision by Giachino & Vailati (*in prep*.) as part of a monographic contribution on the Leptodirini from Greece. However, it seems equally or even more likely to be related to *Bulgariella*, a genus with which it shares not only a reduced basal blade which is completely covered by the tegmen and stylet or flagellum on the endophallus, but also geographical distribution: both genera are found in Stara Planina, a little further east or a little further west. While species of the polyphyletic genus *Albaniola* (*Ceutophyes* series) are found further south; of all its species, those found in eastern Greece, Rhodopes and Pangaion (*Albaniola casalei*, *Albaniola giachinoi* and *Albaniola macedonica*), could be related to *Beronia*; it seems less justified to propose a relationship with those of Dinaric distribution.

Distribution. Bulgaria, Western Stara Planina.

Species

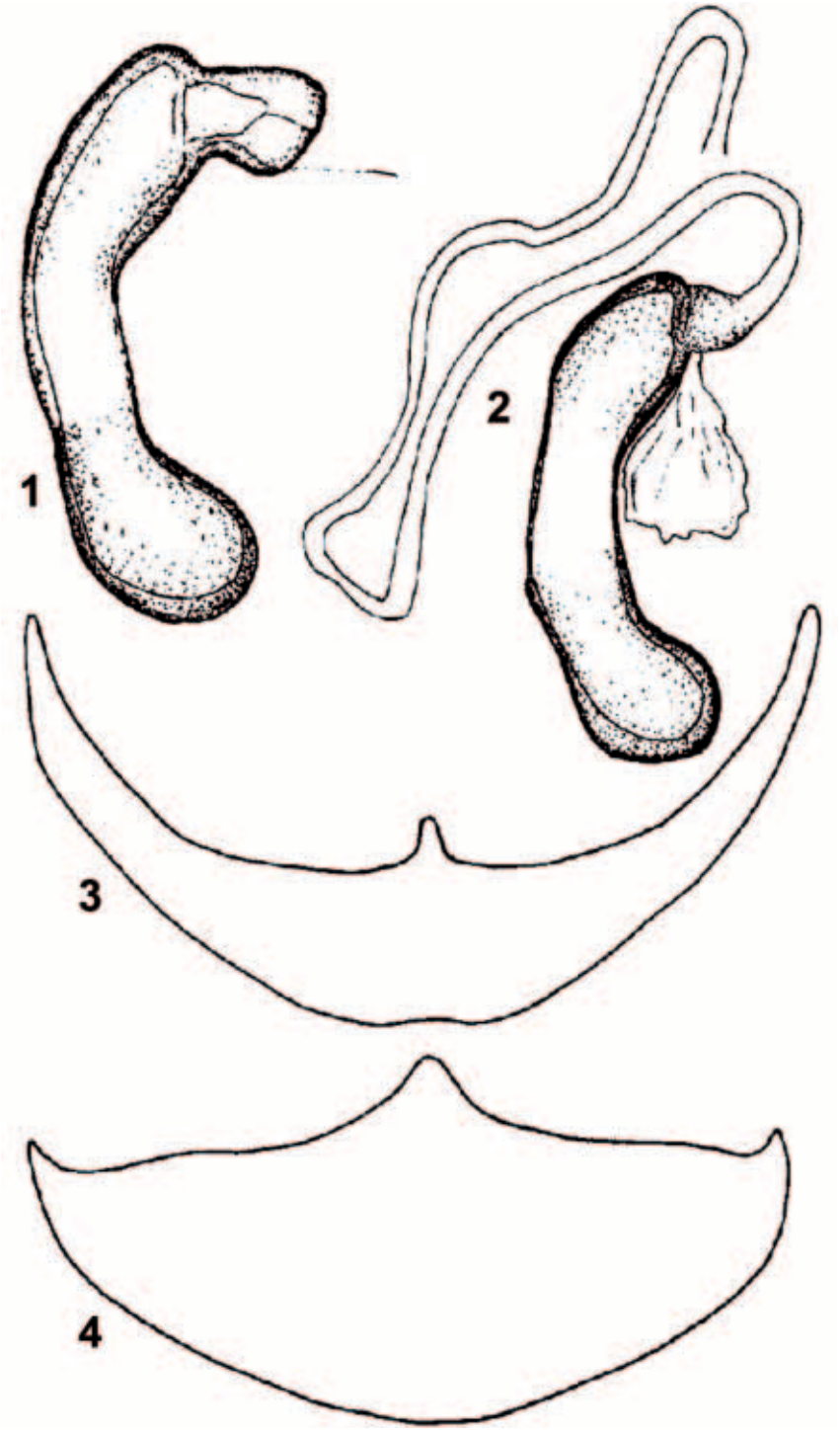
Beronia andreevi Giachino & B.V. Guéorguiev, 2008
Beronia andreevi Giachino & B.V. Guéorguiev, 2008: 94.

Beronia micevi V.B. Guéorguiev, 1960
Beronia micevi V.B. Guéorguiev, 1960a: 608.

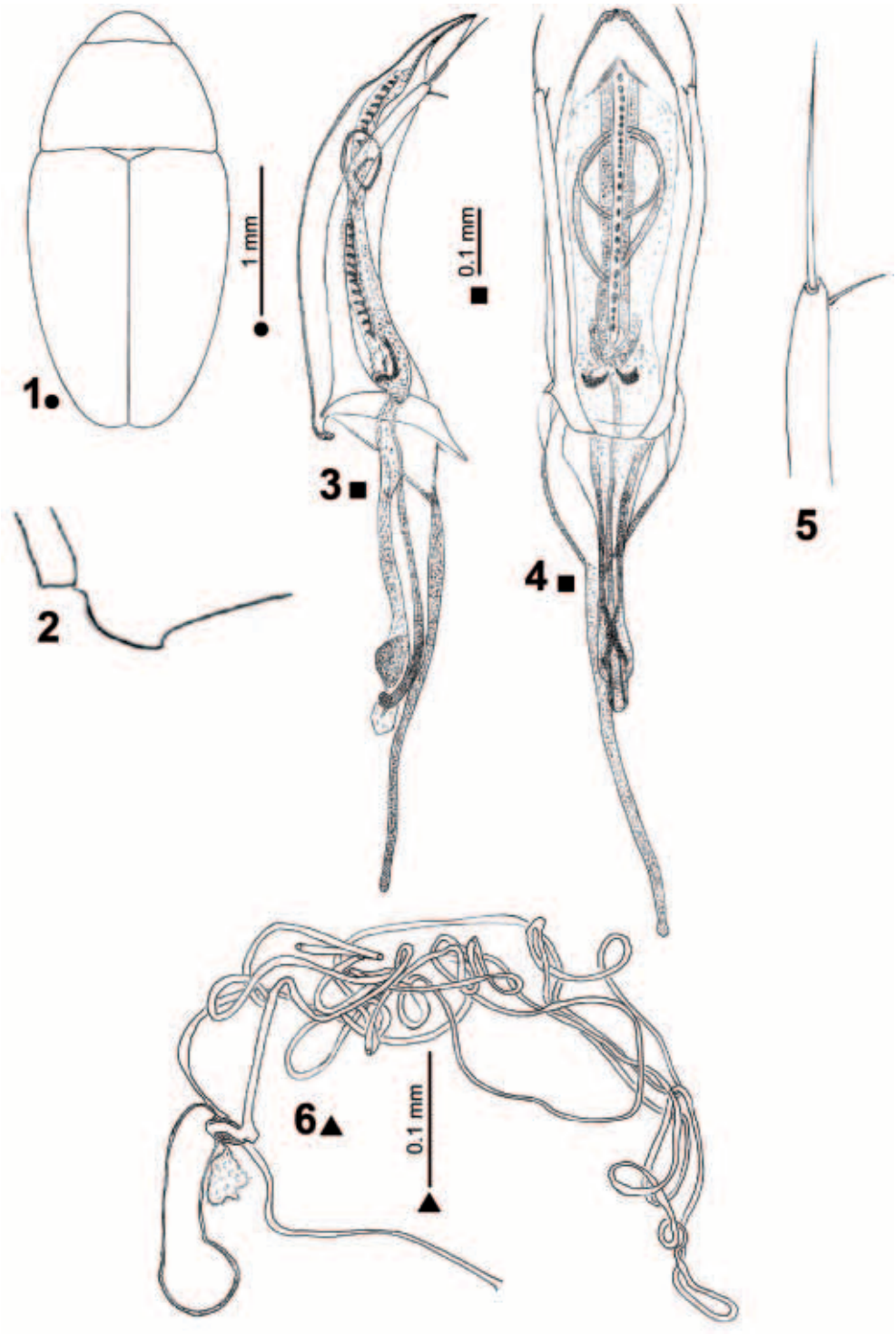
3.1.5.4 Series ***Beroniella***

Monogeneric series, the characters are related in the diagnosis of the genus.

Discussion. Based on the available morphological data, the genus *Beroniella* should also be considered as belonging to the series *Leptodirus*, *Apholeuonus* group (Giachino & B.V. Guéorguiev, 2008). However, its complex armed endophallus coincides with a relatively frequent pattern in taxa distributed by Stara Planina in Bulgaria; also the strongly transverse sclerotized phanerae of the middle region of the endophal-



FIGURES 54.1–54.4: *Balcanobius* series. Spermathecal complex of: (**1**) *Balcanobius etropolensis,* (**2**) *Genestiellina gueorguievi*. Female, uroventrite VIII of: (**3**) *B. etropolensis,* (**4**) *G. gueorguievi*. All figures modified from Giachino (1992).



FIGURES 55.1–55.6: *Beronia* series. *B. micevi*: (**1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of the paramere. (**6**) Spermathecal complex of *B. andreevi*. All figures modified from Giachino & B.V. Guéorguiev (2008).

lus is similar to that of *Beronia*; in addition it shares with *Beronia* and *Bulgariella* a reduced basal blade completely covered by the tegmen. Taxa of the *Apholeuonus* group of the *Leptodirus* series have simpler, sparsely armed, or almost unarmed endophalli (except *Adelopidius*). On the other hand, close phylogenetic relationships between the Balkan and Dinarid faunas appears not likely in general, asthese two mountain massifs are separated by the Tertiary Pannonian basin since the Miocene (Langian, 15.97-13.82 My) (Popov *et al*. 2004). Following the same argument phylogenetic links between *Hexaurus* and *Bathyscia montana* were deemed refuted.

Genus ***Beroniella*** Giachino & V.B. Guéorguiev, 1991
Beroniella Giachino & V.B. Guéorguiev, 1991 [1990]: 193.

Type species. *Beroniella tetevensis* Giachino & V.B. Guéorguiev, 1991 by original designation (habitus in Fig. 56.1).

Diagnosis. Small size, between 1.8–2.2 mm, with bathyscioid facies (Fig. 56.1). Body globose, short, strongly convex and very little narrowed backwards. Integument shiny with very fine, dense and non-aligned punctation. Pubescence fine, short, lying and dense.

Head: Retractable with blurred occipital carina, slightly longer than wide and as wide as the anterior area of pronotum; anophthalmous.

Antennae: Rather long, reach half the length of body, in them club slightly differentiated with antennomeres subcylindrical. First antennomere a little shorter than the second one; 8th antennomere very small and little thickened, almost twice as long as wide; 11th one somewhat longer than the 9th with apex little sharp.

Pronotum: Convex and very transverse, almost twice as wide as long, with lateral edges regularly arcuated. Maximum width very close to base that is narrower than the anterior area of elytra; posterior vertices slightly sharp and acute angles.

Elytra: Ovoid, short and convex, together slightly longer than wide, with the maximum width in the basal third and apical area in rounded arc. Punctation disordered, without transverse striolae and parasutural stria. Abdomen completely covered by elytra.

Legs: Short, quite robust, with fine pubescence; anterior tibiae with an external spur and a comb at apical and external edges. Male protarsi pentameres with the first three tarsomeres dilated, the first one being narrower than the apex of protibia. Pro- and metatibiae straight, mesotibiae arcuated; femora not dilated in apical part.

Mesoventral keel (Fig. 56.2): In lateral view high, laminar, with anterior and ventral edges convex, the latter slightly wavy in posterior part, with short pubescence. In ventral view this area is widened. Vertex widely rounded with obtuse angle. Posterior apophysis is prolonged over a large part of the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and robust. In lateral view (Fig. 56.3), ventral face sharply bended in the apical third; dorsal face in a wide regular arc until the apical fifth, that presents the first part slightly concave, the final part beveled and the apex little sharp. In dorsal view (Fig. 56.4) sides subparallel, apex wide, truncated with a wide and very shallow slit. Basal lamina short with posterior edge broadly arcuated in dorsal view.

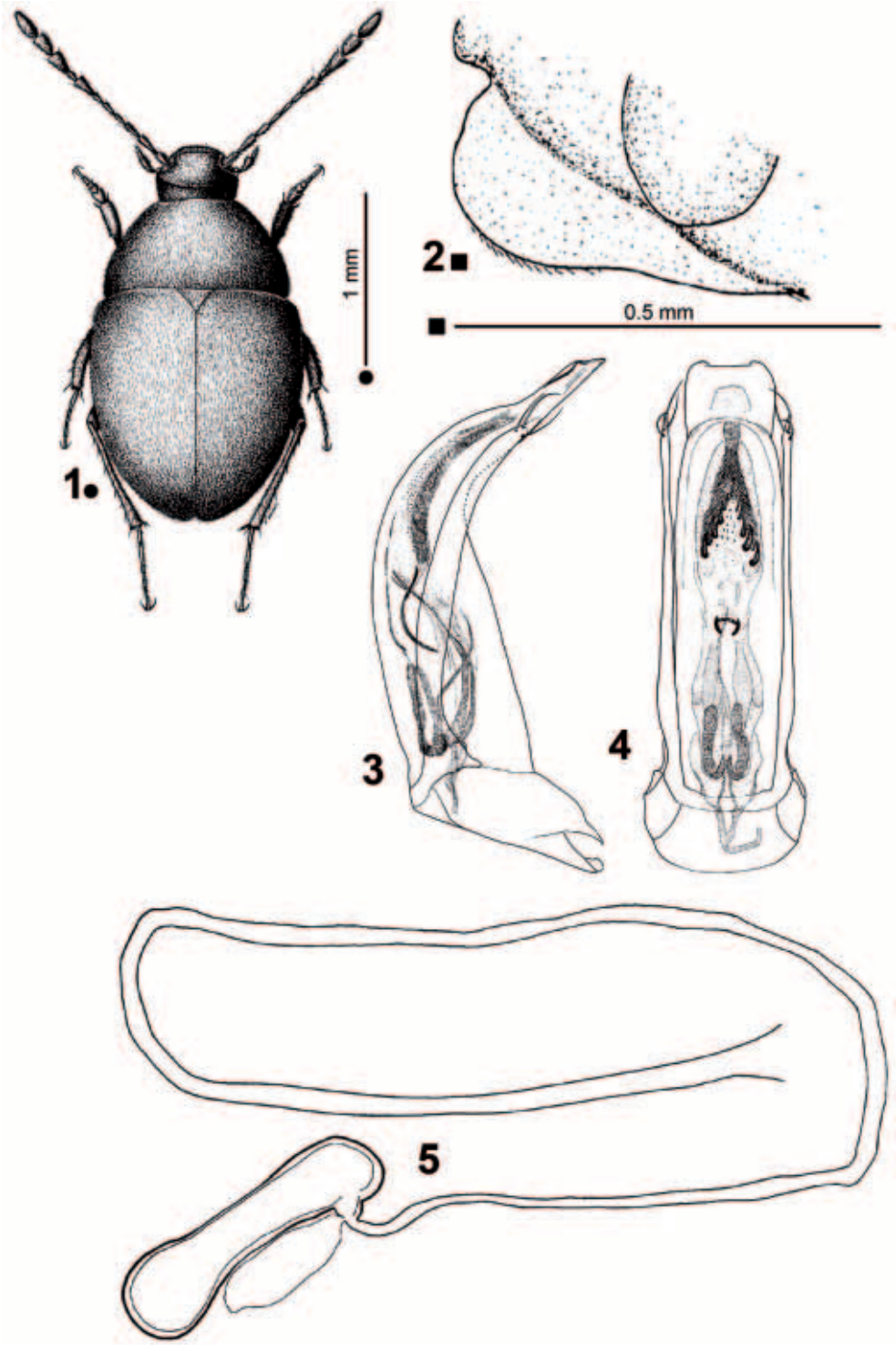
Endophallus (Fig. 56.4): It shows a well-developed and complex armor. In basal part there is a developed «Y»-piece attached to two inverted and symmetrical cane phanerae. In apical part they are two symmetrical and robust groups of several tooth-shape pieces and grouped bundles of elongated spinulae.

Parameres: Thin, unarched and shorter than the median lobe. Club undifferentiated but with a small membranous lobe and three rather long setae inserted into outer face, one apical and two subapical with equidistant pores. Ventral blade of tegmen as long and wide as the basal lamina.

Spermathecal complex (Fig. 56.5): Spermatheca small and elongated, with apical and basal lobes well sclerotized and similar width; the apical globose and the basal elongated; junction duct straight and poorly sclerotized. Spermatic duct about seven times longer than the spermatheca, without a differentiated nodule, although the area of attachment of duct and spermathecal gland to the basal lobe is somewhat dilated.

Female uroventrite VIII: Unknown.

Discussion. Giachino & V.B. Guéorguiev (1991) point out that this genus should be placed in the phyletic series of *Apholeuonus* (*sensu* Jeannel, 1924a) and in «Leptodirina subtribe» of V.B. Guéorguiev (1976) by presenting several common characters. Aedeagus, such as three setae and membranous lobe at the apex of parameres, in addition to tibiae provided with an external spur and protibiae with a comb. On the other hand, and within the phyletic subgroup of



FIGURES 56.1–56.5: *Beroniella* series. *B. tetevensis*: (**1**) Habitus (modified from Giachino & V.B. Guéorguiev 1991), (**2**) Pterothorax, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Spermathecal complex. Figs **2–5** modified from Giachino & V.B. Guéorguiev (1990).

Apholeuonus it should be placed near the genera *Icharonia* and *Setnikia* due to its similar body shape and several general characters of aedeagus. This statement is questionable (see commentaires in Discussion section of *Beroniella* series) and its validity has to be examined by using molecular analysis, which has not yet been done.

Distribution. Type locality is the cave of Djado Draganovata Dupka in Stara Planina mountains, near the city of Teteven in the province of Lovech, Northwestern Bulgaria.

Species

Beroniella tetevensis Giachino & V.B. Guéorguiev, 1991
Beroniella tetevensis Giachino & V.B. Guéorguiev, 1991 [1990]: 194.

3.1.5.5 Series ***Bulgariella*** Giachino & B.V. Guéorguiev, 2008

Monogeneric series, the characters are related in the diagnosis of the genus.

Discussion. This series was defined on a morphological basis by Giachino & B.V. Guéorguiev (2008). No molecular data are available. Pretner (1963a), in his description of *Tranteeviella bulgarica* (now considered synonym of *Bulgariella tranteevi*), approaches this taxon to the phyletic lineage of *Apholeuonus* (*sensu* Jeannel 1924a). However already Giachino & B.V. Guéorguiev (2008) show how a set, in *Bulgariella*, of certain morphological characters such as the peculiar shape of the basal part of the median lobe of aedeagus, the presence in the distal part of the protibiae of a comb – short and incomplete –, and of a external spur to the apex of the protibiae, cause some interpretation problems. In fact, these authors do not share the interpretation proposed by Pretner (1963a) and partially adopted by Perreau (2000), who inserts this taxon in the subtribe Leptodirina. However, the phyletic lineage of *Apholeuonus* is composed of species that present a morphology of the aedeagus very different from that of *Bulgariella*. The median lobe of aedeagus in lateral view bears some resemblance to that of *Ceutophyes karamani*, being slender and elongate with the basal bulb reduced and covered by the tegmen, although in *Ceutophyes* the bulb has a long laminar extension. The endophallus has a long stylet or pseudo-flagellum like the one found in *Babuniella* or *Maroniella*. Its hypothetical relationship with the *Apholeuonus* group of the *Leptodirus* series could be based on homoplasies. Biogeographical arguments point in this direction: their distribution areas are separated by the vast Pannonian basin. It seems more likely to be related to *Beronia* and *Beroniella*, genera with which it shares not only a reduced basal blade totally covered by the tegmen and stylet or flagellum on the endophallus, but also its geographic distribution: all these genera are found in Stara Planina, Bulgaria. *Bulgariella* is the only genus in the region that has no spiculum on the Female uroventrite VIII. Consequentally Giachino & B.V. Guéorguiev (2008) considered to insert *Bulgariella* in a separate phyletic lineage with uncertain affinities and characterised by: the basal part of the median lobe of aedeagus very short and abruptly curved, protibiae equipped in the distal part by a short, incomplete, comb and of an external apical spur.

Genus ***Bulgariella*** Karaman, 1958
Bulgariella Karaman, 1958: 225.
Tranteeviella Pretner, 1963b [1958]: 59 (Type species. *Tranteeviella bulgarica* Pretner, 1963).
Parodromus Buresch: V.B. Guéorguiev, 1965b: 154 (*Nomen nudum*).

Type species. *Bulgariella tranteevi* Karaman, 1958 by monotypy (habitus in Fig. 57.1).

Diagnosis. A medium sized, 2.2 mm. Pholeuonoid facies (Fig. 57.1).

Antennae: Elongated, reaching half of the elytra when stretched backwards; with first article shorter than the second one.

Pronotum: Elongated, narrower than the elytra, with sides sinuated posteriorly.

Elytra: Elongated, with maximum width at about half length. Apex strongly emarginated on the inside, so as to appear pointed. Parasutural stria absent; disc without transversal striolae.

Legs: Male protarsi pentameres and slightly dilated, protibiae bearing in the distal part a short and incomplete external comb and an external apical spur. Meso-and metatibiae without apical basket.

Mesoventral keel (Fig. 57.2): Moderately elevated with rounded front edge; not prolonged posteriorly on the metaventrite.

Suture of the metaventrite (Fig. 57.2, 57.3): Runs close to the coxal cavity, except in the anterior half where it delimits a narrow elongated arched area.

Metatergal apparatus: Unknown.

Metendosternite (Fig. 57.4): «V»-shaped. Arms long and narrow, slightly more than two and a half times the length of the trunk; narrow furcal posterior plate on the arms and the keel of the arm delimits two parts of posterior plate; no apical process or apophysis observed, this part being very narrow and curved inwards. Furcal trunk short and broad, as long as the widest part.

Median lobe of aedeagus: Very elongated, narrow and slender. In lateral view (Fig. 57.5) straight in central part and distal one slightly curved with the basal part very sharply curved. In dorsal view (Fig. 57.6) apex in shape of ogive.

Endophallus (Fig. 57.6): Bearing a complex, symmetrical, median phanera, which originates from a single basal stylet. Basal «Y»-piece apparently absent.

Parameres (Fig. 57.7): Thin, elongated, shorter than the median lobe. Exhibiting three apical, subequal, setae.

Spermathecal complex: Unknown.

Female uroventrite VIII (Fig. 57.8): Posterior medial apical area forms an arcuate protruding lobe due to tapering lateral margins; sub-rectilinear anterior margins merging in the medial area to form a reduced lobe, but no distinct spiculum.

Discussion. See the Discussion section in *Bulgariella* series.

Distribution. Bulgaria, Central Stara Planina.

Species

Bulgariella tranteevi Karaman, 1958
Bulgariella tranteevi Karaman, 1958: 226.
Tranteeviella bulgarica Pretner, 1963b [1958]: 60.
Parodromus panegensis Buresh: Guéorguiev, 1965b: 154 (*Nomen nudum*).

3.1.5.6 Series ***Ceuthophyes***

Diagnosis. Small to medium-large sized more or less elongated, bathyscioid body shape.

Head: With evident occipital carina (sometimes lacking in central part); anophthalmous.

Antennae: Short to relatively long. First antennomere as long as, or shorter than the second one; all antennomeres longer than wide.

Pronotum: Transverse, convex, as wide as, or wider than, the elytral base. Lateral sides not sinuate posteriorly.

Elytra: More or less elongated, oval; very finely punctate or with punctation reduced; without parasutural stria and with or without transverse striolae.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Figs 59.1–59.5): More or less high and not prolonged on the metaventrite. Front edge from straight to decidedly curved, forming an angle toothed or not.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Figs 59.6): Extremely reduced, with apophysis of the alacrista completely absent or very reduced.

Metendosternite (Fig. 59.7): Large, stout, not «V»-shaped but with furcal arms and subtriangular furcal plate. Arms apophysis large and not hooked.

Median lobe of aedeagus: Elongated or hugely elongated, curved in lateral view (Figs 60.1–60.6), sometimes sinuated or bisinuate in the distal third or irregularly curved. Apex, in dorsal view (Figs 61.1–61.7) more or less ogive-shaped and pointed, sometimes broadly rounded. Basal blade very large, sometimes hypertrophic and prolonged in a narrow ribbon-like band, long from one to six times the median lobe itself.

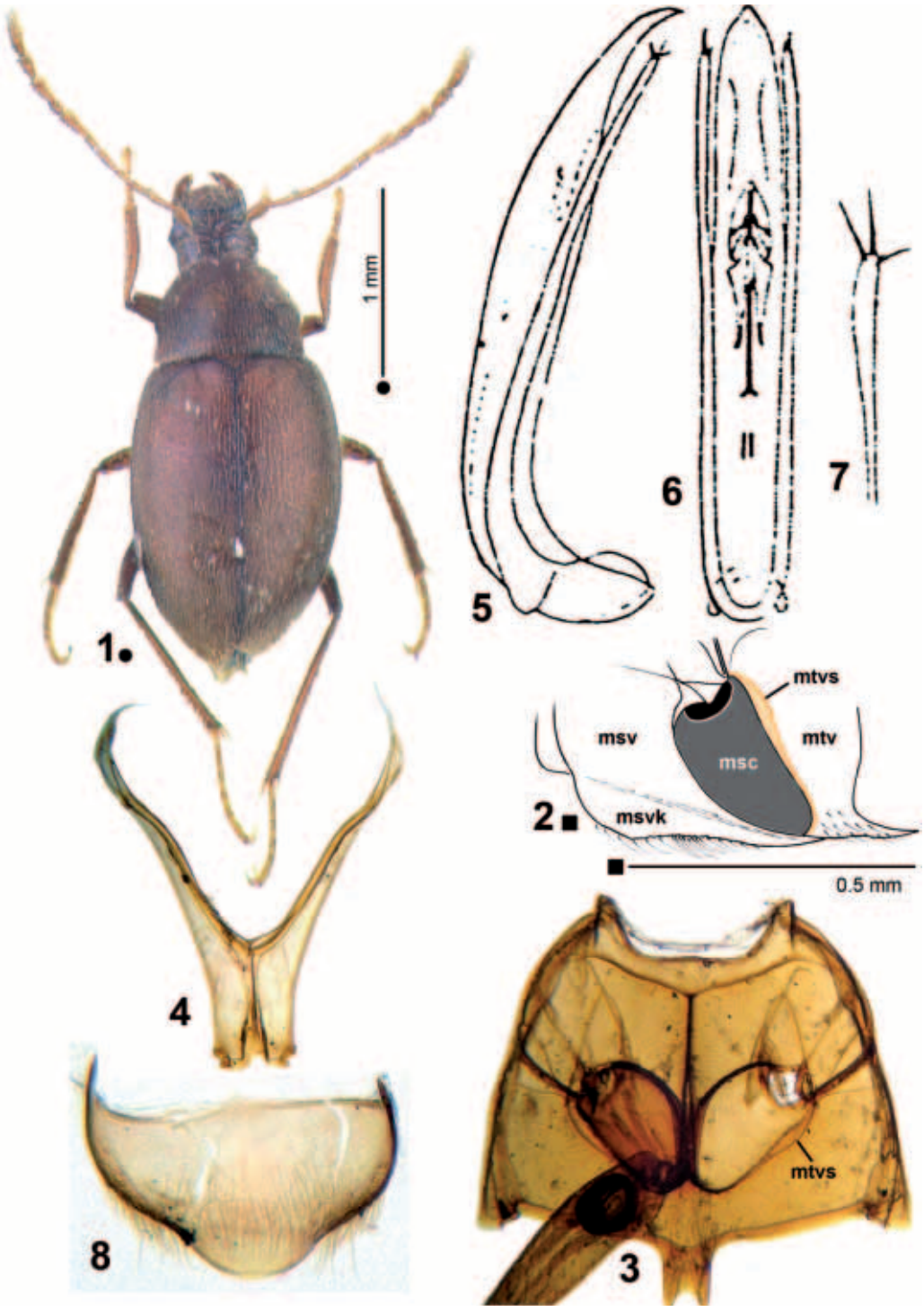
Endophallus (Figs 61.1–61.3, 61.5, 61.6): Without basal «Y»-piece. Bearing one or two long flagellum sometimes exceeding the basal blade of the median lobe. Median area without phanerae or with two poorly sclerotized phanerae of different shape.

Parameres (Figs 62.3–62.9): From slightly longer to slightly shorter than the median lobe. Normally bearing three setae sometimes modified in spiniform shape and distinctly orientated in opposite directions; but sometimes are presents 5–6 setae. Tegmen with basal blade from developed to very develop.

Spermathecal complex (Figs 63.1–63.5): Spermatheca well or slightly sclerotized, more or less kidney-shaped, composed by two fused spherical parts. Ductus long and thin, dilated or not.

Female uroventrite VIII (Fig. 63.6, 63.7): With spiculum of different shape.

Discussion. This lineage is based only on morphological data and defined following Jeannel (1924a) and subsequent authors, as V.B. Guéorguiev (1976) and to a great extent Perreau (2000, 2004). The genus *Albaniola* is clearly polyphyletic, as evidenced by its extensive distribution across a vast geographical range. It is present in the Krujé district of Albania (Dinarides), the Rhodopes Mountains Massif, and Mount Pangaion in the easternmost region of Greece. Additionally, it is



FIGURES 57.1–57.8: *Bulgariella* series. *Bulgariella tranteevi*: (**1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Pterothorax in ventral view, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere, (**8**) Female, uroventrite VIII. Figs **5–7** modified from Pretner (1958). Abbreviations: **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture.

present in the eastern coastal mountain ranges of Greece. Therefore, it can be postulated that each species group (Dinarides, eastern Greek coastal ranges and Rhodopes-Pangaion) should be phylogenetically related to different clades of those populating the region, the *Anthroherpon* series (Dinarides), the Euboea-*Atticiella* series (eastern Greek coastal ranges) and the *Rhodopiola* group of the *Sophrochaeta* series (Rhodopes-Pirin) are the most probable candidates.

The genus *Albaniola* (*sensu auctorum*) is currently being revised in occasion of the monographic study on Leptodirini from Greece (see Discussion section in genus *Albaniola*). *Babuniella*, *Ceutophyes*, *Ochridiola* and *Purkynella* have smaller areas limited to the Dinarides, and *Hussonella* is a very localised genus in the eastern coastal ranges of Greece. No molecular data are available about any genera of this series.

KEY TO GENERA

1. First antennomere as long as the second, or slightly longer 2
- First antennomere more or less short than the second 4

2. Pronotum wider than the elytra. In male, protibiae dilated in club and metatibiae arcuated ....*Purkynella*
- Pronotum as wide as, or narrower than the elytra. In male, protibiae not dilated and metatibiae straight ..3

3. Habitus wide and depressed. Elytra with strong punctation. Mesoventral keel very low (Figs 59.1–59.3). Metaventrite not carinated. Meso- and metatibiae compressed .....*Albaniola*
- Habitus ovoid and convex. Elytra with very fine punctation. Mesoventral keel high and angular. Metaventrite carinated at the base. Meso- and metatibiae cylindrical ..... *Ceuthophyes*

4. Elytra striolate crosswise, at least in the front half .....*Ochridiola*
- Elytra dotted.....5

5. Top of the elytra leaving the pigidium uncovered. Mesoventral keel without sharp angle forward..... .....*Hussonella*
-Top of the elytra far beyond the pygidium. Mesoventral keel at a sharp angle forward (Figs 59.4, 59.5).... .....*Babuniella*

Genus ***Albaniola*** Jeannel, 1924
Albaniola Jeannel, 1924a: 43.

TYPE SPECIES. *Bathyscia* (s. str.) *merditana* Apfelbeck, 1907 by original designation (for the habitus see that of the similar species *Albaniola moraveci* in Fig. 58.1).

DIAGNOSIS. Medium sized, 1.8–2.5 mm, with bathyscioid body (Fig. 58.1).

Head: With complete occipital carina; anophthalmous.

Antennae: Relatively short; first antennomere as long as, or shorter than the second one.

Pronotum: Transverse, convex, as wide as, or wider than, the elytral base. Lateral side not sinuate posteriorly.

Elytra: Elongated, oval; without parasutural stria and without transverse striolae.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket and compressed.

Mesoventral keel (Figs 59.1–59.3): More or less high and not prolonged on the metaventrite. Front edge from straight to decidedly curved, forming an obtuse angle that is not, or very slighly, toothed. Ventral edge not very thick.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 59.6): With very short apophysis of the alacrista, limited to the base of elytra; long and subtriangular metascutum wings.

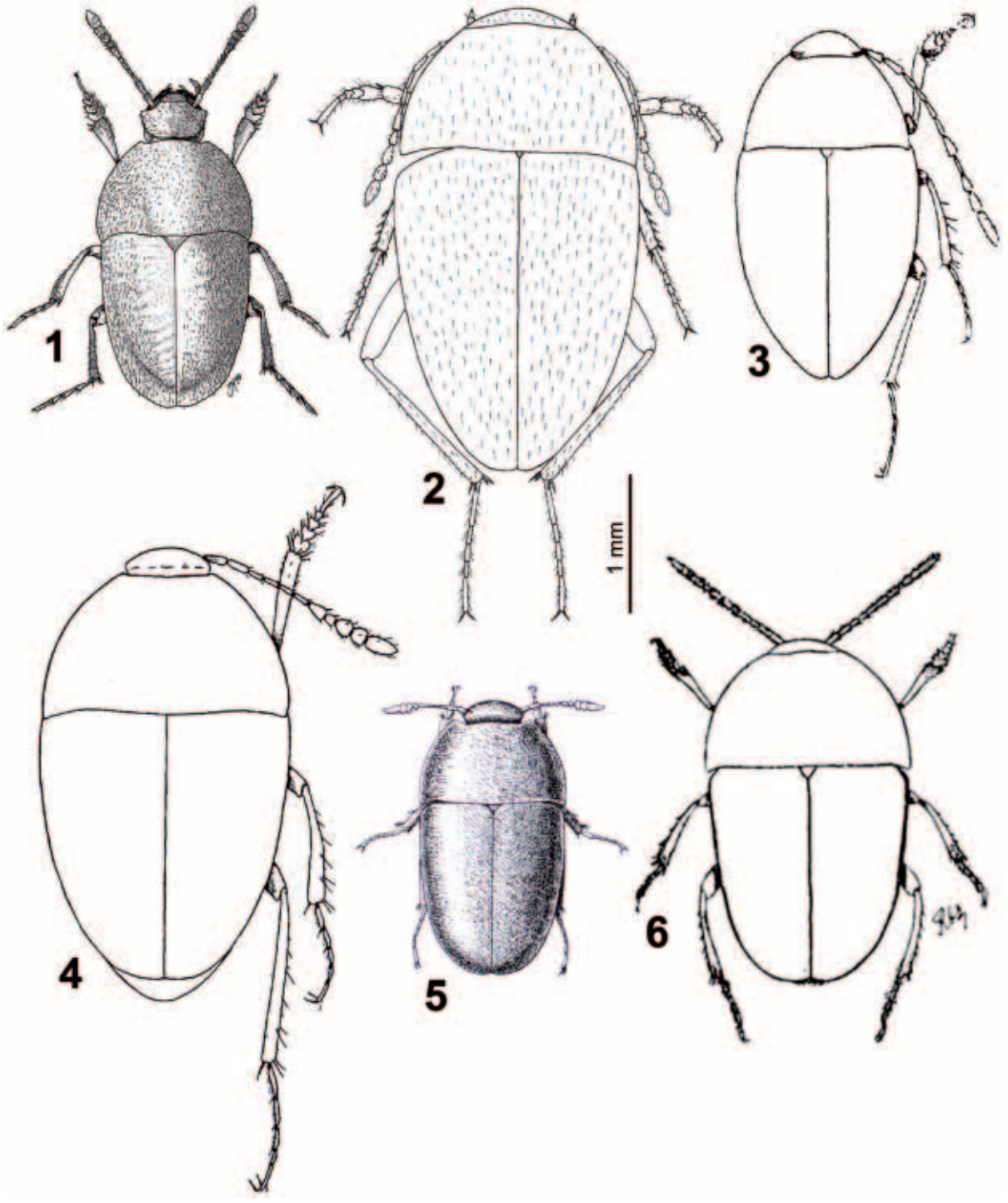
Metendosternite: Unknown.

Median lobe of aedeagus: Elongated, curved in lateral view (Fig. 60.1) sometimes sinuated, or bisinuate, in the distal third. Apex, in dorsal view (Figs 61.1–61.4) more or less ogive-shaped and pointed sometimes broadly rounded; apex slightly deviated from the axis in *Albaniola acutipennis* (Fig. 61.4). Basal blade hypertrophic, long from one to two times the median lobe itself.

Endophallus (Fig. 61.2, 61.3): Without basal «Y»-piece. Bearing a long flagellum that runs along the entire length of the median lobe, including the ribbon-like extroflexion of the basal blade, where it ends with a kind of ampulla.

Parameres (Jeannel 1924a): From slightly longer to slightly shorter than the median lobe. Stout and distinctly sinuated in dorsal view, sometimes also in lateral view. Bearing three setae, two apical and one subapical; four setae in *Albaniola acutipennis* (Fig. 62.4).

Spermathecal complex (Fig. 63.1–63.3): Sper-



FIGURES 58.1–58.6: *Ceuthophyes* series. Habitus of: (**1**) *Albaniola moraveci* (modified from Udržal & Moravec 1999), (**2**) *Babuniella jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**3**) *Ceuthophyes karamani* (modified from Jeannel 1924a), (**4**) *Hussonella remyi* (modified from Jeannel 1934), (**5**) *Ochridiola marinae* (modified from Sbordoni 1971), (**6**) *Purkynella rambouseki* (modified from Knirsch 1926).

matheca more or less kidney-shaped, slightly sclerotized, with the distal part preceded by a relatively large hyaline part; distal and basal lobes similar in length and width. Spermathecal gland hyaline, of modest size. Ductus long and thin, gradually thickened and dilated in the terminal part, near the spermatheca.

Female uroventrite VIII (Fig. 63.6): With ventral edge, subrettilinear anteriorly. Spiculum long and narrow.

Discussion. Already Udržal & Moravec (1999) note strong morphological differences between the known species and propose the subdivision of the genus *Albaniola* into three groups of species. Due to a personal communication it is known to us (Giachino & Vailati *in prep*.) that there will be a more pronounced devision into several genera (at least eight, in addition to the nominotypical genus) which will host at least eight of the 13 species currently assigned (plus numerous others, at least 15 unpublished). Therefore here it is only possible to provide a morphological description of the genus only based on the known species belongs to the true *Albaniola*: the type species *A. merditana* plus *A. gambarii*, *A. moraveci*, *A. rambouseki* and *A. ulbrichi*.

Distribution. *Albaniola* (*sensu auctorum*) is distributed in Albania, Republic of North Macedonia and Greece.

Species

Albaniola acutipennis Jeannel, 1934*
Albaniola acutipennis Jeannel, 1934b: 92.

Albaniola casalei Giachino, 1989*
Albaniola casalei Giachino, 1989: 38.

Albaniola gambarii Rampini & Zoia, 1995
Albaniola gambarii Rampini & Zoia, 1995: 317.

Albaniola giachinoi M. Etonti, 1989*
Albaniola giachinoi M. Etonti, 1989: 259.

Albaniola macedonica Casale, Giachino & M. Etonti, 1990*
Albaniola macedonica Casale, Giachino & M. Etonti, 1990: 556.

Albaniola merditana (Apfelbeck, 1907)
Bathyscia (s. str.) *merditana* Apfelbeck, 1907e: 520.
Pholeuonella merditana Apfelbeck: Jeannel, 1910a: 29.
Bathysciola (Pholeuonella) merditana Apfelbeck: Jeannel, 1914b: 15.
Albaniola merditana Apfelbeck, 1907: Jeannel, 1924a: 43.

Albaniola moraveci Udržal & Moravec, 1999
Albaniola moraveci Udržal & Moravec, 1999: 33.

Albaniola olympicola Casale, 1981*
Albaniola olympicola Casale, 1981: 38.

Albaniola rambouseki Knirsch, 1931
Albaniola Rambouseki Knirsch, 1931: 2.
Albaniola rambouseki Knirsch: Perreau, 2000: 295.

Albaniola remyi Jeannel, 1934*
Albaniola Remyi Jeannel, 1934b: 91.
Albaniola remyi Jeannel: Perreau, 2000: 295.

Albaniola thessalica (Reitter, 1887)*
Bathyscia thessalica Reitter, 1877: 276.
Bathyscia (?) *thessalica* Reitter: Jeannel, 1910a: 46.
Albaniola thessalica Reitter: Jeannel, 1934b: 93.

Albaniola ulbrichi Jeannel, 1929
Albaniola ulbrichi Jeannel, 1929b: 80.

Albaniola xanthina M. Etonti & Giachino, 1994*
Albaniola xanthina M. Etonti & Giachino, 1994: 401.

Genus ***Babuniella*** Karaman, 1954
Hussonella (*Babuniella*) Karaman, 1954b: 70.
Babuniella Karaman, 1954: S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 311.

Type species. *Hussonella* (*Babuniella*) *ovata* Karaman, 1954 by monotypy (for the habitus see that of the similar species *Babuniella jovanhadzii* in Fig. 58.2).

Diagnosis. Medium size, 3.0-3.5 mm, with more or less elongated body; bathyscioid body shape (Fig. 58.2).

Head: Subquadrate, with complete occipital carina; anophthalmous.

Antennae: Relatively long, reaching the basal fourth of the elytra. First antennomere as long as, or

* Work in progress, species belonging to different genera.

little shorter than the second one; 8th antennomere longer than wide, not transverse.

Pronotum: Transverse, convex, as wide as, or a little wider than the elytral base. Lateral side not posteriorly sinuated. Disc microreticulate and scarcely punctate .

Elytra: Elongated, oval; rounded apically; without parasutural stria but otherwise arranged in irregular transversally striolation.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Figs 59.4, 59.5): More or less high, but still obtuse, with more or less prominent tooth. Posterior apophysis not prolonged on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated. In lateral view (Fig. 60.2) sinuate in the apical third. In dorsal view (Fig. 61.5, 61.6) laterally impressed and constricted in its apical third with apex ogivete, rounded or pointed. Basal blade large but not prolonged in a narrow ribbon-like band.

Endophallus (Fig. 61.5, 61.6): Without basal «Y»-piece. Bearing a flagellum as long as the median lobe, not exceeding the basal blade of the median lobe. Median area without phanerae. Apical area with an unequal phanera formed by thorny bundles or by an ampulla-shaped piece.

Parameres (Fig. 62.4, 62.5): Longer or as long as the median lobe, apically thin, protruding exteriorly and not pointed distally (in lateral view). Bearing three setae: two dorsal subapical and one lateral subapical interior.

Spermathecal complex (Fig. 63.4): Spermatheca small, well sclerotized, composed by two lobes spherical fused, both large; undifferentiated union duct. Spermatic duct thin, largely expanded at the insertion into the spermatheca.

Female uroventrite VIII: Unknown.

Discussion. No molecular data about *Babuniella* are available, so its assignment to this phyletic series is made only on a morphological basis. Genus probably closely related to *Hussonella*, of which it was considered a subgenus before its elevation to the rank of genus by S. Ćurčic *et al*. (2005).

Distribution. In the northern and central parts of the Republic of North Macedonia.

Species

Babuniella jovanhadzii S. Ćurčić & Mihajlova, 2005
Babuniella jovanhadzii S. Ćurčić & Mihajlova: *in*, S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 312.

Babuniella ovata (Karaman, 1954)
Hussonella (*Babuniella*) *ovata* Karaman, 1954b: 70.
Babuniella ovata (Karaman): S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 312.

Babuniella prouzai (Urdžal & Moravec, 1999)
Hussonella (*Babuniella*) *prouzai* Urdžal & Moravec, 1999: 39.
Babuniella prouzai (Urdžal & Moravec): S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 312.

Genus ***Ceuthophyes*** Jeannel, 1924
Ceuthophyes Jeannel, 1924a: 43.
Ceutophyes Jeannel: Laneyrie, 1967: 608.

Type species. *Ceuthophyes Karamani* Jeannel, 1924 by original designation (habitus in Fig. 58.3).

Diagnosis. Medium-large size, 2.5–5.0 mm, with more or less elongated or elliptic body shape; bathyscioid facies (Fig. 58.3).

Head: With complete occipital carina; anophthalmous.

Antennae: Relatively long and thin, as long as half of body length. First antennomere as long as or shorter than the second one.

Pronotum: Transverse, convex, as wide as the elytral base. Lateral side not sinuate posteriorly.

Elytra: More or less elongated, oval; without parasutural stria and without transverse striolae; each elytron separately rounded at tip.

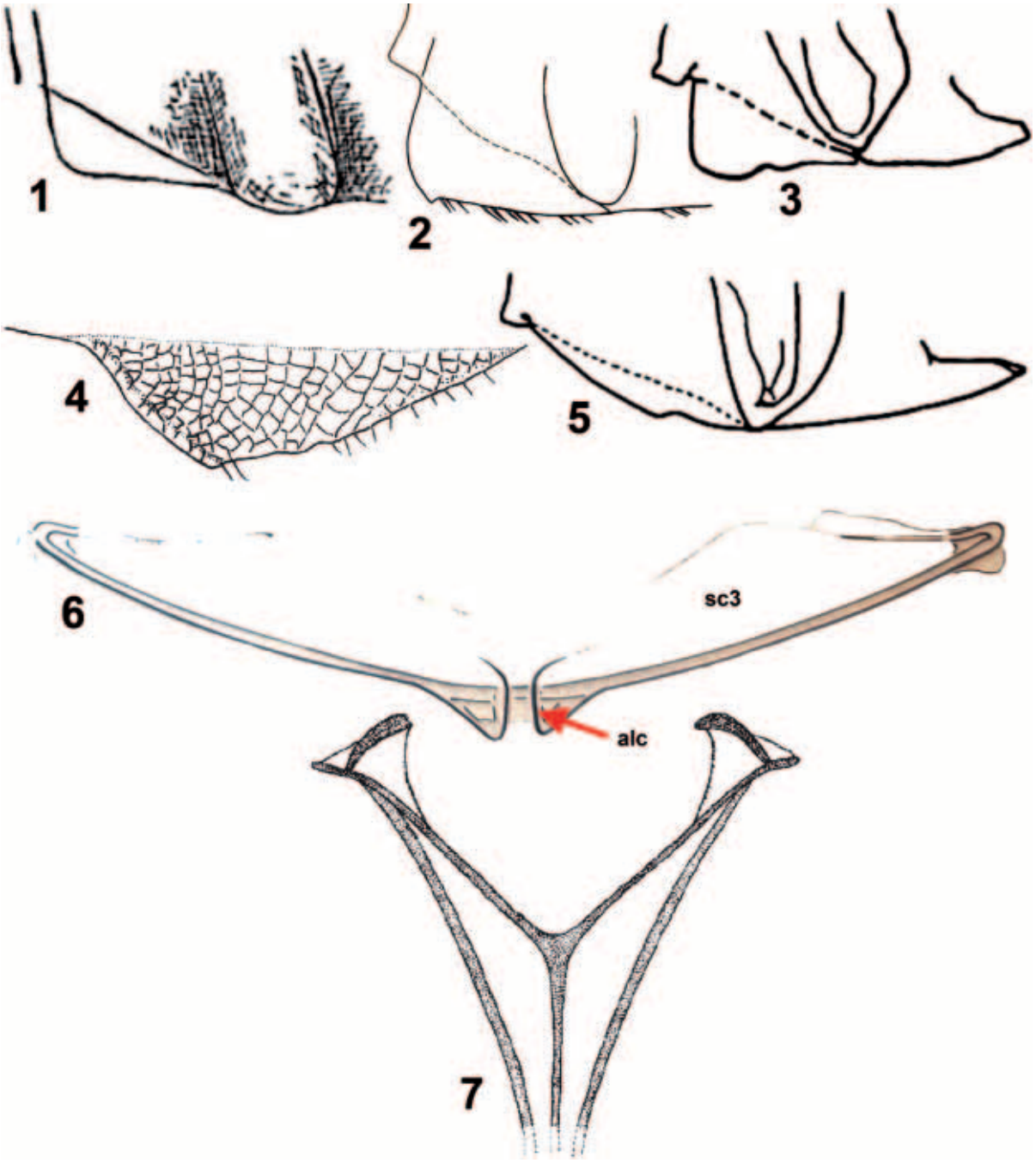
Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Jeannel 1924a): High, with straight front edge and sharp but non -toothed angle. Ventral border posteriorly strongly thickened, not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus: «Metatergal apparatus reduced;» (B.V. Guéorguiev 2007).

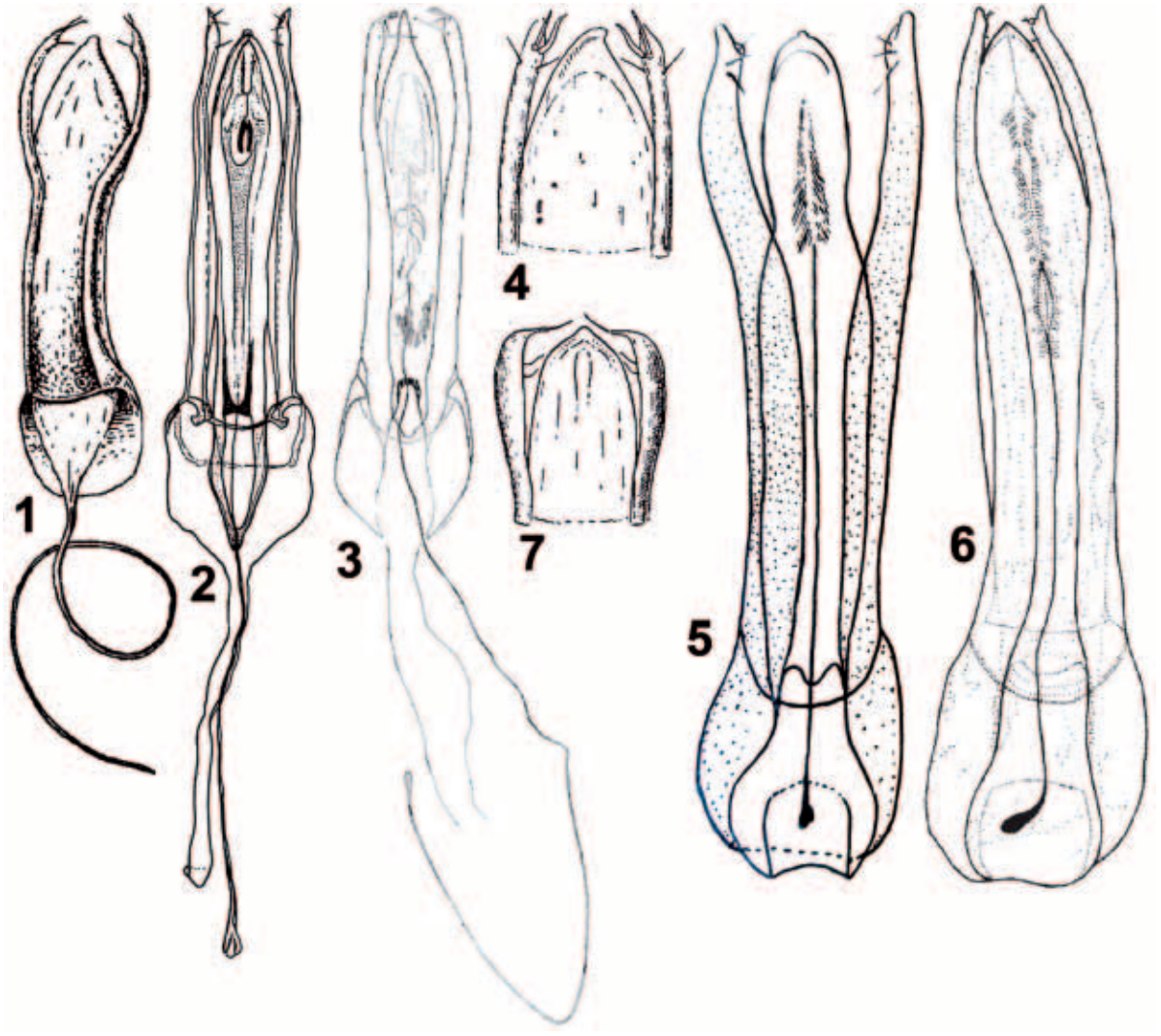
Metendosternite (Fig. 59.7): Large, stout, not «V»-shaped, with subtriangular posterior furcal plate; arms somewhat longer than the furcal trunk. Arms apophysis large and not hooked. Furcal trunk



FIGURES 59.1–59.5: *Ceuthophyes* series. Pterothorax in lateral view of: (**1**) *Albaniola rambouseki* (modified from Knirsch 1931), (**2**) *A. gambarii* (modified from Rampini & Zoia 1995), (**3**) *A. moraveci* (modified from Udržal & Moravec 1999), (**4**) *Babuniella jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**5**) *B. prouzai* (modified from Udržal & Moravec 1999). Metatergal apparatus, ventral view of metanotum and axillaria of: (**6**) *A. thessalica* (modified from Rampini & Zoia 1995). Metendosternite of: (**7**) *Ceuthophyes enormis* (modified from B.V. Guéorguiev 2007). Abbreviations: **alc**, alacrista; **sc3**, metascutum.



FIGURES 60.1–60.6: *Ceuthophyes* series. Aedeagus in lateral view of: (**1**) *Albaniola moraveci* (modified from Udržal & Moravec 1999), (**2**) *Babuniella jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**3**) *Ceuthophyes karamani* (modified from Jeannel 1924a), (**4**) *Hussonella remyi* (modified from Jeannel 1934), (**5**) *Ochridiola marinae* (modified from Sbordoni 1971), (**6**) *Purkynella rambouseki* (modified from Knirsch 1926).



FIGURES 61.1–61.6: *Ceuthophyes* series. Aedeagus in dorsal view of: (**1**) *Albaniola merditana* (modified from Jeannel 1924a), (**2**) *A. moraveci* (modified from Udržal & Moravec 1999), (**3**) *A. macedonica* (modified from Casale *et al.* 1990), (**4**) *A. acutipennis*, apical part (modified from Jeannel 1934), (**5**) *Babuniella ovata* (modified from Karaman 1954), (**6**) *B. jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**7**) *Hussonella remyi*, apical part (modified from Jeannel 1934).

somewhat longer than the part of maximum width.

Median lobe of aedeagus (Fig. 60.3): Hugely elongated; apical orifice equipped with large chitinised ligules, reaching the level of the apex of the median lobe. Basal blade prolonged in a long, flexible, chitinised stripe; this blade, five to six times the median lobe long, is partially twisted to a spiral and continues into abdomen, probably adherent to the ejaculatory duct.

Endophallus: Without basal «Y»-piece. Equipped with a long slender dorsal flagellum. Jeannel (1924a), referring to *C. karamani*, indicates that it has an unarmed endophallus, while both Karaman (1954a, 1968) and B.V. Guéorguiev (2007) illustrate that the aedeagi of *C. karamani*, *C. bukoviki*, *C. lazaropolensis* and *C. enormis* have a long slender flagellum.

Parameres (Fig. 62.6): Large and thick, as long as the median lobe. Apex stout and rounded, bearing a membranous lobe and 5–6 setae in different position – only three in the original description by Jeannel

(1924a) –. Tegmen with basal blade very developed. Parameres dorsally connected by a dorsal band in proximal position.

Spermathecal complex: Unknown.

Female uroventrite VIII (Fig. 63.7): With distal edge widely rounded and subrectilinear basal edge. Spiculum large, subtriangular and rounded apex.

Discussion. No molecular data on *Ceuthophyes* are available, so his assignment to this phyletic series is made only on a morphological basis.

Distribution. Albania and Republic of North Macedonia. Unpublished data highlight its presence also in Greece (Giachino & Vailati *in prep*.).

Species

Ceuthophyes bishoffi G. Müller, 1936
Ceuthophyes Bishoffi G. Müller, 1936: 62.
Ceuthophyes bishoffi Müller: Perreau, 2000: 256.

Ceuthophyes bukoviki Karaman, 1968
Ceuthophyes bukoviki Karaman, 1968: 197.

Ceuthophyes enormis B.V. Guéorguiev, 2007
Ceuthophyes enormis B.V. Guéorguiev, 2007: 76.

Ceuthophyes karamani Jeannel, 1924
Ceuthophyes Karamani Jeannel, 1924a: 45.
Ceuthophyes karamani Jeannel: Perreau, 2000: 256.

Ceuthophyes lazaropolensis Karaman, 1954
Ceuthophyes lazaropolensis Karaman, 1954a: 45.

Genus ***Hussonella*** Jeannel, 1934
Hussonella Jeannel, 1934b: 96.

Type species. *Hussonella Remyi* Jeannel, 1934 by original designation (habitus in Fig. 58.4).

Diagnosis. Medium size, 2.8–3.2 mm, with bathyscioid body (Fig. 58.4).

Head: With complete occipital carina; anophthalmous.

Antennae: Relatively long, reaching the basal fourth of elytra. First antennomere little shorter than the second one; the 8th antennomere short, as long as wide.

Pronotum: Transverse, convex, as wide as the elytral base. Lateral side not posteriorly sinuated.

Elytra: Oval; without parasutural stria and no transversal striolation.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Jeannel 1934): Very high, without tooth. Not prolonged on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated and regularly curved in lateral view (Fig. 60.4). In dorsal view (Fig. 61.7), broad and flattened at the apex, which is subtriangularly pointed. Basal blade large, almost half the length of the entire median lobe, but not prolonged in a narrow ribbon-like band.

Endophallus (Jeannel 1934): Without basal «Y»-piece, scaly, with a large longitudinal and median thickening, at the base of which a basal canal, with a large initial spherical swelling, opens. This contains two articulated phanerae that extend into two flagelli, one short and an other one almost as long as the entire endophallus.

Parameres (Fig. 62.8): As long as the median lobe. Apex, in lateral view, in the shape of a transverse blade and bearing three setae, two located ventrally are curved and a third one inserted apically on an internal, sharp expansion of the apex, clearly visible in dorsal view.

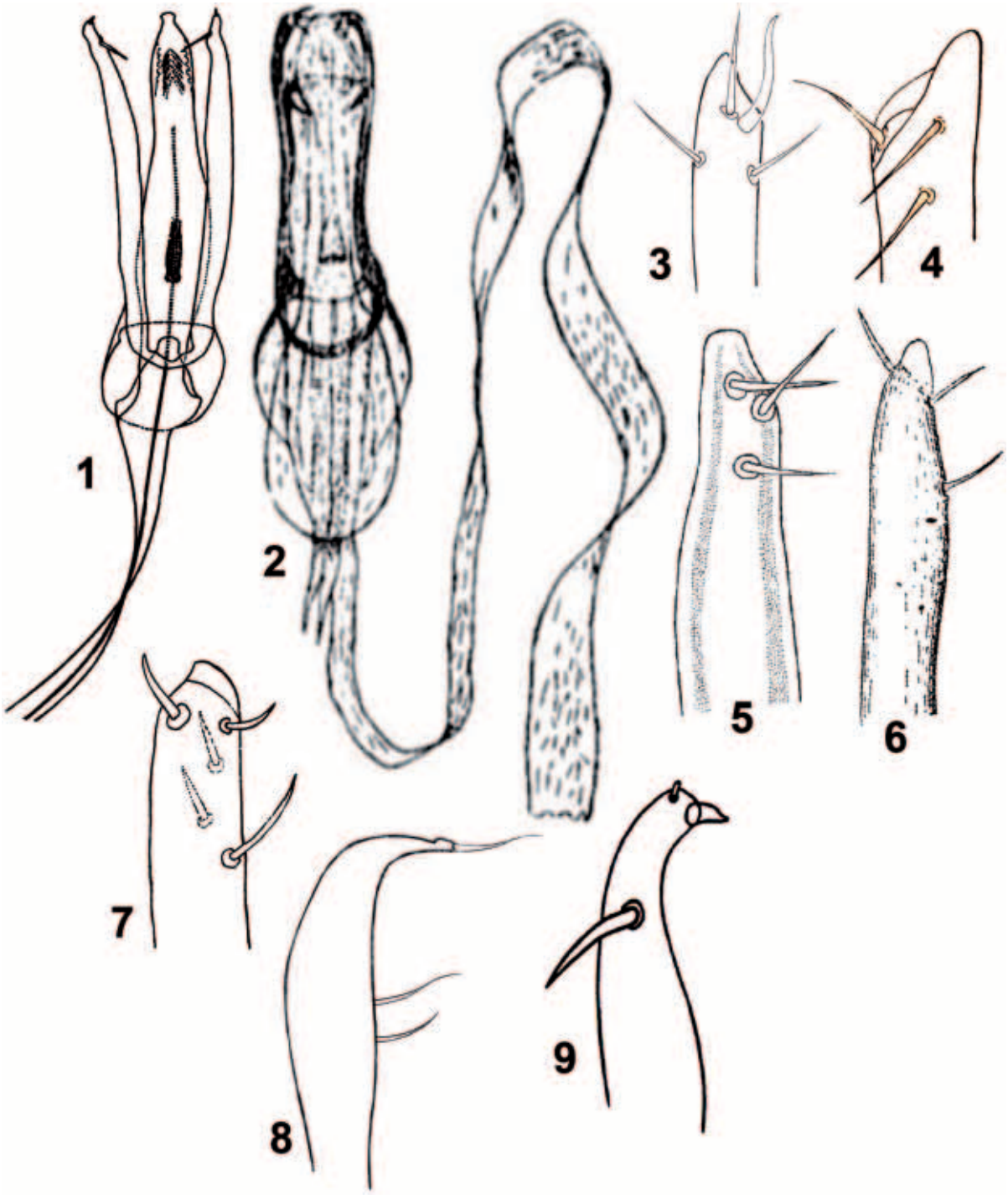
Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. No molecular data on *Hussonella* are available, so his assignment to this phyletic series is made only on a morphological basis. Genus probably closely related to *Babuniella*, considered a subgenus of *Hussonella* by Perreau (2000), before its elevation to the rank of genus by S. Ćurčic *et al*. (2005).

Distribution. Greece, Macedonia, Nomos de Pella, Temna cave in Zbanska Stena.

Species

Hussonella remyi Jeannel, 1934
Hussonella Remyi Jeannel, 1934b: 96.
Hussonella (*Hussonella*) *remyi* Jeannel: Perreau, 2000: 257.
Hussonella remyi Jeannel: S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 312.



FIGURES 62.1–62.9: *Ceuthophyes* series. Aedeagus in dorsal view of: (**1**) *Ochridiola marinae* (modified from Sbordoni 1971), (**2**) *Purkynella rambouseki* (modified from Knirsch 1926). Apex of the paramere of: (**3**) *Albaniola acutipennis* (redrawn from Jeannel 1934), (**4**) *Babuniella ovata* (modified from Karaman 1954), (**5**) *B. jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**6**) *Ceuthophyes karamani* (modified from Jeannel 1924a), (**7**) *C. karamani* (modified from Karaman 1968), (**8**) *Hussonella remyi* (redrawn from Jeannel 1934), (**9**) *Ochridiola marinae* (modified from Sbordoni 1971).

Genus ***Ochridiola*** Sbordoni, 1971
Ochridiola Sbordoni, 1971a: 29.

Type species. *Ochridiola marinae* Sbordoni, 1971 by original designation (habitus in Fig. 58.5).

Diagnosis. Small size, 1.8–2.0 mm, bathyscioid body (Fig. 58.5).

Head: With incomplete occipital carina (lacking in central part); anophthalmous.

Antennae: Short; first antennomere shorter than the second one, the 11th two times longer than the 10th. Antennal club very evident and flat, starting from the 7th antennomere.

Pronotum: Transverse, convex, as wide as the elytral base. Lateral side not sinuate posteriorly.

Elytra: Oval, not elongated; without parasutural stria and with transverse striolae.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Sbordoni 1971a): High, with convex and strongly arcuated anterior margin; ventral margin rectilinear and flattened dorso-ventrally. Not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Sbordoni 1971a): Extremely reduced, apophysis of the alacrista completely absent.

Metendosternite: Unknown.

Median lobe of aedeagus: Large, little and not regularly arcuated. In lateral view (Fig. 60.5) slightly bisinuated, ending with a beak-shaped apex. In dorsal view (Fig. 62.1) strongly restricted in the distal portion, with a dilated apex in shape of rounded arrowhead. Basal blade prolonged in a broad band with little sclerotized and about twice the median lobe long.

Endophallus (Fig. 62.1): Without basal «Y»-piece, bearing a long dorsal flagellum starting, with an ampulla, at the base of the long basal blade of the median lobe and extends to the apex of the median lobe. Median area with two sclerotized phanerae in shape of smooth strips. Apical area with a small phanera consisting of squat lateral teeth and central small spines.

Parameres (Fig. 62.9): Thick, in lateral view strongly arcuated along their entire length with apex decidedly hooked upwards. Bearing three setae, one large, proximal, internal and two distal with a characteristic spiniform shape, one conical and one rod-like.

Spermathecal complex (Fig. 63.5): Spermatheca strongly narrowed and little sclerotized in the median area. Distal lobe spherical and proximal lobe oval, somewhat more elongated, both of similar width and well sclerotized. Ductus about seven times the length of the spermatheca and devoid of dilatations. Spermathecal gland well-developed, hyaline, inserted at the outlet of the ductus into spermatheca.

Female uroventrite VIII: Unknown.

Discussion. No molecular data on *Ochridiola* are available, so his assignment to this phyletic series is made only on morphological characters following the works of Sbordoni (1971a).

Distribution. Republic of North Macedonia, Galičica Planina.

Species

Ochridiola marinae Sbordoni, 1971
Ochridiola marinae Sbordoni, 1971a: 33.

Genus ***Purkynella*** Knirsch, 1926
Purkynella Knirsch, 1926: 59.

Type species. *Purkynella Rambouseki* Knirsch, 1926 by original designation (habitus in Fig. 58.6).

Diagnosis. Small-medium size, 2.2–2.7 mm, with bathyscioid body (Fig. 58.6).

Head: With evident occipital carina; anophthalmous.

Antennae: Short; first antennomere as long as the second one; the 11th two times longer than the 10th one. Antennal club poorly evident and flat, starting from the 7th antennomere.

Pronotum: Transverse, convex, larger than the elytral base. Lateral side not sinuate posteriorly. Pronotum disc transversally striated in the basal part.

Elytra: Oval, short, not elongated; without parasutural stria and with transverse striolae.

Legs: Male protarsi pentameres and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Knirsch 1926): High, with anterior edge slightly curved and ventral one subrettilinear, modestly toothed. Not extended on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Large, in lateral view (Fig. 60.6) strongly and irregularly bent downwards, first at the apical third and then just before the apex. In dorsal view (Fig. 62.2) stout, slightly concave on the

sides. Due to the strong downward curvature of the distal part, it is impossible in this position to see the entire apical part, this appears wide, with a blunt tip, and with a horseshoe-shaped marginal reinforcement. Basal blade large, broadly oval and prolonged in a narrow chitinised band, approximately three times the length of the median lobe.

Endophallus (Fig. 62.2): Without basal «Y»-piece; equipped with an ejaculatory duct, starting just beyond the basal blade of the median lobe, which extends into a thin flagellum that occupies the entire length of the median lobe. Flagellum surrounded in the basal part by very thin, long, extremely dense and inclined teeth. In the central part there is a vaguely omega-shaped phanera.

Parameres (Knirsch 1926): Shorter than the median lobe, thin and regularly curved in lateral view. In dorsal view the apexes are bent inward at right angles and equipped with three setae. Parameres joined dorsally by a narrow basal chitinised band. Ventral blade of the tegmen large and rounded in dorsal view.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. No molecular data on *Purkynella* are available, so its assignment to the phyletic series is based only on morphological analysis.

Distribution. Republic of North Macedonia, Nižepolje, Mont Pelister.

Species

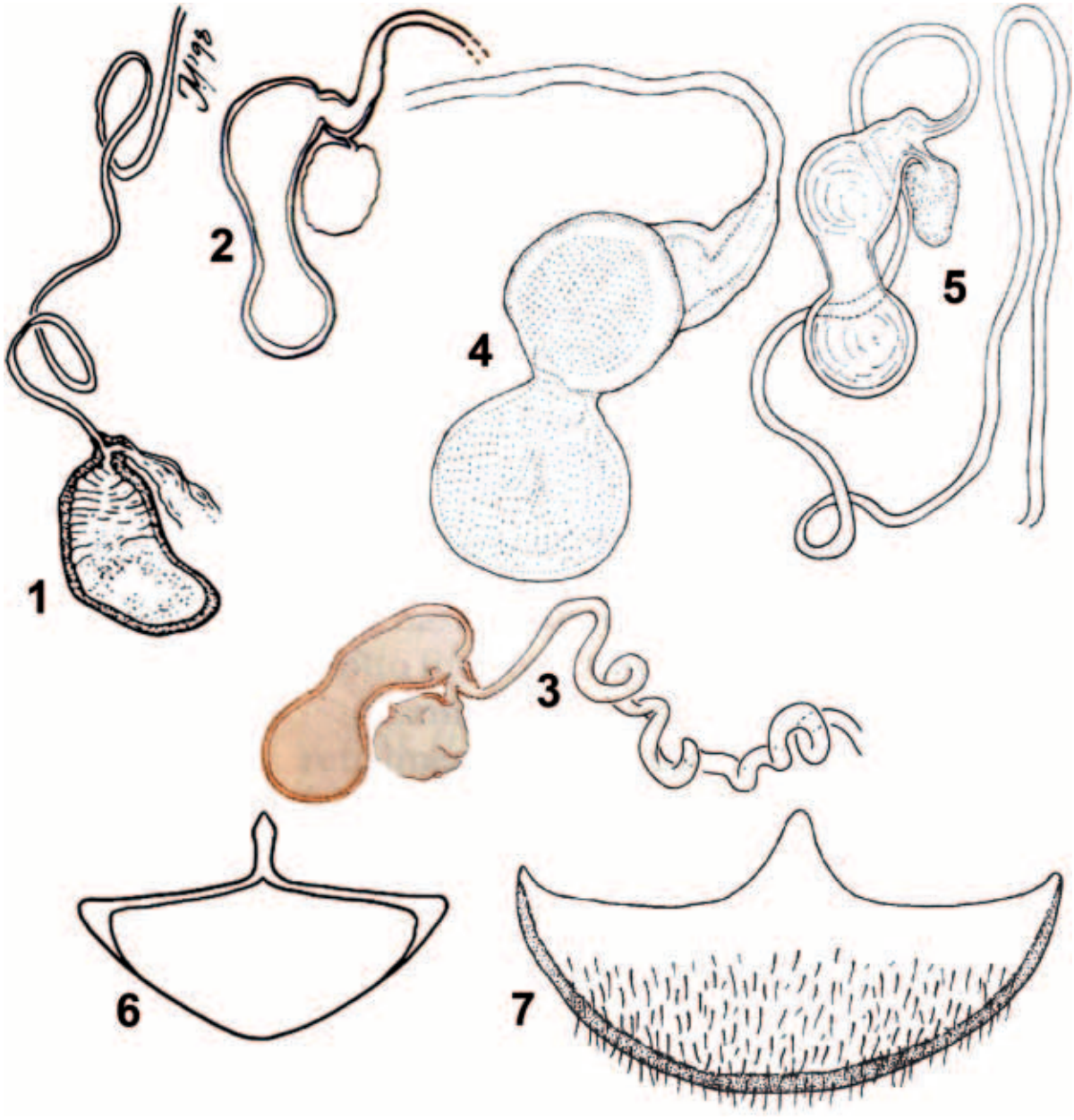
Purkynella rambouseki Knirsch, 1926
Purkynella Rambouseki Knirsch, 1926: 59.
Purkynella rambouseki Knirsch: Perreau, 2000: 257.

3.2 Clade ***Leptodirus-Anthroherpon***

The Anthroherponina composition after Perreau (2004) consists of the genera *Anthroherpon*, *Croatodirus*, *Hadesia*, *Leptomeson*, *Parantrophilon* and *Remyella*. Later, the genra *Nauticiella*, *Kircheria, Graciliella* and, with some reservation, *Riberius* were described and incorporated into this subtribe (Moravec & Mlejnek 2002; Giachino & Vailati 2006; Njunjić *et al*. 2016; Giachino & Casale 2022). Giachino & Vailati (2006) expressed doubts about the monophyly of the subtribe and Giachino & Casale (2022) recognised that in an morphological characters link *Riberius* to Anthroherponina, although preliminary molecular data from A. Faille indicate that it is not directly related to the *Anthroherpon* lineage; in these, unspecified molecular data also suggest that *Kircheria* is related to *Hadesia* and *Anthroherpon*. Njunjić *et al*. (2016) identified homoplasies and postulated the polyphyletism of *Anthroherpon* but do not comment on the phylogenetic coherence of the subtribe. Njunjić *et al*. (2017) incorporated the genera *Remyella*, *Rozajella* and *Speonesiotes* and it seems, although it is not the subject of the mentioned work, that *Remyella* is excluded from Anthroherponina and has to be incorporated into Leptodirina as a sister genus of *Rozajella*. This in turn indirectly provides evidence for the polyphyletism of Leptodirina (*sensu* Perreau 2000). Njunjić *et al*. (2018) incorporated more genera into their analysis and as an additionalresult they gained more evidence for the polyphyletism of Leptodirina (*sensu* Perreau 2000). Delić *et al*. (2023) studied all genera of Anthroherponina (*sensu* Jeannel 1924a) except *Riberius*. However, they incorporate *Nauticiella*, *Parantrophilon*, *Kircheria* and *Velebitodromus* into the molecular analysis. In terms of taxonomic finding from this, it became apparent that *Parantrophilon* is a synonymy of *Anthroherpon.*This result of the molecular analysis confirmed what was demonstrated by Čeplík & Hlavâč (2022) in morphological studies a year earlier.

Molecular results suggest that the subtribe, as currently establised, may not represent the phylogenetic relations; this claim became particularly apparent by the genetically distant position of the genus *Remyella* (Leptodirina sensu Perreau 2000) in the Southern Dinarides clade; Anthroherponina (sensu Jeannel 1924a) should therefore only include the genera distributed in the Southern Dinarides, such as *Anthroherpon*, *Hadesia*, *Graciliella*, *Kircheria*, *Leptomeson* and *Nauticiella*, and exclude *Remyella*. he presence of the raiming two genera *Croatodirus* and *Velebitodromus* from the Northern Dinaric clade are probably found to ba associated with the Sourthern Dinaric Clade due to evolutionary convergence triggered by their hygropetricolous lifestyle as previously suggested by Polak *et al*. (2016). Therefore, in its current conception Anthroherponina (*sensu* Jeannel 1924a), it may not reflect phylogenetic relationship but the formation of a group of similar ecological requirements e.g. similar habitats, so it is concluded that the genera *Croatodirus* and *Velebitodromus*, of the Northern Dinaric clade, should be excluded from this group of genera.

The general tree topology of Delić and co-workers (2023: Fig. 3) is congruent with the results in the study presented here (Tree-1: Fig. 1H; Tree-2: Fig. 2), although some genera occupy different positions on the



FIGURES 63.1–63.5: *Ceuthophyes* series. Spermathecal complex of: (**1**) *Albaniola moraveci* (modified from Udržal & Moravec 1999), (**2**) *A. gambarii* (modified from Rampini & Zoia 1995), (**3**) *A. thessalica* (modified from Rampini & Zoia 1995), (**4**) *Babuniella jovanhadzii* (modified from S. Ćurčić *et al.* 2005), (**5**) *Ochridiola marinae* (modified from Sbordoni 1971). Female uroventrite VIII of: (**6**) *A. moraveci* (modified from Udržal & Moravec 1999), (**7**) *Ceuthophyes enormis* (modified from B.V. Guéorguiev 2007).

phylogentic tree; the most important cases are discussed in the following:

– The position of *Nauticiella* as the sister genus of *Hadesia* with support >0.99 is accepted, even though no species of these genera was included in our analysis. This is mainly due to the high support and the mearly identical structure of the aedeagus in both genera.

– *Parantrophilon spelaeobatoides* is sister to *Anthroherpon hoermanni* although with indeterminate support, supposedly <0.90 (Delić *et al*. 2023).

– *Kircheria beroni* is sister to the *Hadesia* + *Nauticiella* + *Anthroherpon* + *Leptomeson* + *Graciliella* clade with support >0.99 (Delić *et al*. 2023). In our analysis in Tree-1 *Kircheria dritae* is sister to *Leptomeson* + *Graciliella* with very low support, 1.4/56 (Fig. 1H), in Tree-2, however, it is sister to the entire clade with the exception of *Hadesia* (Fig. 2) also with fairly low support, 87.6/78, albeit this position results in a topology which is closer to the one of Delić *et al*. (2023). Given that the support is much higher then in Tree-1, in which the two topologies are more similar, the position of Delić *et al*. (2023) for *Kircheria beroni* is adopted.

– The entire set of genera (*Anthroherpon*, *Hadesia*, *Graciliella*, *Kircheria*, *Leptomeson* and *Nauticiella*) forms the Southern Dinaric clade as described in Delić *et al*. (2023). It corresponds to *Anthroherpon* group of this study.

– *Remyella* has the same position in the present study then in that of Delić *et al*. (2023). The clade including *Remyella* (Fig. 2) also incorporates the genera *Riberius, Rozajella* and *Pholeuonella*; this then constitutes the Northern Dinaric clade of Delić *et al*. (2023) that corresponds to the *Pholeuonella* group of this study. On a morphological basis, the genus *Laneyriella* has been incorporated into this group.

– *Velebitodromus* is a sister to *Croatodirus* with good support, >0.99, and *Leptodirus* is inserted in a basal position with indeterminate support <0.90 (Delić *et al.* 2023). In Tree-1 *Croatodirus* derives from the basal cladogenesis of *Apholeuonus* group with support 95.9/100 and the entire clade is sister to *Leptodirus* group with support 100/100; the Tree-2 topology is identical. Consequently, *Velebitodromus* will be included as sister to *Croatodirus* in *Apholeuonus* group.

3.2.1 Series ***Neobathyscia*** Perreau, 2000 sensu novo

Diagnosis. Medium size, 2.0–4.2 mm, with bathyscioid to pholeuonoid shape, more or less convex, pubescent body. Depigmented.

Head: Retractable, with complete occipital carina; anophthalmous.

Antennae: Long, reaching if stretched backwards the middle of the elytra, with the first antennomere shorter, longer, or as long as the second one.

Pronotum: Transverse with regularly arcuated sides, not sinuated posteriorly or elongate, with arcuated sides anteriorly, deeply sinuate posteriorly.

Elytra: Relatively long, ovoid, more or less convex, regularly attenuated in the posterior half; apex rounded, not dimorphic. Disc with microsculpture transversely aligned or not; parasutural stria absent.

Legs: Thin and relatively long. Protarsi tetrameres in both sexes and not dilated in the male; protibiae without external comb at apex (with the exception of *Neobathyscia* and *Sinuicollia*); meso- and metatibiae without complete apical basket.

Mesoventral keel (Figs 66.1–66.5): Low to high, with or without deep anterior basal hollow. Anterior margin prominent, securiform, or straight, or variously curved and slightly or widely rounded; anterior angle rounded, not toothed. Prolonged or not on the metaventrite.

Suture of the metaventrite: Only known in *Aphaotus* (Fig. 66.1) and *Neobathyscia* (Fig. 66.4). It describes a soft curve from the upper part to the distance of 2/3, running subsequently parallel to the mesocoxal cavity.

Metatergal apparatus: Only known in *Aphaotus* (Fig. 66.6), *Halbherria* (Fig. 66.7) and *Neobathyscia* (Fig. 66.8). It is characterised by having extremely reduced apophysis of the alacrista.

Metendosternite: Only known in *Aphaotus* (Fig. 67.1), *Halbherria* (Fig. 67.2) and *Neobathyscia* (Fig. 67.3). In «V», with the furcal trunk short; in the furcal arms a protuberance on the inner surface and a reduced but evident anterior furcal plate.

Median lobe of aedeagus: In lateral view (Figs 68.1–68.5) abruptly bent and constricted ventrally in the basal third and distally thickened or straight, unfolded and unconstricted in the basal third and not distally thickened. In dorsal view (Figs 68.6–68.10) with apex unarmed, dentate or crenelated; or with the preapical part equipped with more or less developed coaxial teeth or with apex simple or more or less distinctly bi-lobed or tri-lobed. Basal blade of median lobe, roughly parallel, narrower than the basal lamella of the tegmen and without posterior expansion.

Endophallus (Figs 68.6–68.10): Basal «Y»-piece absent; mid-apical sclerites in number of two or three: two in form of parallel lamellae or phanerae of tiny spines.

Parameres (Figs 69.1–69.5): From thin to espe-

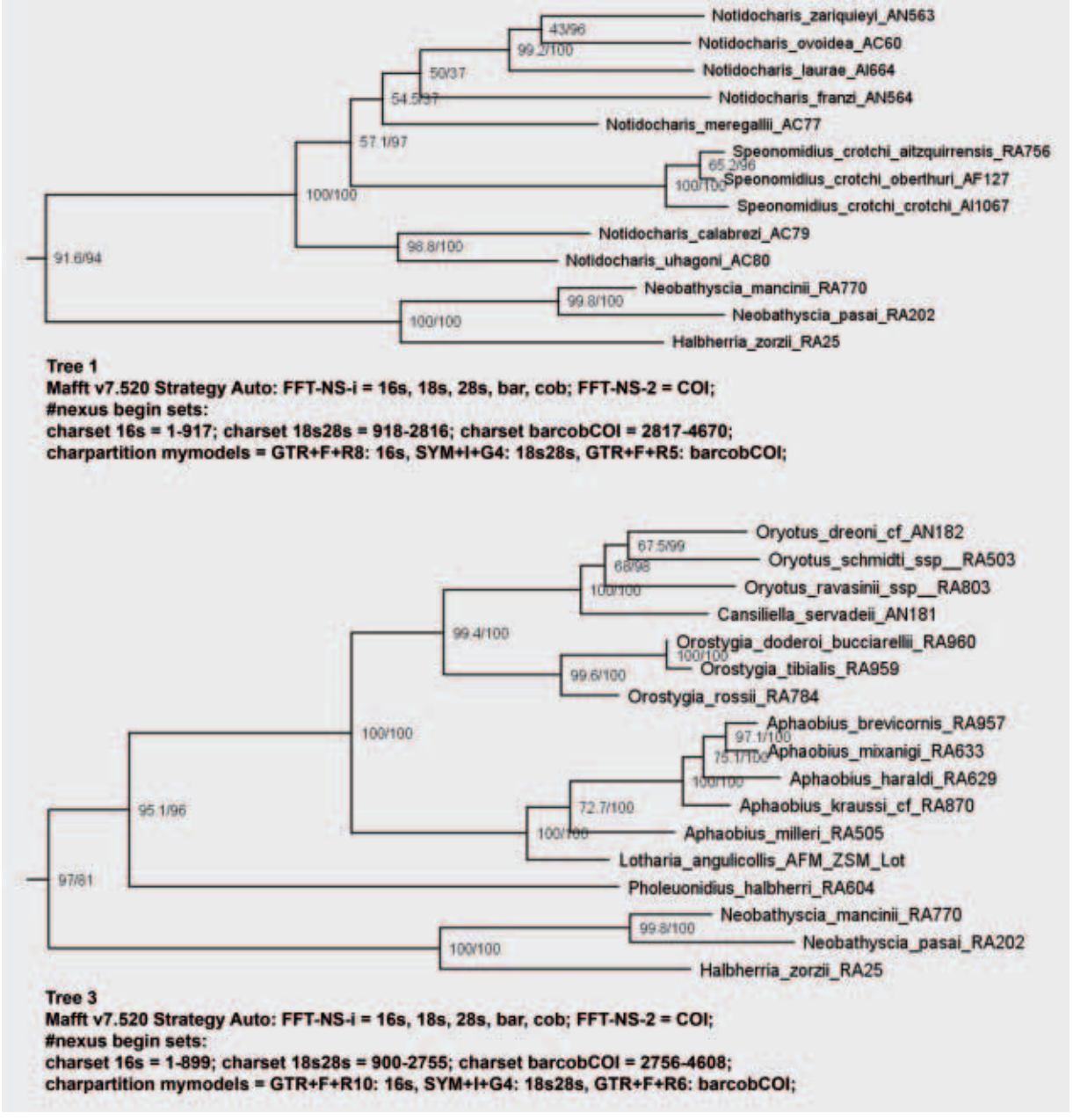


FIGURE 64: Comparison of the topology obtained in Tree-1 and Tree-3 by applying different evolutionary methods to the respective analysis. Tree-3 (analysis data in the Material and Methods section) shows only one alternative position of the *Neobathyscia* clade: *Neobathyscia* sister to the *Speonomidius* series in Tree-1 or sister to the *Oryotus* series in Tree-3.

cially thick, shorter, longer or as long as the median lobe; sometimes apically expanded, with or without laminar lobe. Bearing 2–5 apical setae.

Styli of the ovipositor: Developed, but sometimes completely atrophied.

Spermathecal complex: Spermatheca (Figs 69.6–69.10) in shape of a question mark or «C»-shaped, with the apical lobe more developed. Spermathecal ductus without basal sclerites.

Female uroventrite VIII (Figs 69.11–69.15): With

spiculum from short to long, more or less stout or acute.

Discussion. Congruity of this phyletic series, for which molecular data are present only for the genera *Neobathyscia* and *Halbherria*, is supported also by the recent contribution of Perreau (2019). Herein a cladistic approach on a morphological basis identifies *Neobathyscia* as the sister group of a complex consisting of the genera *Sinuicollia*, *Aphaotus*, *Halbherria* and *Lessiniella*. For Perreau (2000) *Bathysciotes* must be included in this series and for Perreau (2019) *Bathysciotes* + *Redensekia* is the sister group of the series.

Aphaotus, *Halbherria*, *Lessiniella* and *Sinuicollia* – share the mesoventral keel prolonged forward, a character considered unsual (Figs 66.1–66.3, 66.5). The *Halbherria* + *Sinuicollia* clade – share endophallus structures with two mid-apical sclerites in form of long, narrow or thick, lamellae (Figs 68.7, 68.10).

A problematic issue arose since it is currently constituted by its position inside the phylogenetic tree, where it is positioned, with an average high support, 91.6/94 as sister group of the *Speonomidius* series in Tree-1 (Fig. 2) or to support 90.6/97 in Tree-2 (Fig. 2)., In addition together with the latter series it joins the *Leptodirus* and *Hartigiella* series with a support of 80.7/17 in Tree-1 (Fig. 2) or only joins the *Leptodirus* series with a support of 67.6/34 in Tree-2 (Fig. 2). From a zoogeographically and morphologically point of view the topology found in either tree are not very congruent as they position them in a series of the Central-Eastern Alps although the both series are of Iberian distribution.

In the past, on a morphological basis, *Neobathyscia* series has always been related to *Oryotus*; in one of the analysis carried out, this position was indeed obtained (Fig. 64: Tree-3) with good support, 97/81. Currently it is not possible to rule out a future shift towards the *Oryotus* series of this clade because the molecular data of many of taxa of the *Neobathyscia* series are still missing. Concerning the availability of molecular data it has to be stated that data are missing for many *Neobathyscia* (7) are missing, almost all *Halbherria* (10), all *Aphaotus* (8), as well as all *Lessiniella* (2) and *Sinuicollia* (1). We actually have data for only on three specific taxa out of 31.

In this series there are peculiarities in the styli of the ovipositor present, so that it will be indicated in each genus if they are atrophied or not. In other series this structure has not been described since no significant differences are apparent.

Key to genera

1. Pholeuonoid shape (Fig. 65.3). Pronotum deeply sinuate posteriorly. Mesoventral keel low and posterior apophysis not prolonged on the metaventrite (Fig. 66.3). Median lobe of aedeagus short: in dorsal view slightly bifurcated, strongly widened near the apex, whic is protruding in a short tongue (Figs 68.3, 68.8). Endophallus with two mid-apical sclerites in form of long and thick lamellae (Fig. 68.8) .....*Lessiniella*
- Bathyscioid shape (Figs 65.4, 65.5), rarely pholeuonoid, in this case the pronotum slightly sinuate (i.e. *Halbherria daffneri*). Mesoventral keel high and the apophysis extends over the metaventrite (Figs 66.1, 66.2, 66.4). Median lobe and endophallus of aedeagus another way (Figs 68.1, 68.2, 68.4–68.7, 68.9, 68.10) 2

2. Mesoventral keel not prolonged on the metaventrite (Fig. 66.5). Protibiae with external comb. Apical part of the median lobe simple, in shape of sharp beak (Figs 68.5, 68.10). Parameres very robust, apically expanded, with two setae (Fig. 69.5) .....*Sinuicollia*
- Mesoventral keel, prolonged on the metaventrite (Figs 66.1, 66.2, 66.4). Protibiae with or without external comb. Apical part of the median lobe more or less rounded (Fig. 68.7), bifurcated (Fig. 68.9) or trilobed (Fig. 68.6). Parameres otherwise with 3 apical setae (Figs 69.1, 69.2, 69.4) 3

3. Mesoventral keel with prominent anterior margin, with a deep notch behind the anterior margin and beginning of the ventral margin (Fig. 66.1). Median lobe tri-lobed with apical mid-part lanceolate and lateral parts almost as long as the central expansion, tapering and curving inward (Figs 68.1, 68.6) .....*Aphaotus*
- Mesoventral keel with anterior margin not or slightly prominent, if there is a notch it is shallow (Figs 66.2, 66.4). Median lobe simple or bifurcated (Figs 68.7, 68.9) 4

4. Protibiae without external comb. Antennae with first antennomere as long as or shorter than the second. Mesoventral keel not prolonged over the entire metaventrite (Fig. 66.2). Endophallus with two mid-apical sclerites in form of long, narrow or thick, lamellae (Fig. 68.7). Female with styli developed .....
.....*Halbherria*
- Protibiae with external comb. Antennae with the first antennomere longer than the second. Mesoventral keel prolonged over the entire metaventrite (Fig. 66.4). Endophallus with mid-apical sclerites in form of two par-

allel phanerae of tiny spines (Fig. 68.9). Female with styli completely atrophied .....*Neobathyscia*

Genus ***Aphaotus*** Breit, 1914
Aphaotus Breit, 1914: 58.

Type species. *Aphaotus Jurečeki* Breit, 1914 by subsequent designation (habitus in Fig. 65.1).

Diagnosis. Medium size, 2.6–3.9 mm, with bathyscioid shape (Fig. 65.1); with elongated, poorly convex and pubescent body.

Head: Retractable, with complete occipital carina.

Antennae: Long, reaching if stretched backwards the middle of the elytra, with the first antennomere as long as or shorter than the second one.

Pronotum: Broad, transverse, with regularly and long arcuated sides, not sinuated posteriorly; with maximum width just before the base; apex rounded, not dimorphic

Elytra: Long, ovoid, poorly convex, regularly attenuated in the posterior half, apex rounded, not dimorphic. Disc with punctation not transversely aligned.

Legs: Thin and relatively long. Males protarsi tetrameres and not dilated; protibiae without external comb at apex; mesotibiae straight and provided with spines on the external margin; metatibiae straight; meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 66.1): Low to high, with deep anterior basal hollow. Anterior margin prominent, securiform and slightly or widely rounded; anterior angle rounded and connected to the ventral margin which is hollow and noticably toothed. Prolonged posteriorly on the metaventrite.

Suture of the metaventrite (Fig. 66.1): It describes a soft curve from the upper part around 2/3 of the structure, then runs parallel to the mesocoxal cavity.

Metatergal apparatus (Fig. 66.6): The apophysis of the alacrista is very short, with blunt apices, and the wings of the metascutum very reduced.

Metendosternite (Fig. 67.1): In «V». Furcal arms long, twice as long as the furcal trunk with a wide apical apophysis, a protuberance on the inner surface and a reduced but evident anterior furcal plate on the furcal arms; posterior furcal plate slightly wider in the lower third. Furcal trunk short, although clearly longer than the widest area.

Median lobe of aedeagus: In lateral view (Fig. 68.1) more or less regularly arcuate. In dorsal view (Fig. 68.6) trifurcated, strongly widened near the apex with lateral expansion about as long as the central expansion and parallel to the axis of the median lobe. Basal blade short, roughly parallel, narrower than the basal blade of the tegmen, without posterior expansion.

Endophallus (Fig. 68.6): Basal «Y»-piece absent; two mid-apical sclerites in form of long and narrow lamellae.

Parameres (Fig. 69.1): Thin as long as or slightly longer than the median lobe; bearing 2, 3 or 4 apical setae. There are aedeagi with two setae in one paramere and three in the other.

Styli of the ovipositor: Not atrophied.

Spermathecal complex: Spermatheca (Fig. 69.6) in shape of a question mark with the basal lobe undifferentiated. Spermathecal ductus without a basal sclerites.

Female uroventrite VIII (Fig. 69.11): With spiculum very short, less than 1/10 as long as the width of the uroventrite.

Discussion. In absence of molecular data, the genus *Aphaotus* is assigned to the *Neobathyscia* series on a morphological basis. Supported in this also by the recent contribution of Perreau (2019). Giachino & Vailati (2005a) established two groups of species based on morphological characteristics, structures of the aedeagus and distribution area of the species.

Distribution. Italy. Veneto, Monte Pasubio, Monte Grappa, Sette Comuni, Asiago and Folgaria-Tonezza uplands. Trentino, Monte Baldo and Monte Mandriola.

Species

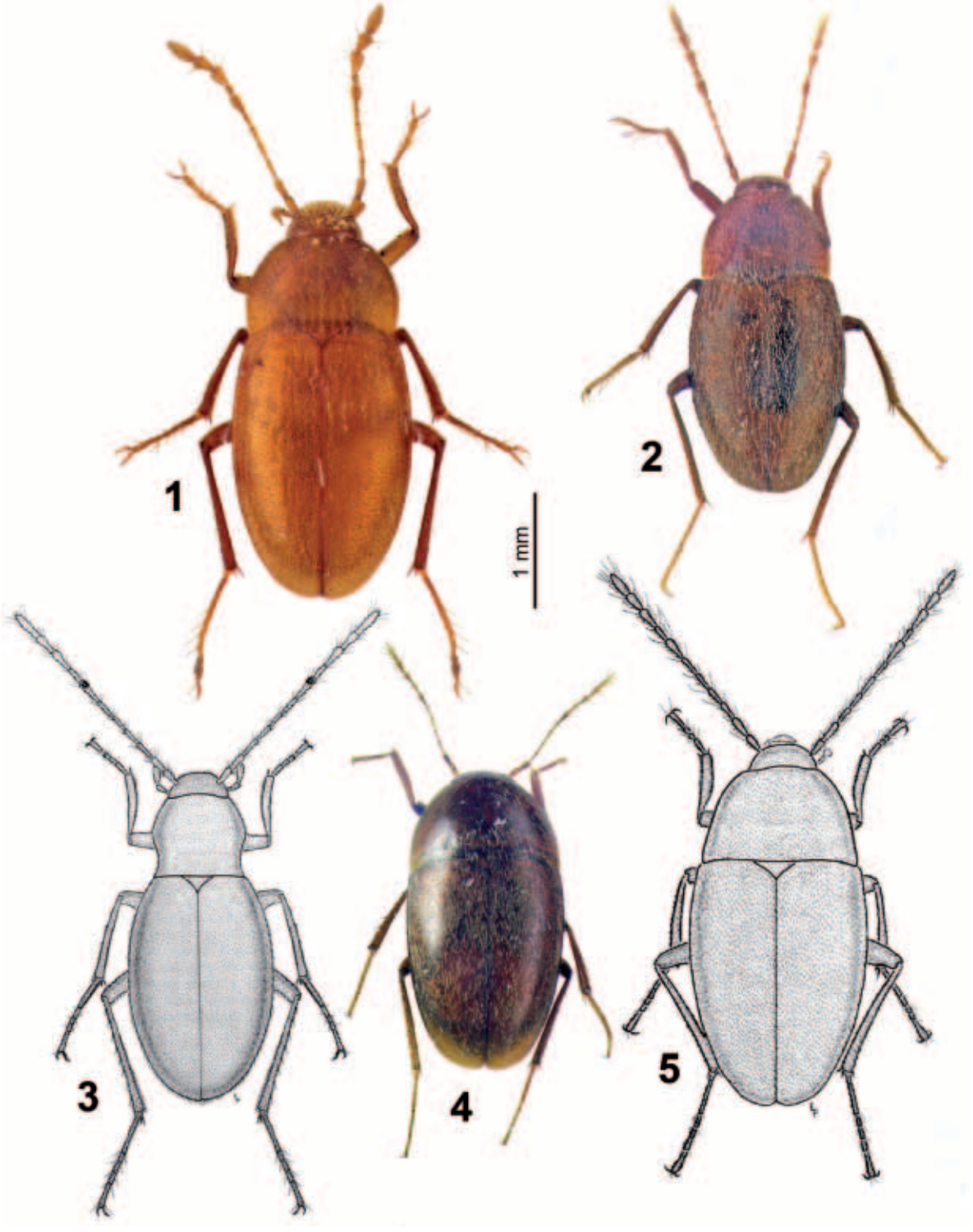
«*jureceki* group» *sensu* Giachino & Vailati, 2005a
Aphaotus jureceki Breit, 1914
Aphaotus Jurečeki Breit, 1914: 59.
Aphaotus jureceki Breit: Perreau, 2000: 180.

Aphaotus genesti Giachino & Vailati, 2005
Aphaotus genesti Giachino & Vailati, 2005a: 348.

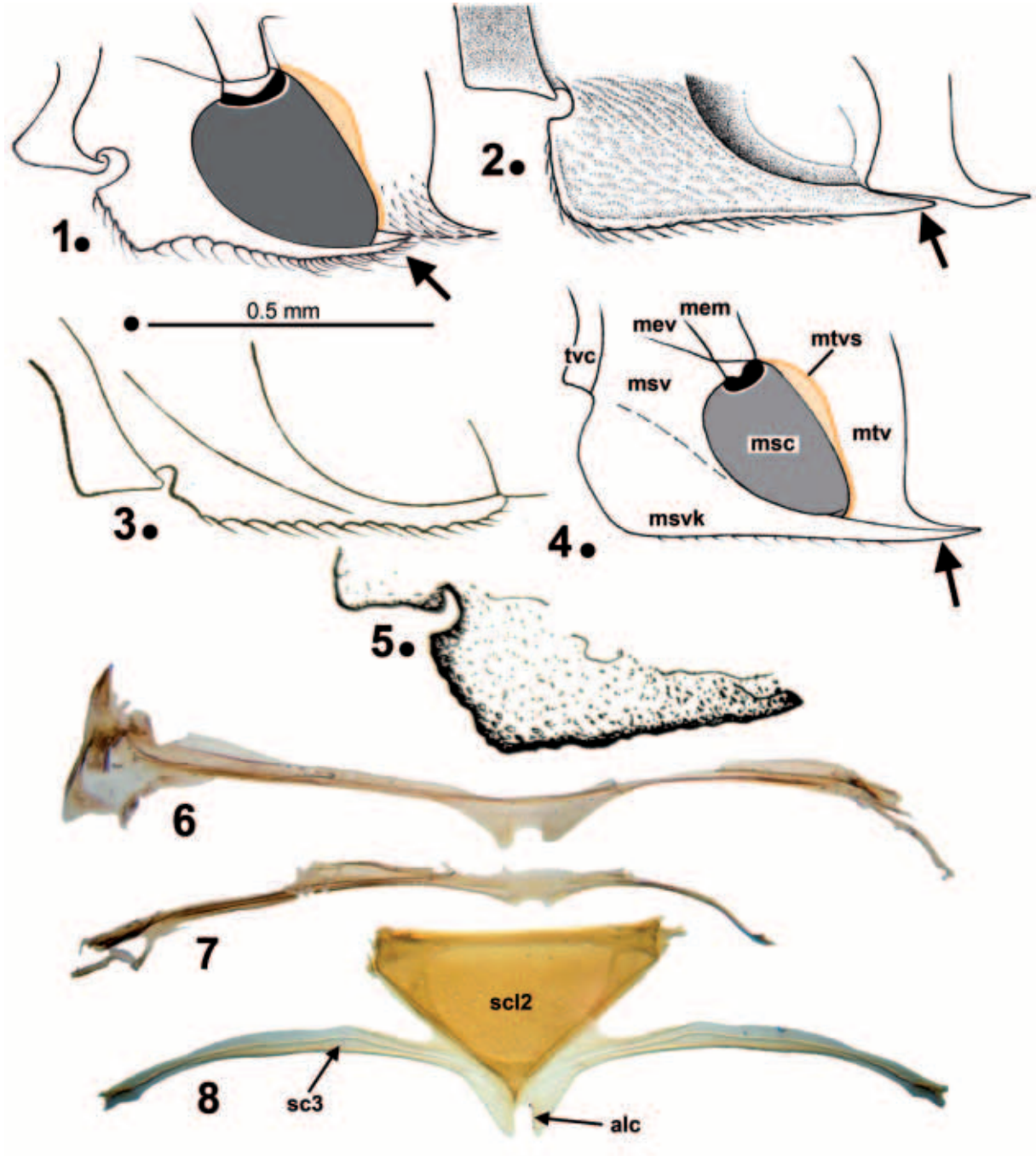
Aphaotus biancoi Giachino & Vailati, 2005
Aphaotus biancoi Giachino & Vailati, 2005a: 350.

Aphaotus martinellii Giachino & Vailati, 2005
Aphaotus martinellii Giachino & Vailati, 2005a: 352.

Aphaotus cadamuroi Busulini, 1958
Aphaotus cadamuroi Busulini, 1958: 16.



FIGURES 65.1–65.5: *Neobathyscia* series. Habitus of: (**1**) *Aphaotus jureceki*, (**2**) *Halbherria tamaninii*, (**3**) *Lessiniella berica* (modified from Piva 1993), (**4**) *Neobathyscia mancinii*, (**5**) *Sinuicollia dalpiazi* (modified from Piva 2008).



FIGURES 66.1–66.8: *Neobathyscia* series. Pterothorax in lateral view of: (**1**) *Aphaotus jureceki*, (**2**) *Halbherria carlini* (modified from Vailati 2017), (**3**) *Lessiniella trevisioli* (modified from Pavan 1941), (**4**) *Neobathyscia mancinii*, (**5**) *Sinuicollia dalpiazi* (modified from Paoletti 1977). Metatergal apparatus, ventral view of metanotum and axillaria of: (**6**) *A. jureceki*, (**7**) *H. zorzii*, (**8**) *N. pasai*. Black arrow pointing towards the keel extended over the metaventrite. Abbreviations: **alc**, alacrista; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **mtvs**, metaventral suture; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **sc3**, metascutum; **scl2**, mesoscutellum; **tvc**, transverse collar.

«*nivalis* group» *sensu* Giachino & Vailati, 2005a
Aphaotus nivalis G. Müller, 1931
Aphaotus nivalis G. Müller, 1931c: 7.
Aphaotus nivalis ssp. *nivalis* Müller, 1931: Piva, 1986: 140.

Aphaotus granulosus Piva, 1986
Aphaotus nivalis ssp. *granulosus* Piva, 1986: 141.
Aphaotus granulosus Piva, 1986: Giachino & Vailati, 2005a: 360.

Aphaotus pivai Giachino & Vailati, 2005
Aphaotus pivai Giachino & Vailati, 2005a: 364.

Aphaotus grottoloi Giachino & Vailati, 2005
Aphaotus grottoloi Giachino & Vailati, 2005a: 370.

Genus ***Halbherria*** Conci & Tamanini, 1951
Halbherria Conci & Tamanini, 1951: 125.

Type species. *Aphaotus Tamaninii* G. Müller, 1931 by original designation (habitus in Fig. 65.2).
Diagnosis. Medium size, 2.3–4.2 mm, with bathyscioid (Fig. 65.2) to pholeuonoid body shape; with elongated, poorly convex and pubescent body.

Head: Retractable, with complete occipital carina.

Antennae: Long, reaching if stretched backwards tothe middle of the elytra; with the first antennomere as long as or shorter than the second one.

Pronotum: Broad, transverse, with regularly and long arcuated sides, sinuate or not posteriorly; with maximum width just before the base.

Elytra: Long, ovoid, poorly convex, regularly attenuated in the posterior half; apex rounded, not dimorphic. Disc with microsculpture not transversely aligned.

Legs: Thin and relatively long. Males protarsi tetrameres and not dilated; protibiae without external comb at apex; mesotibiae slightly arcuated and provided with spines on the external margin; metatibiae straight; meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 66.2): High with straight or diversely curved front edge, not toothed but equipped with a basal hollow. Anterior margin prominent. Extended posterior process or apophysis on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 66.7): The apophysis of the alacrista is very short and the wings of the metascutum are strongly reduced.

Metendosternite (Fig. 67.2): In «V». Furcal arms long, two and a half times longer than the furcal trunk, with a wide apical apophysis, a protuberance on the inner surface and a reduced but evident anterior furcal plate on the furcal arms; posterior furcal plate slightly wider in the lower third. Furcal trunk short, although clearly longer than the widest area.

Median lobe of aedeagus: In lateral view (Fig. 68.2) abruptly bent and constricted ventrally in the basal third and distally thickened; or straight, unfolded and unconstricted in the basal third and not distally thickened. In dorsal view (Fig. 68.7) with apex unarmed, dentate or crenellated; or with the preapical part equipped with more or less developed coaxial teeth; or, again, with apex distinctly tri-lobed. Basal blade short, without posterior expansion.

Endophallus (Fig. 68.7): Basal «Y»-piece absent; two mid-apical sclerites in form of long, narrow or thick, lamellae.

Parameres (Fig. 69.2): Thin, as long as, or shorter than the median lobe; bearing three apical setae

Styli of the ovipositor: Not atrophied.

Spermathecal complex: Spermatheca (Fig. 69.7) in shape of a question mark, with a indistinct differentiation of the apical and basal sclerotized lobes. Spermathecal ductus without a basal sclerites.

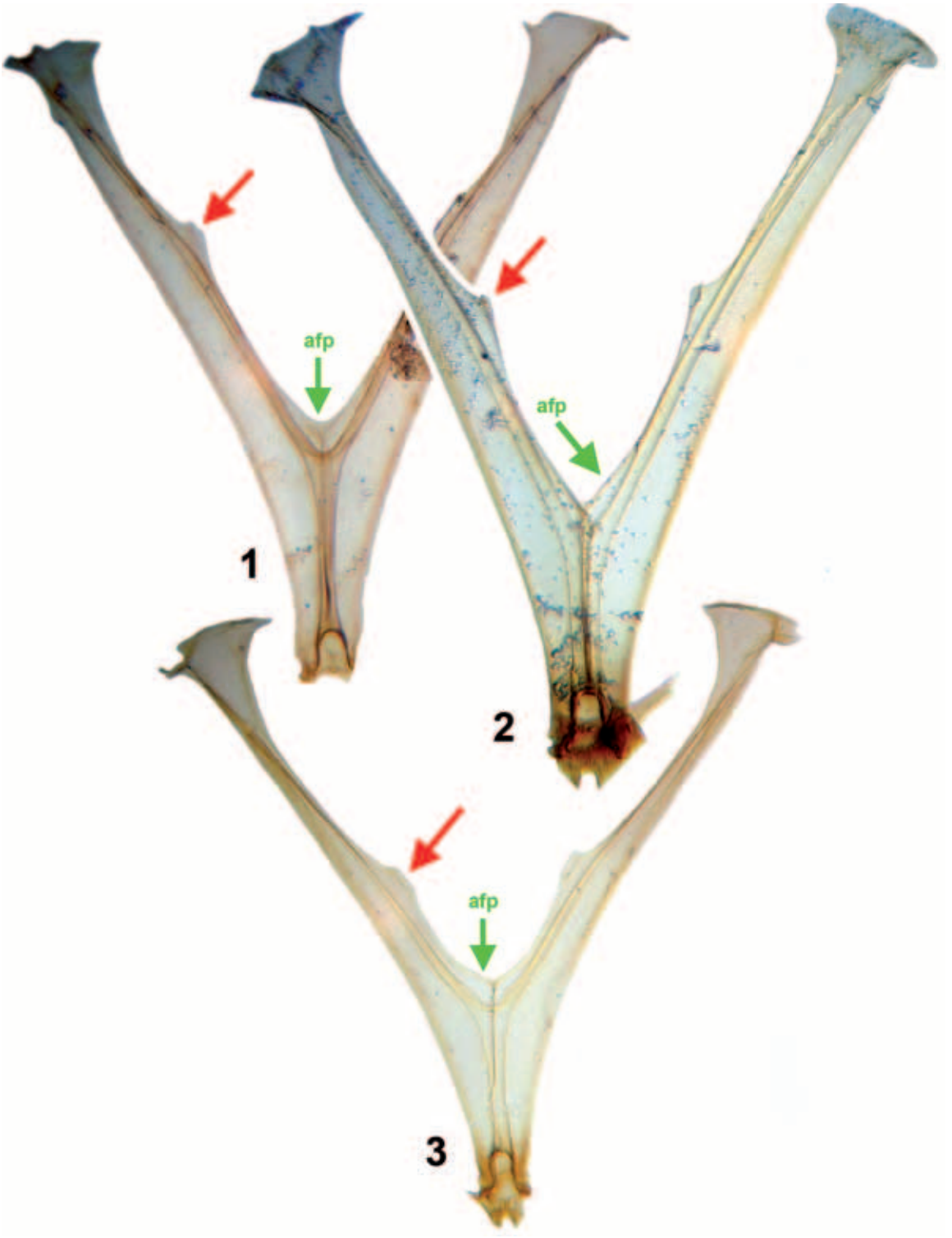
Female uroventrite VIII (Fig. 69.12): With spiculum stout and more or less long.

Discussion. Molecular data (Fig. 1I) assigns the genus *Halbherria* to the *Neobathyscia* series with a very high support, 100/100. This position is supported also by the recent contribution of Perreau (2019). Giachino & Vailati (2005a) established three groups for the nine known species, based on the morphology of the aedeagus. Later Vailati (2017b) describes *H. carlini* and conserves the three groups, but also considers the biogeographic distribution of the species. It seems closely related to *Sinuicollia* with which it shares the same structures equally arranged on the endophallus.

Distribution. Italy. Veneto, Vicenza, Altipiano di Sette Comuni, Rovereto, Vicentino (Recoaro); Belluno, massif of Piani Eterni; Verona, Monti Lessini. Trentino, Monte Pasubio, north slope of Monte Mandriola and massif of Monte Baldo. Trentino-Alto-Adige, Trento, Monte Obante.

Species

«*cimbrica* group» *sensu* Giachino & Vailati, 2005a
Halbherria cimbrica Piva, 1985
Aphaotus (Halbherria) cimbrica Piva, 1985: 301.
Halbherria cimbrica (Piva): Perreau, 2000: 180.



FIGURES 67.1–67.3: *Neobathyscia* series. Metendosternite of: (**1**) *Aphaotus jureceki*, (**2**) *Halbherria zorzii*, (**3**) *Neobathyscia pasai*. The red arrow indicates an internal protuberance; the green arrow indicates the anterior furcal plate (**afp**) (Opitz, 2019).

«*stephani* group» *sensu* Giachino & Vailati, 2005a
Halbherria stefani (Breit, 1914)
Aphaotus stefani Breit, 1914: 60.
Halbherria stefani (Breit): Paoletti, 1977: 47.
Halbherria mandriolensis Conci & Tamanini, 1951: 131.

Halbherria zorzii (Ruffo, 1950)
Aphaotus zorzii Ruffo, 1950: 131.
Halbherria zorzii (Ruffo): Conci & Tamanini, 1951: 136.

Halbherria genesti Giachino & Vailati, 2005
Halbherria genesti Giachino & Vailati, 2005a: 326.

Halbherria daffneri Perreau, 2019
Halbherria daffneri Perreau, 2019: 374.

«*tamaninii* group» *sensu* Giachino & Vailati, 2005a
Halbherria carlini Vailati, 2017
Halbherria carlini Vailati, 2017b: 106.

Halbherria tamaninii G. Müller, 1931
Aphaotus tamaninii G. Müller, 1931b: 5.
Halbherria tamaninii (Müller): Conci & Tamanini, 1951: 127.
Halbherria tamaninii tamaninii (Müller): Perreau, 2000: 181.

Halbherria pacei Piva, 1988
Halbherria tamaninii pacei Piva, 1988: 17.
Halbherria pacei Piva, 1988: Giachino & Vailati, 2005a: 332.

Halbherria pivai Giachino & Vailati, 2005
Halbherria pivai Giachino & Vailati, 2005a: 334.

Halbherria pasubiana Giachino & Vailati, 2005
Halbherria pasubiana Giachino & Vailati, 2005a: 335.

Halbherria vericoi Piva, 1984
Halbherria vericoi Piva, 1984: 208.

Genus ***Lessiniella*** Pavan, 1941
Lessiniella Pavan, 1941: 201.

Type species. *Lessiniella trevisioli* Pavan, 1941 by original designation (for the habitus see that of the similar species *Lessiniella berica* in Fig. 65.3).

Diagnosis. Medium size, 2.8–3.2 mm, with pholeuonoid shape (Fig. 65.3); with elongated, convex and pubescent body.

Head: Retractable, with complete occipital carina.

Antennae: Long, reaching, if stretched backwards to the middle of the elytra, with the first antennomere shorter than the second one.

Pronotum: Elongate, with arcuated sides anteriorly, deeply sinuate posteriorly; with maximum width just at the middle.

Elytra: Long, ovoid, convex, regularly attenuated in the posterior half; apex rounded, not dimorphic. Disc with punctuatuion not transversely aligned.

Legs: Thin and long. Males protarsi tetrameres and not dilated; protibiae without external comb at apex; mesotibiae straight and provided with thin spines on the external margin; metatibiae straight; meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 66.3): Low, with deep anterior basal hollow. Anterior margin slightly prominent and straight or widely rounded; anterior angle rounded and connected to the ventral margin, which is hollow and noticably toothed. Not prolonged posteriorly on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: In lateral view (Fig. 68.3) more or less regularly arcuate. In dorsal view (Fig. 68.8) slightly bifurcated, strongly widened near the apex, which is protruding in a short tongue. Basal blade short, roughly parallel, narrower than the basal blade of tegmen, without posterior expansion.

Endophallus (Fig. 68.8): Basal «Y»-piece absent; two mid-apical sclerites in form of long and thick lamellae.

Parameres (Fig. 69.3): Especially thick, shorter than the median lobe; bearing 3–5 apical setae.

Styli of the ovipositor: Not atrophied.

Spermathecal complex: Spermatheca (Fig. 69.8) «C»-shaped, with a indistinct differentiation of the apical and basal sclerotized lobes. Spermathecal ductus without a basal sclerites.

Female uroventrite VIII (Fig. 69.13): With spiculum short, less than 1/10 as long as the width of the uroventrite.

Discussion. In absence of molecular data, the genus *Lessiniella* is assigned to the *Neobathyscia* series on a morphological basis. Supported is this taxonomic classification also by the recent contribution of Perreau (2019).

Distribution. Italia. Veneto, Vicenza prov., Monti Berici and Monti Lessini.

Species

Lessiniella berica Piva, 1993
Lessiniella berica Piva, 1993: 121.

Lessiniella trevisioli Pavan, 1941
Lessiniella trevisioli Pavan, 1941: 203.

Genus ***Neobathyscia*** G. Müller, 1917
Neobathyscia G. Müller, 1917: 639.

Type species. *Bathyscia antrorum* Dodero, 1900 by subsequent designation (for the habitus see that of the similar species *Neobathyscia mancinii* in Fig. 65.4).
Diagnosis. Medium size, 2.0–3.0 mm, with bathyscioid shape (Fig. 65.4); with short, convex and pubescent body.

Head: Retractable, with complete occipital carina.

Antennae: Long, reaching, if stretched backwards to the middle of the body, with the first antennomere just longer than the second one.

Pronotum: Broad, very transverse, with regularly and long arcuated sides, not sinuated posteriorly, with maximum width at the base which is as wide as the elytral base.

Elytra: Relatively long, ovoid, convex, regularly attenuated in the posterior half; apex rounded, not dimorphic. Disc with microsculpture transversely aligned or not.

Legs: Thin and relatively long. Males protarsi tetrameres and not dilated; protibiae slightly enlarged, provided with two robust spurs (one external and another one internal) and with external comb at apex; mesotibiae straight and provided with spines on the external margin; metatibiae slightly arcuated; meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 66.4): High, from rounded to subrectilinear anteriorly, without a basal hollow; vertex without tooth and obtuse angle; posterior process prolonged over the whole metaventrite.

Suture of the metaventrite (Fig. 66.4): Slightly separated from the coxal cavity in the upper 2/3rd and delimiting a small arched area, then it runs very close to the coxal cavity.

Metatergal apparatus (Fig. 66.7): The apophysis of the alacrista are very short with sharp apices and the wings of the metascutum are very reduced.

Metendosternite (Fig. 67.3): In «V». Furcal arms long and narrow, almost two and a half times longer than the furcal trunk, with a wide apical apophysis, a protuberance on the inner surface and a reduced but evident anterior furcal plate on the furcal arms; posterior furcal plate very narrow or absent in the apical half of the arm. Furcal trunk short, although clearly longer than the widest area.

Median lobe of aedeagus: Short and wide, with ventral side more or less regularly arcuate (Fig. 68.4) and apex bifurcated (Fig. 68.9); normally attenuated at apex. Basal blade roughly parallel, narrower than the basal lamella of the tegmen and without posterior expansion.

Endophallus (Fig. 68.9): Basal «Y»-piece absent; mid-apical sclerites in form of two parallel phanerae of tiny spines.

Parameres (Fig. 69.4): Thin, shorter or as long as the median lobe; sometimes apically expanded, with or without laminar lobe. Bearing three apical setae.
Styli of the ovipositor: Completely atrophied.

Spermathecal complex: Spermatheca (Fig. 69.9) in the form of courgette, with a weak differentiation of the apical and basal sclerotized lobes. Spermathecal ductus without a basal sclerites.

Female uroventrite VIII (Fig. 69.14): With spiculum short, less than 1/10 as long as the width of the uroventrite.

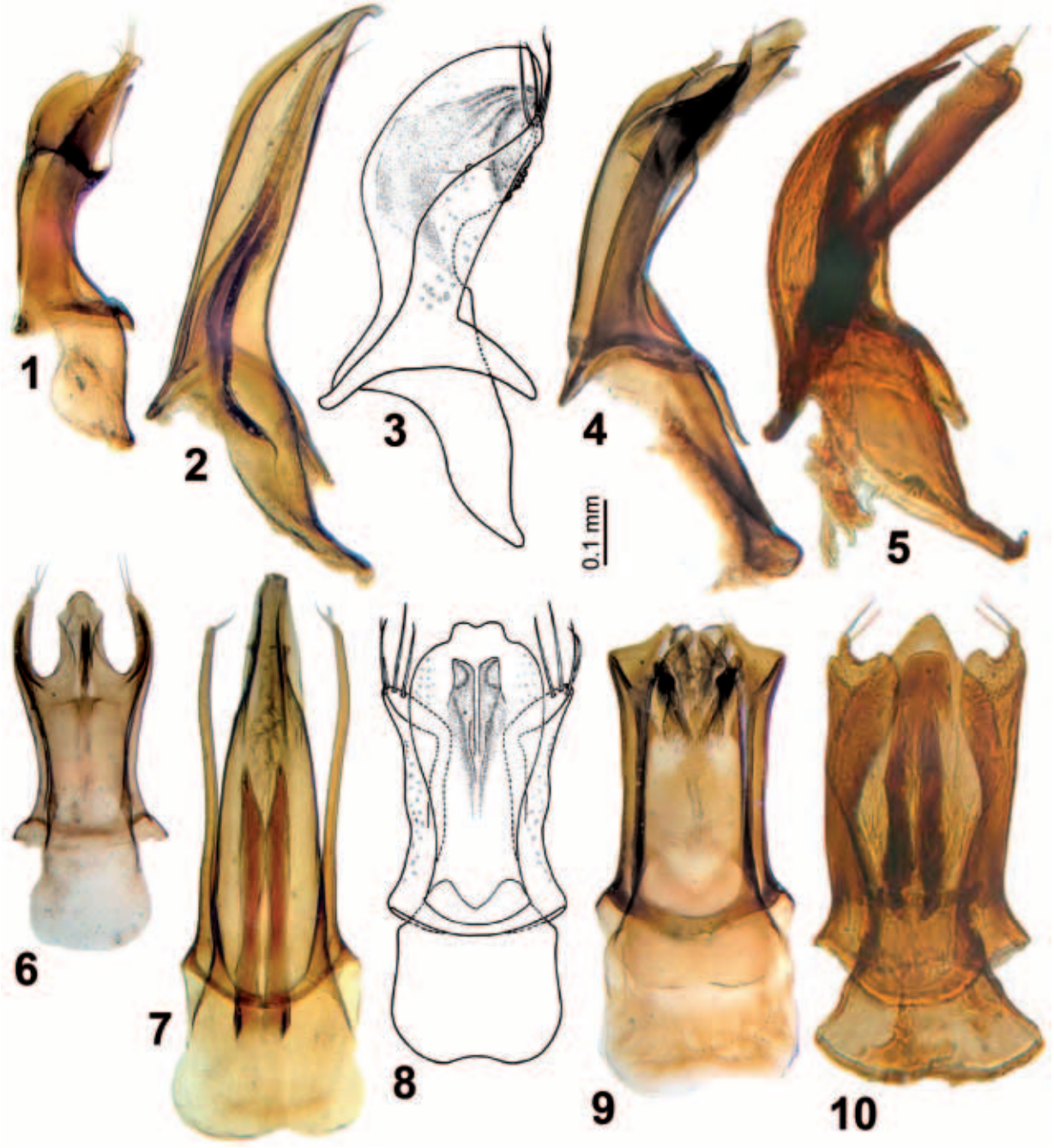
Discussion. Molecular data (Fig. 1I) assign it to the *Neobathyscia* series, the nominotypical genus of the series and the genus *Halbherria* with a very high support (100/100). This position is supported also by morphological data as published in the recent work of Perreau (2019).

Distribution. Italy. Trentino-Alto-Adige, Trento, Rovereto. Veneto, north of Monte Pasubio, within the Adige and Brenta valleys. Veneto, Verona, Monte Lessini; Vicenza, Chiampo, Valdagno, Isola Vicentina, Caltrano and Solagna (Monte del Grappa); Treviso, Monte Pallon.

Species

Neobathyscia affinis Piva, 1984
Neobathyscia affinis Piva, 1984: 205.

Neobathyscia antrorum (Dodero, 1900)
Neobathyscia antrorum antrorum (Dodero, 1900)
Bathyscia antrorum Dodero, 1900: 415.
Speonesiotes antrorum Dodero: Jeannel, 1910a: 39.
Bathyscia antrorum var. *brachycera* Dodero, 1900: 415.
Neobathyscia antrorum antrorum (Dodero): Perreau, 2000: 191.



FIGURES 68.1–68.10: *Neobathyscia* series. Aedeagus in lateral view of: (**1**) *Aphaotus jureceki*, (**2**) *Halbherria tamaninii*, (**3**) *Lessiniella trevisioli* (modified from Piva 1993), (**4**) *Neobathyscia mancinii*, (**5**) *Sinuicollia dalpiazi* (modified from Perreau 2019). Aedeagus in dorsal view of: **(6)** *A. jureceki*, (**7**) *H. tamaninii*, (**8**) *L. trevisioli* (modified from Piva 1993), (**9**) *N. mancinii*, (**10**) *S. dalpiazi* (modified from Perreau 2019).

Neobathyscia antrorum fenzoi Rallo, 1971
Neobathyscia antrorum fenzoi Rallo, 1971: 545.

Neobathyscia fabianii (Dodero, 1904)
Bathyscia (Aphaobius) Fabianii Dodero, 1904a: 55.
Bathyscia Fabianii Dodero: Jeannel, 1908a: 299.
Speonesiotes Fabianii Dodero: Jeannel, 1910a: 39.
Neobathyscia Fabianii Dodero: G. Müller, 1917: 639.
Neobathyscia fabianii (Dodero): Paoletti, 1977: 46.

Neobathyscia isabelae Piva, 1984
Neobathyscia isabelae Piva, 1984: 203.

Neobathyscia leccei Piva, 1984
Neobathyscia leccei Piva, 1984: 204.

Neobathyscia lessinica G. Müller, 1934
Neobathyscia lessinica G. Müller, 1934: 179.

Neobathyscia mancinii Jeannel, 1924
Neobathyscia mancinii mancinii Jeannel, 1924
Neobathyscia Fabianii Mancinii Jeannel, 1924a: 58.
Neobathyscia Mancinii (Jeannel): Ruffo, 1938: 98.
Neobathyscia mancinii mancinii Jeannel: Perreau, 2000: 192.
Neobathyscia mancinii ruffoi Piva, 2008
Neobathyscia mancinii ruffoi Piva, 2008: 11.

Neobathyscia pasai Ruffo, 1950
Neobathyscia pasai Ruffo, 1950: 129.

Neobathyscia roboretana G. Müller, 1931
Neobathyscia roboretana G. Müller, 1931b: 9.

Genus ***Sinuicollia*** Piva, 2008
Sinuicollia Piva, 2008: 7.

Type species. *Neobathyscia dalpiazi* Paoletti, 1977 by original designation (habitus in Fig. 65.5).

Diagnosis. Medium size, 3.0–3.3 mm, with bathyscioid shape (Fig. 65.5); with elongated, poorly convex and pubescent body.

Head: Retractable, with complete occipital carina.

Antennae: Long, reaching, if stretched backwards to the middle of the body, with the first antennomere shorter than the second one.

Pronotum: Broad, transverse, with regularly and long arcuated sides anteriorly, slightly sinuate posteriorly; with maximum width at the base.

Elytra: Relatively long, ovoid, poorly convex, regularly attenuated in the posterior half, apex rounded, not dimorphic. Disc with microsculpture not transversely aligned.

Legs: Thin and relatively long. Males protarsi tetrameres and not dilated; protibiae with external comb at apex; mesotibiae slightly arcuated and provided with spines on the external margin; metatibiae straight; meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 66.5): High, subrettilinear anteriorly, but blunt, not toothed and with a basal hollow; not prolonged on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Robust. In lateral view (Fig. 68.5) ventral side regularly arcuate. In dorsal view (Fig. 68.10) distinctly constricted in the basal third, then enlarged in the distal half; apex simple in shape of sharp beak. Basal blade wider than the basal blade of tegmen; without posterior expansion.

Endophallus (Fig. 68.10): Basal «Y»-piece absent; mid-apical sclerites in number of three: two in form of long and thick lamellae, and another one, single, preapical.

Parameres (Fig. 69.5): Particularly thick, as long as the median lobe; apically expanded, with lobe bearing two setae.

Styli of the ovipositor: Not or completely atrophied.

Spermathecal complex: Spermatheca (Fig. 69.10) in shape of a question mark with the basal lobe undifferentiated. Spermathecal ductus without a basal sclerites.

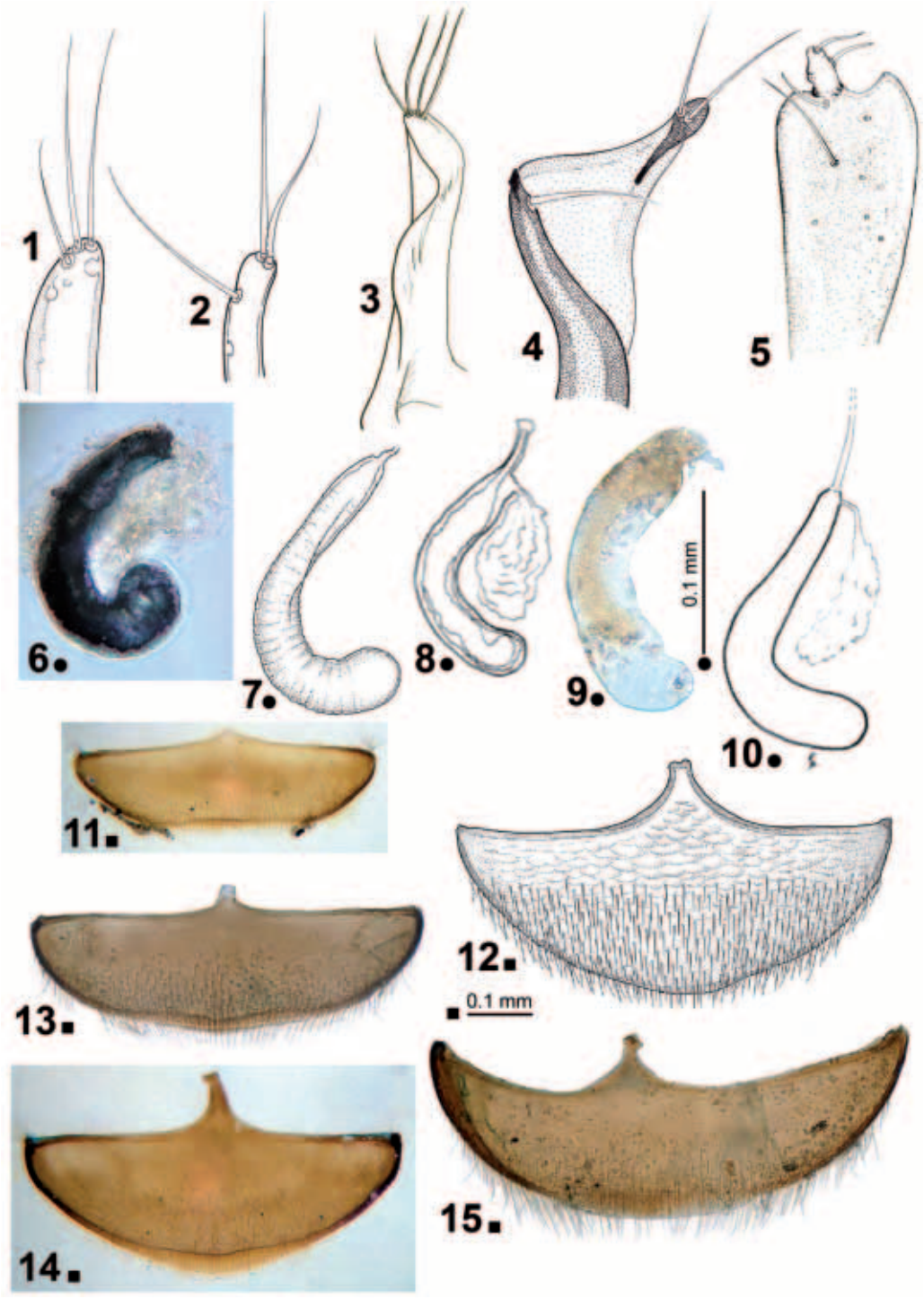
Female uroventrite VIII (Fig. 69.15): With spiculum long and acute.

Discussion. In absence of molecular data, the genus *Sinuicollia* is assigned to the *Neobathyscia* series on a morphological basis. Supported in this also by the recent work of Perreau (2019). It seems closely related to *Halbherria* with which it shares the same structures which are equally arranged on the endophallus.

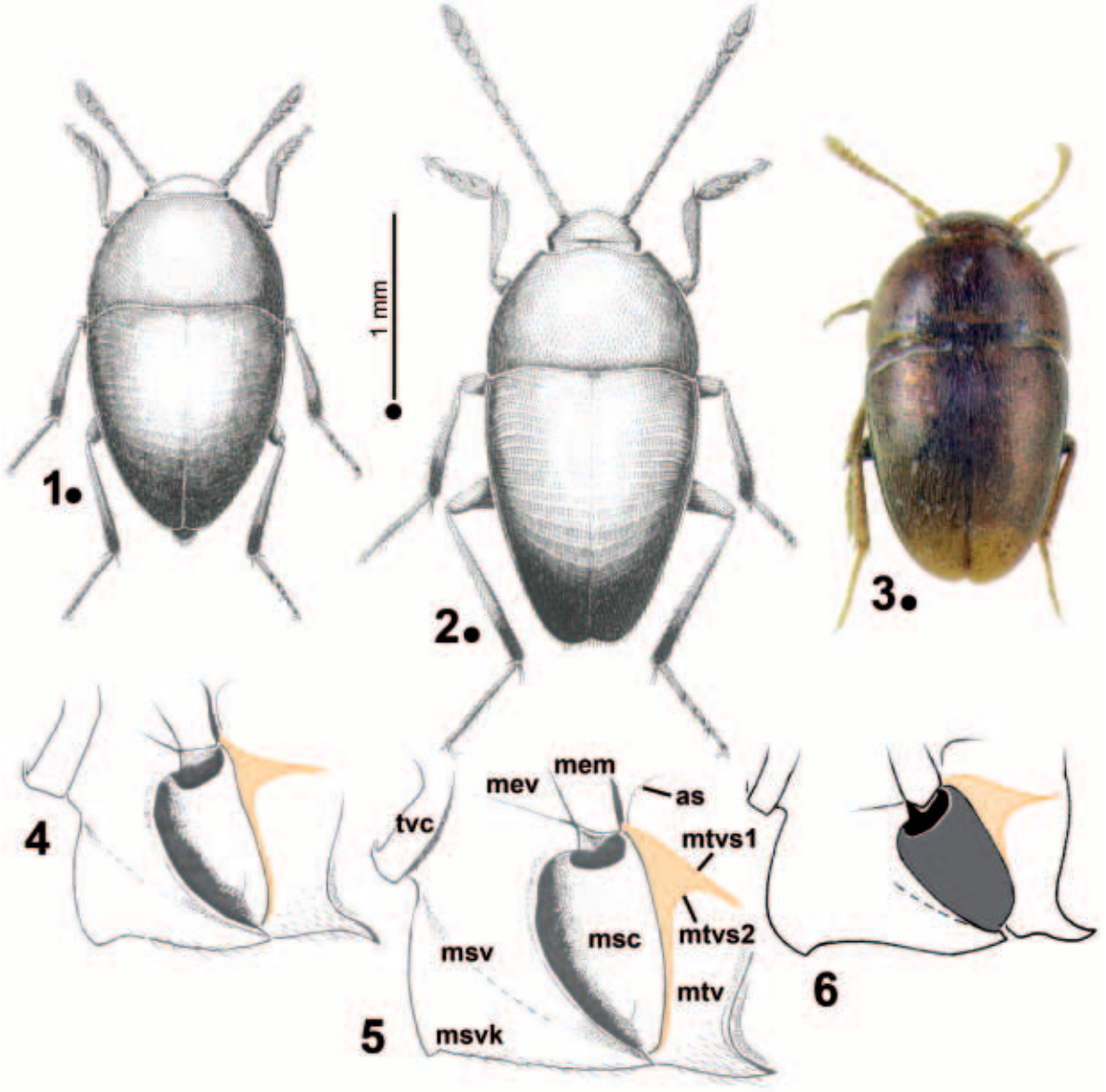
Distribution. Italy. Veneto, Vette Feltrine and Lagorai-Cima d'Asta-Coppolo mountains.

Species

Sinuicollia dalpiazi (Paoletti, 1977)
Neobathyscia dalpiazi Paoletti, 1977: 42.
Sinuicollia dalpiazi (Paoletti, 1977): Piva, 2008: 8.



FIGURES 69.1–69.15: *Neobathyscia* series. Apex of the parameres of: (**1**) *Aphaotus jureceki*, (**2**) *Halbherria tamaninii*, (**3**) *Lessiniella trevisioli* (modified from Pavan 1941), (**4**) *Neobathyscia mancinii*, (**5**) *Sinuicollia dalpiazi* (modified from Paoletti 1977). Spermatheca of: (**6**) *A. jureceki*, (**7**) *H. carlini* (modified from Vailati 2017), (**8**) *L. trevisioli* (modified from Piva 1993), (**9**) *N. mancinii*, (**10**) *S. dalpiazi* (modified from Piva 2008). Female uroventrite VIII of: (**11**) *A. jureceki*, (**12**) *H. carlini* (modified from Vailati 2017), (**13**) *L. berica* (modified from Perreau 2019), (**14**) *N. mancinii*, (**15**) *S. dalpiazi* (modified from Perreau 2019).



FIGURES 70.1–70.6: *Speonomidius* series. Habitus of: (**1**) *Notidocharis uhagoni*, (**2**) *Speonomidius crotchi crotchi*, (**3**) *Uhagoniella zariquieyi* **comb. nov.** Pterothorax in lateral view of: (**4**) *N. uhagoni*, (**5**) *S. c. crotchi*, (**6**) *U. laurae* **comb. nov.** Figs **1**, **2**, **4**, **5** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs1-2**, metaventral sutures; **tvc**, transverse collar.

3.2.2 Series ***Speonomidius*** Salgado, 2000

Diagnosis. Lenght 1.5–2.7 mm. Bathyscioid shape.

Head: With complete occipital carina; last article of maxillary palps short and conical; anophthalmous or with residual eyes formed by few ommatidia.

Antennae: Short, of 11 articles.

Elytra: With transverse striolae; without parasutural stria or very blurred.

Legs: Males protarsi pentamerous and more or less dilated; tetramerous and always gracile in females.

Endophallus: With two regions.

Parameres: Shorter than the median lobe with a club more or less differentiated and highly variable chaetotaxy in the shape and number of setae, four or more setae.

Spermathecal complex: Spermatheca shows a junction or union duct little or not differentiated at the basal lobe, and sclerotized basal process.

Discussion. Four apomorphies can be identified, which when considered collectively facilitate the definition of the representatives of this series. These characters are thefollowing: elytra with manifest transverse striolae; mesoventral keel high and short; sutures of the metaventrite delimit a triangle with an acute angle, apex narrowed and sharp, and the lower part of the suture runs parallel and contiguous to the edge of the mesocoxal cavity; and spermathecal complex with a more or less sclerotized basal process that joins at the dorsal side of the copulatory bag.

The series appears as sister to the *Neobathyscia* series with the genera *Neobathyscia* + *Halbherria* with acceptable support, 91.6/94. *Neobathyscia* was considered to be close to *Oryotus* due to its morphological characteristics and, in fact, in one of the analyzes carried out – Tree-3 with evolutionary models: GTR+F+R10: 16s, SYM+I+G4: 18s-28s, GTR+F+R6: bar-cob-COI (Fig. 64) – it was placed sister to *Oryotus* with fairly good support, 97/81. Both *Speonomidius* and *Neobathyscia* are two robust clades that remain conjointed with all their species in any analysis regardless of usage of different evolutionary models for each of the partitions. However, their status within Leptodirini can change and this has been observed for all series that derive from the most basal cladogenesis. Their position is therefore somewhat uncertain. The *Speonomidius* series + *Neobathyscia* series set is the sister group of the *Leptodirus* series with very low support, 80.7/17, so changes in position have also been noted in different analysis.

The position of the genus *Speonomidius* representing a derived state within *Notidocharis* implies the establishment of synonymy between these two genera, or the description of a genus for the *Notidocharis zariquieyi* clade, *Uhagoniella* gen. nov. This last option has been chosen: since both the support, as well as the morphology and geographical distribution justify a change in taxonomic classification.

Key to genera

1. Wings of the metascutum (sc3) narrow (Fig. 71.1). Apical part of the median lobe of aedeagus lanceolate in dorsal view (Fig. 72.4). Club of the parameres with 4–5 setae long and robust, of which only one is very short and fine (Figs 72.8, 72.9) .....*Notidocharis*
- Wings of the metascutum (sc3) comparatively wide (Figs 71.2, 71.3). Apical part of the median lobe of aedeagus widely arched in dorsal view (Figs 72.5, 72.6). Club of the parameres with numerous setae (Figs 72.10, 72.12–72.15), generally of uniform thickness, only one species with 5–7, in this case two longer and more robust, the others very short and thin (Figs 72.11) 2

2. Size less than 2.0 mm. Species with vestigial eyes, about half a dozen ommatidia. Antennae with the 11th article twice as long as the 10th. Metendosternite with the apical area of the furcal arms in arc and the external apex very sharp (Fig. 71.6). Club of the parameres with numerous setae (Figs 72.12–72.15) of almost uniform thickness, only one species between 5–7 setae (Fig. 72.11). Basal lobe of the spermatheca very poorly differentiated and short, of the same size as the middle region and much smaller in diameter than the apical (Fig. 71.9, 71.10).....
.....*Uhagoniella* gen. nov.
- Size greater than 2.0 mm. Anophthalmous species. Antennae with the 11th article somewhat longer than the 10th. Metendosternite with the apical area of the furcal arms straight and the external apex not very tipped (Fig. 71.5). Club of parameres with numerous setae, 2–3 much longer and thicker, the rest very fine and short, forming a penicillum (Fig. 72.10). Basal lobe of the spermatheca globose, elongated and larger than the apical (Fig. 71.8) .....*Speonomidius*

Genus ***Notidocharis*** Jeannel, 1956
Notidocharis Jeannel, 1956a: 5.

Type species. *Adelops uhagoni* Sharp, 1872 by original designation (habitus in Fig. 70.1).

Diagnosis. Size range between 1.6–1.8 mm. Body shape ovoid, broad and convex (Fig. 70.1). Pubescence short, lying and yellowish.

Head: With the occipital carina complete and angularly protruding to the sides. Eyes reduced and pigmented, formed by about 15 ommatidia.

Antennae: Short, slightly longer than the middle of the elytral suture; club well differentiated with the 8th, 9th, and 10th articles transverse, the 11th being twice the length of the 10th.

Pronotum: Very transverse, as wide as or slightly wider than the area of broadest part of the elytra, with lateral margins regularly arched and acute posterior vertices. Smooth, with very little punctation. Females somewhat more robust than males with slightly more convex elytra.

Elytra: Strongly fused, short and wide, more or less progressively narrowed, with regularly arched margins up to the apex, which is rounded; maximum width near the base, with the parasutural stria

rudimentary or poorly marked; thin transverse striolae, close and fuzzy towards the sides.

Legs: Short and quite robust; males protarsi dilated, but narrower than greatest width of the tibiae; mesotibiae somewhat curved and metatibiae straight.

Mesoventral keel (Fig. 70.4): With the anterior border somewhat arched and without a rim; narrow ventral border with a slightly concave in the anterior area and in general somewhat serrated; angle almost right and vertex rounded or with a marked tooth; posterior process very slightly surpasses mesocoxal cavities.

Sutures of the metaventrite (Fig. 70.4): Delimit a triangular area with a very acute angle and the vertex elongated, narrow and sharp, both sutures join and extend into a single suture that reaches the posterior margin of the metaventrite; the lower suture adjoining the edge of the mesocoxal cavity is prolonged for two-thirds of the length of the cavity.

Metatergal apparatus (Fig. 71.1): Wings of the metascutum narrow and elongated, about three times as long as wide; the apophysis of the alacrista short, little prolonged.

Metendosternite (Fig. 71.4): Furcal arms as long as the furcal trunk, with the apex curved and very tipped, without terminal apophysis; posterior lamina narrows near apical area and slightly arched margin. Trunk slightly longer than the area of greatest basal width and the median keel with a slight posterior divergence.

Median lobe of aedeagus: Long. In lateral view (Fig. 72.1) both the dorsal and the ventral sides regularly arched, with a little sharp apex. In dorsal view (Fig. 72.4), the sides are slightly arched, with the apical area narrowed and lanceolate.

Endophallus (Fig. 72.4): It is divided into two regions, the armor being very different in the two species of this genus. One has a well-developed stylet and arched pieces articulated at its base, as well as an elongated group of fine scaling towards the middle; the other, the basal stylet rudimentary and surrounded in the lower part by diffuse arched fibres, in the apex of some small elongated pieces somewhat more sclerotized and towards the middle apical part an elongated group of squamosities and spinules. Reinforcing bands narrow and somewhat diffuse in the apical region.

Parameres (Figs 72.8, 72.9): Quite robust with a double curve, the latter facing outwards; distinctly shorter than the median lobe; the club elongated but slightly dilated, 4–5 setae are inserted into it, 3–4 long and robust and one very small.

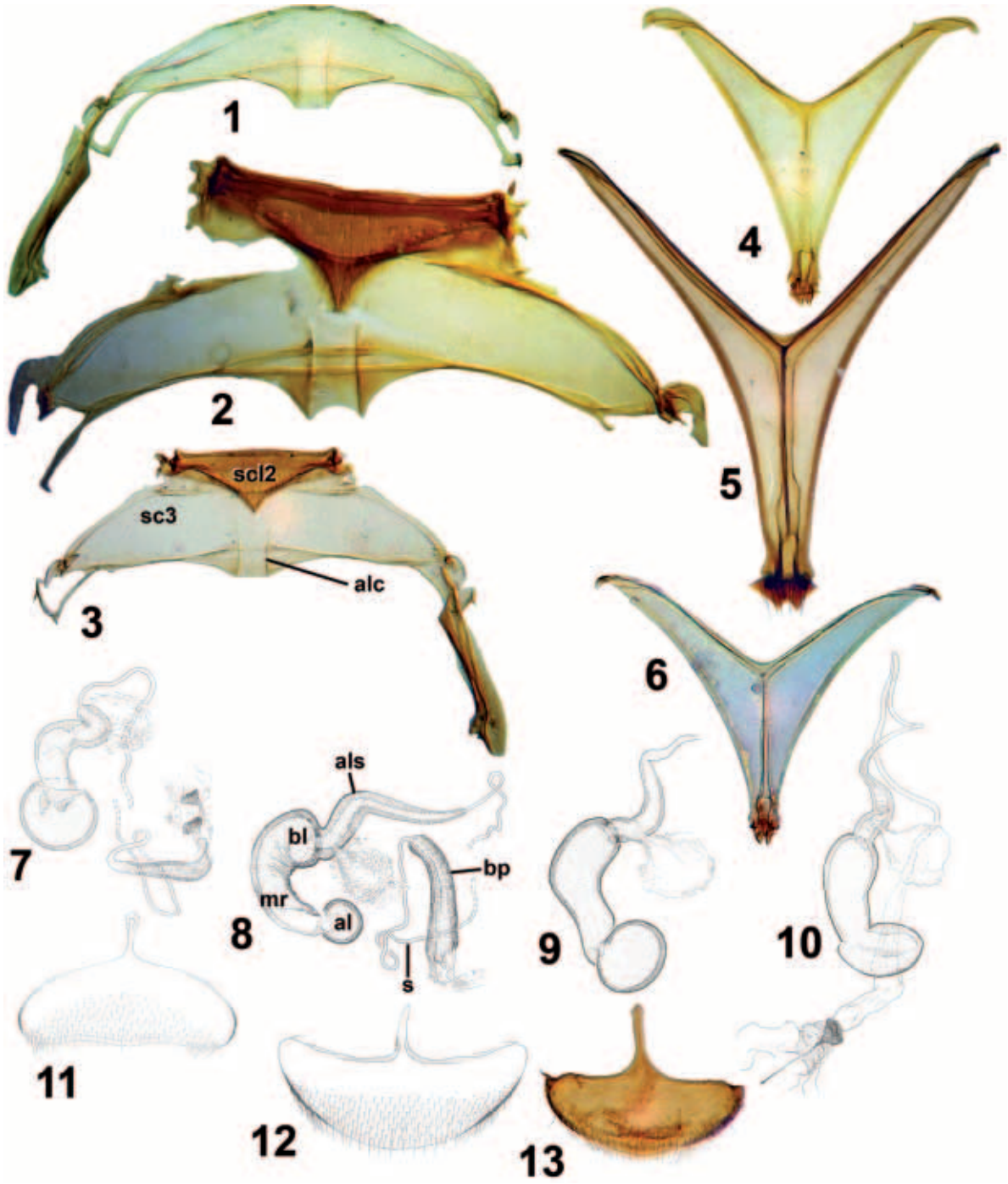
Spermathecal complex (Fig. 71.7): The spermatheca does not show differentiation of a merged duct between the basal and middle parts forming a continuous structure; the apical lobe is spherical and much wider than the basal one; the spermatic duct is 3–4 times the length of the spermatheca, it widens in the area where it joins the spermatheca and the area where the spermathecal gland empties; at the end it joins the dorsal side of the copulatory in form of a little sclerotized structure which is more or less elongated..

Female uroventrite VIII (Fig. 71.11): Spiculum short and narrow, sometimes slightly dilated at the apex.

Discussion. In the phylogenetic tree (Fig. 1I) *Notidocharis* is situated as a sister group to the clade consisting of the genera *Speonomidius* and *Uhagoniella* gen. nov. This relationship is confirmed by a very high support 100/100 in the analysis.

This genus is characterised by: present residual eyes slightly pigmented; parasutural stria very diffuse, formed by some distant and blurred points; mesoventral keel short and the posterior apophysis slightly extends beyond the mesocoxal cavities; sutures of the metaventrite delimit a triangular area, with the apex narrow, sharp and elongated; apical part of the median lobe of aedeagus, in dorsal view, narrowed and lanceolate; endophallus with a long or rudimentary stylet; parameres recurved and the apical area facing outwards, with four or five setae, one of them short; spermatheca short, with a very dilated apical lobe and a narrower basal one, continuous with the undifferentiated middle region; spermatic duct very thin, 3–4 times the length of the spermatheca, ends in a slightly sclerotized piece, the basal process; VIII uroventrite of the female with a short and thin spiculum.

The genus *Notidocharis* belonged to the primitive «Supraflagellates» (Jeannel 1955; Giachino *et al*. 1998), which seemed well characterised by the armor of the endophallus, a character on which Laneyrie (1967) and V.B. Guéorguiev (1976) based their classification. This genus was created by Jeannel in 1956, taking *Adelops uhagoni* as the type species, described by Sharp in 1872, which was included in the genus *Bathyscia* by M. de la Escalera (1898), which later Jeannel (1924a) considered to belong to the genus *Speocharis* and later in 1956 the same author transferred it to the genus *Notidocharis*. Due to its external morphology, *Notidocharis* could be confused with species of the genus *Uhagoniella* gen. nov. and with *Quaesticulus adnexus* or with *Quaesticulus canis* comb. nov., mostly because of the size, body shape and great similarity in the antennal articles, especially those of the club (Salgado 1983a, 1983b). It clearly differs from *Quaesticulus* species by presenting



FIGURES 71.1–71.13: *Speonomidius* series. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Notidocharis uhagoni*, (**2**) *Speonomidius crotchi crotchi*, (**3**) *Uhagoniella zariquieyi* **comb. nov.** Metendosternite of: (**4**) *N. uhagoni*, (**5**) *S. c. crotchi*, (**6**) *U. zariquieyi* **comb. nov.** Spermathecal complex of: (**7**) *N. uhagoni,* (**8**) *S. c. crotchi*, (**9**) *U. zariquiey* **comb. nov.**, (**10**) *U. franzi* **comb. nov.** Female uroventrite VIII of: (**11**) *N. uhagoni*, (**12**) *S. c. crotchi*, (**13**) *U. zariquieyi* **comb. nov.** Figs **7**–**12** modified from Salgado *et al*. (2008). Abbreviations: **al**, apical lobe; **alc**, alacrista; **als**, apical lobe of the spermiduct; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sc3**, metascutum; **scl2**, mesoscutellum; **sg**, spermathecal gland.

residual eyes, transverse elytral striation and having a short mesoventral keel, in addition to large differences in the aedeagus; and from the species of *Uhagoniella* gen. nov. by the narrower wings of the metascutum, by the shape of the apical part of the median lobe of aedeagus and by the club chaetotaxy in the parameres, and also, depending on the species, by clear differences in the structures of the endophallus. In a cladistic analysis carried out by Salgado & Tizado (2005) a phylogenetic tree was built with all the *Notidocharis* species, in which two distinct branches were identified, one included the group formed by *N. uhagoni* and *N. calabrezi*, and the other grouped the remaining *Notidocharis* species (= *Uhagoniella* gen. nov.).

Distribution. Spain. The distribution area in the Cantabrian region is wide, from Asturias foothills of the Sierra del Sueve to Álava, Sierras de Urquilla and Salvada. The species of this genus have been captured in the Spanish provinces of Álava, Asturias, Burgos, Cantabria and Palencia (Fresneda & Salgado 2017a). The two species are basically muscicolous, humicolous or endogeous and, with certain frequency they can be found in the entrance part of the caves and even reach quite deep parts, especially if there is an abundance of organic matter.

Species

Notidocharis calabrezi Giachino & Salgado, 1989
Notidocharis calabrezi Giachino & Salgado, 1989: 12.

Notidocharis uhagoni (Sharp, 1872)
Adelops Uhagoni Sharp, 1872: 271.
Bathyscia Uhagoni Sharp: Heyden, 1881: 243.
Bathyscia (*Bathyscia*) *Uhagoni* Sharp: Reitter, 1885a [1884]: 38.
Speocharis Uhagoni Sharp: Jeannel, 1910a: 30.
Notidocharis Uhagoni Sharp: Jeannel, 1956a: 10.
Notidocharis Uhagoni castilianus Jeannel, 1956a: 10.
Notidocharis uhagoni (Sharp): Giachino & Salgado, 1989: 3.

Genus ***Speonomidius*** Jeannel, 1924
Speonomus (*Speonomidius*) Jeannel, 1924a: 130.
Speonomidius Jeannel, 1924: Salgado, 2000: 56.

Type species. *Bathyscia mazarredoi* Uhagón, 1881 by original designation (for the habitus see that of the similar subspecies *Speonomidius crotchi crotchi* in Fig. 70.2).

Diagnosis. Size ranging between 2.5–2.7 mm. Bathyscioid shape (Fig. 70.2), with elliptical, convex and elongated body shape. Integument covered with a dense, uniform and lying pilosity. Sculpture formed by irregular punctation in the pronotum and by transverse striolae in the elytra, very clear especially in the area of the disc. Depigmented.

Head: Anophthalmous.

Antennae: Short, with cylindrical articles and club slightly thickened; the second antennomere being the longest, from the 8th to the 10th almost as long as wide, and the 11th slightly longer than the 10th.

Pronotum: Transverse, with arched sides and the greatest width at the base.

Elytra: Elongated, the widest part near the base and somewhat acuminate at the apex, with regularly curved sides; not differentiated parasutural stria, although some specimens show a rudiment formed by 5–8 distant points that are located in the basal part.

Legs: Short and not very robust. Males protarsi as wide or wider than the apical area of the tibiae; with very fine spines on the mesotibiae and the spurs much more developed than the spines.

Mesoventral keel (Fig. 70.5): High and short, with the anterior border somewhat convex and without a rim; ventral border narrow and slightly serrated; angle almost right and vertex with a clear tooth, somewhat hooked. Not prolonged over the metaventrite.

Sutures of the metaventrite (Fig. 70.5): The two sutures delimit a triangular area with a very acute angle and the vertex facing the ventral face is elongated, very narrow and very sharp, almost reaching the posterior edge of the metaventrite; the inferior suture extends mostly contiguously the inferior border of the mesocoxal cavity.

Metatergal apparatus (Fig. 71.2): With the wings of the metascutum very wide and united; the apophysis of the alacrista short and the separation between them wide, being the apophysis reduced.

Metendosternite (Fig. 71.5): Furcal arms straight and longer than the furcal trunk, with the apical area not arched and not very sharp, without terminal apophysis; posterior lamina tapers progressively towards the apex, with the margin arched. Trunk almost twice as long as the area of greatest basal width and the median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 72.2) arched with the dorsal medial area slightly sunken and the apex curved and sharp. In dorsal view (Fig. 72.5), widened towards the middle, then progressively narrows to end in an arched apex.

Endophallus (Fig. 72.7): With two distinct regions:

the basal one, with arched phanerae that articulate to a quite robust stylet, bifurcated at its base and almost as long as half the median lobe; the apical one with almost its entire surface covered by numerous scaliness and spines, with the two well visible reinforcing bands.

Parameres (Fig. 72.10): Shorter than the median lobe, arched towards the middle of its length and ending in a club poorly differentiated, in which three main setae and numerous small and minute setae are inserted in the manner of a penicillum.

Spermathecal complex (Fig. 71.8): Spermatheca small, little but uniformly sclerotized, with the basal lobe elongated and somewhat wider than the apical one, which is smaller and spherical; junction duct undifferentiated. Spermatic duct short, forms a thick nodule at the point of junction with the spermatheca, then filiform and joins the copulatory bag through a basal piece elongated and sclerotized. There is a spermathecal gland.

Female uroventrite VIII (Fig. 71.12): Spiculum clearly shorter than the length of the uroventrite, fine, slightly curved and the apex sharp.

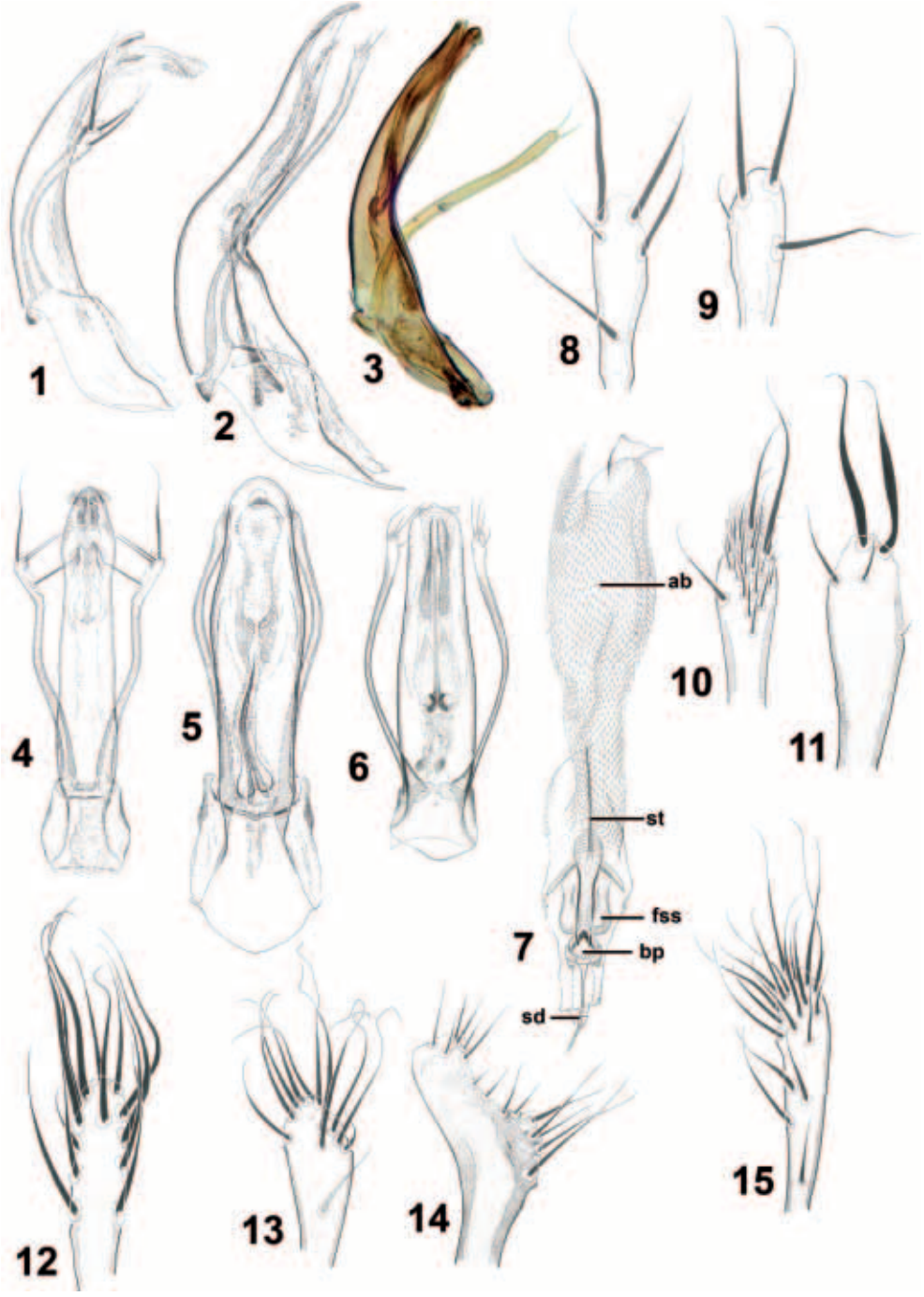
Discussion. *Speonomidius* is sister of *Uhagoniella* gen. nov. with support 57.1/97 (Fig. 1I). Jeannel (1924a) established the subgenus *Speonomidius* within the genus *Speonomus*, a taxonomic position preserved by Bellés *et al*. (1978) and Perreau (2000), which is why they include it in the phyletic series *Speonomus*. This genus has numerous characters that define it; Español (1950) summarised them as follows: absence of parasutural stria, particular structure of a piece in the endophallus, which he calls «inverted «Y»-piece», and in the apical area presence of the parameres of a penicillum of setae, but without apical lamina. Español (1974) kept for this genus the same four species established by Jeannel (1924a), but years later (Español & Bellés 1980b) point out that *Speonomus* (*Speonomidius*) *crotchi* is a polytypic species, and established four subspecies. Salgado (2000) raised *Speonomidius* to a generic category, given the characteristics contained in the endophallus and, above all, the basal piece of the spermatheca, which is highly sclerotized and has the shape of an elongated piece, and furthermore, the genus *Speonomidius* is included in the new phyletic series *Speonomidius* (Salgado 2000), which is considered closer to the phyletic series *Quaestus* than to the phyletic series *Speonomus*. The reasons for the exclusion of the *Speonomus* series are due to the following reasons: (1) the endophallus is divided into two distinct regions (Dupré 1992) and it lacks a true «Y»-piece, being in fact a flagellum or stylet as it is characteristic for *Quaestus*; (2), the morphological characteristics (shape of the body, structure of the mesoventral keel and relationship between the antennal articles) are more similar to the representatives of the *Quaestus* series. (3) In addition to these characters, one could add the general shape of the spermatheca which is also closer to the *Quaestus* series.

Molecular phylogeny (Fig. 1I) revealed that *Speonomidius crotchi* with its four subspecies and *Uhagoniella* gen. nov. are a group derived from the clade *Notidocharis*. It is noteworthy that the mesoventral keel and sutures of the metaventrite, as well as the endophallus and the apex of the parameres, in addition to the spermathecal complex, are similar between these genera. Concerning the differences the larger body size and anophthalmina if *Speonomidius* as well was the gracile and elongated antennae and legs might be valid charactersitics; in addtion the peculiar shape of the stylet of the endophallus and the penicillum at the club of the parameres.

Distribution. Spain. *Speonomidius crotchi* ssp. is a strictly hypogean species that shows a restricted area of distribution: the territories located between Álava (Sierras de Entzia and Urquilla), Gipuzkoa (valley of the river Deva and Sierra de Aitzgorri) and Navarra (Peña Orobe) (Fresneda & Salgado 2017a).

Species

Speonomidius crotchi (Sharp, 1872)
Speonomidius crotchi aitzquirrensis (Bolívar, 1921)
Speonomus (*Speonomus*) *aitzquirrensis* Bolívar, 1921: 532.
Speonomus (*Speonomidius*) *aitzquirrensis* Bolívar: Jeannel, 1924a: 165.
Speonomidius crotchi aitzquirrensis (Bolívar): Salgado, 2000: 57.
Speonomidius crotchi crotchi (Sharp, 1872)
Adelops crotchi Sharp, 1872: 270.
Bathyscia (Bathyscia) crotchi Sharp: Reitter, 1885a [1884]: 36.
Speonomus (Sp*eonomus*) *crotchi* (Sharp): Jeannel, 1910a: 34.
Speonomus (*Speonomidius*) *crotchi* (Sharp): Jeannel, 1924a: 165.
Speonomidius crotchi crotchi (Sharp): Salgado, 2000: 57.
Speonomidius crotchi mazarredoi (Uhagón, 1881)
Bathyscia mazarredoi Uhagón, 1881: 123.
Speonomus (Sp*eonomus*) *Mazarredoi* (Uhagón): Jeannel, 1910a: 34.



FIGURES 72.1–72.15: *Speonomidius* series. Aedeagus in lateral view of: (**1**) *Notidocharis uhagoni*, (**2**) *Speonomidius crotchi crotchi*, (**3**) *Uhagoniella zariquieyi* **comb. nov.** Aedeagus in dorsal view of: (**4**) *N. uhagoni*, (**5**) *S. c. crotchi*, (**6**) *U. zariquieyi* **comb. nov.** Endophallus of: (**7**) *S. c. crotchi*. Apex of the paramere of: (**8**) *N. uhagoni*, (**9**) *N. calabrezi*, (**10**) *S. c. crotchi*, (**11**) *U. zariquieyi* **comb. nov.**, (**12**) *U. franzi* **comb. nov.**, (**13**) *U. laurae* **comb. nov.**, (**14**) *U. meregallii* **comb. nov.**, (**15**) *U. ovoidea* **comb. nov.** Figs **1**, **2**, **4**–**15** modified from Salgado *et al*. (2008). Abbreviations: **ab**, apical sac; **bp**, basal piece; **fss**, phanerae of the stylet; **sd**, spermiduct; **st**, stylet.

Speonomus (*Speonomidius*) *Mazarredoi* (Uhagón): Jeannel, 1924a: 165.
Speonomidius crotchi mazarredoi (Uhagón): Salgado, 2000: 57.
Speonomidius crotchi oberthuri (Jeannel, 1909)
Speonomus oberthuri Jeannel, 1909b: 470.
Speonomus (*Speonomidius*) *oberthuri* (Jeannel): Jeannel, 1924a: 165.
Speonomus (*Speonomidius*) *mazarredoi* ssp. *oberthuri* Jeannel: Español, 1965b: 52.
Speonomidius crotchi oberthuri (Jeannel): Salgado, 2000: 57.

Genus ***Uhagoniella*** nov.
https://zoobank.org/NomenclaturalActs/B165B146-1EAA-4445-B4B7-7206B58D6427

Type species. *Speocharis zariquieyi* Jeannel, 1924 by present designation (habitus in Fig. 70.3).

Diagnosis. Size range between 1.5–1.8 mm. Body oval, wide, more or less convex and in some cases somewhat attenuated posteriorly (Fig. 70.3). Sculpture of the pronotum composed of extremely fine points, hardly visible; integument of the elytra shiny, with a weak microsculpture aligned transversely. In general, females are somewhat more robust than the males.

Head: With complete occipital carina and residual eyes with traces of pigmentation that are located on the anterior face of the pyramid that form the temporal angles and where some ommatidia can be seen.

Antennae: Short, somewhat longer than half the elytral suture, with the club clearly thickened and the 11th article twice or more than twice as long as the 10th and the 2nd equal to or slightly longer than the 11th and always longer than the 1st.

Pronotum: Convex and clearly transverse, with regularly arched sides, not narrowed backward and the base as wide as or slightly wider than the basal area of the elytra; acute angles and sharp vertices projecting backwards.

Elytra: Short and solidly united at the suture line; about twice as long as the pronotum, with the greatest width near the base, then progressively narrowing to the rounded apices; well-defined transverse striolae and in some cases it is observed a parasutural stria formed by blurred and very discontinuous points.

Legs: Short and somewhat robust; males protarsi of variable width, depending on the species; mesotibiae straight or somewhat curved and metatibiae straight.

Abdomen: In some species, a small elliptical pit can be seen in the last abdominal segment of the male, located in the middle anterior area of the ventral face.

Mesoventral keel (Fig. 70.6): More or less high and short; the posterior prolongation generally does not exceed the mesocoxal cavities, with the anterior border between straight and slightly arched, the apex toothed, only rounded in one species; the inferior border narrow, with a slight inflection in the anterior area and in some cases slightly serrated.
Sutures of the metaventrite (Fig. 70.6): The two sutures define a triangular area with a very acute angle and an apex elongated, narrow and pointed. When they come together they form a suture whose prolongation can reach the posterior margin of the metaventrite; the suture in the lower part is adjacent with the middle of the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 71.3): Wings of the metascutum wide and slightly elongated, about twice as long as wide; the apophysis of the alacrista short, little prolonged.

Metendosternite (Fig. 71.6): Furcal arms arched, somewhat longer than the furcal trunk, with the apex curved and very sharp, without terminal apophysis; posterior lamina narrows near the apical area and the margin is slightly arched. Trunk as long as the part of greatest basal width and the median keel with a slight posterior divergence.

Median lobe of aedeagus: Long, almost a third of the length of the body. In lateral view (Fig. 72.3), slightly arched, in a regular curve. In dorsal view (Fig. 72.6) broad middle area and arched sides, then narrows and subparallel sides, ending in an apex broadly arched; only in *Uhagoniella ovoidea* comb. nov. the apex is sub-rectilinear with a minute protuberance in the middle.

Endophallus (Fig. 72.6): In all species a long flagellum is observed, except in *Uhagoniella laurae* comb. nov.; in the basal part there are sclerotized pieces overlapping and symmetrical, they are variable in shape and articulate at the base of the stylet; furthermore, towards the middle part, elongated groups of more or less developed spines and scales; in the apical region there are reinforcing bands.

Parameres: In general, thin, always arched in the middle part, in some cases recurved in the apical part, with the club more or less differentiated; numerous setae are inserted into it of the same or variable length that do not form a penicillum and are generally thin (Figs 72.12–72.15); only *Uhagoniella zariquieyi* comb. nov. it has between 5–7 short setae, of which two are somewhat longer and more robust (Fig. 72.11).

Spermathecal complex (Figs 71.9, 71.10): Spermatheca small, with the apical lobe between oblong and spherical, it is somewhat wider than the basal lobe; the union duct and the area of the basal lobe little or not at all differentiated; spermatic duct about three times longer than the spermatheca; forms a small nodule or enlargement in the anterior area, where the spermathecal gland empties, and at the end joins the dorsal face of the copulatory bag by an elongated piece weakly sclerotized, the basal piece.

Female uroventrite VIII (Fig. 71.13): Apical border broadly arched and a faint arched impression in the middle near the posterior border; the spiculum quite long, narrow and the apical area may be slightly dilated.

Etimology. The genus is honored to the Spanish entomologist and biospeleologist Serafín P.M. de Uhagón Bedía (1845–1904), who worked on the study of cave fauna and was the first one to be dedicated a species belonging to the Leptodirini, *Adelops uhagoni* Sharp, 1872.

Discussion. This genus is the sister of *Speonomidius* although with a considerable genetic distance; the phylogenetic tree (Fig. 1I) shows a support 57.1/97 between both. The characters that allow these two sister genera to be differentiated have been indicated in the genus key and in the diagnosis of *Uhagoniella* gen. nov. In the cladistic analysis that gave rise to the phylogenetic tree for the genus *Notidocharis* (Salgado & Tizado 2005) two branches were joint into one, this one group of associated species, corresponds to the group identified by the molecular analysis as being linked to *Uhagoniella* gen. nov., and in the other the species of *Notidocharis* are grouped. The differentiating characters between both genera have already been pointed out in the Discussion section of the genus *Notidocharis*.

Distribution. Spain. They are distributed over a wide area between the slopes of the Picos de Europa (Espinama, Cantabria, the easternmost datum), and the Sierra de Linares (Lugo), as the westernmost. The are references on collecting sides are reported from the provinces of Cantabria, León and Lugo (Fresneda & Salgado 2017a). They are muscicolous, humicolous and endogeous species that with certain frequency are collected in the entrance area or at a certain depth in the caves.

Species

Uhagoniella franzi (Jeannel, 1956) comb. nov.
Notidocharis Franzi Jeannel, 1956a: 7.
Notidocharis espanyoli Comas, 1987: 135.
Notidocharis franzi Jeannel: Giachino & Salgado, 1989: 9.

Uhagoniella laurae (Salgado & Giachino, 1991) comb. nov.
Notidocharis laurae Salgado & Giachino, 1991: 135.

Uhagoniella meregallii (Giachino & Salgado, 1989) comb. nov.
Notidocharis meregallii Giachino & Salgado, 1989: 10.

Uhagoniella ovoidea (Jeannel, 1956) comb. nov.
Notidocharis ovoideus Jeannel, 1956a: 9.
Notidocharis ovoidea Jeannel: Salgado, Blas & Fresneda, 2008: 401.

Uhagoniella zariquieyi (Jeannel, 1924) comb. nov.
Speocharis Zariquieyi Jeannel, 1924a: 59.
Notidocharis Zariquieyi Jeannel: Jeannel, 1956a: 8.
Notidocharis Zariquieyi asturiensis Jeannel, 1956a: 8.
Notidocharis zariquieyi (Jeannel): Giachino & Salgado, 1989: 5.

3.2.3 Series ***Leptodirus*** Jeannel, 1910 sensu novo

A remarkable variety of forms are present in the genera that make up this series. There are bathyscioid and pholeuonoid body shapes, both with the pronotum more or less transverse, with stubby forms (i. e. *Bathyscimorphus*), with thick and globose forms (i. e. *Apholeuonus*) or more thin and elongated ones (i. e. *Parapropus*). There are also leptodiroid shapes with narrow and elongated pronotum and very globose abdomen (i. e. *Astagobius*) or scaphoid (i.e. *Croatodirus*). A high level of specialisation is known from this group, which has been already highlighted by Jeannel (1924a) Especially the level of integuments it becomes apparent, this can be completely, or partially glabrous, pubescent or equipped with long erect setae. The *Leptodirus* series has high support in any of the molecular analysis (Fig. 2), in Tree-1 with 78.1/93 and in Tree-2 with 96/96; it is sister to the clade formed by the series *Speonomidius* + *Neobathyscia* with low support, 80.7/17 in Tree-1 and 67.6/34 in Tree-2.

Jeannel (1924a), established a «phyletic series of *Apholeonus*» in which, in addition to the nominotypi-

cal genus, the following genera are included: *Adelopidius*, *Icharonia*, *Setnikia*, *Leonhardia*, *Antrosedes*, *Charonites*, *Haplotropidius*, *Spelaites*, *Protobracharthron* and *Parapropus*. This phyletic series, according to Jeannel (1924a) would be flanked by the phyletic series of *Spelaedromus* (with the nominotypical genus plus *Speoplanes*) and *Leptodirus* (with the nominotypical genus plus *Astagobius*). Subsequently, Casale *et al*. (1993) described the male of *Roubaliella* and assigned it to this phyletic series. Polak & Mulaomerović (2021) described the genus *Rudogorites*, assigning it on a morphological basis to the phyletic series of *Apholeuonus*. This systematic structure is largely confirmed by our phylogram of Figure 1I. Some morphological characters that have been considered valid to systematically structure the tribe are inconsistent. The most important of these characters are:

– Relative length of first and second antennomeres, where the first is shorter than the second, valid in all genera of clade of *Leptodirus* series except in genera *Croatodirus* and *Bathysciotes*.

– Presence of a membranous lobe at apex of paramers. Its presence characterises the genera of phyletic series of *Apholeuonus* (*sensu* Jeannel 1924a) with the exclusion of *Parapropus* (Fig. 1I). This situation is coherent, even if molecular data of many genera are lacking, from the grouping *Apholeuonus* + *Charonites* whose clade has a support 54/100 (Fig. 1I).

– Tetramerism of protarsi in males. Within a phyletic series of genera with always pentameric protarsi, characterised by a clade with support 77.5/99 (Fig. 1I), appear four tetrameric genera (*Bathysciotes, Spelaeobates, Prospelaeobates* and *Deleemaniella*).

Recently Mizerakis *et al*. (2022) revised the genus *Speoplanes* and defined its systematic position on a molecular basis, as sister group of the clade *Apholeuonus* + *Charonites*.

The genera of the *Leptodirus* series groups have been grouped into «complexes» in accordance with Jeannel (1924a), V.B. Guéorguiev (1976), Casale & Jalžić (1988) or Perreau (2000, 2004), also adding molecular results and the morphologic study. It was hypothesised on this, assuming that these complexes correspond to the subclades, that fairly certainly form these groups and that they can only be confirmed (or refuted) by future molecular studies of the to date still excluded genera for which there are no molecular data available. It is even possible that some of the «complexes» should be considered a «group» although it is taxonomically irrelevant, therefore in order to standardise the terminology used in other series, instead of «complex» the term «subgroup» will be used.

The structure observed in other highly divers clades, such as the *Euryspeonomus* group (series *Speonomus*) is repeated: similarly in this large clade there is a succession of basal cladogenesis with small bathyscioid forms (*Sphaerobathyscia*, *Bathyscimorphus* and *Bathysciotes*) and cladogenesis derived from larger elongate forms (*Leptodirus*, *Astagobius*, *Spelaeobates,* etc.).

KEY TO GROUPS

1. Apex of the parameres with apical membranous lobe (Figs 90.3, 90.4).....*Apholeuonus* group-pars
- Apex of the parameres without apical membranous lobe (Fig. 74.5, 74.6, 76.7, 76.8, 76.9, 90.5, 103.6, 103.8).....2

2. Oral appendages with long setae .....
.....*Croatodirus* (*Apholeuonus* group-pars)
- Oral appendages without long setae 3

3. Endophallus with a «Y»-piece (Fig. 74.2, 74.4) …
.....*Sphaerobathyscia* group
- Endophallus without a «Y»-piece (Fig. 76.4, 76.6, 102.1, 102.3–102.9,).....4

4. Male protarsi tetramerous.....
.....*Spelaeobates* subgroup (*Leptodirus* group-pars)
- Male protarsi pentamerous.....5

5. Sizes between 1.4–2.6 mm and bathyscioid body shape (Fig. 75.1–75.3); body shape ovoid or oblong-rounded, wide, strongly convex and little attenuated backwards, and without physogastric elytra.....
.....*Bathyscimorphus* group
- Sizes between 5.5–7.0 mm and leptodiroid body shape (Fig. 96.1, 97.2): pronotum slender, laterally compressed, and physogastric elytra .....
.....*Leptodirus* subgroup (*Leptodirus* group-pars)

3.2.3.1 ***Sphaerobathyscia*** group Perreau, 2000

In the molecular phylogeny *Sphaerobathyscia* appears in the trees as the most basal clade of the *Leptodirus* series and links to all other clades with a support of 78.1/93 in Tree-1 and 96/96 in Tree-2 (Figs 1I, 2). We insert *Redensekia* in this group in absence of molecular data; it shows an endophallus with (at least) one «Y»-shaped basal piece as observed in *Sphaerobathyscia.* Jeannel (1924a) himself, places some of them in the «Théléomorphes» of division III, leaving them in an isolated. Perreau (2000) includes both gen-

era in the «phyletic series *Sphaerobathyscia*». The clade of *Sphaerobathyscia* + *Redensekia* to date has to be considered as a grouping of convenience. Although based on phyletic interpretations given by different authors (Jeannel 1924a; Karaman 1953; V.B. Guéorguiev 1974a; Perreau 2000), its real taxonomic value can only be decided in future molecular analysis.

Key to genera

1. Larger body size (2.6–2.7 mm). Pronotum very transverse, three times as wide as long, very large basally and very narrow anteriorly (Fig. 73.1) ....*Redensekia*
- Smaller body size (1.2 mm). Pronotum transverse, 1.8 times wider than long (Fig. 73.2) ....*Sphaerobathyscia*

Genus ***Redensekia*** Karaman, 1953
Redenšekia Karaman, 1953: 109.

Type species. *Redenšekia likana* Karaman, 1953 by original designation (for the habitus see that of the similar subspecies *Redensekia likana kosiniensis* in Fig. 73.1).

Diagnosis. Small size, 2.6–2.7 mm, short and bathysciod in shape (Fig. 73.1). Pubescence short, dense of brown hairs.

Antennae: Moderately long, with first antennomere shorter than the second one. Antennomeres 3rd–6th oval, elongated and narrow; 8th antennomere oval, longer than wide; 7th antennomere almost as wide as the 9th and 10th, but longer than these; the 9th almost as long as wide; the 11th oval, twice as long as wide.

Pronotum: Very transverse, very enlarged posteriorly and very narrow anteriorly. Sides regularly and slightly rounded apically, not sinuated posteriorly, with maximum width at the base.

Elytra: Oval, compact, wider than the pronotum, with maximum width in the basal third. Parasutural stria absent, disc without transverse striolae. Wide apical area slightly subtruncate.

Legs: Short; protibia with internal spur trifid and comb at the distal and external lateral margin. Meso- and metatibiae equipped with an apical basket. Male protarsi tetrameres and not dilated.

Mesoventral keel (Fig. 73.3): High, with anterior edge in convex arc and ventral edge not furrowed, vertex with tooth; posterior process not extended on metaventrite.

Suture of the metaventrite (Fig. 73.3): In sinuous arc that delimits a well manifested area in the upper two thirds and very reduced in the lower third.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Large and strongly curved ventrally in lateral view (Fig. 74.1). In dorsal view (Fig. 74.3), compact with subparallel sides, ogival to subtruncated at apex, which is slightly concave. Basal blade of the median lobe short and lacking posterior apophysis.

Endophallus (Fig. 74.3): Basal part with a «Y»-piece, whose two branches appear long, converging, ogival and slightly curved towards the ventral side. Central branch narrow and pointed in lateral view (Fig. 74.1).

Parameres (Fig. 74.5): Shorter than the median lobe, narrow; apex equipped with three long setae. Dorsal belt of tegmen narrow and weakly chitinised, ventral part of tegmen short and weakly chitinised.

Spermathecal complex: Spermatheca (Fig. 74.7) in the form of an elongated bag, with lobes and union duct poorly differentiated, although the area of the proximal lobe is the widest and most elongated; thin spermatic duct joins the spermatheca without a dilated area.

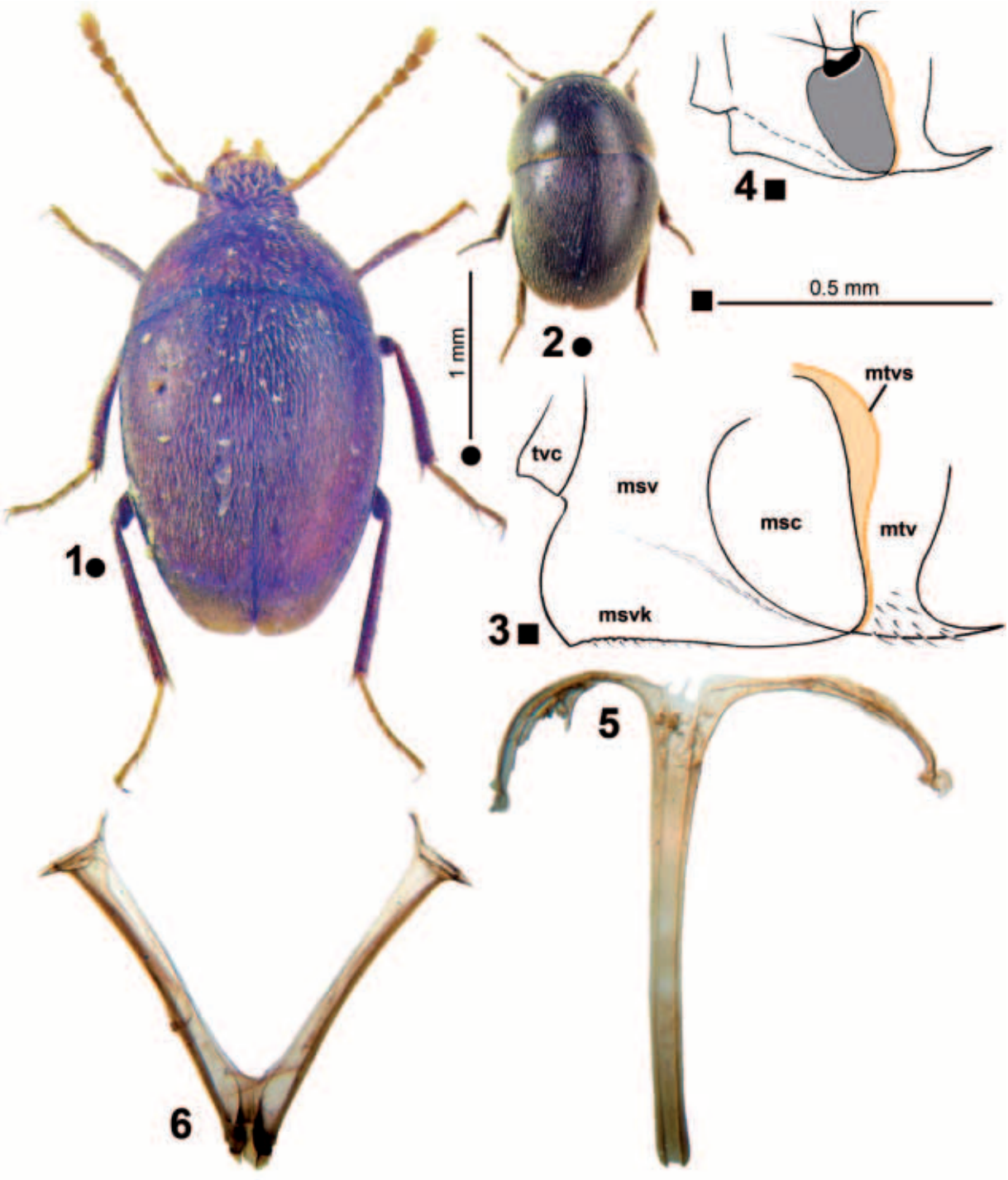
Female uroventrite VIII (Fig. 74.9): Spiculum very short and broad, subtruncated; sides of the anterior edge straight.

Discussion. Genus never revised after its original description (Karaman 1953). According to the author *Redensekia* belongs to the «Théléomorphes» of the Division III of Jeannel (1924a), attaching it to the genus *Sphaerobathyscia* from which, however, it differs for several external characters and for the shape of aedeagus. Despite this attempt, the actual systematic position of *Redensekia* can only be defined by future molecular analysis.

Distribution. Known from some caves in western Croatia, Lika region.

Species

Redensekia likana Karaman, 1953
Redensekia likana kosiniensis Pretner, 1963
Redensekia likana subsp. *kosiniensis* Pretner, 1963a: 63.
Redensekia likana likana Karaman, 1953
Bathysciotes Khevenhülleri subsp. *croaticus* L. Miller: Jeannel, 1911a: 426.
Redenšekia likana Karaman, 1953:109.
Redensekia likana likana Karaman: Perreau, 2000: 199.



FIGURES 73.1–73.6: *Leptodirus* series, *Sphaerobathyscia* group. Habitus of: (**1**) *Redensekia likana kosiniensis*, (**2**) *Sphaerobathyscia hoffmanni*. Pterothorax in lateral view of (**3**) *R. l. kosiniensis*, (**4**) *S. hoffmanni*. (**5**) Metatergal apparatus and (**6**) Metendosternite of *S. hoffmanni*. Abbreviations: **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

Genus ***Sphaerobathyscia*** G. Müller, 1917
Sphaerobathyscia G. Müller, 1917: 637.

Type species. *Batyscia hoffmanni* Motschulsky, 1856 by monotypy (habitus in Fig. 73.2).

Diagnosis. Very small size 1.2 mm, with females somewhat more robust than males. Body shape bathyscioid, very convex and slightly compressed laterally towards the middle (Fig. 73.2). The microsculpture is composed of fine dots, more marked on elytra, and arranged in a disorderly way. Integument between the dots smooth and shiny. Pubescence long, spaced and lying down.

Head: Wider than long, with a complete occipital carina; anophthalmous.

Antennae: Short, slightly exceeding the base of the pronotum; club thickened with flattened antennomeres, the first being similar to the second in length and width. Antennomeres 8th, 9th and 10th transverse.

Pronotum: Transverse and convex, almost twice as wide as long, with sides regularly arcuated and not narrowed backwards. Maximum width near the base, as wide as the maximum width of elytra.

Elytra: Short, about 1.1 times longer than wide, with the maximum width towards the basal third, then narrow very little to the apex, which is very slightly truncated. Parasutural stria lacking without transverse striolae.

Legs: Short and quite robust. Anterior tibiae with a comb formed by a regular row of short and equal spines on the apical edge and much of the outer edge. Tibiae not spiny, with well-developed internal spurs. Male protarsi tetrameres and thin.

Mesoventral keel (Fig. 73.4): High; anterior edge straight, with rounded to slightly tapering vertex, angle right; lower border is wide in middle area and with groove, convex in the posterior half. Posterior process short, does not reach the metaventrite.

Suture of the metaventrite (Fig. 73.4): Almost parallel of edge of the metacoxal cavity and delimits a narrow, slightly wider area in the mid-apical part.

Metatergal apparatus (Fig. 73.5): Well developed, wings of metascutum long, narrow and arched; apophysis of alacrista very long with unsharp apices, almost as long as the base of elytra.

Metendosternite (Fig. 73.6): «V»-shaped; arms very long and very narrow, slightly more than three times longer than the trunk, with well-developed apophyses. Very short furcal trunk, as long as the widest part of the trunk.

Median lobe of aedeagus: Quite robust. In lateral view (Fig. 74.2) ventral side little arcuated, dorsal side with a depression towards the apical quarter and this part oriented towards the ventral face; apex sharp. In dorsal view (Fig. 74.4) flattened, lateral sides subparallel from the base to the middle part, then arcuated; this area being the widest, to progressively narrow to apex that is quite sharp; in the middle part, they are two transverse grooves, one straight anterior more diffuse and another posterior arcuated and deeper. Basal blade of the median lobe broad and oval.

Endophallus (Fig. 74.4): The bottom of basal area shows a basal «Y»-piece; with the dorsal branches long and arcuated as thin as the flagellum that is straight. On both sides of apical part of the flagellum, they are two small tooth-shape pieces quite well sclerotized. In apical region, they are the two bands of reinforcement that are short and somewhat diffuse.

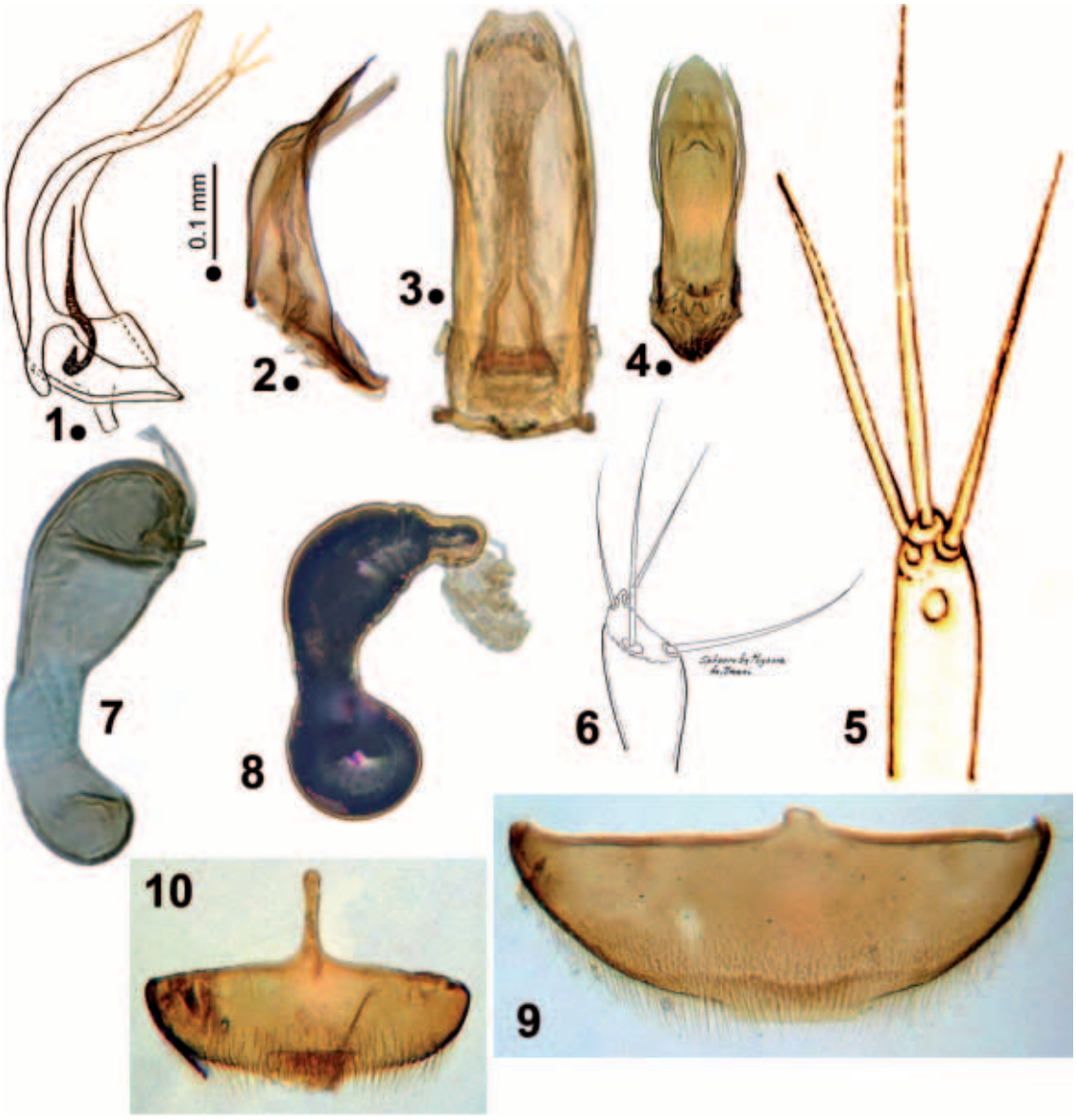
Parameres (Fig. 74.6): Narrow and somewhat shorter than the median lobe. Apical club is differentiated. Bearing at apex four setae, inserted two by two; the two apical being slightly shorter than the two basal. Ventral lamina of the tegmen short and somewhat narrower than the basal one.

Spermathecal complex: Spermatheca (Fig. 74.8) with three regions well differentiated, being the apical and basal lobes well sclerotized and junction duct short and hyaline. Apical lobe large and spherical, wider than the basal, which is oval; at the bottom shows a small bulb into which the spermatic duct and spermathecal gland flow.

Female uroventrite VIII (Fig. 74.10): Spiculum long, quite narrow and apex in arc. Posterior edge slightly wavy with a transverse spot in the middle area of the urosternite, very close to the posterior apex.

Discussion. Perreau (2000) includes *Sphaerobathyscia* in Bathysciotina where this genus gives name to its own phyletic series in which *Redensekia* is also included. *Sphaerobathyscia* derives from the basal clade of the *Leptodirus* series, with support 78.1/93 in Tree-1 and 96/96 in Tree-2 (Figs 1I, 2). There are no consistent morphological characters that link *Sphaerobathyscia* and *Redensekia*, nor are there any linking these genera to the *Leptodirus* series. Information on their evolutionary relationships is provided by molecular (Fig. 1I) and biogeographical data.

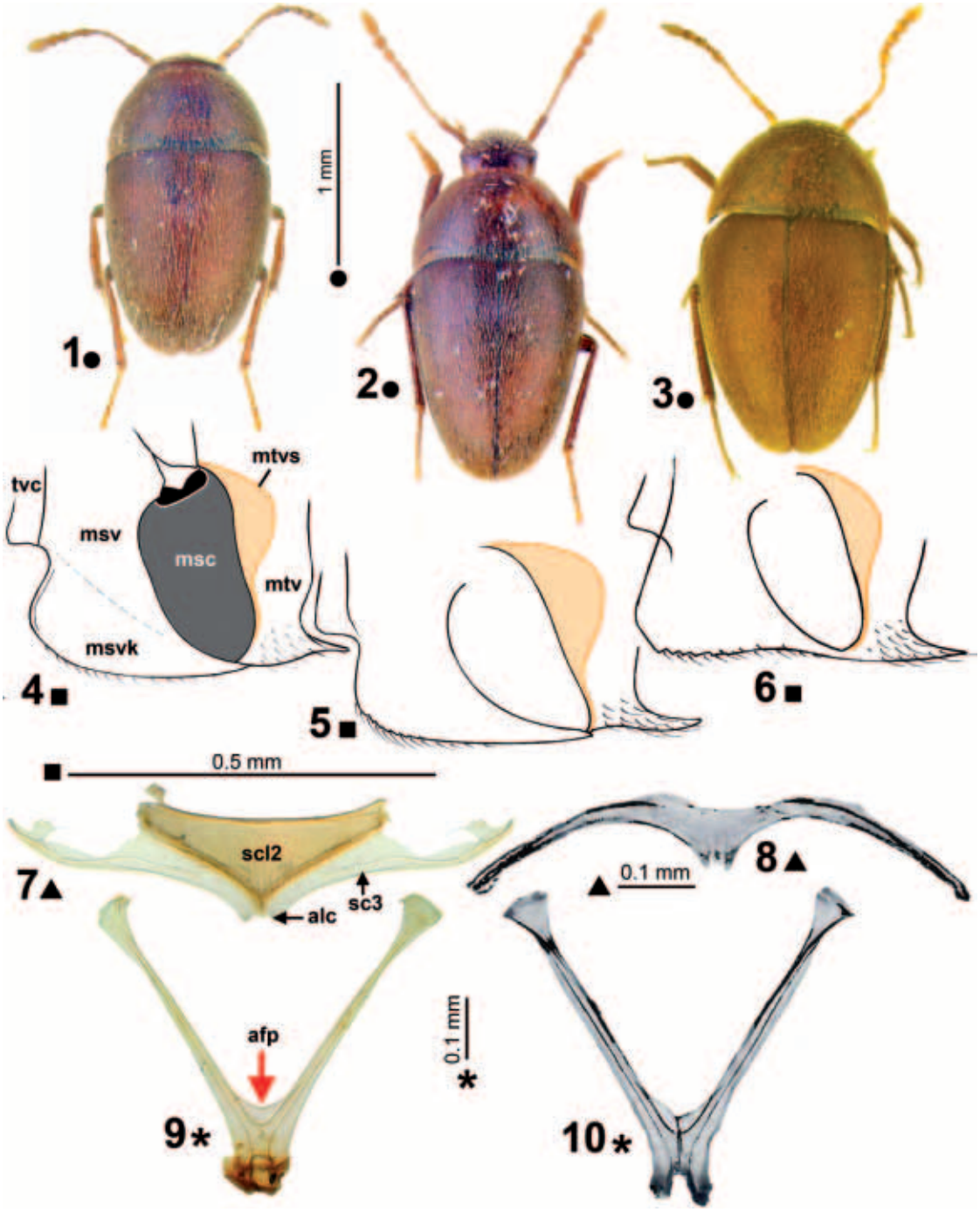
Distribution. Monospecific genus that colonises two caves located near Nebrasina in the Italian municipality of Duino-Aurisina a few kilometers from Trieste and another wider karst area with several cavities in Central and Western Slovenia linked to the Dinaric Alps in the Carniola region.



FIGURES 74.1–74.10: *Leptodirus* series, *Sphaerobathyscia* group. Aedeagus in lateral view of: (**1**) *Redensekia likana likana*, (**2**) *Sphaerobathyscia hoffmanni*. Aedeagus in dorsal view of: (**3**) *R. l. likana*, (**4**) *S. hoffmanni*. Apex of the paramere of: (**5**) *R. l. likana*, (**6**) *S. hoffmanni*. Spermatheca of: (**7**) *R. l. kosiniensis*, (**8**) *S. hoffmanni*. Female uroventrite VIII of: (**9**) *R. l. kosiniensis*, (**10**) *S. hoffmanni*. Figs **1**, **5** modified from Karaman (1953); Figs **3**, **7** modified from Perreau (2019).

Species

Sphaerobathyscia hoffmanni (Motschulsky, 1856)
Batyscia Hoffmanni Motschulsky, 1856: 36.
Pholeuonidius orientalis Meggiolaro, 1966: 70.
Bathysciotes Hoffmanni Motschoulsky: Jeannel, 1910a: 37.
Bathyscia (*Bathysciotes*) *Hoffmanni* Motsch.: Jeannel, 1914b: 16.
Sphaerobathyscia hoffmanni Motschoulsky: G. Müller, 1917: 637.
Sphaerobathyscia Hoffmanni Motschoulsky, 1856: Jeannel, 1924a: 273.



FIGURES 75.1–75.10: *Leptodirus* series, *Bathyscimorphus* group. Habitus of: (**1**) *Bathyscimorphus* (*Bathyscimorphus*) *byssinus byssinus,* (**2**) *B.* (*Drovenikia*) *sagarum*, (**3**) *Bathysciopsis sternalis*. Pterothorax in lateral view of: (**4**) *B.* (*B.*) *b. byssinus*, (**5**) *B.* (*D.*) *sagarum*, (**6**) *Bathysciopsis sternalis*. Metatergal apparatus of: (**7**) *B.* (*B.*) *b. acuminatus,* (**8**) *B.* (*D.*) *sagarum* (modified from Bognolo 2002). Metendosternite of: (**9**) *B.* (*B.*) *b. acuminatus* (**10**) *B.* (*D.*) *sagarum* (modified from Bognolo 2002). Abbreviations: **afp**, anterior furcal plate; **alc**, alacrista; **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture; **sc3**, metascutum; **scl2**, mesoscutellum; **tvc**, transverse collar.

3.2.3.2 ***Bathyscimorphus*** group

Diagnosis. All representatives of this group are genera characterised by have small sizes, between 1.4–2.6 mm and bathyscioid facies. Body shape ovoid or oblong-rounded, wide, strongly convex and little attenuated backwards. Antennae inserted on the medium third of the head. Male protarsi pentameres. Median lobe of aedeagus short and stout, or thin and elongate. Endophallus armed with various sclerotized pieces. Parameres robust or thin or shorter, as long as, or somewhat longer or shorter, than the median lobe. Apical part bearing a crown of about 15 setae (*Bathyscimorphus*), or with two setae (*Bathysciopsis*).

Discussion. G. Müller (1941) and Perreau (2000) point out *Bathyscimorphus*, *Bathysciopsis* and *Ceuthmonocharis* as close genera, although the first two presents a well-developed endophallus armor, while in *Ceuthmonocharis* is defenseless. For this reason the latter genus has been transferred to the subgroup *Leptodirus* (see Discussion section of *Ceuthmonocharis*).The genus *Bathyscimorphus* that belongs to this group joins the groups *Leptodirus* – with the *Spelaeobates* and *Leptodirus* subgroups – and *Apholeuonus* with a support 75.7/99 Fig. 1I).

Key to genera

1. Parameres bearing two setae (Fig. 76.9)..... .....*Bathysciopsis*
- Parameres bearing a crown of about 15 setae (Figs 76.7, 76.8)..... 2
2. Metaventrite with keel. Endophallus without apical sclerification (Fig. 76.4) ....*Bathyscimorphus* (*Bathyscimorphus*)
- Metaventrite without keel. Endophallus with two apical phanerae (Fig. 76.5) .... *Bathyscimorphus* (*Drovenikia*)

Genus ***Bathyscimorphus*** Jeannel, 1910
Bathyscimorphus Jeannel, 1910a: 21.

Type species. *Bathyscia byssina* Schiødte, 1848 by original designation (habitus in Fig. 75.1).

Diagnosis. All representatives are small in size, between 1.4–2.2 mm and bathyscioid facies.

Elytra: Short, altogether slightly longer than wide, with apical border in arc more or less pronounced. Elytral disk with punctation disordered, without transverse striolae and parasutural stria.

Legs: Short, thin, with fine pubescence; protibiae with a well-developed comb; male protarsi pentameres with first three tarsomeres dilated, the first being as wide or somewhat wider than the apical part of protibia.

Metendosternite: Furca in «V», with the trunk shorter and the two arms proportionally longer.

Median lobe of aedeagus: Shorter or more or less elongated, describing in lateral vision a wide regular arc with the terminal sector sinuate. In dorsal vision the apex is rounded, acuminate or with lateral protrusions.

Endophallus: With a well-developed armor.

Subgenus ***Bathyscimorphus***

Diagnosis. Small size, between 1.4–2.2 mm and bathyscioid facies (Fig. 75.1). Body ovoid, short, strongly convex and little attenuated backwards. Integument bright and punctate, with dots very fine and numerous. Pubescence yellowish, fine, lying and dense.

Head: Retractable with full and well-marked occipital carina; anophthalmous.

Antennae: Thin, reaching half of the length of the body, with club slightly differentiated, and all antennomeres longer than wide, the first being as long and as thick as the second one.

Pronotum: Convex and very transverse, two or almost twice as wide as long, with lateral edges regularly arcuated. Maximum width very close to base, which is somewhat narrower than, or as wide as, the anterior edge of elytra. Posterior vertices slightly sharp, with acute angles.

Elytra: Short, altogether slightly longer than wide, with apical border in arc more or less pronounced. Elytral disk with punctation disordered, without transverse striolae and parasutural stria.

Mesoventral keel (Fig. 75.4): High, laminar, with anterior and ventral edges a little arcuated, narrow and smooth; vertex rounded with angle slightly obtuse; posterior extension does not reach the metaventrite, but joins a keel that runs throughout the metaventrite.

Suture of the metaventrite (Fig. 75.4): In sinuous curve, distant in the upper two thirds so it covers a wide arched area, and very close to the coxal cavity in the lower third.

Metatergal apparatus (Fig. 75.7): With the apophysis of the alacrista wide with rounded tips and short, and the wings of the metascutum short, narrow and arched.

Metendosternite (Fig. 75.9): «V»-shaped with fur-

cal arms very thin and long, three times longer than the trunk. Posterior lamina very narrow along the arms and widened in trunk area. Terminal process or apophysis highly developed. Trunk short, at the base as wide as long with median keel wide.

Median lobe of aedeagus: Elongated, arcuated, weak to well sclerotized. In lateral view (Fig. 76.1), the ventral face describes a wide regular arc, while the dorsal face forms an almost regular arc in its basal two thirds, the apical third being recurved in «S»; dorsal face with two depressions, the anterior one much more developed, apex sharp and curved towards the dorsal face. In dorsal view (Fig. 76.4), sides aresubparallel, then widened towards the apical part; near apex, sides are widely rounded to converge in a rounded or somewhat acuminate apex; in some cases, the edges have between 5–7 reduced setae before the curvature of the apical area.

Endophallus (Fig. 76.4): With a well-developed armor. In basal area, a thick arcuated piece is observed in the background to which is attached in its dorsal middle part a flagellum not very long, thick at the base and filiform in apical part. In addition there are two laminar structures between basal piece and flagellum, a typical structure of this genus and which Jeannel (1924a) calls «papilionoid structure». In the middle region there are two lateral and two central pieces very close, both elongated, and above two elongated groups of small thorns. Apical area unarmed, with two rather short reinforcement bands.

Parameres (Fig. 76.7): Robust, as long as, or somewhat longer, than the median lobe; apical part arcuated inwards with club more or less pronounced, cylindrical or conical in shape with truncated apex; bearing a crown of about 15 setae not very long and of different length.

Spermathecal complex: Spermatheca elongated (Fig. 76.10), with apical and basal lobes well sclerotized and similar in width; apical lobe globose and basal elongated; hyaline junction duct, bent into an obtuse angle and somewhat longer than the basal lobe. Spermathecal duct with a well sclerotized nodule before the junction with the spermatheca and in this area the spermathecal gland conduit is inserted.

Female uroventrite VIII (Fig. 76.13): The posterior margin describe three arcs, there is an elongated macula parallel and very close to the edge; the sides of the anterior margin are arranged in slight descending arcs that are joined in the middle and form a very short spiculum with a triangular appearance.

Discussion. Molecular analysis includes this genus into phyletic series of *Leptodirus*. It appears in the tree of figure 1I in a basal position; it joins the groups *Leptodirus* and *Apholeuonus* with a good support (75.7/99). Due to its external morphological characters it is probably close to the genus *Bathysciopsis*, while for some structures of endophallus it seems more related to genus *Apholeuonus*; both genera belong to this series. In addition, this genus presents a unique feature in *Leptodirus* series: the presence of many setae in apical area of parameres.

Distribution. This genus has a wide range and colonizes many cavities from the northwestern region of Slovenia, to the karst areas southeast of the Lika plain in Croatia (Perreau 2000; Bognolo 2002).

Species

Bathyscimorphus (***Bathyscimorphus***) ***byssinus*** (Schiødte, 1848)
Bathyscimorphus (***Bathyscimorphus***) ***byssinus acuminatus*** (L. Miller, 1855)
Adelops acuminatus L. Miller, 1855: 507.
Bathyscia acuminata Mill.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *acuminata* Mill.: Reitter, 1885a [1884]: 19.
Bathyscimorphus byssinus subsp. *acuminatus* L. Miller: Jeannel, 1910a: 44.
Bathysciola (*Bathyscimorphus*) *byssina* subsp. *acuminata* Miller: Jeannel, 1914b: 6.
Bathyscimorphus byssinus acuminatus Mill.: G. Müller, 1914: 1027.

Bathyscimorphus (***Bathyscimorphus***) ***byssinus byssinus*** (Schiødte, 1848)
Bathyscia byssina Schiødte, 1848: 79.
Bathyscia (*Bathyscia*) *byssina* Schiødt.: Reitter, 1885a [1884]: 19.
Adelops byssinus Schiødte: L. Miller, 1855: 507.
Bathyscia Byssina Schiødte, 1891: 8.
Bathyscimorphus byssinus Schiødte: Jeannel, 1910a: 44.
Bathysciola (*Bathyscimorphus*) *byssina* Schiødte: Jeannel, 1914b: 6.
Bathyscimorphus byssinus Subsp. *byssinus* Schiødte, 1849: Jeannel, 1924a: 339.
Bathyscimorphus byssinus byssinus (Schiødte): Perreau, 2000: 200.

Bathyscimorphus (***Bathyscimorphus***) ***croaticus*** Bognolo, 2002
Bathyscimorphus croaticus Bognolo, 2002: 6.

Bathyscimorphus (***Bathyscimorphus***) ***uskokensis*** (G. Müller, 1911)
Bathyscia byssina uskokensis G. Müller, 1911c: 176.
Bathysciola (*Bathyscimorphus*) *byssina* subsp. *uskokensis* J. Müller: Jeannel, 1914b: 6.
Bathyscimorphus byssinus Subsp. *uskokensis* J. Müller, 1911: Jeannel, 1924a: 339.
Bathyscimorphus uskokensis (Müller): Bognolo, 2002: 7.

Subgenus ***Drovenikia*** Bognolo, 2002
Drovenikia Bognolo, 2002: 7.

Type species. *Adelops globosus* L. Miller, 1855 by original designation (for the habitus see that of the similar species *Bathyscimorphus* (*Drovenikia*) *sagarum* in Fig. 75.2).

Diagnosis. Species of small size, 1.6–2.2 mm, and bathyscioid facies (Fig. 75.2). The most relevant differences with the subgenus *Bathyscimorphus* are:

Elytra: More elongated and less convex.

Mesoventral keel (Fig. 75.5): Metaventrite without keel and with a concavity in the anterior part.

Suture of the metaventrite (Fig. 75.5): The suture delimits a slightly more developed superficial one.

Metatergal apparatus (Fig. 75.8): Wings of metascutum slightly longer, narrower and more arched.

Metendosternite (Fig. 75.10): Furca very similar to that of the subgenus *Bathyscimorphus*, but with the furcal trunk somewhat shorter and arms proportionally longer.

Median lobe of aedeagus: Generally shorter. In lateral view (Fig. 76.2), apical part more curved. In dorsal view (Fig. 76.5), apical part of lobe wider in several species, whereas with lateral protrusions in others

Endophallus (Fig. 76.5): The most important differentiating character being the presence in the apical region of two sclerotized and symmetrical pieces that are arranged transversely in evaginated sac.

Parameres (Fig. 76.8): Generally slightly more globular; bearing a crown of about 15 setae not very long and of different length.

Spermathecal complex (Fig. 76.11): Spermatheca elongated, with apical lobe spherical and smaller than the basal one, which is ovoid, both well sclerotized. Hyaline junction duct, not bent and somewhat longer than the basal lobe. Spermathecal duct with a sparsely developed nodule attached to the basal lobe and very close to the junction between the two leads to the spermathecal gland duct.

Female uroventrite VIII (Fig. 76.14): With short and wide spiculum, triangular in shape.

Discussion. See Discussion section of the subgenus *Bathyscimorphus.*

Distribution. Slovenia; several caves or MSS of Orehovški kras, Senožeški, Velike Lipljene, Logařska planota, mount Nanos, Logatec, Cerknišca lake, mount Unec and mount Snežnik. Croatia; several caves of Lika and Gorski Kotar.

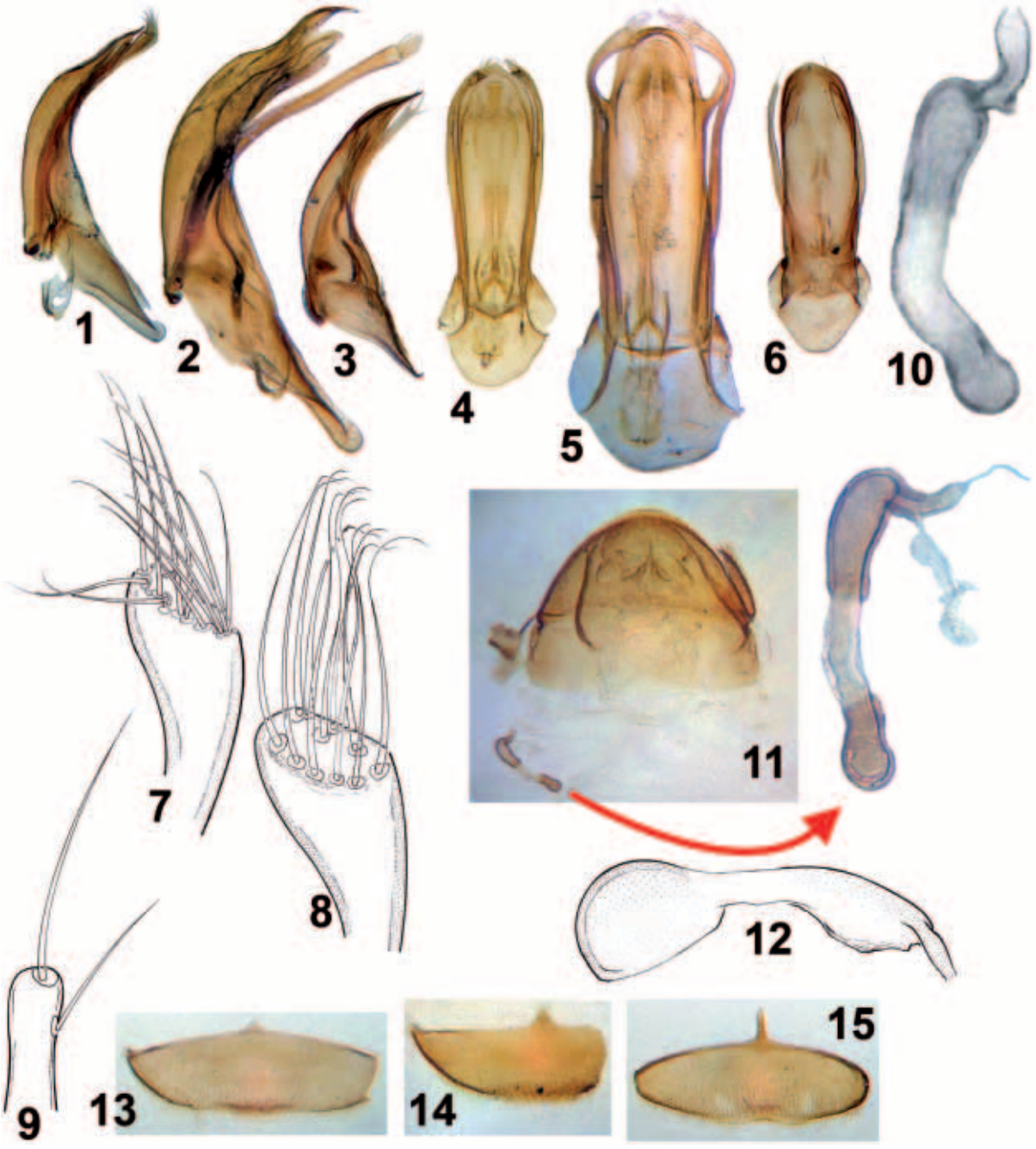
Species

Bathyscimorphus (***Drovenikia***) ***adriaticus*** G. Müller, 1914
Bathyscimorphus byssinus adriaticus G. Müller, 1914: 1028.
Bathyscimorphus (*Drovenikia*) *adriaticus* (Müller): Bognolo, 2002: 10.

Bathyscimorphus (***Drovenikia***) ***globosus*** (L. Miller, 1855)
Adelops globosus L. Miller, 1855: 507.
Bathyscia (*Bathyscia*) *globosa* Mill.: Reitter, 1885a [1884]: 19.
Bathyscimorphus globosus L. Miller: Jeannel, 1910a: 44.
Bathyscimorphus ovatus G. Müller, 1914: 1027.
Bathysciola (*Bathyscimorphus*) *globosa* Miller: Jeannel, 1914b: 6.
Bathyscimorphus (*Drovenikia*) *globosus* (Miller): Bognolo, 2002: 7.

Bathyscimorphus (***Drovenikia***) ***kladniki*** Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *kladniki* Bognolo, 2002: 10.

Bathyscimorphus (***Drovenikia***) ***likanensis*** (Reitter, 1890)
Bathyscimorphus (***Drovenikia***) ***likanensis likanensis*** (Reitter, 1890)
Bathyscia likanensis Reitter, 1890: 191.
Bathyscimorphus byssinus subsp. *likanensis* Reitter: Jeannel, 1910a: 44.
Bathysciola (*Bathyscimorphus*) *byssina* subsp. *likanensis* Reitter: Jeannel, 1914b: 6.
Bathyscimorphus likanensis Reitter, 1890: Jeannel, 1924a: 340.
Bathyscimorphus (*Drovenikia*) *likanensis* (Reitter): Bognolo, 2002: 15.



FIGURES 76.1–76.15: *Leptodirus* series, *Bathyscimorphus* group. Aedeagus in lateral view of: (**1**) *Bathyscimorphus* (*Bathyscimorphus*) *byssinus byssinus*, (**2**) *Bathyscimorphus* (*Drovenikia*) *sagarum*, (**3**) *Bathysciopsis sternalis*. Aedeagus in dorsal view of: (**4**) *B.* (*B.*) *b. byssinus*, (**5**) *B.* (*D.*) *sagarum*, (**6**) *Bathysciopsis sternalis*. Apex of the paramere of: (**7**) *B.* (*B.*) *b. byssinus*, (**8**) *B.* (*D.*) *sagarum*, (**9**) *Bathysciopsis sternalis*. Spermathecal complex of: (**10**) *B.* (*B.*) *b. byssinus* (modified from Bognolo 2002), (**11**) *B.* (*D.*) *adriaticus* with magnification of the spermatheca, (**12**) *Bathysciopsis sternalis*. Female uroventrite VIII of: (**13**) *B.* (*B.*) *b. byssinus*, (**14**) *B.* (*D.*) *adriaticus*, (**15**) *Bathysciopsis sternalis*.

Bathyscimorphus* (*Drovenikia*) *likanensis stilleri Bognolo, 2002
Bathyscimorphus stilleri Bognolo, 2002: 15.

Bathyscimorphus* (*Drovenikia*) *posarinii Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *posarinii* Bognolo, 2002: 11.

Bathyscimorphus* (*Drovenikia*) *pretneri Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *pretneri* Bognolo, 2002: 112.

Bathyscimorphus* (*Drovenikia*) *sagarum Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *sagarum* Bognolo, 2002: 9.

Bathyscimorphus* (*Drovenikia*) *serkoi Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *serkoi* Bognolo, 2002: 8.

Bathyscimorphus* (*Drovenikia*) *slavkoi Bognolo, 2002
Bathyscimorphus (*Drovenikia*) *slavkoi* Bognolo, 2002: 14.

Bathyscimorphus* (*Drovenikia*) *trifurcatus Jeannel, 1924
Bathyscimorphus trifurcatus Jeannel, 1924a: 340.
Bathyscimorphus (*Drovenikia*) *trifurcatus* Jeannel: Bognolo, 2002: 13.

Genus ***Bathysciopsis*** G. Müller, 1941
Bathysciopsis G. Müller, 1941: 213.

Type species. *Bathysciopsis sternalis* G. Müller, 1941: 213 by monotypy (habitus in Fig. 75.3).

Diagnosis. Size 1.8–1.9 mm. Facies bathyscioid, being body shape oblong-elongated, wide and generally very convex (Fig. 75.3). Pubescence short, lying down, thin and yellowish.

Head: With a blunt occipital carina and a punctation of very small and very distant points.

Antennae: Short and thin, do not reach the middle part of the elytra. Antennomeres of club elongated and somewhat widened. The first being clearly shorter than the second; 7th subconical, twice as long as wide, 8th small, almost as long as wide, and 11th pointed, being the longest and most robust.

Pronotum: Clearly transverse, twice as wide as long, with maximum width at the base, as wide as the anterior margin of elytra. Lateral margins little arcuated, not sinuated before the base, with posterior vertices sharp and protruding backwards; angles acute. Dorsal part subtly reticulate and minutely punctate.

Elytra: Strongly welded, convex, short and broad, about 1.25 times longer than wide. Progressively narrowed, with lateral margins poorly arcuated to apex, which is subacute. Maximum width close to the base; fairly strong punctation, with the points unordered and without visible transverse striation; parasutural stria obsolete.

Legs: Short. Male protarsi pentameres and slightly dilated. Protibiae with a poorly-developed apical comb and a short internal spur; meso- and metatibiae with four apical spurs, two internal and two external, and poorly developed baskets.

Mesoventral keel (Fig. 75.6): High, lamina-shaped, with anterior edge very convex, ventral edge widened and with setae, vertex rounded between the edges; meso- and metaventrite fused together in the ventral region, no suture visible.

Suture of the metaventrite (Fig. 75.6): The suture both in the apical area and in the basal third is close to the coxal cavity, in the rest it delimits a wide arched area.

Metaventrite: With a median fovea having a tuft of hairs somewhat longer than the normal pubescence of the body; according to G. Müller (1941) this particularity is unique. However, this structure, as pointed out by G. Müller, is not observed in the specimens we have examined.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus (Fig. 76.3, 76.6): Proportionally short and narrow. In lateral view (Fig. 76.3), apical area almost straight and sharp, strongly sclerotized, without depression before the apex. In dorsal view (Fig. 76.6), the subrectilinear sides delimit an equal width up to the apical part, which has a slightly lanceolate apex. Basal blade elongated and slightly arcuated.

Endophallus (Fig. 76.6). With a short stylet in the basal region and two diffuse phaneres on both sides of the base; in the middle region there are two more phaneres, and between these phaneres and the stylet a band of inconspicuous spinules.

Parameres (Fig. 76.3, 76.9): Thin and shorter than the median lobe. Undilated apex into which two setae are inserted, a long apical and a shorter pre-apical insertions.

Spermathecal complex (Fig. 76.12): Spermatheca small, elongated and slightly sclerotized, with three

well differentiated regions; distal lobe most developed and subspherical in shape, the dorsal and anterior part spherical, the ventral part straight; proximal lobe elongated and somewhat irregular, and between the two a well differentiated, hyaline and narrower junction duct. Spermatic duct thin, joining without nodule the posterior part of the proximal lobe.

Female uroventrite VIII (Fig. 76.15): Mid-apical area of the posterior margin concave with a parallel, slightly arcuate macula; sides of the anterior margin gently arched, joining a long, narrow, pointed spiculum.

Discussion. G. Müller (1941) at the time of description, did not provide a description of the male genitalia, neither did he illustrate the habitus or any other structure. In the same, this author relatated *Bathysciopsis* to *Bathyscimorphus* and *Ceuthmonocharis,* a position maintained by later authors (V.B. Guéorguiev 1976; Perreau 2000, 2004). We consider it appropriate, in the absence of a review of the problem, and in absence of molecular data, to maintain this position. A very striking homoplasy is observed at the apex of the parameres: a long apically inserted and a shorter preapical inserted setae. This feature is identical to that found in the genus *Beronia* (basal clade) from the Balkan mountain range of Bulgaria. In addition, the endophallus is similar to that of *Leptomeson* (*Anthroherpon* series), with the presence of a basal stipe and two diffuse phaneres in the median region, a character which is probably also homoplasic.

Distribution. Bosnia-Herzegovina, Germec planina.

Species

Bathysciopsis sternalis G. Müller, 1941
Bathysciopsis sternalis G. Müller, 1941: 213.

3.2.3.3 ***Apholeuonus*** group Jeannel, 1910 sensu novo

Diagnosis. The characteristics of this group are:

– A relative length of first and second antennomeres, where the first is shorter than the second; this character is valid in all the genera of the clade of *Apholeuonus* group except in the genera *Croatodirus* and *Velebitodromus*.

– Presence of a membranous lobe at apex of parameres. characterizes character shared by the genera of the phyletic series of *Apholeuonus* (*sensu* Jeannel 1924a) with the exclusion, however, of *Parapropus* and, as identified on a molecular basis, of *Croatodirus*. This situation is expressed very well, even if molecular data of many genera are lacking, from the grouping *Apholeuonus* + *Charonites* whose clade has a support of 54/100.

– Pentamerism of protarsi in males; all the genera of this phyletic group show pentameric protarsi.

Discussion. This group is represented in the molecular analysis by the genera *Apholeuonus*, *Parapropus*, *Charonites*, *Croatodirus* and *Speoplanes* with a high support of 95.9/100 (Fig. 1I); it it is related to the *Leptodirus* group and the genus *Bathysciotes*, of the *Spelaeobates* subgroup, with a very high support 100/100 (Fig. 1I).

Key to subgroups

1. Second antennomere elongated.....2
- Second antennomere short 3

2. First antennomere more robust than the second one; mesoventral keel high (Fig. 81.4).....
.....*Charonites* subgroup
- First antennomere of same thickness as the second; mesoventral keel low or absent (Fig. 82.9) .....
.....*Speoplanes* subgroup

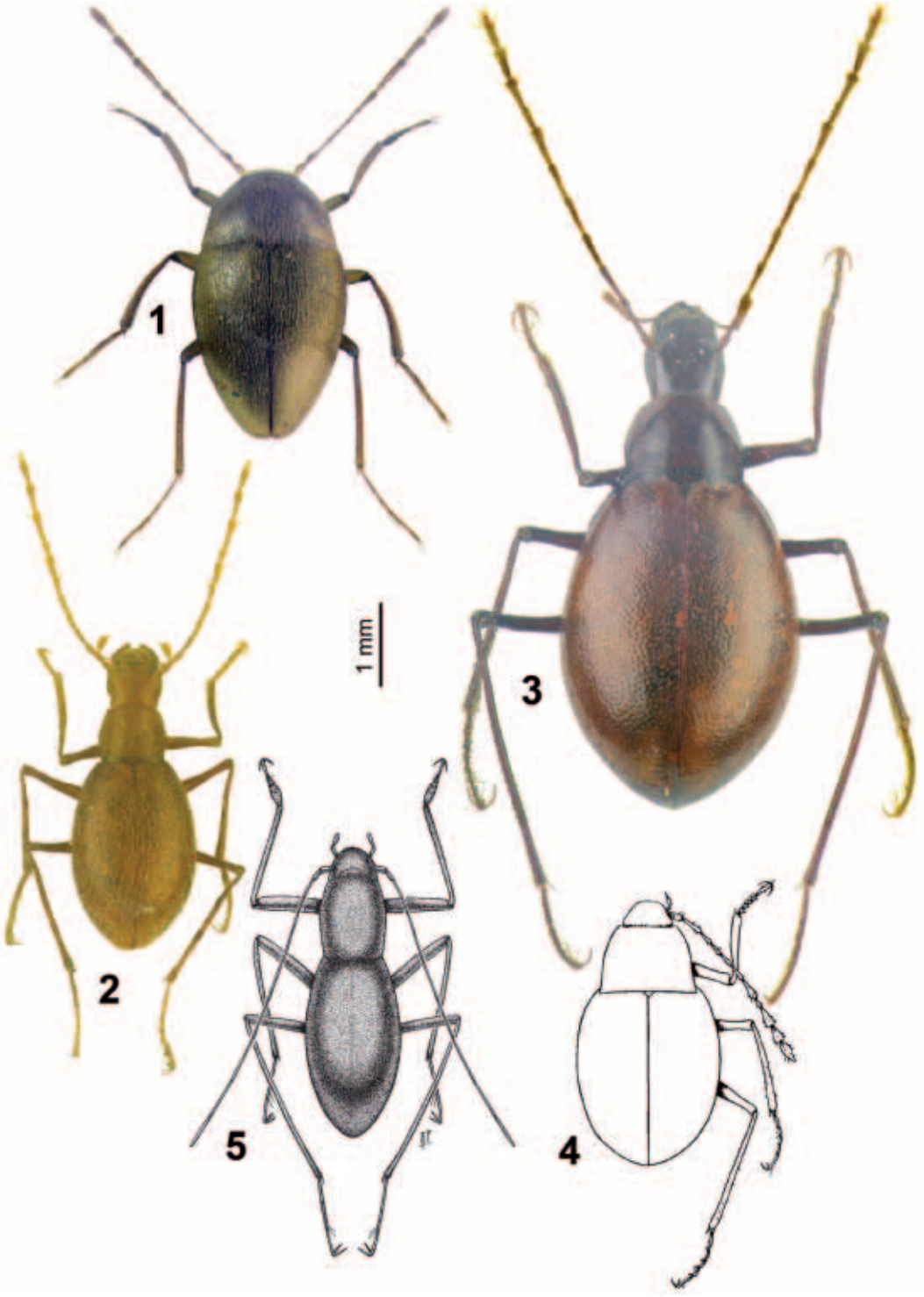
3. Mouth pieces with long setae .....
.....*Croatodirus* subgroup
- Mouth pieces without long setae.....4

4. Leptodiroid facies and body very elongated (Fig. 79.2); pronotum longer than wide; mesoventral keel absent (Fig. 82.3).....*Parapropus* subgroup
- Subpholeuonoid, pholeuonoid or bathyscioid facies and body globose and slightly elongated (Figs 77.1, 77.3, 79.1) – only very elongated in *Spelaites* (Fig. 80.3) –; pronotum as wide as long or wider than long; mesoventral keel low, high or slightly prominent, but always visible (Figs 82.1, 82.4, 82.6).....
.....*Apholeuonus* subgroup

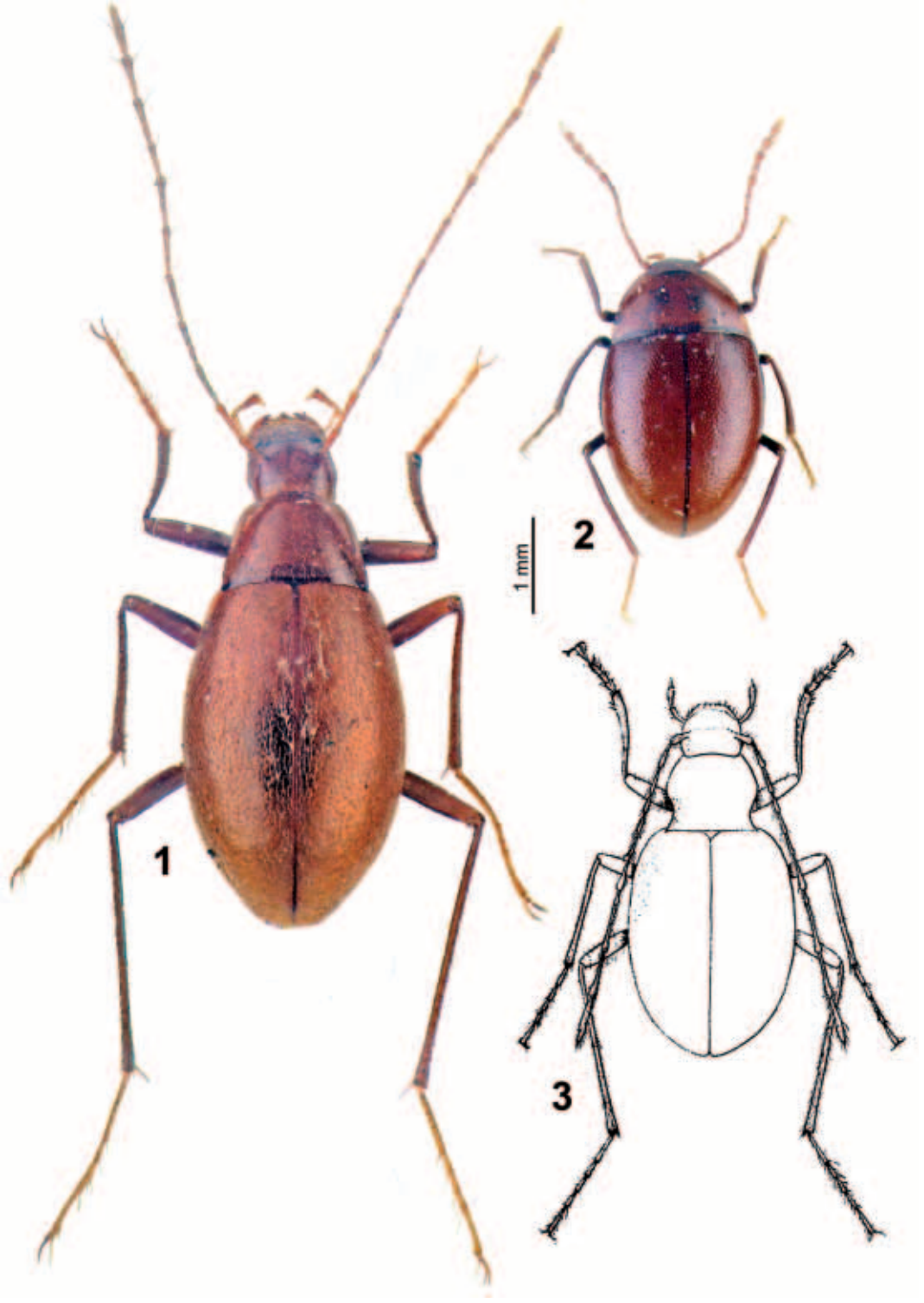
Croatodirus subgroup

Diagnosis. Buccal areas with long setae allowing the filtering of water and organic matter; antennae inserted in the posterior third or fourth of the head; endophallus without armor and parameres without apical membranous lobe.

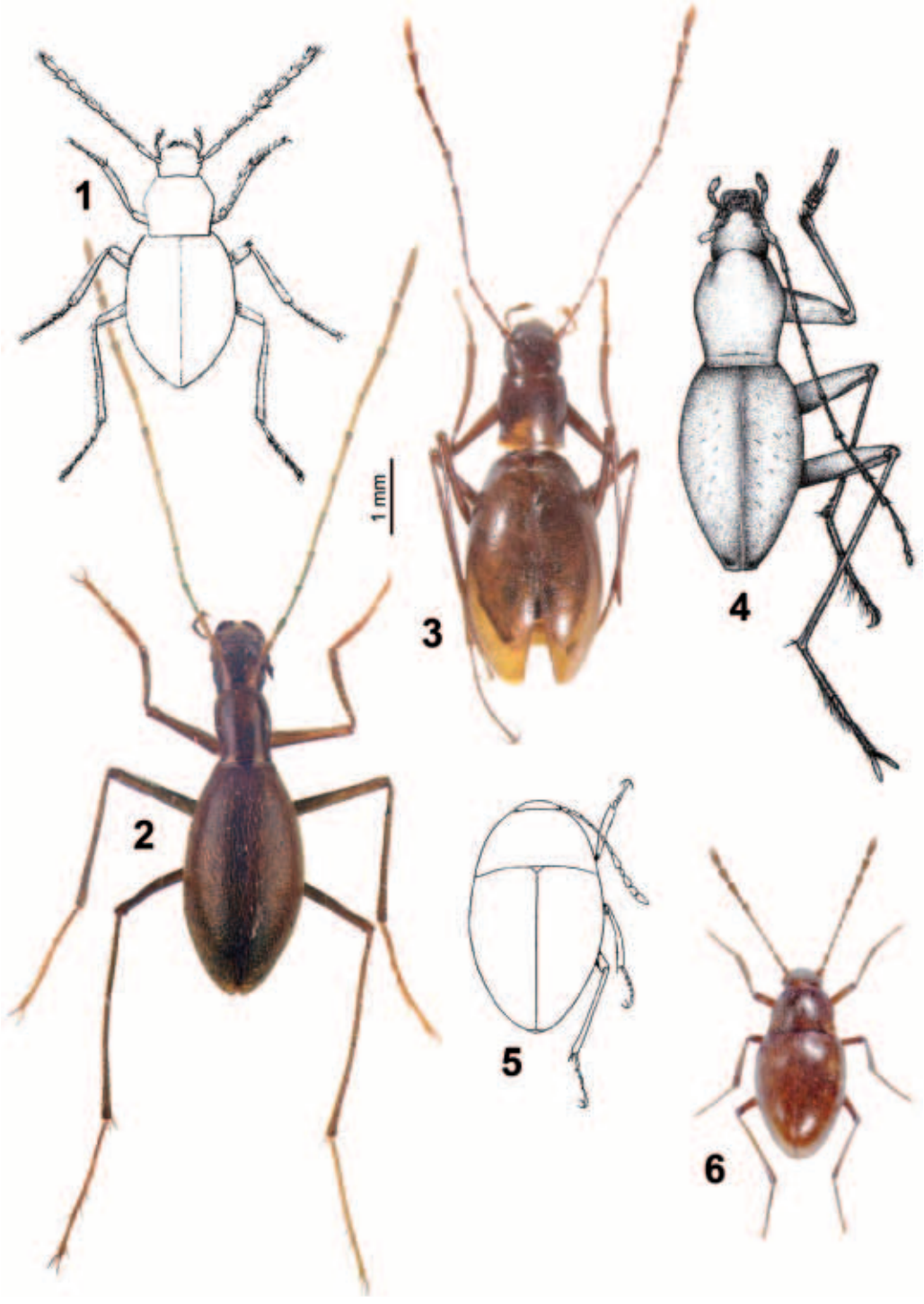
Discussion. Delić *et al.* (2023) established phylogenetic relationships between the genera of the Anthro-



FIGURES 77.1–77.5: *Leptodirus* series, *Apholeuonus* group. Habitus of: (**1**) *Adelopidius neumanni*, (**2**) *Antrosedes speluncarius*, (**3**) *Apholeuonus nudus nudus*, (**4**) *Charonites matzenaueri matzenaueri* (modified from Jeannel 1924a), (**5**) *Croatodirus bozicevici* (modified from Casale 2000).



FIGURES 78.1–78.3: *Leptodirus* series, *Apholeuonus* group. Habitus of: (**1**) *Haplotropidius taxi subinflatus*, (**2**) *Icharonia leonhardiana*, (**3**) *Katobatizon antennarium* (modified from Knirsch 1927).



FIGURES 79.1–79.6: *Leptodirus* series, *Apholeuonus* group. Habitus of: (**1**) *Leonhardia reitteri mersa* (modified from Knirsch 1927), (**2**) *Parapropus sericeus taxi*, (**3**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al.* 2014), (**4**) *Radziella styx* (modified from Casale & Jalžić 1988), (**5**) *Roubaliella biokovensis* (modified from Jeannel 1925), (**6**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021).

herponina from the Dinaric mountains, they show that the genera *Velebitodromus* and *Croatodirus* are sister with good support, >0.99 (Delić *et al*. 2023). In Tree-1 (Fig. 1I) *Croatodirus* derives from the basal cladogenesis of *Apholeuonus* group with support 95.9/100 and the entire clade is sister to *Leptodirus* group with support 100/100; the Tree-2 topology is identical (Fig. 2) and *Croatodirus* is related with support 94.5/99. Consequently, *Velebitodromus* will be included as sister to *Croatodirus* in *Apholeuonus* group.

Key to genera

1. Medium-large size, between 3.5–5.8 mm, with pholeuonoid facies (Fig. 77.5). Median lobe of aedeagus robust (Figs 85.5, 87.6) .....*Croatodirus*
- Small-medium size, 2.7–3.4 mm, with sub-leptodiroid facies (Fig. 80.5). Median lobe of aedeagus slender (Figs 86.7, 89.4).....*Velebitodromus*

Genus ***Croatodirus*** Casale, Giachino & Jalžić, 2000
Croatodirus Casale, Giachino & Jalžić, 2000b: 84.

Type species. *Croatodirus bozicevici* Casale, Giachino & Jalžić, 2000 by original designation (habitus in Fig. 77.5).

Diagnosis. Medium-large size, between 3.5–5.8 mm. General body shape narrow and elongated, with pholeuonoid facies (Fig. 77.5). Body colour dark reddish, with opaque integument.

Head: Elongated, somewhat longer than wide, not retractable, without occipital carina, shorter and narrower than pronotum. Anophthalmous. Buccal areas, or oral appendages, with long setae allowing the filtering of water and organic matter. Punctation fine with short and yellowish hairs, pubescence denser in clypeus and labrum.

Antennae: Inserted in the posterior fourth of the head. Very long and thin, somewhat longer than the length of the body; antennomeres from 3rd to 11th of similar thickness, without differentiated club; first antennomere thicker and longer than the second; antennomeres 7th to 11th longer, with the 9th being the longest and the 11th the shortest.

Pronotum: Large, subrectangular, somewhat longer than wide, between 1.1–1.2 times longer than wide. Little convex, with maximum width in the middle or slightly in front of the middle and narrower than elytra. Lateral edges with the anterior middle part gently arcuated; posterior lateral half very slightly sinuated near the base or more constricted and somewhat more sinuated. Anterior part of similar width to the posterior or basal area. Posterior vertices non-protruding with obtuse angles. Pubescence dense, fine, short and lying.

Elytra: Elongated oval, between 1.7–1.8 times longer than wide, very convex and narrowed towards the apical part, with its maximum width in the middle. Apexes non-sharp, in narrow or subtruncated arches that completely cover pygidium. Punctation dense, shallow and non-transversely aligned. Pubescence dense, short, fine and lying down. Parasutural stria absent.

Legs: Very long and thin; femora widened in basal area; protibiae slightly widened in apical area, without apical comb or internal or external spurs. Pro- and metatibiae straight, mesotibiae slightly arcuated. Male protarsi pentameres, with the first three tarsomeres dilated, the first being somewhat wider than the anterior protibial apex. Tarsal claws long and slightly widened.

Mesoventral keel (Casale *et al*. 2000b): Absent; mesocoxal cavities contiguous.

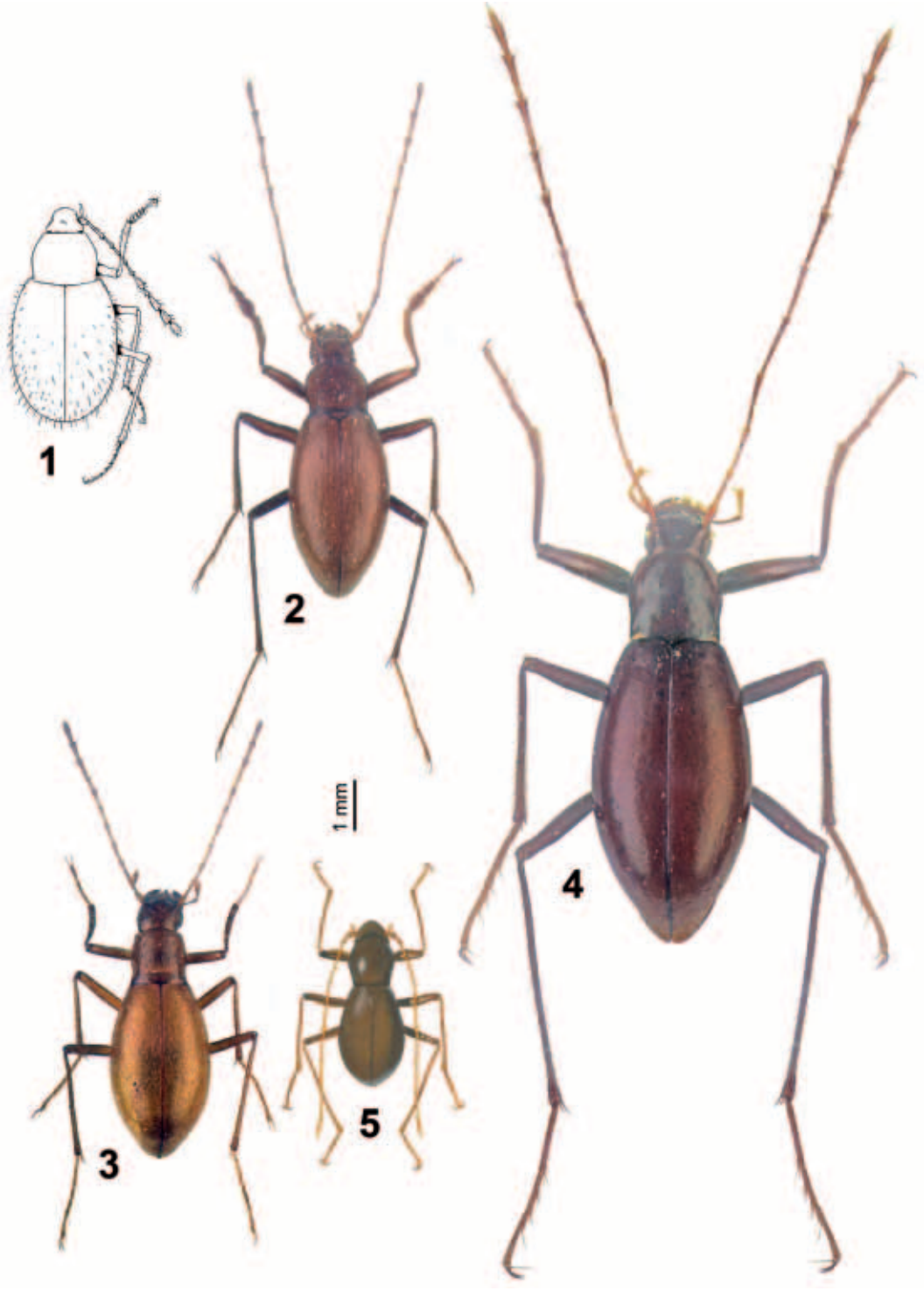
Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Medium sized and robust. Arcuated in lateral view (Fig. 85.5), with the ventral face not sinuate and the dorsal one arcuated in its first part and sinuate in the apical third;apical part straight, narrow and sharp. In dorsal view (Fig. 87.6), widened in the two-thirds of its length, then gradually narrowed to apex, which can form a more or less protruding lobe with a sharp, arcuated or truncated tip. Basal blade long in lateral view, with the apical area curly and very arcuated. In dorsal view, posterior margin in broad arch, sometimes low-cut in the middle and with a short or very short posterior middle keel. Basal lamina longer and somewhat narrower than the ventral lamina of tegmen.

Endophallus (Fig. 87.6): Unarmored; in some species with a strip of poorly sclerotized scales in the middle part.

Parameres (Fig. 90.5): As long as, or somewhat longer than the median lobe, curved inwards in the apical area, without a differentiated club and with three setae of similar length and thickness: two external distal with insertion pores nearby and another one internal preapical with insertion point further away.

Spermathecal complex (Fig. 91.4): Spermatheca small, weakly sclerotized, with apical area dilated, gradually decreasing in thickness until its junction with the spermatic duct. This one of uniform thickness and about two and a half times longer than the spermatheca. Spermathecal gland lacking.



FIGURES 80.1–80.5: *Leptodirus* series, *Apholeuonus* group. Habitus of: (**1**) *Setnikia leonhardi* (modified from Jeannel 1924a), (**2**) *Spelaeodromus pluto*, (**3**) *Spelaites grabowskii*, (**4**) *Speoplanes biokovensis*, (**5**) *Velebitodromus smidai* (modified from Casale *et al.* 2012).

Female uroventrite VIII (Fig. 93.4): Without spiculum, but a membranous basal part and the apical one slightly sclerotized, arcuated in its posterior edge and with two groups of short and thick setae.

Discussion. All specimens of *Croatodirus* were found mostly in places of water drainage (hygropetricolous habitat), or very close to such places (Casale *et al*. 2000b, 2004). The general characters of the body, and the mouthparts with modified setae, suggest an «hadesian» way of life, that it is adapted to filter water and organic matter from stalagmitic walls (Casale *et al*. 2004).

As assumed for other highly specialized Leptodirini, e.g. the species of genera *Hadesia*, *Radziella*, *Tartariella*, *Nauticiella*, *Kircheria* and *Riberius*, among others, all sharing similar morphological adaptations, it is quite possible, but not probable, that they share phylogenetic affinities. A careful examination shows many morphological characters that allow *Croatodirus* to be associated with the phyletic lineage of *Anthroherpon.* These characters are, among others, a scaphoid facies, subrectangular pronotum, insertion point of antennae and first antennomere longer than the second one, absence of mesoventral keel and contiguous mesocoxal cavities, protibiae without apical comb and without external spurs and femora dilated in basal area. However, some other morphological features also suggest that it might be related to the phyletic lineage of *Leptodirus*, such as a non-pedunculated pterothorax, the very small genital segment in male, or a medium-sized aedeagus with unarmed endophallus (Casale *et al*. 2000b).

The recent availability on GeneBank of the molecular sequences of *Croatodirus* (See Appendix 2: KX223671, KX223659, KX223624 and KX223635) has allowed us to position this genus in our tree. As shown in figure 1I *Croatodirus* take place as a sister group of *Apholeuonus* + *Speoplanes* + *Charonites* + *Parapropus* subgroups with a high support, 95.9/100. The alleged affinities with *Anthroherpon* are therefore to the consequence of simple homoplasies linked to phenomena of morphological adaptation to similar living conditions. Instead, the supposed affinity with the phyletic series of *Leptodirus* is confirmed. Delić *et al.* (2023) show that the genera *Velebitodromus* and *Croatodirus* are sister with good support, >0.99 (Delić *et al*. 2023).

Distribution.Three species belong to the genus *Croatodirus*, each linked to a single massif of the Dinaric karst in Croatia: on Učka mountains (*C. bozicevici* in the cave of Kaverna), on Velebit mountains (*C. casalei* in Slovačka jama pothole) and Gorski kotar mountains (*C. ozimeci* in Lokvarka Cave). Recently (Delić 2017) pointed out the presence of *Croatodirus* in a cave of Brezno treh src, Cifre, in Snežnik mountains in Slovenia, a village very close to border with Croatia.

Species

Croatodirus bozicevici Casale, Giachino & Jalžić, 2000
Croatodirus bozicevici Casale, Giachino & Jalžić, 2000b: 87.

Croatodirus casalei Giachino & Jalžić, 2004
Croatodirus casalei Giachino & Jalžić *in* Casale, Giachino & Jalžić, 2004: 303.

Croatodirus ozimeci Casale, Giachino & Jalžić, 2004
Croatodirus ozimeci Casale, Giachino & Jalžić, 2004: 306.

Genus ***Velebitodromus*** Casale, Giachino & Jalžić, 2004
Velebitodromus Casale, Giachino & Jalžić, 2004: 311.

Type species. *Velebitodromus smidai* Casale, Giachino & Jalžić, 2004 by original designation (habitus in Fig. 80.5).

Diagnosis. Small-medium size, 2.7–3.4 mm, with sub-leptodiroid body, large, sub-rectangular pronotum and ovate elytra (Fig. 80.5); pubescent, dark reddish; depigmented.

Head: Elongate, not retractile, without occipital carina; anophthalmous. Mouth parts bearing long setae, i.e. for filtering water and organic matter; clypeus and labrum with dense and long pubescence. Penultimate labial palpomere long and apically dilated; apical palpomere very short.

Antennae: Inserted on the posterior third of the head, very long and slender, similar in both sexes, and widely exceeding the elytron apex; first antennomere widened, longer than the second one; the 11th antennomere shorter than the 10th.

Pronotum: Large, slightly longer than wide, with its maximum width just before the middle, subrectangular in shape; lateral sides regularly rounded anteriorly, distinctly sinuated basally, with hind angles obtuse but evident; basal margin as wide as the base of elytra. Disc subconvex, covered by dense, short and decumbent pubescence. Pterothorax not pedunculate.

Elytra: Elongate-ovate, strongly convex, with their maximum width at the apical third, not truncate and

moderately attenuate at apex, similar in both sexes. Microsculpture not forming transversal rows; disc with short, thin pubescence; parasutural stria absent.

Legs: Very long and slender, with femora thickened basally. Protibiae not widened at apex, without apical comb of spines and without outer and inner spurs. Male protarsi five-segmented, with three dilated tarsomeres; basal tarsomere wider than the apex of protibia. Meso- and metatibiae with inner, simple apical spur and apical row of very short spines; tarsal claws long, slightly widened.

Mesoventral keel (Casale *et al*. 2004): Absent. Mesocoxal cavities contiguous.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Small sized, slender. In lateral view (Fig. 86.7) slightly arcuate. In dorsal view (Fig. 89.4), parallel sides and rounded at apex. Basal lamina arcuate, curly shaped, without ventral keel.

Endophallus: Without sclerotized structures.

Parameres (Figs 90.19, 90.20): Narrow or widened and slightly or distinctly longer than the median lobe, moderately dilated at apex, each furnished with three or four short and stout setae (two or three in apical position, one in pre-apical position, respectively), similar in size and length.

Spermathecal complex (Fig. 92.9): Spermatheca membranous, sac-like, very narrow and elongated, widened and slightly sclerotized only at apex.

Female uroventrite VIII: Without spiculum.

Discussion. See Discussion on the genus *Croatodirus*.

Distribution. Croatia. Known from few caves in Velebit massif, Dinaric chain.

Species

Velebitodromus smidai Casale, Giachino & Jalžić, 2004
Velebitodromus smidai Casale, Giachino & Jalžić, 2004: 313.

Velebitodromus ozrenlukici Lohaj, Mlejnek & Jalžić, 2012
Velebitodromus ozrenlukici Lohaj, Mlejnek & Jalžić *in* Casale, Jalžić, Lohaj & Mlejnek, 2012: 144.

Charonites subgroup

It is characterised by having the first antennomere more robust than the second one, a high mesoventral keel and by the presence of a very small «Y»-piece in ventral position at the bottom of basal region of the endophallus, with the apex of the parameres with a membranous lobe. As *Charonites* is the only genus in the subgroup, its characteristics are the ones of the genus. See genus Discussion section about its position in the tree.

Genus ***Charonites*** Apfelbeck, 1907
Charonites Apfelbeck, 1907a: 304.

Type species. *Charonites matzenaueri* Apfelbeck, 1907 by monotypy (habitus in Fig. 77.4).

Diagnosis. Small size, between 2.5–3.3 mm. Body globose, elliptical and elongated with pholeuonoid facies (Fig. 77.4). Colour reddish, more or less dark, rather bright integument. Pubescence yellowish, short, scattered and raised. Punctation strong and deep, with points more or less separated.

Head: Small and elongated, wider than long and narrower than the pronotum; occipital carina blurred; anophthalmous.

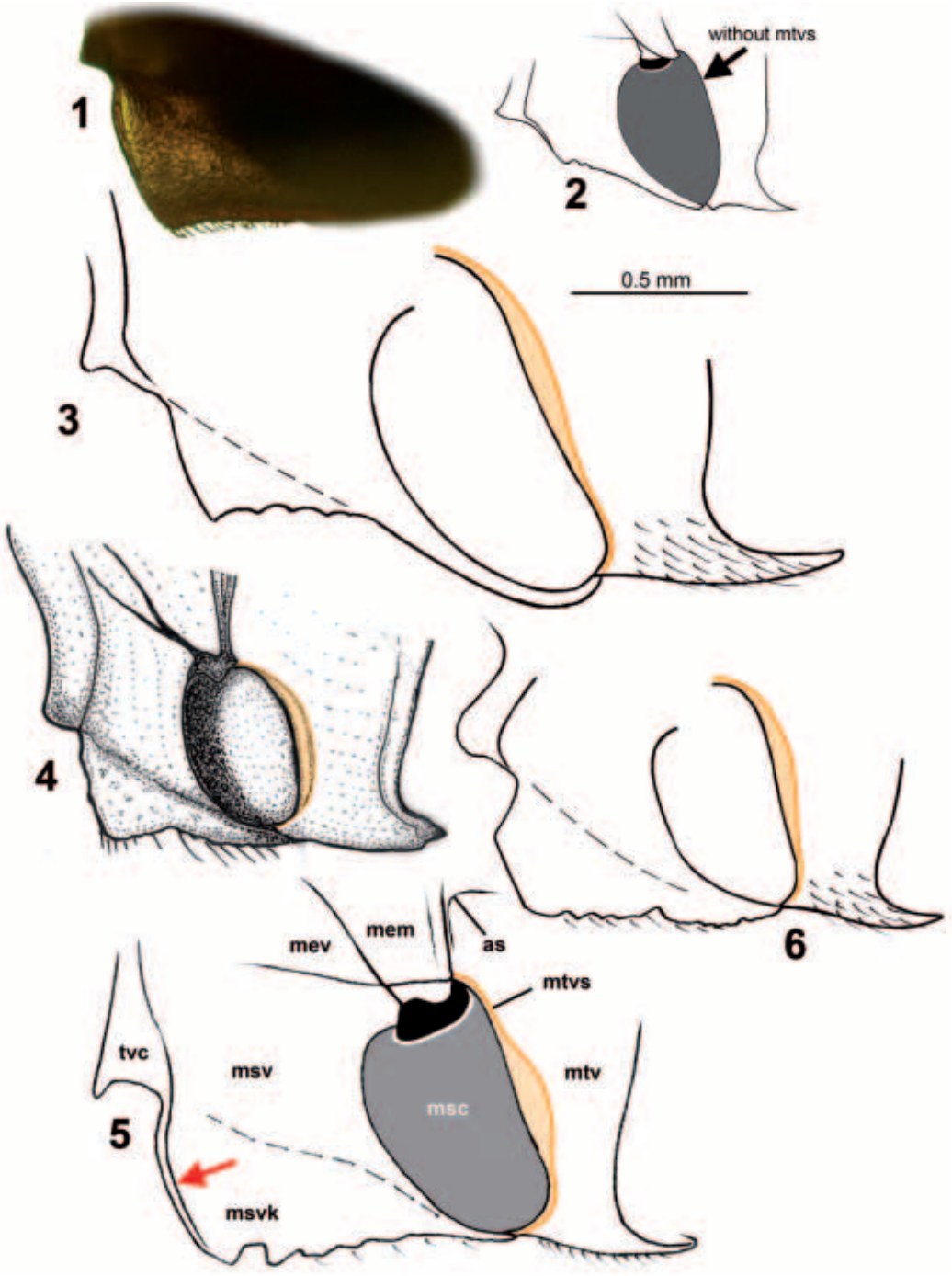
Antennae: Rather short, they can exceed the middle area of elytra, with the first antennomere more robust than the second one, which is between two and three times longer; club thick with antennomeres subconic, the 8th very small and as long as, or somewhat longer than, wide.

Pronotum: Bell-shaped or subrectangular, transverse (1.5–1.7 wider than long), little convex, narrower than the elytra, with maximum width at base, which is wider than anterior area. Lateral margins widen progressively from anterior area to base, throughout the anterior half in smooth and regular arch; concave in its posterior half. Some species with two elongated depressions on both sides of the pronotum, near the base. Sharp and protruding vertices to sides; basal angles acute.

Elytra: Short and convex, 1.3–1.4 times longer than wide together, with maximum width towards basal third. Sides regularly arcuated, as well as apical parts; shoulders rounded and blurred. Pubescence dense and dotted deeper than in other parts of body. Parasutural stria lacking and transverse striation absent.

Legs: Quite long and thin; protibiae with a visible comb, although not very developed, in apical half of outer edge. Protarsi pentameres undilated in males; meso- and metatibiae without external spurs; basal area of femora dilated in club.

Mesoventral keel (Fig. 81.4): High, almost trapezoidal, depending on species, vertex more or less



FIGURES 81.1–81.6: *Leptodirus* series, *Apholeuonus* group. Pterothorax in lateral view of: (**1**) *Adelopidius ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**2**) *Antrosedes speluncarius*, (**3**) *Apholeuonus nudus nudus*, (**4**) *Charonites matzenaueri matzenaueri* (modified from Polak & Mulaomerović 2021), (**5**) *Haplotropidius pubescens* (red arrow pointing to a groove parallel to the anterior margin), (**6**) *Icharonia leonhardiana*. Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

hooked or angular. Anterior border little convex, ventral one slightly low in middle, with setae and prolongation of the posterior apophysis which does not or slightly exceed the metaventrite.

Suture of the metaventrite (Fig. 81.4): In form of a regular arch from anterior to posterior apex of mesocoxal cavity, it delimits a narrow and elongated area.

Metatergal apparatus (Fig. 83.3): With short and wide metascutum wings; apophysis of the alacrista very long, almost as long as wings of metascutum.

Metendosternite: Unknown.

Median lobe of aedeagus: Short and narrow. In lateral view (Fig. 85.4), regularly arcuated. In dorsal view (Fig. 87.5), with subparallel and somewhat sinuous sides, which narrow gently towards apical area, the apex arcuated and not sharp.

Endophallus (Fig. 87.5): At bottom of basal region, there is a very small «Y»-piece in ventral position. Above this piece, two dorsal lateral branches that merge towards the ventral face and form a wide phanera similar to a spoon with dorsal concavity. In addition, they are two other small well sclerotized phanerae on both sides of phanera in spoon.

Parameres (Fig. 90.4): Curved, bent, thick at base and thiner with uniform thickness along middle and apical areas, between as long as, or somewhat longer than the median lobe. Apex with a membranous lobe, more or less developed depending of the species, and three short setae: in general two apical, somewhat longer and more robust, and an internal subapical smaller and oriented inwards.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Jeannel (1924a) pointed out that the closest genus is *Adelopidius* by presenting similarities in several external morphological characters and especially in male genitalia. V.B. Guéorguiev (1976) places this genus in the subtribe Leptodirina close to *Adelopidius*, as well as Perreau (2000) within the phyletic series of *Apholeuonus*. In Tree-1 it is included in *Leptodirus* series and *Charonites* joins *Apholeuonus* + *Speoplanes* + *Parapropus* with a support of 54.3/99 (Fig. 1I).

Charonites derives from a basal cladogenesis within the *Apholeuonus* group. There is a great genetic distance with respect to the other representatives of its group; this shows the possibility that other undiscovered genera can be found in its branch. Therefore, it should probably form its own group; this would also be the case of *Croatodirus*, with an even more basal cladogenesis and also joined by a long branch.

Distribution. The genus colonizes caves towards centre and south of Bosnia-Herzegovina, mostly in karst areas near Sarajevo.

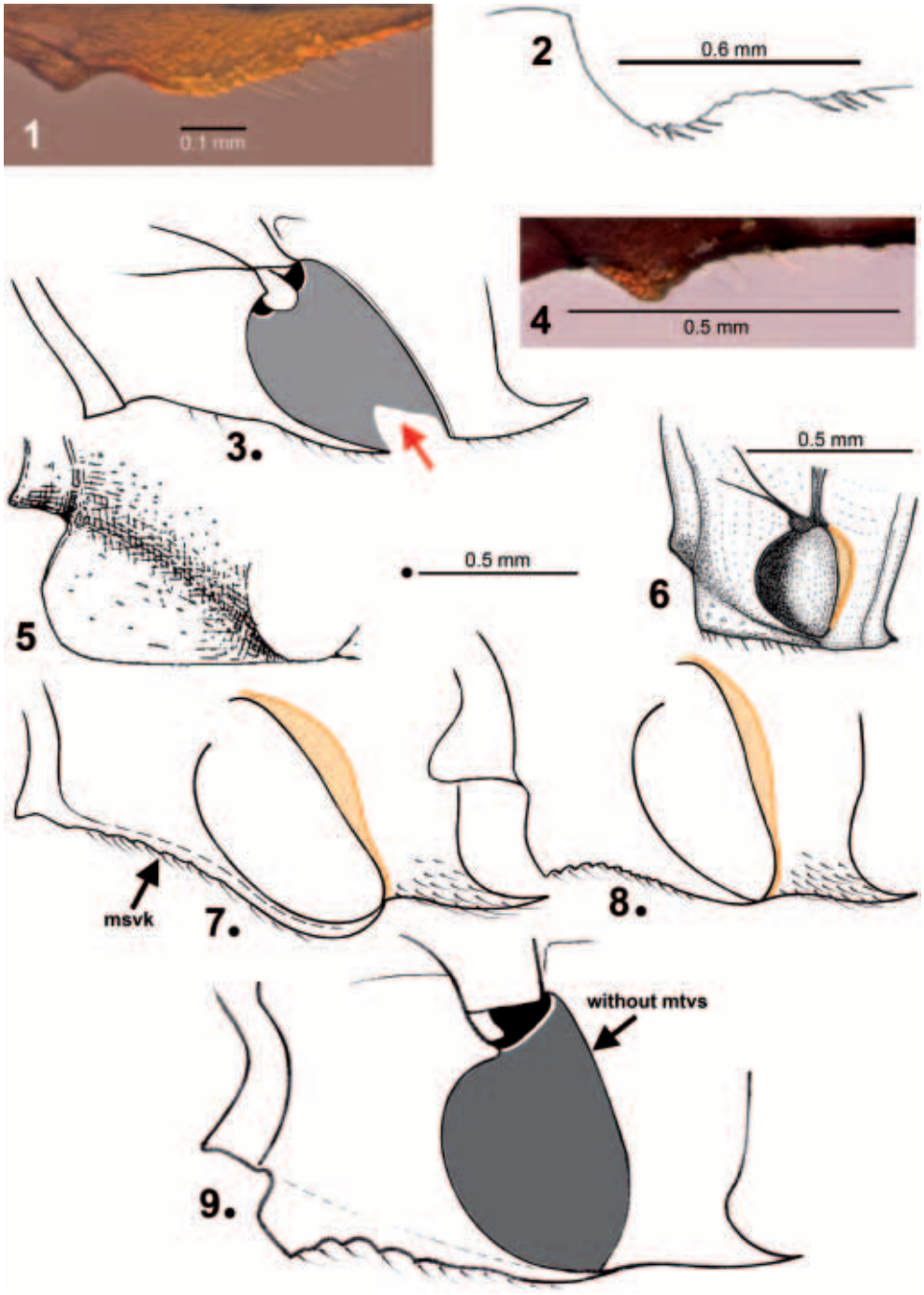
Species

Charonites matzenaueri Apfelbeck, 1907
Charonites matzenaueri apfelbecki Jeannel, 1924
Charonites Matzenaueri Subsp. *Apfelbecki* Jeannel, 1924a: 365.
Charonites matzenaueri apfelbecki Apfelbeck: Perreau, 2000: 207.
Charonites matzenaueri matzenaueri Apfelbeck, 1907
Charonites Matzenaueri Apfelbeck, 1907a: 304.
Charonites Matzenaueri Subsp. *Matzenaueri* Apfelbeck, 1907: Jeannel, 1924a: 365.
Charonites exilis Reitter, 1911a: 174.
Charonites Matzenaueri ab. *sinuatocollis* Apfelbeck, 1919: 270.
Charonites matzenaueri matzenaueri Apfelbeck: Perreau, 2000: 207.

Charonites scheibeli Apfelbeck, 1919
Charonites Scheibeli Apfelbeck, 1919: 269.
Charonites Scheibeli ab. *subimpressus* Apfelbeck, 1919: 269 (*Nomen nudum*).
Charonites scheibeli Apfelbeck: Perreau, 2000: 207.

Charonites weiratheri Reitter, 1911
Charonites weiratheri prosternalis Jeannel, 1924
Charonites Weiratheri Subsp. *prosternalis* Jeannel, 1924a: 365.
Charonites weiratheri prosternalis Jeannel: Perreau, 2000: 207.
Charonites weiratheri pygmaeus Jeannel, 1924
Charonites Weiratheri Subsp. *pygmaeus* Jeannel, 1924a: 366.
Charonites weiratheri pygmaeus Jeannel: Perreau, 2000: 208.
Charonites weiratheri weiratheri Reitter, 1911
Charonites Weiratheri Reitter, 1911a: 173.
Charonites Noesskei Apfelbeck, 1919: 270.
Charonites Weiratheri Subsp. *Weiratheri* Reitter, 1911: Jeannel, 1924a: 365.
Charonites weiratheri weiratheri Reitter: Pretner, 1974: 10.

Charonites orlovacensis Reitter, 1913
Charonites orlovacensis Reitter, 1913a: 154.
Charonites (s. str.) *Zoppai* Subsp. *orlovacensis* Reitter, 1913: Jeannel, 1924a: 366.



FIGURES 82.1–82.9: *Leptodirus* series, *Apholeuonus* group. Pterothorax in lateral view of: (**1**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014), (**2**) *Leonhardia hilfi* (modified from Perreau 1999), (**3**) *Parapropus sericeus sinuaticollis* (red arrow pointing to the confluent mesoventral cavities), (**4**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al.* 2014), (**5**) *Roubaliella biokovensis* (modified from Jeannel 1925), (**6**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**7**) *Spelaeodromus pluto*, (**8**) *Spelaites grabowskii*, (**9**) *Speoplanes biokovensis*. Abbreviations: **msvk**, mesoventral keel; **mtvs**, metaventral suture.

Charonites zoppae orlovacensis Reitter: Perreau, 2000: 208.

Charonites zoppae G. Müller, 1912
Charonites Zoppae G. Müller, 1912: 302.
Charonites Zoppai J. Müller: Jeannel, 1914b: 49.
Charonites zoppae zoppae Müller: Perreau, 2000: 208.

Parapropus subgroup

Characterised by leptodiroid facies, body very elongated, pronotum longer than wide, mesoventral keel absent and endophallus without sclerotized «Y»-piece. The *Parapropus* subgroup is sister to clade *Speoplanes* + *Apholeuonus* with support 56.2/98 (Fig. 1I). Being the only genus in the subgroup, the characteristics that define it are those of the genus. For its position in the tree, see genus Discussion section.

Genus ***Parapropus*** Ganglbauer, 1899
Leptonotus Motschulsky, 1869: 253 (*Nom. praeocc.* Homonymy with *Leptonotus* Kaup, 1853 – Pisces –; Type species. *Leptoderus sericeus* Schmidt, 1852).
Leptodirus (*Propus*) Abeille de Perrin, 1878: 149 (*Nom. praeocc.* Homonymy with *Propus* Onken, 1816 – Reptilia –; *Propus* Cope, 1876 – Reptilia –; Type species. *Leptoderus sericeus* Schmidt, 1852).
Parapropus Ganglbauer, 1899: 84.
Propus G. Müller, 1901: 28.
Reinholdina Giachino & Moravec, 2009: 38 (Type species. *Reinholdina deelemanorum* Giachino & Moravec, 2009).

Type species. *Leptoderus sericeus* Schmidt, 1852 by monotypy (for the habitus see that of the similar subspecies *Parapropus sericeus taxi* in Fig. 79.2).

Diagnosis. Size between 4.0–6.3 mm. Body shape leptodiroid, narrowed, little globose and very elongated (Fig. 79.2). Integument colour yellowish, with microsculpture in general fine without order. Pubescence yellowish, short, thin, lying down and more or less dense depending on region of body.

Head: Elongated, non-retractable, without full occipital carina and narrower than the anterior part of pronotum; anophthalmous. Punctation fine, distant and shallow.

Antennae: Very long, between as long as and longer than the length of body. Antennomeres all thin and elongated, first antennomere the widest, between 2–3 times shorter than the third one, antennomeres 7th–11th the longest.

Pronotum: Elongated, variable in length, but always longer than wide, marginal edge full. Sides arcuated anteriorly, concave and more or less sinuated in the basal part which is the narrowest. Widest part being slightly in front of the middle part. Posterior vertices more or less prominent and sharp, with angles rights to slightly obtuse. Punctation with points larger and spaced than on head.

Elytra: Very narrow anteriorly and very long compared to pronotum, about twice as long as wide, with maximum width towards half. Disc convex and more or less dilated; apexes well rounded and more or less separated. Normally two narrow basal impressions are present. Punctation formed by points larger and closer than in pronotum. No transverse striolation and parasutural stria, although this stria is present only in *P. vitorogensis*.

Legs: Very long and thin; protibiae combless with very reduced or absent spurs. Males protarsi pentameres, width of tarsomeres in males very variable from thin to very dilated, but always wider than the apex of protibia. Femora straight and not dilated towards the basal part.

Mesoventral keel (Fig. 82.3): Lacking, with the ventral edge slightly sinuate with some distant setae. Mesocoxal cavity open inferiorly.

Suture of the metaventrite (Fig. 82.3): Very close to the edge of mesocoxal cavity, not differentiated.

Metatergal apparatus (Fig. 83.5): Very small, with the wings of metascutum very narrow, very long and without sutures; apophysis of the alacrista without apical nodule, with basal processes very reduced.

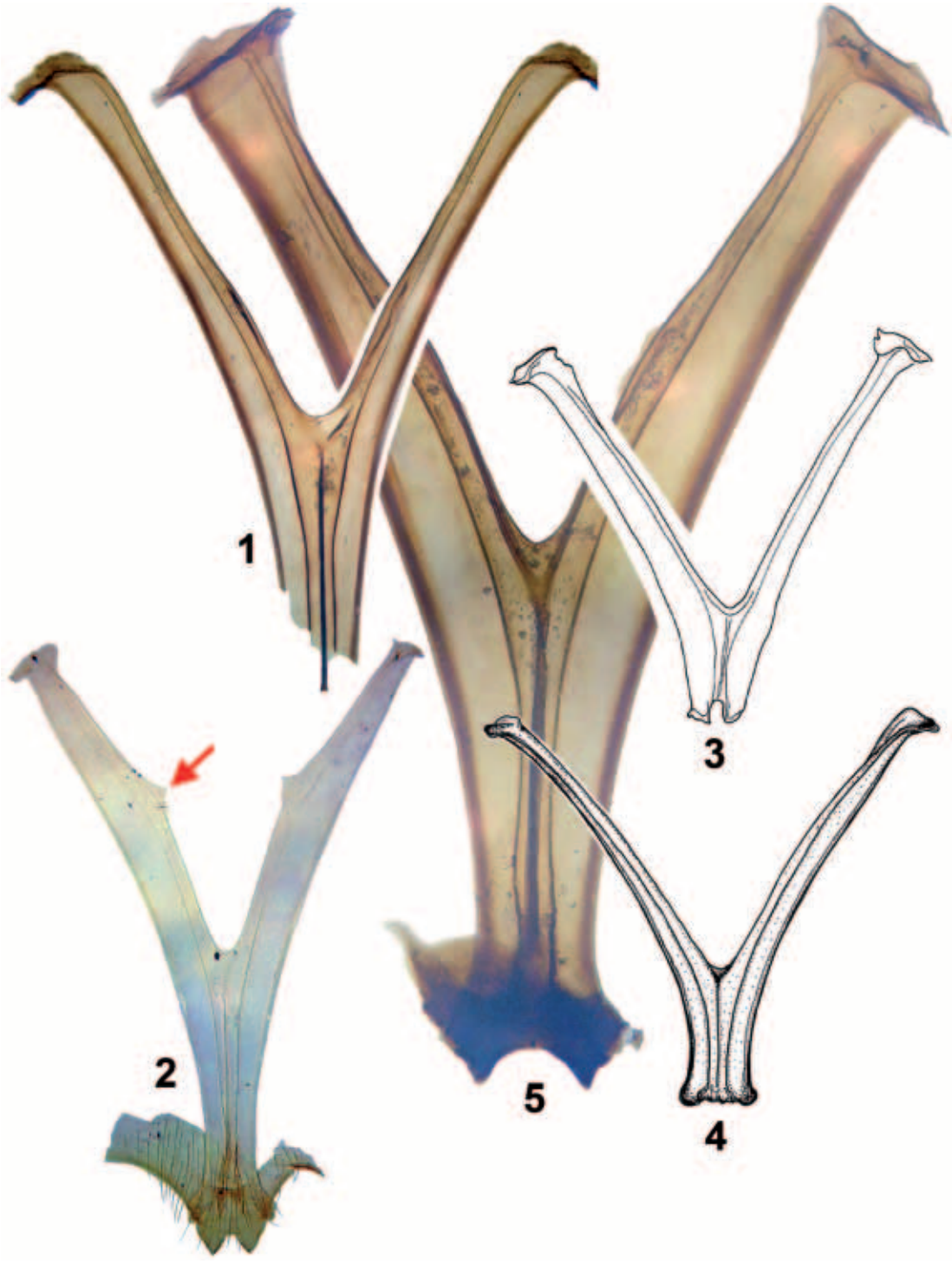
Metendosternite (Fig. 84.2): Furcal arms quite wide and clearly longer than the trunk, with apical process or apophysis poorly developed; with a prominent expansion towards the middle of the inner face of the arms, remains of the anterior plate. Posterior plate well visible along arms and trunk, narrowed toward the anterior and posterior parts and wider in the middle part. Trunk twice as long as width at the base and middle keel with short posterior divergence.

Median lobe of aedeagus: Long and robust, in almost regular arc in lateral view (Fig. 85.10), with apex short, sharp and bent towards the ventral face. In dorsal view (Fig. 88.3), with slightly sinuate sides along the basal and middle parts, broadly arcuated in apical part, then narrowed towards the apex, which is more or less rounded.

Endophallus (Fig. 88.3): Without «Y»-piece in basal region. Middle region with two dorsal bars



FIGURES 83.1–83.9: *Leptodirus* series, *Apholeuonus* group. Metatergal apparatus of: (**1**) *Antrosedes speluncarius*, (**2**) *Apholeuonus nudus nudus*, (**3**) *Charonites scheibeli (*modified from Polak & Mulaomerović 2021), (**4**) *Haplotropidius pubescens*, (**5**) *Parapropus sericeus sinuaticollis*, (**6**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**7**) *Rudogorites simonei (*modified from Polak & Mulaomerović 2021), (**8**) *Speoplanes giganteus* (modified from Mizerakis *et al*. 2022). Metendosternite of: (**9**) *Antrosedes speluncarius*, (**10**) *Apholeuonus n. nudus*. Figs **1**, **9** modified from Čeplík 2023. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.



FIGURES 84.1–84.4: *Leptodirus* series, *Apholeuonus* group. Metendosternite of: (**1**) *Haplotropidius pubescens*, (**2**) *Parapropus sericeus sinuaticollis* (red arrow pointing to a prominent expansion in the inner face of the arm), (**3**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**4**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**5**) *Speoplanes biokovensis*.

joined in a single laminar phanera with concave anterior edge and protruding and sharp lateral areas. Apical region with two reinforcement bands well differentiated.

Parameres (Fig. 90.10): Neither dilated nor bent. Although elongated, parameres do not reach the apex of median lobe. Three setae in apical area. Apex generally protruding and narrow in which a fairly robust seta is inserted, the other two below and with close insertion, with the external usually longer than the internal.

Spermathecal complex: Spermatheca (Fig. 91.8) small and curved, with apical and basal lobes very sclerotized; duct short and hyaline. Apical lobe very developed and spherical, slightly wider than the basal lobe, which is longer. Spermatic duct long, poorly sclerotized and quite thick; no spermathecal gland present.

Female uroventrite VIII (Fig. 94.2): Posterior edge in arc that narrows to form a fairly sharp apical middle area. Sides of the anterior edge straight with spiculum long, narrow; apex in a rounded arc.

Discussion. Phylogram in figure 1I, shows that genus *Parapropus* is the sister group of the clade *Apholeuon* + *Speoplanes* with a support of 56.2/98. This situation confirms the assumptions of Jeannel (1924a) that included *Parapropus* into the phyletic series of *Apholeuonus*.

Distribution. The nine species and fourteen subspecies colonize many caves of the Dinaric mountain range from Bosnia-Herzegovina (most of the species), Croatia and Slovenia.

Species

Parapropus brevicollis G. Müller, 1911
Parapropus brevicollis G. Müller, 1911b: 234.

Parapropus ganglbaueri Ganglbauer, 1899
Parapropus ganglbaueri ganglbaueri Ganglbauer, 1899
Parapropus ganglbaueri Ganglbauer, 1899: 85.
Parapropus Ganglbaueri Ganglbauer: Jeannel, 1910a: 43.
Parapropus Ganglbaueri Subsp. *Ganglbaueri* Ganglbauer, 1899: Jeannel, 1924a: 378.
Parapropus ganglbaueri ganglbaueri Ganglbauer: Perreau, 2000: 211.

Parapropus ganglbaueri humeralis Apfelbeck, 1907
Parapropus humeralis Apfelbeck, 1907: 318.
Parapropus Ganglbaueri subsp. *humeralis* Apfelbeck: Jeannel, 1910a: 43.
Parapropus ganglbaueri humeralis Apfelbeck: Perreau, 2000: 212.

Parapropus ganglbaueri obenbergeri Mařan, 1943
Parapropus Ganglbaueri Obenbergeri Mařan, 1943: 96.
Parapropus ganglbaueri obenbergeri Mařan: Perreau, 2000: 212.

Parapropus ganglbaueri weiratheri G. Müller, 1941
Parapropus Ganglbaueri Weiratheri G. Müller, 1941: 217.
Parapropus ganglbaueri weiratheri G. Müller: Pretner, 1974: 10.

Parapropus ganglbaueri zepcensis Mařan, 1943
Parapropus Ganglbaueri zepcensis Mařan, 1943: 96.
Parapropus ganglbaueri zepcensis Mařan: Perreau, 2000: 212.

Parapropus insignis G. Müller, 1937
Parapropus insignis G. Müller, 1937: 110.

Parapropus jasminkoi Polak, 2015
Parapropus jasminkoi Polak, 2015: 95.

Parapropus neumanni G. Müller, 1911
Parapropus sericeus Neumanni G. Müller, 1911a: 4.
Parapropus Neumanni J. Müller, 1911: Jeannel, 1924a: 378.
Parapropus neumanni Müller, 1911: Lakota, Hlaváč, Lohaj & Čeplík, 2014: 598.
Reinholdina deelemanorum Giachino & Moravec, 2009: 40.

Parapropus nonveilleri G. Müller, 1937
Parapropus Nonveilleri G. Müller, 1937: 110.
Parapropus nonveilleri Müller: Perreau, 2000: 212.

Parapropus pfeiferi Apfelbeck, 1908
Parapropus Pfeiferi Apfelbeck, 1908: 417.
Parapropus pfeiferi Apfelbeck: Perreau, 2000: 212.

Parapropus sericeus (F.J. Schmidt, 1852)
Parapropus sericeus augustae G. Müller, 1941
Parapropus sericeus Augustae G. Müller, 1941: 217.
Parapropus sericeus augustae G. Müller: Pretner, 1974: 11.

Parapropus sericeus intermedius (C. Hampe, 1870)
Leptoderus intermedius C. Hampe, 1870: 332.
Parapropus sericeus Subsp. *intermedius* Hampe, 1870: Jeannel, 1924a: 377.
Parapropus intermedius Hampe: G. Müller, 1907: 197.
Parapropus sericeus Schmidt: Jeannel, 1911a: 515.

Parapropus sericeus minutus Absolon & Mařan, 1943
Parapropus sericeus minutus Absolon & Mařan, 1943: 95.

Parapropus sericeus muelleri Jeannel, 1924
Parapropus sericeus Subsp. *Mülleri* Jeannel, 1924a: 377.
Parapropus sericeus mülleri Jeannel: Perreau, 2000: 213.

Parapropus sericeus sericeus (F. J. Schmidt, 1852)
Leptoderus sericeus F. J. Schmidt, 1852: 382.
Leptodirus (*Propus*) *sericeus* Schmidt: Abeille de Perrin, 1878: 150.
Parapropus sericeus Schmidt: Jeannel, 1910a: 43.
Propus sericeus Schmidt: Wichmann, 1926 [1924]: 123.
Parapropus sericeus sericeus (Schmidt): Perreau, 2000: 213.

Parapropus sericeus simplicipes G. Müller, 1911
Parapropus sericeus simplicipes G. Müller, 1911a: 3.

Parapropus sericeus sinuaticollis Absolon & Mařan, 1943
Parapropus sericeus sinuaticollis Absolon & Mařan, 1943: 94.

Parapropus sericeus stilleri Reitter, 1914
Parapropus Stilleri Reitter, 1914: 263.
Parapropus Neumanni J. Müller, 1911: Jeannel, 1924a: 378.
Parapropus sericeus stilleri Reitter: Perreau, 2000: 213.

Parapropus sericeus taxi G. Müller, 1911
Parapropus sericeus Taxi G. Müller, 1911a: 3.
Parapropus sericeus Absoloni Mařan, 1943, *in* Absolon & Mařan, 1943: 94.
Parapropus sericeus taxi Müller: Perreau, 2000: 213.

Parapropus vitorogensis S. Ćurčić, Pešić & B. Ćurčić, 2012
Parapropus vitorogensis S. Ćurčić, Pešić & B. Ćurčić, 2012: 1230 *in* S. Ćurčić *et al*. (2012).

Speoplanes subgroup

This subgroup belongs to the *Apholeuonus* group, *Leptodirus* series, as already assumed by V.B. Guéorguiev (1976) and recorded by Perreau (2000, 2004). It is characterised by the second antennomere not shortened and elongated and a mesoventral keel low or absent. Jeannel (1924a) established a separate phyletic lineage for the two genera *Speoplanes* and *Spelaedromus*, to which we now add, according to the hypotheses of Casale & Jalžić (1988), *Radziella*, allied to the group of *Leptodirus*. *Speoplanes* was recently revised by Mizerakis *et al*. (2022). This subgroup provisionally combines three genera, *Speoplanes*, *Spelaedromus* and *Radziella*, the last two of uncertain position and lacking, now, molecular data. This clade is sister to the *Apholeuonus* subgroup with support of 85.7/100 (Fig. 1I).

Key to genera

1. Small to medium-large body, 1.7–5.5 mm; legs with dilated claws; mouthparts specialized for filtering running water ..... *Radziella*
- Large to very large body, 6–8 mm; legs without dilated claws; mouthparts not modified..... 2

2. Large body, 6 mm; antennae shorter, just exceeding the elytral apex ..... *Spelaeodromus*
- Very large body, 8 mm; antennae very long, longer than the elytra ..... *Speoplanes*

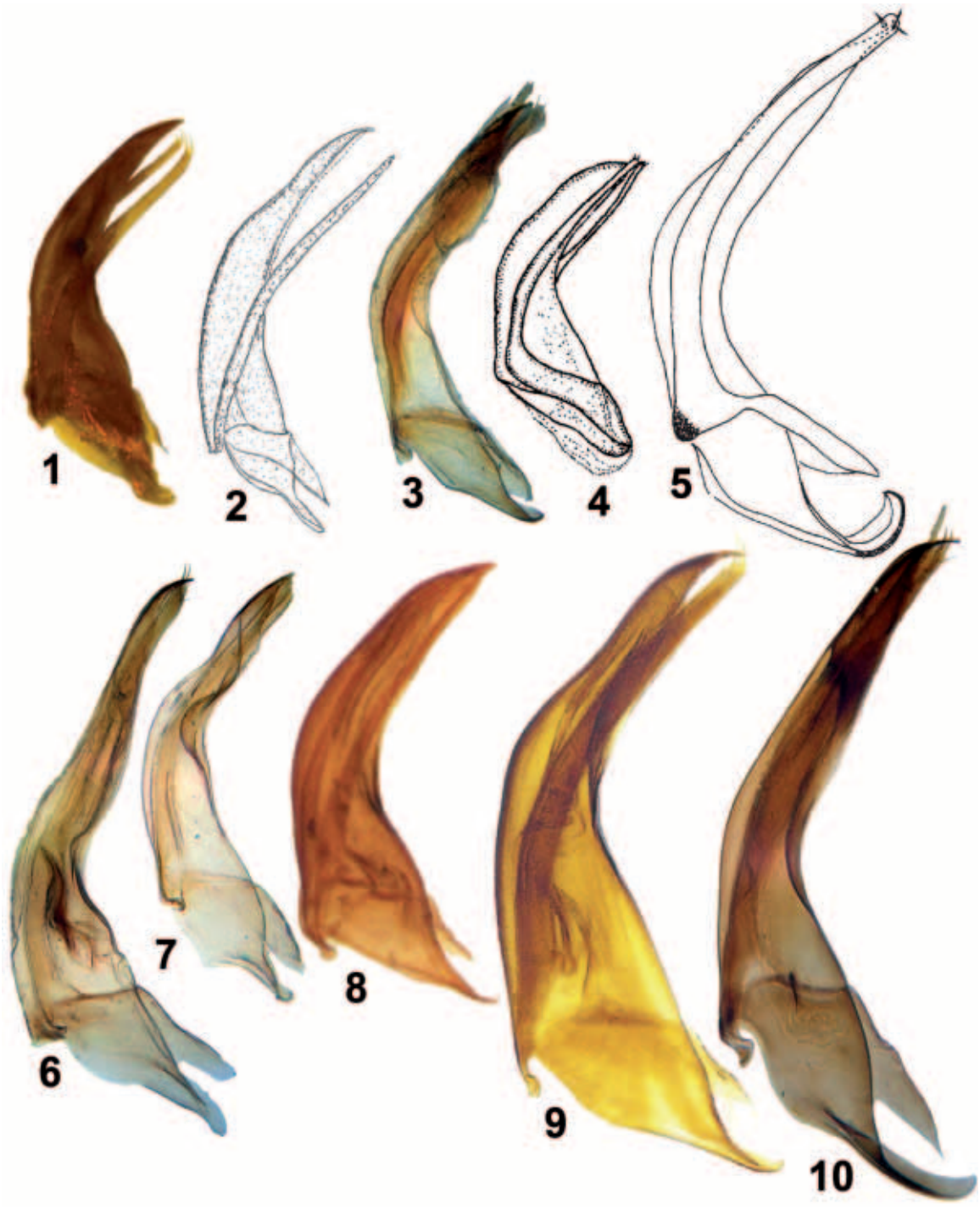
Genus ***Radziella*** Casale & Jalžic, 1988
Radziella Casale & Jalžic, 1988: 352.

Type species. *Radziella styx* Casale & Jalžic, 1988 by original designation (habitus in Fig. 79.4).

Diagnosis. Small sized species, 1.6–2.2 mm. Facies leptodiroid (Fig. 79.4), body shape elongated, narrowed forward and backward. Colour dark reddish. Integument glossy, dorsally smooth, microsculpture of irregular meshes. Pubescence absent on pronotum, short, fine, yellowish and scattered on elytra. Ventral surface largely covered with a dense pubescence of hydrophobic hairs.

Head: Elongated, somewhat longer than wide, non-retractable, without occipital carina; sides subparallel and narrower than pronotum; anophthalmous. Mouth appendages modified to collect food in a liquid environment.

Antennae: Very long and thin, longer than the length



FIGURES 85.1–85.10: *Leptodirus* series, *Apholeuonus* group. Aedeagus in lateral view of: (**1**) *Adelopidius ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**2**) *Antrosedes longicollis* (modified from Čeplík 2023), (**3**) *Apholeuonus nudus nudus,* (**4**) *Charonites orlovacensis* (modified from S. Ćurčić *et al*. 2002), (**5**) *Croatodirus bozicevici* (modified from Casale *et al*. 2000), (**6**) *Haplotropidius pubescens*, (**7**) *Icharonia leonhardiana*, (**8**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014), (**9**) *Leonhardia solaki* (modified from S. Ćurčić *et al.* 2021), (**10**) *Parapropus sericeus sinuaticollis.*

of the body in male, as long as the body in females; 2nd antennomere one and a half times longer than the 1st, the latter somewhat thicker. Non-dilated club, antennomeres slightly thickened at the top, with the 11th antennomere very small, ovoid, almost half-shorter than the 10th; the 5th being the longest antennomere.

Pronotum: Convex, large and robust, about 1.3 times longer than wide; anterior margin protruding forward in rounded arc covering the basal area of the neck. Basal margin slightly arcuated and narrower than the base of the elytra. Lateral margins rectilinear in the anterior part, in soft, regular arc, towards the anterior third that is the widest part (in females this part is more protruding) and very slightly sinuated in the posterior half (in females much more concave with the basal margin as wide as the base of the elytra). Posterior vertices rounded in males, sharp, and more protruding outward in females. Posterior angles sharper in females than in males.

Elytra: Convex, oval and little elongated (1.6 times longer than wide), covering the pygidium. Lateral margins widely arcuated, with the widest area in the middle, this area a little wider than the pronotum. Apices wide, subtruncated, in females in front of the apex the sides retracted and emarginate. Elytral suture with a slight keel protrusion along the midline. No parasutural stria.

Legs: Long and very robust; tibiae straight and femora widened in the middle part. Tarsi all pubescent both dorsally and ventrally. Protibiae with a robust, dentiform, internal spur, the apical comb reduced to a few small setae. Male protarsi pentameres with the first four tarsomeres dilated; the first being wider than the apical part of the protibia. Claws large, widened, arcuated and concave on the ventral side.

Mesoventral keel (Casale & Jalžic 1988): Low, in shape of a small triangle with the apex in tooth.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Very long, large and robust. Curved in «S» In lateral view (Fig. 86.2), with the basal curve much wider than the apical one; apex robust, sharp, slightly curved towards dorsally and behind a dorsal prominence in shape of a crest. In dorsal view (Fig. 88.5), base wide progressively narrowing on parallel sides in the basal third. In the apical two-third, sides are sinuous and widening progressively, ending in a rounded tip. Basal blade short and subsequently narrowed, as long as and somewhat narrower than the ventral blade of the tegmen.

Endophallus (Fig. 88.5): Without sclerifed pieces, only faint scales in the basal and apical part, none in the middle. Poorly defined apical reinforcement bands.

Parameres (Fig. 90.12): Very thin and long, somewhat shorter than, or as long as, the median lobe. In lateral view, in wide curve, and in dorsal view, with the apical area curved inwards. Apex without differentiated club and bearing three short and subequal setae with close insertion pores.

Spermathecal complex (Fig. 92.2): Spermatheca small and elongated with the three regions well defined. Apical lobe spherical, basal lobe elliptical, both well sclerotized and similar width. Junction duct very narrow, short and hyaline; spermatic duct thin, short, about twice as long as the spermatheca; no spermathecal gland.

Female uroventrite VIII: Unknown.

Discussion. This genus has been included in the subtribe Leptodirina (Newton 1998; Perreau 2000). Casale & Jalzić (1988) pointed out that byits leptodiroid facies, shape of pronotum, elytra, antennae and legs, the genus present a similar degree of evolution than the genera *Spelaites*, *Spelaeodromus* and *Protobracharthron*, among others. The peculiar morphology of the buccal appendages adapted to the unique way of feeding and the presence of robust claws adapted to its peculiar way of life is convergently found in the genera *Cansiliella* (*Oryotus* series), and *Hadesia* (*Anthroherpon* series). In spite of the fact that *Radziella* is a clearly isolated genus by its unique set of characters, it is probably closely related to the genera *Speoplanes* and *Spelaeodromus* with which it shares external morphological characteristics and various structures of the genitalia, We therefore include it tentatively in the same phyletic line, an hypothesis that will need to be confirmed by obtention of molecular data.

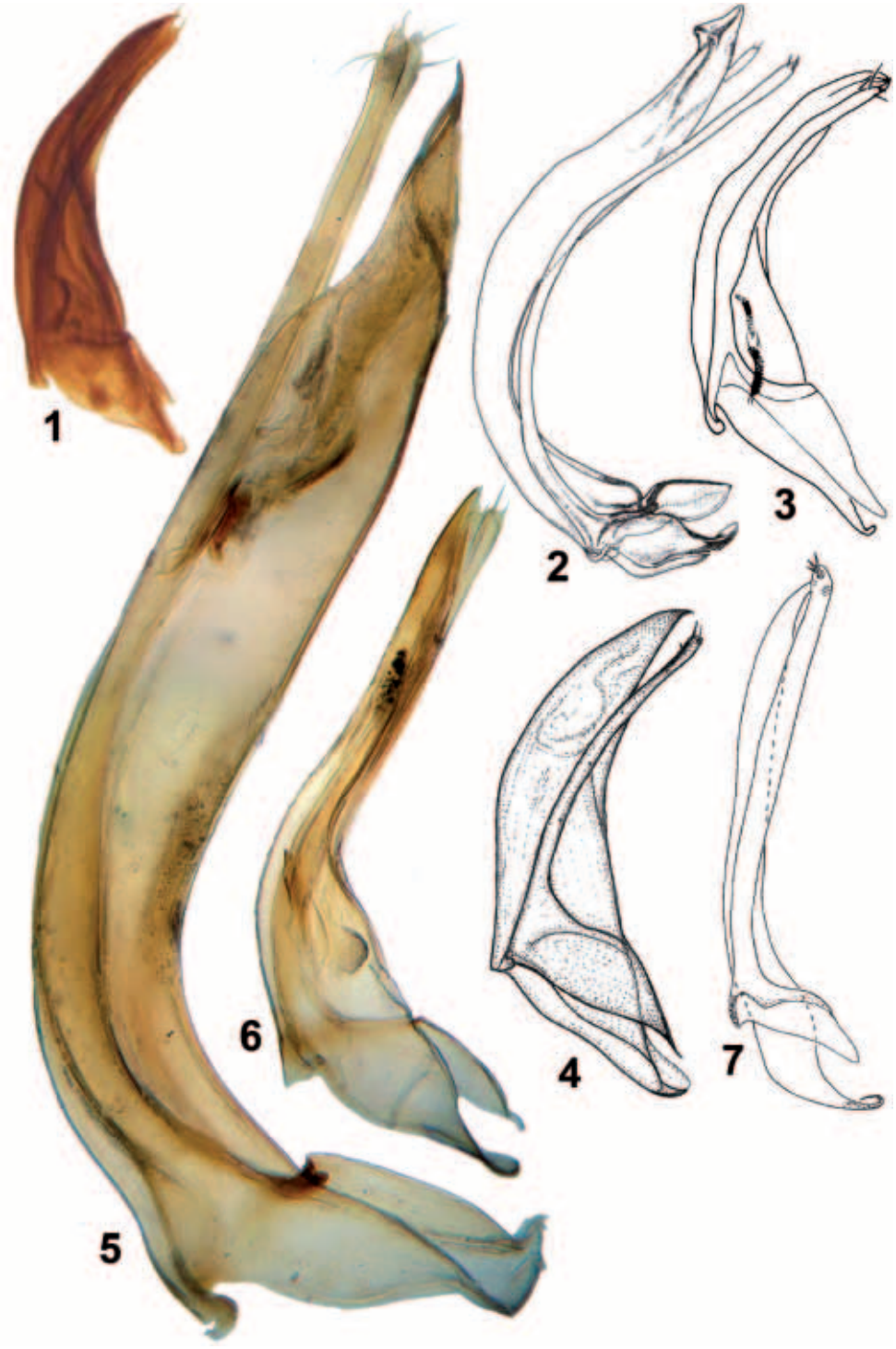
Distribution. Croatia. A cave dwelling genus known from two nearby pits, Pretnerova jama (-252 m) and Stara jama (-576 m), both on mount Biokovo in the broad central Dalmatian karst (Casale & Jalzić 1988).

Species

Radziella styx Casale & Jalžić, 1988
Radziella styx Casale & Jalžić, 1988: 352.

Genus ***Spelaeodromus*** Reitter, 1885
Spelaeodromus Reitter, 1885a [1884]: 13.

Type species. *Pholeuon pluto* Reitter, 1881 by monotypy (habitus in Fig. 80.2).



FIGURES 86.1–86.7: *Leptodirus* series, *Apholeuonus* group. Aedeagus in lateral view of: (**1**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al*. 2014), (**2**) *Radziella styx* (modified from Casale & Jalžić 1988), (**3**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**4**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**5**) *Spelaeodromus pluto*, (**6**) *Spelaites grabowskii*, (**7**) *Velebitodromus smidai* (modified from Casale *et al*. 2004).

DIAGNOSIS. Large size, 5.0–6.0 mm. Facies pholeuonoid (Fig. 80.2), with body shape very elongated, narrowed forward, wider backwards. Colour light brown. Integument covered with fine pubescence, very short and lying down, more abundant in elytra. Punctation dense and deep, with small dots on the head, somewhat larger and similar on the pronotum and elytra.

Head: Small, somewhat longer than wide, a little wider than the anterior edge of the pronotum and narrower than its widest part; without occipital carina; anophthalmous.

Antennae: Long and thin, as or almost as long as the length of the body. 2nd antennomere one and a half times longer than the 1st, the latter thicker; poorly dilated club and unthickened antennomeres at the top, with the 11th as long as the 10th and somewhat shorter than the 9th; 8th thin, almost three times longer than wide.

Pronotum: Convex, slightly wider than long, 1.0–1.1 times wider than long. Base straight, wider than the anterior edge and slightly narrower than the elytral base. Lateral margins arcuated in the anterior part, with arc a little more pronounced between the anterior third and the middle region, that is the widest part, and concave in the posterior third or half. Vertices sharp and slightly protruding outwards; posterior angles acute.

Elytra: Very convex, oval and very elongated (1.9–2.0 times longer than wide in males; 1.7–1.8 in females), far exceeding the pygidium. Lateral margins compressed and widely arcuated, with the widest area between the middle and the anterior third. Posterior third narrowing very strongly, apices sharp. Humeral rim angular at the beginning,wider in the anterior third. No parasutural stria.

Legs: Long and quite robust; males protarsi pentameres and very dilated, the first tarsomere being much wider than the apical part of the protibia, this without comb or very reduced. Protibiae slightly arcuated, meso- and metatibiae straight; femora dilated in the previous three quarters.

Mesoventral keel (Fig. 82.7): Almost null or very low, in this case it extends along the metaventrite. Anterior edge slightly concave, posterior convex and haired; vertex formed by a small thorn.

Suture of the metaventrite (Fig. 82.7): Arch-shaped, which is sinuous in the basal third and delimits a somewhat wider area in the apical third.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Very long, large and very robust. Curved in «S» in lateral view (Fig. 86.5), with the apex very sharp and slightly curved towards the dorsal face. In dorsal view (Fig. 89.1), sides subparallel and narrow basally, slightly widened towards the median part; apical part narrower, apex sharp or triangular with a slightly sharp tip. Basal blade short and narrowed posteriorly, as long and as wide as the ventral blade of the tegmen.

Endophallus (Fig. 89.1): presence of a long and slightly blurred stylet in the basal part. Median part with a pair of thorny pieces on disc, more or less oval. Apical region with two long reinforcement bands more or less marked that reach the middle part.

Parameres (Fig. 90.16): Elongated and thin, somewhat shorter than or as long as the median lobe, with the apical area slightly dilated or somewhat forked and widened. Apex with or without a small-elongated membranous lobe. Club armed with three almost equal setae, two apical with close insertion pores, and a subapical, latero-dorsal seta located below.

Spermathecal complex (Figs 92.5, 92.6): Spermatheca elongated and membranous; apical lobe spherical, basal lobe elliptical, somewhat narrower and undifferentiated junction duct. Spermatic duct thin and without spermathecal gland. According to Polak (2002) the spermatheca shows the three well-differentiated regions, a sclerotized apical and basal lobe and a hyaline junction part.

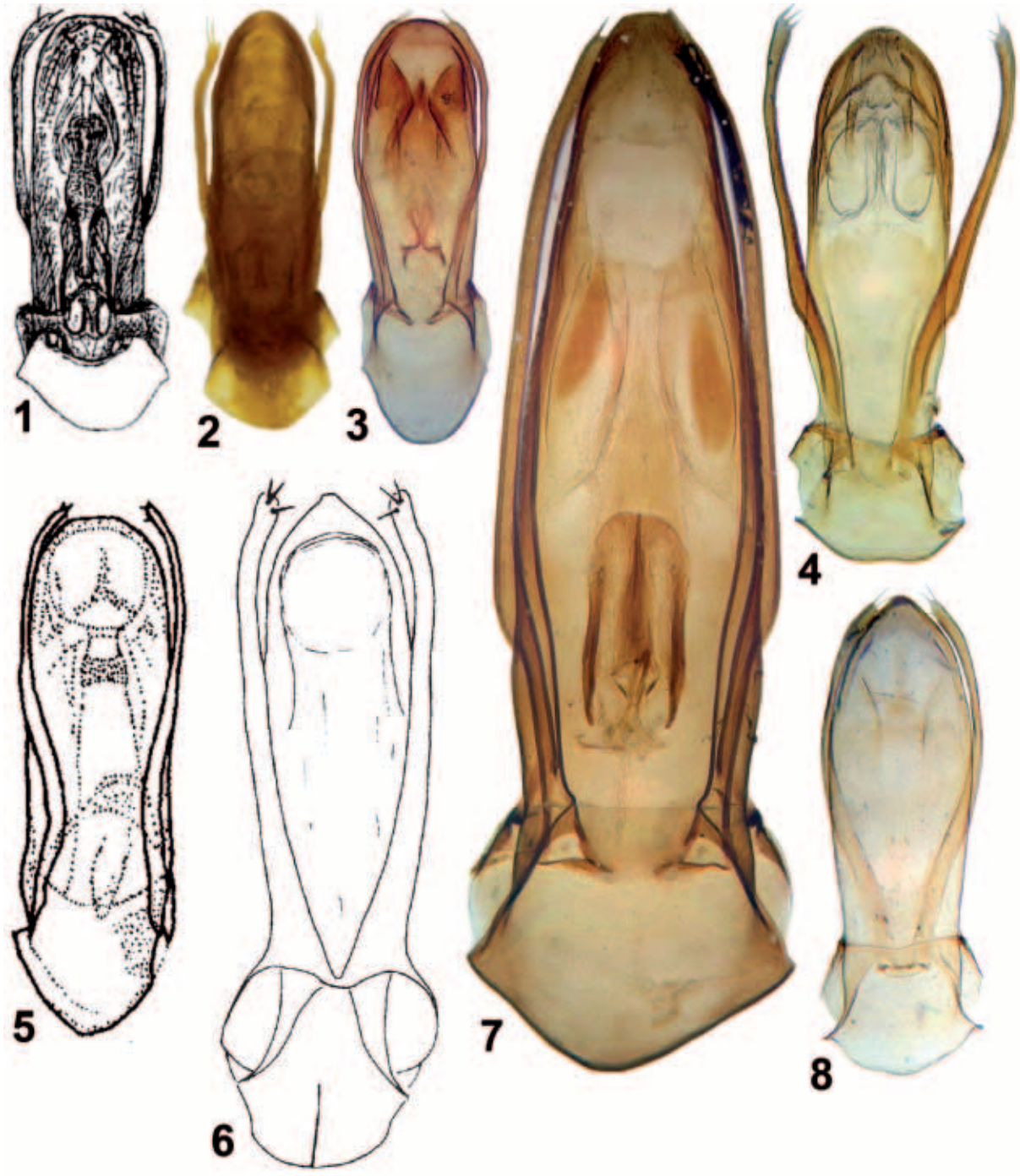
Female uroventrite VIII (Fig. 94.6): Apical edge broadly and regularly arched, somewhat less marked in the middle part; basal edge with straight, ascending sides converging at the spiculum, which is rather long and narrow with a bevelled apex.

DISCUSSION. This genus is included in the subtribe Leptodirina (V.B. Guéorguiev 1976; Newton 1998; Perreau 2000) and very similar to *Speoplanes* in its external morphological characters and in some structures of genitalia. It was therefore included in the *Speoplanes* series by Jeannel (1924a).

DISTRIBUTION. Two species found in karstic areas of the western part of the Dinaric Alps. *Spelaeodromus pluto* occurs in cold caves of the Velebit Mountains (NW Croatia); *Spelaeodromus sneznikensis* in Brezno-I cave, in the mountainous area of Snežnik (SW Slovenia).

Species

Spelaeodromus pluto (Reitter, 1881)
Pholeuon pluto Reitter, 1881a: 214.
Spelaeodromus Pluto Reitt.: Reitter, 1885a [1884]: 13.



FIGURES 87.1–87.8: *Leptodirus* series, *Apholeuonus* group. Aedeagus in dorsal view of: (**1**) *Adelopidius boksevicensis* (modified from Knirsch 1927), (**2**) *A. ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**3**) *Antrosedes speluncarius*, (**4**) *Apholeuonus nudus nudus,* (**5**) *Charonites orlovacensis* (modified from S. Ćurčić *et al*. 2002), (**6**) *Croatodirus bozicevici* (modified from Casale *et al*. 2000), (**7**) *Haplotropidius pubescens*, (**8**) *Icharonia leonhardiana*.

Spelaeodromus sneznikensis Polak, 2002
Spelaeodromus sneznikensis Polak, 2002: 6.

Genus ***Speoplanes*** G. Müller, 1911
Apholeuonus (*Speoplanes*) G. Müller, 1911a: 2.
Speoplanes G. Müller, 1911: Jeannel, 1924a: 381.

Type species. *Apholeuonus* (*Speoplanes*) *giganteus* G. Müller, 1911 by original designation (for the habitus see that of the similar species *Speoplanes biocovensis* in Fig. 80.4).

Diagnosis. Size very large, 8.0–8.2 mm. Body shape very elongated, narrowed forward and more marked backwards; facies scaphoid (Fig. 80.4). Colour dark brown. Tegument glabrous, with only a few short hairs; without defined punctation, but with a marked microsculpture which gives it a mat appearance.

Head: Short, somewhat wider than long, slightly wider than the anterior part of pronotum and narrower than the widest area of pronotum; without occipital carina; anophthalmous.

Antennae: Very long and thin, almost one and a half times longer than the length of the body. 2nd antennomere almost two and a half times longer than the 1st, the latter thicker; club poorly dilated and antennomeres very slightly thickened at top, with the 11th antennomere shorter than the 10th; the 8th very long and thin, almost six times longer than wide.

Pronotum: Robust, convex, slightly (1.1 times) longer than wide. Base straight, wider than the anterior margin and somewhat narrower than the elytral base. Lateral margins gently arcuated in the anterior two-thirds, with the widest area towards the middle and concave in the posterior third. Vertices sharp and very little protruding outwards; basal angles right.

Elytra: Scaphoid, very convex, oval and very elongated, 1.9–2.0 times longer than wide, extending well beyond the pygidium. Lateral margins mostly arcuated in the anterior two-thirds, narrow and slightly concave in the posterior third, with the widest area behind the mid-part; sharp apices. In dorsal view, shoulders blurred and without humeral ridge. Parasutural stria lacking.

Legs: Very long and thin; males protarsi pentameres and very dilated; the first tarsomere being wider than the apex of the protibia, which featuresa a very reduced comb. Protibiae slightly arcuated outwards, meso- and metatibiae straight; femora widened in the basal half.

Mesoventral keel (Fig. 82.9): Small and low, the anterior edge protruding and straight, sharp vertex, with setae and serrated ventral edge.

Suture of the metaventrite (Fig. 82.9): Without suture.

Metatergal apparatus (Fig. 83.8): With narrow and long metascutum wings; apophysis of the alacrista very long and tips not sharp.

Metendosternite (Fig. 84.5): Well developed, not «Y»-shape. Robust arms somewhat longer than the trunk, posterior plate of similar width along the arms and trunk, the apophysis poorly developed. Furcal trunk long, about twice as long as the widest area.

Median lobe of aedeagus: Very long, large and very sclerotized. Not recurved in lateral view, with the ventral face very arcuated towards the anterior two-thirds; the apical area sharp, narrow and not curved. Basal sides subparallel in the basal two-thirds in dorsal view (Fig. 89.3), then gradually narrow in the apical third; apex sharp. Basal blade of the median lobe quite long and arcuated posteriorly, longer than and as wide as the ventral blade of the tegmen.

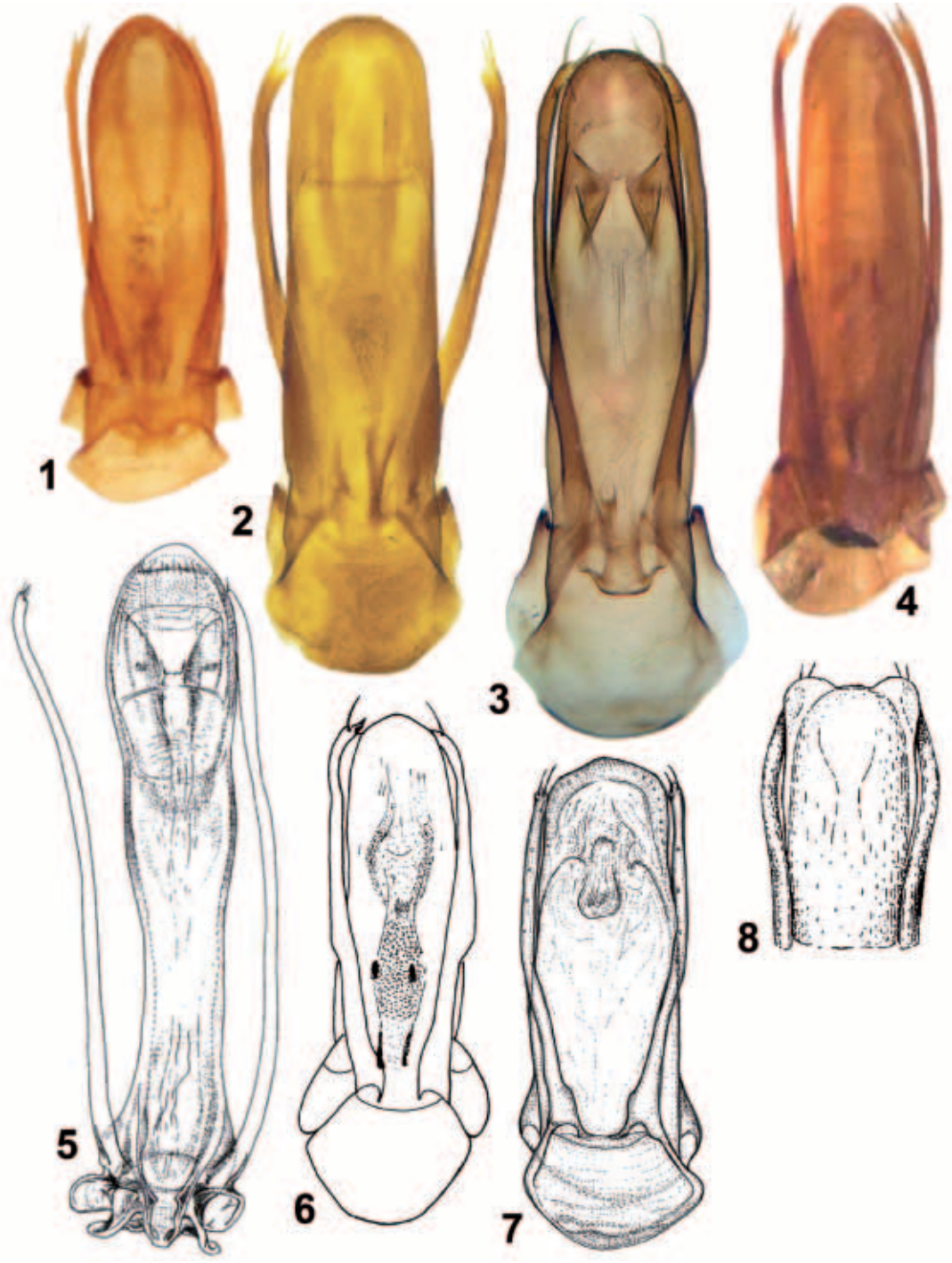
Endophallus (Fig. 89.3): Basal region with, at the base of the sac, a very small ventral «Y»-piece and above two robust and long dorsal bars with sharp apical areas that converge upwards. Apical region with two long reinforcement bands that run through the middle of the sac.

Parameres (Fig. 90.18): Elongated and thin, somewhat bent in the middle and somewhat shorter than or as long as the median lobe. Apical part not dilated and somewhat recurved inwards, with a small, elongated, membranous lobe. Apex armed with three subequal setae, two apical with the insertion pores nearby, and the third subapical, latero-dorsal with the pore shifted downward.

Spermathecal complex (Fig. 92.8): Spermatheca weakly sclerotized, with well defined regions, basal part oblong, junction duct narrower and hyaline, and apical part spherical and somewhat wider. Spermathecal duct relatively long with a small dilated area at the junction to the spermatheca.

Female uroventrite VIII (Fig. 95.2): With straight anterior edges and a well-developed spiculum.

Discussion. Sister of *Apholeuonus* from which it is separated by a significant genetic distance (Fig. 1I), support is 85.7/100. G. Müller (1911a) included *Speoplanes* as a subgenus of *Apholeuonus*. However, Jeannel (1924a) points out that it has no affinity with this genus, but is phylogenetically closer to *Spelaeodromus*, from which it differs in its external morphology by a much larger size, and the lack of pubescence and punctation. In addition, the armor of the endophallus is very different between both genera. The most re-



FIGURES 88.1–88.8: *Leptodirus* series, *Apholeuonus* group. Aedeagus in dorsal view of: (**1**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014), (**2**) *Leonhardia solaki* (modified from S. Ćurčić *et al.* 2021), (**3**) *Parapropus sericeus sinuaticollis*, (**4**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al*. 2014), (**5**) *Radziella styx* (modified from Casale & Jalžić 1988), (**6**) *Roubaliella biokovensis*, (modified from Casale *et al.* 1993), (**7**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**8**) *Setnikia leonhardi* (modified from Jeannel 1924a).

cent addition by Mizerakis *et al*. (2022) and Vrbica *et al*. (2024) has helped to clarify its systematic position and substantially align it with Jeannel (1924a) hypothesis.

Distribution. Croatia and Bosnia-Herzegovina. Colonize several cold caves on Biokovo and Mosor Mounts, near the Adriatic coast in southern Dalmatia.

Species

Speoplanes biocovensis G. Müller, 1934
Speoplanes biocovensis biocovensis G. Müller, 1934
Speoplanes giganteus biocovensis G. Müller, 1934: 180.
Speoplanes biocovensis Müller, 1934: Mizerakis *et al.* 2022: 590.

Speoplanes biocovensis bosnicus Vrbica, Vesović, Rađa & S. Ćurčić, 2024
Speoplanes biocovensis bosnicus Vrbica, Vesović, Rađa & S. Ćurčić, 2024: 425.

Speoplanes giganteus (G. Müller, 1911)
Apholeuonus (Speoplanes) giganteus G. Müller, 1911a: 2.
Speoplanes giganteus J. Müller: Jeannel, 1914b: 50.

Apholeuonus subgroup

Generic subgroup established in part on a molecular basis and as well as other other genera which were characterised by synapomorphies as belonging to the subgroup if no molecular data were available. Synapomorphies considered are:

– Relative length of first and second antennomere, with the first shorter than the second.

– Pronotum as wide as long or wider than long.

– Presence of a membranous lobe at apex of parameres.

The large *Apholeuonus* subgroup is sister to *Speoplanes* subgroup with support, 85.7/100 (Fig. 1I).

Key to genera

1. Bathyscioid facies and body shape spherical (Fig. 79.5) with pronotum only little narrower than elytra . .....*Roubaliella*
- Body shape sub-pholeuonoid (Fig. 79.6), pholeuonoid (Fig. 79.3) sub-scaphoid (Fig. 78.1) or scaphoid (Fig. 77.3) with pronotum shorter or longer than wide; bigger species with elongated legs 2

2. Pronotum distinctly narrower than elytra width; body shape pholeuonoid (Fig. 79.3), sub-scaphoid (Fig. 78.1) or scaphoid (Fig. 77.3), pronotum distinctly longer than wide, widest at the middle length, lateral sides strongly, slightly or not sinuate 3
- Pronotum slightly narrower than elytra width; body shape sub-pholeuonoid (Figs 77.1, 78.2, 79.6), pronotum wider than long, widest at the posterior edge, lateral sides concave, straight or slightly sinuate 10

3. Robust species, body length more than 4.5 mm; second antennomere length sub-equal to third antennomere..... 4
- Slender species, body length less than 4.5 mm; second antennomere distinctly longer than third antennomere..... 7

4. Pronotum distinctly wider as head width 5
- Pronotum approximately wide as head width..... 6

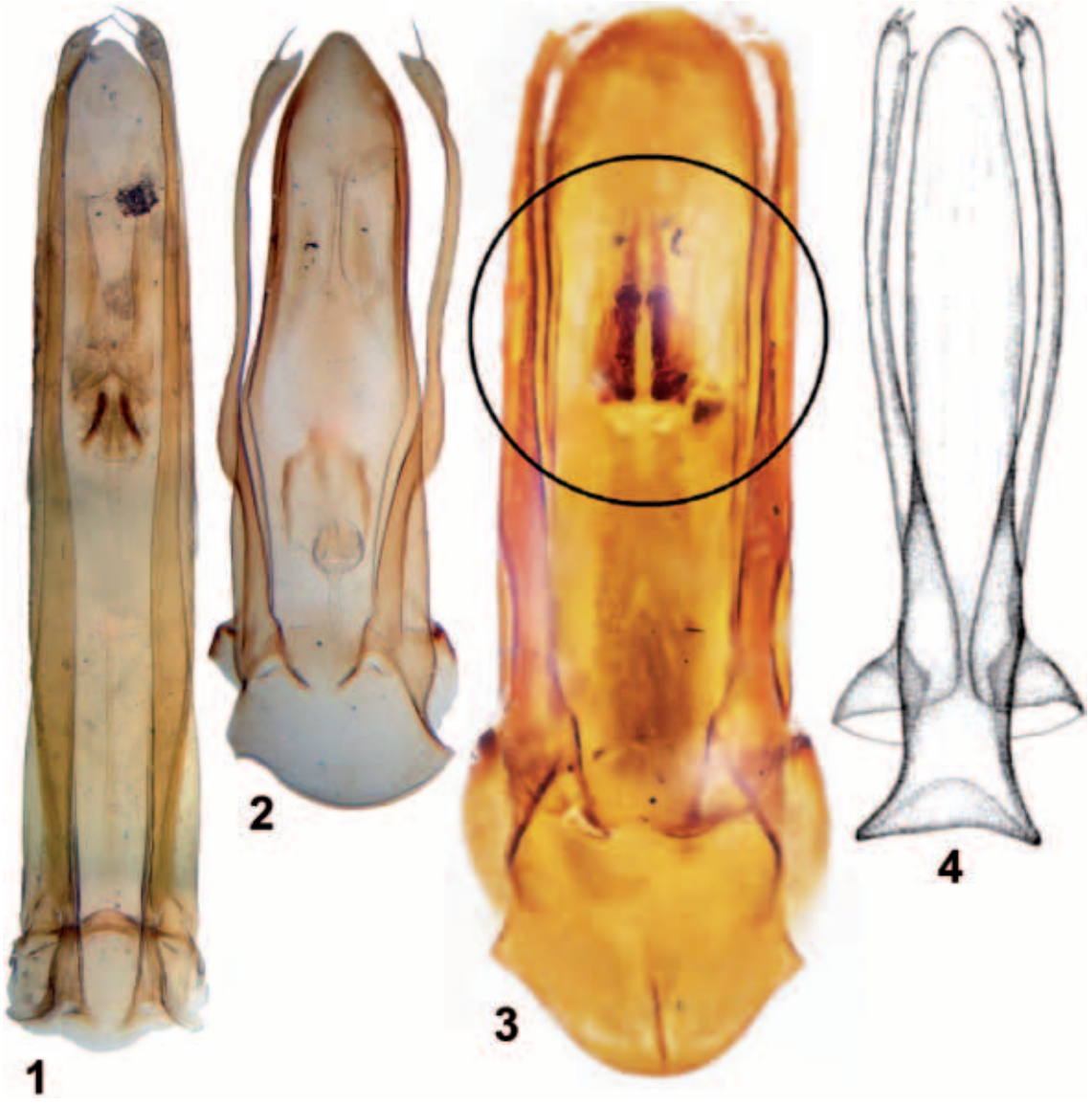
5. Elytra strongly inflated with surface almost glabrous and shiny effect; mesoventral keel reduced to strong dent (Fig. 81.3) .....*Apholeuonus*
- Elytra inflated with short and sparse pubescence; mesoventral keel high, not reduced (Fig. 81.5)..... .....*Haplotropidius*

6. First antennomere distinctly shorter, but less than two times shorter than the second; mesoventral keel (Fig. 82.8); sides of the apical half of the median lobe straight and the apex sharper.....*Spelaites*
- First antennomere two times shorter than the second; mesoventral keel reduced to strong wide dent (Fig. 82.4); apical half of the median lobe sides more arched and the apex less tapering ....*Protobracharthron*

7. Pronotum approximately wide as head width; mesoventral cavities separated with an extension of mesoventrite without a keel (Fig. 81.2) .*Antrosedes*
- Pronotum distinctly wider as head width; mesoventral cavities separated with an extension of mesoventrite with well-developed keel (Fig. 82.1, 82.2,) 8

8. Elytra surface shiny, with sparse long and erected setae; sides of pronotum slightly sinuate; pronotum slightly longer or as long as wide.....*Setnikia*
- Elytra surface covered with short setae; lateral edges of the pronotum strongly sinuate; pronotum slightly wider than long.....9

9. Apical area of median lobe wider and tip subtruncate (Fig. 88.2); parameres without club (Fig. 90.9);



FIGURES 89.1–89.4: *Leptodirus* series, *Apholeuonus* group. Aedeagus in dorsal view of: (**1**) *Spelaeodromus pluto*, (2) *Spelaites grabowskii*, (**3**) *Speoplanes giganteus* (modified from Mizerakis *et al*. 2022), (**4**) *Velebitodromus ozrenlukici* (modified from Casale *et al.* 2012).

spermatheca with longer and narrower union duct (Fig. 91.7) ..... *Leonhardia*
- Apical area of the median lobe narrower and sharper (Fig. 88.1); club of the parameres somewhat differentiated (Fig. 90.8); spermatheca with shorter and wider union duct (Fig. 91.6) .....*Katobatizon*

10. Elytra surface densely and fine punctate cowered with short, dense and recumbent setae; femora straight, not widened at apex; male protarsomeres distinctly dilated .....*Adelopidius*
- Elytra strongly, sparsely and deeply foveolated punctate, almost glabrous or cowered with short sparse and erected setae; each seta growing from the bottom of a small depressed point; femora distinctly widened at apex; male protarsomeres not dilated.....11

11. Elytra almost glabrous with shiny effect; globular body shape with pronotum distinctly wider than its length .....*Icharonia*
- Elytra covered with short and sparse erected setae; slightly prolonged body shape with pronotum slightly wider than its length, bell-like form .....
.....*Rudogorites*

Genus ***Adelopidius*** Apfelbeck, 1907
Adelopidius Apfelbeck, 1907a: 305.

Type species. *Pholeuonopsis sequensi* Reitter, 1902 by monotypy (for the habitus see that of the similar species *Adelopidius neumanni* in Fig. 77.1).

Diagnosis. Length 2.7–3.8 mm. Body shape with pholeuonoid facies (Fig. 77.1). Elliptical and elongated or oval and shorter body, thicker and quite convex. Body colour brown. Microsculpture with weak, fine, numerous and dense dotting. Pubescence short, dense and lying down, usually raised on head.

Head: Retractable, between something wider than long and as long as wide, with occipital carina more or less marked; anophthalmous.

Antennae: Thin, long, can reach the apex of the elytra, always somewhat shorter in females. Antennomeres of club apically thicker; first antennomere almost three times shorter than the second, and 8th short, width and elongated.

Pronotum: Bell shape, transverse, 1.7–1.8 times wider than long; base clearly wider than the anterior border and slightly narrower than the elytral base; maximum width usually at the base. Lateral margins sigmoid, arcuated in anterior half and more or less concave or sinuous in posterior half, with sharp posterior vertices, somewhat outward-oriented and acute angles. Disc little convex, sometimes with two lateral, longitudinal impressions near the base.

Elytra: Between elliptical and ovoid (1.2–1.4 longer than wide together), wider than pronotum; maximum width about at one-fifth basal of elytra length; gradually narrow backwards, with rounded apexes; obtuse and rounded shoulders. Parasutural stria lacking.

Legs: Long and slender; anterior tibiae slightly curved, with a comb and without external spurs. Males protarsi pentameres, the first four protarsomeres somewhat widened.

Mesoventral keel (Fig. 81.1): Well developed, high, triangular, with vertex little angular and angle obtuse. Anterior edge more or less convex and posterior one concave or almost straight in its anterior half, with some teeth and setae along the edge. Posterior prolongation does not reach the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Arcuated, robust and not very long. In lateral view (Fig. 85.1), dorsal face in regular arc, with sharp apex curved towards ventral face. In dorsal view (Figs 87.1, 87.2), with sides subparallel and slightly sinuous; apical area very little narrows and describes a non-sharp arc.

Endophallus (Fig. 87.1): Basal «Y»-piece well-developed, middle area with a strong dorsal tooth flanked by two small and elongated lateral pieces. Apical part with two reinforcement bands that reach the middle part.

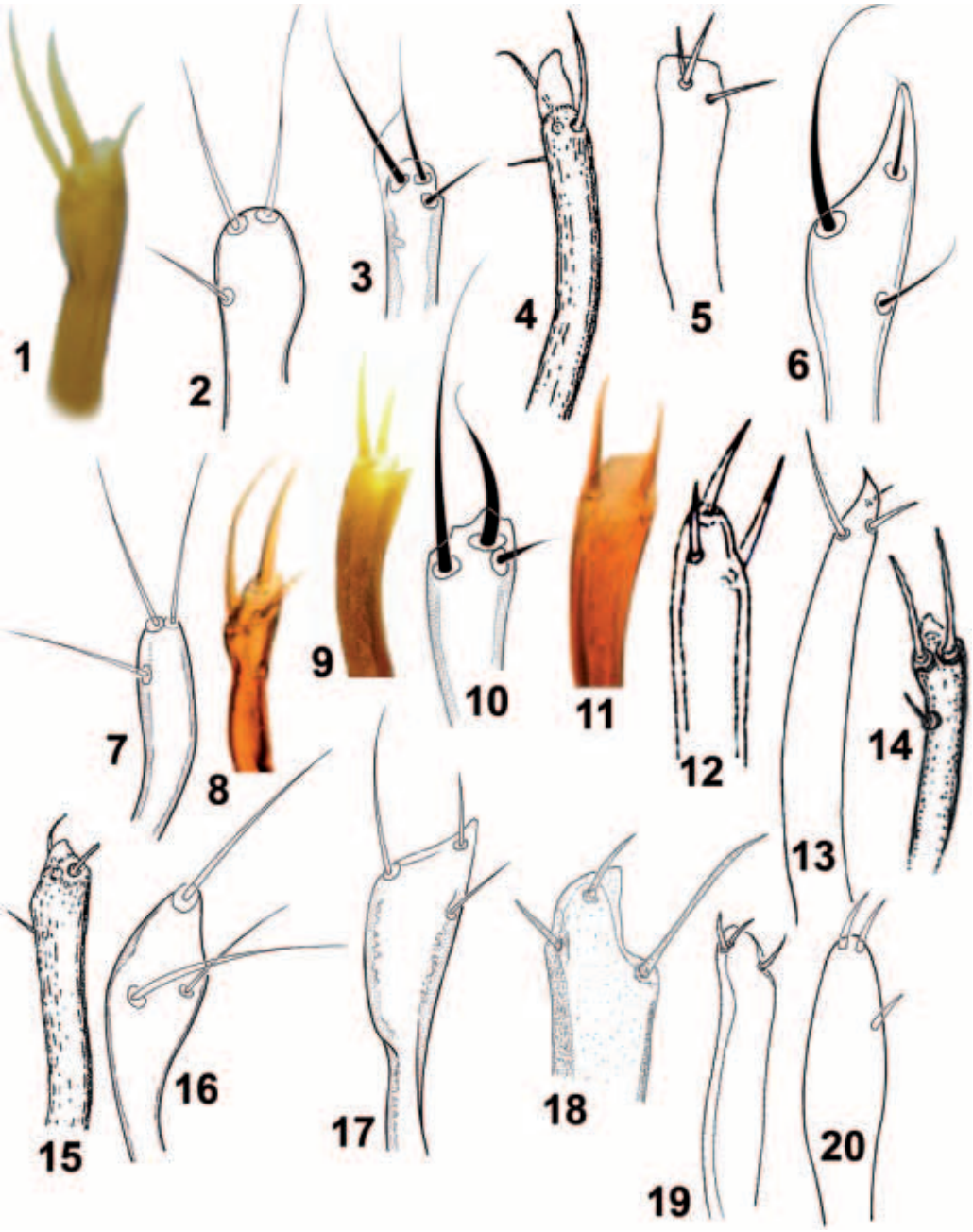
Parameres (Fig. 90.1): Quite long and not very robust, curved inwards in apical area, shorter than the middle lobe. Apical club little or not differentiated, sharp or rounded, in some species with a small membranous lobe. Armed with three setae, two apical somewhat longer and more robust than preapical one, that is directed inward.

Spermathecal complex: Spermatheca (Fig. 91.1) small and curved, with three well differentiated areas; apical lobe spherical and as wide as, but shorter than the basal one. Between them, they are an area of hyaline and narrower union.

Female uroventrite VIII (Fig. 93.1): Apical margin broadly arcuated; spiculum short and wide, with truncated apex.

Discussion. Jeannel (1924a) includes this genus in «Brachyscapes», Division IV, phyletic series *Apholeuonus* in which he points out variety of forms, but no bathyscioid. This was also pointed out by V.B. Guéorguiev (1976) and included it in the subtribe Leptodirina. In addition, Perreau (2000), following the criteria of the two previous authors, included *Adelopidius* in the subtribe Leptodirina and phyletic series of *Apholeuonus*. Unfortunately, there are no molecular data to confirm this classification, although the morphology of aedeagus of *Adelopidius*, that is very similar to that of *Apholeuonus*, compels us to adopt this assumption.

Distribution. The ten cave-dwelling species of this genus colonise caves in karst mountainous areas of Central and Northwestern Bosnia-Herzegovina (S. Ćurčić *et al.* 2018).



FIGURES 90.1–90.20: *Leptodirus* series, *Apholeuonus* group. Apex of the paramere of: (**1**) *Adelopidius ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**2**) *Antrosedes speluncarius*, (**3**) *Apholeuonus nudus nudus,* (**4**) *Charonites matzenaueri matzenaueri* (modified from Jeannel 1924a), (**5**) *Croatodirus bozicevici* (modified from Casale *et al*. 2000), (**6**) *Haplotropidius pubescens*, (**7**) *Icharonia leonhardiana*, (**8**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014), (**9**) *Leonhardia solaki* (modified from S. Ćurčić *et al*. 2021), (**10**) *Parapropus sericeus sinuaticollis*, (**11**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al*. 2014), (**12**) *Radziella styx* (modified from Casale & Jalžić 1988), (**13**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**14**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**15**) *Setnikia leonhardi* (modified from Jeannel 1924a), (**16**) *Spelaeodromus pluto*, (**17**) *Spelaites grabowskii*, (**18**) *Speoplanes giganteus* (modified from Mizerakis *et al*. 2022), (**19**) *Velebitodromus smidai* (modified from Casale et al. 2004), (**20**) *V. ozrenlukici* (redrawn from Casale *et al*. 2012).

Species

Adelopidius boksevicensis Knirsch, 1928
Adelopidius boksevicensis Knirsch, 1928 [1927]: 107.

Adelopidius bufonis Knirsch, 1928
Adelopidius bufonis Knirsch, 1928 [1927]: 106.
Adelopidius Arndti Weirather: Knirsch, 1928: 107 (*Nomen nudum*).

Adelopidius hrustovacensis S. Ćurčić, Pavićević & Mulaomerović, 2018
Adelopidius hrustovacensis S. Ćurčić, Pavićević & Mulaomerović: 526 *in* S. Ćurčić *et al*. (2018).

Adelopidius kuchtae Breit, 1911
Adelopidius kuchtae Breit, 1911a: 113.
Adelopidius Kuchtai Breit: Jeannel, 1914b: 48.

Adelopidius ljubacevoensis S. Ćurčić, Pavićević & Mulaomerović, 2018
Adelopidius ljubacevoensis S. Ćurčić, Pavićević & Mulaomerović: 529 *in* S. Ćurčić *et al*. (2018).

Adelopidius neumanni G. Müller, 1911
Adelopidius neumanni G. Müller, 1911a: 2.
Adelopidius Neumanni J. Müller: Jeannel, 1911a: 498.

Adelopidius ovatus Jeannel, 1934
Adelopidius ovatus Jeannel, 1934d: 158.

Adelopidius pougarjensis S. Ćurčić, Pavićević & Rađa, 2018
Adelopidius pougarjensis S. Ćurčić, Pavićević & Rađa: 533 *in* S. Ćurčić *et al*. (2018).

Adelopidius sequensi (Reitter, 1902)
Pholeuonopsis sequensi Reitter, 1902b: 223.
Adelopidius Sequensi Reitt.: Apfelbeck, 1907a: 305.
Adelopidius sequensi (Reitter): Perreau, 2000: 204.

Adelopidius weiratherianus Reitter, 1913
Adelopidius weiratherianus Reitter, 1913b: 173.
Adelopidius Weiratherianus Reitt.: Jeannel, 1914b: 48.

Genus ***Antrosedes*** Reitter, 1912
Antrosedes Reitter, 1912a: 326.

Type species. *Antrosedes speluncarius* Reitter, 1912 by monotypy (habitus in Fig. 77.2).

Diagnosis. Medium size, 4.0 mm, with pholeuonoid facies (Fig. 77.2). Body shape elongated, forward narrowed. Colour yellowish-reddish. Pubescence short and scattered, somewhat raised. Punctation dense and deep, with small dots on head, larger and similar on pronotum and elytra.

Head: Large, somewhat wider than long, slightly wider than the anterior area of pronotum and as wide, or almost as wide as, the widest area of pronotum. Occipital carina lacking.

Antennae: Long and thin, as long as, or somewhat longer than, the length of body. Second antennomere twice as long as the first; club little dilated, with 11th antennomere as long as the 10th; 8th thin, about twice as long as it is wide.

Pronotum: Subsquared, very convex and little transverse, up to 1.2 times wider than long. Base straight, as wide as the anterior area and narrower than the elytral base. Lateral margins slightly arcuated in the anterior area, with arc a little more pronounced in middle part, which is the widest area; somewhat concave in the posterior third. Basal angles right.

Elytra: Ovoid, elongated (1.5 times longer than wide as a whole), convex, narrowed backwards with rounded apexes and apical part of pygidium visible from above; maximum width towards the apical third; marginal ridge visible; parasutural stria lacking.

Legs: Long and thin; males protarsi pentameres and undilated; protibiae with a visible comb, but little developed in apical area, somewhat arcuated, meso- and metatibiae straight; femora dilated in basal area.

Mesoventral keel (Fig. 81.2): Very low, with only a slight prominence and serrated along the middle anterior part; vertex blunt.

Suture of the metaventrite (Fig. 81.2): Lacking.

Metatergal apparatus (Fig. 83.1): Small, with metascutum wings long and very narrow; apophysis of alacrista of medium length with sharp tips.

Metendosternite (Fig. 83.9): «V»-shaped; furcal arms long, about three times the length of the trunk, with arched apical area and reduced apophysis; posterior lamina progressively narrowing from trunk to apex of arm. Furcal trunk broad and short, wider than long, «V»-shaped base with tapering tips.

Median lobe of aedeagus: Elongated and quite robust. In lateral view (Fig. 85.2), clearly arcuated, with a gentle depression in apical third followed by an arcuated area towards the apex that is sharp and slightly curved towards the ventral face. In dorsal view (Fig. 87.3), with sides subparallel that gradually narrow to the rounded apex.

Endophallus (Fig. 87.3): With a well-developed

«Y»-piece at the bottom of sac and, above, two fairly wide sigmoid lateral pieces. In addition, they are two long reinforcement bands in apical region that reach the middle part.

Parameres (Fig. 90.2): Elongated and thin somewhat shorter than the middle lobe, with apical area little dilated and slightly sinuated; rounded apex with an elongated membranous lobe. Club armed with three unequal setae, two apical rather long and robust with the insertion pores nearby, and one subapical, inferior and internal with pore further away, thinner and smaller.

Spermathecal complex: Spermatheca (Fig. 91.2) in the form of an elongated sac, with poorly differentiated regions, the apical lobe in the form of a bonnet, a short and less sclerotized junction part and the basal lobe more elongated and wide; a very short spermatic duct joins the basal lobe, that ends in the spermathecal gland.

Female uroventrite VIII (Fig. 93.2): Basal margins straight, with long and narrow gastral spiculum, and rounded tip.

Discussion. *Antrosedes* presents great similarities in many external morphological characters and male genitalia with genera *Adelopidius, Apholeuonus* and *Leonhardia* (Jeannel, 1924a), but without a molecular analysis its phylogenetic relationships with respect to these genera are particularly doubtful due to the absence of phanerae in endophallus.

Distribution. Genus with two cave-dweling species that are located in karst areas near central Bosnia-Herzegovina: *Antrosedes longicollis* in Kruščica cave, near Vitez, and *A. speluncarius* in several caves of Visočica mountain, near Konjic; in these caves coexisting with *Icharonia leonhardiana leonhardiana*.

Species

Antrosedes longicollis Pretner, 1970
Antrosedes longicollis Pretner, 1970c: 155.

Antrosedes speluncarius Reitter, 1912
Antrosedes speluncarius Reitter, 1912a: 326.

Genus ***Apholeuonus*** Reitter, 1889
Apholeuonus Reitter, 1889a: 297.

Type species. *Hexaurus nudus* Apfelbeck, 1889 by monotypy (habitus in Fig. 77.3).

Diagnosis. Length 5.5–7.5 mm. Pholeuonoid body facies (Fig. 77.3), narrow pronotum and a very marked false physogastria. Integument alutaceous and glabrous or almost glabrous, with fine and superficial punctation on head and pronotum, being larger, deeper and more spaced on elytra.

Head: Not retractable, without occipital carina; anophthalmous.

Antennae: Thin, long but do not reach the apex of elytra. First antennomere much shorter than the second, all much longer than wide, except the first and, in some species, the second one.

Pronotum: Small and somewhat convex, subsquared, always somewhat wider than long with maximum width at the base, that is as wide as the elytral base. Lateral sides arcuated in middle part, with weakly curvature pointing forward and not, or only slightly, sinuated in basal part before posterior angles.

Elytra: Very large and very convex, with maximum width towards the middle, with apical areas narrowed, more or less sharp or protruding. Both sutural stria and transverse striolae lacking.

Legs: Long, slender, with males protarsi pentameres and generally weakly dilated. Anterior tibiae with a comb and without external spur. Femora widen in apical area.

Mesoventral keel (Fig. 81.3): It is divided into two parts, the anterior part in the shape of a small triangle with the anterior edge slightly arched, the ventral edge slightly serrated and the sharp apex in-between; the posterior part continues in a very low apophysis that surrounds the coxal cavity and reaches the anterior edge of the metaventrite.

Suture of the metaventrite (Fig. 81.3): Slightly sinuous arch in the basal third and close to the coxal cavity, the area it delimits being very narrow.

Metatergal apparatus (Fig. 83.2): Wings of metascutum long and wide; apophysis of alacrista very long with sharp apexes.

Metendosternite (Fig. 83.10): Furcal arms longer like the furcal trunk; furcal plate retains same width of posterior edge in a smooth continuous arc; terminal process thick. Furcal trunk twice as long as wide; median furcal keel wide and in the posterior area very divergent.

Median lobe of aedeagus: In lateral view (Fig. 85.3), at an obtuse angle with distal end short and little sharp. Dorsal face gently arcuated, in some cases apical third somewhat convex. In dorsal view (Fig. 87.4), apical part with shapes widely arched and sharp.

Endophallus (Fig. 87.4): Characterised by basal region with a small dorsal tooth and two lateral pieces in form of wide triangular spiny plates.

Parameres (Fig. 90.3): Thin, as long, or somewhat

longer, than the apex of median lobe, they end in a poorly developed and more or less sharp membranous lobe. Apical part without a defined club, where three setae are inserted, two apical, long and robust with insertion pores nearby, and an internal lower one, generally further away, more thin and small.

Spermathecal complex (Fig. 91.3): Spermatheca in tubular shape, wide and short. Small apical lobe located on same plane of middle region, which is hyaline and similar section to that of lobes; basal lobe somewhat more developed than apical one. Spermatic duct long, about four times the length of spermatheca and uniform width. Spermathecal gland well-developed and deformed.

Female uroventrite VIII (Fig. 93.3): Spiculum long and wide, with a rounded apex; very slightly sinuous arched posterior edge.

Discussion. Phylogenetic tree (Fig. 1I) shows a clade including the genera *Apholeuonus* and *Speoplanes* has a support of 85.7/100, and thas as sister genus *Parapropus* with a joint support of 56.2/98. This preliminary result seems to support Jeannel´s (1924a) hypothesis about a phyletic series of *Apholeuonus* (a subgroup in our case) well separated from other groups of which will be focused on later in detail. For this reason, on a purely morphological basis, we insert provisionally in this point of tree the genera *Rudogorites, Adelopidius*, *Icharonia*, *Setnikia*, *Katobatizon*, *Leonhardia*, *Antrosedes*, *Haplotropidius*, *Spelaites*, *Protobracharthron* and *Roubaliella*; for each genus, the morphological characteristics suggesting its inclusion in this group shall be indicated.

Distribution. Distribution area disjointed, colonising limestone massifs of Central and Southeastern of Bosnia-Herzegovina.

Species

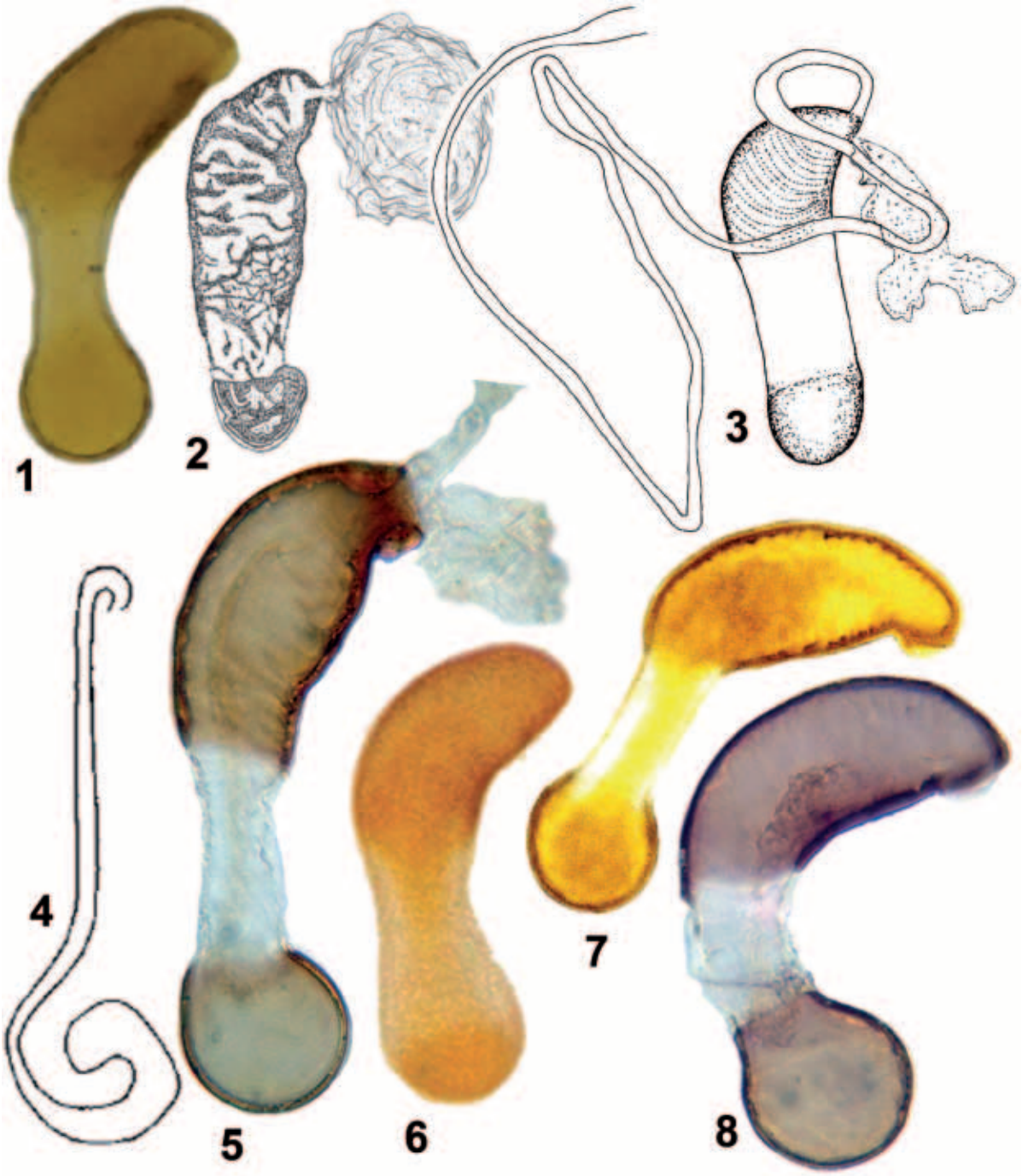
Apholeuonus absoloni Giachino & V.B. Guéorguiev, 1995
Apholeuonus absoloni Giachino & V.B. Guéorguiev, 1995: 208.

Apholeuonus insignis Giachino & V.B. Guéorguiev, 1995
Apholeuonus insignis Giachino & V.B. Guéorguiev, 1995: 210.

Apholeuonus leonhardi Giachino & V.B. Guéorguiev, 1995
Apholeuonus leonhardi Giachino & V.B. Guéorguiev, 1995: 205.

Apholeuonus longicollis Reitter, 1904
Apholeuonus longicollis longicollis Reitter, 1904
Apholeuonus nudus longicollis Reitter, 1904c: 255.
Apholeuonus longicollis Reitter: Jeannel, 1910a: 42.
Apholeuonus longicollis longicollis Reitter, 1904: Giachino & V.B. Guéorguiev, 1995: 194.
Apholeuonus longicollis pretneri Giachino & V.B. Guéorguiev, 1995
Apholeuonus longicollis pretneri Giachino & V.B. Guéorguiev, 1995: 199.
Apholeuonus longicollis sequensi Reitter, 1906
Apholeuonus sequensi Reitter, 1906a: 97.
Apholeuonus Sequensi: Reitter, 1906b: 129.
Apholeuonus longicollis Reitter: Jeannel, 1910a: 42.
Apholeuonus Sequensi Setniki Reitter, 1912c: 254.
Apholeuonus longicollis subsp. *Setniki* Reitt.: Jeannel, 1914b: 50.
Apholeuonus longicollis Subsp. *Sequensi* Reitter, 1906: Jeannel, 1924a: 355.
Apholeuonus curticollis Jeannel, 1924a: 354.
Apholeuonus ampliatus Knirsch, 1928: 107.
A. longicollis jeanneli Fagniez: Pretner, 1969 [1968]: 28.
Apholeuonus longicollis sequensis Reitter: Perreau, 2000: 206.

Apholeuonus nudus (Apfelbeck, 1889)
Apholeuonus nudus nudus (Apfelbeck, 1889)
Hexaurus nudus Apfelbeck, 1889: 63.
Apholeuonus knoteki Reitter, 1906c: 237.
Apholeuonus nudus: Apfelbeck, 1894: 513.
Apholeuonus nudus nudus (Apfelbeck, 1889): Giachino & V.B. Guéorguiev, 1995: 179.
Apholeuonus nudus cryophilus Jeannel, 1924
Apholeuonus nudus cryophilus Jeannel, 1924a: 353.
Apholeuonus nudus ledenjacensis S. Ćurčić, Pavićević & Antić, 2018
Apholeuonus ledenjacensis S. Ćurčić, Pavićević & Antić, 2018: 544 *in* S. Ćurčić *et al*. (2018).
Apholeuonus nudus petrovici Pretner, 1963
Apholeuonus nudus petrovici Pretner, 1963c: 133.
Apholeuonus nudus sturanyi Apfelbeck, 1906
Apholeuonus sturanyi Apfelbeck, 1906b: 113.
Apholeuonus nudus subsp. *Sturanyi* Apfelbeck: Jeannel, 1910a: 43.
Apholeuonus nudus sturanyi Apfelbeck, 1906: Giachino & V.B. Guéorguiev, 1995: 184.
Apholeuonus nudus winkleri Jeannel, 1924
Apholeuonus nudus winkleri Jeannel, 1924a: 354.



FIGURES 91.1–91.8: *Leptodirus* series, *Apholeuonus* group. Spermatheca of: (**1**) *Adelopidius ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**2**) *Antrosedes speluncarius* (modified from Čeplík 2023), (**3**) *Apholeuonus absoloni* (modified from Giachino & V.B. Guéorguiev 1995), (**4**) *Croatodirus casalei* (modified from Casale *et al*. 2004), (**5**) *Haplotropidius pubescens*, (**6**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014), (**7**) *Leonhardia solaki* (modified from S. Ćurčić *et al*. 2021), (**8**) *Parapropus sericeus sinuaticollis*.

Genus ***Haplotropidius*** G. Müller, 1903
Apholeuonus (Haplotropidius) G. Müller, 1903a: 89.
Haplotropidius Müller, 1903: Jeannel, 1910a: 22.

Type species. *Apholeuonus (Haplotropidius) pubescens* G. Müller, 1903 by subsequent designation (for the habitus see that of the similar species *Haplotropidius taxi subinflatus* in Fig. 78.1).

Diagnosis. Large size, 5.5–6.5 mm. Pholeuonoid facies, with body elongated, narrowed anteriorly and dilated backwards (Fig. 78.1). Integuments of head and pronotum almost smooth, with very faint hardly visible punctation. However, dots are numerous, quite large, shallow and well isolated on elytra. Colour bright reddish. Pubescence of head and pronotum very small, with only very scattered small hairs, somewhat more numerous in lateral areas of the pronotum; well-developed on elytra with numerous yellowish hairs, somewhat raised, quite long and well independent.

Head: Almost as long as wide, without occipital carina and narrower than the pronotum.

Antennae: Very long and filiform, although somewhat shorter than the length of body, without a differentiated club in both sexes. First antennomere about two-thirds the length of the second one, with 8th being the longest and 9th of length similar to 11th.

Pronotum: Quite convex and slightly transverse, with shapes between trapezoids and subsquares. Sides arcuated or more or less subrectilinear, in some cases somewhat sinuous in basal part, with basal border as wide as, or wider than, the anterior one. Base narrower than the anterior area of elytra; with a thin marginal flange along the entire pronotum.

Elytra: Globose and very convex, about 1.5 times longer than wide as a whole, with maximum width being a little behind the middle part. Sides gently arcuated and progressively narrowed backwards, with apexes not very sharp. Shoulders blurred, without humeral rim. Parasutural stria lacking.

Legs: Long, with tibiae thin and femora much more robust, but not dilated in apical area; males protarsi pentameres and not widened. Protibiae slightly curved with a reduced crown of spines on the anterior edge and a small internal spur. Meso- and metatibiae straight, the first with a spur and the second one with two internal spurs; external spurs lacking.

Mesoventral keel (Fig. 81.5): Normally high, with anterior ridge and posterior process does not exceed the mesocoxal cavity. Depending on species, the anterior edge is more or less convex, with vertex more or less rounded and angle obtuse. Posterior edge more or less long and more or less toothed.

Suture of the metaventrite (Fig. 81.5): Runs close to the edge of mesocoxal cavity, except in middle area where it separates a little, and delimits a narrow and elongated area, somewhat wider in middle area.

Metatergal apparatus (Fig. 83.4): With the metascutum wings short and broad, triangular in shape; apophysis of the alacrista very long and developed, with apexes little sharp.

Metendosternite (Fig. 84.1): «V»-shaped. Furcal arms long and quite robust, one and a half times the length of trunk. Keel of the arms ends in a hooked structure, with a visible but poorly developed process, with a posterior plate of uniform width and a slightly concave edge. Trunk long, about twice as long as the area with the greatest width.

Median lobe of aedeagus: In lateral view (Fig. 85.6), little arcuated with the dorsal face and, below, the apical area slightly concave, being apical area somewhat convex with apex sharp and oriented towards the ventral face. Sides, in dorsal view (Fig. 87.7), in regularly curved arches that narrow progressively towards the apex, which is subtruncated and little arcuated. Basal lobe and ventral blade of the tegmen short, the former being somewhat wider.

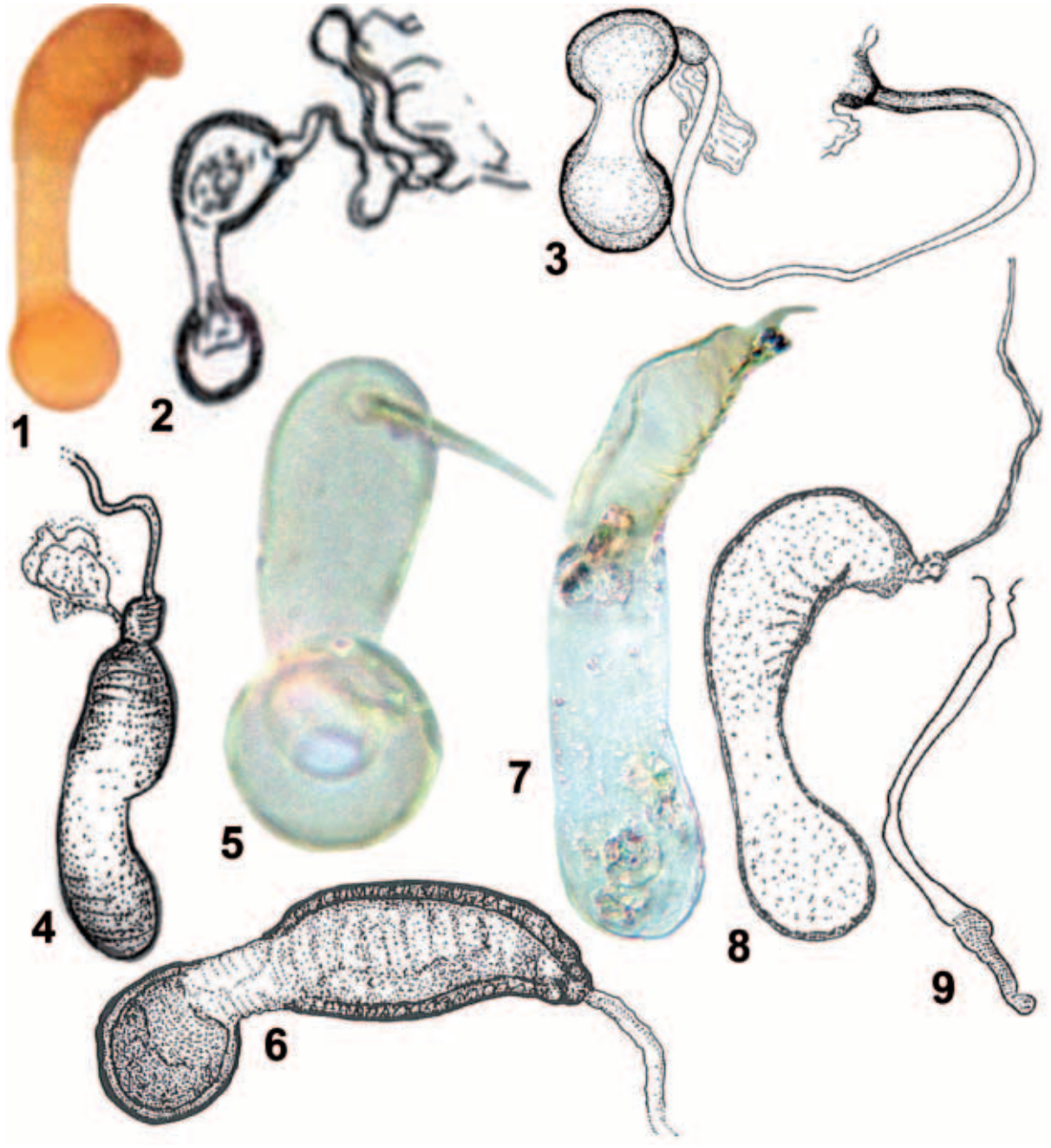
Endophallus (Fig. 87.7): Characterised by a very special armor, in which the «Y»-piece in the basal region is rudimentary. Middle region with two dorsal pieces merged to form a large phanera similar to a wide and long reed in form of a dorsal spoon. Apical region with two ovoid structures above the two reinforcement bands that reach the middle area of median lobe.

Parameres (Fig. 90.6): Somewhat shorter than the median lobe; with apical area somewhat dilated, widened at base and with a more or less sharp extension, with three setae. Lower seta, normally with latero-internal insertion; two are shorter and thinner, and the third is longer and more robust.

Spermathecal complex: Spermatheca quite long (Fig. 91.5) and not arcuated, with apical lobe spherical, hyaline junction duct narrower than the lobes; basal lobe as wide as the apical and twice as long. Spermathecal gland and spermatic duct meet very close to the basal lobe in a more widened area.

Female uroventrite VIII (Fig. 93.5): Posterior margin in a broad arc, with spiculum long, a little compressed towards the middle and with apex dilated.

Discussion. *Haplotropidius* has always been considered sister and very similar to *Apholeuonus*. Differences should be observed in: strongly developed pubescence, punctation of elytra being more numer-



FIGURES 92.1–92.9: *Leptodirus* series, *Apholeuonus* group. Spermathecal complex of: (**1**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al.* 2014), (**2**) *Radziella styx* (modified from Casale & Jalžić 1988), (**3**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**4**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**5**) *Spelaeodromus pluto*, (**6**) *Spelaeodromus sneznikensis* (modified from Polak 2002), (**7**) *Spelaites grabowskii*, (**8**) *Speoplanes giganteus* (modified from Mizerakis *et al.* 2022), (**9**) *Velebitodromus smidai* (modified from Casale *et al*. 2004).

ous and obvious, form of pronotum (most trapezoidal or subrectangular) and femora not dilated in apical part. There are no molecular data to confirm the proposed relationship by phylogenetic analysis.

DISTRIBUTION. All caves colonised by species of this genus are located in foothills or mountains of Dinaric Mountains range in middle part of Dalmatia region (Croatia) and in mountains of Cabulja, Cvrstnica, Plasa, Prolog and Vran in the north and east of Bosnia-Herzegovina.

Species

Haplotropidius cadeki Jeannel, 1927
Haplotropidius Cadeki Jeannel, 1927: 114.
Haplotropidius cadeki Jeannel: Perreau, 2000: 208.

Haplotropidius mariani G. Müller, 1913
Haplotropidius mariani cabuljenis G. Müller, 1930
Haplotropidius Mariani cabuljenis G. Müller, 1930: 20.
Haplotropidius mariani cabuljenis Müller, 1930: Perreau, 2000: 208.
Haplotropidius mariani cvrstnicensis G. Müller, 1930
Haplotropidius Mariani cvrstnicensis G. Müller, 1930: 20.
Haplotropidius mariani cvrstnicensis Müller, 1930: Perreau, 2000: 208.
Haplotropidius mariani mariani G. Müller, 1913
Haplotropidius Mariani G. Müller, 1913b: 158.
Haplotropidius Marianii J. Müller: Jeannel, 1914b: 49.
Haplotropidius mariani mariani Müller: Perreau, 2000: 209.

Haplotropidius pubescens (G. Müller, 1903)
Haplotropidius pubescens livnensis G. Müller, 1926
Haplotropidius pubescens sbsp. *livnensis* G. Müller, 1926b: 157.
Haplotropidius pubescens subsp. *pubescens* Müller: Jeannel, 1924a: 369.
Haplotropidius pubescens pubescens (G. Müller, 1903)
Apholeuonus (Haplotropidius) pubescens G. Müller, 1903a: 78.
Haplotropidius pubescens J. Müller: Jeannel, 1910a: 42.
Apholeuonus (Haplotropidius) bokori Csiki, 1912b: 512.
Haplotropidius Bokori Csiki: Jeannel, 1914b: 49.
Haplotropidius pubescens Subsp. *pubescens* J. Müller, 1903: Jeannel, 1924a: 369.
Haplotropidius pubescens svilajensis G. Müller, 1917
Haplotropidius pubescens svilajensis G. Müller, 1917: 624.

Haplotropidius taxi (G. Müller, 1903)
Haplotropidius taxi novaki G. Müller, 1926
Haplotropidius taxi subsp. Novaki G. Müller, 1926b: 156.
Haplotropidius taxi novaki Müller: Perreau, 2000: 209.
Haplotropidius taxi subinflatus (Apfelbek, 1907)
Apholeuonus Taxi subinflatus Apfelbek, 1907: 303.
Apholeuonus subinflatus Apfelbeck: Jeannel, 1910a: 42.
Haplotropidius taxi subinflatus (Apfelbek): Perreau, 2000: 209.
Haplotropidius taxi taxi (G. Müller, 1903)
Apholeuonus (Haplotropidius) Taxi G. Müller, 1903a: 83.
Haplotropidius Taxi J. Müller: Jeannel, 1910a: 42.
Protobracharthron Gyleki Obenberger, 1917 [1916]: 19.
Haplotropidius taxi taxi Müller: Perreau, 2000: 209.

Haplotropidius vranensis Knirsch, 1927
Haplotropidius vranensis heteromorphus Knirsch, 1929
Haplotropidius vranensis heteromorphus Knirsch, 1929 [1928]: 87.
Haplotropidius vranensis vranensis Knirsch, 1927
Haplotropidius vranensis Knirsch, 1927a: 13.
Haplotropidius vranensis vranensis Knirsch: Perreau, 2000: 210.

Genus ***Icharonia*** Reitter, 1912
Icharonia Reitter, 1912b: 334.

TYPE SPECIES. *Icharonia leonhardiana* Reitter, 1912 by monotypy (habitus in Fig. 78.2).

DIAGNOSIS. Length, 3.0 mm. Body shape short, oval, globose and convex, subpholeuonoid facies (Fig. 78.2). Colour reddish, very bright. Integuments glabrous or almost glabrous, with setae very short and very scattered on elytra. Punctation fine, superficial on head, and pronotum, points being larger, deeper and spaced on elytra.

Head: Wider than long, not retractable and without occipital carina; anophthalmous.

Antennae: Quite long as they reach half-length of

the body. Second antennomere almost three times the length of the first one; club with thick antennomeres, 8th being slightly longer than wide and 11th sharp and almost twice the length of 10th one.

Pronotum: Bell-shaped, very transverse (1.9–2.0 times wider than long), with maximum width at base. Anterior area much narrower than the base and this somewhat narrower than the base of elytra; sides slightly arcuated up to basal third, in this area sinuated with vertices sharp and facing outwards. Angles acute; two small arcuated depressions on sides of pronotum, very close to base.

Elytra: Globose, convex and very short (1.03–1.06 times longer than wide), with maximum width towards basal third and with rounded apical area. Shoulders well-marked and full marginal flanging, visible from above. No transverse striation and messy punctation. Parasutural stria absent.

Legs: Short, thin with male protarsi pentameres, and undilated. Anterior tibiae with an apical comb, in part well-developed on outer edge. Femora widened in apical area.

Mesoventral keel (Fig. 81.6): High and well-developed, with anterior edge slightly convex and vertex little rounded. Posterior apophysis does not reaching the metaventrite.

Suture of the metaventrite (Fig. 81.6): It forms a very little sinuous arch and the area bordering the coxal cavity is very narrow.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Arcuated, little sclerotized and not very long. In lateral view (Fig. 85.7), dorsal face in regular arc with sharp apex curved towards the ventral face. In dorsal view (Fig. 87.8) sides subparallel and slightly sinuated; apical area very little narrow and in shape a non-sharp arc.

Endophallus (Fig. 87.8): Without sclerotized pieces.

Parameres (Fig. 90.7): Quite long and not very robust, arcuated inwards in apical area, shorter than the median lobe. Club undifferentiated, sharp, with a small membranous lobe. Armed with three setae, two apical longer and more robust with the insertion pores nearby, and another preapical further away that is directed inward.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. *Icharonia* presents great similarities in many external morphological characters and male genitalia with genera *Adelopidius* and *Apholeuonus* (Jeannel, 1924a), but without a molecular analysis its phylogenetic affinities with respect to these genera are doubtful due to absence of phanerae in endophallus.

Distribution. Bosnia-Herzegovina. It colonises cavities in karst areas near west and southwest of Sarajevo, in Visočica and Treskavica mountains.

Species

Icharonia leonhardiana Reitter, 1912
Icharonia leonhardiana leonhardiana Reitter, 1912
Icharonia leonhardiana Reitter, 1912b: 334.
Icharonia Leonhardiana Reitt.: Jeannel, 1914b: 48.
Icharonia leonhardiana leonhardiana Reitter: Perreau, 2000: 210.

Icharonia leonhardiana trescavicensis G. Müller, 1925
Icharonia leonhardiana trescavicensis G. Müller, 1925: 77.
Icharonia Leonhardiana subsp. *trescavicensis* J. Müller: Jeannel, 1925: 77.

Genus ***Katobatizon*** Knirsch, 1928
Anomalocerina Weirather: Knirsch, 1928 [1927]: 112 (*Nomen nudum*).
Katobatizon Knirsch, 1928 [1927]: 109.
Type species. *Katobatizon antennarium* Knirsch, 1928 by original designation (habitus in Fig. 78.3).

Diagnosis. Average length, 3.4–3.8 mm. Body shape elongated and rather convex, oval, with pholeuonoid facies (Fig. 78.3). Colour grayish-red. Integument with weak, bright and microsculpture; pubescent.

Head: Rounded, between slightly longer than wide, or as long as wide; as wide as, or slightly narrower than anterior part of pronotum, but clearly narrower than the wider part of pronotum and shorter; without occipital carina. With dense pubescence and punctation. Anophthalmous.

Antennae: Thin, long, reach or exceed a little the middle of elytra, always somewhat shorter in females. First antennomere shorter than the second one; 8th short, at least twice as long as wide; 9th and 10th of similar length and dilated in apical area, somewhat longer the 9th; 11th the longest, with sharp apex.

Pronotum: Bell-shaped, little convex and little transverse, 1.2–1.3 times wider than long; base wider than anterior border and narrower than the elytral base. Maximum width slightly just before the middle, lateral margins sigmoid, arcuated in anterior half and

concave in the posterior one. Posterior vertices sharp, outward facing and acute angles; pubescence dense, short, lying; punctation dense.

Elytra: Convex, elongated oval, between 1.5–1.7 times longer than wide as a whole, with maximum width just before the middle and clearly wider than pronotum; they gradually narrow backwards, with non-sharp apexes. Shoulders obtuse and rounded. Pubescence lying down and dense especially on disc; punctation with points numerous and somewhat larger and deeper than on head and pronotum. Parasutural stria present, somewhat blurred.

Legs: Long, slender; femora non-constricted in apical part; protibiae slightly curved inwards, with an apical comb and some spines on the external apical margin. Males protarsi pentameres, with first four tarsomeres very slightly widened.

Mesoventral keel (Fig. 82.1): Low, with anterior margin straight, vertex rounded and angle obtuse. Posterior process does not reach the metaventrite; posterior margin concave in anterior part, convex and slightly toothed with setae in posterior part.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated, arcuated and robust. In lateral view (Fig. 85.8), thickened with ventral and dorsal sides in regular arc; dorsal face slightly sinuated in the apical third, with a straight and sharp apex. In dorsal view (Fig. 88.1), with sides subparallel that widen slightly in basal area and in front of the middle; apical area short, that narrows regularly to the rounded apex.

Endophallus (Fig. 88.1): Little sclerotized and without a defined «Y»-piece, only in the basal middle area there are structures in form of teeth and some scales. The distal area shows two narrow reinforcement bands that reach the middle part.

Parameres (Fig. 90.8): Quite long and not very robust, slightly curved inwards in apical area, somewhat shorter than the median lobe. Club little differentiated and irregular, basally widened and constricted before the apex. Bearing three setae, one apical – robust and long –, the other two preapical (one with external insertion, long), the other one (shorter) with internal insertion.

Spermathecal complex: Spermatheca (Fig. 91.6) small and curved towards the basal third, with three well-differentiated regions. A spherical apical lobe, as wide although shorter than the basal one, between them there is a short area of hyaline union, somewhat narrower.

Female uroventrite VIII (Fig. 93.6): Little widened, with apical edge in arched little narrowed; arcuate anterior margins that meet to form the spiculum quite long and narrow with apex truncated.

Discussion. Knirsch (1928), at the time of description, assigning *Katobatizon* to the genus *Setnikia* based on external characters. On the other hand, many of the external morphological features and structures of male and female genitalia are present in genera *Leonhardia* and *Protobracharthron*. Considering these similarities the genus *Katobatizon* should be included in the series of *Leptodirus* and subgroup of *Apholeuonus*. No molecular data are available to confirm this hypothetical relationship.

Distribution. Species of this genus colonise the karst of the Dinaric Mountains in two localitys: one on Mount Vlašić (Pećinica Cave), the other on mount Dnolučka (Jama Ispol Puta and Snježara wells). These three capture sites are near Jajce, in central region of Bosnia-Herzegovina (S. Ćurčić *et al*. 2014).

Species

Katobatizon antennarium Knirsch, 1928
Katobatizon antennarium Knirsch, 1928 [1927]: 109.
Anomalocerina Zariquieyi Weirather: Knirsch, 1928 [1927]: 112.

Katobatizon apfelbecki S. Ćurčić & Rađa, 2014
Katobatizon apfelbecki S. Ćurčić & T. Rađa *in* S. Ćurčić, T. Rađa, Mulaomerović, Vrbica, Antić, B. Ćurčić, B. Rađa & Vesović, 2014: 925.

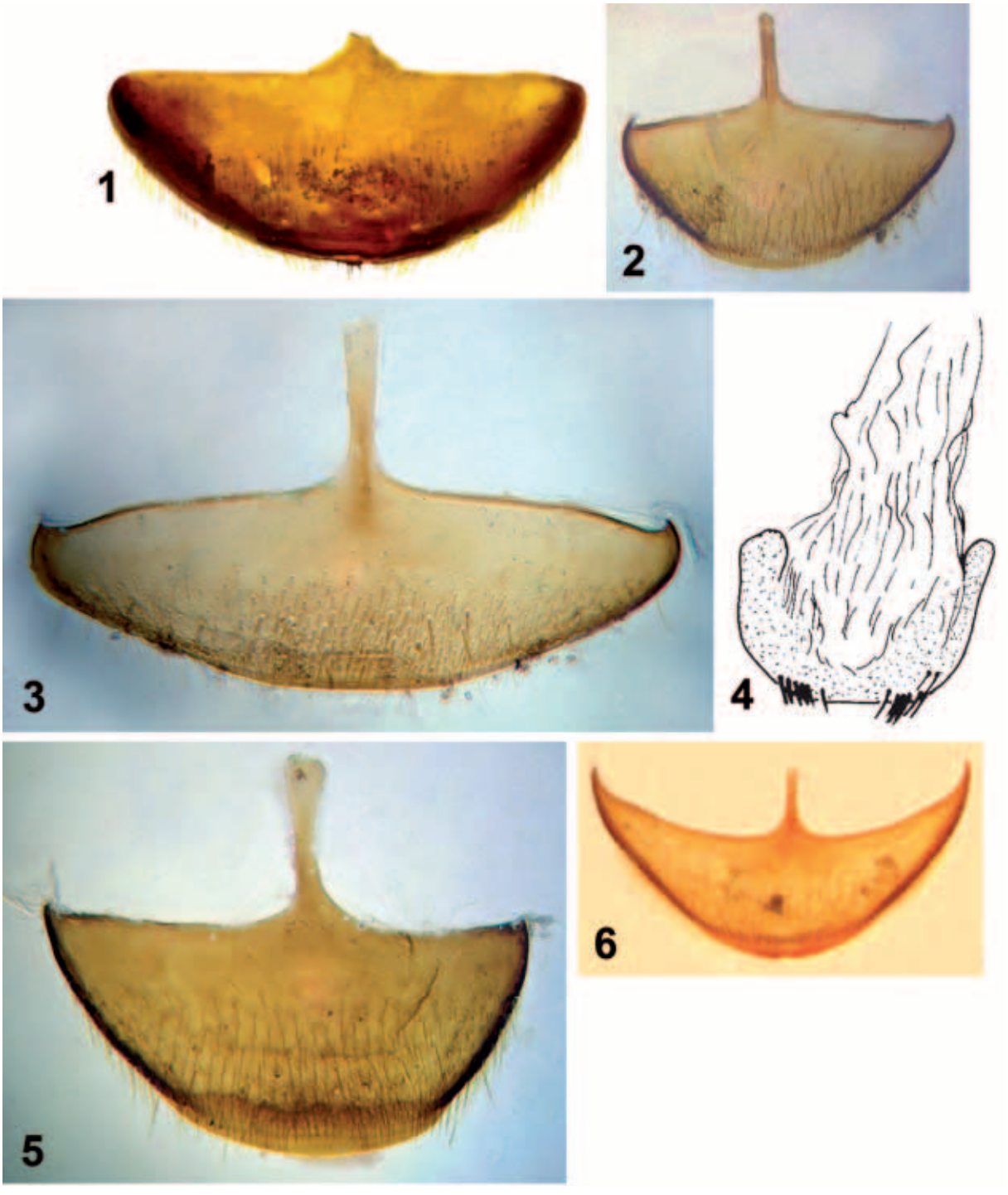
Genus ***Leonhardia*** Reitter, 1901
Leonhardia Reitter, 1901: 128.

Type species. *Leonhardia hilfi* Reitter, 1901 by monotypy (for the habitus see that of the similar species *Leonhardia reitteri mersa* in Fig. 79.1).

Diagnosis. Length, 2.8–4.0 mm. Body shape narrow and very narrow anteriorly; with pholeuonoid facies (Fig. 79.1). Colour reddish-brown, with bright integument and microsculpture. Pubescence short, small in number, slightly raised on head, lying on pronotum and elytra. Punctation dense and shallow, with smaller dots on head.

Head: Not retractable without occipital carina; as long as wide or a little longer than wide and somewhat narrower than the pronotum. Anophthalmous.

Antennae: Inserted towards the middle area of



FIGURES 93.1–93.6: *Leptodirus* series, *Apholeuonus* group. Female uroventrite VIII of: (**1**) *Adelopidius ljubacevoensis* (modified from S. Ćurčić *et al*. 2018), (**2**) *Antrosedes speluncarius,* (**3**) *Apholeuonus nudus nudus*, (**4**) *Croatodirus bozicevici* (modified fom Casale *et al*. 2000), (**5**) *Haplotropidius pubescens*, (**6**) *Katobatizon apfelbecki* (modified from S. Ćurčić *et al*. 2014).

head, quite long and thin, in general exceeding half of elytra in males, not so in females. Second antennomere twice as long as the first, this one somewhat thicker; antennomeres of club widened in apical part, clearly longer than wide, the 8th being at least a little longer than wide; the 11th is the longest of all and sharpened apically.

Pronotum: Bell-shaped, little transverse, 1.1–1.2 times wider than long, with maximum width towards anterior third. Base somewhat narrower than the base of elytra. Lateral margins gently arcuated in anterior area, more widely arcuated a little in front of the middle and sinuous in posterior area. Posterior vertices rather sharp, little protruding outwards, with right angles.

Elytra: Oval and convex, wider than pronotum, quite elongated, between 1.5–1.6 times longer than wide together; maximum width near the middle part; sides gently arcuated, with well-marked shoulders; apexes rounded, little narrowed. Parasutural stria laking.

Legs: Long, slender; tibiae slightly curved; protibiae with a well-developed comb on the apical fourth of outer edge; males protarsi pentameres, slightly enlarged, first one being narrower than apical edge of the protibia; femora widened in basal area and narrowed towards apical area.

Mesoventral keel (Fig. 82.2): Short and high, with vertex more or less angular and angle obtuse. Anterior border usually convex; ventral border denticulated or rounded with setae, and concave anteriorly; posterior process does not reaching metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated and quite robust. In lateral view (Fig. 85.9), arcuated, with ventral face concave, being basal two-thirds of dorsal face flattened; apical third with a mild depression followed by an arcuated area towards apex, which is sharp and slightly curved towards ventral face. In dorsal view (Fig. 88.2), basal area widened, then subparallel and, in apical area, gradually narrows to rounded apex.

Endophallus (Fig. 88.2): At the bottom of sac, a very small «Y»-piece and two more or less developed lateral sclerosities. In the middle of basal region a fine dorsal tooth and above this tooth a broad scaly longitudinal band. In addition, they are two long reinforcement bands, in apical region that reachs the middle region.

Parameres (Fig. 90.9): Elongated and thin, somewhat shorter than the median lobe, with apical area curved inwards. Apex more or less rounded with a membranous lobe more or less evident depending on species. In general, a defined club is not observed, in it three unequal setae are inserted, two somewhat longer and more robust apical with insertion pores nearby, and one subapical, inferior and internal with pore farther away, thinner and smaller.

Spermathecal complex: Spermatheca (Fig. 91.7) elongated showing three distinct parts, an apical spherical, an elongated oblong basal, as wide as apical one, both well sclerotized, and among them a middle part or duct of union, long, narrower and hyaline.

Female uroventrite VIII (Fig. 94.1): With well-developed spiculum, narrowed apical area and ogival apex; anterior edges in regular concave arches.

Discussion. *Leonhardia* exhibits great similarities in many external morphological characters and male genitalia with genera *Adelopidius* and *Apholeuonus* (Jeannel 1924a). However, without a molecular analysis its phylogenetic affinity with respect to these genera remains doubtful, particularly due to the absence of phanerae in endophallus.

Distribution. Genus with six species and five subspecies distributed on limestone massifs of centre and southwest of Bosnia-Herzegovina (S. Ćurčić *et al*. 2018).

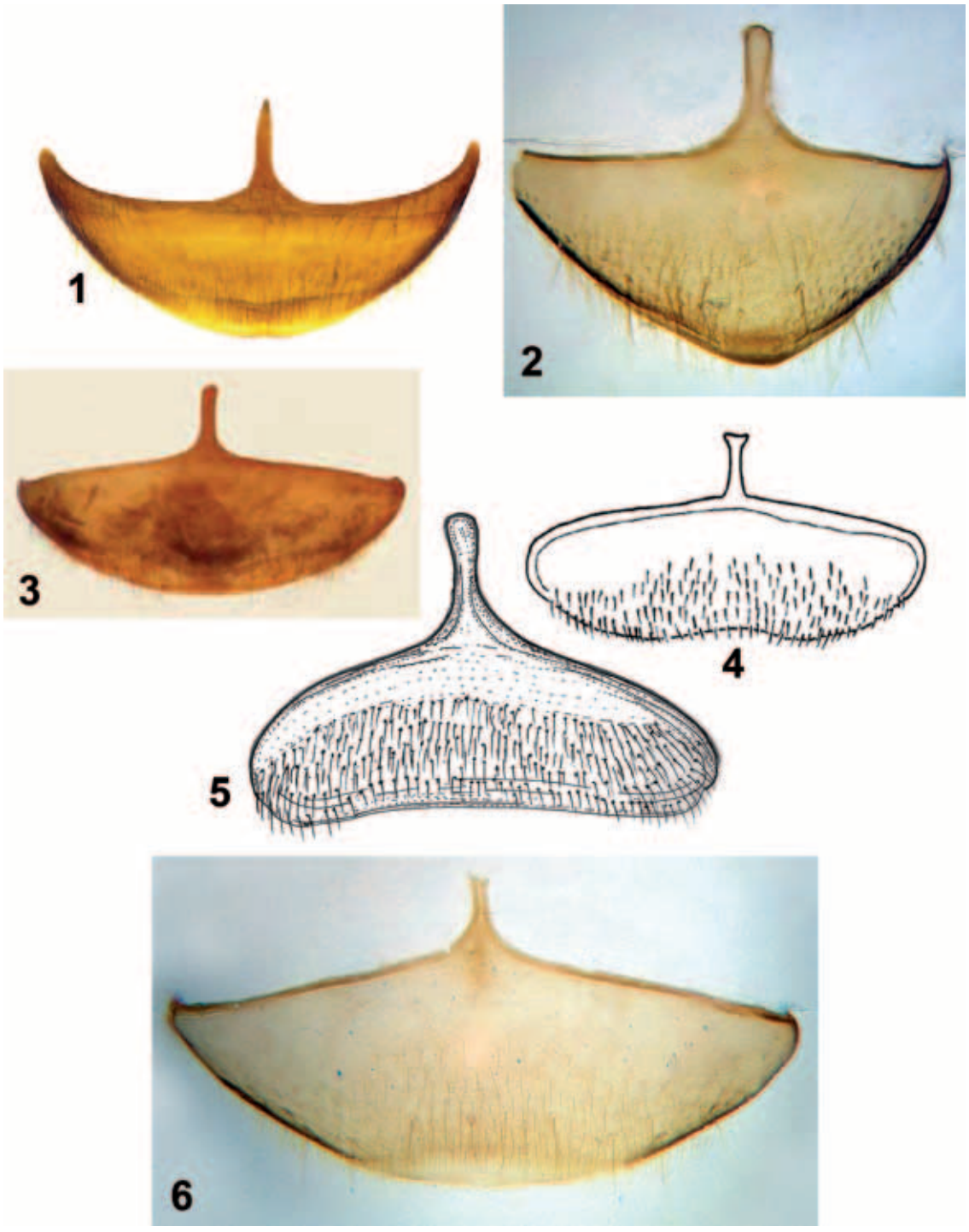
Species

Leonhardia delminiumica Nonveiller, Pavićević, Rađa & Vujčić-Karlo, 2002
Leonhardia delminiumica Nonveiller, Pavićević, Rađa & Vujčić-Karlo, 2002: 166.

Leonhardia droveniki Perreau, 1999
Leonhardia droveniki Perreau, 1999: 402.

Leonhardia hilfi Reitter, 1901
Leonhardia hilfi hilfi Reitter, 1901
Leonhardia hilfi Reitter, 1901:128.
Leonhardia Hilfi Reitter: Jeannel, 1910a: 42.
Leonhardia hilfi hilfi Reitter: Perreau, 2000: 210.
Leonhardia hilfi robusta Knirsch, 1928
Leonhardia hilfi robusta Knirsch, 1928 [1927]: 113.

Leonhardia jajcensis S. Ćurčić & Rađa, 2014
Leonhardia jajcensis S. Ćurčić & Rađa, 2014 *in* S. Ćurčić, T. Rađa, Mulaomerović, Vrbica, Antić, B. Ćurčić, B. rađa & Vesović, 2014: 920.



FIGURES 94.1–94.6: *Leptodirus* series, *Apholeuonus* group. Female uroventrite VIII of: (**1**) *Leonhardia solaki* (modified from S. Ćurčić *et al*. 2021), (**2**) *Parapropus sericeus sinuaticollis*, (**3**) *Protobracharthron dusinae* (modified from S. Ćurčić *et al.* 2014), (**4**) *Roubaliella biokovensis* (modified from Casale *et al*. 1993), (**5**) *Rudogorites simonei* (modified from Polak & Mulaomerović 2021), (**6**) *Spelaeodromus pluto*.

Leonhardia reitteri Breit, 1902
Leonhardia reitteri mersa Knirsch, 1928
Leonhardia reitteri mersa Knirsch, 1928 [1927]: 113.

Leonhardia reitteri reitteri Breit, 1902
Leonhardia reitteri Breit, 1902: 89.
Leonhardia Reitteri Breit: Reitter, 1902b: 223.
Leonhardia reitteri ssp.*retusa* Knirsch, 1928 [1927]: 113.
Leonhardia Willneri Weirather: Knirsch, 1928 [1927]: 113 (*Nomen nudum*).
Leonhardia reitteri reitteri Breit: Perreau, 2000: 211.
Leonhardia reitteri zariquieyi G. Müller, 1937
Leonhardia Reitteri sbsp. nv. *Zariquieyi* G. Müller, 1937: 109.
Leonhardia reitteri zariquieyi G. Müller: Pretner, 1974: 10.

Leonhardia sebesicensis S. Ćurčić, Pavićević & Mulaomerović, 2018
Leonhardia sebesicensis S. Ćurčić, Pavićević & Mulaomerović, 2018 *in* S. Ćurčić *et al.* 2018: 536.

Leonhardia solaki S. Ćurčić, Rađa, Vesović & Vrbica 2021
Leonhardia solaki S. Ćurčić, Rađa, Vesović & Vrbica 2021 *in* S. Ćurčić *et al.* 2021: 73.

Genus ***Protobracharthron*** Reitter, 1889
Protobracharthron Reitter, 1889a: 297.

Type species. *Hexaurus reitteri* Apfelbeck, 1889 by monotypy (for the habitus see that of the similar species *Protobracharthron dusinae* in Fig. 79.3).

Diagnosis. Length, 4.5–5.0 mm. Pholeuonoid facies with body shape elongated and very narrowed anteriorly (Fig. 79.3). Colour between reddish and dark reddish. Integument shiny and finely microsculptured; pubescence short, spaced and raised; punctation without order, fine, dense and shallow, the points being somewhat larger and deeper on elytra.

Head: Not retractable and without occipital carina; longer than wide, between 1.2–1.5 times, slightly narrower than the widest part of pronotum and a little shorter. Anophthalmous.

Antennae: Very long and thin, in males as long as, or somewhat longer than the length of body, in females they do not reach the apical part of elytra. Second antennomere between just over two and three times longer than the first, this one somewhat thicker. Antennomeres of club somewhat dilated in apical area; 8th about three times longer than wide; 11th as long as the 10th and somewhat shorter than 9th.

Pronotum: Narrow, as wide or slightly longer than wide, 1.0–1.2 times longer than width, with maximum width between the third and the anterior half. Base as wide as or somewhat wider than anterior area, and as wide as the base of elytra. Lateral margins gently arcuated in the anterior area, more widely arcuated a little in front of middle and strongly sinuated in the posterior third. Posterior vertices between little and quite sharp, somewhat protruding outwards with angles between sharp and straight.

Elytra: Oval, elongated, 1.8–1.9 times longer than wide overall – much shorter in females, about 1.6 – and very convex; maximum width in the middle part and much wider than pronotum. Sides arcuated, with blurred shoulders; marginal ridge not visible or slightly visible in the humeral region seen from above; apical areas rounded, little narrowed. Parasutural stria visible.

Legs: Long, slender; protibiae with an apical comb prolonged on apical fourth of the outer edge, somewhat curved. Femora dilated in basal part and subapically constricted; males protarsi pentameres, very weakly enlarged.

Mesoventral keel (Fig. 82.4): Triangular and very short, with anterior edge straight, vertex rounded or dentiform and posterior border a little convex with some setae and very low, does not reaching metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated and quite robust. In lateral view (Fig. 86.1), arcuated, with ventral face concave, being the basal two thirds of the dorsal face almost flattened and the apical third with a soft depression; towards the apex an arcuated area that is sharp and slightly curved towards the ventral face. In dorsal view (Fig. 88.4), basal area somewhat widened, then subparallel and in apical area gradually narrows to the rounded apex. Basal blade short, as wide as and somewhat longer than the ventral lamina of tegmen; apical edge of the basal blade in arc.

Endophallus (Fig. 88.4): Bearing at the bottom of basal region a small «Y»-piece and filamentous lateral structures; in centre of the middle area two small teeth and in apical area two longitudinal reinforcement bands.

Parameres (Fig. 90.11): Elongated and thin, somewhat shorter than the median lobe, with apical part curved inwards and somewhat dilated. Apex more or less rounded and somewhat membranous on the inner

edge; each paramere bearing three short, sharp setae and nearby insertion pores. One, somewhat more robust, in an external apical position; another oriented inwards, in a pre-apical position; and the third, also interior, somewhat below the other two.

Spermathecal complex: Spermatheca (Fig. 92.1) elongated with three distinct parts, spherical apical, elongated oblong basal as wide as the apical, both well sclerotized, and between them a middle part, or duct of union, narrower and hyaline that is longer than the diameter of the apical lobe.

Female uroventrite VIII (Fig. 94.3): Two and a half times wider than long; spiculum well-developed and narrow, with rounded apex; posterior edge broadly arcuated with an arched spot in middle area near the edge.

Discussion. *Protobracharthron* is regarding many external morphological characters similar to *Spelaites* of phyletic subgroup of *Apholeuonus* (Jeannel, 1924a; V.B. Guéorguiev, 1976) and *Leonhardia*. However, by morphology of aedeagus and spermathecal complex alone, it seems probable that is is close to *Katobatizon* and to *Leonhardia*, both in *Leptodirus* series. There is no molecular analysis to confirm the suggested affinity.

Distribution. Genus with two cave-dwelling species that have colonised small karst areas in close proximity to each other and belonging to the limestone massifs in Central Bosnia-Herzegovina. *Protobracharthron reitteri* is only known from a cave near Kreševo, municipality west of Sarajevo, and *P. dusinae* was captured in Dusina cave, near the village of Dusina and municipality of Fojnica west of Sarajevo.

Species

Protobracharthron dusinae S. Ćurčić, Rađa & Mulaomerović, 2014
Protobracharthron dusinae S. Ćurčić, Rađa & Mulaomerović *in* S. Ćurčić, T. Rađa, Mulaomerović, Vrbica, Antić, B. Ćurčić, B. Rađa & Vesović, 2014: 929.

Protobracharthron reitteri (Apfelbeck, 1889)
Hexaurus Reitteri Apfelbeck, 1889: 63.
Protobracharthron reitteri Apfelbeck: Reitter, 1889a: 297.
Protobracharthron Reitteri: Apfelbeck, 1894: 514.

Genus ***Roubaliella*** Jeannel, 1925
Roubaliella Jeannel, 1925: 74.

Type species. *Roubaliella biokovensis* Jeannel, 1925 by original designation (habitus in Fig. 79.5).

Diagnosis. Average length, 2.9–3.1 mm. Body shape subglobose, very convex and narrowed backwards; with bathyscioid facies (Fig. 79.5). Colour bright brown. Integument with weak microsculpture; punctation fine, with numerous dots on head and pronotum, the largest and most distant points on elytra. Pubescence short, lying down and dense.

Head: Retractable, somewhat wider than long, with occipital carina complete, but very little protruding; anophthalmous.

Antennae: Short, do not reach the half of elytra; club differentiated with the thickest antennomeres in apical part. First antennomere clearly shorter than the second, this one somewhat longer than the 3rd; the 8th short, as long as wide; 11th conical and the longest.

Pronotum: Very transverse, two or almost twice as wide as long. Lateral margins gently arcuated and not sinuated posteriorly; maximum width at the base, that is as wide as or slightly narrower than the base of elytra. Basal edge broadly arcuated; posterior vertices and angles sharps.

Elytra: Very convex, between ellipticals and ovoids, relatively short, 1.1–1.2 times longer than wide together; maximum width in front of the half, in this area somewhat wider than pronotum; they gradually narrow backwards, with apexes not sharp, subtruncated. Parasurural stria lacking.

Legs: Slender and relatively long. Protibiae straight, with a comb in apical area and anterior half of the outer margin. Males protarsi pentameres, with the first three tarsomeres dilated; the first being somewhat narrower than the apex of protibia. Mesotibiae somewhat arcuated, metatibiae straight. Femora distally undilated.

Mesoventral keel (Fig. 82.5): Well developed, high and laminar; anterior edge prominent and convex, posterior one smooth or slightly serrated and narrow, does not extend to metaventrite; vertex widely rounded with very obtuse angle.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 83.6): Metascutum wings very narrow and very long; apophysis of the alacrista long and narrow.

Metendosternite (Fig. 84.3): Furcal arms more than two and a half times the length of trunk; posterior lamina slightly narrower in apical area with slightly concave edge in the arm-trunk junction area; terminal process or apophysis well-developed. Furcal trunk short, as long as wide measured in the point of union

with arms. Middle keel of trunk diverges in posterior area.

Median lobe of aedeagus: Short, robust and arcuated. In lateral view (Fig. 86.3), dorsal and ventral sides sinuated, apex robust, sharp, and curved towards the ventral face. In dorsal view (Fig. 88.6), sides little arcuated, subparallels; apical area wide with apex rounded. Basal blade relatively long, posterior edge arcuated, somewhat longer and a little narrower than the ventral blade of tegmen.

Endophallus (Fig. 88.6): «Y»-piece very small; median area with two pairs of small pieces poorly sclerotized, the basal somewhat longer, and an elongated group of scales; two short reinforcement bands with reduced scales are present.

Parameres (Fig. 90.13): Thick in basal half somewhat shorter than the median lobe, sinuated and arcuated inwards in the apical part. Club undifferentiated, but apex strongly sharpened, bearing three preapical setae; the two upper ones shorter with insertion pores close and in internal position, and the lower one longer and more robust, pore the most distant with dorsal-external position.

Spermathecal complex (Fig. 92.3): Spermatheca small, with globose and sclerotized apical and basal lobes, somewhat more developed the apical; junction duct short and hyaline. Spermatic duct just over twice the length of spermatheca, with a small nodule at its junction with the basal lobe, with somewhat wider and sclerotized area of attachment to copulatory pouch; there is spermathecal gland.

Female uroventrite VIII (Fig. 94.4): Almost three times wider than long, with posterior edge concave in the middle part; with the anterior edges in descending arcs that join to form a well-developed spiculum, narrow with apex straight and widened.

Discussion. Jeannel (1925) points out that this genus is highly similar in in terms of morphological characters to *Adelopidius*, except for the shape of pronotum and shortness of antennae, for this reasons it is seems likely that it belongs to the phyletic series of *Apholeuonus*. V.B. Guéorguiev (1976) not knowing the male morphology included it in Leptodirina as a genus «*incertae sedis*». However, Casale *et al*. (1993) confirm the position of *Roubaliella* in the phyletic series of *Apholeuonus*. Considering the morphological characteristics of the genitalia it appears to be close to *Leonhardia*. In the same work it is also pointed out that it is the only genus in this series with bathyscioid facies. It also shows other characters such as the shape of apical part and position of parameres setae, the presence of a protibial comb and the pubescence indicate direct relations with several genera of this subgroup such as *Antrosedes*, *Charonites* and *Haplotropidius*. All these characters seemingly confirm its classification as part of *Apholeuonus* group, hence belonging to the clade series of *Leptodirus*, but a confirmation by molecular analysis might be needed to confirm the relationship.

Distribution. Croatia. Known from superficial subterranean habitat (MSS) and small caves especially from mount Sveti Jure in Biokovo Mountains, near the coast in Central Dalmatia region (Jeannel 1925; Casale *et al*. 1993).

Species

Roubaliella biokovensis Jeannel, 1925
Roubaliella biokovensis Jeannel, 1925: 76.

Genus ***Rudogorites*** Polak & Mulaomerović, 2021
Rudogorites Polak & Mulaomerović, 2021: 547.

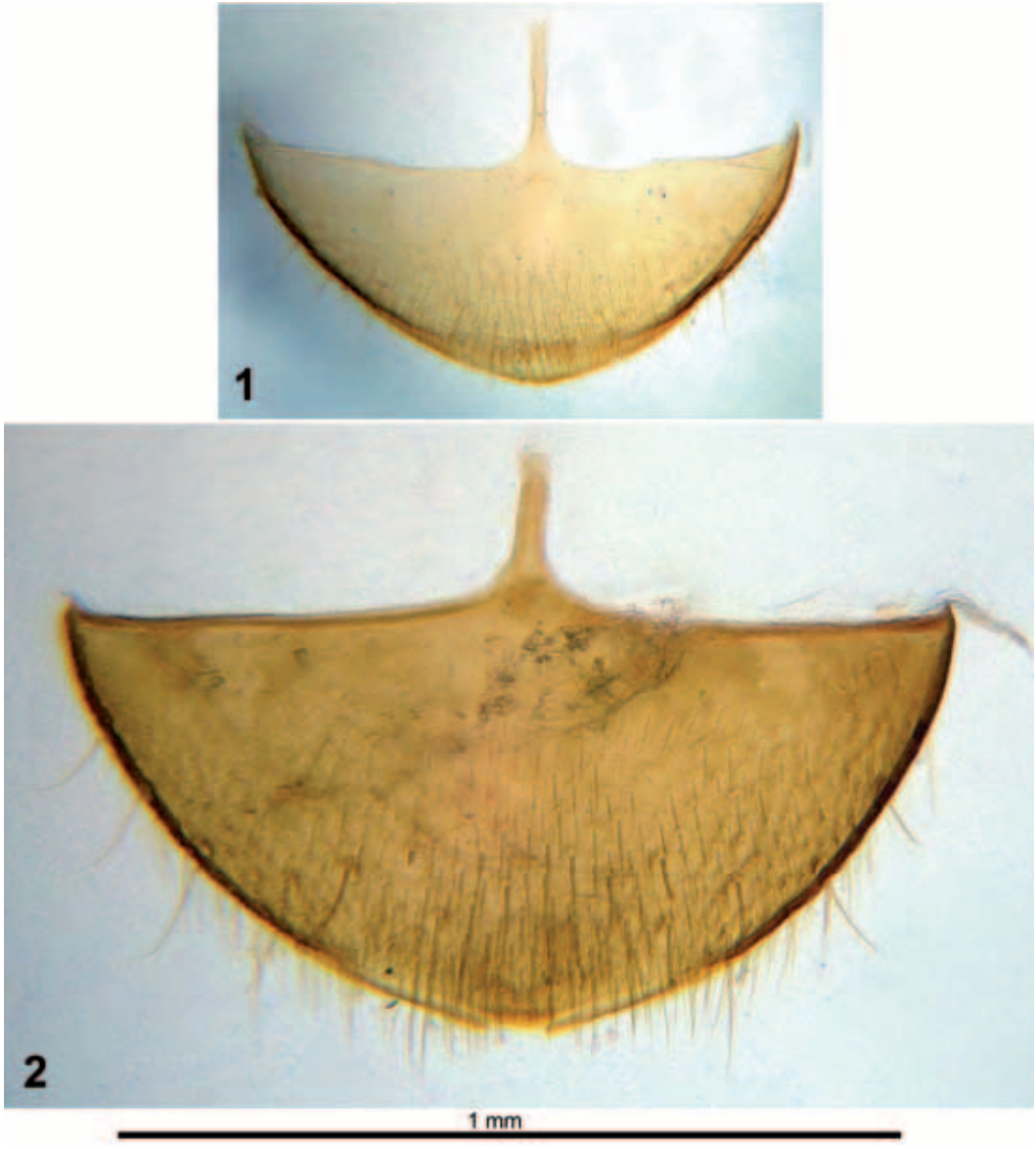
Type species. *Rudogorites simonei* Polak & Mulaomerović, 2021 by original designation (habitus in Fig. 79.6).

Diagnosis. Genus of small sized, between 2.4–3.5 mm, with pholeuonoid facies (Fig. 79.6). Body globose, elliptical and elongated. Colour dark reddish, quite bright integument, with paler antennae and legs. Pubescence yellowish, short and raised, more dispersed on the head, uniform and abundant on pronotum and elytra. Punctation strong and deep, with dots more or less separated.

Head: Small, somewhat wider than long, as wide as the anterior part of the pronotum, but narrower than the widest area of the same; without occipital carina; anophthalmous.

Antennae: Moderate length, reach two thirds of the length of the body, being somewhat shorter and more robust in females. Antennomeres longer than wide; club differentiated with subconical antennomeres, wider at the apex. First antennomere shorter than the second, the latter one and a half times longer, and also longer than the 3rd. 11th elliptical and the longest of all.

Pronotum: Bell-shaped, transverse, 1.4–1.5 wider than long, slightly convex, narrower than the elytra, with the maximum width at the base that is wider than the anterior edge. Lateral margins widen progressively from the anterior area to the base, throughout the an-



FIGURES 95.1–95.2: *Leptodirus* series, *Apholeuonus* group. Female uroventrite VIII of: (**1**) *Spelaites grabowskii*, (**2**) *Speoplanes biokovensis*.

terior half forming a smooth and regular arc, in the posterior one concave, with more prominent concavity in the male. Vertices sharp and somewhat protruding sideways; angles acute.

Elytra: Convex, oval-elongated, 1.3–1.4 times longer than widths altogether, proportionally more short in the female. Maximum width towards the basal third; sides regularly arcuated, as well as apical parts; shoulders rounded and blurred. Punctation deeper and more spaced than in other parts of the body. Parasutural stria and transverse striolation absent.

Legs: Rather long and thin. Tibiae slightly arched; protibiae with a comb visible in the apical area and on the outer lateral edge. In addition, flattened and grouped setae in the two thirds of the inner edge are also present on meso- and metatibiae. Males protarsi

pentamerous and non-widened; basal area of the femora widened. Claws long, narrow, sharp and regularly curved.

Mesoventrite (Polak & Mulaomerović, 2021: Fig. 7): With bifid posterior medial process, short and narrow, in addition to the suture between the mesoventrite and mesepisternum atrophied in the anterior area.

Mesoventral keel (Fig. 82.6): Well developed, hight and triangular; anterior edge slightly convex; ventral border straight, with setae; prolongation reaches the posterior edge of the mesocoxal cavities. Vertex non-sharp with right angle.

Suture of the metaventrite (Fig. 82.6): It forms a regular arc from the anterior to the posterior apex of the mesocoxal cavity, bounded area narrow.

Metatergal apparatus (Fig. 83.7): With the metascutum wings short and wide; the apophysis of the alacrista very reduced with sharp apices.

Metendosternite (Fig. 84.4): «V»-shaped. Furcal arms a little more than twice the length of the trunk, narrow, with the apical area slightly dilated and the terminal process or apophysis reduced; posterior plate of similar width along the arm and trunk, the posterior edge being concave in the area of merging of arms and trunk. Furcal trunk almost one and a half times longer than width of the basal part. Middle keel of the trunk does not diverge in the posterior area.

Median lobe of aedeagus: Quite long and wide. In lateral view (Fig. 86.4), thick, with ventral side little arcuated and the dorsal one more curved in the middle area, with the apex very short, sharp and curved towards the ventral face. In dorsal view (Fig. 88.7), with subparallel sides, of similar width from the base to the apical part forming a wide arc with a slight rounded protrusion in the middle. Basal blade of medium length, wide with rounded posterior margin in dorsal view, and invaginated in lateral view. Ventral blade of the tegmen somewhat shorter and narrower than the basal blade.

Endophallus (Fig. 88.7): Basal part without «Y»-piece and without sclerotized structures, only in the middle apical part very weakly scaled.

Parameres (Fig. 90.14): In dorsal view slightly arcuated towards the middle, then straight; similar width throughout its length, somewhat shorter than the median lobe and without differentiated club. Apical part with a small membranous lobe at the apex and three setae, two apical ones of similar length with close insertion pores and another shorter, latero-internal, subapical with the pore farther away.

Spermathecal complex: Spermatheca (Fig. 92.4) short, with apical and basal lobes sclerotized, ovoid and similar width; junction duct very short and hyaline. Spermatic duct and gland lead to a small sclerotized nodule that attaches to the basal lobe of the spermatheca.

Female uroventrite VIII (Fig. 94.5): A little more than twice as wide as long with surface very pubescent and a slightly concave porterior margin; posterior margins in descending arcs that meet in the middle part and form a spiculum long, narrowed in the middle, with rounded apex.

Discussion. According to Polak & Mulaomerović (2021) this genus belongs to the phyletic group of *Apholeuonus* or as Jeannel (1924a) and Perreau (2000) stated the phyletic series of *Apholeuonus*. It exhibits similar morphological characters as *Apholeuonus* and all the genera that belong to this phyletic group. The most closely related seems *Charonites* (a separate sister genus of *Apholeuon* + *Parapropus* subgroup in our tree of Fig. 1I) from which it is separated by the different length of the first antennomere, the shape of the comb of the protibiae, the development of the suture between mesoventrite and mesepisternum, the shape of the mesoventral keel, the atrophy of the apophysis of the alacrista – metatergal apparatus – and different structures in the endophallus. To date the relationship postulated is based on morphology only and is so far not confirmed by molecular analysis due to the lack of data.

Distribution. Bosnia-Herzegovina. Known only from Lijina Cave (Lijina Pećina) located in the municipality of Kreševo, about 20 km west of Sarajevo (Polak & Mulaomerović 2021).

Species

Rudogorites simonei Polak & Mulaomerović, 2021
Rudogorites simonei Polak & Mulaomerović, 2021: 548.

Genus ***Setnikia*** Breit, 1913
Setnikia Breit, 1913a: 13.

Type species. *Setnikia leonhardi* Breit, 1913 by monotypy (habitus in Fig. 80.1).

Diagnosis. Medium sized, 4.0 mm. Subpholeuonoid facies (Fig. 80.1) with body elliptical, narrowed in head and pronotum and widened in elytra. Colour reddish bright. Punctation very strong and very deep, especially on elytra; yellowish, long and bristly pubescence on elytra.

Head: Large, slightly longer than wide, almost as wide as the anterior area of the pronotum; non-retractable, without occipital carina; anophthalmous.

Antennae: Quite long, but shorter than body length, exceeding first half length of elytra, with club antennomeres dilated. Second antennomere almost twice as long as the first; 8th very small somewhat longer than wide; 11th sharp and a little longer than 10th.

Pronotum: Rather small, little transverse, 1.23 times wider than long, with disc little convex. Base wider than anterior border, but somewhat narrower than base of elytra. Lateral margins anteriorly little arcuated, in posterior third narrows and concave; sharp vertices, little protruding and almost right angle.

Elytra: Oval-elongated, wide, 1.3 times longer than wide together, and depressed over disc. Much wider than pronotum the widest area around the midline; lateral margins regularly arcuated with rounded apexes. No transverse striation and no parasutural stria.

Legs: Thin and quite long; males protarsi pentameres and slightly dilated. Anterior tibiae with a well-developed comb, mainly in apical half of outer edge. Tibiae straight and femora dilated into club in apical area.

Mesoventral keel (Breit 1913a): Quite high and wide, with angular vertex and posterior prolongation does not reach the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Arcuated, little sclerotized. In dorsal view (Fig. 88.8), with sides subparallel and slightly sinuated; apical area with two rounded lateral expansions that frame rounded apex of median lobe.

Endophallus (Jeannel 1924a): With a well-developed basal «Y»-piece. Two elongated lateral, sigmoids phanerae, that widen towards ventral face with a sclerotized structure in form of a small hood above the «Y»-piece in the middle.

Parameres (Fig. 90.15): Quite long, arcuated inward in apical part, as long as median lobe. Apex with little differentiated club, with a very small sharp membranous lobe, which makes apex appear acuminate. Apex bearing three short and subequal setae, two apical with insertion pores nearby, and another preapical further away that is directed inwards.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. The genus *Setnikia* presents unique characters in its external morphology, such as body shape and pubescence; also concerning such of male genitalia: lateral expansions in apical area of median lobe, shape of club of the parameres and sclerotized pieces of endophallus. These characters separate it from genera that are considered more closely related such as *Icharonia* in which colouration, punctation and similar apical shape of femora, or in *Adelopidius* and *Apholeuonus* with a certain similarity in shape of aedeagus and structures of endophallus are the separating characters. These doubts can only be resolved once molecular data on this genus will be available.

Distribution. Bosnia-Herzegovina. It colonizes cavities in Treskavica mountains, south of Sarajevo.

Species

Setnikia leonhardi Breit, 1913
Setnikia leonhardi Breit, 1913a: 13.
Setnikia Leonhardi Breit: Jeannel, 1914b: 49.

Genus ***Spelaites*** Apfelbeck, 1907
Spelaïtes Apfelbeck, 1907a: 303.
Spelaetes Apfelbeck, 1907c: 315.

Type species. *Spelaïtes grabowskii* Apfelbeck, 1907 by monotypy (habitus in Fig. 80.3).

Diagnosis. Length 5.0–5.5 mm. Body shape very elongated and very narrowed anteriorly; with pholeuonoid facies (Fig. 80.3). Colour reddish with bright integument and microsculpture. Pubescence fine, with sparce hair coat, quite long and raised, especially on elytra; punctation dense and shallow, with smallest dots on head.

Head: Not retractable and without occipital carina. A little longer than wide and as wide as the anterior area of pronotum, but narrower than the widest area of pronotum; anophthalmous.

Antennae: Inserted towards the middle area of head, long and thin, almost reaching the apex of elytra. 2nd antennomere twice as long as the 1st, this one somewhat thicker. Antennomeres of club somewhat widened in apical part, all clearly longer than wide, the 8th being about three times longer than wide; 11th as long as 10th and shorter than 9th.

Pronotum: Narrow and convex, as wide or slightly longer than wide, with maximum width towards the anterior third. Base somewhat wider than the anterior area and as wide as the base of elytra; middle area 0.5 times narrower than elytra. Lateral margins gently arcuated anteriorly, somewhat more arcuated in middle

part and sinuated in the posterior one; basal vertices quite sharp, somewhat protruding outwards and almost right angles.

Elytra: Ovoid, dilated, very convex and elongated, 1.7 times longer than wide together; wider than pronotum, with maximum width a little above the middle. Sides regularly arcuated, with blurred shoulders and rounded apical areas. Marginal flange not visible from above. Parasutural stria lacking.

Legs: Long and slender; males protarsi pentameres, weakly enlarged, first one being clearly narrower than the apical part of protibia; tibiae straight, protibiae with a comb reduced to a few spines in apical area; femora not narrowed towards apical area.

Mesoventral keel (Fig. 82.8): Well developed, with convex front edge and concave posterior edge, serrated and silky; apex with tooth and sub-ctilinear angle.

Suture of the metaventrite (Fig. 82.8): Arch-shaped, which is sinuous in the basal third and delimits a somewhat wider area in the apical third.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Quite long and robust. In lateral view (Fig. 86.6), little arcuated; apical area with apex sharp and oriented towards the ventral face. In dorsal view (Fig. 89.2), sides in almost regular arches that progressively narrow towards the apex, which is arcuated.

Endophallus (Fig. 89.2): Characterised by a very special armor, in which «Y»-piece in basal region is wide and very developed; the two dorsal pieces of middle region merge to form a large wide phanera in the middle with two lateral extensions.

Parameres (Fig. 90.17): Slightly shorter than the median lobe; with apical area somewhat dilated and bearing three setae of similar length with equidistant insertion pores. Normally the lower seta, with latero-internal insertion, is somewhat shorter and less robust.

Spermathecal complex (Fig. 92.7): The spermatheca decreasing in thickness from the apical to the basal part; without distinct parts and all membranous except for the apical part which is slightly sclerotized.

Female uroventrite VIII. (Fig. 95.1): Slightly pointed arched posterior margin; slightly sinuous anterior margins meeting in the middle to form a long, narrow spiculum with a truncated apex.

DISCUSSION. A genus that has been included in the *Leptodirus* series as it exhibits several similar in external morphological characters to the genera *Protobracharthron*, *Haplotropidius* and *Leonhardia*. Differences between them are found in shape of pronotum, pubescence, antennae, mesoventral keel and protibial comb. Although it shows great similarities in genitalia shape with *Haplotropidius* and *Parapropus*. The parts of the endophallus are very similar in *Spelaites* and *Haplotropidius* with some phanerae in the middle region; in *Parapropus* the endophallus is almost unarmed.

DISTRIBUTION. Croatia. Colonises caves on the northern slope of Mosor Mountains near Dugopolje, central Dalmatia (Jeannel 1924a; Perreau 2000).

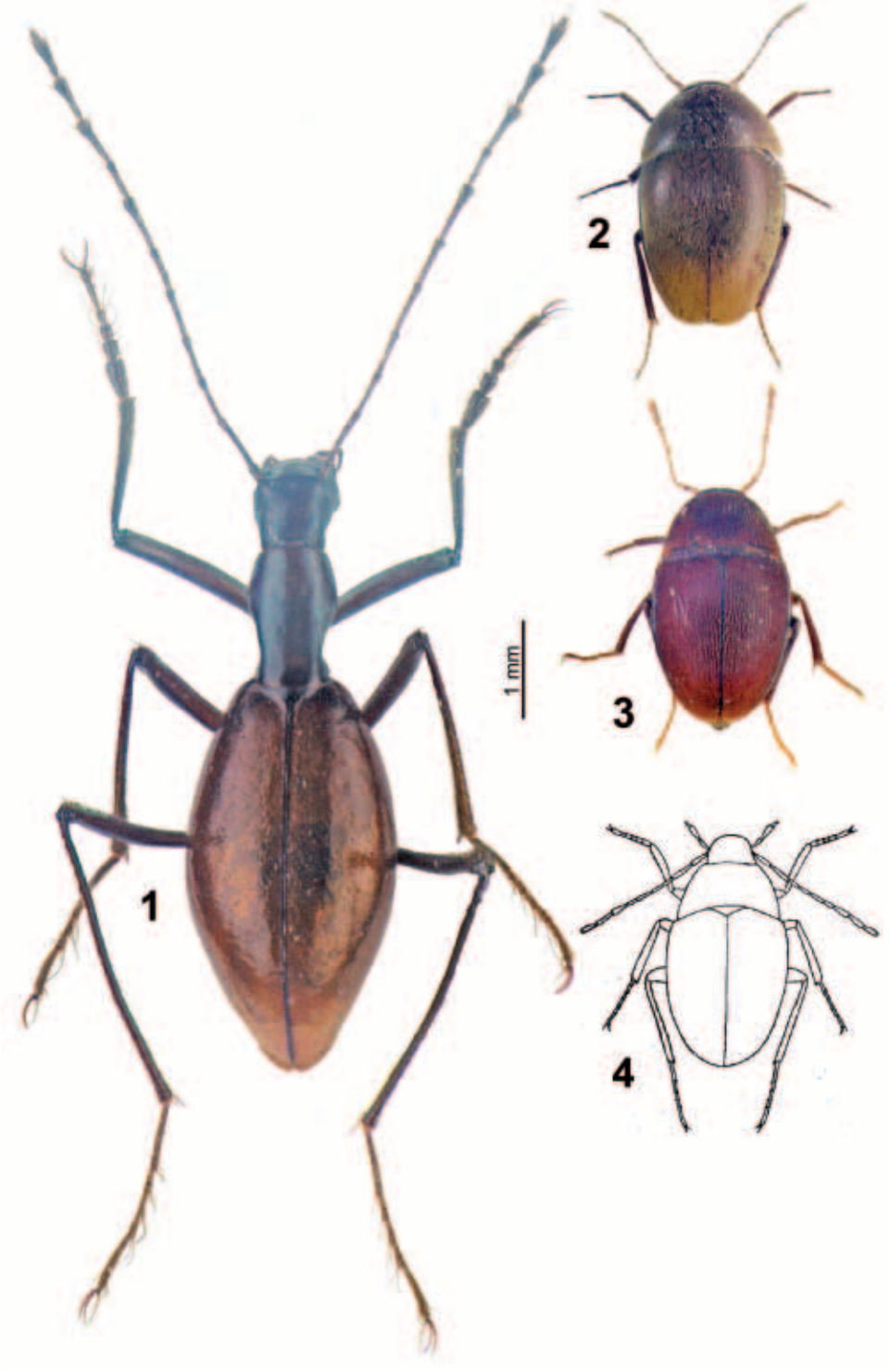
Species

Spelaites grabowskii (Apfelbeck, 1907)
Spelaïtes Grabowskii Apfelbeck, 1907a: 303.
Spelaetes Grabowskii Apfelbeck, 1907c: 316.
Protobracharthron Grabowskii Apfelbeck: Jeannel, 1910a: 43.
Spelaites grabowskii (Apfelbeck): Perreau, 2000: 214.

3.2.3.4 ***Leptodirus*** group

DIAGNOSIS. Genera of this group are characterised by male protarsi pentameres or tetrameres and by specialized or not body shape, ranging from bathysciod to leptodiroid or to scaphoid, depending on generus and species analysed. Antennae inserted in median third of head or in the posterior fourth. Relative length of first and second antennomere, where the first is shorter than, or as long as second. General structure of aedeagus very variable: short and stout, or long and thin; little arcuated or sinuate, with parameres thin and equipped with two or three setae, and endophallus with or without sclerotized structures.

DISCUSSION. The species-richness of this group is based purely on morphological characters, however, the absence of other taxa may well be due to inclusion into other groups also by morphological classification, even though they migh belong to the *Leptodirus* group. This taxonomic uncertainty makes is literally impossible to establish strong synapomorphies defining the group. The main reason for this is likely to be found in the convergent evolutionary process bearing highly specialised and superficially similar moprhologies as adaptations to the subterranean environment. This, in many cases, means that only the availability of molecular data may resolve the real underlying phylogentic relationship amongst these taxa. In the tree presented here (Fig. 1I) this group is sister to the



FIGURES 96.1–96.4: *Leptodirus* series, *Leptodirus* group. Habitus of: (**1**) *Astagobius angustatus laticollis*, (**2**) *Bathysciotes khevenhuelleri croaticus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *freyeri,* (**4**) *C.* (*Rectipenis*) *matjasici* (modified from Pretner 1959).

Apholeuonus group with a support of 100/100; the support between *Leptodirus* and *Spelaeobates* subgroups is 51.9/98. In order to classify subgroups two subgroups were established by a morphological character concering the the number of protarsomeres of the males: *Leptodirus* group (pentamers) and *Spelaeobates* group (tetramers). With this it appears that an other structure of these two subgroups, *Leptodirus* and *Spelaeobates*, developed independently twice in the same clade, this is the unarmed endophallus. This in turns mean that if all those with unarmed endophallus are clustered in the same *Leptodirus* subgroup it suggests that this derived from basal cladogenesis involving the genus *Bathysciotes*. This, however, implies an independent occurrence of the tetramer structure twice. Molecular data will be needed to resolve this problem and sheed light on the evolutionary process leading to the contracditory morphological findings. The position of *Ceuthmonocharis*, transferred from a previous status in the *Bathyscimorphus* group, is also controversial, as it has an unarmed endophallus, therefore it actually could be placed either in the subgroup *Leptodirus* or in the subgroup *Spelaeobates*; we have chosen to place it in the subgroup *Leptodirus* because of its pentamerous male protarsus.

KEY TO SUBGROUPS

1. Males protarsi pentamerous .....
.....*Leptodirus* subgroup
- Males protarsi tetramerous.....
.....*Spelaeobates* subgroup

Leptodirus subgroup

Including the genera *Astagobius*, *Ceuthmonocharis* and *Leptodirus* this subgroup is characterised by species with pentamerous male protarsi and an unarmed endophallus. *Ceuthmonocharis* is bathyscioid and probably derived in a basal cladogenesis of the group; *Astagobius* and *Leptodirus* are characterised by: a slender pronotum that is laterally compressed and without lateral edge, physogastric elytra, antennae inserted in the medium third of head and a first antennomere shorter than the second one. In the phylogenetic tree (Fig. 1I) *Astagobius* and *Leptodirus* form a clade with a very high support, 100/100; this clade is sister to the genus *Bathysciotes* which belongs to the *Spelaeobates* subgroup to which it relatest with a 51.9/98 support.

KEY TO GENERA

1. Size 1.8–2.6 mm; body shape bathyscioid .....
.....*Ceuthmonocharis*
- Size 6.0–7.0 mm; body shape leptodiroid or scaphoid
.....2

2. Body size smaller, 6.0 mm. Elytra elongated, scaphoides (Fig. 96.1) .....*Astagobius*
- Body size larger, 6.5–7.0 mm. Elytra globular, physogastric, leptodiroid shape (Fig. 97.2) .....
.....*Leptodirus*

Genus ***Astagobius*** Reitter, 1886
Astagobius Reitter, 1886a: 315.

TYPE SPECIES. *Leptoderus angustatus* Schmidt, 1852 by subsequent designation (for the habitus see that of the similar subspecies *Astagobius angustatus laticollis* in Fig. 96.1).

DIAGNOSIS. Size 5.5–6.5 mm. Body shape scaphoid, posteriorly very convex and narrow (Fig. 96.1). Colour bright reddish. Pubescence almost absent, with only small and scattered hairs on the apical half of elytra. Integument microsculptured on head and pronotum as a fine and superficial reticulate; punctation is only observed on elytra, which is very scattered with points small and shallow. Females in general are somewhat more robust than males with slightly more bulging elytra.

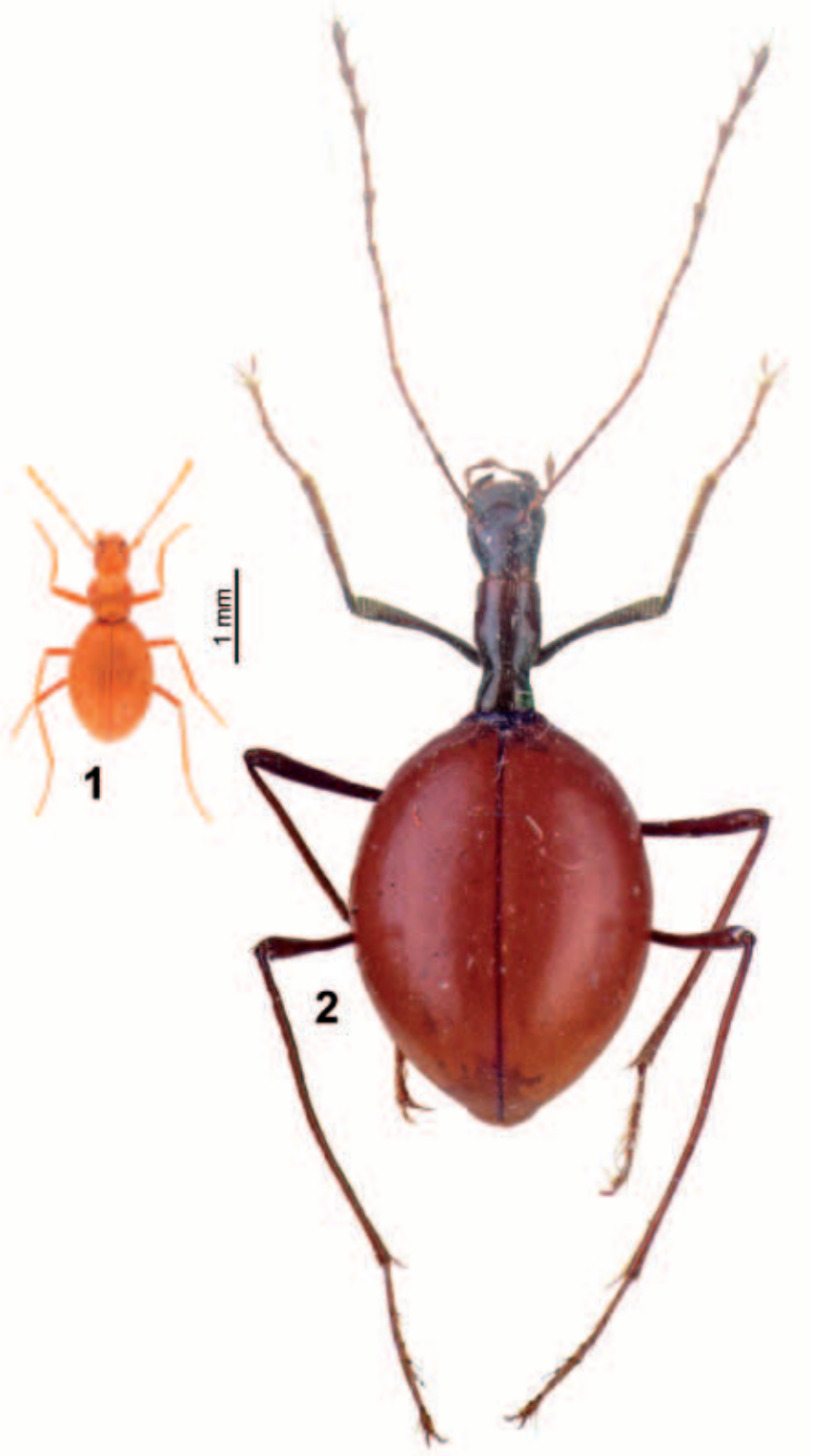
Head: Elongated without occipital carina, from the middle area it narrows progressively and regularly backwards; anophthalmous.

Antennae: Very thin, as long as the body. Second antennomere is the longest and at least three times longer than the first one, which is thicker; antennomeres 9th, 10th and 11th of similar length.

Pronotum: Narrow and elongated, almost twice as long as wide, with sides regularly arcuated in the anterior half; basal part narrowed in convex arc, with maximum width towards the middle. Posterior vertices little sharp, with angles little obtuse.

Elytra: Elliptical, very convex, with a marked physogastria; apical part somewhat sinuated, progressively narrows to the apex which is sharp. Maximum width towards the middle, being almost twice as long as wide; parasutural stria lacking.

Legs: Very long and very thin; male protarsi pentameres, as wide as the apex of the protibiae, these without combs. Protibiae slightly curved, meso- and metatibiae being straight, like femora, these are of similar width throughout their length.



FIGURES 97.1–97.2: *Leptodirus* series, *Leptodirus* group. Habitus of: (**1**) *Deelemaniella pretneri* (modified from Hlaváč *et al*. 2017), (**2**) *Leptodirus hochenwarti hochenwarti*.

Mesoventral keel (Fig. 98.4): Lacking. The mesocoxal cavities are connected.

Suture of the metaventrite (Fig. 98.4): Parallel to the coxal cavity along its entire length, intermediate space very reduced.

Metatergal apparatus (Fig. 99.1): Wings of the metascutum very long, very narrow and arcuated; apophysis of the alacrista very underdeveloped, almost absent.

Metendosternite (Fig. 100.1): Furcal arms long, twice the length of trunk, both progressively narrow towards the apex that is hook-like shaped with terminal process well-developed and with a prominent expansion on the inner face. Posterior edge in soft regular arc; trunk long, twice as wide as long.

Median lobe of aedeagus: Very long and large. In lateral view (Fig. 101.1), curved from base to apex; apical part of dorsal face sinuated with sharp tip curved very sharply towards dorsal face. In dorsal view (Fig. 102.1), apical part not widened with arcuated sides that narrow regularly to the slightly sharp apex. Basal blade long, being short the ventral blade of tegmen.

Endophallus (Fig. 102.1): Totally without basal armor and differentiated pieces.

Parameres (Fig. 103.1): Uniform in thickness, rather thin and somewhat shorter than the median lobe, lack of differentiated club and bearing three setae of medium length, almost equal and inserted apically.

Spermathecal complex (Fig. 104.1): Spermatheca small, straight on dorsal side and arched on ventral side; apical lobe and junctional duct sparsely sclerotized, almost hyaline, the apical lobe being spherical; proximal lobe well sclerotized, irregular appearance and larger than apical lobe; spermatic duct of uniform thickness joins directly into basal lobe, without dilated area.

Female uroventrite VIII (Fig. 104.8): Lateral areas of uroventrite folded inwards; median area of posterior margin concave; lateral sides of anterior margin in smooth ascending arcs that join to form a short and broad spiculum, with cleft apex.

Discussion. The genus *Astagobius* is sister to *Leptodirus* with 100/100 support (Fig. 1I). See the discussion of the genus *Leptodirus*.

Distribution. Colonises Slovenian caves in Carniola region and several karst massifs of Northeastern Croatia.

Species

Astagobius angustatus (F.J. Schmidt, 1852)
Astagobius angustatus angustatus (F.J. Schmidt, 1852)
Leptoderus angustatus F.J. Schmidt, 1852: 381.
Leptodirus robicii Joseph, 1867: 170.
Leptodirus angustatus Schmidt: Joseph, 1872 [1871]: 175.
Leptoderus (*Leptoderus*) *angustatus* Schm.: Reitter, 1885a [1884]: 11.
Astagobius angustatus Schmidt: Reitter, 1886a: 315.
Leptodirus (*Astagobius*) *angustatus* Schmidt: Jeannel, 1910a: 44.
Astagobius angustatus Subsp. *angustatus* Schmidt, 1852: Jeannel, 1924a: 387.

Astagobius angustatus deelemani Pretner, 1970
Astagobius angustatus deelemani Pretner, 1970a: 330, 337.

Astagobius angustatus driolii Pretner, 1970
Astagobius angustatus driolii Pretner, 1970a: 331, 338.

Astagobius angustatus glacialis Pretner, 1955
Astagobius angustatus glacialis Pretner, 1955: 51.

Astagobius angustatus langhofferi Obenberger, 1917
Astagobius angustatus langhofferi Obenberger, 1917 [1916]: 19.
Astagobius angustatus Subsp. *Langhofferi* Obenberger, 1916: Jeannel, 1924a: 387.

Astagobius angustatus laticollis Pretner, 1955
Astagobius angustatus laticollis Pretner, 1955: 51.

Astagobius angustatus vukusici Jalžić, 1982
Astagobius angustatus vukusici Jalžić, 1982: 15.

Astagobius hadzii Pretner, 1970
Astagobius hadzii Pretner, 1970a: 327, 336.

Genus ***Ceuthmonocharis*** Jeannel, 1914
Hohenwartia Jeannel, 1910a: 21.
Ceuthmonocharis Jeannel, 1914a: 68 (Unjustified new replacement name).

Note. From 1914 to the present *Hohenwartia* Jeannel, 1910 has been considered in homonymy with *Hohenwarthia* Letourneux & Bourguignat, 1887 – Mollusca –. However, *Hohenwartia* Jeannel and *Hohenwarthia*

Letourneux & Bourguignat differ in one letter and according to article 56.2 of the International Code of Zoological Nomenclature (ICZN 1999) there is no homonymy and the name of Jeannel (1910a) can be kept. To apply the article 23.9 (ICZN 1999), reversal of precedence, the evidence of article 23.9.1.2 must be provided; the article 23.9.1 of the code must be applied and declared *Hohenwartia* a nomen oblitum and *Ceuthmonocharis a* nomen protectum. The conditions of article 23.9.1.2 are not met and the case has been referred to the Nomenclature Commission; until the case is resolved, the name *Ceuthmonocharis* can continue to be used in accordance with article 23.9.3.

Type species. *Adelops freyeri* Miller, 1855 by original designation (habitus in Fig. 96.3).

Subgenus ***Ceuthmonocharis***

Diagnosis. Size 1.8–2.6 mm. Bathyscioid facies, body shape oblong-rounded, wide and generally very convex (Fig. 96.3). Pubescence short, lying down, thin and yellowish with, in lateral areas of pronotum, longer, robust and raised hairs.

Head: Almost as long as wide, without occipital carina, narrower than pronotum, with a punctation by very small and sparsely dotted.

Antennae: Long and thin, with antennomeres of club elongated and somewhat widened. The first being clearly shorter than the second; the 8th almost

a half times longer than wide and the 11th the longest and most robust. Antennae somewhat shorter and more robust in females.

Pronotum: Clearly transverse, with maximum width at the base or very close to it, as wide as, or slightly narrower than the anterior margin of elytra. Lateral margins little arcuated or subrectilinear, not sinuated before the base, with posterior vertices more or less sharp and more or less protruding backwards; angles acute. Disk with a punctation formed by small and scattered dots.

Elytra: Heavily welded, convex, short and wide, about 1.2 times longer than wide. Narrow more or less progressively, with lateral margins regularly arcuated to apex, which is rounded. Maximum width close to base; punctation quite strong, with points located close to each other and ordered. Marginal furrow well defined along the entire elytral edge; parasutural stria lacking.

Legs: Short; male protarsi pentameres not or slightly dilated. Protibiae with a well-developed apical comb and a short internal spur; meso- and metatibiae bearing thin and long, erect spines and very small external spurs, internal ones more developed.

Mesoventral keel (Fig. 98.6): High in shape of a lamina, with anterior edge subrectilinear, ventral one narrow and ciliated and vertex between them rounded; posterior process reaching the middle area of metaventrite. Intercoxal process of metaventrite very narrow and bifid.

Suture of the metaventrite (Fig. 98.6): In the form of a wavy arch delimiting a well-defined arched area in the apical half and then very close to the coxal cavity in the basal half.

Metatergal apparatus (Fig. 99.3): Wings of metascutum long and very narrow, and well-developed alacrista apophysis with blunt apices.

Metendosternite (Fig. 100.3): «V»-shaped with the arms long and very narrow in the apical half being almost twice as long as the trunk, terminal apophysis small but well visible; posterior furcal lamina narrow and softly arched at the junction of the arm and trunk. Furcal trunk twice as long as the widest part.

Median lobe of aedeagus: Proportionally long and narrow. In lateral view (Fig. 101.3), recurved in an «S»-shape, with apical area strongly sclerotized and the apex sharp and curved towards the ventral face. In dorsal view (Fig. 102.3), compressed laterally little below the middle part, with apex lanceolate. Basal blade elongated and slightly arcuated.

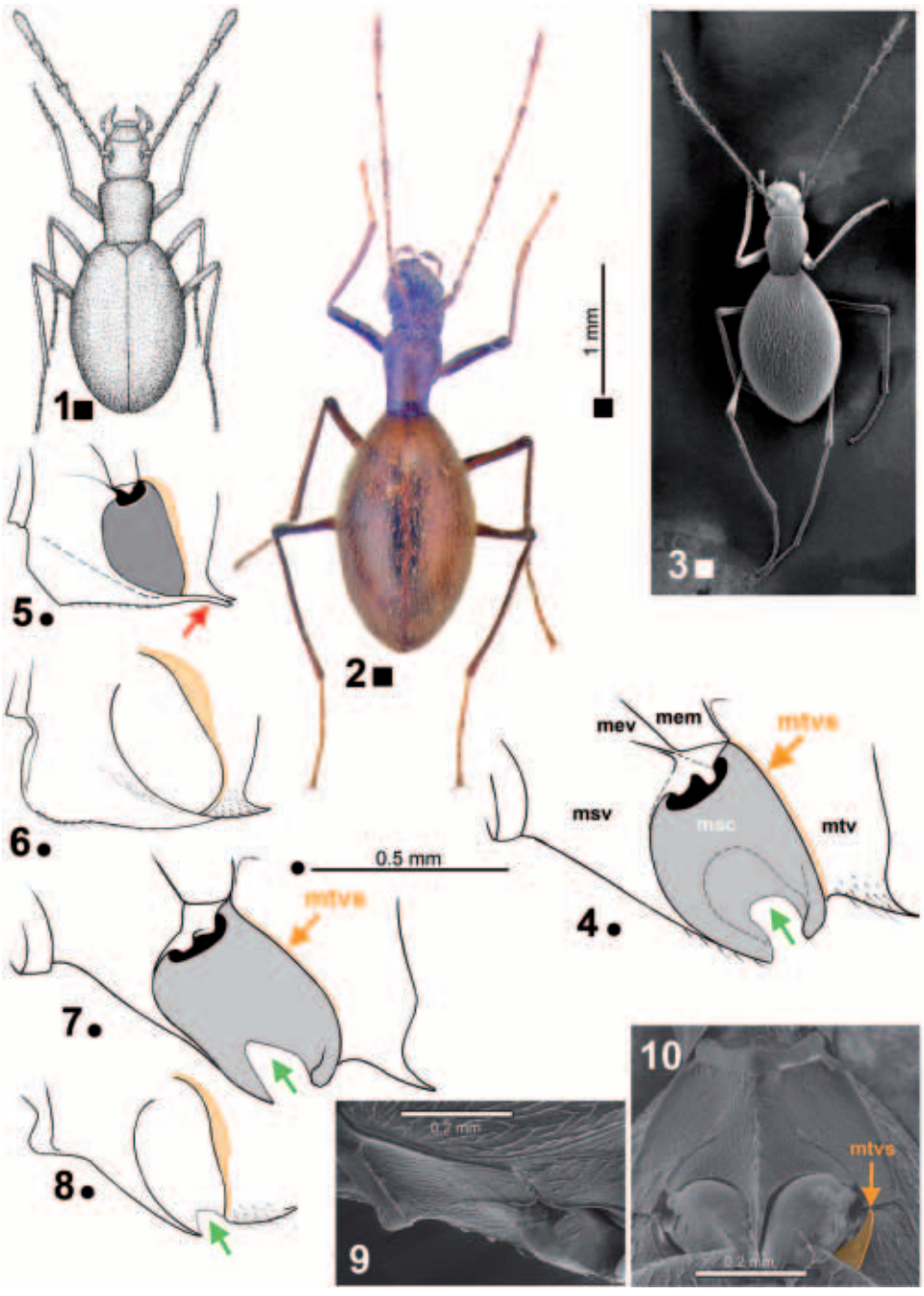
Endophallus (Fig. 102.3): Characterised by being a totally unarmed sac.

Parameres (Fig. 103.3): Thin and slightly shorter than the median lobe. In lateral view recurved with apical part facing dorsally. In dorsal view, a slight latero-external slit is observed before the apical part. Apex not dilated, somewhat sharp and with three short setae inserted equidistantly. Ventral lamina of tegmen short.

Spermathecal complex (Fig. 104.3): Spermatheca small, with very uniform structure and weakly sclerotized. The two globose and well differentiated lobes, the apical one much more developed and the junction duct little differentiated, it is the narrowing part between the two lobes.

Female uroventrite VIII (Fig. 104.10): Posterior edge arcuated, with apical middle part little sclerotized. Spiculum short, slightly widened with beveled apex.

Discussion. Jeannel (1924a) placed *Ceuthmonocharis* into «Brachyscapes Division V», close to the genus *Bathyscimorphus*. Subsequently, Perreau (2000) also maintained the same classification.



FIGURES 98.1–98.10: *Leptodirus* series, *Leptodirus* group. Habitus of: (**1**) *Prospelaeobates bognoloi* (modified from Giachino & Etonti 1996), (**2**) *Spelaeobates* (*Pretneriella*) *kraussi*, (**3**) *S.* (*Spelaeobates*) *coriniensis coriniensis*. Pterothorax in lateral view of: (**4**) *Astagobius angustatus angustatus*, (**5**) *Bathysciotes khevenhuelleri croaticus* (red arrow pointing to the mesoventral keel extended above the entire metaventrite), (**6**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii*, (**7**) *Leptodirus hochenwarti hochenwarti*, (**8**) *S.* (*P.*) *kraussi*, (**9**) *S.* (*S.*) *c. coriniensis*. Pterothorax in ventral view of (**10**) *S.* (*S.*) *c. coriniensis*. Figs **3**, **9**, **10** modified from S. Ćurčić *et al*. 2023. The green arrows indicate the mesocoxal cavities in contact. Abbreviations: **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture.

However, the characters defining «Brachyscapes» and Division V as well as the other divisions of the tribe by Jeannel (1924a) are of no value for establishing phylogenetic relationships for the following reasons:

– The relative length of the first two antennomeres represent a continuum of structural characteristics between «equal» (Euryscapes and Théléomorphes) and «first shorter than the second» (Brachyscapes and Théléomorphes).

– The number of protarsomeres of the male has been shown to have no phylogenetic value as it is a derived state that has appeared in several clades independently (Fig. 15) (See Discussion section of the genus *Speophyes*).

– Tibiae without external spurs, meso- and metatibiae with an apical spine basket («corbeilles» of Jeannel 1924a) and protibiae with spined comb on the external face and at the apex, all these structures are adaptive forms directly influenced by the selective pressure of the environment and, consequently, not useful for establishing taxonomic relationships (see Morphological characters: Legs). Due to their appearance, the former look like walking legs and the latter like digging legs (a hypothesis to be proved). Each of these two forms has occurred independently in several clades (Fig. 15).

The unarmed endophallus of *Ceuthmonocharis* are similar to those found in the genera of the *Leptodirus* group (except *Bathysciotes*), so its transfer into this group appears justified. The classification approach followed here is based on the assumption that an independent appearance of an unarmed endophallus inside the group *Bathyscimorphus* (with no species with unarmed endophallus) as a single event only in this species appears unlikely. It is more parsimonious to place *Ceuthmonocharis* inside the *Leptodirus* group in which this morphological feature is present, even if it is known that unarmed endophalli have occurred independently on at least two occasions (Fig. 1I):

– *Sophrochaeta* group + *Hexaurus*-*Netolitzkya* + *Bathyscia* from Rhodopes, all from the basal clade.

– *Leptodirus* group + *Bathyscia* series of undetermined position, both of the *Leptodirus* series.

In a former classification of this genus it was included in the *Bathyscimorphus* group by Jeannel (1924a) and Perreau (2000), which is sister to the *Leptodirus* and *Apholeuonus* groups (Fig. 1I).

Distribution. It colonises several cavities located in Lower Carniola (Slovenia) along the Sava River, on both banks, between the towns of Domzale and Krsko.

Species

Ceuthmonocharis* (*Ceuthmonocharis*) *freyeri (Miller, 1855)
Adelops freyeri L. Miller, 1855: 506.
Adelops pilosus L. Miller: H. Müller, 1857: 70.
Hohenwartia freyeri Jeannel, 1910a: 25.
Adelops Freyeri L. Miller: Joseph, 1872: 177.
Bathyscia Freyeri Mill.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *Freyeri* Mill.: Reitter, 1885a [1884]: 19.
Hohenwartia Freyeri L. Miller: Jeannel, 1910a: 43.
Ceuthmonocharis Freyeri L. Miller: Jeannel, 1914b: 18.
Ceuthmonocharis Doderoi Jeannel, 1924c: 61.
Ceuthmonocharis (s. str.) *freyeri* L. Miller: Pretner, 1959: 266, 279.
Ceuthmonocharis (s. str.) *doderoi* Jeannel, 1924: Perreau, 2000: 201.

Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkyi (G. Müller, 1908)
Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkyi kodrici G. Müller, 1932
Ceuthmonocharis freyeri kodrici G. Müller, 1932: 13.
Ceuthmonocharis (s. str.) *netolitzkyi* subsp. *kodrici* G. Müller: Pretner, 1959: 268, 280.
Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkyi netolitzkyi (G. Müller, 1908)
Bathyscia freyeri netolitzkyi G. Müller, 1908: 39.
Hohenwartia Freyeri subsp. *Netolitzkyi* J. Müller: Jeannel, 1910a: 43.
Ceuthmonocharis Freyeri subsp. *Netolitzkyi* J. Müller: Jeannel, 1914b: 19.
Ceuthmonocharis Netolitzkyi J. Müller, 1908: Jeannel, 1924a: 344.
Ceuthmonocharis (s. str.) *netolitzkyi* J. Müller: Pretner, 1959: 279.
Ceuthmonocharis (s. str.) *netolitzkyi netolitzkyi* (Müller): Perreau, 2000: 202.

Ceuthmonocharis* (*Ceuthmonocharis*) *pusillus Jeannel, 1924
Adelops schmidti Joseph, 1881: 257 (*Nomen nudum*).
Ceuthmonocharis (*Ceuthmonocharis*) *pusillus* Jeannel, 1924a: 343.

Ceuthmonocharis* (*Ceuthmonocharis*) *robici (Ganglbauer, 1899)
Ceuthmonocharis* (*Ceuthmonocharis*) *robici robici (Ganglbauer, 1899)
Bathyscia (*Bathyscia*) *khevenhülleri robici* Ganglbauer, 1899: 102.

Bathyscia Robici Gglb.: G. Müller, 1908: 38.
Hohenwartia Robici Ganglbauer: Jeannel, 1910a: 43.
Ceuthmonocharis Robici Ganglb.: Jeannel, 1914b: 19.
Ceuthmonocharis (s. str.) *robici* Ganglbauer: Pretner, 1959: 268, 280.
Ceuthmonocharis (s. str.) *robici robici* (Ganglbauer): Perreau, 2000: 202.
Bathyscia heteromorpha Dodero, 1909: 203.
Ceuthmonocharis heteromorphus Dodero: Jeannel, 1924a: 59.
Ceuthmonocharis* (*Ceuthmonocharis*) *robici staudacheri G. Müller, 1919
Ceuthmonocharis robici staudacheri G. Müller, 1919a: 199.
Ceuthmonocharis Staudacheri J. Müller, 1919: Jeannel, 1924a: 344.
Ceuthmonocharis (s. str.) *robici* subsp. *staudacheri* Pretner, 1959: 269, 280.

Subgenus ***Rectipenis*** Pretner, 1959
Ceuthmonocharis (*Rectipenis*) Pretner, 1959: 270.

Type species. *Ceuthmonocharis* (*Rectipenis*) *matjasici* Pretner, 1959: 281 by original designation (habitus in Fig. 96.4).

Diagnosis. The most important characters that allow differentiating subgenus *Rectipenis* from subgenus *Ceuthmonocharis* are the following (Pretner, 1959):

Body (Fig. 96.4): Somewhat more elongated and less convex.

Antennae: Second antennomere only slightly longer than the first one.

Pronotum: Lateral edges in smooth regular arches up to posterior vertices that are sharp and directed backwards. Maximum width observed in the basal part.

Legs: Male protarsi barely dilated.

Mesoventral keel (Pretner 1959): High, with straight anterior and basal edges; vertex forming the edges sharp not rounded.

Median lobe of aedeagus: Small and poorly sclerotized. In lateral view (Fig. 101.4), in unresolved arc in «S», with straight apex. In dorsal view (Fig. 102.4), narrow with parallel sides to the apical area, whose apex describes a slightly sharp arc.

Parameres (Fig. 103.4): Not curved. The apex with three equidistant setae is identical to that of the nominotypic subgenus.

Discussion. Since no molecular data are available, the taxonomic position given by Pretner (1959) is maintained. It is widely agreed on that the genus *Ceuthmonocharis* needs a revision based on modern standards a century after the last one by Jeannel (1924a). Pretner's (1959) image of the habitus (Fig. 96.4) shows antennae with nine antennomeres; this is undoubtedly an observational or drawing error.

Distribution. It is known from two nearby caves near the town of Gabrovka, to the right of the Sava river basin, in Lower Carniola (Slovenia).

Species

Ceuthmonocharis* (*Rectipenis*) *matjasici Pretner, 1959
Ceuthmonocharis (*Rectipenis*) *matjasici* Pretner, 1959: 281.

Genus ***Leptodirus*** F.J. Schmidt, 1832
Leptodirus F.J. Schmidt, 1832a: 9.
Leptoderus F.J. Schmidt, 1852: 381.
Stagobius Schiødte, 1848: 78 (Type species. *Stagobius troglodytes* Schiødte, 1848 = *Leptodirus hochenwarti* Schmidt, 1832).

Type species. *Leptodirus hochenwarti* F.J. Schmidt, 1832 by monotypy (habitus in Fig. 97.2).

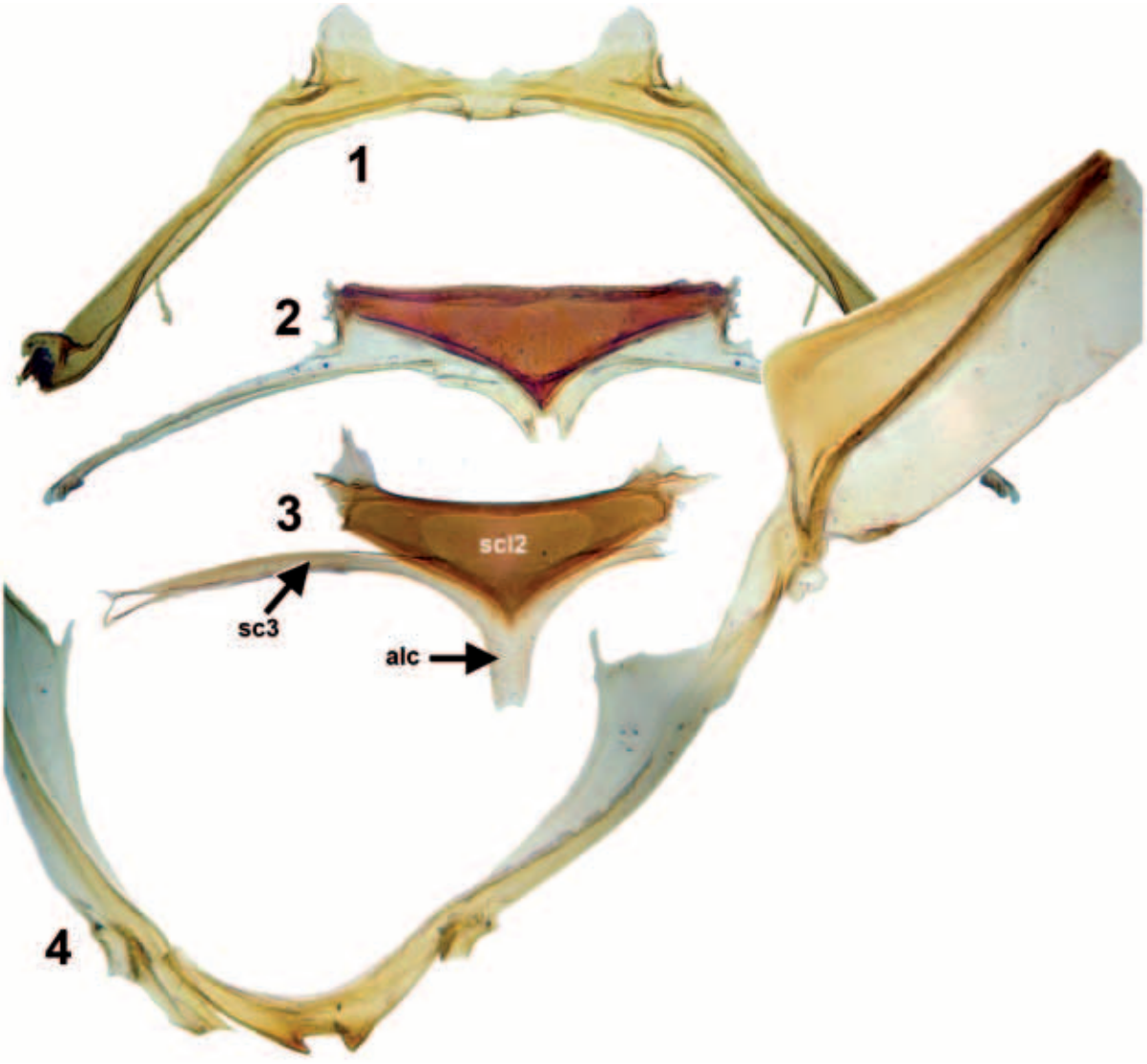
Diagnosis. Size 6.5–7.0 mm. Leptodiroid body shape (Fig. 97.2), very convex and very narrowed anteriorly which gives it a pedunculated appearance. Colour bright reddish somewhat darker on head and pronotum, lighter on elytra. Pubescence reduced, with tiny and very isolated setae on head and pronotum, somewhat longer and scattered on elytra. Integuments smooth, with punctation very superficial and irregular, barely visible, only a few scattered points of different size and shallow on elytra.

Head: Very elongated and progressively narrowed in the posterior part. Antennae are inserted dorsolaterally towards the middle; occipital carina lacking; anophthalmous.

Antennae: Very thin, as long as the length of body, with second antennomere about three times longer than the first; the 7th being the longest and the 9th of similar length than the 11th.

Pronotum: Narrower than head, three or almost three times longer than wide, with the marginal flange blurred. Compressed in the basal third with maximum width in the anterior part.

Elytra: Very globose, more or less spherical, 1.3 times longer than wide as a whole. Somewhat depressed along elytral suture, without marginal flange.



FIGURES 99.1–99.4: *Leptodirus* series, *Leptodirus* group. Metatergal apparatus in ventral view of: (**1**) *Astagobius angustatus angustatus*, (**2**) *Bathysciotes khevenhuelleri tergestinus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii*, (**4**) *Leptodirus hochenwarti hochenwarti*. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Apical area short, somewhat narrowed backwards with apexes little sharp. Parasutural stria lacking.

Legs: Very long; femora with the basal half narrowed and the apical one dilated. Male protarsi pentameres thin or very slightly dilated. Apical area of protibiae without combs and without external spurs, but with a bifid internal one. Meso- and metatibiae without external spurs. Mesotibiae having an internal spur trifid and metatibiae with two internal spurs. Many hairs along the entire length of mesotibiae, but only present in the apical area of metatibiae in which hairs are longer and more distant.

Mesoventral keel (Fig. 98.7): Lacking. The mesocoxal cavities are in contact.

Suture of the metaventrite (Fig. 98.7): Diffuse, not very pronounced, parallel to the coxal cavity and does not delimit an intermediate space.

Metatergal apparatus (Fig. 99.4): Wings of metascutum very long and narrow; apophysis of alacrista reduced to two small lobes.

Metendosternite (Fig. 100.4): Furcal arms long, almost twice the length of trunk; with a prominent expansion on the inner face of the arms. Keel of arms ends in a hooked structure, without a defined process. Posterior plate of almost uniform width and slightly concave edge, towards the middle a reduced anterior lamina. Trunk clearly longer than wide and the middle keel marked with a posterior divergence.

Median lobe of aedeagus: Short and well sclerotized dorsally. In lateral view (Fig. 101.5), very slightly curved, with the apical area hooked towards the ventral side. In dorsal view (Fig. 102.6), basal part narrow with sides parallel in first half then widens to form a spoon-like structure with ventrally concave and apex in form of a slightly narrowed arc; on the terminal third a ventral hair coat projecting from the sides. Basal blade in lateral view small upward curved tongue in the mid-apical area; in dorsal view, short with a gently arched posterior margin, ventral blade of tegmen shorter and of similar width.

Endophallus (Fig. 102.6): Unarmed.

Parameres (Fig. 103.6): Not dilated or bent; somewhat shorter than the median lobe, without apical club and with three short setae, of similar length and equidistant insertion pores.

Spermathecal complex (Fig. 104.4): With three well differentiated regions consisting of the basal lobe which is most sclerotized and developed; the apical lobe subspherical and small, and the union duct short and hyaline.

Female uroventrite VIII (Fig. 104.11): Posterior edge arcuated with an apical middle part little sclerotized and slightly concave. Spiculum sub-triangular, short, considerably wide with apex iforming an arc.

Discussion. Jeannel (1924a) established a phyletic series of *Leptodirus*, to which he assigned the genera *Leptodirus* and *Astagobius*. Subsequently, in his catalog, Perreau (2000) also included the genera *Albanodirus*, *Leptostagus* and *Petkovskiella* in this phyletic series. Available molecular data confirm the phyletic series of *Leptodirus* as understood by Jeannel, while with regard to the genera added later (Perreau 2000) no molecular data are available on*Albanodirus*, *Leptostagus* and *Petkovskiella*.

Examination of the phylogram of figure 1I shows that in the *Leptodirus* group the genus *Leptodirus* is sister to genus *Astagobius* with a 100/100 support. This phylogram branch can be considered as a separate group This group is defined in this work and named «*Leptodirus* group». The other genera, for which no molecular data are available, are provisionally considered to associated with the *Leptodirus* clade.

The genetic distance (Fig. 1I) between RA504 (ssp. *hochenwarti*) and AC51 (ssp. *reticulatus*), with support 99.9/100 indicate that these two taxa are separated and valid species. However, as data of the other four subspecies are missing in the analysis, no taxonomical reevaluation was carried out.

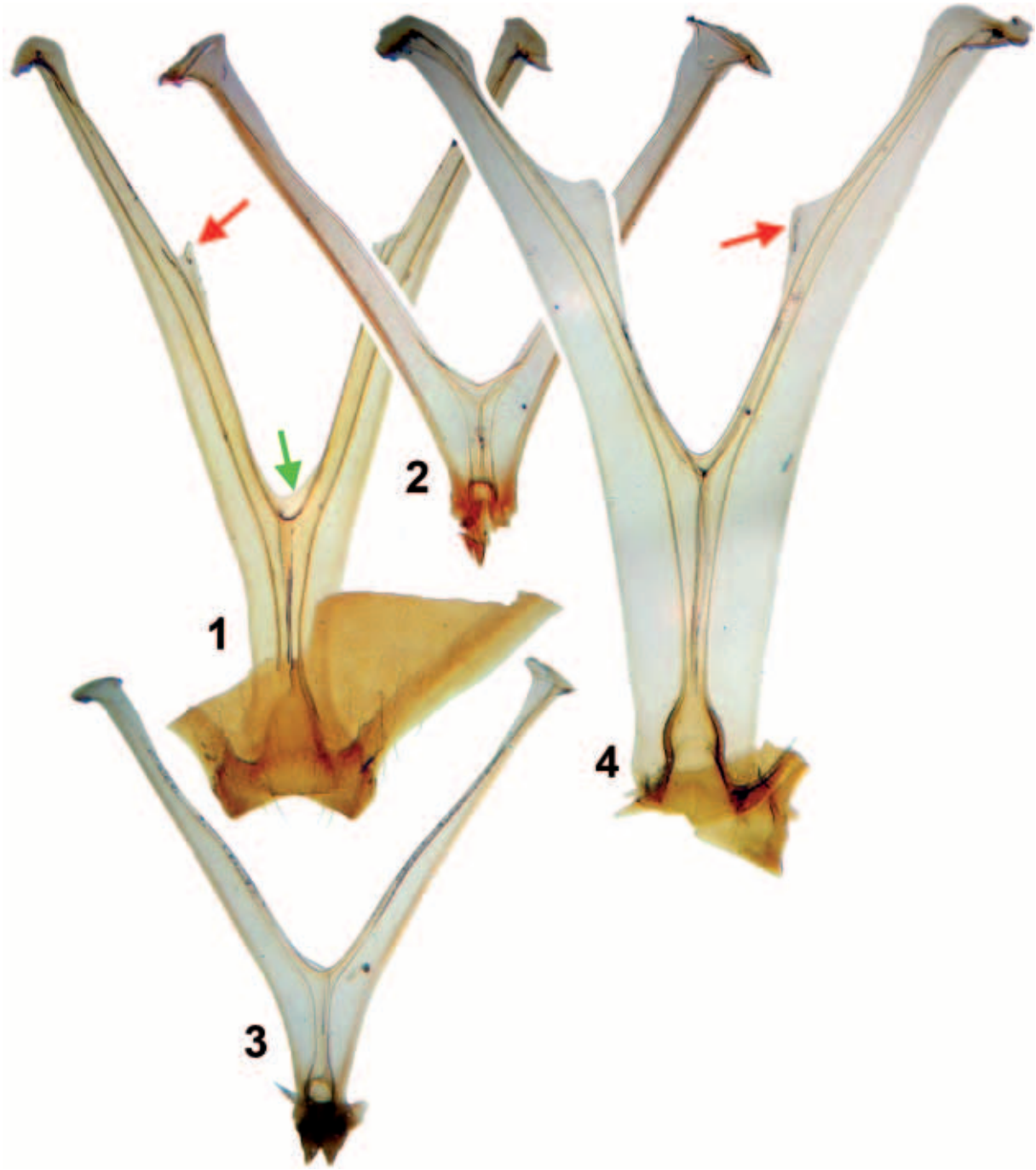
Distribution. The six known subspecies of this genus colonise several caves of the karst of Trieste (Italy), Istria, the mountainous regions of Gorski Kotar and Velebit (Croatia), Kras and further east in the region of Dolenjsko (Slovenia).

Species

Leptodirus hochenwarti F.J. Schmidt, 1832
Leptodirus hochenwarti croaticus Pretner, 1955
Leptodirus hochenwarti croaticus Pretner, 1955: 56.

Leptodirus hochenwarti hochenwarti F.J. Schmidt, 1832
Leptodirus hochenwartii F.J. Schmidt, 1832a: 9.
Leptodirus Hochenwartii Schmidt, 1832b: 83.
Leptodirus Hohenwartii: Schmidt, 1852: 381.
Leptoderus (*Leptoderus*) *Hohenwarti* Schm.: Reitter, 1885a [1884]: 11.
Leptoderus Hohenwarti: Bachofen, 1912: 28.
Leptodirus hochenwarti subsp. *hochenwarti* Schmidt: Pretner, 1955: 54.
Stagobius troglodytes Schiødte, 1848: 79.
Stagobius Troglodytes Schiødte, 1891: 13.
Leptodirus hohenwartii dechsmannii Joseph, 1872: 175.
Leptodirus Hohenwarti var. *Deschmanni* Joseph: Jeannel, 1910a: 44.
Leptodirus grouvellei Jeannel, 1910d: 29.
Leptodirus hohenwarti ab. *grouvellei* Schmidt: Schatzmayr, 1911: 65.
Leptodirus Grouvellei Jeannel: Jeannel, 1911a: 534.
Leptodirus Hohenwarti var. *Grouvellei* Jeannel: Jeannel, 1914b: 48.
Leptodirus hochenwarti hochenwarti Schmidt: Perreau, 2000: 218.

Leptodirus hochenwarti pretneri G. Müller, 1926
Leptodirus hohenwarti pretneri G. Müller, 1926a: 146.
Leptodirus Hohenwarti reticulatus var. *Pretneri* G. Müller, 1926b: 158.
Leptodirus hochenwarti subsp. *Pretneri* G. Müller: Pretner, 1955: 59.



FIGURES 100.1–100.4: *Leptodirus* series, *Leptodirus* group. Metendosternite of: (**1**) *Astagobius angustatus angustatus* (green arrow pointing to the anterior furcal plate), (**2**) *Bathysciotes khevenhuelleri tergestinus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii*, (**4**) *Leptodirus hochenwarti hochenwarti*. Red arrows indicates an internal protuberance.

Leptodirus hochenwarti reticulatus G. Müller, 1904
Leptodirus hohenwarti reticulatus G. Müller, 1904a: 3.
Leptodirus Hohenwarthi reticulatus G. Müller, 1905: 32.
Leptodirus hohenwarti reticulatus bachofeni Schatzmayr, 1911: 65.
Leptoderus Hohenwarti f. *Bachofeni*: Bachofen, 1912: 28.

Leptodirus hochenwarti schmidti Motschulsky, 1856
Leptodirus schmidtii Motschulsky, 1856: 35.
Leptoderus Schmidtii Motsch.: Motschulsky, 1869: 253.
Leptodirus Hohenwarthi var. *Schmidti* Mots: Abeille de Perrin, 1878: 153.
Leptodirus Hohenwarthi subsp. *schmidti* Motsch.: Schatzmayr, 1911: 65.
Leptodirus hochenwarti subsp. *schmidti* Motschulsky: Pretner, 1955: 57.

Leptodirus hochenwarti velebiticus Pretner, 1970
Leptodirus hochenwarti velebiticus Pretner, 1970a: 323.

Spelaeobates subgroup

Diagnosis. Subgroup genera characterised by male protarsi tetrameric, parameres thin and equipped with three apical setae, and endophallus without sclerotized structures. *Bathysciotes* is the only one of the subgroup with an endophallus armed with sclerotized structures; it probably derives from the basal cladogenesis.

Body shape more or less specialised, ranging from bathyscioid or pholeuonoid to leptodiroid; antennae inserted in basal or median third of head.

Discussion. V.B. Guéorguiev (1974a) established for the genus *Spelaeobates* the subtribe Spelaeobatina, following the approach of Jeannel (1924a), who had introduced it as a phyletic lineage within the tribe Antroherpona. Following the unpublished molecular data obtained by S. Polak (*pers. comm.* 2022), the genera of this group do not require the status of a subtribe as Spelaeobatina. *Spelaeobates* is closely related to *Prospelaeobates* and *Deelemaniella*, and all form a sister group within the *Leptodirus* lineage. In the tree of figure 1I the genus *Bathysciotes*, which belongs to *Spelaeobates* subgroup genera, joins with support of 51.9/98 the clade of the *Leptodirus* subgroup and both to the *Apholeuonus* group with 100/100 support.

Key to genera

1. Body-shape bathyscioid (Fig. 96.2).....*Bathysciotes*
- Body-shape scaphoid-leptodiroid (Fig. 98.2, 98.3) or pholeuonoid (Fig. 97.1, 98.1) 2

2. Body-shape scaphoid or leptodiroid (Fig. 98.2, 98.3). Antennae inserted in basal fourth of head 3
- Body-shape pholeuonoid (Fig. 97.1, 98.1). Antennae inserted in medium third of head 4

3. First protarsomere dilated in males. In dorsal view, the sides of the median lobe narrow progressively to the apex and in this area it is truncated (Fig. 103.9)...
.....*Spelaeobates* (*Spelaeobates*)
- First protarsomere not dilated in males. In dosal view, the median lobe narrows towards the apical third and forms a palette structure in the apical part (Fig. 103.8)..... *Spelaeobates* (*Pretneriella*)

4. Parameres bearing three long setae (Fig. 103.7).....
.....*Prospelaeobates*
- Parameres bearing two long setae (Fig. 103.5) .....
.....*Deelemaniella*

Genus ***Bathysciotes*** Jeannel, 1910
Bathysciotes Jeannel, 1910a: 15.

Type species. *Adelops khevenhülleri* L. Miller, 1852 by original designation (for the habitus see that of the similar subspecies *Bathysciotes khevenhuelleri croaticus* in Fig. 96.2).

Diagnosis. Size between 2.4–2.8 mm. Bathyscioid body shape, short, oval and very convex (Fig. 96.2). Colour reddish-brown with integument entirely covered by fine, short, lying, yellowish and tight pubescence.

Head: With full occipital carina, little marked, and a fine and scattered punctation; anophthalmous.

Antennae: Thin and proportionally long, reaching or exceeding half of the body length, 1st and 2nd antennomeres are the most robust and of similar length. Antennal club differentiated with all the antennomeres longer than wide.

Pronotum: Very transverse (width/length ratio = 1.9), with maximum width at the base or a little earlier. Base as wide as the anterior margin of elytra. Anterior margin much narrower than posterior. Posterior part of lateral margins more or less and regularly curved. Posterior vertices little sharp and acute angles with fine and scattered punctation.

Elytra: Slightly longer than wide (width/length ratio = 1.1), with maximum width along the anterior half or in basal third. Posterior part decreasing in regular curve to apex in wide arc. Punctation very fine and very close; no transverse striolae, no parasutural stria.

Legs: Short, protarsi in both sexes tetrameres and thin; anterior tibiae with a comb of short and equal spines in much of the apical outer edge.

Mesoventral keel (Fig. 98.5): High, with anterior edge convex or somewhat broken, forming an obtuse angle with vertex more or less rounded. Lower edge slightly sinuated with setae, and with rounded edge. Posterior process prolonged above all the metaventrite.

Suture of the metaventrite (Fig. 98.5): Describes an continuous arc; little separated from the edge of mesocoxal cavity delimiting a narrow and elongated area.

Metatergal apparatus (Fig. 99.2): With the wings of the metascutum very narrow, very long and arcuated, apophysis of the alacrista very reduced, with sharp apexes.

Metendosternite (Fig. 100.2): Furcal arms of regular width and very long, three times longer than the furcal trunk, with well-developed terminal processes. Posterior sheet of similar width in all its extension, with posterior lateral rim almost straight. Trunk of the furca as long as the area of greater basal width; thick middle keel without marked posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 101.2), little elongated and very little arcuated, with apical area flattened and apex curved towards the ventral face. In dorsal view (Fig. 102.2), apical area narrowed with concave lateral margins and wide apex in blunt beak. Basal lamina of median lobe elongated into a broad arc with ventral lamina of tegmen reduced.

Endophallus (Fig. 102.2): Basal region without differentiated pieces. Middle region with three groups of spines, medium one poorly developed, other two wider laterally situated. Basal part of apical region with two wide folds arranged in longitudinally progressively decrease from the base and framed by two sclerotized and elongated pieces converging towards the apical part; thorny structures or disordered inserts are observed in this area. In addition, in lateral view and below the folds a long tongue-like structure is observed.

Parameres (Fig. 103.2): Somewhat shorter than the median lobe, arcuated, without a differentiated club. Apical area narrowed, bearing three setae of similar length, two apical and a third a little further away, with internal lateral insertion.

Spermathecal complex (Fig. 104.2): Spermatheca very short, curved and sclerotized evenly. Apical lobe spherical and very developed; the middle duct and the basal lobe form homogenous structure without clear delimination visible, into which; the spermatic duct of hyaline appearance is inserting and somewhat wider in the area of merging; no spermathecal gland is observed.

Female uroventrite VIII (Fig. 104.9): Apical border in wide arc, containing a piece with a macula in the posterior middle area. Spiculum quite long, wide and with an arcuated apex.

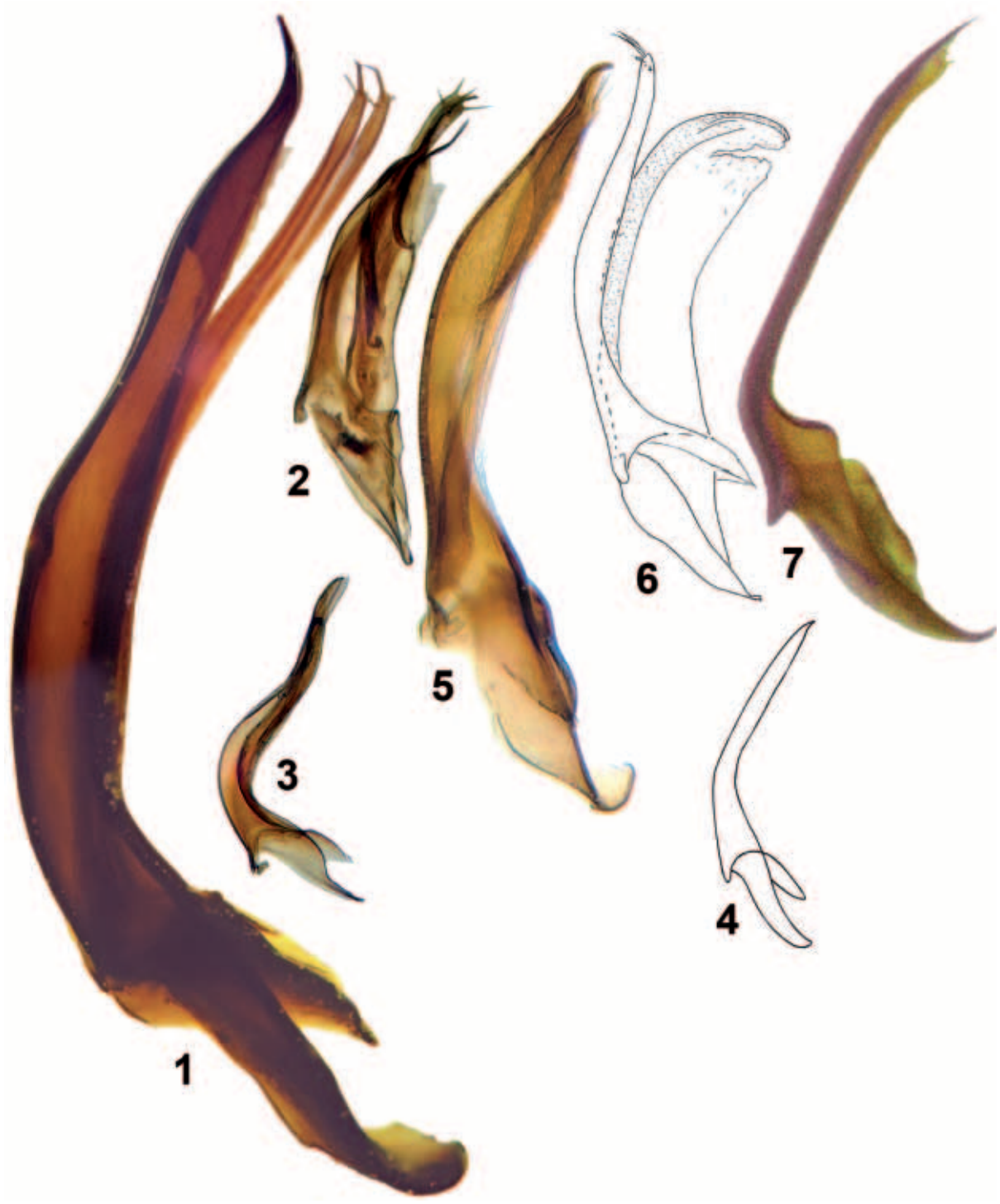
Discussion. Jeannel (1924a) including *Bathysciotes* into the III Division of «Théléomorphes» and with this establishing for this genus a special phyletic series. The main character used by R. Jeannel for this was the tetramerism of male protarsi. V.B. Guéorguiev (1974a) established for the genus the subtribe Bathysciotina. Perreau (2000) on the other hand included *Bathysciotes* into the *Neobathyscia* phyletic series of the Bathysciotina subtribe. In the light of our phylogenetic tree of figure 1I, none of the systematic approaches mentioned above seem hold when compared to the molecular analysis.*Bathysciotes*, although with a not particularly high support (51.8/98), was in fact founf to be the sister group of the clade *Leptodirus* + *Astagobius* within the phyletic series of *Leptodirus*.

Distribution. Monotypical genus with five subspecies widely distributed in caves of Carniola region (Slovenia), the islands of Cres, Krk and Losinj (Croatia) and the Istrian peninsula.

Species

Bathysciotes khevenhuelleri (L. Miller, 1852)
Bathysciotes khevenhuelleri crepsensis G. Müller, 1922
Bathysciotes khevenhülleri crepsensis G. Müller, 1922b: 14.
Bathysciotes Khevenhülleri crepsensis G. Müller, 1923: 6.

Bathysciotes khevenhuelleri croaticus (L. Miller, 1867)
Adelops croaticus L. Miller, 1867: 551.
Bathyscia croatica Mill.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *croatica* Mill.: Reitter, 1885a [1884]: 19.
Aphaobius Khevenhülleri sbsp. *croatica* Mill.: G. Müller, 1908: 39.
Bathysciotes Khevenhülleri subsp. *croatica* L. Miller: Jeannel, 1910a: 38.
Bathysciotes Khevenhülleri subsp. *croaticus* L. Miller: Jeannel, 1911a: 426.



FIGURES 101.1–101.7: *Leptodirus* series, *Leptodirus* group. Aedeagus in lateral view of: (**1**) *Astagobius angustatus angustatus*, (**2**) *Bathysciotes khevenhuelleri croaticus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii,* (**4**) *C.* (*Rectipenis*) *matjasici* (modified from Pretner 1959), (**5**) *Leptodirus hochenwarti reticulatus*, (**6**) *Prospelaeobates bognoloi* (modified from Giachino & Etonti 1996), (**7**) *Spelaeobates* (*Spelaeobates*) *novaki* (modified from S. Ćurčić *et al.* 2023).

Bathyscia (*Bathysciotes*) *Khevenhülleri* Müller subsp. *Croatic*a L. Miller: Jeannel, 1914b: 17.
Bathysciotes khevenhuelleri croaticus (Miller): Perreau, 2000: 190.

Bathysciotes khevenhuelleri horvathi (Csiki, 1901)
Bathyscia horvathi Csiki, 1901: 487.
Aphaobius Khevenhülleri sbsp. *Horvathi* Csiki: G. Müller, 1908: 38.
Bathysciotes Khevenhülleri subsp. *Horvathi* Csiki: Jeannel, 1910a: 38.
Bathyscia (*Bathysciotes*) *Khevenhülleri* subsp. *Horvathi* Csiki: Jeannel, 1914b: 17.
Bathyscia Khevenhülleri horváthi Csiki: Depoli, 1920: 261.
Bathysciotes Khevenhülleri Subsp. *Horváthi* Csiki, 1901: Jeannel, 1924a: 276.
Bathysciotes khevenhuelleri horvathi (Csiki): Perreau, 2000: 191.

Bathysciotes khevenhuelleri khevenhuelleri (L. Miller, 1852)
Adelops khevenhülleri L. Miller, 1852: 131.
Adelops Khevenhülleri Miller: L. Miller, 1855: 506.
Bathyscia Khevenhülleri Mill.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *Khevenhülleri* Mill.: Reitter, 1885a [1884]: 19.
Bathyscia subrotundata Reitter, 1885a [1884]: 19.
Bathyscia (*Bathyscia*) *subrotundata* Reitter, 1885a [1884]: 219.
Bathyscina Khevenhülleri Mill.: Jeannel, 1908a: 299.
Bathysciotes Khevenhülleri L. Miller: Jeannel, 1910a: 37.
Bathyscia (*Bathysciotes*) *Khevenhülleri* L. Miller: Jeannel, 1914b: 16.
Bathysciotes Khevenhülleri Subsp. *Khevenhülleri* L. Miller, 1851: Jeannel, 1924a: 275.
Bathysciotes khevenhülleri Müll.: Baccetti & Sbordoni, 1967: 84.
Bathysciotes khevenhülleri khevenhülleri (Miller): Perreau, 2000: 191.

Bathysciotes khevenhuelleri tergestinus G. Müller, 1922
Bathysciotes khevenhülleri tergestinus G. Müller, 1922b: 14.
Bathysciotes Khevenhülleri Subsp. *tergestinus* J. Müller, 1922: Jeannel, 1924a: 276.

Genus ***Deelemaniella*** Perreau, 2002
Deelemania Perreau, 1999: 400 (*Nom. praeocc*. Homonymy with *Deelemania* Jocque, 1983 – Aranea –).
Deelemaniella Perreau, 2002: 50.

Type species. *Deelemania pretneri* Perreau, 1999 by original designation (habitus in Fig. 97.1).

Diagnosis. Small size, 2.0 mm. Pholeuonoid shape (Fig. 97.1); body narrow, convex and elongated. Integument bright dark reddish; yellowish pubescence, with short, thin and raised hairs.

Head: Elongated; occipital carina fine, generally blurred; anophthalmous.

Antennae: Long, reaching middle area of elytra. Second antennomere elongated, almost a half the length of the first one. All antennomeres longer than wide; antennomeres 7th, 9th and 10th piriform, somewhat widened in apical part; 11th antennomere somewhat longer than 10th, with apical area very narrow.

Pronotum: Almost as long as wide. Lateral margins converging towards base which is strongly narrowed, basal third between subparallel and slightly sinuous,showing greatest width at level of anterior third. Punctation very fine, with dots very close to each other on a clearly micro-cross-linked integument background that gives it a mat appearance.

Elytra: Oval, between 1.4–1.5 times longer than wide, with maximum width in the middle. Transverse striolation and parasutural stria lacking; apical parts rounded. Punctation and micro-cross-linked similar to pronotum.

Legs: Quite long and robust; protibiae combless at apical and external edges. Male protarsi tetrameres and slightly dilated; tibiae with internal spurs; tibiae and femora with fine bristling spines, without apical basket.

Mesoventral keel (Perreau 1999): Very low, vertex non-angular and ventral edge wide.

Suture of the metaventrite, metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus (Fig. 102.5): Short and thick, shape subtriangular, more widened in apical third. Sides slightly concave in basal third and arcuated in apical two thirds, these converge to form a little narrowed and sharp tip. Basal blade short and wide, with posterior edge in concave arc in middle area.

Endophallus (Fig. 102.5): Unarmed, without sclerotized pieces.

Parameres (Fig. 103.5): Widened by half, then thin and as long as the median lobe. Apical area very arcuated, with apex not dilated and bearing two setae, one at the tip and another, subapical, slightly more robust, oriented towards interior.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Relative length of first two antennomeres, absence of comb at apical and sternal edges of protibiae and tetrameres protarsi in male allow to place this genus into subtribe Bathysciina (V.B. Guéorguiev 1974a, 1974b, 1976; «Théléomorphes» group, division II of Jeannel, 1924a). The same characters place *Deelemaniella* in phyletic series of *Leonhardella*, close to the genera *Anillocharis*, *Leonhardella* and *Tartariella*. According to Perreau (1999) there are notable differences between those genera regarding the following characters: absence of external spurs at tibiae, low mesoventral keel, endophallus without basal sclerotized pieces and apical part of parameres with two setae. Recent and unpublished molecular data link *Deelemaniella* to *Spelaeobates* and *Prospelaeobates* inside a *Spelaeobates* group, within a *Leptodirus* series, as sister group of the *Leptodirus* + *Astagobius* lineage (S. Polak, *pers. comm*. 2022).

Distribution. A monospecific genus from two caves on Sitnica mountain, Mackica Cave and Pokraj Sane Cave, both located in Sana Valley in the south-west of Bosnia-Herzegovina.

Species

Deelemaniella pretneri (Perreau, 2002)
Deelemania pretneri Perreau, 1999: 402.
Deelemaniella pretneri Perreau, 1999: Perreau, 2002: 50.

Genus ***Prospelaeobates*** Giachino & M. Etonti, 1996
Prospelaeobates Giachino & M. Etonti, 1996: 66.

Type species. *Prospelaeobates vrezeci* Giachino & M. Etonti, 1996 by original designation (for the habitus see that of the similar species *Prospelaeobates bognoloi* in Fig. 98.1).

Diagnosis. Small size, between 1.8–2.6 mm, pholeuonoid facies, elongated body and small, cordiform pronotum and physogastric elytra (Fig. 98.1).

Head: Non-retractable, without occipital carina; anophthalmous.

Antennae: Inserted at half length of head, moderately elongated, reaching or beyond half of elytra if stretched backwards; antennomeres 7th, 9th and 10th asymmetrically dilated at apex; first antennomere shorter than the second one.

Pronotum: Small, cordiform, with sides little arcuated anteriorly, little sinuated posteriorly, with maximum width at anterior third; base narrower than elytral base.

Elytra: Ovoid, moderately elongated, regularly arcuated in posterior half, moderately physogastria, with transversely non-aligned microsculpture. Parasutural stria absent.

Legs: Long and thin. Male protarsi tetrameres and imperceptibly dilated; protibiae slightly curved and devoid of a real comb on outer margin, but equipped with a series of aligned bristles. Mesotibiae weakly arcuated and equipped with a series of long and weak spines on outer margin; metatibiae straight; meso- and metatibiae equipped with apical basket.

Mesoventral keel (Giachino & M. Etonti, 1996): Low, not prolonged on metaventrite; with non-confluent mesocoxal cavities.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Small; in lateral view (Figs 101.6) stout and poorly arcuated; in dorsal view (Figs 102.7) apex largely rounded.

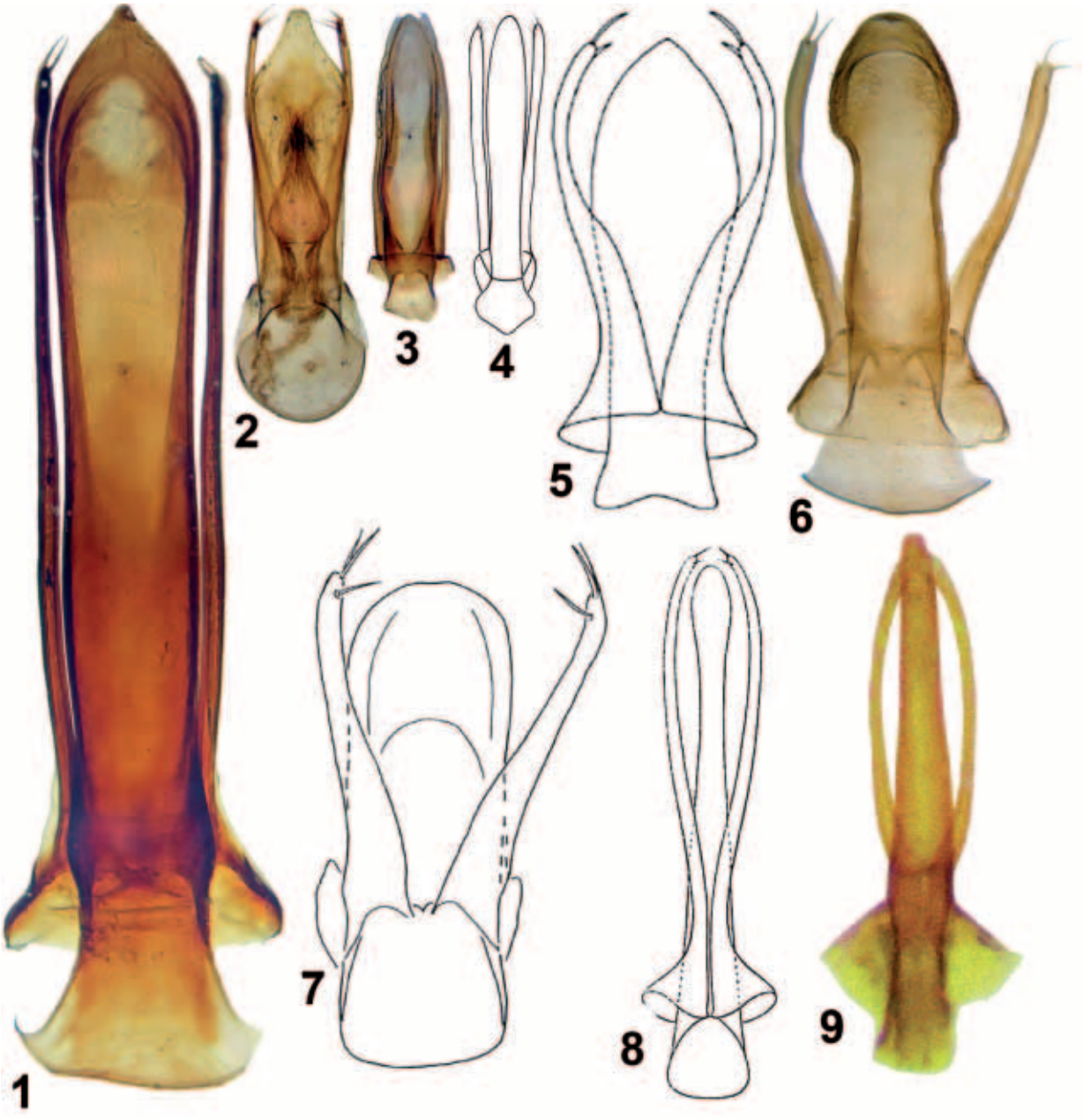
Endophallus (Fig. 102.7): Unarmed, lacking obvious sclerotized structures.

Parameres (Fig. 103.7): Thin, barely exceeding apex of median lobe and equipped with three apical setae.

Spermathecal complex: Spermatheca reniform (Fig. 104.5), little elongated, moderately narrowed at the centre, with proximal lobe slightly more developed and sclerotized than the apical lobe. Spermatic duct with manifest and sclerotized piece at insertion into the spermatheca. Spermathecal gland hyaline, shapeless.

Female uroventrite VIII: Unknown.

Discussion. The taxonomic position as established by Giachino & M. Etonti (1996) based on morphology could not be confirmed by us due to lack of molecular data, however, a personal communication by S. Polak (2022) affirmed that the position in an molecular analysis supports the findings deduced by morphology. *Prospelaeobates*, in fact appears closely related to genus *Spelaeobates* by similarities in characters such as the tetrameric protarsi of malesand aedeagic structure (in particular for the arrangement of apical setae of parameres and the shape of median lobe of aedeagus). Nevertheless there are slo distinct differences concerning the structure of body with less specialised characteristic adaptations to the subterranean environment (less leptodiroid body shape, with less physogastrics elytra, antennae inserted in the middle third of head instead of in basal quarter, less elongated appendages). Unpublished molecular data of *Spelaeobates, Prospelaeobates* and *Deelemaniella* (S. Polak, *pers. comm*. 2022) show these three genera closely related each other. They are the sister group of *Leptodirus* + *Astagobius*.



FIGURES 102.1–102.9: *Leptodirus* series, *Leptodirus* group. Aedeagus in dorsal view of: (**1**) *Astagobius angustatus angustatus*, (**2**) *Bathysciotes khevenhuelleri croaticus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii,* (**4**) *C.* (*Rectipenis*) *matjasici* (modified from Pretner 1959), (**5**) *Deelemaniella pretneri* (modified from Perreau 1999), (**6**) *Leptodirus hochenwarti reticulatus,* (**7**) *Prospelaeobates vrezeci* (modified from Giachino & Etonti 1996), (**8**) *Spelaeobates* (*Pretneriella*) *kraussi* (modified from G. Müller 1903), (**9**) *S.* (*Spelaeobates*) *novaki* (modified from S. Ćurčić *et al.* 2023).

DISTRIBUTION. Known of some caves of Dalmatian coast, in Istria (Slovenia) and on the island of Cres (Croatia).

Species

Prospelaeobates bognoloi Giachino & M. Etonti, 1996
Prospelaeobates bognoloi Giachino & M. Etonti, 1996: 66.

Prospelaeobates brelihi Polak & Bognolo, 2003
Prospelaeobates brelihi Polak & Bognolo, 2003: 18.

Prospelaeobates vrezeci Giachino & M. Etonti, 1996
Prospelaeobates vrezeci Giachino & M. Etonti, 1996: 65.

Genus ***Spelaeobates*** G. Müller, 1901
Spelaeobates G. Müller, 1901: 16.

TYPE SPECIES. *Spelaeobates novaki* G. Müller, 1901 by subsequent designation (for the habitus see that of the similar species *Spelaeobates coriniensis coriniensis* in Fig. 98.3).

DIAGNOSIS. Size small, between 2.5–3.0 mm. Leptodiroid body shape, very convex and very narrowed anteriorly which gives it a pedunculated appearance (Figs 98.2, 98.3). Colour bright reddish somewhat darker on head and pronotum, lighter on elytra. Short, scattered and straightened pubescence.

Head: Oval, large and voluminous, as wide as long. Cheeks protruding, very convex, with sutures between them and sides. Occipital carina differentiated by a smooth curved line with anterior concavity; marked and deeply punctate; anophthalmous.

Antennae: Inserted into posterior quarter of head, very long and very thin, normally exceeding the apex of elytra. Second antennomere as long, or longer than, and as thick as the first one; apical antennomeres with dilated top; 11th rather short, half of 10th one.

Pronotum: As wide as, or almost as wide as, head; longer than width, between 1.4–1.6 times longer than width. Base clearly narrower than anterior margin; sides flanged, at least in posterior half. Regularly convex in anterior half and concave in posterior one, in basal part narrowed and can be somewhat sinuous. Punctation variable, thick, deep and close or fine, superficial and scattered.

Elytra: Pyriform, very convex, being the physogastria very marked; altogether about 1.6 times longer than wide, with basal part very narrow and apical area rounded. Parasutural stria lacking.

Legs: Very long and very thin. Males protarsi tetrameres with the first tarsomere dilated or thin. Anterior tibiae without comb on apical margin, but with a small comb on apical third of outer edge. Femora little widened in apical area.

Mesoventral keel (Figs 98.8, 98.9): High or low with rounded vertex and obtuse angle; posterior edge smooth or toothed. Mesocoxal cavities connected.

Metaventral suture (Figs 98.8, 98.10): In an arc bordering the entire coxal cavity and delimiting a narrow area along the middle part.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Poorly sclerotized, small, thin and narrow. In lateral view (Fig. 101.7), the ventral side at an obtuse angle between the basal area and the mid-apical area, the latter being absolutely straight. In dorsal view (Figs 102.8, 102.9), with sides subparallel to apex, little sharp, or subparallel to apical area that widens being sides arcuated and apex little sharp. Basal blade short and terminally truncated.

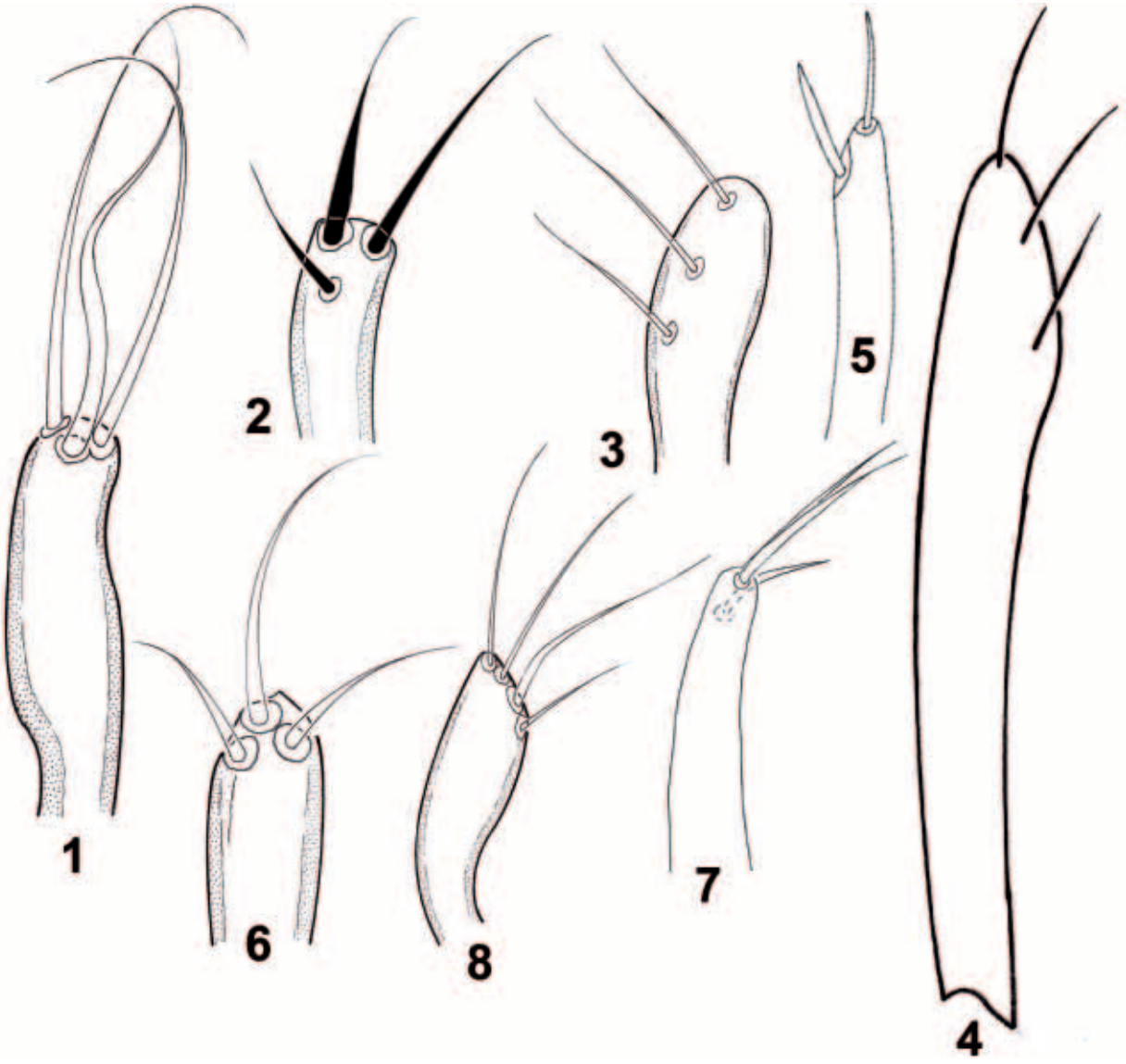
Endophallus (Figs 102.8, 102.9): Without basal armor.

Parameres (G. Müller 1901): Thin and slightly arcuated, somewhat longer than the median lobe. Without differentiated club and three – or four (S. Ćurčić *et al*. 2023) – setae, two apical with insertion pores nearby and a subapical inserted in internal margin, distant, in general somewhat shorter. Ventral blade of tegmen short, flared and wider than basal blade of median lobe.

Spermathecal complex: Spermatheca small (Figs 104.6, 104.7), weakly and uniformly sclerotized and poorly differentiated regions.

Female uroventrite VIII (Figs 104.12, 104.13): With broad, somewhat concave apical margin in the middle or progressively narrowing to form a convex arc; basal margin in a smooth arc without spiculum.

DISCUSSION. Following the «classic» systematic, it appears to be close to the genera *Anthroherpon* and *Leptomeson*, and its facies is very similar to that of *A. spelaebatoides*. Previous authors pointed out that the most obvious differences with these genera are the sides of pronotum lacking a marginal rim; males protarsi are pentameres; second antennomere always shorter and thinner than first one and the absence of a mesoventral keel. There are also marked differences in shape and structures of the aedeagus. Giachino & M. Etonti (1996) in the description of genus *Prospelaeo-*



FIGURES 103.1–103.8: *Leptodirus* series, *Leptodirus* group. Apex of the paramere of: (**1**) *Astagobius angustatus angustatus*, (**2**) *Bathysciotes khevenhuelleri croaticus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii,* (**4**) *C.* (*Rectipenis*) *matjasici* (modified from Pretner 1959), (**5**) *Deelemaniella pretneri* (modified from Perreau 1999)*,* (**6**) *Leptodirus hochenwarti reticulatus,* (**7**) *Prospelaeobates vrezeci* (modified from Giachino & Etonti 1996), (**8**) *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* (redrawn from S. Ćurčić *et al.* 2023).

bates pointed out that this genus is closely related to the genus *Spelaeobates* by exhibiting tetrameric protarsi and presenting a very similar aedeagus.

Now availabile unpublished molecular data of *Spelaeobates, Prospelaeobates* and *Deelemaniella* (S. Polak *pers. comm*. 2022) show these three genera are found to be closely related each other in molecular analysis. Herein they form the sister group of *Leptodirus* + *Astagobius*.

Distribution. Croatia. Colonizes several islands of Croatian archipelago of Dalmatia region.

Subgenus ***Pretneriella*** V.B. Guéorguiev, 1976
Pretneriella V.B. Guéorguiev, 1976: 128.
Type species. *Spelaeobates pharensis* G. Müller, 1901 by original designation (for the habitus see that of the similar species *Spelaeobates kraussi* in Fig. 98.2).

Diagnosis. Differentiating characters of the subgenus according to Jeannel, 1924a and V.B. Guéorguiev, 1976:

– Pronotum with lateral margins flanged along its entire length or only in basal part; punctation strong and deep, or fine and superficial, with dots scattered.

– First protarsomere not dilated in males.

– Mesoventral keel (Fig. 98.8) high, with a smooth posterior edge.

– Aedeagus (Fig. 102.8) with apical area of median lobe widened and parameres with dilated and armed club bearing three setae.

– *Spermathecal complex* (Fig. 104.6): Spermatheca small, slightly sclerotized, slightly arched on the ventral side between the apical lobe and the union part; spherical apical lobe and the union duct and basal lobe form a whole of similar width; the spermatic duct, which is slightly widened in the anterior part, ends in the latter part. No spermathecal gland observed.

– *Female uroventrite VIII* (Fig. 104.12): The lateral margins of the posterior edge progressively tapering to form a narrow arc; the anterior margin in a smooth arc and without spiculum.

Distribution. Croatia. Subgenus whose species have colonized several caves in isolated karst that correspond to islands of Brač, Hvar and Vis.

Species

Spelaeobates* (*Pretneriella*) *bachofeni Breit, 1913
Spelaeobates bachofeni Breit, 1913a: 15.
Spelaeobates Bachofeni Breit: Jeannel, 1914b: 53.
Spelaeobates (*Pretneriella*) *Bachofeni* Breit: V.B. Guéorguiev, 1976: 129.
Spelaeobates (*Pretneriella*) b*achofeni* Breit: Perreau, 2000: 339.

Spelaeobates* (*Pretneriella*) *czernyi Breit, 1913
Spelaeobates Czernyi Breit, 1913a: 14.
Spelaeobates (*Pretneriella*) *czernyi* Breit: V.B. Guéorguiev, 1976: 129.

Spelaeobates* (*Pretneriella*) *kraussi G. Müller, 1903
Spelaeobates kraussi, G. Müller 1903b: 885.
Spelaeobates Kraussi J. Müller: Jeannel, 1910a: 45.
Spelaeobates (Pretneriella) Kraussi Müller: V.B. Guéorguiev, 1976: 129.
Spelaeobates (Pretneriella) kraussi J. Müller: V.B. Guéorguiev, 1990: 239.

Spelaeobates* (*Pretneriella*) *peneckei G. Müller, 1903
Spelaeobates peneckei, G. Müller 1903b: 882.
Spelaeobates Peneckei J. Müller: Jeannel, 1910a: 45.
Spelaeobates (*Pretneriella*) *Peneckei* Müller: V.B. Guéorguiev, 1976: 129.
Spelaeobates brattianus Absolon: Jeannel, 1924a: 397 (*Nomen nudum*).
Spelaeobates (*Pretneriella*) *peneckei* Müller: Perreau, 2000: 339.

Spelaeobates* (*Pretneriella*) *pharensis G. Müller, 1901
Spelaeobates* (*Pretneriella*) *pharensis langhofferi G. Müller, 1931
Spelaeobates pharensis langhofferi G. Müller, 1931a: 205.
Spelaeobates (*Pretneriella*) *pharensis langhofferi* Müller: Perreau, 2000: 339.

Spelaeobates* (*Pretneriella*) *pharensis pharensis G. Müller, 1901
Spelaeobates pharensis G. Müller, 1901: 20.
Spelaeobates (*Pretneriella*) *pharensis* Müller: V.B. Guéorguiev, 1976: 129.
Spelaeobates (*Pretneriella*) *pharensis pharensis* Müller: Perreau, 2000: 340.

Subgenus ***Spelaeobates***

Diagnosis. Differentiating characters of subgenus in accordance with the works of Jeannel (1924a) and (V.B. Guéorguiev (1976):

– Pronotum with lateral margins flanged along its entire length and large, withdeep punctation and nearby dots, frequently touching each other.

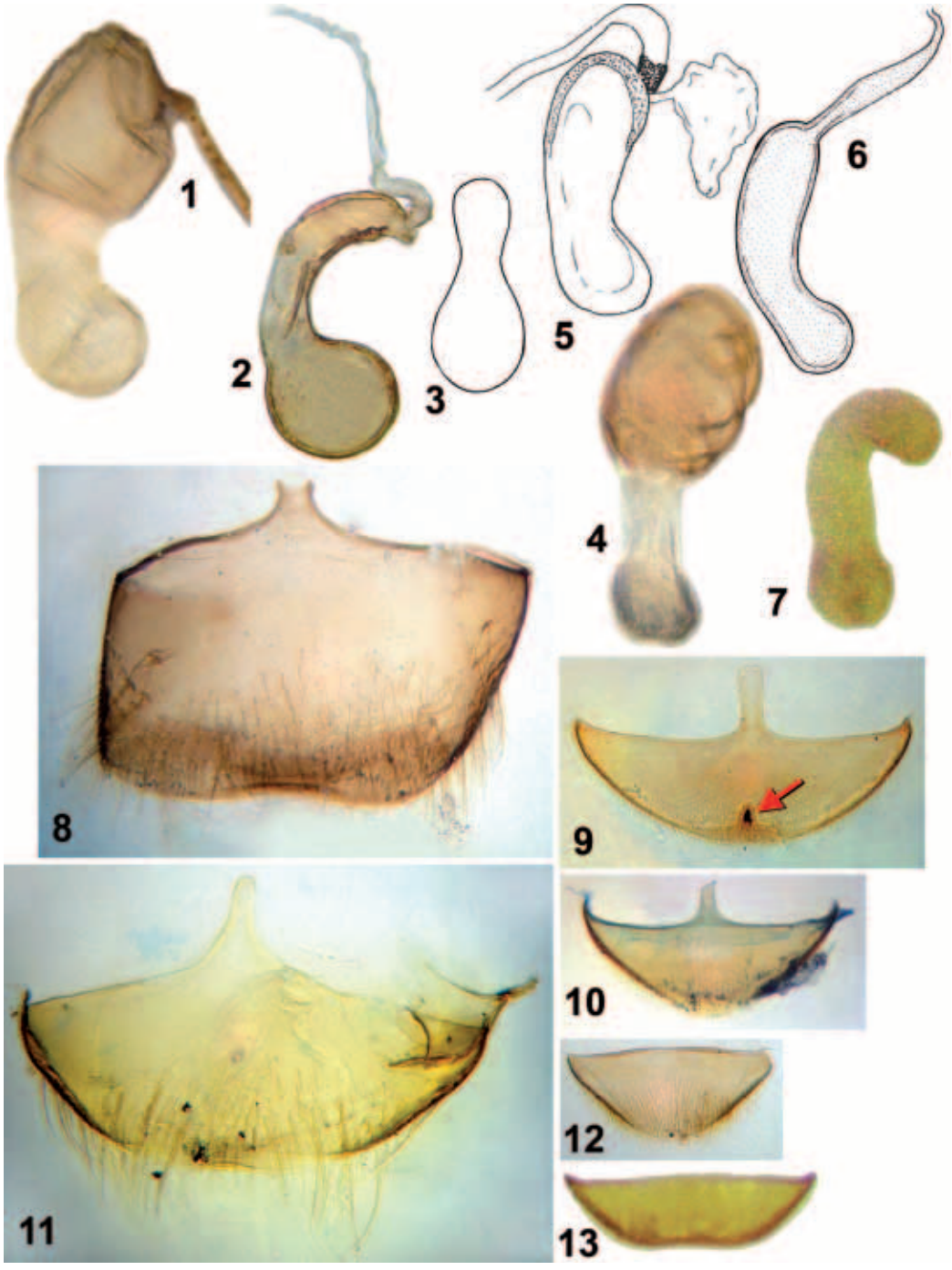
– First protarsomere dilated in males.

– Very low mesoventral keel with rounded vertex (Fig. 98.9).

– Aedeagus (Figs 101.7, 102.9) with apical area of median lobe narrowed and parameres without differentiated club and setae (Fig. 103.8).

– *Spermathecal complex* (Fig. 104.7): Spermatheca weakly and uniformly sclerotized, without distinct regions; the apical part spherical and somewhat wider, the proximal part being elbowed.

– *Female uroventrite VIII* (Fig. 104.13): Posterior margin with broad, slightly concave apical midpart; subrectilinear anterior margin without spiculum.



FIGURES 104.1–104.13: *Leptodirus* series, *Leptodirus* group. Spermatheca of: (**1**) *Astagobius angustatus angustatus*, (**2**) *Bathysciotes khevenhuelleri croaticus*, (**3**) *Ceuthmonocharis* (*Ceuthmonocharis*) *netolitzkii netolitzkii,* (**4**) *Leptodirus hochenwarti reticulatus,* (**5**) *Prospelaeobates vrezeci* (modified from Giachino & Etonti 1996), (**6**) *Spelaeobates* (*Pretneriella*) *krausi,* (**7**) *S.* (*Spelaeobates*) *novaki* (modified from S. Ćurčić *et al.* 2023). Female uroventrite VIII of: (**8**) *A. a. angustatus*, (**9**) *B. k. croaticus* (red arrow pointing to a part with macula in the posterior median part), (**10**) *C.* (*C.*) *n. netolitzkii,* (**11**) *Leptodirus hochenwarti reticulatus,* (**12**) *S.* (*P.*) *kraussi*, (**13**) *S.* (*S.*) *novaki* (modified from S. Ćurčić *et al.* 2023).

Distribution. Croatia. Subgenus that has only colonised Iž Island.

Species

Spelaeobates* (*Spelaeobates*) *coriniensis S. Ćurčić, Vesović, Vrbica & Rađa, 2023
Spelaeobates* (*Spelaeobates*) *coriniensis coriniensis S. Ćurčić, Vesović, Vrbica & Rađa, 2023
Spelaeobates (*Spelaeobates*) *coriniensis* S. Ćurčić, Vesović, Vrbica & Rađa: 26 *in* S. Ćurčić *et al.* 2023.

Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri S. Ćurčić, Vesović, Vrbica & Rađa, 2023
Spelaeobates (*Spelaeobates*) *coriniensis nonveilleri* S. Ćurčić, Vesović, Vrbica & Rađa: 31 *in* S. Ćurčić *et al.* 2023.

Spelaeobates* (*Spelaeobates*) *novaki G. Müller, 1901
Spelaeobates novaki G. Müller, 1901: 19.
Spelaeobates Novaki J. Müller: Jeannel, 1910a: 45.
Spelaeobates (*Spelaeobates*) *novaki* J. Müller: V.B. Guéorguiev 1990: 239.

3.2.4 *Incertae sedis* in series ***Leptodirus***

3.2.4.1 Genus ***Muelleriola*** Giachino & Vailati, 2019
Muelleriola Giachino & Vailati, 2019: 93.

Type species. *Bathyscia sylvestris* Motschulsky, 1856 by original designation (habitus in Fig. 105.1).

Diagnosis. Size ranging between 1.8–2.0 mm. Bathysciod body shape, small, ovoid, with broad prothorax, not wider than elytra (Fig. 105.1); anophthalmous and depigmented.

Antennae: Short, just reaching if stretched backward the base of the pronotum; first article just shorter than the second one, the 8th wider than long, the 11th ogival and twice as long as the former.

Pronotum: With regularly rounded sides, broad and globose, as wide as the elytra, with maximum width in the posterior angles, which are acute and turned backward due to the pronounced sinuosity of the base.

Elytra: Provided with nearly complete and well-marked parasutural stria fading away anteriorly; transverse striolation fine and serrate.

Legs: Hind femurs with unarmed posterior margin. Apex of tibiae fitted with internal polidentated spurs; meso- and metatibiae with incomplete apical baskets of short, sparse spines. Male protarsi pentameres and moderately dilated, clearly narrower than apex of protibiae.

Mesoventral keel (Fig. 105.2): High, the anterior outline nearly vertical and the ventral outline subretilinear forming a nearly right angle, with a barely hinted tooth; posteriorly the apophysis does not exceed the metaventrite or does so slightly.

Suture of the metaventrite (Fig. 105.2): In sinuous curve, distant in the upper two thirds so it covers a wide arched area, and very close to the coxal cavity in the lower third.

Metatergal apparatus (Fig. 105.3): Large, with apophysis of the alacrista about one-third of the length of the elytra; short metascutum wings almost as long as wide and rounded apical parts.

Metendosternite (Fig. 105.4): «V»-shaped, with triangular furcal arms, broad at base; arms somewhat longer than the furcal trunk, with the apical apophysis in a narrow arc and the apex tapering; furcal trunk as long as the widest area.

Median lobe of aedeagus: Elongate in shape. In lateral view (Fig. 105.5), it is broadly curved, slender, and deeply sinuate dorsally in preapical area, with apex pointing markedly downward. In dorsal view (Fig. 105.6) with sides subparallel in basal 2/3, slightly sinuate, then abruptly converging toward apex, which is ogival and broadly rounded, but with a hint of blunt tip.

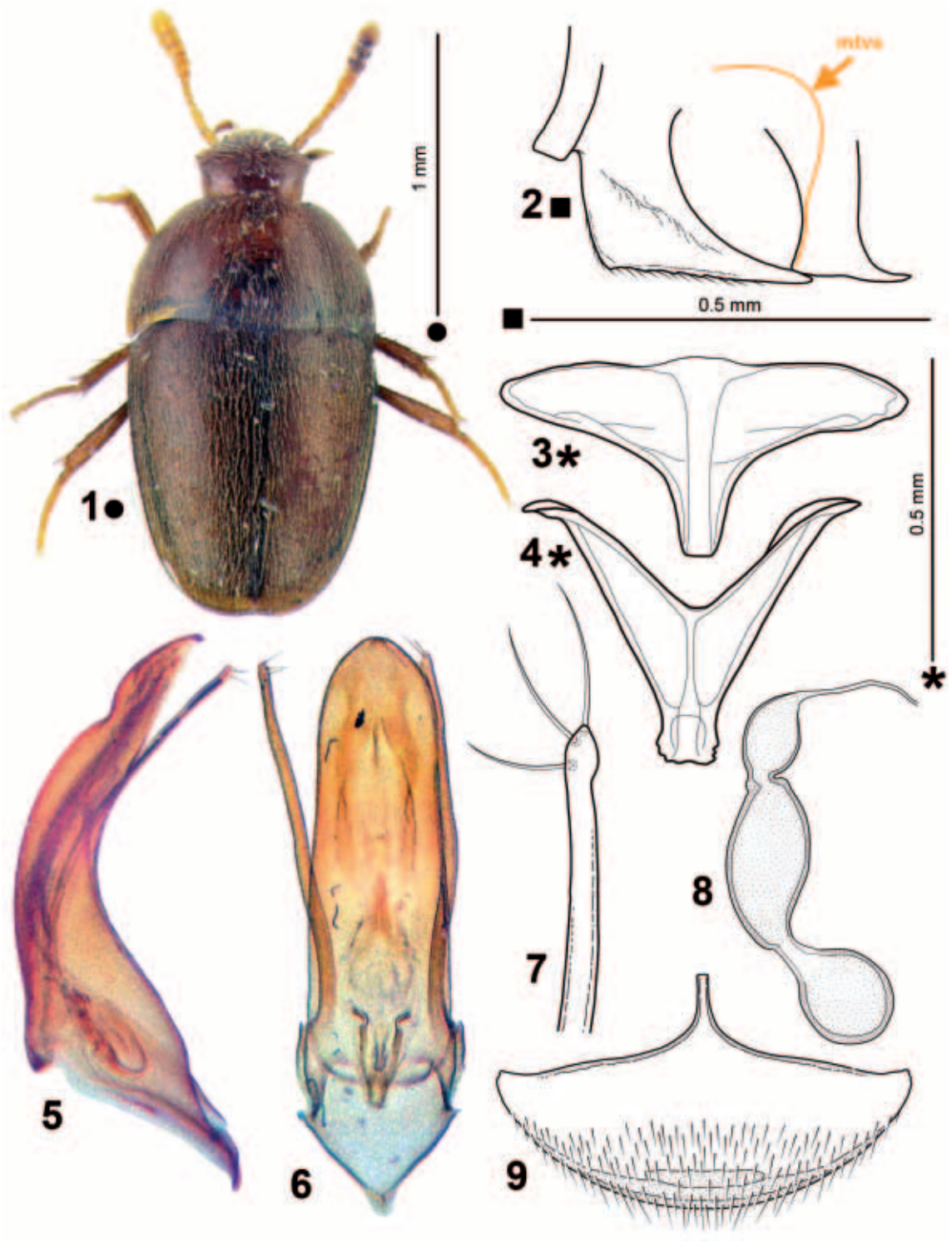
Endophallus (Fig. 105.6): With large, well sclerotized basal «Y»-piece, and lacks a median phanera; two dorsal spinous bundles are present, sinuate and poorly sclerotized.

Parameres (Fig. 105.7): Long and slender, only slightly shorter than the median lobe, with apex, in dorsal view, simple; fitted with three subequal setae: two apical and one subapical, internal.

Spermathecal complex: Spermatheca (Fig. 105.8) large and tri-lobed in appearance; with the proximal lobe elongated and the distal lobe smaller and globular; very short and narrow hyaline union duct, of constriced appearance between lobes; spermatic duct very dilated and sclerotized in the area where it empties into the proximal lobe.

Female uroventrite VIII (Fig. 105.9): Spiculum long, narrow and sharp; posterior border of ventrite in a wide arc and anterior border with slightly convergent sides.

Discussion. Classified by Jeannel (1924a) as the genus *Bathysciola*, it differs from it not only in the shape of the median lobe of aedeagus, but also in the following characters: In dorsal view the apex is lacking the characteristic dorsal, raised, lozenge-shaped structure, the shape of the female abdominal differs in



FIGURES 105.1–105.9: *Muelleriola sylvestris*: (**1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Metatergal apparatus, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere, (**8**) Spermatheca, (**9**) Female uroventrite VIII. Figs **2**–**4**,**7**–**9** modified from Giachino & Vailati (2019). Abbreviations: **mtvs**, metaventrite suture.

the VIII uroventrite and spermatheca, which is almost tri-lobed and characterised by a conspicuous, proximal, sclerotized dilatation of the ductus (Giachino & Vailati 2019). *Muelleriola* also exhibits an overall aedeagus structure similar to that of *Magdelainella* with a sharp, curved apex of the median lobe in lateral view; but the presence of the «Y»-piece in the basal region of the endophallus is striking. In the *Leptodirus* series, which has its distribution area on these territories, there are genera with «Y»-piece in the endophallus: *Adelopidius*, *Antrosedes*, *Charonites*, *Leonhardia*, *Protobracharthron*, *Redensekia*, *Roubaliella*, *Setnikia*, *Spelaeodromus*, *Spelaites*, *Speoplanes* or *Sphaerobathyscia*. Based on this it seems likely that this series we have to focus on to identify close relatives *Muelleriola*. It seems apparent that confirmation of one of this two hypothesis (series *Magdelainella* or *Leptodirus*) can only come from the application of molecular techniques to the entire group.

Distribution. Austria, Slovenia and Croatia.

Species

Muelleriola sylvestris (Motschulsky, 1856)
Bathyscia sylvestris Motschulsky, 1856: 36.
Adelops celatus C. Hampe, 1861: 65.
Adelops Coelatus Hampe: Abeille de Perrin, 1878: 154.
Bathyscia caelata Hampe: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *celata* Hampe: Reitter, 1885a [1884]: 21.
Bathysciola silvestris Motschoulsky: Jeannel, 1910a: 26.
Bathysciola (s. str.) *silvestris* Motschoulsky: Jeannel, 1914b: 12
Muelleriola sylvestris (Motschulsky, 1856): Giachino & Vailati, 2019: 93.

3.2.4.2 Series ***Bathyscia***

Diagnosis. A small to medium sized species, 1.0–3.0 mm. Bathyscioid to pholeuonoid shaped body; depigmented.

Head: With or without occipital carina. Anophthalmous or with rudimentary eyes.

Antennae: With 11 segments, short; first antennomere shortest or as long as the second one.

Elytra: With or without transverse striolae; without parasutural stria.

Legs: Protarsi tetrameres in both sexes, not or slightly dilated in males.

Mesoventral keel: High, only low in *Ravasinia*, complete or short. Ventral tooth present or absent.

Endophallus: Completely hyaline, without any internal structure.

Parameres: Thin or relatively robust, shorter or as long as the median lobe, without differentiated club. Bearing three setae.

Spermathecal complex: Sacciform spermatheca, small, membranous or slightly sclerotized; undifferentiated union duct of the basal lobe; well-developed spermathecal gland.

Discussion. The importance of characters such as tetrameric protarsi in both sexes («Théléomorphes» of Jeannel 1924a), the absence of parasutural stria, parameres without club which are shorter than or as long as the median lobe, and especially an unarmed endophallus indicate that these genera form a very close group. Jeannel (1924a) included it in Division II consisting of *Bathyscia*, *Hexaurus* and *Netolitzkya*. For his part V.B. Guéorguiev (1976) and Perreau (2000) included these genera in the subtribe Bathysciina that is characterised by protibiae without comb and with 2–3 external spurs, meso- and metatibiae without apical basket and with well-developed external spurs. The genera *Bathyscidius* and *Ravasinia* are enclosed in Division III by Jeannel (1924a) or the subtribe Bathysciotina by V.B. Guéorguiev (1976) and Perreau (2000) with the genus *Pseudobathyscidius* characterised due to their protibiae with comb on the apical and external edges and without external spurs, in addition to the meso- and metatibiae with apical basket. No molecular data are available for this series. Perreau (2008) pointed out the monophyly of the *Bathyscidius-Pavicevicia-Ravasinia* set. Perreau (2019) provides a cladistic analysis based on the morphology of Bathysciotina (*sensu* V.B. Guéorguiev, 1976) and placed it in the same clade as the genera *Bathyscidius*, *Pavicevicia* and *Ravasinia*, as well as the genera *Pseudobathyscidius*, *Speonesiotes* and *Albanella*, all with distribution in the Southern Balkan. Although it should be noted that the phylogram largely does not correspond to our trees, obtained on a molecular basis (Fig. 1I). Therefore, only a complete molecular analysis of the complex can resolve the question in the future. In addition, also on a morphological basis Casale *et al*. (1991a) included in the same group the genera *Bathyscia*, *Hexaurus* and *Netolitzkya*. This later was confirmed by the work of Giachino & B.V. Guéorguiev (2008). However, both morphological data (simple aedeagus with unarmed endophallus) and biogeographic data suggest that their relatives can be found among species inhabiting neighboring areas of

the same mountain massif, also with simple aedeagus and unarmed endophallus (see Discussion section of series *Sophrochaeta*). *Hexaurus* and *Netolitzkya* have been included in the basal clade of the *Sophrochaeta* series and the Euboea Island series, Greece (see Discussion section of *Sophrochaeta* series). The Greco-Bulgarian *Bathyscia* from Rhodopes-Pirin mountains, also with unarmed endophallus, probably also belong to the *Hexaurus* series clade.

Key to groups

1. Protibiae without comb and with 2–3 external spurs. Meso- and metatibiae without apical baskets ....*Bathyscia* group
- Protibiae with comb of spines aligned on the outer apical edge and without external spurs. Meso- and metatibiae with baskets on the periphery of the apically truncated area..... *Ravasinia* group

3.2.4.2.1 ***Bathyscia*** group

With the characters indicated as diagnostic for the series and those mentioned in the groups key.

Genus ***Bathyscia*** Schiødte, 1848
Bathyscia Schiødte, 1848: 79.

Type species. *Bathyscia montana* Schiødte, 1848 by subsequent designation (for the habitus see that of the similar subspecies *Bathyscia montana jablanicensis* Ganglbauer, 1899 in Fig. 106.1).

Diagnosis. Small size, 1.0–2.0 mm, bathyscioid body (Fig. 106.1).

Head: With rudimentary eyes or anophthamous.

Antennae: Second antennomere of equal length or as long as the first one.

Pronotum: Convex and transverse, as wide as the elytra, with regularly curved sides and not narrowed at the base.

Elytra: Dotted, not transversely striated, without parasutural stria.

Legs: Males protarsi tetrameres, not or slightly dilated. Protibiae without comb; meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 106.6): High and short, with more or less curved anterior edge and straight ventral edge or variably wavy, but not prolonged on the metaventrite. Ventral tooth present or absent.

Suture of the metaventrite (Fig. 106.6): In the first half it delimits a well-developed arc area and subsequently runs parallel to the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 106.9): With the wings of the metascutum triangular in shape, very broad at the base and twice as long as broad; the processes of the alacrista broad, short and the apices not very sharp, almost rounded.

Metendosternite (Fig. 106.11): «V»-shaped; furcal arms very long and thin, almost four times the length of the trunk, with the apical part arched and the apophysis poorly developed; posterior furcal plate narrow and of equal width along the entire length of the arm, with the posterior flange subrectilinear; there appears to be a reduced anterior furcal plate towards the middle of the arm; furcal trunk as wide as long in the part of maximum width and median keel diverging posteriorly.

Median lobe of aedeagus: Very small, in lateral view (Fig. 107.1: *Bathyscia hungarica*) from regularly curved to sharply bent, or subretilinear or slightly sinuated. In dorsal view (Fig. 107.5), always very elongated and frail, with more or less regularly converging sides and apex from broadly rounded to more or less sharp sub-triangular.

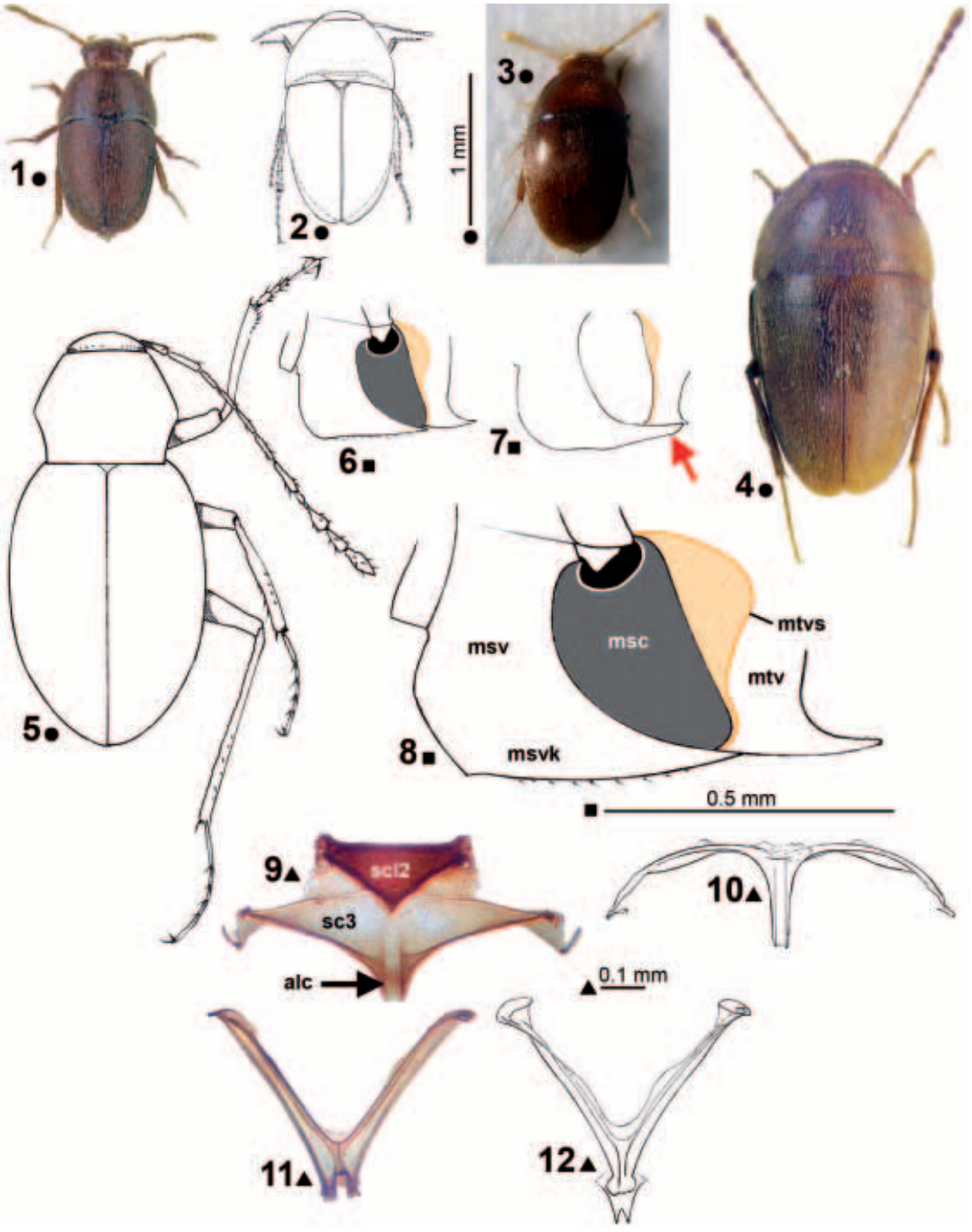
Endophallus (Fig. 107.5): Completely hyaline, without any internal structure.

Parameres (Fig. 108.1): Thin, more or less long than the median lobe. Bearing three setae, one or two apical, the others subapical. Supranumerary setae have rarely been observed.

Spermathecal complex (Figs 108.6; 108.7: *Bathyscia lekanica*): Spermatheca sacciform, annulated, not sclerotized and without differentiated parts, almost devoid of ductus. Very voluminous spermathecal gland (almost as large as the spermatheca) with large and short ductus.

Female uroventrite VIII (Fig. 109.1): A quite long and wide or narrow spiculum with rounded apex.

Discussion. A study of the distribution area of the genus highlights three large areas which are clearly disjuncted: the first one, between Slovenia and Bosnia, for *B. montana*; a second one, Czech Republic, Slovak Republic and Ukraine, for *B. hungarica* and a third one, essentially comprising the mountains located at the border between Greece and Bulgaria (Rhodopi and Pirin mountains) for the numerically more conspicuous contingent of species. Another species from Montenegro, *B. mikati*, originally described as *Bathyscia* has been moved to the genus *Laneyriella* by Hlaváč *et al*. (2017). This disjunction, over such a vast geographical extension, raises the suspicion that the genus, as conceived today, may not



FIGURES 106.1–106.12: *Bathyscia* series. Habitus of: (**1**) *Bathyscia montana jablanicensis,* (**2**) *Bathyscidius* (*Bathyscidius*) *fallaciosus*, (**3**) *B.* (*Ionobathyscidius*) *basarai* (modified from Čeplík *et al.* 2021a), (**4**) *Pavicevicia comottiorum*, (**5**) *Ravasinia lonae* (redrawn from Jeannel 1924a). Pterothorax in lateral view of: (**6**) *B. m. jablanicensis,* (**7**) *B.* (*B.*) *mljetensis* (red arrow pointing to the mesoventral keel extended over the metaventrite), (**8**) *P. comottiorum*. Metatergal apparatus, ventral view of metanotum and axillaria of: (**9**) *B. m. jablanicensis,* (**10**) *B.* (*B.*) *mljetensis*. Metendosternite of (**11**) *B. m. jablanicensis,* (**12**) *B.* (*B.*) *fallaciosus*. Figs **2**, **7**, **10**, **12** redrawn from Polak & Jalžić (2019). Abbreviations: **alc**, alacrista; **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture; **sc3**, metascutum; **scl2**, mesoscutellum.

be monophyletic. Furthermore, it is hypothesised that *Bathyscia hungarica* from the north of the Carpathians is phylogenetically related to the south Carphatians *Sophrochaeta* group of the series *Sophrochaeta*. Also *Bathyscia* from Rhodopes-Pirin are thought to be possibly related to *Hexaurus* and *Netolitzkya* as they share the unarmed endophallus and are found in adjacent mountain ranges: Leptodirini from Rhodopes (it is not known what the *Albaniola* from Rhodopes is related to) were shown to be closely related to those from the Carpathians and Balkan. Only the future availability of molecular data, will probably clarify the question, however to date those data are not available.

Distribution. Slovenia, Bosnia, Czech Republic, Slovak Republic, Ukraine, Greece and Bulgaria.

Species

Bathyscia besucheti Giachino, 1991
Bathyscia besucheti Giachino, 1991: 293.

Bathyscia hungarica (Reitter, 1878)
Adelops Hungarica Reitter, 1878: 63.
Bathyscia hungarica Reitter: Reitter, 1885a [1884]: 20.
Bathyscia montana subsp. *hungarica* Reitter: Jeannel, 1910a: 37.
Bathyscia (s. str.) *montana* subsp. *hungarica* Reitt.: Jeannel, 1914b: 16.

Bathyscia jeannelides Newton, 2015
Bathyscia jeanneli Casale, Giachino & M. Etonti, 1990: 570.
Bathyscia jeannelides Newton, 2015: 4 (*Nomen novum* for *Bathyscia jeanneli* Casale, Giachino & M. Etonti, 1990).

Bathyscia kiparidisi Casale, Giachino & M. Etonti, 1990
Bathyscia kiparidisi Casale, Giachino & M. Etonti, 1990: 572.

Bathyscia lekanica Casale, Giachino & M. Etonti, 1990
Bathyscia lekanica Casale, Giachino & M. Etonti, 1990: 565.

Bathyscia macedonica Casale, Giachino & M. Etonti, 1990
Bathyscia macedonica Casale, Giachino & M. Etonti, 1990: 569.

Bathyscia mimetica Casale, Giachino & M. Etonti, 1990
Bathyscia mimetica Casale, Giachino & M. Etonti, 1990: 563.

Bathyscia montana Schiødte, 1848
Bathyscia montana apfelbecki Ganglbauer, 1899
Bathyscia (s. str.) *montana* var. *apfelbecki* Ganglbauer, 1899: 106.
Bathyscia montana subsp. *Apfelbecki* Ganglbauer: Jeannel, 1910a: 37.

Bathyscia montana forticornis (Joseph, 1872)
Adelops montanus V. *forticornis* Joseph, 1872: 178.
Bathyscia (s. str.) *montana* var. *forticornis* Joseph: Jeannel, 1914b: 16.

Bathyscia montana jablanicensis Ganglbauer, 1899
Bathyscia montana var. *jablanicensis* Ganglbauer, 1899: 107.
Bathyscia montana var. *Apfelbecki-jablanicensis* Ganglbauer: Jeannel, 1910a: 37.
Bathyscia (*Adelopsella*) *Jablonicensis* Ganglb.: J. Sahlberg, 1913: 48.
Bathyscia montana Subsp. *jablanicensis* Ganglbauer: Jeannel, 1924a: 216.

Bathyscia montana montana Schiødte, 1848
Bathyscia montana Schiødte, 1848: 80.
Bathyscia rotundata Motschulsky, 1851: 598.
Bathyscia triangularis Motschulsky, 1851: 594.
Bathyscia valida Motschulsky, 1851: 599.
Adelops montanus Schiødte: L. Miller, 1855: 508.
Adelops montanus V. *longipennis* Joseph, 1872: 178.
Bathyscia (*Bathyscia*) *montana* Schiødt.: Reitter, 1885a [1884]: 20.
Bathyscia montana Subsp. *montana* Schiødte, 1848: Jeannel, 1924a: 216.

Bathyscia raitchevi Casale, Giachino & M. Etonti, 1990
Bathyscia raitchevi Casale, Giachino & M. Etonti, 1990: 571.

Bathyscia thracica Jeannel, 1934
Bathyscia thracica Jeannel, 1934d: 157.

3.2.4.2.2 ***Ravasinia*** group Perreau, 2000 sensu novo

We insert the genera that, in the absence of molecular data, shows an endophallus without sclerotized structures: *Ravasinia*, *Pavicevicia* and *Bathyscidius*. Jeannel (1924a) himself placed some of them in the «Théléomorphes» of Division III, leaving them in an

isolated position or inserting some of them in other «Phyletic series». Following the criteria of Jeannel (1924a), V.B. Guéorguiev (1976) and Perreau (2000) the genera *Bathyscidius*, *Pseudobathyscidius* and *Ravasinia* were included in the Bathysciotina subtribe, to which Perreau (2008) later added *Pavicevicia*. In this monograph, *Pseudobathyscidius* has been transferred based on morphological criteria to the *Pholeuonopsis* group of the *Anthroherpon* series (see Discussion section of the genus *Pseudobathyscidius*).

KEY TO GENERA

1. Body shape pholeuonoid or subpholeuonoid (Fig. 106.5). Pronotum narrower than elytra, with sides not fully curved and more or less sinuous in the basal third, narrowed at the base. Mesoventral keel low ....*Ravasinia*
- Body shape bathyscioid (Figs 106.2–106.4). Pronotum as wide as, or wider than elytra, with regularly curved sides, not narrowed at the base. Mesoventral keel high (Figs 106.7, 106.8).....2
2. Body length greater than 1.9 mm. Head with occipital carina. Antennae long (at least 0.5 times the length of the body with sexual dimorphism) and thin, all antennomeres longer than wide. First protarsomere somewhat dilated in males. Apical part of the median lobe with long parallel-sided narrowing (Fig. 107.8). .....*Pavicevicia*
- Body length less than 1.9 mm. Head without occipital carina or smooth keel. Shorter antennae (at most 0.4 times the length of the body without sexual dimorphism) and more compact, the 9th and 10th antennomeres transverse. First protarsomere not dilated in males. Apical part of the median lobe with very short narrowing and without narrowing (Figs 107.6, 107.7) 3
3. Apical area of the median lobe of aedeagus lanceolate in shape (Fig. 107.6). Apical part of paramere with three setae, 1 or 2 of them subapical (Fig. 108.2). Female uroventrite VIII with spiculum somewhat longer or more triangular and on both sides of the spiculum, in the basal part, the edges straighter or more convex (Fig. 109.3).....*Bathyscidius* (*Bathyscidius*)
- Apical area of the median lobe of the subtriangular aedeagus (Fig. 107.7). Apical area of paramere with three proximally inserted apical setae (Fig. 108.3). Female uroventrite VIII with the spiculum shorter and on both sides of the spiculum, in the basal part, the edges more concave (Fig. 109.4)..... .....*Bathyscidius* (*Ionobathyscidius*)

Genus ***Bathyscidius*** Jeannel, 1910
Bathyscidius Jeannel, 1910a: 15.

TYPE SPECIES. *Bathyscia* (*Bathyscia*) *tristicula* Apfelbeck, 1906 by original designation (for the habitus see that of the similar species *Bathyscidius fallaciosus* in Fig. 106.2).

DIAGNOSIS. Very small size, between 1.2–1.8 mm. Bathyscioid facies, body shape elongated, elliptical and very convex, subsequently not narrowed (Fig. 106.2, 106.3). Colour yellowish to dark reddish. Sculpture consisting of a fine and disordered punctation on the head, pronotum and elytra, where it forms transverse striolae quite separated and strong. Pubescence yellowish, fine, lying down and not very tight, generally disordered.

Head: Retractable, with occipital carina obliterated, not present; anophthalmous.

Antennae: Thin and proportionally short since they only slightly exceed the base of pronotum. First antennomere shorter than the second. Antennomeres of the club flattened, the 8th sub globose and transverse, the 9th and 10th transverse or slightly longer than wide, depending on species; the 11th being the longest and most robust, between 2.2–2.5 the length of the 10th.

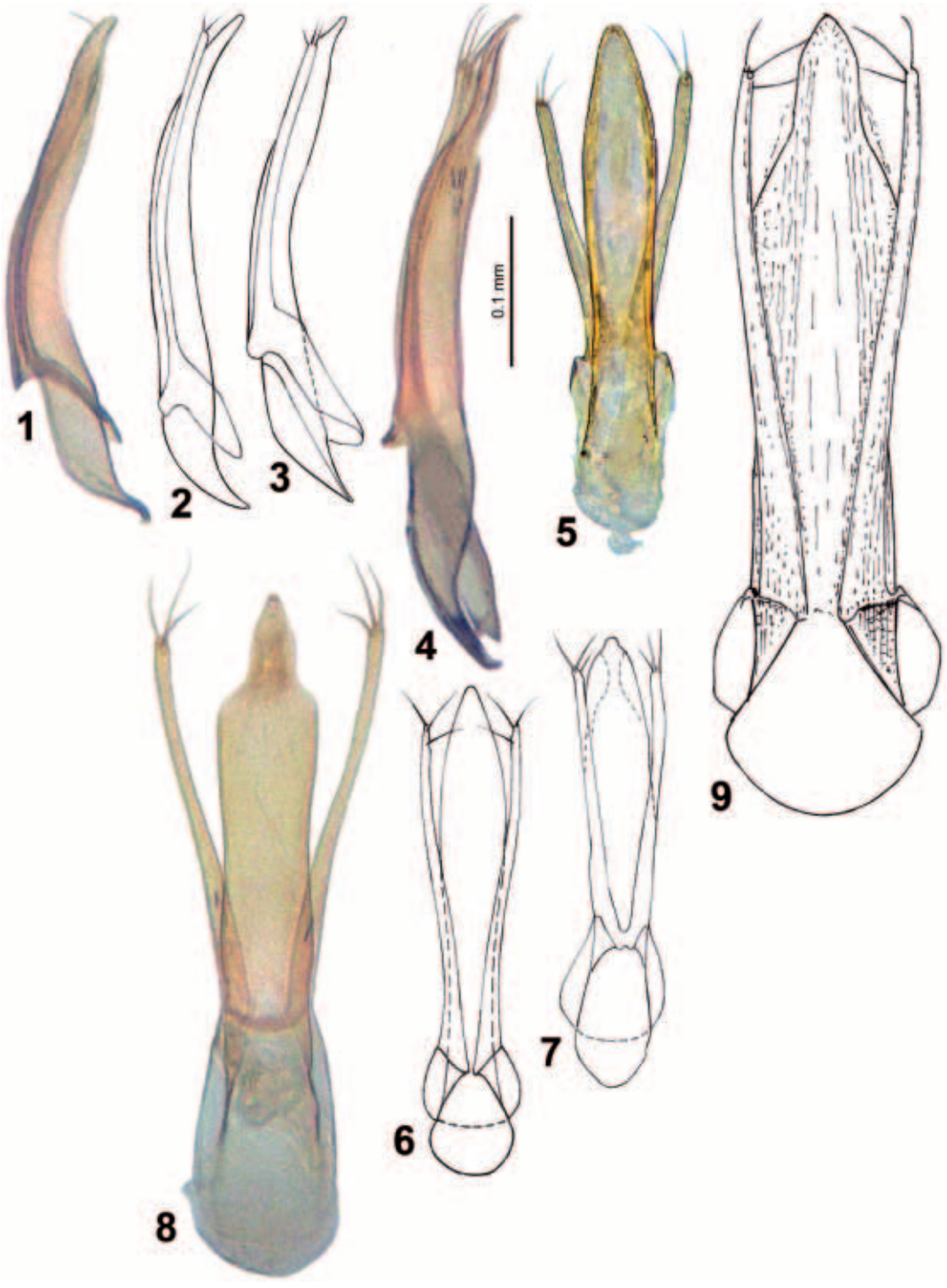
Pronotum: Very convex and transverse, 1.7–1.8 times longer than wide. Sides regularly arcuated with maximum width at the base, or a little before the base, and as wide as or slightly wider than the elytra. Not sinuated in front of the base; posterior vertices sharp and somewhat prolonged over the elytra; angles acute.

Elytra: Oval, slightly longer than wide, 1.2–1.3 times longer than wide, with maximum width near the base. Sides of the basal part broadly rounded diminished in a regular curve towards the rounded apices. Pubescence aligned in transverse striations along the entire length of the elytra; no parasutural stria.

Legs: Moderately short and robust; protarsi tetrameres and non-dilated in both sexes. Protibiae without external spurs, but with a comb of strong spines extending at the apical and lateral outer edges, in the latter one or two-thirds of the length of the tibia. Meso- and metatibiae with apical basket and two large, strong, spurs on the inner apical side.

Mesoventral keel (Fig. 106.7): High well-developed and moderately thick; anterior edge straight or convex, vertex rounded and angle very obtuse. Posterior border straight or slightly convex extends over all, or almost all, of the metaventrite, ventrally flattened and widened.

Suture of the metaventrite (Fig. 106.7): In the



FIGURES 107.1–107.9: *Bathyscia* series. Aedeagus in lateral view of: (**1**) *Bathyscia hungarica,* (**2**) *Bathyscidius* (*Bathyscidius*) *tristiculus*, (**3**) *Bathyscidius* (*Ionobathyscidius*) *rambouseki*, (**4**) *Pavicevicia comottiorum*. Aedeagus in dorsal view of: (**5**) *Bathyscia montana jablanicensis,* (**6**) *B.* (*B.*) *tristiculus* (redrawn from G. Müller 1922), (**7**) *B.* (*I.*) *rambouseki*, (**8**) *P. comottiorum*, (**9**) *Ravasinia lonae* (redrawn from Jeannel 1924a). Figs **2**, **3**, **7** redrawn from Polak & Jalžić (2019).

upper half it delimits a small arc area and the lower half runs parallel to the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 106.10): With metascutum wings very long and narrow; the processes of the alacrista very prolonged and the apices sharp.

Metendosternite (Fig. 106.12): Furcal arms long, more than twice the trunk length, with terminal apophysis well-developed. Posterior lamina narrow and preserved up to the apex, the edge little arcuated. There is also anterior lamina sinuous and somewhat widened towards the middle area. Furcal trunk wide in the basal part, being somewhat wider than long. Middle keel on the trunk does not diverge posteriorly.

Median lobe of aedeagus: Small and thin. In lateral view (Figs 107.2, 107.3), narrow and straight or slightly arcuated. In dorsal view (Figs 107.6, 107.7), elongated with more or less arcuated sides; apical part narrows into a rounded tip, more or less pointed, depending on species. Basal blade more or less long with parallel sides in the basal part, then widens with the posterior edge straight or arcuate.

Endophallus (Figs 107.6, 107.7): Without sclerotized structures.

Parameres (Figs 108.2, 108.3): More or less robust, almost straight, parallel to the median lobe and somewhat shorter than the median lobe. Apical part not dilated, armed with three setae of similar length and thickness with the insertion point depending on the species. Ventral blade of tegmen somewhat wider but shorter than the basal one.

Spermathecal complex: Spermatheca (Figs 108.8–108.9) small, bag-shaped, arcuated, not or weakly sclerotized. Apical lobe rounded, more or less dilated; basal lobe more developed and somewhat wider. Union duct of the lobes not differentiated. Spermathecal gland well-developed, ends into the area where spermatheca and spermatic duct meet, this is very thin.

Female uroventrite VIII (Figs 109.2–109.4): Depending on the species the posterior edge little arched and sinuous or in arc with the middle part pointed and on the edge numerous fine or robust setae. Spiculum of medium length, thin, somewhat arched and rounded apex or in triangle with very sharp upper vertex.

Subgenus ***Bathyscidius***

Diagnosis. Size between 1.2–1.8 mm. Other characteristics see genus description.

Legs: The spines of the comb are stronger and cover about two-thirds of the protibia.

Median lobe of aedeagus (Figs 107.6): Apical part is not narrowed, with the tip pointed or rounded, not subtriangular.

Parameres (Fig. 108.2): The apical part is armed with three setae, two apical setae with insertion pores close to each other and the third subapical with the most distant insertion pore; or one apical and two subapical, in the subapical the insertion is latero-internal.

Females have the IX uroventrite, the genital-ovipositor segment, relatively short, with broad and voluminous stylomeres, subtriangular in shape, with straight outer edges and significantly convex inner ones.

Discussion. No molecular study has been performed showing the position of *Bathyscidius* on the phylogenetic tree, but this genus has marked affinities with *Ravasinia* with its thin and elongated aedeagus model with the narrow and long median lobe, the parameres with three setae and the unarmed endophallus. The genus *Bathyscidius* is included in the tribe Bathysciae, group «Théléomorphes» and Division III according to Jeannel (1924a); in the subtribe Bathysciotina, according to V.B. Guéorguiev (1974a, 1974b, 1976) and in the subtribe Bathysciotina and phyletic series «*Ravasinia*» according to Perreau (2000). Jeannel (1934) described *Bathyscidius remyi,* today synonymous with *Laneyriella andrijevicensis* by Polak & Jalžić (2019). Čeplík *et al*. (2021b) placed *Laneyriella mikati* in the genus *Bathyscidius* (see Discussion section of the genus *Laneyriella*).

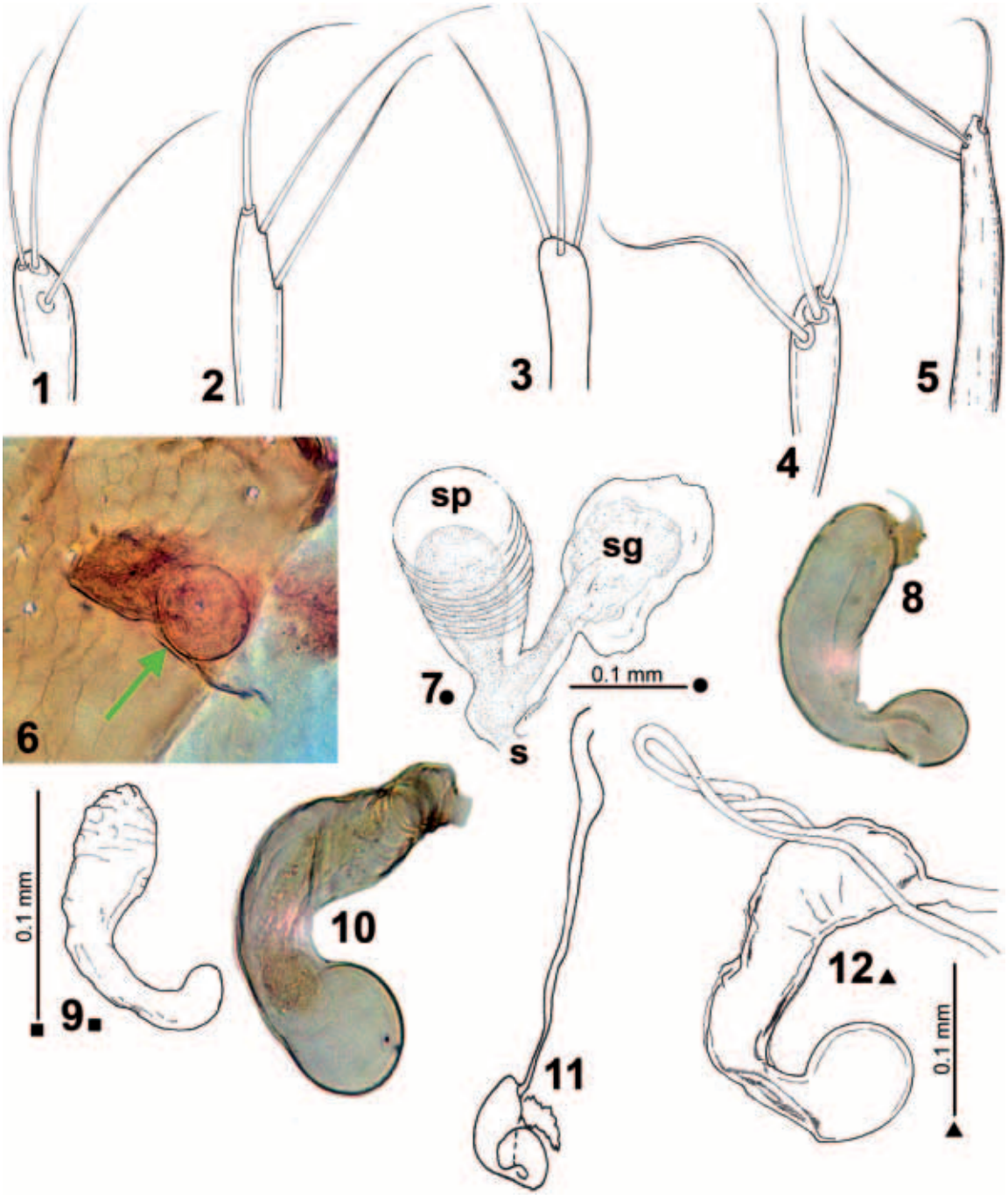
Distribution. Includes seven species distributed along the southern and western Adriatic coast. Croatia, Bosnia-Herzegovina and Montenegro.

Species

Bathyscidius (***Bathyscidius***) ***crnagorensis*** (See Appendix New Species)

Bathyscidius (***Bathyscidius***) ***fallaciosus*** (G. Müller, 1910)
Bathyscia tristicula fallaciosa G. Müller, 1910: 184.
Bathyscidius tristiculus subsp. *fallaciosus* J. Müller: Jeannel, 1911a: 415.
Bathyscidius fallaciosus (Müller, 1910): Polak & Jalžić, 2019: 372.

Bathyscidius (***Bathyscidius***) ***komajiensis*** Polak & Jalžić, 2019
Bathyscidius komajiensis Polak & Jalžić, 2019: 374.



FIGURES 108.1–108.12: *Bathyscia* series. Apex of the paramere of: (**1**) *Bathyscia montana jablanicensis,* (**2**) *Bathyscidius* (*Bathyscidius*) *orjensis*, (**3**) *Bathyscidius* (*Ionobathyscidius*) *rambouseki*, (**4**) *Pavicevicia comottiorum*, (**5**) *Ravasinia lonae* (redrawn from Jeannel 1924a). Spermathecal complex of: (**6**) *Bathyscia montana jablanicensis* (broken spermatheca, green arrow pointing to the apical lobe), (**7**) *B. lekanica* (modified from Casale *et al*. 1990), (**8**) *B.* (*Bathyscidius*) sp. (**9**) *B.* (*I.*) *basarai* (modified from Čeplík *et al.* 2021a), (**10**) *P. comottiorum*, (**11**) *P. comottiorum* (modified from Giachino 2006), (**12**) *R. lonae* (redrawn from Perreau 2019). Figs **2**, **3** redrawn from Polak & Jalžić (2019). Abbreviations: **s**, spermiduct; **sg**, spermathecal gland; **sp**, spermatheca.

Bathyscidius (***Bathyscidius***) ***mikati*** (Udržal, 1995)
Bathyscia mikati Udržal, 1995: 25.
Laneyriella mikati (Udržal, 1995): Hlavac, Perreau & Čeplik, 2017: 113.
Bathyscidius mikati (Udržal, 1995): Čeplik *et al.* 2021: 589.

Bathyscidius (***Bathyscidius***) ***mljetensis*** Polak & Jalžić, 2019
Bathyscidius mljetensis Polak & Jalžić, 2019: 368.

Bathyscidius (***Bathyscidius***) ***orjensis*** Polak & Jalžić, 2019
Bathyscidius orjensis Polak & Jalžić, 2019: 377.

Bathyscidius (***Bathyscidius***) ***tristiculus*** (Apfelbeck, 1906)
Bathyscia (Bathyscia) *tristicula* Apfelbeck, 1906a [1905]: 247.
Bathyscina tristiculus Apfelb.: Jeannel, 1908a: 299.
Bathyscidius tristiculus Apfelbeck: Jeannel, 1910a: 37.
Bathyscia (*Bathyscidius*) *tristicula* Apfelbeck: Jeannel, 1914b: 16.
Bathyscidius tristiculus Subsp. *tristiculus* Apfelbeck, 1907: Jeannel, 1924a: 269.

Subgenus ***Ionobathyscidius*** Polak & Jalžić, 2019
Bathyscidius (*Ionobathyscidius*) Polak & Jalžić, 2019: 380.

Type species. *Bathyscidius rambouseki* Knirsch, 1931 by original designation (for the habitus see that of the similar species *Bathyscidius* (*Ionobathyscidius*) *basarai* in Fig. 106.3).

Diagnosis. Size between 1.4–1.9 mm; habitus in figure 106.3. The most important characters that allow differentiating the subgenus *Ionobathyscidius* from the subgenus *Bathyscidius* are (Polak & Jalžić, 2019):

Legs: In *Ionobathyscidius* the comb is of finer and flatter spines and shorter, covering only the apical third of the protibiae. In the subgenus *Bathyscidius*, the spines of the comb are stronger and cover about two-thirds of the protibia.

Median lobe of aedeagus: Apical part in the subgenus *Ionobathyscidius* gradually ogival, subtriangular, with a rounded, non-pointed tip (Fig. 107.7). In the subgenus *Bathyscidius* apical area is not narrowed with the end pointed or rounded, but not subtriangular (Fig. 107.6).

Parameres (Fig. 108.3): Apex is armed with three erect apical setae with insertion in close proximity, almost together. This structure is not consisting of one or two apical setae and two or one lateral subapical setae, as found in *Bathyscidius*.

Females of the subgenus *Ionobathyscidius* show significant differences in the uroventrite VIII (Fig. 109.4), the spiculum being shorter and on both sides of the spiculum in the basal part the edges more concave, in the spermatheca (Fig. 108.9) the area corresponding to the more elongated joint duct and in the genital-ovipositor with long and narrow stylomeres. While in *Bathyscidius* species have in the uroventrite VIII (Fig. 109.3) the spiculum somewhat longer or more triangular and on both sides of the spiculum in the basal part the edges straighter or more convex, in the spermatheca (Fig. 108.8) the area corresponding to the shorter joining duct and in the genital-ovipositor wider and more voluminous stylomeres.

Distribution. The subgenus is currently represented by three species, two endogean and one cave dwelling that have a more southern distribution than the species of the subgenus *Bathyscidius*; one in the southwest of North Macedonia and the other two in Albania, one in the centre and the other in the southeast.

Species

Bathyscidius (***Ionobathyscidius***) ***basarai*** D. Čeplík, Lakota & J. Čeplík, 2021
Bathyscidius (*Ionobathyscidius*) *basarai* D. Čeplík, Lakota & J. Čeplík, 2021a: 589.

Bathyscidius (***Ionobathyscidius***) ***rambouseki*** Knirsch, 1931
Bathyscidius rambouseki Knirsch, 1931: 3.
Bathyscidius (*Ionobathyscidius*) *rambouseki* Knirsch: Polak & Jalžić, 2019: 381.

Bathyscidius (***Ionobathyscidius***) ***tomoricensis*** G. Müller, 1922
Bathyscidius tristiculus tomoricensis G. Müller, 1922a: 89.
Bathyscidius tomoricensis J. Müller, 1922: Jeannel, 1924a: 269.
Bathyscidius (*Ioniobathyscidius*) *tomoricensis* Müller, 1922: Polak & Jalžić, 2019: 383.

Genus ***Pavicevicia*** Perreau, 2008
Pavicevicia Perreau, 2008: 177.

Type species. *Pavicevicia pretneri* Perreau, 2008 by original designation (for the habitus see that of the similar species *Pavicevicia comottiorum* in Fig. 106.4).

Diagnosis. Medium size, body length 1.9–2.7 mm. Bathyscioid body shape, ovoid elongated, convex and regularly curved (Fig. 106.4). Unpigmented, colour dark reddish, with palpi and antennae somewhat lighter. Integument moderately bright; pubescence evenly distributed, short, fine and lying down. Microsculpture formed by disordered, fine and superficial dots on the head and pronotum, on the elytra lined up in fine transverse striolae more or less marked.

Head: Slightly elongated; occipital carina well marked; anophthalmous.

Antennae: Quite long and thin, reach or exceed half of the elytra. Second antennomere slightly longer than the first one; the 8th non-transverse and the 9th and 10th subequal and somewhat longer than wide, the 11th being the longest and most robust of all the antennomeres.

Pronotum: Transverse, 1.7–1.9 times wider than long, with maximum width near the base being as wide as elytra. Lateral margins regularly arcuated and not sinuous. Posterior vertices sharp and slightly protruding backwards, angles acute.

Elytra: Elliptical, 1.2–1.3 times longer than wide, continue the curvature of the sides of the pronotum. Maximum width near the base; posterior area little narrowed and rounded distally. Parasutural stria absent.

Legs: Proportionally short and little thick, protarsi tetrameres and not dilated in both sexes. Protibiae slightly thickened and provided with a comb along two-thirds of the outer side; meso- and metatibiae straight with an apical basket. Empodium of all tarsi with two setae.

Mesoventral keel (Fig. 106.8): High with the anterior margin arcuated in the upper third and rectilinear in the lower two thirds and the posterior margin smooth, slightly convex; apophysis partially extended over the metaventrite; vertex with a small tooth and angle obtuse.

Suture of the metaventrite (Fig. 106.8): It delimits an ample arched area in the upper two thirds and very close to the coxal cavity in the lower third.

Metatergal apparatus (Giachino, 2006): With the apophysis of the alacrista well-developed.

Metendosternite: Unknown.

Median lobe of aedeagus: Thin, elongated and little arcuated. In lateral view (Fig. 107.4), very little arcuated, with the apical area slightly curved and the apex sharp. In dorsal view (Fig. 107.8), sub rectilinear sides that widen a little before the apical area that is shaped like an elongated triangle with a little sharp tip. Basal blade of the median lobe very elongated with the posterior margin in form of an arc.

Endophallus: Without sclerotized structures.

Parameres (Fig. 108.4): Quite thick and straight or a little arcuated, shorter than the median lobe, without differentiated club; bearing three rather long and robust setae, of similar thickness; the insertion pores nearby, two apical and one subapical, in general somewhat shorter. Ventral blade of the tegmen long, but somewhat shorter and somewhat wider than the basal blade of the median lobe.

Spermathecal complex (Fig. 108.10): Spermatheca small, in sacciform arc, somewhat sclerotized at both ends, spherical and wider apical part; no joint duct between the lobes. Spermatic duct short and thin, somewhat wider in the area of attachment to the copulatory pouch. Spermathecal gland well evident. In the work of Giachino (2006) the spermateca of the specimen used was deformed (Fig. 108.11).

Female uroventrite VIII (Fig. 109.5): With a rather long, narrow spiculum and a pointed apex; without significant difference between the two known species.
Discussion.: If the structure of the endophallus of the genera of Bathysciotina (*sensu* Perreau 2019) is taken into account, the three groups established by Jeannel (1924a) are valid. If the to date known genera are included in these three groups, as done by Perreau (2008) the following picture emerges: First group with an unarmed endophallus and spermateca exhibiting a similar structure: *Bathyscidius*, *Pavicevicia* and *Ravasinia*. Second group with an endophallus with at least one similar or «Y»-shaped basal piece: *Pseudobathyscidius*, *Sphaerobathyscia* and *Redensekia*. Third group with several symmetrical basal pieces: *Speonesiotes* and *Neobathyscia*.

In the study on the phylogeny of the subtribe Bathysciotina based on morphological characters, Perreau (2019) pointed out that the monophyly of the subtribe does not have a significant support and that the genus *Sphaerobathyscia* should be excluded from the subtribe. Also that the phylogenetic status of the other genera of the subtribe remains problematic in terms of monophyly. However at the base of the tree the genus *Ravasinia* is appears as sister of *Pavicevicia* and *Bathyscidius* These genera have in common that they lack sclerotized structures in the endophallus. In the absence of molecular data, we agreed on the position stated by Perreau (2008) in which the lack of sclero-

tized structures in the endophallus *Pavicevicia* is closely related to *Bathyscidius* and *Ravasinia*.

Distribution. Genus with two hypogean species that colonise well-defined areas. *Pavicevicia pretneri* is located in a cave in the Liplje region, Western Serbia; while *Pavicevicia comottiorum* shows a wider distribution by occurance in two distant caves, one located in the region of Liplje, a few kilometers from the cave of *P. pretneri*, the other in the region of Metojia, west of Kosovo.

Species

Pavicevicia comottiorum (Giachino, 2006)
Bathyscidius comottiorum Giachino, 2006: 11.
Pavicevicia comottiorum (Giachino): Perreau, 2008: 178.

Pavicevicia pretneri Perreau, 2008
Pavicevicia pretneri Perreau, 2008: 178.

Genus ***Ravasinia*** G. Müller, 1922

Leonhardella (*Ravasinia*) G. Müller, 1922a: 89.
Ravasinia J. Müller, 1922: Jeannel, 1924a: 271.

Type species. *Leonhardella* (*Ravasinia*) *lonae* G. Müller, 1922 by monotypy (habitus in Fig. 106.5).

Diagnosis. Small size between 2.6–2.9 mm. Pholeuonoid facies with convex body, widening backwards and narrowing forward (Fig. 106.5). Integument bright; pubescence strong, close and lying flat; punctation numerous and fine. Sexual differences very small: the last antennomere a little longer than the penultimate in the male.

Head: Not retractable, always visible from above, with slightly protruding occipital carina; anophthalmous.

Antennae: Thin, reaching up to middle of the elytra; the first antennomere being shorter than the second one; 8th antennomere subglobose, slightly longer than wide; club antennomeres conical, longer than wide, uncompressed and thickened in the apical part; 11th antennomere as thick as the 10th but somewhat longer.

Pronotum: Scarcely wider than long, much narrower than the elytra, as wide at the base as at the top. Sides angular in the middle, slightly rounded forward deeply sinuated behind. Posterior angles right, blunt, no protruding outside, sides parallel before the base and then continuing rectilinear.

Elytra: Ovoid, convex, finely and sparse punctate, arranged unordered; humeral vertices erased; the apex leaves the tip of the pygidium exposed. No parasutural stria.

Legs: Long and quite robust; protibiae without external spurs, but with a comb on the apical edges and half of the outer edge, formed by a row of short and equal spines, somewhat more robust those of the outer edge. Protarsi tetrameres in both sexes, with the first tarsomere somewhat dilated in males; meso- and metatibiae straight, with an apical basket and almost unarmed edges.

Mesoventral keel (Jeannel, 1924a): Very low, not forming an angle, rounded; without posterior extension.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Of the same type as in *Bathyscidius*, small and thin. In lateral view, flattened, narrow and straight (Jeannel, 1924a). In dorsal view (Fig. 107.9), elongated and with more or less straight lateral edges into the apical area; this narrows and is of triangular shape, decreasing towards the apex that is only slighly sharp. Basal blade long with parallel sides in the basal part, then widens and the posterior edge arcuated.

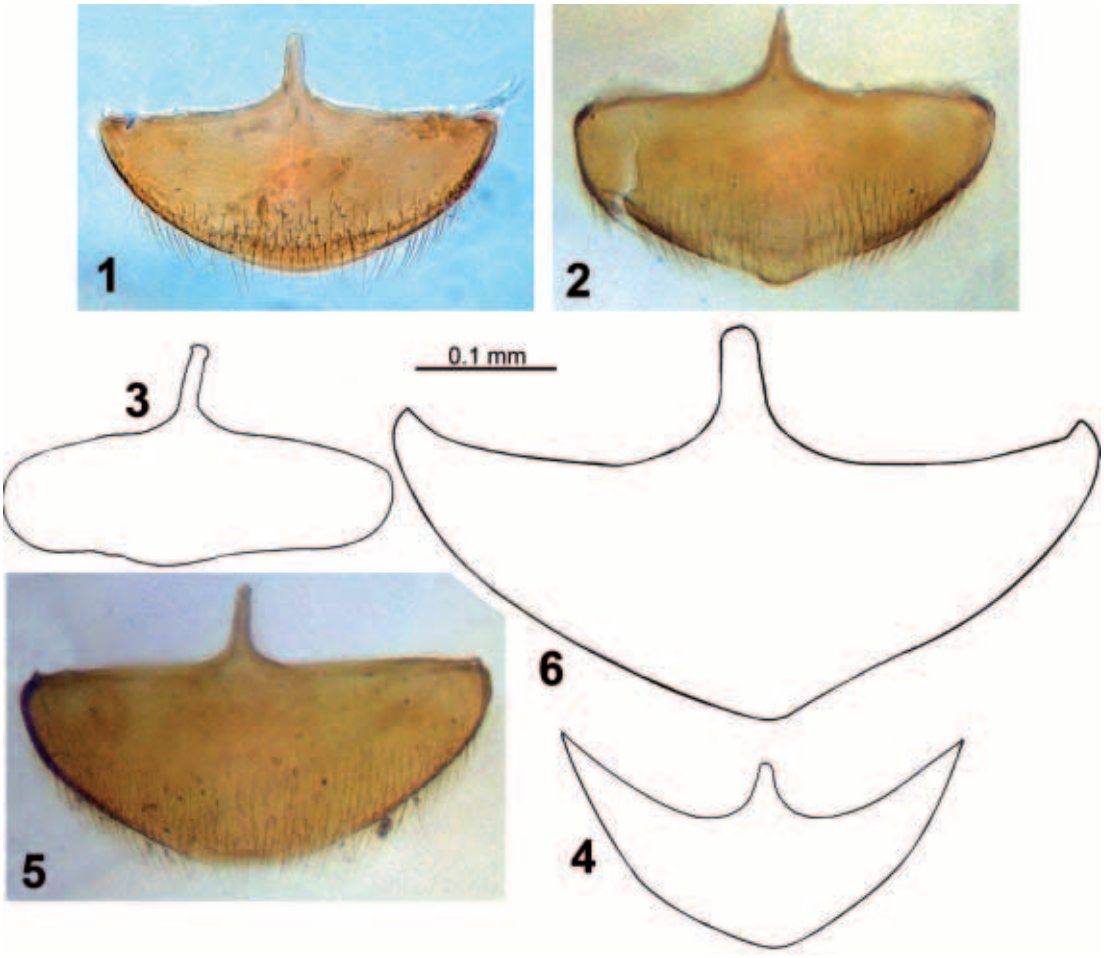
Endophallus (Fig. 107.9): Without any sclerotized structures.

Parameres (Fig. 108.5): Inserted on the dorsal edge of the median lobe as in *Bathyscidius*. Quite robust, thicker in the basal part, then almost straight and somewhat shorter than the median lobe. Apex narrowed, bearing three rather long setae of similar thickness and length, one apical and two others of internal lateral insertion, with the insertion pores almost equidistant. Ventral blade of the tegmen slightly wider but shorter than the basal one.

Spermathecal complex (Fig. 108.12): Spermatheca small and sacciform, somewhat sclerotized at both ends; apical part spherical and of similar width then the basal part; no joint duct is differentiated between the lobes. Spermatic duct long and of uniform thickness, without nodule in the area of attachment at the basal lobe of the spermatheca.

Female uroventrite VIII (Fig. 109.6): The posterior margin in pointed arch; the spiculum rather long, rather wide, with rounded apex and on both sides the edges of the basal margin slightly arched.

Discussion. Jeannel (1924a) noted that *Ravasinia* bears a curious external similarity to *Leonhardella*. Due to the shape and characters of the aedeagus, the



FIGURES 109.1–109.6: *Bathyscia* series. Female uroventrite VIII of: (**1**) *Bathyscia montana jablanicensis,* (**2**) *Bathyscidius* (*Bathyscidius*) sp., (**3**) *B.* (*B.*) *tristiculus*, (**4**) *B.* (*Ionobathyscidius*) *basarai* (redrawn from Čeplík *et al.* 2021a), (**5**) *Pavicevicia comottiorum*, (**6**) *Ravasinia lonae*. Figs **3**, **6** redrawn from Perreau (2019).

genus *Ravasinia* shows notable similarities with the genus *Bathyscidius*, this is the reason for Jeannel (1924a) pointing out that *Ravasinia* represents a special phyletic series related to *Bathyscidius*. V.B. Guéorguiev (1974a) and Newton (1998) included *Ravasinia* and *Bathyscidius* in the subtribe Bathysciotina, as does Perreau (2000), but this author, who included, the two genera indicated, in the «Phyletic series of *Ravasinia*» and added the genus *Pseudobathyscidius*. The clarification of the relationships e.g. the constellation suggested by Jeannel (1924a) requires further investigation using molecular data.

Distribution. Albania. It colonises caves of the Tomor Mountains, near Bérat towards south-central area.

Species

Ravasinia lonae (G. Müller, 1922)
Leonhardella (*Ravasinia*) *Lonae* G. Müller, 1922a: 90.
Ravasinia Lonai J. Müller, 1922: Jeannel, 1924a: 271.
Ravasinia lonae (Müller, 1922): Perreau, 2000: 194.

3.2.5 Series ***Anthroherpon***

The characters that define the «Euryscapes» group of the tribe Bathysciae have no phylogenetic value as shown above. However, some of them used to define what Jeannel (1924a) named «Antroherpona Tribe» are valid for establishing the clade of *Anthroherpon*, *Graciliella*, *Leptomeson*, *Nauticiella* and *Hadesia*, but

not for the other clades of the series, such as the sister group consisting of *Leonhardella*, *Proleonhardella*, *Pholeuonopsis*, *Speonesiotes*, *Pholeuonella*, *Remyella* and *Rozajella*. The characters, here considered synapomorphies of the *Anthroherpon* subclade, are the following:

– Antennae inserted in the posterior quarter of the head.

– Very long and concave claws recurved ladle-shaped.

The rest that defined the tribe also found in one or another of the divisions of Bathysciae proposed by Jeannel (1924a) and may be used only to separate some subclade (or «group»):

– First article of antennae as long as, or longer than the second one.

– No external spurs at the apex of tibiae.

– Anterior tibia without comb or with comb and with a simple, internal spur.

– Meso- and metatibiae with the apex not widened, forming a hollow structure surrounded by rigid spines.

– Femora dilated at base or at apex.

– Feminine genitalia atrophied (lacking of spermatheca and styli).

The monophyly of Leptodirina (*sensu* Perreau 2000) is highly questionable (Perreau & Pavićević 2008b), especially since many species are highly troglobiomorphic and many characters are potentially homoplasic, the same might be true for the *Anthroherpon* series. This question was taken up by the recent works of Njunjić *et al*. (2017), Čeplik & Hlavâč (2022) and Delić *et al*. (2023). The molecular phylogenetic tree presented in the paper of Njunjić *et al*. (2017**)** pointed out, thatin their morphological and molecular analysis, the genera *Leptomeson*, *Anthroherpon* and *Hadesia* are found to be joint inside in the Anthroherponina subtribe and *Speonesiotes* is in the Bathysciotina subtribe.These two clades in the phylogeny are sister clades, and in turn they join the Leptodirina subtribe with a support of 0.99, this includes also the sister genera *Remyella* and *Rozajella*. In the phylogenetic tree (Fig. 1H), three groups are included within the *Anthroherpon* series:

– The *Anthroherpon* group with the genera *Anthroherpon*, *Graciliella*, *Leptomeson*, *Kircheria* and *Hadesia* (+ *Nauticiella*) which are joined with support 100/100.

– The *Pholeuonopsis* group which in turn includes the genera *Leonhardella*, *Pholeuonopsis*, *Proleonhardella* and *Speonesiotes* which are also joined with support 100/100.

– These two groups join with a very significant support, 92.4/100, to the third group *Pholeuonella* that includes *Remyella*, *Riberius*, *Rozajella* and *Pholeuonella* which are themselfes joined with high support, 94.9/100.

The genus *Parantrophilon* is missing from our phylogram, for which we have no molecular data, but is present in the molecular study of Delić *et al*. (2023). Recently it is considered as synonymous with *Anthroherpon* (Čeplík & Hlavâč 2022) and Delić *et al*. (2023) confirmed in his molecular work.

Jeannel (1924a) created the «Antroherpona Tribe» for these genera, which includes *Spelaeobates*, *Parantrophilon*, *Anthroherpon* (with *Leptomeson* as subgenus) and *Hadesia*. Although we do not have further evidence it appears highly likely that this grouping is, at least in part, paraphyletic. Still Perreau (2000) considered this grouping to be valid, with the exception of *Spelaeobates* that was moved to another sub-tribe; by adding *Remyella* Perreau (2000) followed on this Jeannel (1931).

Some other genera (*Croatodirus*, *Hygrodromus*, *Graciliella*, *Kircheria*, *Nauticiella, Velebitodromus* and *Riberius*) were finally described in the beginning of this century (Casale *et al*. 2000b; Moravec & Mlejnek 2002; Casale *et al*. 2004; Giachino & Vailati 2006; Njunjić *et al*. 2016; Giachino *et al*. 2021) and, apart from *Graciliella*, assigned to *Leptomeson* andwith this to *Hadesia* (Njunjić *et al*. 2016). Here *Nauticiella* are sister to *Hadesia*, *Kircheria* and *Velebitodromus* (Delić *et al*. 2023), as well as *Croatodirus* and *Hygrodromus* (Polak 2022 *pers. comm*.), no molecular data were available before this contributions. We will deal with the position of these genera in the part focussing specifically on this groups.

Key to groups

1. Facies leptodiroid or scaphoid. Antennae inserted in the posterior quarter of the head; first antennomere longer than the second .....*Anthroherpon* group
- Different facies, if leptodiroid or scaphoid facies only—*Rozajella* and *Remyella*—, then antennae inserted differently and the first antennomere shorter or equal to the second 2

2. Males protarsi tetrameres .....*Pholeuonopsis* group
- Males protarsi pentameres.....*Pholeuonella* group

3.2.5.1 ***Pholeuonella*** group

Diagnosis. Body shape bathyscioid, leptodiroid or pholeuonoid. Anophthalmous and depigmented. An-

tennae inserted in the central third, or in the back third of the head. First antennomere shorter than or as long as the second one; only in *Riberius* the first antennomer somewhat longer than the second. Elytral disc with, or without, transverse striations. Parasutural stria absent. Male protarsi pentameres, dilated or not. Protibiae with or without apical comb. Tarsal claws dilated or not. Mesoventral keel absent, poorly or well-developed. Median lobe of aedeagus, endophallus, parameres and spermatheca in different shape, depending of the genus.

Discussion. This group is based on morphological characters only very difficult to define. The synapomorphies are masked by an extreme degree of specialisation in the subterranean environment, this is particularly accentuated in these genera.

The entire *Pholeuonella* group is highly consistent with a support of 94.9/100 and joins as a basal group with the *Pholeuonopsis* and *Anthroherpon* groups to form the *Anthroherpon* series with support of 92.4/100 in Tree-1 (Fig. 1H) and of 98.6/100 in Tree-2 (Fig. 2).

Key to genera

1. Facies bathyscioid. Size very small, between 1.0–1.8 mm. Mesoventral keel high, posterior apophysis reaches at least a part of metaventrite (Figs 112.1–112.3, 112.7) 2
- Non-bathyscioid facies. Medium to large size, between 3.2–4.8 mm. Mesoventral keel absent or poorly visible (Figs 112.4–112.6) 5

2. Parameres with three (Fig. 115.2) or four setae (Fig. 115.8); if four setae the apical part with narrowed apex and beveled inner lateral margin 3
- Parameres with more of four setae (Figs 115.1, 115.3, 115.4); only *Laneyriella andrijevicensis* with four setae (see Jeannel, 1924a: Fig. 369).....4

3. VIIIth female uroventrite with two laminar lobes on each side of the spiculum in the basal margin (Fig. 116.10). Endophallus with a long and thin inverted stylet in the basal region (Fig. 114.8). Parameres with three setae (Fig. 115.2) .....*Perreauia* **gen. nov.**
- VIIIth female uroventrite without laminar lobes on the basal margin (Fig. 116.15). Endophallus without a long and thin stylet in the basal region (Fig. 114.14). Parameres with four setae (Fig. 115.8) ....*Serbiana* **gen. nov.**

4. Antennae with 9th and 10th antennomere transverse. Median lobe of aedeagus, in dorsal view, ends in a long sharp tip (Fig. 114.9). Endophallus with a single row of teeth along dorsal middle part (Fig. 114.9). Parameres with apex hooked and five or more apical setae (Fig. 115.4) and a row of two or five very small setae on the inner lateral edge of apical area (Fig. 115.3)..... *Pholeuonella*
- Antennae with 9th and 10th antennomere longer than wide. Median lobe of aedeagus, in dorsal view, more or less sharp (Fig. 114.7). Endophallus unarmed, no sclerotized pieces (Fig. 114.7). Parameres with apical area rounded or with a lateral depression and a group of apical setae between four and eleven of them (Fig. 115.1) .....*Laneyriella*

5. Facies pholeounoid. Clypeus and labrum with dense and long pubescence. Parameres with seven setae at apex (Fig. 115.5) .....*Riberius*
- Non-pholeounoid facies. Clypeus and labrum with no dense and rather short pubescence. Parameres with three setae at apex (Fig. 115.6, 115.7) 6

6. Antennae longer than the body length. Elytra without transverse striolae. Endophallus with two lateral phanerae and a central one in basal area (Fig. 114.10) ..... *Remyella*
- Antennae longer or shorter than the body length. Elytra with transverse striolae. Endophallus without sclerotized structures in basal area (Fig. 114.12, 114.13) ..... *Rozajella*

Genus ***Laneyriella*** V.B. Guéorguiev, 1976
Laneyriella V.B. Guéorguiev, 1976: 127.

Type species. *Bathyscia* (s. str.) *Ganglbaueri* Apfelbeck, 1907 by original designation (habitus in Fig. 110.1).

Diagnosis. Very small size, between 1.0–1.8 mm. Facies bathyscioid, with body ovoid, little elongated, convex and not attenuated backwards (Fig. 110.1); depigmented.

Head: Anophthalmous.

Antennae: Short, reaching the base of pronotum to the middle of body, with dilated club. Antenomeres 4th to 6th clearly longer than wide and 9th-10th somewhat longer than wide in males.

Pronotum: Transverse with the base as wide as the base of elytra; sides regularly arcuated and not sinuated in basal part.

Elytra: With thin and well-separated transverse

striolae, more defined in basal half and more confused in apical half. No parasutural stria.

Legs: Short, with tibiae little thorny; males protarsi pentameres and, depending on species, between narrow or somewhat wider than apex of protibiae; protibiae without external spurs and with comb.

Mesoventral keel (Fig. 112.1): Keel high, the posterior process reaching the middle of the metaventrite; anterior margin with the apical half softly arched and the lower half rectilinear; vertex rounded and obtuse-angled; posterior margin slightly concave in the anterior half and slightly convex in the posterior half, with very small setae.

Suture of the metaventrite (Fig. 112.1): The suture delimits a distinct arched area in the upper two thirds, and is very close to the coxal cavity in the lower third.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: In lateral view (Fig. 114.1) long, straight or slightly arcuated. Apical area, in dorsal view (Fig. 114.7), in a more or less sharp arc, not recurved; sides slightly arched in the basal half and sub-rectilinear in the apical half.

Endophallus (Fig. 114.7): Unarmed, no sclerotized pieces or structures.

Parameres (Fig. 115.1): As long, or somewhat shorter, than median lobe, thick but not compressed, with apical area rounded or with a lateral pit and between seven and eleven fairly long setae depending on species.

Spermathecal complex (Fig. 116.1). Spermatheca small, angled in the apical third, very weak but uniformly sclerotized without distinct regions, the walls of the proximal part being somewhat wrinkled.

Female uroventrite VIII (Fig. 116.9). Posterior margin in wide, very slightly undulating arc; anterior margin with the lateral edges straight and ascending, meeting to form a very long spiculum with the apical area somewhat enlarged and not sharpened.

Discussion. *Laneyriella* is very similar to the genus *Pholeuonella*, and was created for five species of the Balkan Peninsula (Jeannel, 1924a) and two others described later by G. Müller (1934) – *P. staudacheri* and *P. scutariensis* –. V.B. Guéorguiev (1976) described the genus based on very significant differences in copulatory organ: median lobe, parameres and endophallus (see description of genera *Pholeuonella* and *Laneyriella*). The lack of molecular data prevents us from confirming this supposed affinity with *Pholeuonella*.

Čeplík *et al*. (2021b) place *Laneyriella mikati* in the genus *Bathyscidius*. The reason supporting this generic change (Čeplík *et al*. 2021b) is the following: *Bathyscia mikati* was listed (Perreau 2015; Hlaváč *et al*. 2017) inside the genus *Laneyriella*, which belongs to the subtribe Leptodirina; genera from this subtribe have five protarsal segments in males; in the case of the genus *Laneyriella*, the first three male protarsal segments are distinctly dilated. Therefore the species cannot be classified in the genus *Laneyriella.*

Distribution. Species of this genus are known from areas of southern Dalmatia (Croatia), several localities of Montenegro and a locality in north Albania.

Species

Laneyriella andrijevicensis (Jeannel, 1924)
Pholeuonella andrijevicensis Jeannel, 1924a: 332.
Bathyscidius remyi Jeannel, 1934b: 100.
Laneyriella andrijevicensis (Jeannel): V.B. Guéorguiev, 1976: 128.

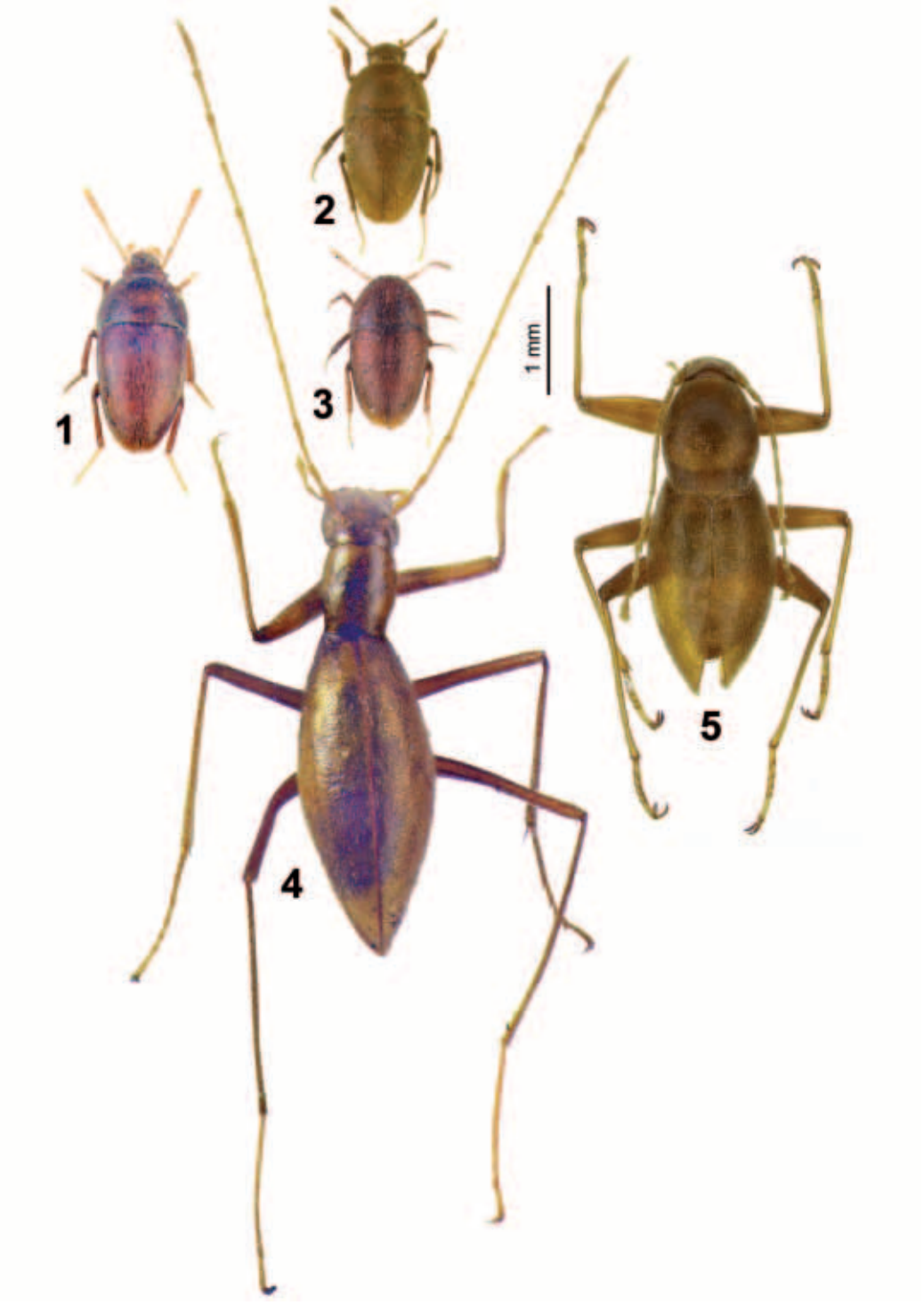
Laneyriella ganglbaueri (Apfelbeck, 1907)
Bathyscia (s. str.) *Ganglbaueri* Apfelbeck, 1907c: 320.
Pholeuonella Ganglbaueri Apfelbeck: Jeannel, 1910a: 29.
Bathysciola (*Pholeuonella*) *Ganglbaueri* Apfelbeck: Jeannel, 1914b: 15.
Laneyriella ganglbaueri (Apfelbeck): V.B. Guéorguiev, 1976: 128.

Laneyriella matchai (Jeannel, 1924)
Pholeuonella Matchai Jeannel, 1924a: 332.
Laneyriella matchai (Jeannel): V.B. Guéorguiev, 1976: 128.

Laneyriella milotiana (Reitter, 1918)
Bathyscia (Pholeuonella) milotiana Reitter, 1918: 153.
Pholeuonella milotiana Reitter, 1918: Jeannel, 1924a: 333.
Laneyriella milotiana (Reitter): V.B. Guéorguiev, 1976: 128.

Laneyriella scutariensis (G. Müller, 1934)
Pholeuonella scutariensis G. Müller, 1934: 178.
Laneyriella scutariensis (Müller): V.B. Guéorguiev, 1976: 128.

Laneyriella staudacheri (G. Müller, 1934)
Pholeuonella staudacheri G. Müller, 1934: 178.
Laneyriella Staudacheri (Müller): V.B. Guéorguiev, 1976: 128.
Laneyriella staudacheri (Müller): Perreau, 2000: 216.



FIGURES 110.1–110.5: *Anthroherpon* series, *Pholeuonella* group. Habitus of: (**1**) *Laneyriella ganglbaueri*, (**2**) *Perreauia dalmatica* **gen. nov. sp. nov**., (**3**) *Pholeuonella erberii erberii,* (**4**) *Remyella propiformis borensis*, (**5**) *Riberius stillicidii* (modified from Giachino & Casale 2022).

Laneyriella stussineri (G. Müller, 1914)
Pholeuonella Stussineri G. Müller, 1914: 1009.
Laneyriella stuessineri (Müller): V.B. Guéorguiev, 1976: 128.

Genus ***Perreauia*** nov.
https://zoobank.org/NomenclaturalActs/5C1066D6-C285-45AF-A4EA-84FB890A381F

Type species. *Perreauia dalmatica* sp. nov. by present designation (habitus in Fig. 110.2).

Description. Small size, between 1.5–1.6 mm. Bathyscioid facies, with body elliptical, elongated, quite convex and attenuated backwards (Fig. 110.2). Colouration reddish-brown; pubescence short and lying down. Depigmented.

Head: Retractile, with little marked but evident occipital carina; anophthalmous.

Antennae: Antennae inserted in the central third; short, not exceeding the base of pronotum, with first antennomere shorter than the second one; widened club and transverse antennomeres, except the 11th.

Pronotum: Transverse and convex, with very fine punctation and a poorly printed microreticulum; maximum width at the base, as wide as the base of elytra; sides regularly and slightly arcuated, not sinuated in basal part; posterior angles acute and pointed vertices.

Elytra: Oval elongated and convex; maximum width very close to base, with fine transverse striolae, well separated and well marked, present throughout the surface of the elytra. Parasutural stria absent.

Legs: Moderately long with tibiae little thorny. Male protarsi pentameres, narrower than the apical part of protibiae. Protibiae without external spurs, but with a well-developed comb on apical and external edge.

Mesoventral keel (Fig. 112.2): High, convex margins and toothless apex; posterior process reaching the metaventrite.

Suture of the metaventrite (Fig. 112.2): It delimits a small arched area in the upper half.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Long and narrow. In lateral view (Fig. 114.2), not arcuated, with the dorsal face flat and the apical part very curved with a very sharp tip. In dorsal view (Fig. 114.8), sub-rectilinear sides nearly until the apex, which abruptly tapers to form a long, curved extension towards the ventral side; the maximum width in the middle part. Long, narrow basal blade with smooth posterior arch.

Endophallus (Fig. 114.8): Sclerotized structures differentiated in the three regions. Basal region with a long and thin inverted stylet; middle region with a narrow sclerotized lamina, sigmoid in lateral view; apical region with two bands in the shape of an inverted «Y» and, on the sides, two spongy structures.

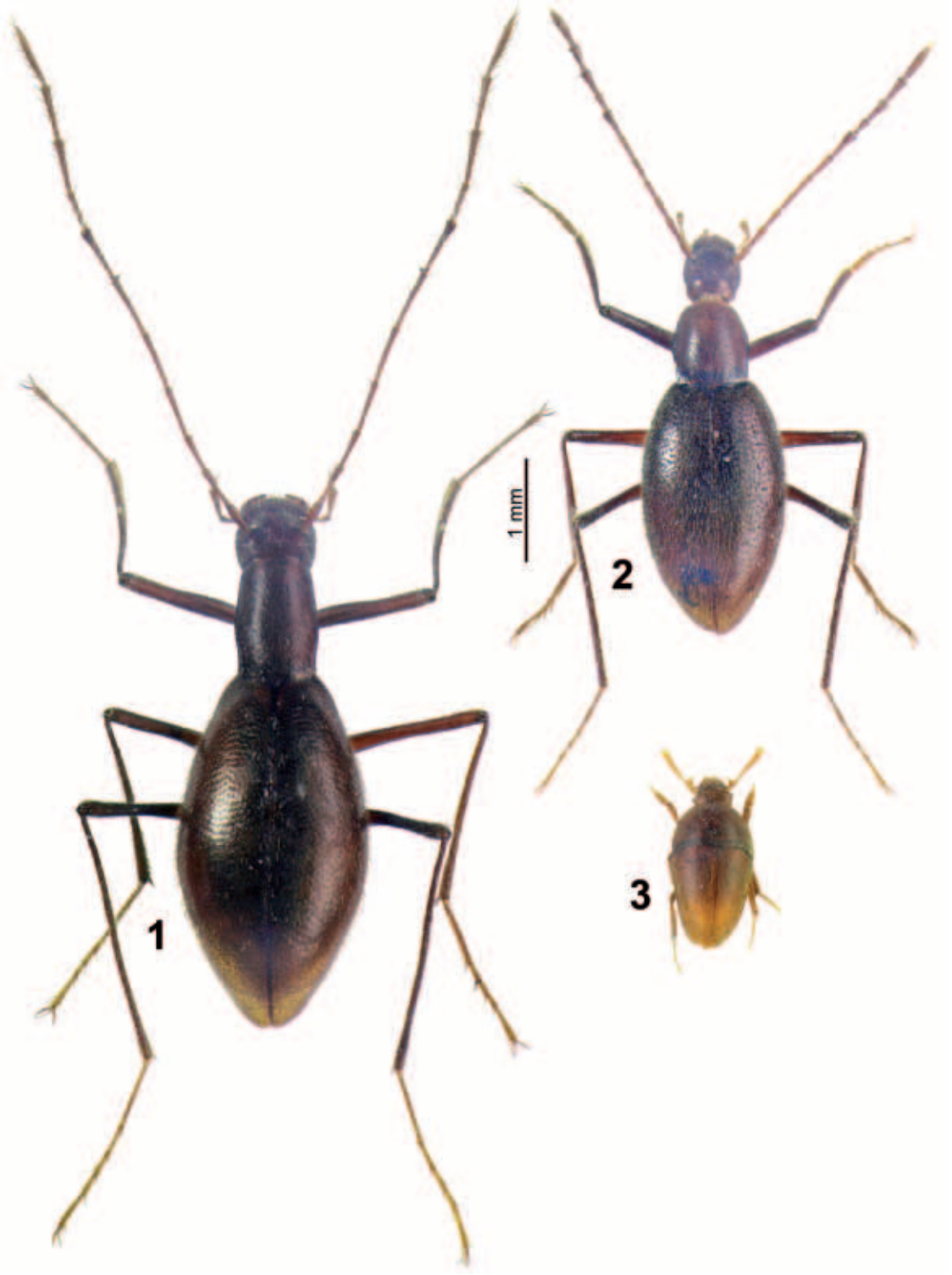
Parameres (Fig. 115.2): Broad, as long as or very slightly shorter than the median lobe and flattened in the apical area, elbow-shaped with a rounded tip. There are three setae of different lengths, two apical, the inner one much thicker and the third subapical.

Female. *Spermathecal complex*: Spermatheca (Fig. 116.2) short and complex, with a rough annular basal lobe, more developed and slightly more sclerotized than the areas corresponding to the short joint duct and the apical lobe, which is spherical.

Female uroventrite VIII (Fig. 116.10): Apical margin in wide arc; basal margin with two laminar lobes on each side of the spiculum, which is long, narrow and with sharp apex.

Etymology. Genus dedicated to our common friend Dr. Michel Perreau (Paris, France), in recognition of his extensive research activity in the field of subterranean fauna in general, and Leiodidae in particular. The name will be considered feminine.

Discussion. *Perreauia* gen. nov. presents a set of characters common with *Pholeuonella* such as: a bathyscioid facies, small size, anophthalmia, the antennomeres 8th to 10th transverse, a transverse pronotum with the base as wide as the base of the elytra, elytra with transverse striolae well separated and lacking parasutural stria, male protarsi pentameres, protibiae without external spurs, with a well-developed comb; endophallus of the aedeagus without «Y»-piece and parameres wide, as long as the median lobe. Females of *Perreauia* gen. nov. show a unique characteristic not observed in any other genus of the *Pholeuonella* group, the two small lobes on the basal margin of the VIII uroventrite (Fig. 116.2); a similar conformation has been observed in *Speonesiotes narentinus latitarsis* and the genus *Adelopsella*, with much more developed lobes (Figs 35.9, 135.9). Therefore, we believe that *Perreauia* gen. nov. is a genus close to the genus *Pholeuonella,* but molecular data are lacking to confirm the supposed affinity between both genera.



FIGURES 111.1–111.3: *Anthroherpon* series, *Pholeuonella* group. Habitus of: (**1**) *Rozajella ognjenovici* **comb. nov.**, (**2**) *Rozajella jovanvladimiri*, (**3**) *Serbiana latitarsis* **gen. nov. sp. nov**.

Species

Perreauia dalmatica sp. nov. (See Appendix New Species)

Genus ***Pholeuonella*** Jeannel, 1910
Pholeuonella Jeannel, 1910a: 8.
Protopholeuonella Laneyrie, 1967: 613 (Type species. *Adelops Erberii* Schaufuss, 1862).

Type species. *Adelops erberii* Schaufuss, 1862 by original designation (habitus in Fig. 110.3).

Diagnosis. Size very small, between 1.3–1.5 mm. Facies bathyscioid, with body elliptical, elongated, quite convex and poorly attenuated backwards (Fig. 110.3). Pubescence short and lying down. Depigmented.

Head: Blurred occipital carina; anophthalmous.

Antennae: Short, not extending beyond the base of the pronotum, with widened club; the 1st antennomere almost as long as the 2nd one; the 4th to 6th slightly longer than wide; the 8th to 10th transverse.

Pronotum: Transverse with base as wide as base of elytra; sides regularly arched and not sinuous in the basal area.

Elytra: With fine, well-separated transverse striae over the entire surface, with those in the medial apical part being well marked.. Parasutural stria absent.

Legs: Short with slightly spiny tibiae. Males protarsi pentamerous and narrower or as wide as the apical part of the protibiae. Protibiae without external spurs, but with a well-developed comb on the apical and external margin.

Mesoventral keel (Fig. 112.3): High, laminar with narrow margins, the ventral one arched and smooth. The posterior process does not exceed half the metaventrite.

Suture of the metaventrite (Fig. 112.3): It delimits a rather well-developed, almost subtriangular area in the upper half and is very close to the coxal cavity in the lower half.

Metatergal apparatus (Fig. 113.1): Wings of metascutum short and narrow; apophysis of alacrista rather long, as long as half the length of a wing, with sharp tips.

Metendosternite (Fig. 113.4): «V»-shaped. Furcal arms long and very narrow, with a well-developed apophysis; very narrow posterior furcal plate along arms and trunk, not reaching the apophysis, and there is a small anterior furcal plate in the apical part of the arm before the apophysis. Trunk short and narrow, about twice as long as wide.

Median lobe of aedeagus: Long and narrow. In lateral view (Fig. 114.3), very little arcuated, before apical area a strong depression, then very curved and with a very sharp tip. In dorsal view (Fig. 114.9), sides arched, concave in the middle part and convex towards the apical third; then gradually diminishing to end in a long, sharp tip. Basal blade long and narrow.

Endophallus (Fig. 114.9): Armed with a single row of highly sclerotized teeth arranged along the dorsal median part and tapering from the basal to the apical part.

Parameres: Broad, compressed and somewhat sinuate, as long as the median lobe, with the apex hooked (Fig. 115.4). Equipped with five fairly stout setae of similar length with insertion pores very close together; bearing on the inner lateral margin of the apical area a row of small, distant setae, usually more than two (Fig. 115.3). Ventral blade of tegmen wider and shorter than basal blade of median lobe.

Spermathecal complex (Fig. 116.3): Spermatheca small, very weakly sclerotized, almost hyaline; apical lobe small and spherical, very short union duct and proximal lobe in a smooth arc, much more elongated and wider than apical.

Female uroventrite VIII (Fig. 116.11): Median area of posterior margin in very slightly protruding arc; sides of anterior margin smoothly arched and meeting to form a short, very sharp spiculum.

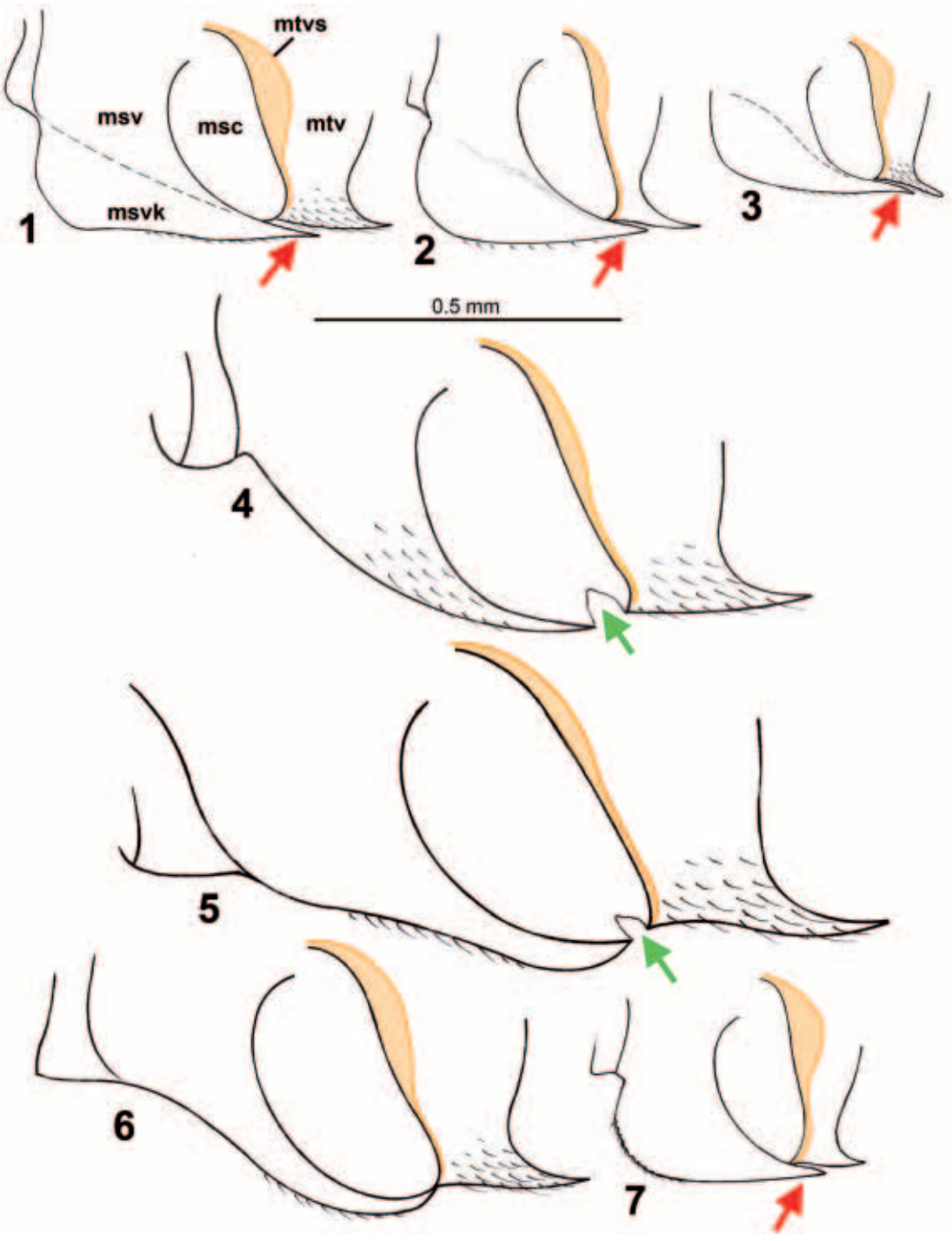
Discussion. In the phylogenetic tree (Fig. 1H), the genus *Pholeuonella* joins the sister clades *Rozajella*, *Remyella* and *Riberius* with a high support (94.9/100). Together they form the *Pholeuonella* group.

Distribution. Distributed in southern Dalmatia (Croatia), western Montenegro, near the Adriatic Sea, and southern Bosnia-Herzegovina, as well as a site near Sarajevo.

Species

Pholeuonella bosnicola (Reitter, 1913)
Bathyscia (*Pholeuonella*) *bosnicola* Reitter, 1913a: 157.
Bathyscia bosnicola Reitt.: G. Müller, 1917: 655.
Pholeuonella bosnicola Reitter: Jeannel, 1924a: 427.

Pholeuonella erberii (Schaufuss, 1862)
Pholeuonella erberii epidaurica Karaman, 1953
Pholeuonella erberi epidaurica Karaman, 1953: 112.
Pholeuonella erberii erberii (Schaufuss, 1862)
Adelops Erberii Schaufuss, 1862b: 145.
Bathyscia Erberi Schauf.: Schaufuss, 1881: xcvii.



FIGURES 112.1–112.7: *Anthroherpon* series, *Pholeuonella* group. Pterothorax in lateral view of: (**1**) *Laneyriella ganglbaueri*, (**2**) *Perreauia dalmatica* **gen. nov. sp. nov**., (**3**) *Pholeuonella erberii erberii*, (**4**) *Remyella propiformis borensis*, (**5**) *Rozajella ognjenovici* **comb. nov.**, (**6**) *Rozajella jovanvladimiri*, (**7**) *Serbiana latitarsis* **gen. nov. sp. nov**. Red arrow pointing to the mesoventral keel prolonged over the metaventrite; green arrow pointing to the confluent mesocoxal cavities. Abbreviations: **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture.

Bathyscia (*Bathyscia*) *Erberi* Schauf.: Reitter, 1885a [1884]: 20.
Pholeuonella Erberi Schaufuss: Jeannel, 1910a: 29.
Bathyscia (*Adelopsella*) *Erberi* Schauf.: J. Sahlberg, 1913: 48.
Bathysciola (*Pholeuonella*) *Erberi* Schaufuss: Jeannel, 1914b: 14.
Pholeuonella erberii erberii (Schaufuss): Perreau. 2000: 216.

Genus ***Remyella*** Jeannel, 1931
Remyella Jeannel, 1931b: 260.

Type species. *Remyella scaphoides* Jeannel, 1931 by original designation (for the habitus see the one of the similar species *Remyella propiformis borensis* in Fig. 110.4).

Diagnosis. Average size, between 3.8–5.5 mm. Body shape narrow and elongated, with scaphoid facies (Fig. 110.4); depigmented. Colour yellowish-brown, with bright integument. Head and pronotum with fine and superficial polygonal microsculpture.

Head: Elongated, somewhat longer than wide, shorter, narrower than pronotum in males, and sometimes as wide as pronotum in females. Punctation clearly visible, with short, yellowish setae scattered throughout. Anophthalmous.

Antennae: Very long and thin, much longer than the body in males, only slightly longer in females. 1st and 2nd antennomeres subequal; the 8th shorter and narrower than the 7th, 9th and 10th.

Pronotum: Bell-shaped, between 1.7–1.9 times as long as wide; convex, with maximum width in the median part, or very close to the median part, and much narrower than the elytra. Lateral margins narrow, being somewhat arched or rectilinear in anterior area and somewhat sinuous in posterior one, as well as entirely and finely flanged. Basal angles obtuse and unplanned posteriorly. Disk with dense or more or less scattered punctation, in this case denser along the posterior margins. Disk bearing short and thin scattered setae.

Elytra: Scaphoid, convex and very elongated, between 2.3–2.6 times longer than wide, without physiogastry. Wider in females than in males, with maximum width slightly in front of the median part. Apexes separated and broadly arched in males, slightly closer together and narrower in females. Disc with dense and deep punctation not aligned transversely, sometimes with rudimentary transverse alignments, but without transverse striae. Rather long, flat-lying bristles. Parasutural stria absent.

Legs: Very long and thin; femora widened, profemora with a dense pubescence of fine and very short setae on ventral surface. Protibiae curved outwards in apical area, without comb on external lateral margin, meso- and metatibiae straight. Male protarsi pentamerous and not dilated.

Mesoventral keel (Fig. 112.4): Absent. Intercoxal process of mesoventrite not reaching the anterior margin of metaventrite.

Suture of the metaventrite (Fig. 112.4): A narrow and elongated area delimited in the upper two thirds, almost non-existent in the lower third.

Metatergal apparatus (Fig. 113.2): Wings of the metascutum very long, very narrow and curved; short and sharp alacrista process.

Metendosternite (Fig. 113.5): In shape of «V» or «U» with long arms and a very short and wide trunk. Arms 3.5 times longer than the trunk, slightly sinuate; posterior plate narrow and only visible in the basal area of arms and in trunk; terminal process widened. Furcal trunk transverse, 1.5 times wider than long; median keel wide and divergent in its posterior part.

Genital segment of male: Complete, clearly differentiated in dorsal and ventral parts, with setae on all dorsal apical edge, or only on sides.

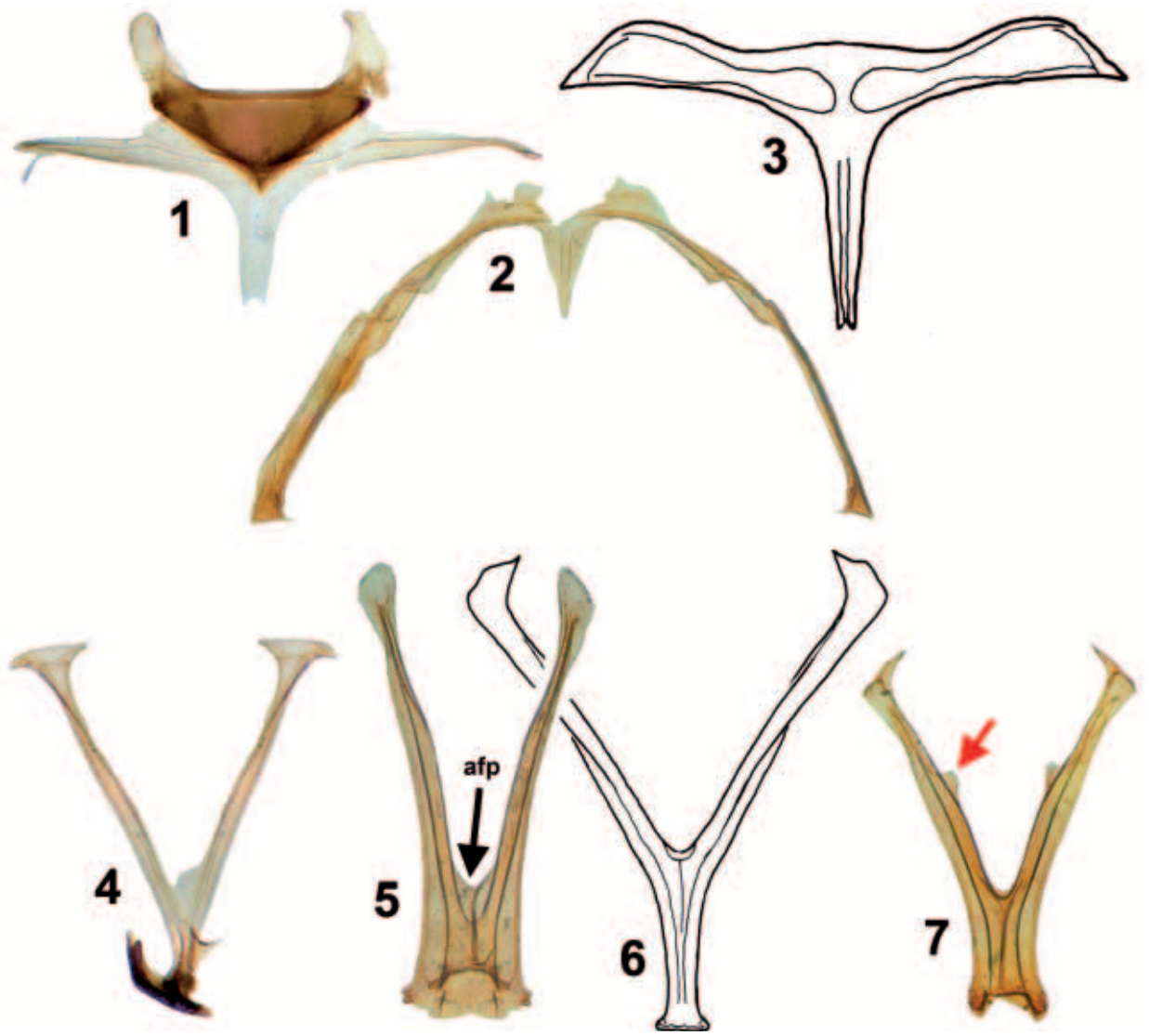
Median lobe of aedeagus: Short and weakly sclerotized. In lateral view, very slightly arched, almost straight, with a flattened, dorsally curved apex. In dorsal view (Fig. 114.10), widened to two-thirds of its length, with subrectilinear sides, then gradually narrowing into an equilateral triangle with straight or slightly concave sides that meet at an already sharp or blunt apex, depending on the species. Basal blade with arched apical area, slightly narrower and as long as the ventral blade of the tegmen.

Endophallus (Fig. 114.10): With two lateral and one central phanerae in basal area, as well as two weak, subapical sclerotized parts in the median part..

Parameres: Longer than the median lobe, curved outward in their middle part and narrowed distally. Three subequal setae are present, one distal and two latero-internal, equidistant, or two apical and one subapical.

Spermathecal complex (Figs 116.4, 116.5): Spermatheca small, weakly sclerotized; «C»-shaped with proximal and medial parts cylindrical, not lobated; distal lobe spherical. Spermatic duct long and of uniform thickness, about four times the length of the spermatheca, without basal sclerotized part. Spermathecal gland hyaline, sponge-shaped.

Female uroventrite VIII (Fig. 116.12): Sparsely pubescent, with scattered setae and posterior edge



FIGURES 113.1–113.7: *Anthroherpon* series, *Pholeuonella* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Pholeuonella erberii erberii*, (**2**) *Remyella javorensis*, (**3**) *Riberius stillicidii*. Metendosternite of: (**4**) *P. e. erberii*, (**5**) *R. javorensis*, (**6**) *R. stillicidii*, (**7**) *Rozajella madzgalji*. Red arrow pointing to an internal protuberance of the arm. Figs **2**, **5**, **7** modified from Njunjić *et al.* 2017; Figs **3**, **6** from Giachino & Casale 2022. Abbreviations: **afp**, anterior furcal plate.

widely arched. Anterior edge with the lateral margins straight, ascending and joining to form a long spiculum, slightly wide and with blunt apex.

Discussion. Morphological and molecular phylogenetic studies by Njunjić *et al*. (2017) place *Remyella* in the subtribe Leptodirina as sister to the genus *Rozajella* with posterior probability = 1.00. Both share morphological characters and live in neighbouring geographical areas. In addition, our molecular results (Fig. 1H) identified a sister relationship between *Remyella* and the genus *Riberius* with support of 87.7/100. The clade formed by these two species is identified as sister to *Rozajella* with a high support (97.1/100).

Distribution. Located in the Pešter polje region, with the following surrounding mountain ranges: Jadovnik (1734 m), Javor (1520 m), Giljeva (1617 m), Ninaja

(1358 m) and Žilindar (1616 m). It corresponds to three isolated karst areas that colonise all four currently known species (Njunjić *et al*. 2017):

– Near Sjenica, south-western Serbia, with two caves hosting *R. javorensis*.

– Near Novi Pazar, on the north-eastern side of Pešter polje, with a single locality in which *R. raskae* lives.

– The third part is an area 25 km long and 10 km wide, oriented NW-SE on the southern border of Pešter polje, along the border between Serbia and Montenegro. Here, in isolated but close areas, occur *R. propiformis,* which lives in two caves in Montenegro and eleven in Serbia, and *R. hussoni* which lives in two caves in Montenegro and five in Serbia.

Species

Remyella hussoni Jeannel, 1934
Remyella propiformis subsp. *Hussoni* Jeannel, 1934b: 103.
Remyella puncticollis Jeannel, 1934b: 103.
Remyella scaphoides hussoni Jeannel, 1934: Giachino & M. Etonti, 1995: 91.
Remyella hussoni Jeannel, 1934: Njunjić, Schilthuizen, Pavićević & Perreau, 2017: 154.

Remyella javorensis S. Ćurčić & B. Ćurčić, 2008
Remyella javorensis S. Ćurčić & B. Ćurčić *in* S. Ćurčić, Waitzbauer, Zolda, Brajković & B. Ćurčić, 2008: 112.

Remyella propiformis Winkler, 1933
Remyella propiformis Winkler, 1933: 78.
Remyella propiformis borensis Winkler, 1933: 78.
Remyella scaphoides droveniki Giachino & M. Etonti, 1995: 91.
Remyella montenegrina S. Ćurčić, Antić, N. Ćurčić & B. Ćurčić, 2013: 1218.
Remyella scaphoides propiformis Winkler, 1933: Giachino & M. Etonti, 1995: 88.
Remyella scaphoides borensis Winkler, 1933: Giachino & M. Etonti, 1995: 90.

Remyella raskae S. Ćurčić & B. Ćurčić, 2008
Remyella raskae S. Ćurčić & B. Ćurčić *in* S. Ćurčić, Waitzbauer, Zolda, Brajković & B. Ćurčić, 2008: 110.

Remyella scaphoides Jeannel, 1931
Remyella scaphoides Jeannel, 1931b: 263.
Remyella scaphoides scaphoides Jeannel, 1931: Giachino & M. Etonti, 1995: 88.

Genus ***Riberius*** Giachino & Casale, 2022
Riberius Giachino & Casale, 2022: 35.

Type species. *Riberius stillicidii* Giachino & Casale, 2022 by original designation (habitus in Fig. 110.5).

Diagnosis. Small size, 3.2–3.3 mm, with pholeounoid appearance (Fig. 110.5), depigmented and pubescent.

Head: Elongate, non-retractile, without occipital carina; clypeus and labrum with dense, long pubescence and a series of anterior setae (labrum) or two lateral groups of three setae (clypeus). Penultimate labial palpomere long and apically dilated; apical palpomere very short and stout. Anophthalmous.

Antennae: Relatively short, inserted at the base of the middle 1/3 of the head, similar in both sexes and not reaching the apex of the elytra, shorter than the length of the body; first antennomere enlarged, longer than the second; the 11th antennomere as long as the 10th.

Pronotum: Large and not dimorphic; only slightly more elongate in male than in female. Sub-ovoidal in shape, with its maximum width just after the middle. Lateral sides regularly rounded anteriorly, subrectilinear basally. Hind angles marked although obtuse; basal margin narrower than the base of elytra. Anterior margin convex. Pterothorax not pedunculate.

Elytra: Elongate-oval, moderately attenuated at the apex. Dimorphic, apex pointed in both sexes, with a small acute, pointed, posterior expansion in the female. Microsculpture sparse, not forming transverse rows; disc with fine, short pubescence; parasutural stria absent.

Legs: Very long and slender, with femora basally thickened. Protibiae slightly enlarged just at apex, without comb but with incomplete apical inner basket of spines and short setae and without outer spurs; inner spurs simple, very small and slender. Male protarsi with five segments, not dilated. Meso- and metatibiae with a simple apical internal spur and an apical basket of very short spines and setae; tarsal claws long and enlarged.

Mesoventral keel: Absent; mesocoxal cavities contiguous.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 113.3): Reduced, with long alacrista apophysis although shorter than wings of the metascutum.

Metendosternite (Fig. 113.6): Thin, «V»-shaped, with narrow furcal arms and short, narrow furcal plate, only visible up to the middle of the arms. Apophysis of the arms well-developed, flexed and pointed in-

wards. Furcal trunk narrow, almost three times longer than wide and slightly more than twice as short as the length of the arms.

Median lobe of aedeagus: Large, thin, ventrally abruptly arched before base; basal lamina of median lobe curved, without ventral keel. Apex, in lateral view (Fig. 114.4), pointed and bisinuate. In dorsal view (Fig. 114.11) very elongate, with sides subparallel almost to apex, which is subtriangular and slightly truncate.

Endophallus (Fig. 114.11): Almost unarmed, with only a short, centro-apical, striated bundle.

Parameres (Fig. 115.5): As long as the median lobe, apically turned outward, each bearing seven setae at apex.

Spermathecal complex (Fig. 116.6): Spermatheca membranous, bean-shaped, only slightly sclerotized, not annulated; short spermatic duct, slightly widened in the middle part.

Female uroventrite VIII (Fig. 116.13): With an evident, apically truncated, spiculum.

Gonapophysis (Giachino & Casale 2022: Fig. 9): Normally developed.

Discussion. The first antennomere of *Riberius* is longer than the second, the male protarsi are pentamerous, the ovipositor is completely atrophied and the spiculum of the Female uroventrite VIII is well-developed (Giachino & Casale 2022). Analysis and evaluation of the taxonomic significance of these characters, together with other morphological characters, in particular those of the male genitalia, lead us to include *Riberius* in the phyletic series of *Anthroherpon*. This series, composed on a molecular basis of at least two clades (*Anthroherpon* + *Graciliella* + *Leptomeson*) and (*Hadesia* + *Nauticiella*), on a morphological basis would seem to base this series on the presence/absence of the spiculum of the 8th female uroventrite. However, because of the presence of a developed apophysis, *Riberius* seems closer to the phyletic lineage of *Anthroherpon* than to *Hadesia*, with which it shares the hygropetricolous lifestyle.
Some preliminary molecular data based on cox1 only (Faille 2021 *pers. comm*. *in* Giachino & Casale 2022) show that: *Kircheria* is close to *Hadesia* and *Anthroherpon*, and *Riberius* is not directly related with the *Kircheria-Hadesia* clade, nor with *Anthroherpon* lineage. This is much more in agreement with the analysis of our recent molecular phylogenetic tree (Fig. 1H), which shows a clear relationship between *Anthroherpon* + *Graciliella* + *Leptomeson* which are part of the same clade; however, *Riberius* which is within the *Anthroherpon* phyletic series is placed in the *Pholeuonella* group clade and is sister to *Remyella* with a support of 87.7/100.

Distribution. Known from a single cave in Northern Albania, into the Nikaj Mërtur Regional Natural Park.

Species

Riberius stillicidii Giachino & Casale, 2022
Riberius stillicidii Giachino & Casale, 2022: 36.

Genus ***Rozajella*** S. Ćurčić, Brajković & B. Ćurčić, 2007
Rozajella S. Ćurčić, Brajković & B. Ćurčić *in* S. Ćurčić, Brajković, B. Ćurčić & Waitzbauer, 2007: 146.
Nonveilleriella Perreau & Pavićević, 2008a: 199 **syn. nov.** (Type species. *Nonveilleriella ognjenovici* Perreau & Pavićević, 2008).

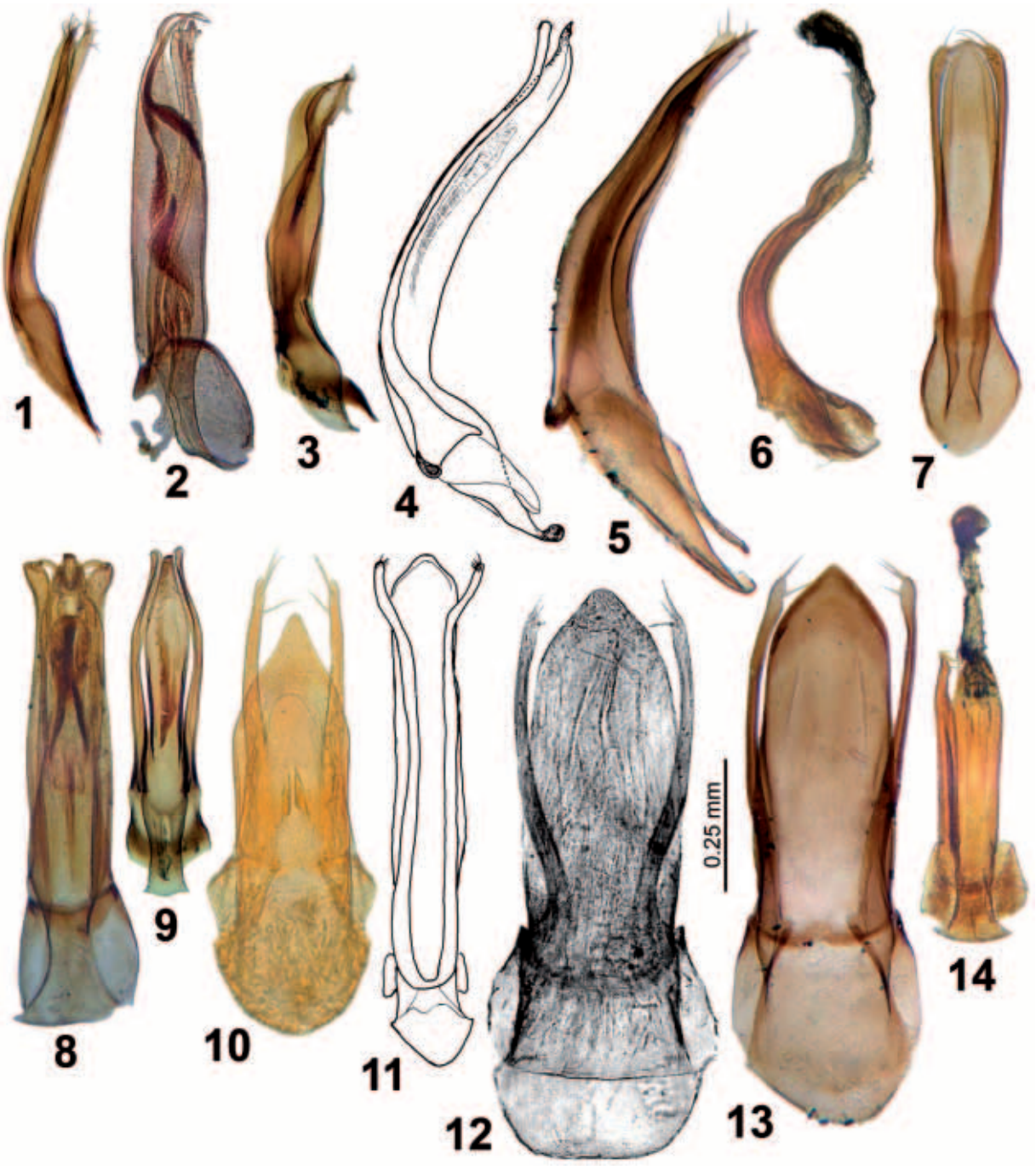
Type species. *Rozajella jovanvladimiri* S. Ćurčić, Brajković & B. Ćurčić, 2007 by original designation (habitus in Fig. 111.2).

Diagnosis. Average size, between 3.2–5.7 mm; females generally larger than males. Body shape narrow and elongated, with facies intermediate between scaphoid and leptodiroid (Fig. 111.2). Colour dark reddish, with bright integument and fine and dense microsculpture. Depigmented.

Head: Slightly elongated and non-retractable, somewhat longer than wide, slightly narrowed towards the base which is slightly narrower than pronotum. Occipital carina absent or only slightly marked; very fine punctation and numerous short, raised setae; anophthalmous.

Antennae: Long and slender, although distinctly shorter or clearly longer than the length of the body. Slightly longer in the male than in the female, and inserted in the central part of the head. First antennomere broader, slightly shorter or as long as the second; 7th, 9th and 10th subconical, widened distally, of which the 10th is the shortest; 11th elongated and with acute apex, the longest of all.

Pronotum: Bell-shaped or subrectangular between 1.2–1.5 times longer than wide; convex, with a maximal width slightly in front of the median part or towards the middle. Slightly narrowed at the base which is almost as wide as the base of the elytra. Lateral margins flanged; in some species the margin is interrupted in the median part. Anteriorly narrow and arched or slightly sinuate. Base concave and sinuate in front of



FIGURES 114.1–114.14: *Anthroherpon* series, *Pholeuonella* group. Aedeagus in lateral view of: (**1**) *Laneyriella ganglbaueri*, (**2**) *Perreauia dalmatica* **gen. nov. sp. nov**., (**3**) *Pholeuonella erberii erberii*, (**4**) *Riberius stillicidii*, (**5**) *Rozajella jovanvladimiri*, (**6**) *Serbiana latitarsis* **gen. nov. sp. nov**. Aedeagus in dorsal view of: (**7**) *L. ganglbaueri*, (**8**) *P. dalmatica* **gen. nov. sp. nov**., (**9**) *P. e. erberii*. (**10**) *Remyella scaphoides* (modified from Njunjić *et al.* 2017), (**11**) *R. stillicidii*, (**12**) *Rozajella ognjenovici* **comb. nov.** (modified from Perreau & Pavićević 2008), (**13**) *R. jovanvladimiri*, (**14**) *S. latitarsis* **gen. nov. sp. nov**. Figs **4**, **11** modified from Giachino & Casale 2022.

the more or less acute and slightly flattened vertices; posterior angles obtuse or acute with sharp vertices. Dorsal surface strongly reticulated; dense punctation of small, shallow dots or thick, deep, spaced punctation. Pubescence raised. Pterothorax not pedunculated.

Elytra: Elliptical, convex and quite elongated, 1.5–1.8 times longer than wide, without physiogastry; maximum width towards the middle with apical area narrowed and apexes in rounded arches; shoulders well marked. Punctation dense and deep, aligned transversely, with transverse striations on all, or at least, a significant part of the elytral disk. Pubescence short or long and raised. Parasutural stria absent.

Legs: Long and thin; tibiae with a crown of thorns in apical area, but no comb on outer margins; without external apical spurs; slightly arcuated outward in basal part. Protibiae and mesotibiae with apical part of internal spurs crenate, simple in metatibiae. Protibiae with apical area slightly curved outwards; femora dilated in basal area and narrowed in distal one. Profemora with fine, sparse, scattered and tiny setae on ventral surface. Male protarsi pentamerous, with the first two tarsomera widened, although narrower than the apex of protibiae, or totally undilated. Claws long and sharp at apex.

Mesoventral keel (Fig. 112.6): Very low, not very marked; the lower margin in slightly concave arc and with setae; the posterior process reaching the anterior area of the coxal cavity. This cavity is open posteriorly.

Suture of the metaventrite (Fig. 112.6): Delimits a narrow, elongated area in the upper half that is almost non-existent in the lower half.

Metatergal apparatus: Unknown.

Metendosternite (Fig. 113.7): «V»-shaped, with long arms and short, wide trunk. Arms 3.5 times longer than trunk, slightly sinuate; posterior plate narrow along entire arm and trunk; small lobe in the mid-anterior area of the arm that is a rudiment of the anterior plate. Terminal process or apophysis prolonged inwards and very sharp. Trunk as long as wide, or very little longer than wide.

Median lobe of aedeagus: Short and little widened. In lateral view (Fig. 114.5), ventrally arcuated, dorsally sinuated, being convex in middle part and apical area a little raised towards dorsal face; apex slightly curved ventrally. In dorsal view (Fig. 114.13), sides slightly arcuated up to three-quarters of apical part, then gradually narrowed in arc to the apex which is more or less sharp. Basal lamina short, with arcuated apical area, somewhat longer than and as wide as ventral blade of tegmen.

Endophallus (Fig. 114.13): Weakly sclerotized, almost unarmed, with only two lateral bands along the median area and numerous short thin or thick spines.

Parameres (Fig. 115.7): Elongated and thin, slightly longer than the median lobe. Apical area dilated, slightly curved inwards with sharp apex, and bearing three setae of similar length: two apical with insertion pores nearby and another preapical and internal slightly offset. Apical club, depending on species, with or without a preapical constriction and with or without an internal concavity.

Spermathecal complex (Fig. 116.7): Spermatheca small, elongated irregular sac-shaped, membranous, although dorsal area a little more sclerotized; spermatic duct thin, somewhat widened in the area of union to the spermatheca, with spermathecal gland.

Female uroventrite VIII (Fig. 116.15): With posterior edge widely arched; anterior edge subrectilinear with spiculum long, apical part slightly widened and sharp, rounded, bifurcated or subtruncate apex, depending on species.

Discussion. A morphological and molecular analysis unambiguously places *Remyella* and *Rozajella* in the subtribe Leptodirina (Njunjić *et al*. 2017), as sister genera. In our phylogenetic tree (Fig. 1H) *Rozajella* is also sister to the genus *Remyella*, as is *Riberius*, which it joins with high support (97.1/100); these join the genus *Pholeuonella* to form the group *Pholeuonella* with high support (94.9/100). This clade is grouped in the *Anthroherpon* series with the groups *Anthroherpon* + *Pholeuonopsi*s with support 92.4/100.

Perreau & Pavićević (2008a) placed the genera *Nonveilleriella* and *Rozajella* in the subtribe Leptodirina for their similar morphological characters and close range, but without phylogenetic evidence. Subsequently, based on morphological and molecular phylogenetic analysis by Njunjić *et al*. (2017), they associated the genera *Remyella* and *Rozajella* with *Nonveilleriella* (without molecular data), this genus being morphologically very similar to *Rozajella*, and gave these three genera the same subtribal assignment. Molecular data are lacking in our tree.

The genera *Rozajella* and *Nonveilleriella* share the following characters (Perreau & Pavićević 2008a): the presence of transverse striations on the elytra, at least over the anterior half of their length, which differentiates these two genera from all other Leptodirina (*sensu* Perreau 2000); a blurred mesoventral keel with a similar metaventral suture (Figs 112.5, 112.6); the protarsi of the male with five segments; the meso- and metatibiae without external apical spurs; the antennae inserted in the central part of the head; the general

shape of the body (especially the shape of the pronotum); the shape of the aedeagus, flat in lateral view, with the apex curved towards the ventral side, and that in dorsal view also correspond to the same model (Figs 114.12, 114.13); the apex of the parameres, with two apical and one preapical insertion setae (Figs 115.6, 115.7); the shape of the spiculum of the 8th female urosternite, long and thin (Figs 116.14, 116.15); the microsculpture of the pronotum; the absence of the external protibial row of spines present in other Leptodirina (*sensu* Perreau 2000); the metendosternite in «V». Thus, it is confirmed that *Nonveilleriella* and *Rozajella* share numerous characters, some exclusive to these two taxa, unlike those presented by the remaining Leptodirina (*sensu* Perreau 2000).

Nonveilleriella and *Rozajella* can be distinguished from each other by the following characters (Perreau & Pavićević 2008a): the pronotal punctation, more spaced in *Nonveilleriella* than in *Rozajella*; the setae of the pronotum, with more spaced insertion and longer setae in *Nonveilleriella*, with denser insertion and shorter setae in *Rozajella*; the proportions of the pronotum, with a length/width ratio greater than 1.5 for *Nonveilleriella* (longer and narrower) and less than 1.4 for *Rozajella* (shorter and wider); by the length of the antennae, much longer in *Nonveilleriella* (Fig. 111.1) than in *Rozajella* (Fig. 111.2).

A pronotum with exactly the same shape (Figs 111.1, 111.2) and different proportions, different punctation and distribution of its setae, and different length of the antennae do not seem to be consistent nor sufficient elements to differentiate two genera: these are the minimum characters expected to distinguish two species belonging to the same genus. Moreover, *Nonveilleriella ognjenovici* is found in the distribution range of *Rozajella*, they share the same territory, a small area at the eastern end of Montenegro (Njunjić *et al*. 2017: Fig. 39). Therefore, the synonymy *Nonveilleriella* Perreau & Pavićević, 2008 syn. nov. = *Rozajella* S. Ćurčić, Brajković & B. Ćurčić, 2007 in S. Ćurčić *et al.* 2007 is established.

Distribution. Species of this genus are known only from south-east Montenegro where they colonise the Dinaric Mountains: two species in nearby karst areas near Berane; a third further afield, near Rožaje; and *Rozajella ognjenovici* comb. nov. found in the pit jama kod Stovarišta near Šoljani on Mount Žljeb, Prokletije Mts., south-east Montenegro (Perreau & Pavićević 2008a).

Species

Rozajella deelemani Perreau & Pavićević, 2008
Rozajella deelemani Perreau & Pavićević, 2008a: 206.

Rozajella jovanvladimiri S. Ćurčić, Brajković & B. Ćurčić, 2007
Rozajella jovanvladimiri S. Ćurčić, Brajković & B. Ćurčić, 2007 *in* S. Ćurčić, Brajković, B. Ćurčić & Waitzbauer, 2007: 148.

Rozajella madzgalji Njunjić, Schilthuizen, Pavićević & Perreau, 2017
Rozajella madzgalji Njunjić, Schilthuizen, Pavićević & Perreau, 2017: 155.

Rozajella ognjenovici **(**Perreau & Pavićević, 2008) comb. nov.
Nonveilleriella ognjenovici Perreau & Pavićević, 2008a: 200.

Genus ***Serbiana*** nov.
https://zoobank.org/NomenclaturalActs/ca68e631-23b9-47be-a9e1-3b09be332eff

Type species. *Serbiana latitarsis* sp. nov. by present designation (habitus in Fig. 111.3).

Description. Small size, between 1.5–1.8 mm. Bathyscioid facies; body short, convex, oval and tapering regularly towards the apical area (Fig. 111.3). Tegument shiny brownish, with fairly long, recumbent. Punctation fine and spaced, finer and more superficial on the pronotum than on the elytra.

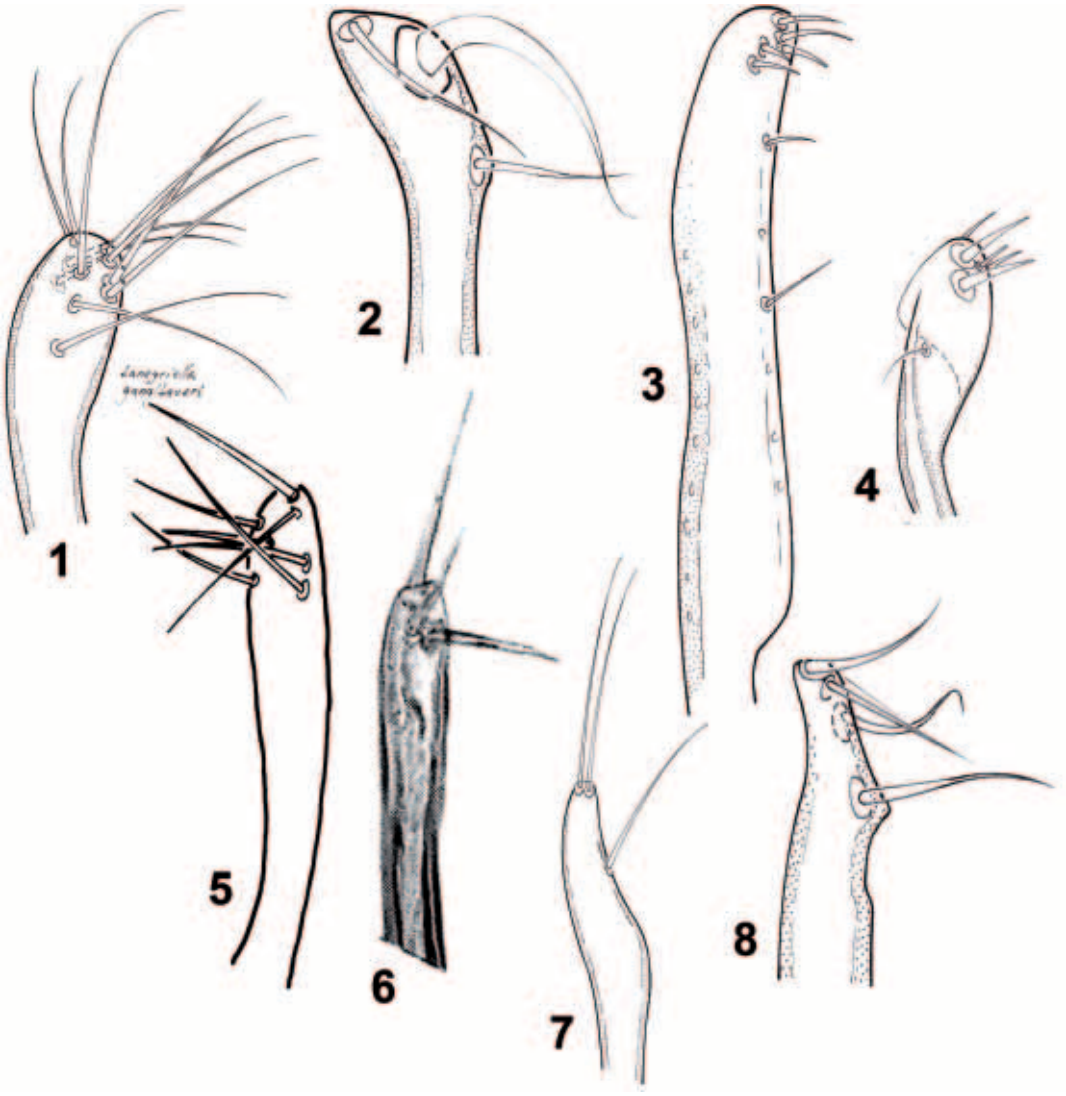
Head: Sub-square, occipital carina blurred, eyes prominent and very small.

Antennae: Short, reaching the base of the pronotum; first antennomere shorter than the second; club differentiated with the 8th, 9th and 10th antennomeres transverse.

Pronotum: Transverse, as wide as the maximum width of the elytra; the posterior vertices acute and prolonged on the elytra.

Elytra: Elongated and oval with the maximum width very close to the base; apical part rounded; transverse striae poorly defined, reduced to a few striae between the base and the median area of the elytra; punctation formed by small dots; without parasutural stria.

Legs: Short and fairly robust; protibiae with comb, with well-developed inner spur, without outer spurs; male protarsi pentamerous and enlarged with first tar-



FIGURES 115.1–114.8: *Anthroherpon* series, *Pholeuonella* group. Apex of the paramere of: (**1**) *Laneyriella ganglbaueri*, (**2**) *Perreauia dalmatica* **gen. nov. sp. nov**., (**3**) *Pholeuonella erberii erberii* (in lateral view), (**4**) *Pholeuonella erberii erberii* (apex in dorsal view), (**5**) *Riberius stillicidii* (modified from Giachino & Casale 2022), (**6**) *Rozajella ognjenovici* **comb. nov.** (modified from Perreau & Pavićević 2008), (**7**) *R. jovanvladimiri*, (**8**) *Serbiana latitarsis* **gen. nov. sp. nov**.

somere clearly wider than apical area of protibia; metatibiae slender, slight arched; meso- and metatibiae without apical basket of spines.

Mesoventral keel (Fig. 112.7): High, with convex anterior and posterior margins, the latter smooth and with a few setae; vertex rounded and very finely serrate and angle very obtuse; posterior process extending over middle of metaventrite.

Suture of metaventrite (Fig. 112.7): It extends a short distance from the edge of the mesocoxal cavity and delimits a small arcuate area in the upper half.

Metatergal apparatus and m*etendosternite*: Unknown.

Median lobe of aedeagus: Moderately long. In lateral view (Fig. 114.6), regularly arcuate, the dorsal margin with a marked depression towards the apical fifth, the apex very sharp and curved towards the ventral side. In dorsal view (Fig. 114.14), sides sub-recti-

linear, gradually widening to the apical fifth, then narrowing to form acute apex. Basal blade well-developed with an arched apical margin. The median lobe of the holotype has the apex broken off; the two pieces were reassembled in the microscopic preparation in their natural position.

Endophallus (Fig. 114.14): It is completely evaginated so that we do not know exactly what parts it has and how they are arranged. It is observed that it has no «Y»-piece and that in the medial and apical regions, there are teeth whose arrangement is undetermined.

Parameres (Fig. 115.8): As long as the median lobe; very thick to the tapering apical region and with four setae. The ventral blade of the tegmen is wider than the basal blade. One of the two parameres is separated from the median lobe.

Female. *Spermathecal complex* (Fig. 116.8): Spermatheca small, arcuate, crook- or hook-shaped, with the basal lobe well sclerotized; basal lobe much longer and wider than apical lobe with posterior area very slightly ringed; apical lobe with parallel sides, slightly arched, with the apical area rounded and somewhat dilated; short and hyaline joint duct, as wide as the posterior area of the apical lobe.

Female uroventrite VIII (Fig. 116.16): Apical margin in wide arc; spiculum long, narrow, with rounded apex.

Etymology. The name refers to Serbia, which hosts the only known species of the new genus. Feminine name.

Discussion. This genus has the first antennomere shorter than the second, the elytra without parasutural striation and with inconspicuous transverse striolation, the protibiae with a comb, a well-developed internal spur and without an external spur, a high and short keel, a uniformly arched median lobe with a dorsal depression, the endophallus without «Y»-piece and with teeth in the median and apical areas and thick parameres with four apical setae. These characteristics are largely shared with *Pholeuonella* and *Perreauia* gen. nov. However, the spermatheca is similar to the genera of the *Pholeuonopsis* group: *Pholeuonopsis*, *Proleonhardella*, *Speonesiotes* or *Tartariella*.

Serbiana gen. nov. is more closely related, albeit with marked differences, to the thin, elongated aedeagus without extensions at both ends found in the *Pholeuonella* group, and as this genus has a sinuous apical end or a depression in the preapical area. The peculiarities of its highly derived aedeagus make it difficult to assign a precise position within the *Anthroherpon* clade, in the *Pholeuonella* or *Pholeuonopsis* groups, until molecular data become available. *Serbiana* **gen. nov**. has been provisionally included in the *Pholeuonella* group.

Distribution. Serbia, Tutin, cave near Godovo.

Species

Serbiana latitarsis sp. nov. (See Appendix New Species)

3.2.5.2 ***Anthroherpon*** group

Diagnosis. Leptodiroid body shape.

Antennae: Inserted in the posterior quarter of the head, with scape longer than pedicel.

Pronotum: Slightly to strongly elongate with or without constriction in posterior third.

Elytra: Elliptically variable.

Mesoventral process: Mesoventrite in the middle posterior area short to strongly elongated, pointed or rounded.

Legs: Protarsi with five tarsomeres in the male, claws well developed.

Aedeagus: Relatively small.

Endophallus: with or without sclerotized structures.

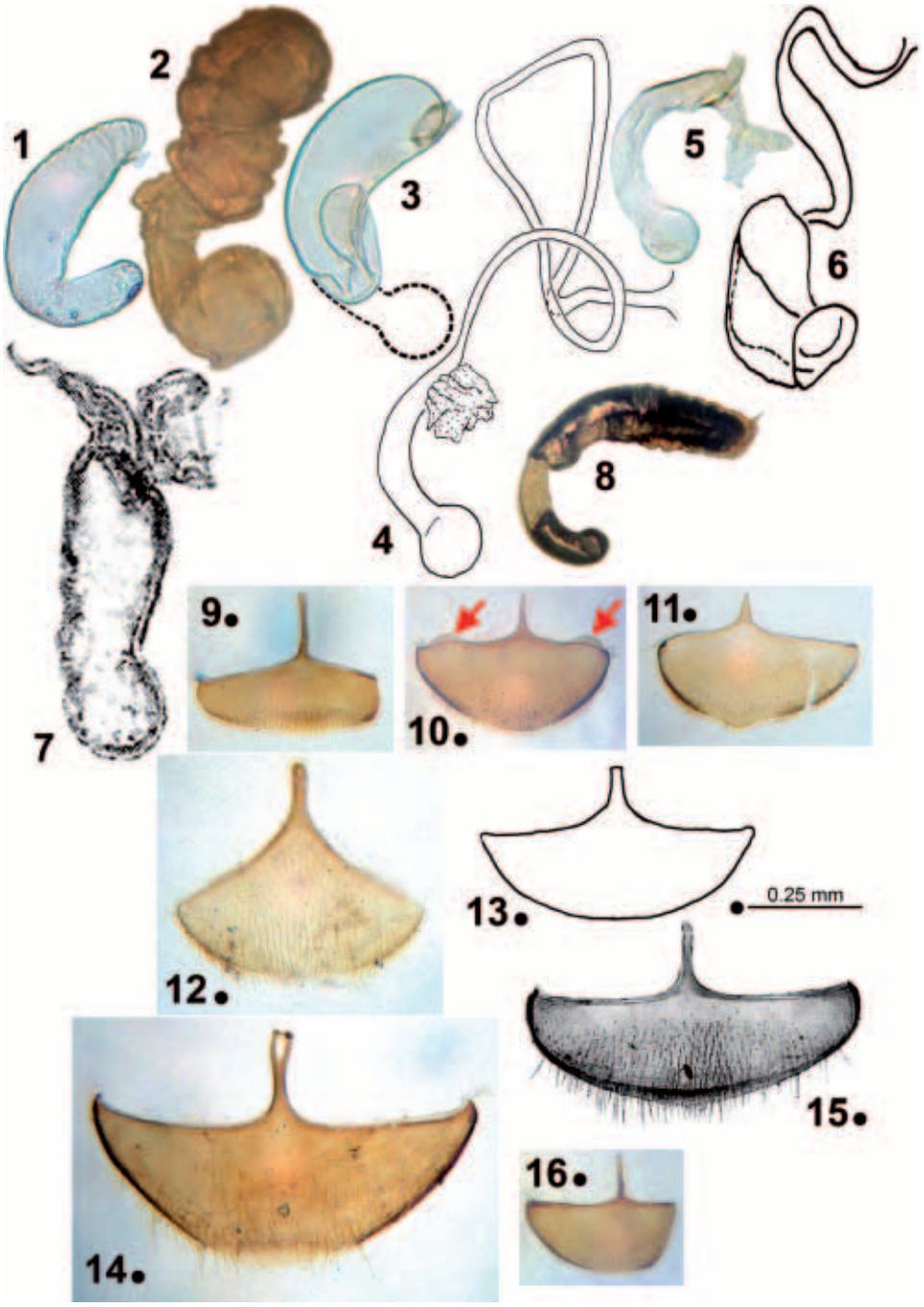
Female uroventrite VIII: Spiculum with or without anterior expansion.

Discussion. In the phylogenetic tree (Fig. 1H) the group shows a very high consistency, with a support of 100/100.

Key to subgroups

1. Mesothorax with peduncle (Figs 117.1, 117.2, 118.2); mouth parts not modified for filtration ....*Anthroherpon* subgroup
- Mesothorax without peduncle (Figs 117.3, 118.1, 118.3) and mouthparts heavily modified to filter organic matter from the water …….. 2

2. Median lobe of aedeagus tubuliform basally, in lateral view with a regular curve and the apex with hook-shaped swayback (Figs 120.2, 120.5) ....*Hadesia* subgroup
- Median lobe of aedeagus not tubuliform at the base, only moderately curved in lateral view and the apex only slightly bent dorsally, lacking the hook-shaped apical notch (Fig. 120.3) .....*Kircheria* subgroup



FIGURES 116.1–116.15: *Anthroherpon* series, *Pholeuonella* group. Spermathecal complex of: (**1**) *Laneyriella ganglbaueri,* (**2**) *Perreauia dalmatica* **gen. nov. sp. nov**., (**3**) *Pholeuonella erberii erberii*, (**4**) *Remyella scaphoides droveniki* (modified from Giachino & Etonti 1995), (**5**) *Remyella propiformis borensis*, (**6**) *Riberius stillicidii* (modified from Giachino & Casale 2022), (**7**) *Rozajella jovanvladimiri* (modified from Perreau & Pavićević 2008), (**8**) *Serbiana latitarsis* **gen. nov. sp. nov**. Female uroventrite VIII of: (**9**) *L. ganglbaueri,* (**10**) *P. dalmatica* **gen. nov. sp. nov**., (**11**) *P. e. erberii*, (**12**) *Remyella p. borensis*, (**13**) *R. stillicidii* (modified from Giachino & Casale 2022), (**14**) *Rozajella ognjenovici*, (**15**) *R. jovanvladimiri* (modified from Perreau & Pavićević 2008), (**16**) *S. latitarsis* **gen. nov. sp. nov**. Red arrow pointing to the laminar lobes on each side of the spiculum.

Kircheria subgroup

As the only genus in the subgroup, its defining characteristics correspond to those of the genus.

Discussion.,The position of *Kircheria* at the base of the complete clade *Anthroherpon* group is adopted from Delić *et al*. (2023). In this paper *Kircheria beroni* is sister to the *Hadesia* + *Nauticiella* + *Anthroherpon* + *Leptomeson* + *Graciliella* clade with support >0.99 (Delić *et al*. 2023: Fig. 3). However, in Tree-1 *Kircheria dritae* is sister to *Leptomeson* + *Graciliella* with very low support, 1.4/56 (Fig. 1H), and in Tree-2 it is sister to the entire clade with the exception of *Hadesia* with also low support, 87.6/78 (Fig. 2), although it is closer to the topology of Delić *et al*. (2023).

Genus ***Kircheria*** Giachino & Vailati, 2006
Kircheria Giachino & Vailati, 2006: 103.

Type species. *Kircheria beroni* Giachino & Vailati, 2006 by original designation (habitus in Fig. 118.1).

Diagnosis. Large size, 8.8–9.3 mm, with head bent in natural position. Body «hadesian» shaped, elongated, very ogival, acute apically, remarkably convex (Fig. 118.1), uniformly covered with a short, very thick and hydrophobous pubescence. Anophthalmous. Colour normally completely brown ferrugineous (yellow-orange in the immature specimens). Some specimens show pronotum, head, femora, tibiae, mandibles and antennomeres 1st-7th darker and elytra, tarsi and antennomeres 8th–11th paler, orange.

Head: Non-retractile. Very elongated, enlarged anteriorly with concave genae, labrum big and robust, mandibles arcuate, decidedly flattened in the basal region, and thickened dorsally in the apical part, with a bidentate apex. Maxillary palpi long, last palpomere, basally stumpy, shorter than the penultimate one. Labium, glossae, paraglossae, labrum, and lateral part of stipes bears long setae with an obvious filtering function.

Antennae: Inserted on the basal fourth of the head. Second antennomere shorter than the first one; third antennomere longest of all; eighth longer than the three subsequent ones, and eleventh shortest of all, except for the second one.

Pronotum: Elongated, cordate, uniformly convex, with sides regularly rounded anteriorly; remarkably sinuate posteriorly starting from the basal third. Basal angles broadly obtuse yet sharp; base remarkably arcuate and projecting posteriorly, wider than the anterior margin. Sides of pronotum finely edged along their entire length (although this edging is not evident in the anterior part when viewed dorsally).

Mesonotum: Mesothoracic peduncle lacking; scutellum big and transverse.

Mesoventrite: Flat.

Elytra: Very elongated, oval, narrow with maximum width at the middle, apex altogether acute, but separately subrounded, more rounded in male and slightly more acute in female, finely keeled laterally. Elytral disc convex, not depressed or flattened along the elytral suture, without transversal striation and without parasutural stria.

Legs: Slender and very elongated. Femora typically enlarged at the base and narrowed towards the apex, flattened, and entirely covered on both sides with a very short and thick hydrophobic pubescence. Tibiae lacking apical spurs; protibiae slightly curved outwards; mesotibiae slightly curved inwards and metatibiae straight. Pro- and mesotibiae strongly enlarged at the distal end; all tibiae covered with a very short and thick hydrophobic pubescence, but all showing a glabrous stripe on the external side. Protarsi pentamerous and not dilated in male; first meso- and metatarsomere very elongated, markedly longer than the fifth. Tarsal claws big, specialized, wide and strongly hollowed spoon-shaped.

Mesoventral keel: Without keel; mesocoxal cavities confluent.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 119.3): Very reduced, with a very short apophysis of the alacrista.

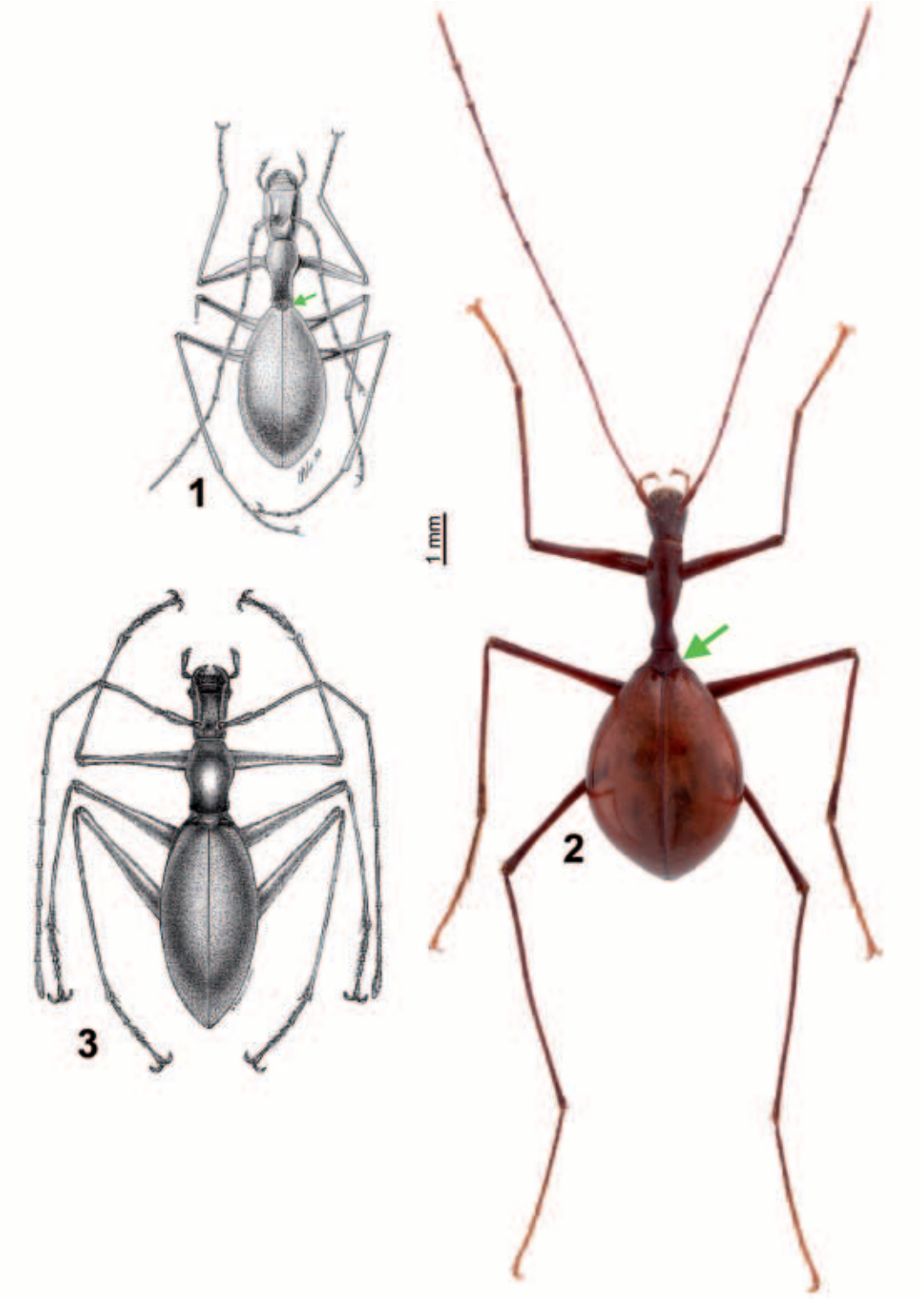
Metendosternite (Fig. 119.7): Not «V»-shaped. Furcal arms slightly longer than the trunk and without a distinct apical apophysis; with a robust furcal trunk and a little more than twice as long as it is wide, relatively narrow and moderately divergent furcal arms.

Male genital segment (Giachino & Vailati 2006): Reduced, wide and oval, without a pronounced ventral apophysis.

Median lobe of aedeagus: In lateral view (Fig. 120.3), slightly and regularly curved from base to apex. Apex slightly upwards and not sharp. In dorsal view (Fig. 120.9), robust and elongated, subparallel sides from the base to pre-apical area; apex more or less truncated or trapezoidal, with right or concave anterior margin. Basal blade short and stumpy.

Endophallus (Fig. 120.9): With a characteristic basal, long phanera, enlarged at base and bifid or not at apex; two, spinuliform bundles are also present in the median-apical area.

Parameres (Fig. 120.15): Parameres short and relatively strong, neatly shorter than median lobe. Apex



FIGURES 117.1–117.3: *Anthroherpon* series, *Anthroherpon* group. Habitus of: (**1**) *Anthroherpon brckoensis* (modified from Giachino & V.B. Guéorguiev 1993), (**2**) *Graciliella apfelbecki apfelbecki* (modified from Njunjić *et al.* 2016), (**3**) *Hadesia vasiceki* (modified from Perreau & Pavićević 2008). Green arrow pointing to the mesothoracic peduncle.

of parameres bearing, on the inner side, three or four apical short, subequal, setae. Tegmen complete, wide and well visible dorsally, ventral blade of the tegmen narrow.

Spermathecal complex (Fig. 121.4): Spermatheca sacciform, shaped like a curved cucumber, uniformly and very poorly sclerotized, with a striated surface, without parts differing one from the other, but only with the distal part slightly dilated; Adnexal gland small and confluent with the insertion of the duct, i.e. proximal. Spermiduct is thin with no dilated areas.

Stylomeres: Lacking.

Female uroventrite VIII (Fig. 121.8): No spiculum.

Discussion. Giachino & Vailati (2006) pointed out that *Kircheria* is well distinct from *Hadesia*: it features a different, lower degree of specialization of the whole body and of the filtering mouthparts; mandibles are apically not polidentated; antennae are proportionally much shorter due to a shorter last antennomere with respect to the penultimate one; a pubescent pronotum with a rebordered lateral margin. Male genitalia of *Kircheria* are different from those of *Hadesia*: the median lobe of aedeagus is not tubuliform at base; the lateral view shows only a moderate curve and the apex is only slightly bent dorsally and lacks the typical, apical hook-shaped notch visible in *Hadesia*; the lateral part does not have preapical swellings like those present in the aedeagus of *Hadesia*. A remarkable morphological difference can also be seen in the smaller male genital segment, which is markedly narrower an more elongate in *Hadesia.*

Our molecular phylogenetic trees (Fig. 2: Tree-1 and Tree-2) and the one proposed by Delić *et al*. (2023) in relation to the position of *Kircheria*, are noted in the discussion section of this group.

Distribution. Known from two caves in the Albanian Alps, in northern Albania.

Species

Kircheria beroni Giachino & Vailati, 2006
Kircheria beroni Giachino & Vailati, 2006: 104.

Kircheria dritae Giachino & Casale, 2022
Kircheria dritae Giachino & Casale, 2022: 36.

Anthroherpon subgroup

See *Anthroherpon* group diagnosis.

Discussion. The *Anthroherpon* clade is sister to the *Hadesia* clade with very high support (100/100) (Fig. 1H). These two clades form the *Anthroherpon* group with six genera – including *Nauticiella* (Delić *et al*. 2023) – and the nodes are well supported with the exception of the one shared by *Kircheria* and *Graciliella* + *Leptomeson* the two sister genera; the position of *Kircheria* at the base of the complete clade is adopted from Delić *et al*. (2023).

Key to genera

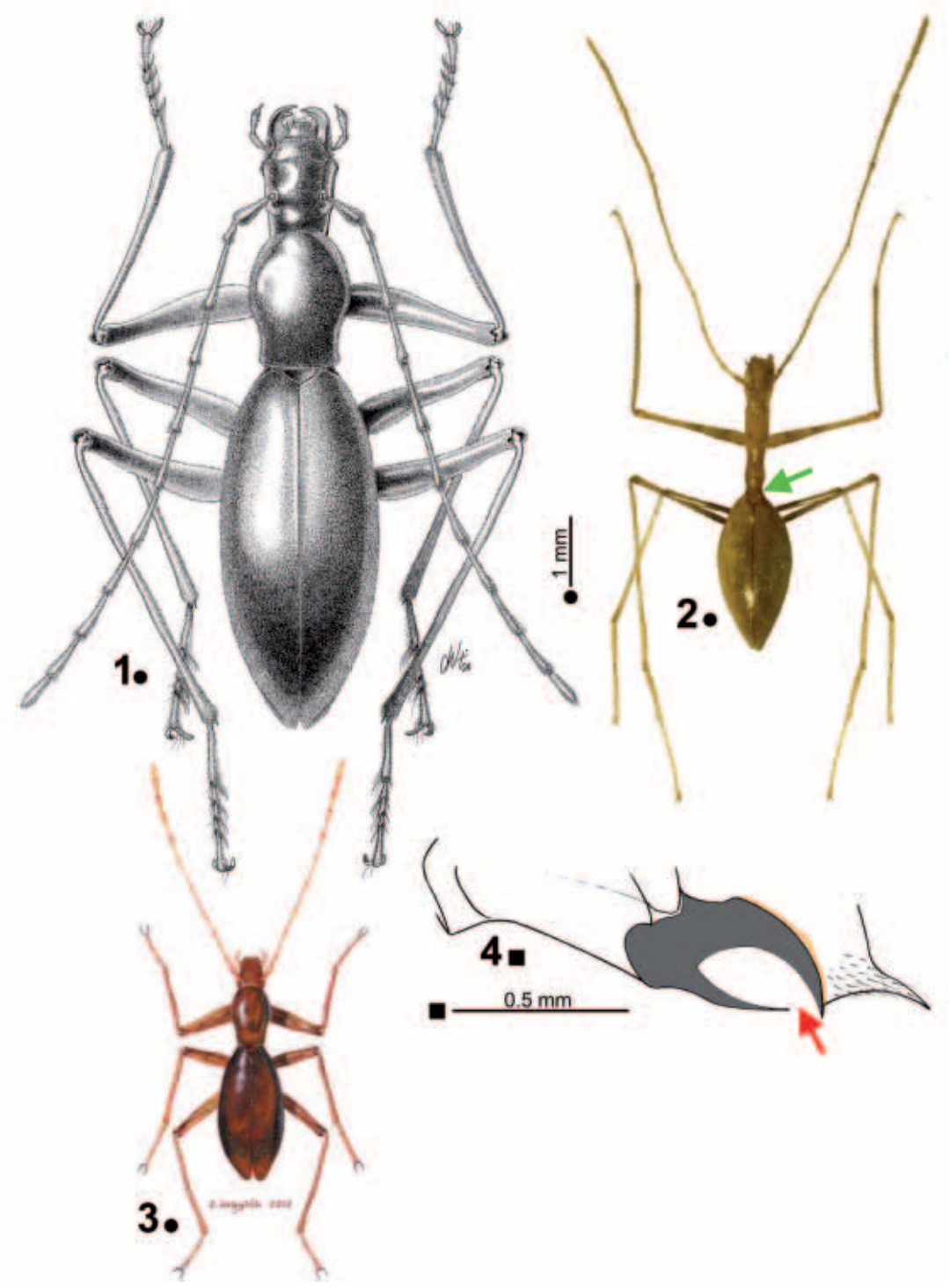
1. Mesothoracic peduncle, in general with a constriction in the middle (Fig. 118.2). Endophallus with basal armature (Fig. 120.10).....*Leptomeson*
- Mesothoracic peduncle without constriction (Figs 117.1, 117.2). Endophallus without basal armature (Figs 120.6, 120.7).....2

2. Mesothoracic peduncle in general poorly developed, wider behind than in front (Fig. 117.1). Antennae in general, with the 11th antennomere much longer than the 10th, and the 5th not the longest.....
.....*Anthroherpon*
- Mesothoracic peduncle very elongated, wider in front (Fig. 117.2). Antennae with the 11th antennomere almost as long as the 10th, and the 5th the longest of all ..... *Graciliella*

Genus ***Anthroherpon*** Reitter, 1889
Anthroherpon Reitter, 1889a: 294.
Anthroherpon (*Eumecosoma*) G. Müller, 1901: 29 (Type species. *Antroherpon stenocephalum* Apfelbeck, 1901).
Euantroherpon Absolon, 1913b: 108 (Type species. *Leptoderus Hoermanni* Apfelbeck, 1889).
Protantroherpon Absolon, 1913b: 108 (Type species. *Leptoderus cylindricollis* Apfelbeck, 1889).
Antrophilon Absolon, 1913b: 100 (Type species: *Antrophilon primitivum* Absolon, 1913).
Parantrophilon Noesske, 1914: 17 (Type species: *Parantrophilon spelaebatoides* Noesske, 1914).

Type species. *Leptoderus cylindricollis* Apfelbeck, 1889 by subsequent designation (for the habitus see that of the similar species *Anthroherpon brckoensis* in Fig. 117.1).

Diagnosis. Size ranging from 4.0–9.0 mm. Body shape leptodiroid, thinner to more robust, very convex and narrowed anteriorly, which gives a pedunculated appearance (Fig. 117.1). Colouration orange to bright



FIGURES 118.1–118.4: *Anthroherpon* series, *Anthroherpon* group. Habitus of: (**1**) *Kircheria beroni* (modified from Giachino & Vailati 2006), (**2**) *Leptomeson soltensis* (modified from Ćurčić *et al.* 2019), (**3**) *Nauticiella stygivaga* (modified from Moravec & Mlejnek 2002). Pterothorax in lateral view of (**4**) *Anthroherpon ganglbaueri ganglbaueri*. Green arrow pointing to the mesothoracic peduncle. Red arrow pointing to the confluent mesocoxal cavities.

reddish, normally head and pronotum being somewhat darker. Pubescence very variable, the pronotum of some specimens may have developed setae in the medio-posterior area and in others the setae are very short and scattered or glabrous, the setae always being erect. In the elytra, the pubescence is between very long and short, generally bristly and dense, although there are a few representatives that are glabrous and shiny. The microsculpure and punctation of integument are also variable.

Head: Sub-cylindrical or quadrangular, as wide as long or a little longer than wide, cheeks not or slightly convex; shorter than the pronotum and between the same width and a little wider than it. Anophthalmous.

Antennae: Very long and slender, the first antennomere being longer and thicker than the 2nd, and the latter three to four times shorter than the 3th. The 8th, although very long, is a little shorter than the 7th; the 9th to 11th articles are of similar length, although the 11th is often longer than the 10th; no differentiated club.

Pronotum: Variable in length and shape, between 2.5 and 4 times longer than wide. Dorsal surface convex and, often, with two impressions towards the anterior half; sides without marginal rim, in some cases a fine rim at base. Two areas clearly differentiated; the anterior one-half has regularly arched sides and is longer and wider than the posterior half. Depending on the group of species, the sides of the posterior half are more or less strongly compressed and either straight, arched or sinuous. Microreticulation more or less marked or smooth with the punctation from fine and superficial to strong and deep, with nearby or scattered points.

Mesonotum: Anterior part, depending on the species of some groups, more or less narrowed, with or without a short mesothoracic peduncle (Fig. 119.1). Movements in the sagittal plane occur between these two regions of the thorax – pronotum and mesonotum –.

Elytra: Very convex, overall longer than wide, of variable shape, generally pyriform, but sometimes elliptical or even subspherical; the basal area between convex, and more or less flattened, and marginal rim barely visible from above and apical part more or less narrowed. Without parasutural stria. Females tend to have more dilated elytra. On elytra, points are fine or strong and more widely spaced, and microreticulation, when present, more or less marked.

Legs: Very long; the protibiae normally somewhat thicker and arched inwards, protarsi pentamerous in male, normally without dilatation. Femora more or less dilated along the basal area depending on the group of species, and gradually taper to the top.

Mesoventral keel (Fig. 118.4): Missing; mesocoxal cavity open.

Suture of the metaventrite (Fig. 118.4): Very small area between the cavity and the suture, as the suture is very close to the mesocoxal cavity throughout its length.

Metatergal apparatus (Figs 119.1, 119.2): Strongly modified, it seems to be the only Leptodirini without alacrista apophysis; the wings of the metascutum are joined together without any intermediate structure.

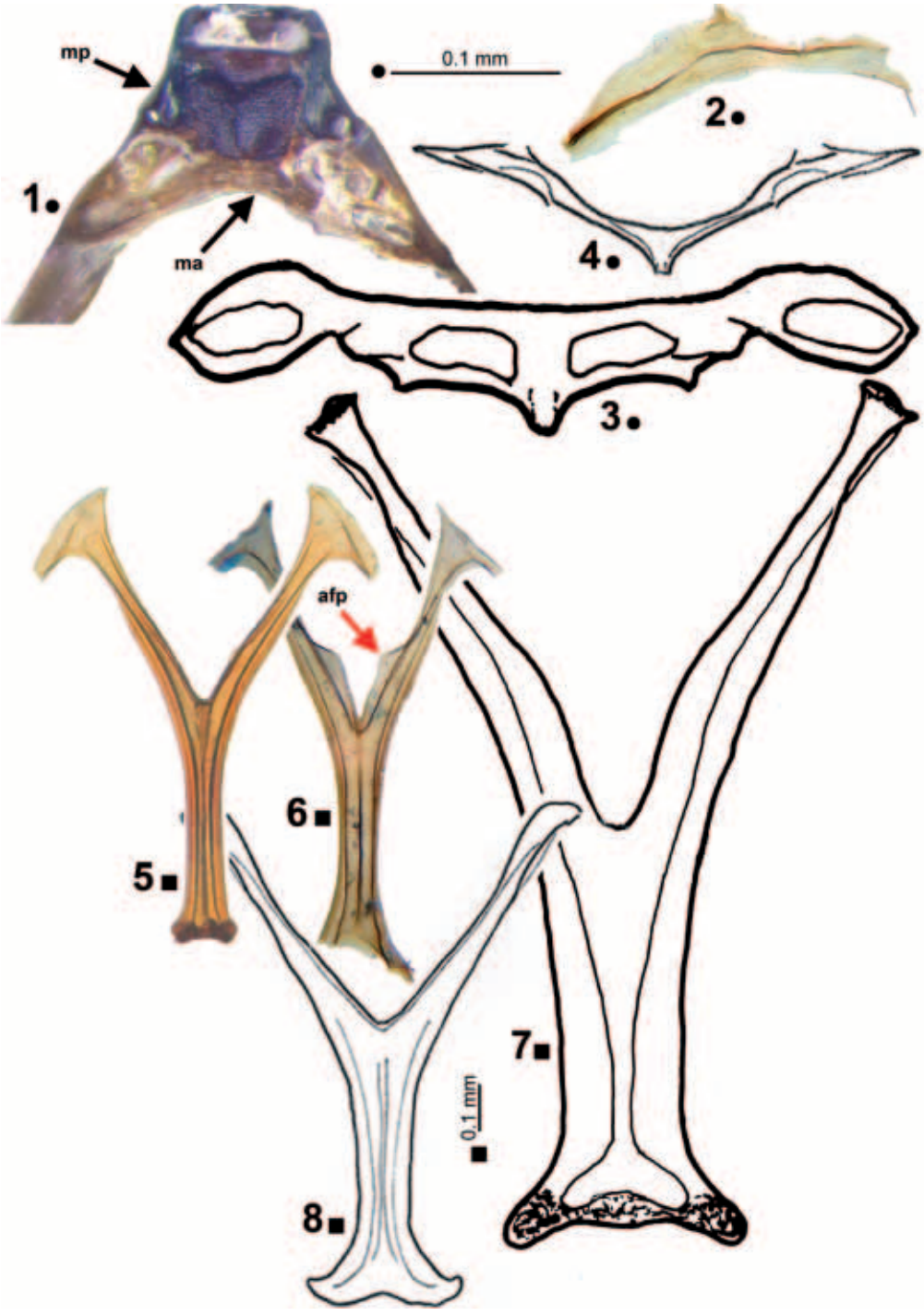
Metendosternite (Figs 119.5, 119.6): In shape of a «Y». Furcal arms as long as the trunk, with the terminal process very dilated. Posterior lamina of the furca with convave edge; narrow in arms and trunk, in both it retains the same width but does not reach the apical area of the arms. Very long trunk, 3.4 times longer than wide at the base, the median keel with a posterior divergence. The photo of the metendosternite of a specimen of *Anthroherpon hoermanni* ssp. (Fig. 119.6) shows the same structure as the one examined by Njunjić *et al*. (2017) (Fig. 119.5), but with a singular difference: the existence of an anterior furcal plate on the lower inner half of the arms.

Median lobe of aedeagus: Rather short, poorly sclerotized and highly variable in shape. In lateral view (Fig. 120.1), more or less arched in the basal region, then more or less straight or flattened, and in some with a more or less marked dorsal depression between the middle and the basal third. In dorsal view (Fig. 120.6), sides are in regular arc, straight, sub-rectilinear or sinuous, and convergent to form an apical part that can be triangular, more or less narrowed, with the apex little to very sharp, or arched. Basal lamina long and more or less oval.

Endophallus (Fig. 120.6): Basal armature lacking.

Parameres (Fig. 120.12): Very variable, between longer and shorter than the middle lobe, straight, sinuous and more or less arched. With uniform thickness although the basal area is generally somewhat broader, without differentiated club and, in some species, with a preapical constriction. Apex sharp to rounded, with two-three setae normally of similar length and well-differentiated insertion pores: one or two apical and one preapical whose insertion varies between the dorsal face and the inner edge; in a few cases the insertion of pores of the three setae are very close, or with an apical long and two shorter setae. Ventral lamina of the tegmen short and usually somewhat wider than the basal lamina of median lobe.

Spermathecal complex (Fig. 121.1): Spermatheca short, weakly sclerotized and without distinct regions,



FIGURES 119.1–119.8: *Anthroherpon* series, *Anthroherpon* group. Metatergal apparatus of: (**1**) *Anthroherpon ganglbaueri ganglbaueri*, (**2**) *A. hoermanni* ssp., (**3**) *Kircheria dritae*, (**4**) *Leptomeson vuicae*. Metendosternite of: (**5**) *A. primitivum* (modified from Njunjić *et al.* 2017), (**6**) *A. hoermanni* ssp., (**7**) *K. dritae*, (**8**) *L. vuicae*. Figs **3**, **7** modified from Giachino & Casale 2022; Figs **4**, **8** from Giachino *et al*. 2021. Abbreviations: **afp**, anterior furcal plate; **ma**, metatergal apparatus; **mp**, mesothoracic peduncle.

although the region corresponding to the proximal lobe is somewhat more sclerotized than that corresponding to the union duct and apical lobe. Spermatic duct without nodule or other dilated area, directly attached to the proximal lobe.

Female uroventrite VIII (Fig. 121.7): Posterior margin with the median area somewhat less sclerotized than the lateral edges, and a short, wide and not sharp spiculum.

Discussion. The phylogenetic tree (Fig. 1H) clearly identifies a strongly supported global relationship between the analysed species of *Anthroherpon* (99.8/100), this *Anthroherpon* clade has as the sister group the complex of the phyletic lineages of *Leptomeson* + *Graciliella,* all of them forming a clade together with the *Hadesia* clade (100/100). Some taxonomic and systematic considerations are necessary for *Anthroherpon* phyletic line. Beyond the appropriate identification and separation of *Graciliella* from *Anthroherpon* by Njunjić *et al*. (2016) and the proposed synonymy of *Parantrophilon* with *Anthroherpon* (Čeplik & Hlavâč 2022) a revision of the genus is necessary. Based on a modern approach, both classical morphological and molecular, a revision is necessary to better define a series of taxa so far considered, or described, as subspecies on the basis of a «systematic attitude» largely inherited by the great past specialists (Absolon, Jeannel, G. Müller or Winkler). In fact, it is well known that external morphology, in this genus, seems to be more determining than the morphology of the genitalia, which vary in the same species from cave to cave.The taxonomic weight to be attributed to one or other of these character sets is often the subject of doubt on the part of the specialist, who has often based his decision solely on his own perception and sensitivity.

Distribution. A genus with a wide distribution in the subterranean environment and described from numerous cavities located along the southern chain of the Dinaric Alps in the western part of the Balkan Peninsula: southern Croatia, Bosnia-Herzegovina, Montenegro, and northern Albania.

Species

Anthroherpon cylindricollis (Apfelbeck, 1889)
Anthroherpon cylindricollis cylindricollis (Apfelbeck, 1889)
Leptoderus cylindricollis Apfelbeck, 1889: 61.
Anthroherpon cylindricolle Apfelbeck: Apfelbeck, 1894: 511.
Anthroherpon (s. str.) *cylindricolle* Subsp. *cylindricolle* Apfelbeck: Jeannel, 1924a: 414.
Anthroherpon cylindricolle cylindricolle (Apfelbeck): Giachino & Guéorguiev, 1993 [1992]: 288.

Anthroherpon cylindricollis scaphium Reitter, 1908
Anthroherpon cylindricolle scaphium Reitter, 1908b: 20.
Anthroherpon (s. str.) *cylindricolle* Subsp. *scaphium* Reitter: Jeannel, 1914b: 54.

Anthroherpon cylindricollis thoracicum Apfelbeck, 1907
Antroherpon cylindricolle thoracicum Apfelbeck, 1907b: 402.
Anthroherpon (s. str.) *cylindricolle* subsp. *thoracicum* Apfelbeck: Jeannel, 1911a: 550.

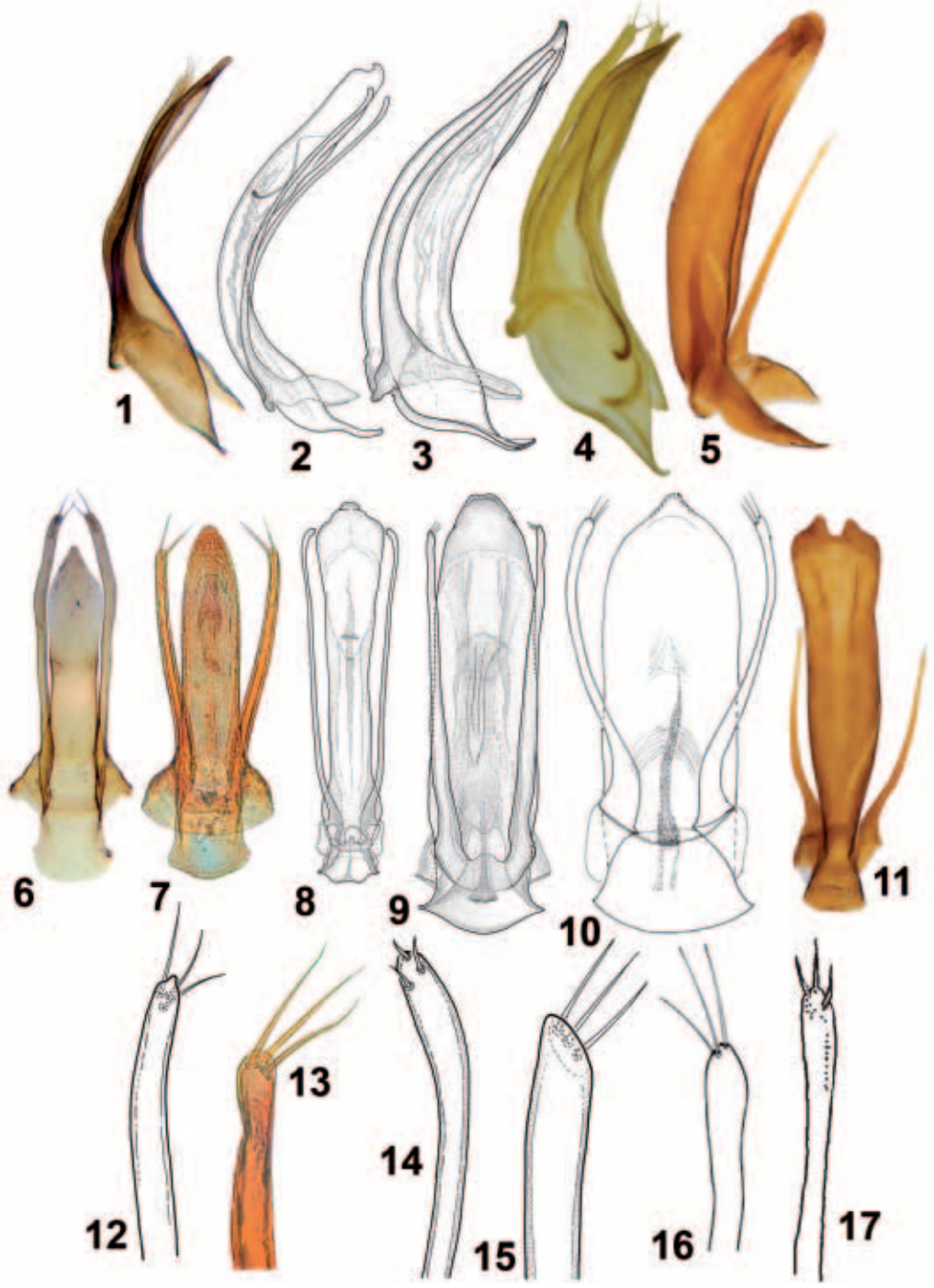
Anthroherpon brckoensis Giachino & V.B. Guéorguiev, 1993
Antroherpon brckoensis Giachino & V.B. Guéorguiev, 1993 [1992]: 293.

Anthroherpon cecai Njunjić, Perreau & Pavićević, 2015
Anthroherpon cecai Njunjić, Perreau & Pavićević, 2015: 408.

Anthroherpon charon Reitter, 1911
Antroherpon Charon Reitter, 1911a: 173.
Antroherpon (s. str.) *Charon* Reitt.: Jeannel, 1914b: 54.
Antroherpon charon Reitter: Pretner, 1974: 11.

Anthroherpon elongatum Giachino & V.B. Guéorguiev, 1993
Antroherpon elongatum Giachino & V.B. Guéorguiev, 1993 [1992]: 298.

Anthroherpon erebus Breit, 1913
Anthroherpon erebus erebus Breit, 1913
Antroherpon Erebus Breit, 1913c 237.
Antroherpon affinis Breit, 1913b 357.
Antroherpon (s. str.) *Erebus* Breit: Jeannel, 1914b: 54.
Antroherpon (s. str.) *affnis* Breit: Jeannel, 1914b: 54.
Antroherpon (s. str.) *Erebus* Subsp. *Erebus* Breit, 1913: Jeannel, 1924.
Antroherpon erebus Breit: V.B. Guéorguiev, 1990: 260.
Anthroherpon erebus scheibeli Jeannel, 1924
Antroherpon (s. str.) *erebus* Subsp. *scheibeli* Jeannel, 1924a: 418.
Anthroherpon erebus scheibeli Jeannel: Perreau, 2000: 163.



FIGURES 120.1–120.17: *Anthroherpon* series, *Anthroherpon* group. Aedeagus in lateral view of: (**1**) *Anthroherpon ganglbaueri ganglbaueri,* (**2**) *Hadesia vasiceki,* (**3**) *Kircheria beroni,* (**4**) *Leptomeson soltensis* (modified from Ćurčić *et al.*, 2019), (**5**) *Nauticiella numerosa*. Aedeagus in dorsal view of: (**6**) *A. hoermanni* ssp.*,* (**7**) *Graciliella apfelbecki apfelbecki*, (**8**) *H. vasiceki,* (**9**) *K. beroni*, (**10**) *L. biokovensis*, (**11**) *N. numerosa*. Apex of the paramere of: (**12**) *A. urdzali* (modified from Giachino & Vailati, 2005)*,* (**13**) *G. metohijensis*, (**14**) *H. vasiceki,* (**15**) *K. beroni*, (**16**) *L. biokovensis*, (**17**) *N. stygivaga* (modified from Moravec & Mlejnek 2002). Figs **3**, **9**, **15** modified from Giachino & Vailati 2006; Figs **5**, **11**, from Delić *et al.* 2023; Figs **7**, **13** from Njunjić *et al.* 2016; Figs **10**, **16** from Giachino *et al.* 2011.

Anthroherpon ganglbaueri Apfelbeck, 1894
Anthroherpon ganglbaueri alticola Knirsch, 1927
Antroherpon alticola Knirsch, 1927b: 45.
Antroherpon (s. str.) *Ganglbaueri* subsp. *alticola* Knirsch: Jeannel, 1930, l'Abeille, 34: 138.
Antroherpon ganglbaueri alticola Knirsch: V.B. Guéorguiev, 1990: 252.

Anthroherpon ganglbaueri distinguendum G. Müller, 1913
Antroherpon Ganglbaueri distinguendum G. Müller, 1913c: 160.
Antroherpon (s. str.) *Ganglbaueri* subsp. *distinguendum* J. Müller: Jeannel, 1914b: 54.
Antroherpon (s. str.) *distinguendum* J. Müller, 1913: Jeannel, 1924a: 415.
Antroherpon ganglbaueri distinguendum J. Müller: V.B. Guéorguiev, 1990: 251.

Anthroherpon ganglbaueri ganglbaueri Apfelbeck, 1894
Antroherpon Ganglbaueri Apfelbeck, 1894: 513.
Antroherpon (s. str) *Ganglbaueri* Apfelbeck: Jeannel, 1914b: 54.
Antroherpon (s. str.) *Ganglbaueri* subsp. *Ganglbaueri*: Jeannel, 1930e: 138.
Antroherpon ganglbaueri Apfelbeck: V.B. Guéorguiev, 1990: 251.
Antroherpon ganglbaueri ganglbaueri Apfelbeck: Giachino & V.B. Guéorguiev, 1993 [1992]: 291.

Anthroherpon ganglbaueri intermedium Winkler, 1938
Antroherpon Ganglbaueri ssp. *intermedium* Winkler, 1938: 219.
Antroherpon ganglbaueri intermedium Winkler: V.B. Guéorguiev, 1990: 252.

Anthroherpon garbellii Giachino & Vailati, 2005
Anthroherpon garbellii Giachino & Vailati, 2005b: 157.

Anthroherpon gueorguievi Giachino & Vailati, 2005
Anthroherpon gueorguievi Giachino & Vailati, 2005b: 157.

Anthroherpon harbichi Reitter, 1913
Antroherpon Harbichi Reitter, 1913a: 153.
Antroherpon (s. str.) *Harbichi* Reitt.: Jeannel, 1914b: 54.
Antroherpon harbichi Reitter: V.B. Guéorguiev, 1990: 249.

Anthroherpon hoermanni (Apfelbeck, 1889)
Anthroherpon hoermanni hoermanni (Apfelbeck, 1889)
Leptoderus Hoermanni Apfelbeck, 1889: 62.
Antroherpon Hoermanni Apfelbeck: Apfelbeck, 1894: 512.
Antroherpon Hörmanni Apfelbeck: Jeannel, 1910a: 46.
Antroherpon Bokori Csiki, 1912b: 512.
Antroherpon (s. str.) *Bokori* Csiki: Jeannel, 1914b: 54.
Antroherpon (s. str.) *Hörmanni* Apfelbeck: Jeannel, 1914b: 54.
Antroherpon (s. str.) *Hörmanni* Subsp. *Hörmanni* Apfelbeck, 1889: Jeannel, 1924a: 419.
Antroherpon hoermanni Apfelbeck: V.B. Guéorguiev, 1990: 262.
Antroherpon hoermanni hoermanni (Apfelbeck, 1889): Giachino & V.B. Guéorguiev, 1993 [1992]: 310.

Anthroherpon hoermanni hoffmanni Giachino & V.B. Guéorguiev, 1993
Antroherpon hoermanni hoffmanni Giachino & V.B. Guéorguiev, 1993 [1992]: 310.

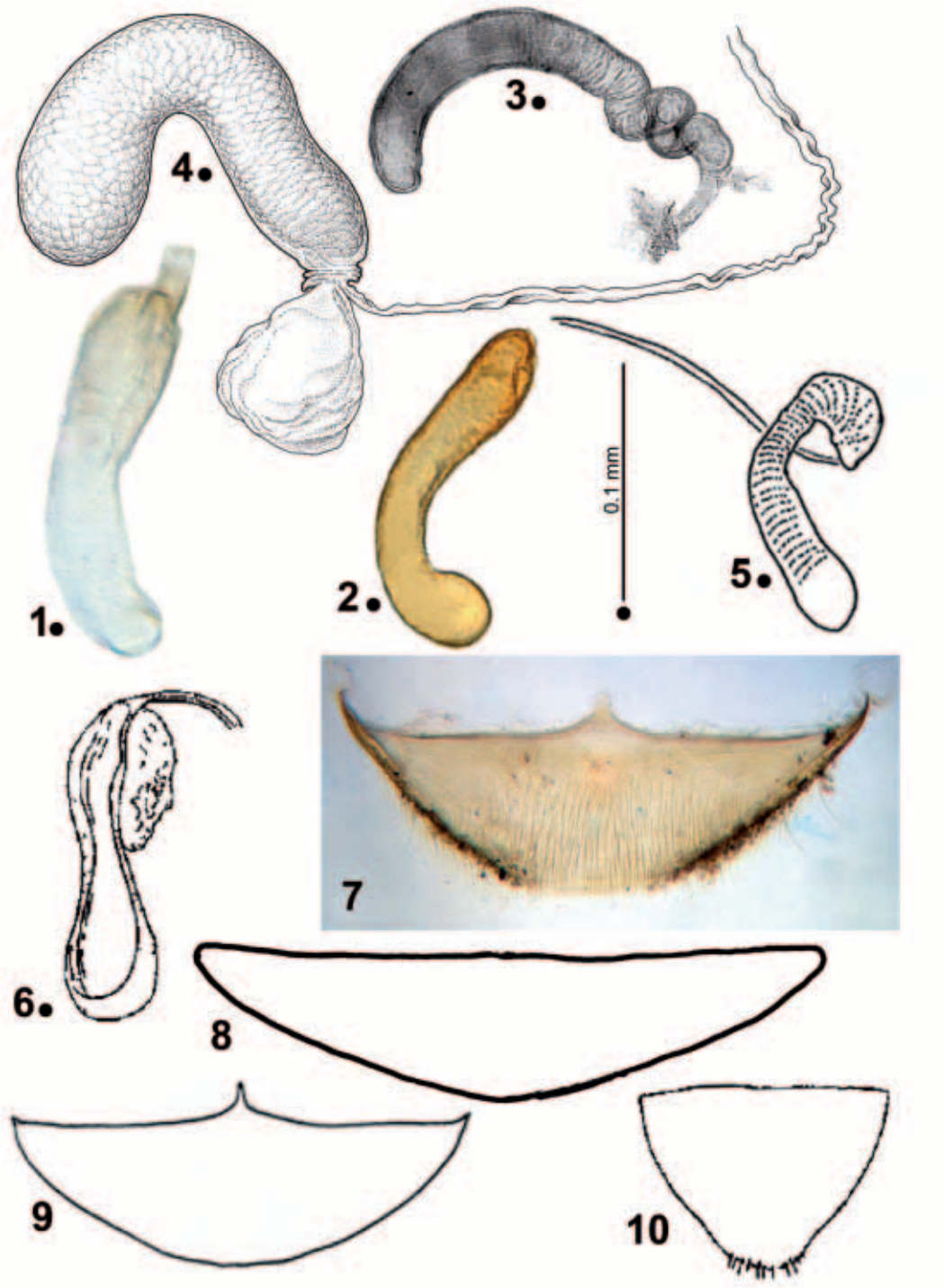
Anthroherpon hoermanni hypsophilum Apfelbeck, 1907
Antroherpon Hoermanni hypsophilum Apfelbeck, 1907b: 402.
Antroherpon (s. str.) *Hörmanni* subsp. *hypsophilum* Apfelbeck: Jeannel, 1914b: 54.
Antroherpon hoermanni hypsophilum Apfelbeck: V.B. Guéorguiev, 1990: 263.

Anthroherpon hoermanni orlovacensis V.B. Guéorguiev, 1990
Antroherpon hoermanni orlovacensis V.B. Guéorguiev, 1990: 264.

Anthroherpon hoermanni sericeum Jeannel, 1930
Antroherpon Hörmanni ssp. *sericeum* Jeannel, 1930e: 146.
Antroherpon hoermanni sericeum Jeannel: Pretner, 1974: 11.

Anthroherpon hossei Winkler, 1925
Antroherpon Hossei Winkler, 1925: 143.
Antroherpon (s. str.) *Hossei* Winkler: Jeannel, 1930e: 140.
Antroherpon hossei Winkler: Pretner, 1974: 11.

Anthroherpon latipenne Apfelbeck, 1907
Anthroherpon latipenne attenuatum Jeannel, 1934
Antroherpon matzenaueri subsp. *attenuatum* Jeannel, 1934d: 160.
Antroherpon Luciani subsp. *attenuatum* Jeannel: G. Müller, 1937: 117.



FIGURES 121.1–121.10: *Anthroherpon* series, *Anthroherpon* group. Spermathecal complex of: (**1**) *Anthroherpon hoermanni* ssp., (**2**) *Graciliella ozimeci* (modified from Njunjić *et al.* 2016), (**3**) *Hadesia vasiceki* (modified from Perreau & Pavićević 2008), (**4**) *Kircheria beroni* (modified from Giachino & Vailati 2006), (**5**) *Leptomeson vuicae*, (**6**) *Nauticiella stygivaga*. Female uroventrite VIII of: (**7**) *A. hoermanni* ssp., (**8**) *K. dritae* (modified from Giachino & Casale 2022), (**9**) *L. vuicae*, (**10**) *N. stygivaga*. Figs **5**, **8** modified from Giachino *et al.* (2021); Figs **6**, **10** from Mlejnek & Moravec (2003).

Antroherpon latipene attenuatum Jeannel: Pretner, 1974: 11.

Anthroherpon latipenne gottli Zariquiey, 1927
Antroherpon Matzenaueri subsp. *gottli* Zariquiey, 1927: 163.
Antroherpon brevipenne Knirsch, 1928 [1927]: 115.
Antroherpon Matzenaueri Gottli Zariquiey: Jeannel, 1929a: 297.
Anthoherpon (s. str.) *matzenaueri* subsp. *Göttli* Zariquiey: Jeannel, 1930e: 142.
Antroherpon Luciani subsp. *Göttli* Zariquiey: G. Müller, 1937: 117.
Antroherpon latipenne Göttli Zar.: Jeannel, 1947d: 47.
Antroherpon latipenne goettli Zariquiey: Pretner, 1974: 11.

Anthroherpon latipenne latellai Giachino & Vailati, 2005
Anthroherpon latipenne latellai Giachino & Vailati, 2005b: 153.

Anthroherpon latipenne latipenne Apfelbeck, 1907
Antroherpon Matzenaueri var. *latipenne* Apfelbeck, 1907b: 401.
Antroherpon Matzenaueri subsp. *latipenne* Apfelbeck: Jeannel, 1910a: 45.
Antroherpon latipenne Apf.: Jeannel, 1947d: 47.
Antroherpon Luciani G. Müller, 1913b: 128.
Antroherpon (s. str.) *Luciani* J. Müller: Jeannel, 1914b: 55.
Antroherpon (s. str.) *Matzenaueri* subsp. *Luciani* Müller: Jeannel, 1930e: 142.
Antroherpon latipenne Luciani J. Müll.: Jeannel, 1947d: 47.
Antroherpon (s. str.) *Matzenaueri* Apfelbeck: Jeannel, 1924a: 416.
Antroherpon latipenne latipenne Apfelbeck, 1907: Giachino & V.B. Guéorguiev, 1993 [1992]: 297.

Anthroherpon latipenne punctipennis Jeannel, 1930
Antroherpon (s. str.) *matzenaueri* subsp. *punctipennis* Jeannel, 1930e: 142.
Antroherpon Luciani subsp. *punctipenne* Jeannel: G. Müller, 1937: 117.
Antroherpon latipenne punctipenne Jeann.: Jeannel, 1947d: 47.
Anthroherpon latipenne punctipennis Jeannel: Perreau, 2000: 159.

Anthroherpon matulici Reitter, 1903
Antroherpon Matulici Reitter, 1903b: 216.
Antroherpon (s. str.) *echinatum* Jeannel, 1924a: 416.
Antroherpon (s. str.) *Matuliči* Reitt.: Jeannel, 1914b: 55.
Antroherpon (s. str.) *Matulici* subsp. *Matulici* Reitter: Jeannel, 1930e: 139.
Antroherpon (s. str.) *Matulici* subsp. *echinatum* Jeannel: Jeannel, 1930e: 139.
Antroherpon matulici Reitter: V.B. Guéorguiev, 1990: 249.

Anthroherpon matzenaueri Apfelbeck, 1907
Anthroherpon matzenaueri augustae Zariquiey, 1927
Antroherpon Augustae Zariquiey, 1927: 160.
Antroherpon Augustae subsp. *Bocki* Zariquiey, 1927: 161.
Antroherpon peduncularium Knirsch, 1928 [1927]: 114.
Antroherpon peduncularium ssp. *discrepans* Knirsch, 1928 [1927]: 121.
Antroherpon Augustae subsp. *Augustae* Zariquiey: Jeannel, 1930e: 139.
Antroherpon Matzenaueri Augustae Zar.: Jeannel, 1947d: 47.
Antroherpon matzenaueri augustae Zariquiey: Pretner, 1974: 11.
Anthroherpon matzenaueri augustae Zariquiey: Perreau, 2000: 155.

Anthroherpon matzenaueri matzenaueri Apfelbeck, 1907
Antroherpon Matzenaueri Apfelbeck, 1907b: 401.
Antroherpon (s. str.) *Matzenaueri* Apfelbeck: Jeannel, 1914b: 55.
Antroherpon (s. str.) *Matzenaueri* subsp. *Matzenaueri* Apfelbeck: Jeannel, 1930e: 139.
Antroherpon matzenaueri Apfelbeck: V.B. Guéorguiev, 1990: 250.
Antroherpon matzenaueri matzenaueri Apfelbeck, 1907: Giachino & V.B. Guéorguiev, 1993 [1992]: 290.
Antroherpon Hawelkai Knirsch, 1929 [1928]: 95.
Antroherpon Augustae subsp. *Hawelkai* Knirsch: Jeannel, 1930e: 139.
Antroherpon matzenaueri ab. *dilatatus* Apfelbeck: J. Müller, 1913b: 129.

Anthroherpon matzenaueri taliensis Zariquiey, 1927
Antroherpon Augustae subsp. *taliensis* Zariquiey, 1927: 160.
Antroherpon Matzenaueri subsp. *taliensis* Zariquiey: G. Müller, 1937: 117.
Antroherpon matzenaueri talienes (Zariquiey): Pretner, 1974: 12.
Antroherpon matzenaueri taliensis Zariquiey: V.B. Guéorguiev, 1990: 251.

Anthroherpon piesbergeni Zariquiey, 1927
Antroherpon Piesbergeni Zariquiey, 1927: 161.
Antroherpon (s. str.) *Piesbergeni* Zariquiey: Jeannel, 1930e: 140.
Antroherpon piesbergeni Zariquiey: Pretner, 1974: 12.

Anthroherpon pozi Absolon, 1913
Antroherpon pozi Absolon, 1913a: 1.
Antroherpon (s. str.) *Poži* Absolon: Jeannel, 1914b: 55.

Anthroherpon primitivum (Absolon, 1913)
Anthroherpon primitivum jeanneli Winkler, 1925
Antroherpon Jeanneli Winkler, 1925: 143.
Antroherpon (s. str.) *primitivum* subsp. *Jeanneli* Winkler: Jeannel, 1930e: 140.
Antroherpon primitivum jeanneli (Winkler): Pretner, 1974: 12.
Antroherpon primitivum jeanneli Winkler: V.B. Guéorguiev, 1990: 253.

Anthroherpon primitivum primitivum (Absolon, 1913)
Antrophilon primitivum Absolon, 1913b: 101.
Antroherpon (*Antrophilon*) *primitivum* Absolon: Jeannel, 1914b: 55.
Antroherpon primitivum Absolon: G. Müller, 1914: 1027.
Antroherpon (s. str.) *primitivum* subsp. *primitivum* Absolon: Jeannel, 1930e: 140.
Antroherpon primitivum (Absolon): V.B. Guéorguiev, 1990: 252.
Antroherpon primitivum primitivum (Absolon, 1913): Giachino & V.B. Guéorguiev, 1993 [1992]: 295.

Anthroherpon pygmaeum (Apfelbeck, 1889)
Anthroherpon pygmaeum pygmaeum (Apfelbeck, 1889)
Leptoderus pygmaeus Apfelbeck, 1889: 61.
Anthroherpon pygmaeus Apfelbeck: Reitter, 1889a: 294.
Antroherpon pygmaeum: Apfelbeck, 1894: 512.
Antroherpon (s. str.) *pygmaeum* Apfelbeck: Jeannel, 1914b: 55.
Antroherpon (s. str.) *pygmaeum* subsp. *pygmaeum* Apfelbeck: Jeannel, 1930e: 144.
Antroherpon pygmaeum pygmaeum (Apfelbeck, 1889): Giachino & V.B. Guéorguiev, 1993 [1992]: 307.

Anthroherpon pygmaeum stricticolle Jeannel, 1930
Antroherpon (s. str.) *pygmaeum* subsp. *stricticolle* Jeannel, 1930e: 144.
Antroherpon pygmaeum stricticolle Jeannel: V.B. Guéorguiev, 1990: 261.

Anthroherpon scutariensis Giachino & V.B. Guéorguiev, 1993
Antroherpon scutariensis Giachino & V.B. Guéorguiev, 1993 [1992]: 308.

Anthroherpon shtarensis Giachino & Casale, 2022
Anthroherpon shtarensis Giachino & Casale, 2022: 38.

Anthroherpon sinjajevinja Njunjić, Perreau & Pavićević, 2015
Anthroherpon sinjajevinja Njunjić, Perreau & Pavićević, 2015: 404.

Anthroherpon spelaebatoides (Noesske, 1914)
Parantrophilon spelaebatoides Noesske, 1914: 21.
Anthroherpon spelaeobatoides (Noesske, 1914): Čeplík & Hlaváč, 2022: 555.

Anthroherpon stenocephalum Apfelbeck, 1901
Anthroherpon stenocephalum noesskei Jeannel, 1924
Antroherpon (s. str.) *stenocephalum* Subsp. *Noesskei* Jeannel, 1924a: 417.
Antroherpon stenocephalum noesskei Jeannel: V.B. Guéorguiev, 1990: 260.

Anthroherpon stenocephalum stenocephalum Apfelbeck, 1901
Antroherpon stenocephalum Apfelbeck, 1901: 15.
Antroherpon (*Eumecosoma*) *stenocephalum* Apfelbeck: G. Müller, 1901: 29.
Antroherpon (s. str.) *stenocephalum* Apfelbeck: Jeannel, 1914b: 55.
Antroherpon (s. str.) *stenocephalum* Subsp. *stenocephalum* Apfelbeck, 1901: Jeannel, 1924a: 417.
Antroherpon stenocephalum stenocephalum Apfelbeck, 1901: Giachino & V.B. Guéorguiev, 1993 [1992]: 304.

Anthroherpon subalpinum Jeannel, 1924
Antroherpon subalpinum Jeannel, 1924a: 418.

Anthroherpon taxi G. Müller, 1913
Anthroherpon taxi albanicum Apfelbeck, 1919
Antroherpon albanicum Apfelbeck, 1919: 271.
Antroherpon (s. str.) *albanicum* Apfelbeck, 1919: Jeannel, 1924a: 417.
Antroherpon (s. str.) *albanicum* subsp. *albanicum* Apfelbeck: Jeannel, 1930e: 141.
Antroherpon (s. str.) *taxi* subsp. *albanicum* Apf.: Winkler, 1938: 220.

Anthroherpon taxi albanicum (Apfelbeck): Perreau, 2000: 162.

Anthroherpon taxi boschi Zariquiey, 1927
Antroherpon Winkleri subsp. *Boschi* Zariquiey, 1927: 162.
Antroherpon montenegrinum Knirsch, 1928 [1927]: 118.
Antroherpon Winkleri Boschi Zariquiey: Jeannel, 1929a: 297.
Antroherpon (s. str.) *albanicum* subsp. *Boschi* Zariquiey: Jeannel, 1930e: 141.
Antroherpon albanicum gracile Winkler, 1933: 77.
Antroherpon albanicum Boschi Zar.: Jeannel, 1947d: 48.
Antroherpon albanicum boschi Zariquiey: Pretner, 1974: 11.
Antroherpon taxi boschi Zariquiey: V.B. Guéorguiev, 1990: 258.

Anthroherpon taxi hercegovinum Winkler, 1938
Antroherpon taxi hercegovinum Winkler, 1938: 220.

Anthroherpon taxi lemur Knirsch, 1929
Antroherpon lemur Knirsch, 1929: 96.
Antroherpon albanicum lemur Kn: Jeannel, 1947d: 48.
Antroherpon taxi lemur Knirsch: V.B. Guéorguiev, 1990: 258.
Antroherpon (s. str.) *Matzenaueri* subsp. *Matzenaueri* Apfelbeck: Jeannel, 1930e: 142.
Antroherpon (s. str.) *albanicum* subsp. *ledenicense* Jeannel, 1934d: 159.
Anthroherpon albanicum ledenicense Jeannel: Pretner, 1974: 11.

Anthroherpon taxi muelleri Zariquiey, 1927
Antroherpon Winkleri subsp. Mülleri Zariquiey, 1927: 162.
Antroherpon grebense Knirsch, 1928 [1927]: 119.
Antroherpon Winkleri Mülleri Zariquiey: Jeannel, 1929a: 297.
Antroherpon albanicum subsp. *Mülleri* Zariquiey: Jeannel, 1930e: 141.
Antroherpon albanicum muelleri Zariquiey: Pretner, 1974: 11.
Antroherpon taxi muelleri Zariquiey: V.B. Guéorguiev, 1990: 257.

Anthroherpon taxi pretneri Giachino & Vailati, 2005
Anthroherpon taxi pretneri Giachino & Vailati, 2005b: 156.

Anthroherpon taxi remyi Jeannel, 1931
Antroherpon (s. str.) *albanicum* ssp.*Remyi* Jeannel, 1931b: 265.
Antroherpon albanicum Remyi Jeann.: Jeannel, 1947d: 48.
Antroherpon taxi remyi Jeannel: V.B. Guéorguiev, 1990: 258.

Anthroherpon taxi sydowi Zariquiey, 1927
Antroherpon Winkleri subsp. *Sydowi* Zariquiey, 1927: 162.
Antroherpon albanicum subsp. *Sydowi* Zariquiey: Jeannel, 1930e: 142.
Antroherpon albanicum sydowi (Zariquiey): Pretner, 1974: 11.
Antroherpon taxi sydowi Zariquiey: V.B. Guéorguiev, 1990: 257.

Anthroherpon taxi taxi G. Müller, 1913
Antroherpon Taxi G. Müller, 1913b: 159.
Antroherpon (s. str.) *Taxi* J. Müller: Jeannel, 1914b: 55.
Antroherpon taxi Müller: V.B. Guéorguiev, 1990: 256.
Antroherpon taxi taxi J. Müller, 1913: Giachino & V.B. Guéorguiev, 1993 [1992]: 301.

Anthroherpon taxi trezzii Giachino & Vailati, 2005
Anthroherpon taxi trezzii Giachino & Vailati, 2005b: 154.

Anthroherpon taxi winkleri Zariquiey, 1927
Antroherpon Winkleri Zariquiey, 1927: 162.
Antroherpon velare Knirsch, 1928 [1927]: 118.
Antroherpon velare divergens Knirsch, 1928 [1927]: 122.
Antroherpon albanicum subsp. *Winkleri* Zariquiey: Jeannel, 1930e: 141.
Antroherpon albanicum malissorum Winkler, 1933: 77.
Antroherpon albanicum winkleri Zariquiey: Pretner, 1974: 11.
Antroherpon albanicum divergens (Knirsch): Pretner, 1974: 11.
Antroherpon albanicum winkleri Zariquiey: V.B. Guéorguiev, 1990: 257.
Antroherpon taxi winkleri Zariquiey, 1928: Giachino & V.B. Guéorguiev, 1993 [1992]: 302.

Anthroherpon udrzali Giachino & Vailati, 2005
Anthroherpon matzenaueri udrzali Giachino & Vailati, 2005b: 150.
Anthroherpon udrzali Giachino & Vailati, 2005: Njunjić, Perreau & Pavićević, 2015: 410.

Anthroherpon weiratheri Reitter, 1913
Antroherpon Weiratheri Reitter, 1913a: 154.
Antroherpon (s. str.) *Weiratheri* Reitt.: Jeannel, 1914b: 55.
Antroherpon weiratheri Reitter: Pretner, 1974: 12.

Anthroherpon winneguthi Apfelbeck, 1919
Antroherpon Winneguthi Apfelbeck, 1919: 271.
Antroherpon (s. str.) *Winneguthi* Apfelbeck, 1919: Jeannel, 1924a: 418.
Anthroherpon winneguthi Apfelbeck, 1919: Perreau, 2000: 163.

Anthroherpon zariquieyi Jeannel, 1930
Antroherpon (s. str.) *Zariquieyi* Jeannel, 1930e: 145.
Antroherpon zariquieyi Jeannel: Pretner, 1974: 12.

Genus ***Graciliella*** Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016
Graciliella Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 350.

Type species. *Antroherpon apfelbecki apfelbecki* G. Müller, 1910 by original designation (habitus in Fig. 117.2).

Diagnosis. Large size, between 6.7–9.1 mm. Leptodiroid facies (Fig. 117.2) with extremely long and slender appendages, very elongated head and pronotum, hemispherical elytra, and totally depigmented. Colouration between orange and bright reddish, in general head and pronotum being somewhat darker.

Head: Elongated, between 1.5–2 times longer than wide, being clearly shorter than pronotum. Anterior part is the widest and wider than pronotum; surface shiny with a superficial micro-reticulation; pubescence, when present, very sparse and short. Base of terminal maxillary palpomere with a comb or dorsal ridge of robust and short setae. Anophthalmous.

Antennae: Inserted in the posterior quarter of the head, very long and very thin, much longer than the body length. First antennomere longer than the second one; the 11th somewhat longer than the 10th and the 5th the longest of all; without differentiated club.

Pronotum: Long and narrow, between 2.5–4 times longer than wide, with maximum width in the anterior third. Anterior area longer than the posterior one, with arcuated or sub-rectilinear sides and, in some cases, very slightly concave. Posterior area very narrow and concave. Surface shiny, with little marked but evident micro-reticulation, with none, or sparse, more or less long pubescence, most of them in the posterior area.

Mesonotum: Mesothoracic peduncle elongated, without constriction, slightly wider than long, or as long as wide.

Elytra: Elliptical, wide and with a marked physogastry, always somewhat longer than broad as a whole. Depending on the species, maximum width towards the middle and the apical part, and more rounded or more acuminate. Surface smooth, shiny or matt, normally with a very superficial micro-sculpture, as the punctation, which, if present, is spaced and irregular. Pubescence also, if they are not glabrous, scattered and can be short or long. No parasutural stria.

Legs: Very long, thin and pubescent; protibiae straight or slightly arcuated, meso- and metatibiae straight. Femora dilated and widened in the basal area, then progressively narrow towards the distal area; protarsi not dilated, pentameres in males.

Mesoventral keel (Njunjić *et al*. 2016): Not present. Mesoventrite without process between the mesocoxae, cavities being confluent.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: It is long, narrow, with a lanceolate shape, and apical area more or less narrowed, but not sharp. Rather short, little sclerotized and highly variable in shape. In lateral view, more or less arcuated in the basal region, then is more or less straight or flattened and, in some, with a more or less marked dorsal depression between the middle and the basal third. In dorsal view (Fig. 120.7), sides are in regular arc, straight, sub-rectilinear or sinuated, that converge to form an apical part that can be triangular, more or less narrowed. Apex between little and very sharp, or arcuated, with apex more or less sharp. Basal blade long and more or less oval.

Endophallus (Fig. 120.7): Without any sclerotized structures.

Parameres (Fig. 120.13): As long as, or somewhat shorter than the median lobe. Normally thin and of uniform thickness up to the apical area, that is narrow with a blunt apex and no differentiated club, or with a weak preapical constriction and slightly dilated in apical area. Apical area bearing three setae of similar length and width.

Spermathecal complex: Spermatheca (Fig. 121.2) weakly sclerotized, without differentiated lobes, in shape of a «J», short and slightly dilated in the apical area.

Female uroventrite VIII (Njunjić *et al*. 2016): With a well-developed and narrow spiculum.

Discussion. On Fig. 1H it is shown that *Graciliella* and *Leptomeson* are sister genera with a high support in the molecular phylogeny (96.2/100); together with *Kircheria*, with has only a very low support of 1.4/56 in Tree-1, is adopted the position of *Kircheria* at the base of the whole clade *Anthroherpon* group of Delić *et al*. (2023).

These three genera join *Anthroherpon* with a support of 82.7/94. All of this also supported by the external morphology with various characters that are likely synapomorphic, such as the shape and length of the pronotum and mesothoracic peduncle, the mesoventrite with or without a process and the endophallus of the aedeagus with or without a stylet (Njunjić *et al*. 2016). The authors, by molecular analysis, also show that *Graciliella* and *Leptomeson* are found to be sister genera with highest support. Thus, *Graciliella* differs from *Anthroherpon* by the very elongated mesothoracic peduncle, the elytra more spherical and the absence of mesoventral process with confluent cavities. *Leptomeson* differs from *Anthroherpon* by the larger size, by the mesothoracic peduncle with constriction and wider posterior area, by the median lobe of aedeagus more elongated and narrow and especially without a stylet in the endophallus.

Distribution. Genus located in the mountain chain of the Dinaric Alps in the western part of the Balkan Peninsula with caves attached to the calcareous massifs of Bosnia-Herzegovina, Montenegro, Albania and Croatian Dalmatia region.

Species

Graciliella absoloni (V.B. Guéorguiev, 1990)
Antroherpon absoloni V.B. Guéorguiev, 1990: 265.
Graciliella absoloni (Guéorguiev, 1990): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 360.

Graciliella apfelbecki (G. Müller, 1910)
Graciliella apfelbecki apfelbecki (G. Müller, 1910)
Antroherpon apfelbecki G. Müller, 1910: 186.
Antroherpon kauti Apfelbeck, 1911: 216.
Antroherpon Apfelbecki J. Müller: Jeannel, 1911a: 560.
Antroherpon (s. str.) *Apfelbecki* J. Müller: Jeannel, 1914b: 54.
Antroherpon Kauti Apfelbeck, 1916: 346.
Antroherpon (s. str.) *Apfelbecki* subsp. *Apfelbecki* Müller: Jeannel, 1930e: 147.
Antroherpon apfelbecki apfelbecki J. Müller, 1910: Giachino & V.B. Guéorguiev, 1993 [1992]: 316.
*Graciliella apfelbecki apfelbecki (*Müller, 1910): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 356.

Graciliella apfelbecki schwienbacheri (Giachino & Vailati, 2005)
Anthroherpon apfelbecki schwienbacheri Giachino & Vailati, 2005b: 159.
Graciliella apfelbecki schwienbacheri (Giachino & Vailati, 2005): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 357.

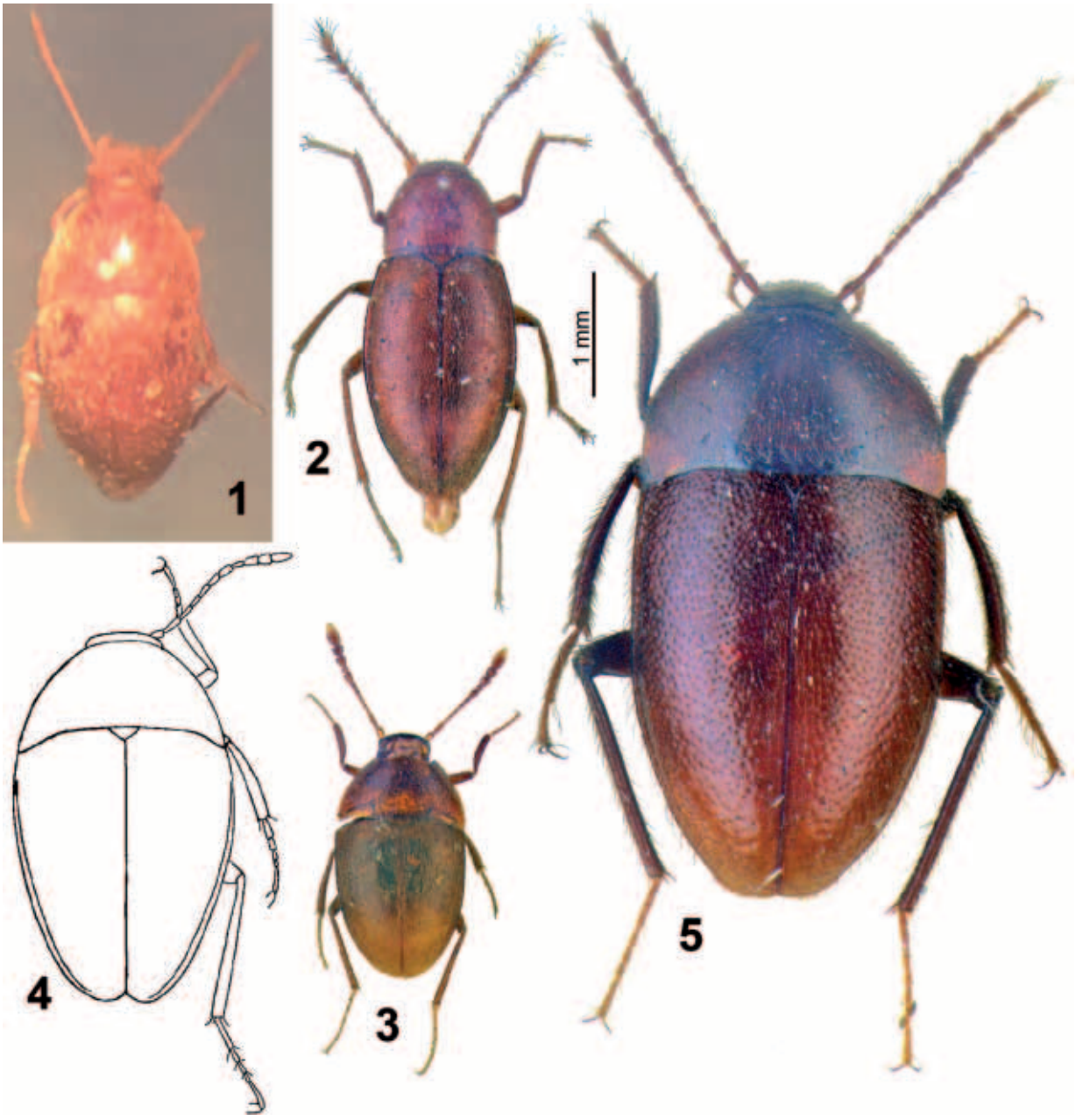
Graciliella apfelbecki sculptifrons (Winkler, 1925)
Antroherpon Apfelbecki sculptifrons Winkler, 1925: 144.
Antroherpon (s. str.) *Apfelbecki* subsp. *sculptifrons* Winkler: Jeannel, 1930e: 147.
Antroherpon apfelbecki sculptifrons Winkler: Pretner, 1974: 11.
Graciliella apfelbecki sculptifrons (Winkler, 1925): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 357.

Graciliella apfelbecki scutulatum (Giachino & V.B. Guéorguiev, 1993)
Antroherpon scutulatum Giachino & V.B. Guéorguiev, 1993 [1992]: 317.
Anthroherpon apfelbecki scutulatum Giachino & Guéorguiev: Perreau & Pavićević, 2008b: 212.
Graciliella apfelbecki scutulatum (Giachino & Guéorguiev, 1993): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 357.

Graciliella kosovaci Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016
Graciliella kosovaci Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 353.

Graciliella lahneri (Matcha, 1916)
Antroherpon Lahneri Matcha, 1916: 63.
Antroherpon (s. str.) *Lahneri* Matcha, 1916: Jeannel, 1924a: 420.
Antroherpon apfelbecki lahneri Matcha: V.B. Guéorguiev, 1990: 265.
Graciliella lahneri (Matcha, 1916): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 358.

Graciliella metohijensis (Zariquiey, 1927)
Antroherpon Apfelbecki subsp. *Metohijensis* Zariquiey, 1927: 163.
Antroherpon (s. str.) *Apfelbecki* subsp. *metohiensis* Zariquiey: Jeannel, 1930e: 147.



FIGURES 122.1–122.5: *Anthroherpon* series, *Pholeuonopsis* group. Habitus of: (**1**) *Albanella lonae,* (**2**) *Anillocharis stenopterus*, (**3**) *Anisoscapha klimeschi misella*, (**4**) *Augustia weiratheri* (modified from Zariquiey 1928), (**5**) *Blattochaeta matchai*.

Antroherpon apfelbecki metohijense Zariquiey: Pretner, 1974: 11.
Graciliella metohijensis (Zariquiey, 1928): Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 357.

Graciliella ozimeci Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016
Graciliella ozimeci Njunjić, Perreau, Hendriks, Schilthuizen & Deharveng, 2016: 356.

Genus ***Leptomeson*** Jeannel, 1924
Antroherpon (*Leptomeson*) Jeannel, 1924a: 400.
Leptomeson Jeannel: V.B. Guéorguiev, 1990: 267.

Type species. *Antroherpon leonhardi* Reitter, 1902 by original designation (for the habitus see that of the similar species *Leptomeson soltensis* in Fig. 118.2).

Diagnosis. Size between 4.0–7.0 mm. Leptodiroid facies, with a very elongated body and very marked physogastry (Fig. 118.2). Depigmented. Colouration bright reddish, normally with legs and antennae somewhat lighter. Microsculpture very weak on the head, between marked and almost blurred on pronotum, well defined on elytra. Pubescence on both head and pronotum is almost, or non-existent.

Head: Very elongated, about 1.5–2 times longer than wide, without occipital keel; maximum width in the anterior area and wider than the pronotum Anophthalmous.

Antennae: Very long and thin, with the first antennomere longer than the second one. Eleventh, compared to the ninth or tenth, always longer in males, may be shorter in females.

Pronotum: Narrow and very elongated, subrectangular or bottle-shaped, between 2.5–4 times as long as wide. Anterior or distal part, somewhat wider and longer than the posterior or basal area. With two more or less marked concavities on the sides, one in the middle of the anterior area and another in the posterior one, narrower and at the beginning of the basal area, in general it is more sinuated and usually reborded in the final part. Punctation is sparse, like the pubescence that are erect.

Mesonotum: Mesothoracic peduncle highly developed, usually restricted in the middle, and as wide as long or, somewhat, longer than wide; sometimes as long as the basal area of pronotum.

Elytra: Pyriform or elongated elliptical, very convex, more or less widened laterally; depending on this shape, the apical area is more rounded or more acuminate. Punctation, depending on the species, can be superficial or strong and close or spaced, but without transverse striolation. Likewise pubescence that can be between short and long, more or less raised, generally spaced, and in some representatives glabrous. No parasutural stria.

Legs: Very long and thin; tibiae straight, not widened distally. Femora dilated and widened in the basal area, then progressively narrowed towards the distal area. Protarsi pentameres, non-dilated, in males; claws long and slightly widened.

Mesoventral keel: Not present. Mesoventrite without process between the mesocoxae, cavities being confluent.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 119.4): Reduced, with long and narrow metascutum wings and posterior process reduced to a stump.

Metendosternite (Fig. 119.8): In shape of «Y». Furcal arms narrow and as long as the trunk, with a short and rounded terminal process; posterior lamina of the furca with convave margin, tapers towards the apical part of the arms. Trunk very long, between 3.5–4 times longer than wide, base forms two arcuated and sharp lobes.

Median lobe of aedeagus: Short and wide, very sclerotized. In lateral view (Fig. 120.4), little arcuated. In dorsal view (Fig. 120.10) rounded or sub-rectilinear laterally, with the short apical part already rounded or sub-triangular and the apex more or less prominent, but not acuminate. Basal blade short and widened.

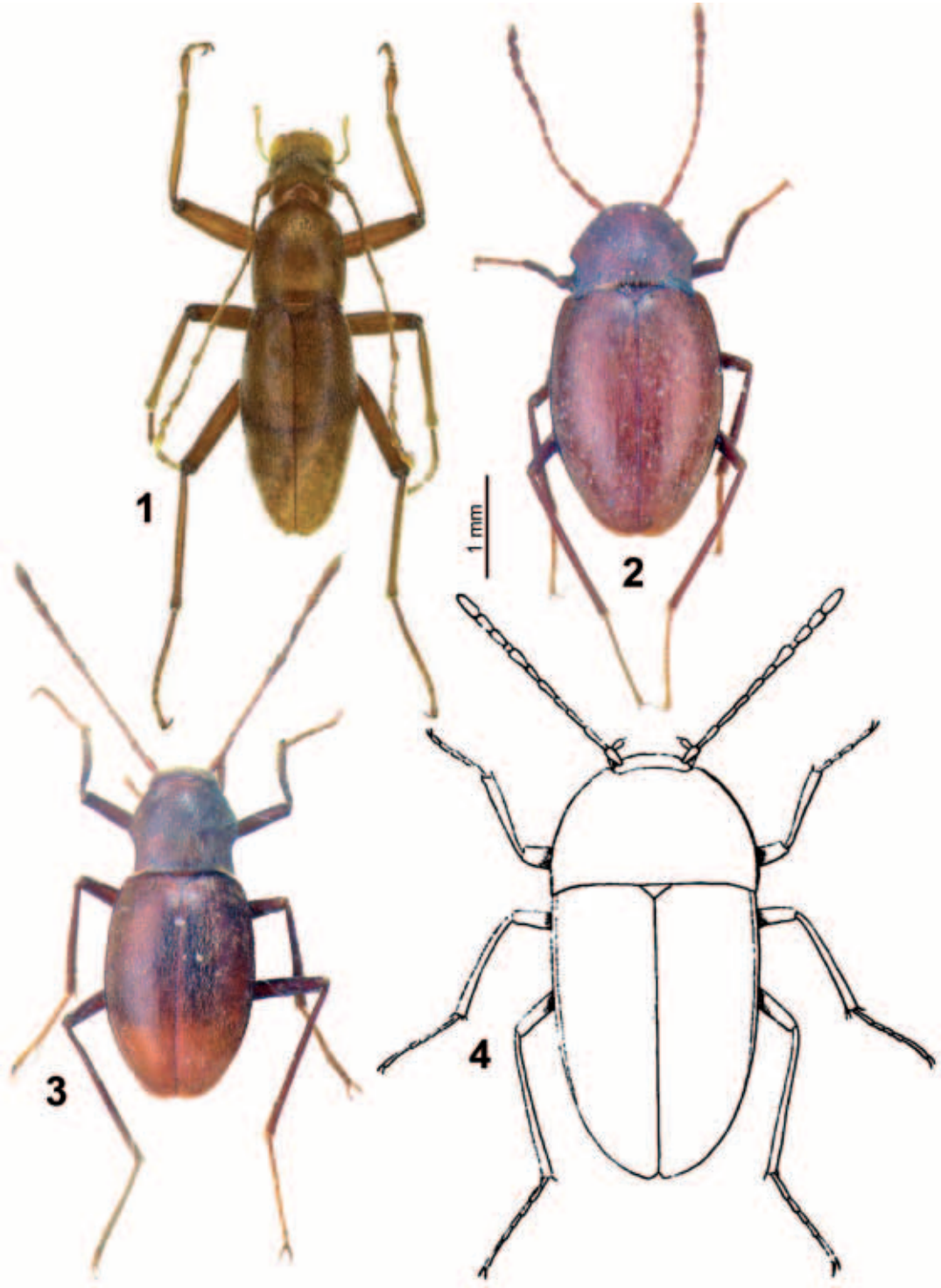
Endophallus (Fig. 120.10): Provided with a basal structure, with two juxtaposed ventral pieces that correspond to the «Y»-piece and form a widened stylet at the base, which is located in the middle part and direct towards the apex.

Parameres (Fig. 120.16): They are as long as, or somewhat shorter than the middle lobe, thin and regularly curved. Apex twisted or not, with three apical setae of similar length, or four setae, three apical and one subapical inserted on the inner margin. Ventral blade of the tegmen short and as wide as the basal blade.

Spermathecal complex (Fig. 121.5): Spermatheca short, largely striated and quite sclerotized, there are no different lobes or union ducts, with a sacciform or pyriform appearance with regular width along the middle area, or the anterior area wider. Spermatic duct very thin with spermathecal gland, although hyaline, well differentiated.

Female uroventrite VIII (Fig. 121.9): With short, fine and sharp spiculum in the middle anterior part.

Discussion. Jeannel (1924a) established *Leptomeson* as a subgenus of *Anthroherpon*. Subsequently V.B. Guéorguiev (1990) changed the status of *Leptomeson* to sta genus. Njunjić *et al*. (2016) in a molecular study established *Leptomeson* and *Graciliella* as sisters genera as a unit and both genera join the clade formed by *Hadesia* + *Anthropherpon* as such. In our molecular phylogenetic tree (Fig. 1H), *Leptomeson* is also sister to the genus *Graciliella* with a high support, 96.2/100, and these two genera together with *Kircheria* join *An-*



FIGURES 123.1–123.4: *Anthroherpon* series, *Pholeuonopsis* group. Habitus of: (**1**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**2**) *Leonhardella (Leonhardella) angulicollis*, (**3**) *L. (Leonhardellina) antennaria* ssp., (**4**) *Pholeuodromus jeanneli* (modified from Knirsch 1929).

throherpon with a support of 82.7/94. *Leptomeson* presents all morphological characters similar to *Arthroherpon* (see Discussion section about *Graciliella*).

DISTRIBUTION. It colonises various cavities in calcareous massifs of central and eastern Bosnia-Herzegovina (five species and three subspecies) and of insular and continental Dalmatia in Southern Croatia (seven species and one subspecies).

Species

Leptomeson biokovensis Giachino, Bregović & Jalžić, 2011
Leptomeson biokovensis Giachino, Bregović & Jalžić, 2011: 363.

Leptomeson bujasi Giachino, Bregović & Jalžić, 2011
Leptomeson bujasi Giachino, Bregović & Jalžić, 2011: 356.

Leptomeson dalmatinus Giachino, Bregović & Jalžić, 2011
Leptomeson dalmatinus Giachino, Bregović & Jalžić, 2011: 365.

Leptomeson dombrowskii (Apfelbeck, 1907)
Leptomeson dombrowskii dombrowskii (Apfelbeck, 1907)
Antroherpon Dombrowskii Apfelbeck, 1907a: 303.
Antroherpon (s. str.) *Dombrowskii* Apfelbeck: Jeannel, 1914b: 54.
Antroherpon (*Leptomeson*) *Dombrowskii* Apfelbeck, 1907: Jeannel, 1924a: 421.
Antroherpon dombrowskii (Apfelbeck, 1907): Jalžić, 1984: 57.
Leptomeson dombrowskii (Apfelbeck): V.B. Guéorguiev, 1990: 268.
Leptomeson dombrowskii dombrowskii (Apfelbeck): Perreau, 2000: 165.

Leptomeson dombrowskii pubipenne (G. Müller, 1941)
Antroherpon Dombrowskyi pubipenne G. Müller, 1941: 217.
Antroherpon dombrowskyi pubipenne G. Müller: Pretner, 1974: 12.
Leptomeson dombrowskyi pubipenne (Müller): Perreau, 2000: 165.

Leptomeson leonhardi (Reitter, 1902)
Antroherpon Leonhardi Reitter, 1902a: 208.
Antroherpon (s. str.) *Leonhardi* Reitt.: Jeannel, 1914b: 55.
Antroherpon (*Leptomeson*) *Leonhardi* Reitter: Jeannel, 1924a: 420.
Leptomeson leonhardi (Reitter): V.B. Guéorguiev, 1990: 268.

Leptomeson loreki (Zoufal, 1904)
Antroherpon Loreki Zoufal, 1904: 20.
Antroherpon kraussi G. Müller, 1904b: 38.
Antroherpon (s. str.) *Loreki* Zoufal: Jeannel, 1914b: 55.
Antroherpon (*Leptomeson*) Loreki Zoufal: Jeannel, 1924a: 420.
Leptomeson loreki (Zoufal): V.B. Guéorguiev, 1990: 268.

Leptomeson radjai Giachino, Bregović & Jalžić, 2011
Leptomeson radjai Giachino, Bregović & Jalžić, 2011: 360.

Leptomeson raguzi Giachino, Bregović & Jalžić, 2011
Leptomeson raguzi Giachino, Bregović & Jalžić, 2011: 367.

Leptomeson soltensis S. Ćurčić & Rađa, 2019
Leptomeson soltensis S. Ćurčić & Rađa *in* S. Ćurčić, Vesović, Lazović, Pantelić, & Rađa, 2019: 195.

Leptomeson svircevi (G. Müller, 1929)
Leptomeson svircevi knirschi V.B. Guéorguiev, 1990
Leptomeson svircevi knirschi V.B. Guéorguiev, 1990: 269.

Leptomeson svircevi svircevi (G. Müller, 1929)
Antroherpon Svircevi G. Müller, 1929: 137.
Antroherpon (*Leptomeson*) *Svircevi* Müller: Jeannel, 1930e: 147.
Leptomeson svircevi (G. Müller): V.B. Guéorguiev, 1990: 269.
Leptomeson svircevi svircevi (G. Müller): Perreau, 2000: 165.

Leptomeson vuicae Giachino, Casale & Jalžić, 2021
Leptomeson vuicae Giachino, Casale & Jalžić, 2021: 63.

Hadesia subgroup

Subgroup consisting of genera that, from the morphological point of view, presents a series by a common body structures such as: shape of mouth part, insertion of antennae, second antennomere shorter than the first one, female genitalia with styli fully atrophied, VIII. female uroventrite without spiculum and tarsal claws dilated. All these genera living in a hygropetric environments, *Hadesia* and *Nauticiella*. *Kircheria*, of the *Anthroherpon* subgroup, exhibit the same characters. As shown in the tree in figure 1H, derived from our molecular phylogenetic analysis, the genera *Hadesia* is sister to the group consisting of, *Anthroherpon* + *Leptomeson* + *Graciliella* + *Kircheria* with a support of 100/100 and together they constitute the «*Anthroherpon* group». In our opinion, on the basis of morphological and molecular data, to this clade only belong the genera *Hadesia* and *Nauticiella*.

Key to genera

1. Large size, 5.9–8.6 mm. Apical part of the median lobe of aedeagus, in lateral view, with a small depression before the preapical hump that is more or less pronounced (Fig. 120.2); apex with a small hooked tooth; in dorsal view, apical part widened and trilobed appearance (Fig. 120.8). Endophallus with a long flagellum or stylet widened or cup-shaped at the base (Fig. 120.8) ..... *Hadesia*
- Small to medium size, 2.5–3.4 mm. Apical part of the median lobe of aedeagus, in lateral view, without a small depression and apex not hooked (Fig. 120.5); in dorsal view, bilobed (Fig. 120.11). Endophallus without sclerotized structures (Fig. 120.11) ..... *Nauticiella*

Genus ***Hadesia*** G. Müller, 1911
Hadesia G. Müller, 1911c: 175.

Type species. *Hadesia vasiceki* G. Müller, 1911 by monotypy (habitus in Fig. 117.3).

Diagnosis. Size between 5.9–8.6 mm. General shape elongated elliptical and depigmented, with leptodiroid facies (Fig. 117.3). The colour between bright reddish and dark reddish, antennae and legs being lighter.

Head: Elongated, quadrangular, longer than wide, with concave cheeks; shorter than, and between as wide, or somewhat narrower, than pronotum; surface microreticulate, with some points in the occipital area, without occipital keel. Forehead dotted and with fine and distant setae at the central part. Labrum trapezoidal, bearing numerous long dorsal setae; a median incision is present at the anterior edge. Mandibles robust, with apical area widened and flattened and the edge equipped with about seven short teeth; labrum very developed and protruding with two groups of robust ventro-lateral setae. Anophthalmous.

Antennae: Inserted on the posterior quarter of head, very long and very thin, longer than the length of the body. First antennomere forms elongated club, about three times longer than the second one; the 3rd as long as the sum of 1st and 2nd; the 9th to 11th antennomeres similar in length and width, without a differentiated club.

Pronotum: Cylindrical and elongated, between 1.5–2.0 times longer than wide, very convex. Lateral edges rounded in the anterior half and concave in the posterior half, with the edges not or slightly sinuate; no marginal ridge. Maximum width at the anterior third; with a superficial and smooth microreticulation, or with a fine and scattered dotting; disc glabrous or with some scattered short setae.

Mesonotum: No mesothoracic peduncle.

Elytra: Elliptical, elongated, two, or somewhat more than twice as long as wide as a whole, with the maximum width towards the middle. Apical area slightly conical, with preapical area of epipleura not, or slightly, toothed in males and with a more or less prominent tooth in females, followed by a more or less marked indentation towards the apex. Humeral region of epipleura thickened or flattened, dependent on the species. Marginal ridge visible in dorsal view. Discal pubescence compact, silky in appearance, with short, grouped, regular distibuted and hydrophobic setae. No punctation observed, but a small granulated area nearby. Elytral disk lacks transversal striolae, without parasutural stria.

Legs: Long and thin; tibiae thin and straight; protibia and mesotibia without apical basket of spines, but with a group of short, dense bristles in distal area and a row of short, fine spines along the inner edge. All tibiae without comb on external margin and without external apical spur, but with two short and thick internal spurs. Femora widened along the basal area, and then gradually tapering to the top. Protarsi pentamerous, not dilated, in males, both in males and females, widely ciliated on ventral side and lateral edges with longer bristles. Claws very large and thick, spoon-shaped, with apical area recurved. First visible uroventrite, in females, with two highly-visible lateral depressions or fissures; absent in males.

Mesoventral keel: Lacking; mesoventrite without process between mesocoxae, the cavities being confluent.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Long, large and well sclerotized. In lateral view (Fig. 120.2), arcuated, with a small depression before the preapical hump that is more or less pronounced; apex with a small hooked tooth. In dorsal view (Fig. 120.8), with more or less parallel sides, with a narrow basal area, then widened and trilobed appearance in apical part; apex more or less developed and with more or less sharp triangular beak (*H. vasiceki*) or a wide hump (*H. asamo*).

Endophallus (Fig. 120.8): Enclosing a long flagellum, or stylet-shaped phanera, located on the dorsal part of the apical half of the median lobe. This stylet has a widened or cup-shaped base, something similar to that of species of genus *Quaestus*; in addition, many small spines are present on the walls of the middle part. Between the apical and middle part two well-developed reinforcing bands are present.

Parameres (Fig. 120.14): Thin and sharp, arcuated between middle and apical part, somewhat shorter than the median lobe. Without a distinct club; apex very narrow or rounded with 3–4 very short setae, generally not easy to see. If three: two subapical and one apical somewhat longer (Polak *et al*. 2016); if four: two short, subapical, and two apical of variable length within the same population (Perreau & Pavićević 2008b).

Spermathecal complex (Fig. 121.3): Spermatheca in shape of elongated arcuated sac, with uniform and weak sclerification; distal area sharp, rounded or somewhat dilated, basal area with spiral-shaped structures. Spermathecal gland hyaline, but visible, empties into base of spermatheca in union with spermatic duct, which is very thin, cylindrical or flattened and about 1.5 times longer than spermatheca; generally with a widened area before joining the copulatory bursa.

VIII and IX female uroventrites (Perreau & Pavićević 2008b): VIII without spiculum in the anterior medial area. IX without gonostyles and gonocoxites.

Discussion. A genus with good support and clearly separated from its sister clade formed by *Anthroherpon* and *Leptomeson* (Polak *et al*. 2016). Easily differentiated by these genera by body pubescence, ventrolateral dimples on the first female uroventrite, endophallus with singular flagellum and shape of apical setae of parameres. In turn, Njunjić *et al*. (2016) also confirmed it through a combined morphological-molecular analysis, so that *Hadesia* forms the sister clade of *Anthroherpon*, and *Leptomeson* forms another sister clade with *Graciliella*, with species that were part of *Anthroherpon* (*sensu auctorum*). Also, Perreau & Pavićević (2008b) pointed out that *Hadesia* and *Kircheria* were sister genera. In recent work, Delić *et al*. (2023) regard *Nauticiella* and *Hadesia* as sisters and with this clade separated from *Anthroherpon*. In our phylogenetic study (Fig. 1H), the genus *Hadesia*, with a support of 100/100 is sister of *Anthroherpon* + *Leptomeson* + *Graciliella* + *Kircheria*.

Paying attention to some morphological characters common in *Hadesia* and *Kircheria*, which from our point of view have to be considered important synapomorphies. These are in females are the complete atrophy of gonocoxites and gonostyles and the total lack of anterior apophysis of VIII uroventrite (Giachino & Vailati 2006; Giachino & Casale 2022). For this reason, in this contribution on a morphological base and on preliminary molecular data (Giachino & Casale 2022) we consider *Kircheria* as belonging to the «*Anthroherpon* group».

Distribution. They colonise caves of the SW Dinaric karst, corresponding to parts of the republics of Bosnia-Herzegovina and Montenegro.

Species

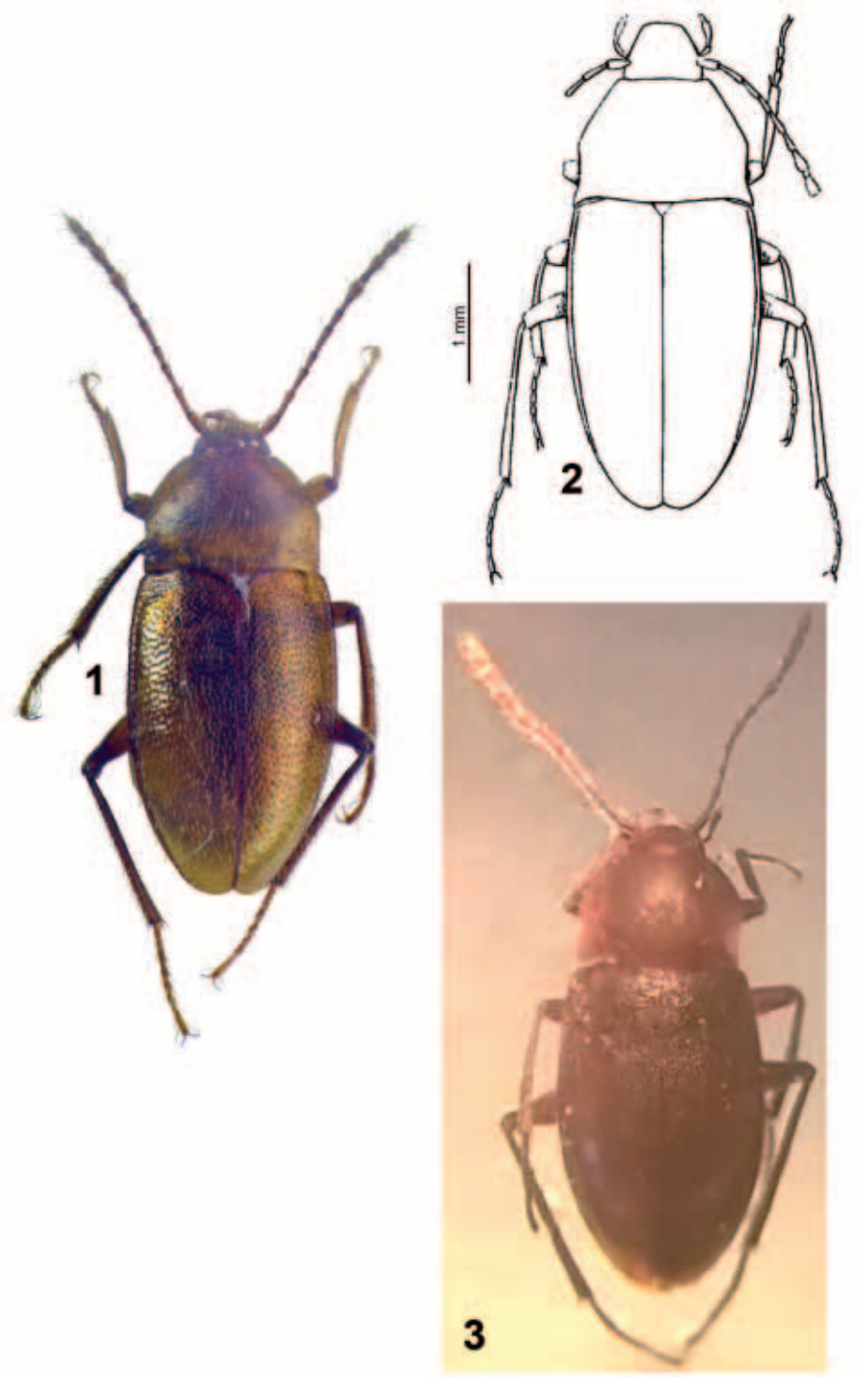
Hadesia asamo Perreau & Pavićević, 2008
Hadesia vasiceki weiratheri Zariquiey: Pretner, 1974: 12.
Hadesia orjensis V.B. Guéorguiev, 1990: 270 (*Nomen nudum*).
Hadesia asamo Perreau & Pavićević, 2008b: 219.

Hadesia lakotai Perreau & Pavićević, 2008
Hadesia lakotai Perreau & Pavićević, 2008b: 217.

Hadesia persephonae Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023
Hadesia persephonae Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023: 8.

Hadesia ticari Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023
Hadesia persephonae Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023: 11.

Hadesia vasiceki G. Müller, 1911
Hadesia Vasiceki G. Müller, 1911c: 175.
Hadesia vasiceki J. Müller: V.B. Guéorguiev, 1990: 269.
Hadesia vasiceki vasiceki Müller: Perreau, 2000: 164.



FIGURES 124.1–124.3: *Anthroherpon* series, *Pholeuonopsis* group. Habitus of: (**1**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii grabowskii*, (**2**) *P.* (*Scotosites*) *spaethi* (modified from Knirsch 1929), (**3**) *P.* (*Silphanillus*) *leonhardi*.

Hadesia weiratheri Zariquiey, 1927
Hadesia vasiceki subsp. *Weiratheri* Zariquiey, 1927: 163.
Hadesia vasiceki weiratheri Zariquiey: Pretner, 1974: 12.
Hadesia weiratheri Zariquiey: Perreau & Pavićević, 2008b: 224.

Hadesia zetae Delić, Polak & Trontelj, 2016
Hadesia zetae Delić, Polak & Trontelj, 2016: 245.

Genus ***Nauticiella*** Moravec & Mlejnek, 2002
Nauticiella Moravec & Mlejnek, 2002: 294.

Type species. *Nauticiella stygivaga* Moravec & Mlejnek, 2002 by original designation (habitus in Fig. 118.3).

Diagnosis. Small size, between 2.5–3.3 mm. General shape of the body narrow and elongated, with scaphoid facies (Fig. 118.3); depigmented. Brown colouration, with antennae and tarsus somewhat lighter.

Head: Wide, slightly longer than wide, not retractable, a little convex and somewhat narrower than the pronotum; without occipital keel. Pubescence yellowish, consisting of short or long setae, scattered and lying down; punctation little differentiated, dots very fine. Mouthparts such as clypeum, labrum, labium, maxillary and labial palpi modified and covered with long and dense pubescence. Anophthalmous.

Antennae: Long and thin, inserted in the posterior quarter of the length of the head, being between somewhat shorter or somewhat longer than body length; first antenomere much more robust and longer than the second one, the 2nd, 10th and 11th being in general the shortest antenomeres, 11thsubconic.

Pronotum: Subrectangular, slightly convex with the middle part sometimes flattened, about 1.5 times longer than the widest area and the maximum width in front or a little behind the middle, depending on the species. Lateral edges strongly and regularly arcuated from the middle part to the anterior base, being more or less concave in the posterior third. Angles subrectangular, with vertices non-protruding laterally; base of the pronotum almost straight. Dorsal surface with a fine and dense punctation; pubescence short and scattered.

Mesonotum: Not pedunculated.

Elytra: Elongated and moderately convex, between 2.0–2.5 times longer than wide; lateral margins regularly rounded and flanged, gradually narrow backwards, with the apical parts obtusely separated and the apexes rounded in males. Apical part, in females, narrow sharply, the apexes being very narrow, elongated and sharp. Punctation denser and thicker than in the pronotum, without transversal striolation. Pubescence well-developed, dense and lying; parasutural stria lacking.

Legs: Very long and thin, covered with fine pubescence. Femora widened along the basal area, and then, starting from the middle, gradually tapering to the top. Protibiae with the inner margin of the apical part slightly concave, without comb of short apical external spines, nor basket and nor internal spurs. Protarsi pentameres in males, with the first tarsomere moderately dilated, almost as wide as the apical part of the protibia; meso- and metatibiae slightly sinuous. Tarsal claws dimorphic, simple, long and not widened in metarsi; pro- and mesotarsal claws, widened, spoon-shaped.

Mesoventral keel: Lacking.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Quite long and robust. In lateral view (Fig. 120.5), regularly arcuated. In dorsal view (Fig. 120.11), somewhat widened in the basal two-thirds and concave in the apical third, with the apical area widened, bilobed and clearly cleft in the middle. Basal blade of the median lobe short, little widened and posterior margin in arc, almost as wide as the ventral blade of tegmen that is also short.

Endophallus (Fig. 120.11): Without sclerotized structures.

Parameres (Fig. 120.17): Long and thin, shorter than the median lobe; apical area a little sinuated. Club slightly thickened, bearing three short setae, two apical and one preapical inserted near the apex.

Spermathecal complex (Fig. 121.6): Spermatheca small, in shape of elongated sac; apical lobe subspherical and membranous, wider than the basal lobe which is oval, somewhat sclerotized and separated by a narrower and hyaline area. Spermatic duct thin and short; spermathecal gland small. Mlejnek & Moravec (2003) do not clarify whether or not female of *Nauticiella stygivaga* presents styles. From the description and drawings provided would seem absent.

Female uroventrite VIII (Fig. 121.10): With a slight depression in the middle area of the anterior edge, without spiculum; posterior edge narrows moderately towards the apical area.

Discussion. The species of this genus live in semiaquatic habitat, they have mouth parts strongly modified to be able to filter the organic matter out of the

water that runs through the walls of the caves (Lohaj *et al*. 2012). The y present a series of common body characters such as: shape of mouth part, insertion of antennae, 2nd antennomere shorter than the first one, female genitalia with styli fully atrophied, Female uroventrite VIII without spiculum and tarsal claws dilated, with several genera inhabiting in the same environment: *Hadesia*, *Nauticiella* or *Kircheria*. In other genera, with hygropetricolous way of life similar modifications of the mouth parts are present, therefore this is considered to be a simple convergence due to a specialised habitat; this finding is supported by the morphology of divergent genera such as: *Radziella*, *Tartariella*, *Croatodirus*, *Velebitodromus*, *Hygrodromus* or *Cansiliella*. Delić *et al.* (2023) pointed out that the clear phylogenetic relationship between the genera *Hadesia* and *Nauticiella*, establisehed by molecular analysis, placing these genera in the same clade as sisters with a support of >0.99.

Distribution. Only known from two cavities in the southern area of Bosnia-Herzegovina, the well of Bravenik, in the village of Grab, municipality of Trebinje, and the cave of Vjetrenica, Popovo polje, in the village of Zavala, municipality of Ravno.

Species

Nauticiella djokici Lohaj, Čeplík, Mlejnek & Lakota, 2012
Nauticiella djokici Lohaj, Čeplík, Mlejnek & Lakota, 2012: 179.

Nauticiella numerosa Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023
Hadesia persephonae Delić, Lohaj, Brestovanský, Čáha & Jalžić, 2023: 14.

Nauticiella stygivaga Moravec & Mlejnek, 2002
Nauticiella stygivaga Moravec & Mlejnek, 2002: 294.

3.2.5.3 ***Pholeuonopsis*** group

The analysis, on a morphological basis, of mutual affinities by genera assigned to this group is, when molecular data are lacking, very complicated. They are probably masked by phenomena of convergence presented by most specialized taxa towards subterranean environment, or by reverse phenomena of state of some characters. The characters series normally used for suprageneric systematics appears in this case not informative. Despite this, it seems correct to report these characters and their state to stimulate further investigation of them. The set of characters presented by this group are: Bathyscioid or pholeuonoid body; first antennomere shorter than the second one; legs with protarsi tetrameres in males and protibiae without comb (except *Albanella* and *Speonesiotes*, although reduced comb); absent parasutural stria (except *Proleonhardella remyi*); median lobe of aedeagus stout; endophallus with various internal structures, depending by genus. Particularly striking is the shape of the median lobe of aedeagus with an apical prolongation visible both in lateral and dorsal view; also with a prolongation of the basal lamina except *Anisoscapha* (and if its inclusion in this group is confirmed also of *Pseudobathyscidius*). Likewise, the spermatheca is very characteristic, with the median region prolonged and the apical lobe very poorly developed and scarcely or not at all sclerotized. *Hygrodromus*, although it presents the general characteristics of the group, does not coincide neither in the shape of the median lobe of aedeagus nor in the spermatheca, which introduces doubts for its inclusion in this group.

In the phylogenetic tree (Fig. 1H) *Pholeuonopsis* group is supported by 100/100; the group as sister of the clade *Anthroherpon* group with support 48.9/92; includes the genera *Pholeuonopsis*, *Leonhardella*, *Proleonhardella* and *Speonesiotes* with molecular data available, as well as other genera for which molecular data are not available.

It should be noted that in this group there are several genera which are preferentially endogean and are only known from the few specimens of their respective type series. Thus, in some of these cases no material has been available for study or no published figures of the various fundamental structures have been found.

Key to genera

1. Pholeuonoid or subpholeuonoid facies. Body elliptical and very elongated. Basal part of pronotum narrowed and concave or sinuated sides 2
- Bathyscioid facies. Body usually ovoid and wide, in some cases slightly elliptical and elongated. Basal part of pronotum unnarrowed, with regular or moderately curved sides..... 9

2. Mouth parts modified for filtration, with long setae brushes. Median lobe of aedeagus, in dorsal view, with apical part subtriangular and slightly truncate (Fig. 131.9). Basal lamina of median lobe without tongue (Fig. 131.9). Endophallus without sclerotized structures (Fig. 131.9).....*Hygrodromus*

- Unmodified mouth parts, without setae brushes. Median lobe of aedeagus, in dorsal view, narrow and forms a triangular ledge (Figs 131.5–131.8, 131.10, 131.11, 132.1–132.7). Basal lamina of the median lobe with tongue (Figs 131.5, 131.7, 131.8, 131.10, 131.11, 132.1–132.7). Endophallus with sclerotized structures.....3

3. Pronotum as long as wide, or slightly longer than width. Mesoventral keel atrophied. Endophallus without basal stylet, (Fig. 132.6) .....*Tartariella*
- Pronotum as long as wide or transverse. Mesoventral keel well evident, high (Figs 126.5–126.9, 127.1–127.8). Endophallus with well-developed basal stylet (Fig. 132.7)..... 4

4. Eighth antennomere elongated, at least twice as long as width. Elytra with pubescence short and lying down, without long, raised or erect setae. Pronotum with the sides of the basal third strongly concave....5
- Eighth antennomere subglobose or cylindrical, as long as wide, or at most one and a half times longer than wide. Elytra with long and raised pubescence, very long and erect setae especially in the posterior area of elytra. Pronotum with the sides of the basal third slightly concave..... 6

5. Size between 3.0–4.0 mm; antennae with the 11th antennomere, in males, longer than the 10th; elytra with shoulders angular or protruding; apical part of the median lobe of aedeagus in very sharp triangle and narrow base (Fig. 131.10); parameres as long as the median lobe, of uniform thickness to the apical area … .....*Leonhardella* (*Leonhardella*)
- Size between 4.0–4.5 mm; antennae with the 11th antennomere as long as the 10th in both sexes; elytra shoulders rounded; apical part of the median lobe of aedeagus in a blunt triangle with a broad base (Fig. 131.11); parameres more thin, and shorter than the median lobe ..... *Leonhardella* (*Leonhardellina*)

6. Protarsi of males strongly dilated. Median lobe of aedeagus long, in dorsal view, apical part forms a poorly developed and depressed triangular beak, with a rounded tip (Fig. 131.5); parameres somewhat longer than median lobe.....*Anillocharis*
- Protarsi of males not or slightly dilated. Median lobe of aedeagus shorter, in dorsal view, in the apical area forms a well-developed triangular beak, clearly depressed at the base, with a rounded or sharp tip (Fig. 132.1). Parameres somewhat longer or shorter than the median lobe.....7

7. Pronotum at the level of the base as wide as the base of the elytra. Humeral angles of the elytra do not pass outwardly the posterior angles of the pronotum .... *Pholeuonopsis* (*Scotosites*)
- Pronotum at base level narrower than base of elytra. Humeral angles of the elytra protruding and outwardly surpass the posterior angles of the pronotum..... 8

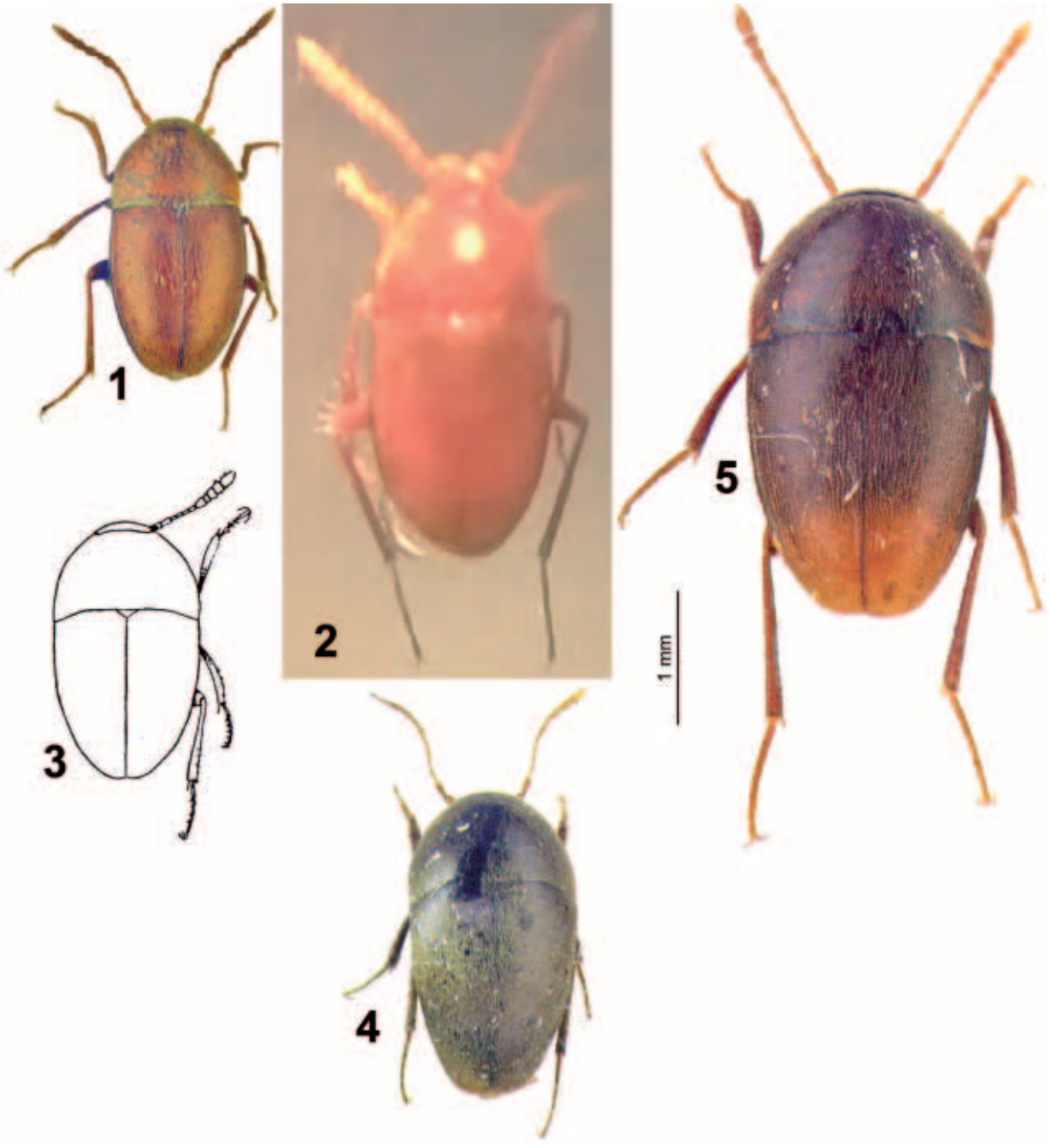
8. Basal edge of the prosternum projecting backwards from the anterior coxae. Mesoventral keel hight but very short, only extends along a third of mesoventrite, with straight anterior edge ....*Pholeuonopsis* (*Silphanillus*)
- Basal edge of the prosternum deeply notched on the midline, does not pass the anterior coxae. Mesoventral keel over entire mesoventrite, with anterior edge arched (Fig. 127.4)..... .....*Pholeuonopsis* (*Pholeuonopsis*)

9. Elytra with transverse striolation 10
- Elytra without transverse striolation.....14

10. Elytra with transverse striolation in the anterior and middle areas. Protibiae without comb. Ventral edge of the mesoventral keel wide, triangular-shaped and with a marked groove (Fig. 126.6). Endophallus with a robust and quite long stylet in bottom of sac (Fig. 131.6) .....*Anisoscapha*
- Elytra with transverse striolation in the entire elytra. Protibiae with comb. Ventral edge of the mesoventral keel more or less widened, without groove. Endophallus with one or two pairs of elongated basal pieces (Figs 131.7, 131.8, 132.3–132.5) 11

11. Antennae with the 8th antennomere longer than wide. Elytra with apex sexually dimorphic, widely arcuated in males, narrower and sharper in females. Males protarsi dilated. Median lobe of aedeagus very elongated, at least six times as long as it is wide and apparently unarmed endophallus (Fig. 131.4) ....*Albanella*
- Antennae with the 8th antennomere slightly longer than wide or very transverse . Elytra similar in both sexes, more or less arched or more or less cuneiform. Males protarsi gracile or little dilated. Median lobe of aedeagus shorter and wider, about three or four times longer than wide and endophallus with more or less differentiated phanerae (Figs 131.7, 131.8, 132.2–132.5, 132.7) 12

12. Antennae short, thick, do not exceed the base of pronotum; antennomeres non-detached and trape-



FIGURES 125.1–125.5: *Anthroherpon* series, *Pholeuonopsis* group. Habitus of: (**1**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**2**) *P.* (*Pholeuonillus*) *adolfi*, (**3**) *Speonesiotes* (*Crivosiella*) *brachycerus* (modified from Jeannel 1941), (**4**) *S.* (*Kulzeria*) *muelleri*, (**5**) *S.* (*Speonesiotes*) *narentinus latitarsis*.

zoidal with the base as wide as the apical area; 8th antennomere very transverse, twice as wide as long ....*Speonesiotes* (*Crivosiella*)
- Antennae surpass the base of the pronotum, with the apical antennomeres detached and narrow at the base; 8th slightly wider than long or a little longer than wide 13

13. Elytra with sides more or less arched backwards and regularly rounded apical areas. Endophallus without hyaline ampoule in the basal part and with four large strongly sclerotized phanerae (Fig. 132.5)..... ..... *Speonesiotes* (*Speonesiotes*)
- Elytra more or less cuneiform, with sides rectilinear backwards, apical areas narrowed and usually obliquely truncated. Endophallus with a hyaline ampoule at the basal part and two weakly sclerotized phanerae (Fig. 132.4).....*Speonesiotes* (*Kulzeria*)

14. Endophallus without sclerotized structures in the middle and/or upper part (Figs 131.7, 132.7) 15
- Endophallus with sclerotized structures in the middle and/or upper part (Figs 131.8, 132.2)..... 16

15. Parameres longer than the median lobe of aedeagus (Fig. 131.7). Endophallus with a short stylet in the centre of the basal area and on the sides two small arc-shaped phanerae (Fig. 131.7) .....*Augustia*
- Parameres shorter than the median lobe of aedeagus (Fig. 132.7). Endophallus with stylet in the centre of the basal area, surrounded by a bilobed hyaline ampoule (Fig. 132.7).....*Weiratheria*

16. Antennae with the 8th antennomere small and subsquared. Pronotum as wide as the elytra, with sides very narrowed at the base..... ..... *Proleonhardella* (*Pholeuonillus*)
- Antennae with the 8th antennomere generally more than one and a half times longer than wide, if shorter ovoid. Pronotum narrower than the elytra, some cases as wide as the elytra, and not or slightly narrowed at the base 17

17. Small or very small size, between 1.3–2.5 mm, exceptionally 3.5 mm. Short and lying pubescence. Pronotum somewhat narrower than the elytra .... *Proleonhardella* (*Proleonhardella*)
- Larger size, between 3.5–5.5 mm. Pubescence long and raised, with hairs longer and more erect in lateral and apical areas of elytra. Pronotum as wide as the elytra 18

18. Body shape elliptical, more elongated. Mesoventral keel high and laminar, anterior border not notched at the base and subrectilinear; narrow ventral border. Endophallus is unknown..... *Pholeuodromus*
- Body shape ovoid, wider. Mesoventral keel high and robust, subquadrangular; anterior border deeply notched at base, straight or convex; ventral border quite wide and transverse collar very developed (Fig. 126.7). Endophallus with a pair of short dentiform phanerae in the centre of the basal region (Fig. 131.8) .....*Blattochaeta*

Genus ***Albanella*** G. Müller, 1914
Speonesiotes (*Albanella*) G. Müller, 1914: 1006.
Albanella Müller, 1914: Perreau, 2019: 377.

Type species. *Speonesiotes* (*Albanella*) *Lonae* G. Müller, 1914 by original designation (habitus in Fig. 122.1).
Diagnosis. (G. Müller 1914): Small size between 2.0–2.8 mm, with the same facies and general characteristics as *Speonesiotes* s. str. General body shape more elongated and narrowed (Fig. 122.1). Depigmented.

Head: Wide with fine occipital carina; anophthalmous.

Antennae: Thin and long, clearly exceed the base of pronotum, with antennomeres unlinked and the 8th somewhat longer than wide.

Elytra: Little elongated, with apex sexually dimorphic, widely arcuated in males, being in females narrower and sharper.

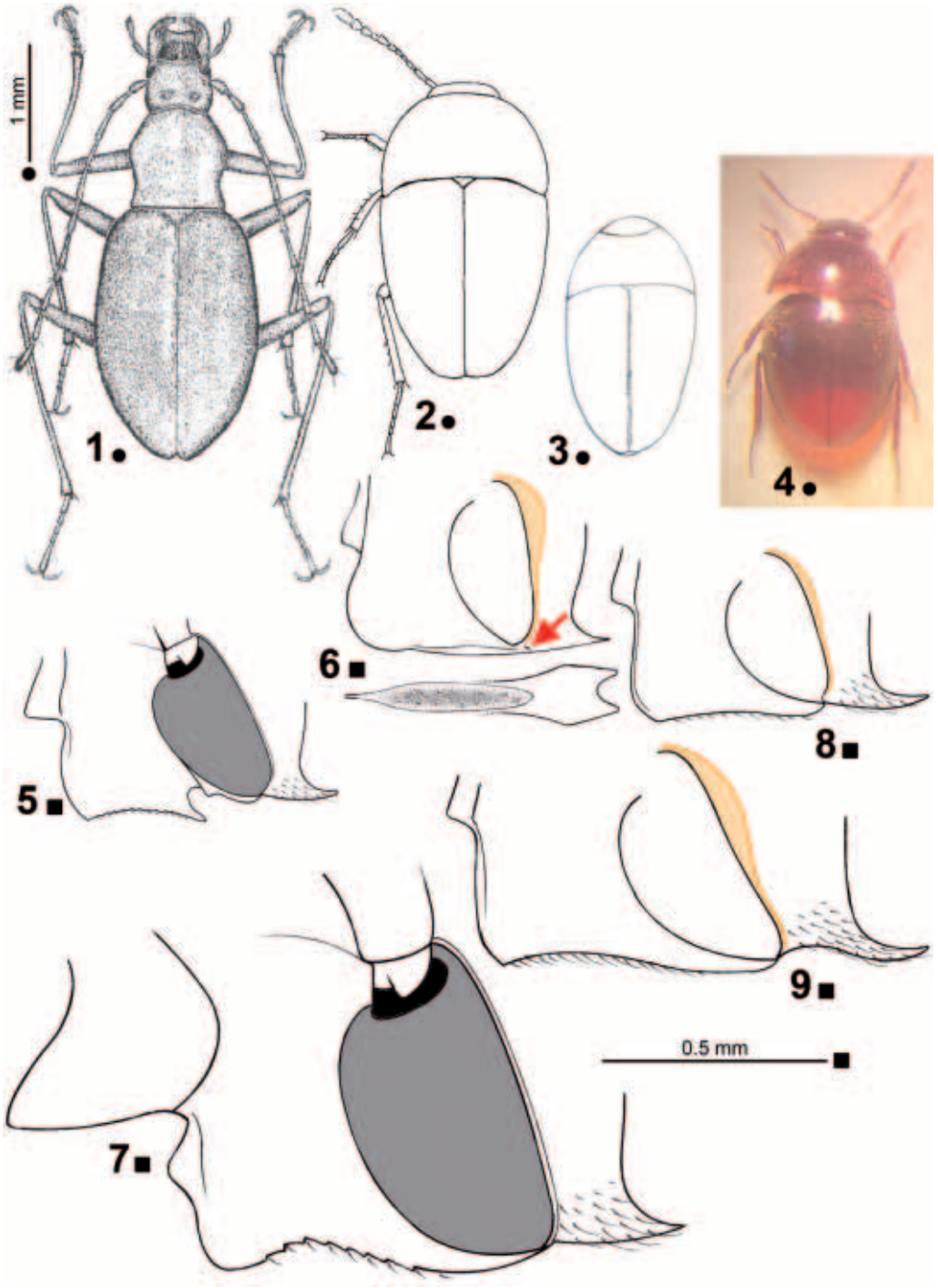
Legs: Male's protarsi tetrameres well dilated, but narrower than the top of protibiae. Very short lateral row of spines of protibia, only extending on half the length of the protibia; without an external apical tibial spur.

Mesoventral keel: Hight, with ventral edge convex and wide. Posterior apophysis does not extend to the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated and narrowed, at least six times longer than it is wide. In lateral view (Fig. 130.1), not very thick, it describes a smooth regular arc; in dorsal view (Fig. 131.4), narrow and with sub-rectangular sides that narrow in the apical part and form a triangular structure. Basal blade short and as wide and long as the ventral blade of the tegmen, with a marked tubercle over the middle area of the posterior edge.

Endophallus (Fig. 131.4): Apparently unarmed.



FIGURES 126.1–126.9: *Anthroherpon* series, *Pholeuonopsis* group. Habitus of: (**1**) *Tartariella durmitorensis durmitorensis* (modified from Nonveiller & Pavićević 1999), (**2**) *Weiratheria bocki* (modified from Zariquiey 1928), (**3**) *Pseudobathyscidius serbicus* (modified from Karaman 1964), (**4**) *Henrotiella eubeensis*. Pterothorax in lateral view of: (**5**) *Anillocharis stenopterus*, (**6**) *Anisoscapha klimeschi misella* (and ventral view), (**7**) *Blattochaeta matchai*, (**8**) *Leonhardella* (*Leonhardella*) *angulicollis*, (**9**) *L.* (*Leonhardellina*) *antennaria* ssp. Red arrow pointing to the lateral mesoventrite-metaventrite suture.

Parameres (Figs 130.1, 133.1): Long and slender, as long as or slightly shorter than the middle lobe. In lateral view, sharp, sinuous final part; in dorsal view, elongated club very poorly differentiated and three rather long setae, two apical and the third subapical.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. With the same facies and general characteristics as *Speonesiotes* s. str. By Jeannel (1924a), V.B. Guéorguiev (1976) and Perreau (2019), the following characters of *Albanella* differs from the genus *Speonesiotes*: General body shape more elongated and narrowed; antennae thin and long, clearly exceed the base of pronotum, with antennomeres unlinked and the 8th somewhat longer than wide; elytra little elongated, with apex sexually dimorphic, widely arcuated in males, being in females narrower and sharper; male's protarsi tetrameres well dilated, but narrower than the top of protibiae; very short lateral row of spines of protibia, only extending on half the length of the protibia; without an external apical tibial spur; the main character of differentiation is in the median lobe of aedeagus, which is much more elongated and narrowed, at least six times longer than it is wide.

The above-mentioned characters justify, following Perreau (2019), raising the subgenus *Albanella* to genus rank. This status has been implicitely foreboded by Zariquiey (1928) who described *Albanella reissi*, without any comments while until now; all other authors have used *Albanella* as a subgenus of *Speonesiotes* (Perreau 2019).

Perreau (2019) provides a cladistic analysis on a morphological basis of Bathysciotina (*sensu* V.B. Guéorguiev 1976) and a cladogram that largely does not correspond to our tree obtained on a molecular basis (Fig. 1H). Despite this, in the cladogram proposed by Perreau (2019), *Albanella* appears taxonomically close (albeit with a largely unresolved clade at its base) to *Speonesiotes* and its subgenera. Only a complete molecular study of the complex of genera and subgenera related to *Speonesiotes* will be able to settle the question in the future.

The species of this genus do not seem to be well known and many morphological structures have never been figured.

Distribution. Known from two caves in northern Albania near the border of Montenegro and several caves in southwestern Montenegro.

Species

Albanella lonae (G. Müller, 1914)
Albanella lonae lonae G. Müller, 1914
Speonesiotes (*Albanella*) *Lonae* G. Müller, 1914: 1006.
Speonesiotes (*Albanella*) *Lonai* J. Müller, 1914: Jeannel, 1924a: 290.
Speonesiotes (*Albanella*) *lonae lonae* Müller: Perreau, 2000: 194.
Albanella lonae lonae (Müller, 1914): Perreau, 2019: 377.

Albanella lonae zoufali (Reitter, 1918)
Bathyscia (Speonesiotes) Zoufali Reitter, 1918: 153.
Speonesiotes (*Albanella*) *Lonai* J. Müller, 1922: Jeannel, 1924a: 291.
Speonesiotes (*Albanella*) *Lonai* sbsp. *Zoufali* Reitt.: G. Müller, 1937: 107.
Speonesiotes (*Albanella*) *lonae zoufali* (Reitter): Perreau, 2000: 194.
Albanella lonai zoufali (Reitter, 1918): Perreau, 2019: 377.

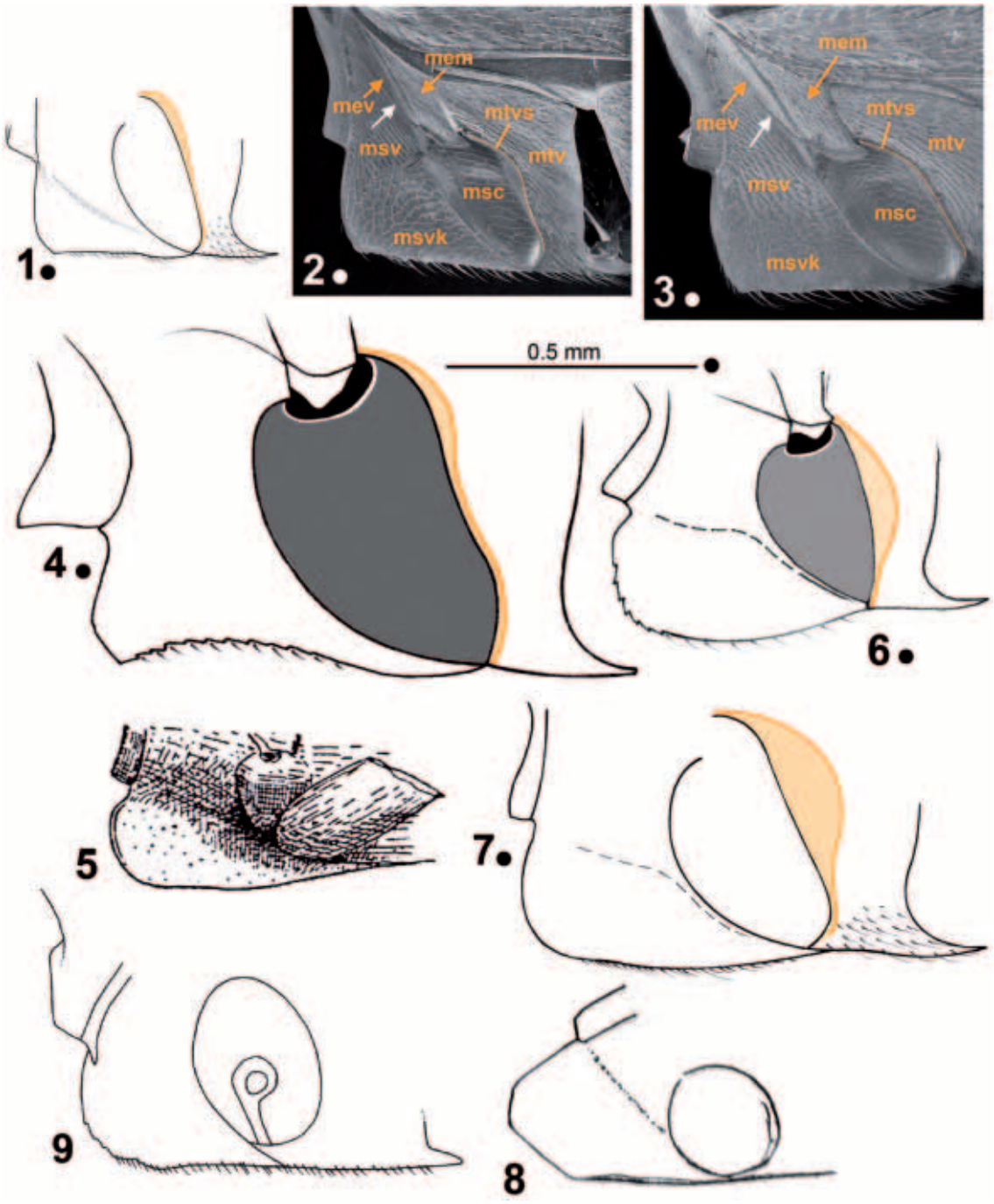
Albanella reissi (Zariquiey, 1928)
Albanella Reissi Zariquiey, 1928 [1927]: 158.
Speonesiotes (Albanella) Reissi Zariquiey: Jeannel, 1941: 125.
Speonesiotes Reissi Zariquiey: Pretner, 1974: 10.
Speonesiotes (*Albanella*) *reissi* (Zariquiey): Perreau, 2000: 194.
Albanella reissi Zariquiey, 1928: Perreau, 2019: 377.

Albanella scutariensis (G. Müller, 1934)
Speonesiotes (*Albanella*) *scutariensis* G. Müller, 1934: 179.
Albanella scutariensis (Müller, 1934): Perreau, 2019: 377.

Genus ***Anillocharis*** Reitter, 1903
Anillocharis Reitter, 1903c: 231.

Type species. *Anillocharis Ottonis* Reitter, 1903 by original designation (for the habitus see that of the similar species *Anillocharis stenopterus* in Fig. 122.2).

Diagnosis. Small size, between 2.5–3.0 mm. Facies pholeuonoid or subpholeuonoid; body elliptical, very elongated and little convex; widened towards the middle and narrowed towards two ends, posterior more narrowed (Fig. 122.2). Colour reddish yellowish.



FIGURES 127.1–127.9: *Anthroherpon* series, *Pholeuonopsis* group. Pterothorax in lateral view of: (**1**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**2**) *P.* (*P.*) *tarensis*, (**3**) *P.* (*P.*) *serboocidentalis*, (**4**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**5**) *Speonesiotes* (*Crivosiella*) *brachycerus* (modified from Jeannel 1941), (**6**) *S.* (*Kulzeria*) *muelleri*, (**7**) *S.* (*Speonesiotes*) *narentinus latitarsis*, (**8**) *Pseudobathyscidius serbicus* (modified from Karaman 1964), (**9**) *Henrotiella eubeensis* (modified from B.V. Guéorguiev 2007). Figs **2**, **3** modified from S. Ćurčić *et al*. 2021. Abbreviations: **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msv**, mesoventrite; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral sutures. White arrow pointing the mesoepimere-mesoepiventrite suture.

Pubescence long and abundant, lying and accompanied on elytra by longer and raised setae; microsculpture more or less marked throughout body. Depigmented.

Head: Rather small, non-retractable, with occipital carina; largely punctate , with points smaller than in pronotum and elytra, being in these stronger; anophthalmous.

Antennae: Moderately long and robust, reaching or exceeding half length of body. Antennomeres, 2^{d} short and oval, 3rd to 7th clearly longer than wide and pubescent. Club rather thick, with antennomeres dilated at top; second a little more than a time and half longer than first one; eighth cylindrical and much longer than wide or oval barely longer than wide; eleventh ovoid, longer than tenth.

Pronotum: Transverse, 1.2–1.3 times wider than long, somewhat bell-shaped, with middle and basal areas of equal width, this one somewhat narrower than, or as wide as, elytral base. Anterior lateral margins rounded and weakly sinuous in basal third. Basal angles almost straight with sharp vertices, somewhat protruding outwards.

Elytra: Very elongated, 1.8–1.9 times longer than wide, little convex, regularly arcuated to the apex, this rounded. Maximum width at anterior third, which is wider than pronotum; shoulders well marked. Punctation small and dense, without transverse striation and without parasutural stria.

Legs: Long and quite robust; male's protarsi tetrameres, with the first tarsomere dilated, being narrower than or as wide as, apex of protibia; thin in females. Protibiae straight, without comb at apical and external edges; mesotibiae somewhat arcuated and finely thorny; metatibiae straight.

Mesoventral keel (Fig. 126.5): Well developed, high and triangular, with rounded, sharp or hooked vertex and obtuse angle. Anterior border convex, posterior one rectilinear or concave, sometimes slightly denticulated; subsequent prolongation does not reach metaventrite and the tip is somewhat distant from the coxal cavity.

Suture of the metaventrite (Fig. 126.5): Throughout its entire course, it is very close to the coxal cavity.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Long, stout and well sclerotized. In lateral view (Fig. 130.2), both the ventral concavity and the dorsal convexity are very marked, the apical area is sinuous, sharp and curved towards the ventral face. In dorsal view (Fig. 131.5), subparallel sides, somewhat arcuated, narrow sharply in apical part to form a poorly developed, depressed, triangular beak, with a slightly sharp tip. Basal blade broad and subtriangular, with a small tongue in posterior middle area.

Endophallus (Fig. 131.5; Jeannel 1924a: Fig. 274): With three well differentiated areas. Short basal, at the bottom of sac a robust stylet, quite long and widened at base. Short middle area, with two symmetrical groups of well-sclerotized spines, more developed basal than apical. Long apical area, with two narrow and short bands of reinforcement since they do not exceed the middle of this area.

Parameres (Fig. 133.2): Long and slender, slightly longer than median lobe with the apical area curved inwards; elongated club with three setae, two inserted on the inner side and the third apical, with the pores of insertion closer between the two apical ones.

Spermathecal complex: Spermatheca (Fig. 134.1) small, with globose, hyaline apical lobe, undifferentiated union duct and a long, well sclerotized basal or proximal lobe; spermatic duct and spermathecal gland lead into an unwidened area at the end of the basal lobe.

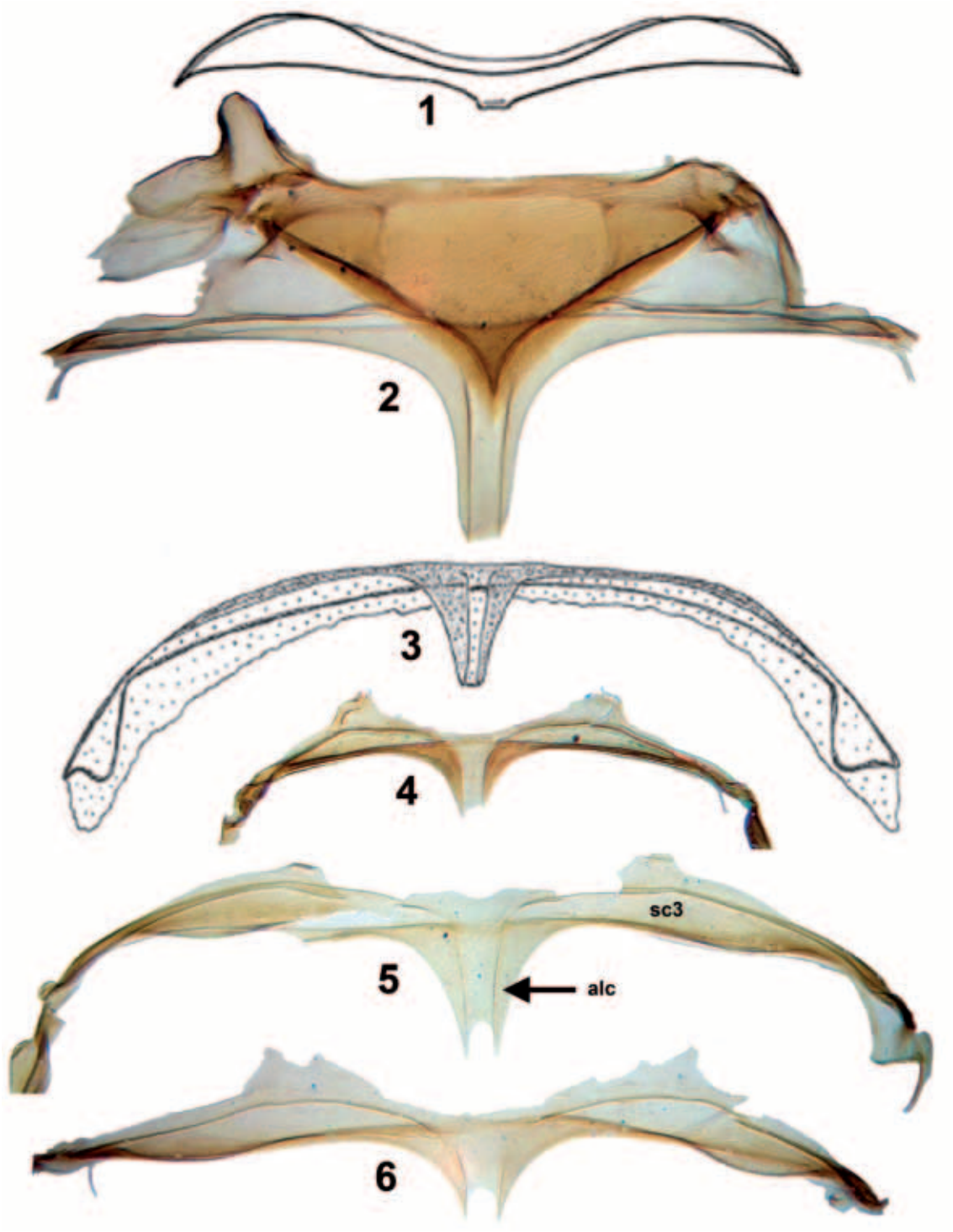
Female uroventrite VIII (Fig. 135.1): Triangular in appearance, with straight anterior margins, short and narrow spiculum with sharp tip and a «pore field» at the base.

Discussion. Without molecular studies that allow the position of *Anillocharis* in phylogenetic tree, it can be observed that it shows several morphological characters that bring it closer to several genera of *Leonhardella* phyletic lineage (Jeannel 1911, 1924a). Especially to *Pholeuonopsis* by general shape of the body, antennae and pubescence, but not by protarsi that are thin. Aedeagus, especially, are very similar, with triangular apical structure in median lobe and tongue in basal blade, and a well-developed stylus in bottom of sac.

Distribution. Four species and two subspecies from caves of Dinaric karst region, between central and southern Bosnia-Herzegovina and northern Montenegro.

Species

Anillocharis hawelkai G. Müller, 1937
Anillocharis Hawelkai G. Müller, 1937: 107.
Anillocharis hawelkai Müller: Perreau, 2000: 181.



FIGURES 128.1–128.6: *Anthroherpon* series, *Pholeuonopsis* group. Metatergal apparatus of: (**1**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**2**) *Leonhardella (Leonhardella) angulicollis*, (**3**) *Pholeuonopsis* (*Pholeuonopsis*) *herculeana* (modified from Čeplík 2021), (**4**) *Proleonhardella* (*Proleonhardella*) *epimikes* **sp. nov**., (**5**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**6**) *S.* (*Speonesiotes*) *narentinus latitarsis*. Abbreviations: **alc**, alacrista; **sc3**, metascutum.

Anillocharis ottonis Reitter, 1903
Anillocharis Ottonis Reitter, 1903c: 231.
Anillocharis ottonis Reitter: Perreau, 2000: 181.

Anillocharis stenopterus Formánek, 1906
Anillocharis stenopterus matzenaueri Jeannel, 1924
Anillocharis stenopterus subsp. *Matzenaueri* Jeannel, 1924a: 254.
Anillocharis stenopterus matznaueri Jeannel: Perreau, 2000: 181.

Anillocharis stenopterus stenopterus Formánek, 1906
Anillocharis stenoptera Formánek, 1906: 151.
Anillocharis Platonia Reitter, 1907b: 344.
Anillocharis stenopterus Formánek: Jeannel, 1910a: 40.
Anillocharis stenopterus Subsp. *stenopterus* Formánek: Jeannel, 1924a: 254.
Anillocharis Ottonis subsp. *plutonius* Reitter: Jeannel, 1910a: 40.

Anillocharis tenuilimbatus Jeannel, 1934
Anillocharis tenuilimbatus Jeannel, 1934d: 158.

Genus ***Anisoscapha*** G. Müller, 1917
Proleonhardella (*Anisoscapha*) G. Müller, 1917: 616.
Anisoscapha Müller, 1917: Jeannel, 1924a: 245.

Type species. *Proleonhardella* (*Anisoscapha*) *Winkleri* G. Müller, 1917 by original designation (for the habitus see that of the similar species *Anisoscapha klimeschi misella* in Fig. 122.3).

Diagnosis. Size wery small, between 1.8–2.0 mm. Facies bathyscioid, body elliptical and elongated, very narrowed posteriorly (Fig. 122.3). Colour reddish yellow, not very bright. Pubescence simple, short, dense and recumbent. Depigmented.

Head: Small, with occipital carina blurred; anophthalmous; densely dotted, with points smaller than in pronotum and elytra.

Antennae: Moderately long and robust, as long, or almost as long, as half the length of body, club thick; first antennomere shorter than the second one; eighth very small and little transverse.

Pronotum: Very transverse (1.8–1.9 times wider than long), almost semicircular, with the wider area slightly ahead of the base, as wide as, or somewhat narrower than, the elytra; lateral margins regularly arcuated.

Elytra: Elongated, 1.5–1.6 times longer than wide, very narrowed posteriorly and generally not very convex. Apexes sharp, separate rounded in females. Maximum width in the anterior third. Disc fine and dense dotting, with the points aligned transversely in a more or less defined striae in the anterior and middle parts. Points without order and more scattered, and somewhat larger, in the apical part; unrounded shoulders. Parasutural stria absent.

Legs: Short and not very robust; protarsi tetrameres and very weak dilated in males, thin in females. Protibiae straight, little thorny, without comb on the outer and apical margins and with external spur; mesotibiae somewhat curved; metatibiae straight, both relatively narrow and bristling with some fine spines.

Mesoventral keel (Fig. 126.6): High, with the anterior edge subrectilinear and the ventral edge wide, triangular-shaped and with a marked groove; vertex in wide arc and very obtuse angle. Posterior apophysis does not extend to the metaventrite. Meso- and mesoventrite are welded; the suture is visible laterally.

Suture of the metaventrite (Fig. 126.6): It delimits a narrow arched area in the upper half and is very close to the coxal cavity in the lower half.

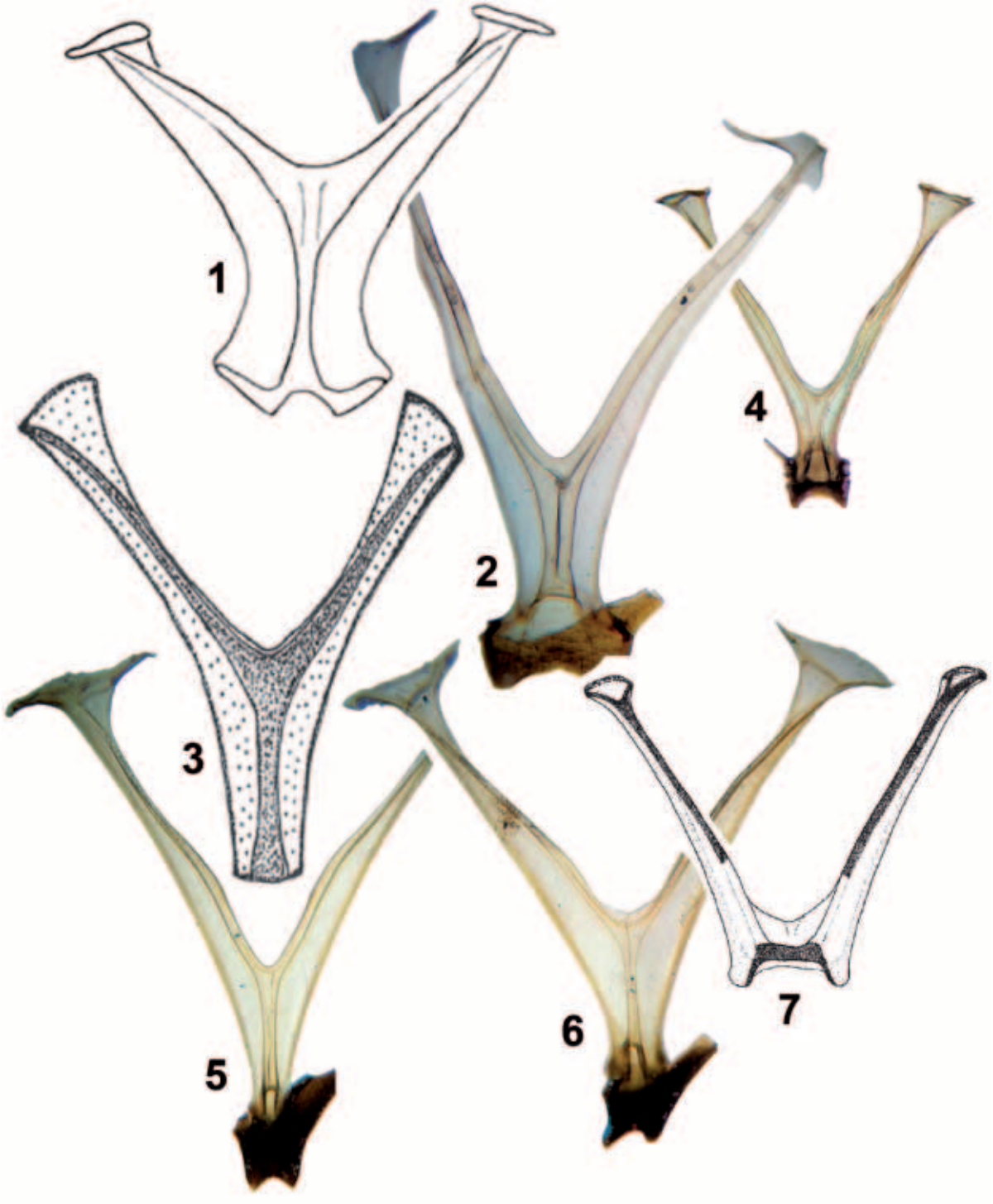
Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated, between five to eight times longer than wide, well sclerotized. In lateral view (Fig. 130.3), ventral face rectilinear, dorsal face in a smooth, regular arc, both faces tapering apically and forming a blunt beak. In dorsal view (Fig. 131.6), the basal two-thirds with arcuated sides (it is the widest area); between this area and the apical third, narrower, with a concavity. Apical part, short, shows a small triangular beak with a rounded tip and a small depression in the middle of base. Basal blade broad, oval, with no posterior middle tongue, or only a very small prominence.

Endophallus (Fig. 131.6): Bottom of sac with a long and quite robust stylus. Middle area with short, well-sclerotized spines, in small number and above or both sides of the stylus; apical area with two narrow, sinuous and short, reinforcement bands.

Parameres (Fig. 133.3): Thin, somewhat shorter than the median lobe; apex with oblong club, little dilated and with three equal setae, two at the apex with the insertion pores nearby and the third further away, inserts in the inner edge and oriented towards the interior.

Spermathecal complex (Fig. 134.2): Spermatheca small, rod-shaped, with the basal lobe well sclerotized, much larger and wider than the joining duct and the apical lobe, the latter rounded and both membranous. Spermatic duct is very thin and joins the spermatheca without a dilated part.



FIGURES 129.1–129.7: *Anthroherpon* series, *Pholeuonopsis* group. Metendosternite of: (**1**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**2**) *Leonhardella (Leonhardella) angulicollis*, (**3**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii* (modified from Čeplík 2021), (**4**) *Proleonhardella* (*Proleonhardella*) *epimikes* **sp. nov**., (**5**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**6**) *S.* (*Speonesiotes*) *narentinus latitarsis*, (**7**) *Henrotiella eubeensis* (modified from B.V. Guéorguiev 2007).

Female uroventrite VIII (Fig. 135.2): Apical margin in wide arc; basal margins straight, spiculum short, wide, with rounded apex.

Discussion. No molecular analysis have been carried out. Jeannel (1911, 1924a) included the genus *Anisoscapha* in the phyletic series of *Leonhardella*, in which he has also included *Pholeuonopsis* as a group. *Anisoscapha* differs from the more morphologically similar genera *Anillocharis*, *Blattochaeta* and *Proleonhardella* in the shape of body, especially in the pronotum, elytra, mesoventral keel and protarsomeres of males and, in addition, to the shape and different structures of aedeagus.

Distribution. At present, two species and two subspecies belong to this genus, that have colonized a small karst area of central Dalmatia, between the border areas of western central Bosnia-Herzegovina (Mount Troglav) and southern Croatia (Svilaja planina and Trilj). Representatives mostly endogean (or from MSS), collected under much buried stones, and some captures in cavities.

Species

Anisoscapha klimeschi (G. Müller, 1917)
Anisoscapha klimeschi klimeschi (G. Müller, 1917)
Proleonhardella (Anisoscapha) Klimeschi G. Müller, 1917: 623.
Anisoscapha Klimeschi J. Müller, 1917: Jeannel, 1924a: 245.
Anisoscapha klimeschi klimeschi (Müller): Perreau, 2000: 182.

Anisoscapha klimeschi misella G. Müller, 1934
Anisoscapha Klimeschi misella G. Müller, 1934: 180.
Anisoscapha klimeschi misella Müller: Perreau, 2000: 182.

Anisoscapha winkleri (G. Müller, 1917)
Proleonhardella (Anisoscapha) Winkleri G. Müller, 1917: 616.
Anisoscapha Winkleri J. Müller, 1917: Jeannel, 1924a: 247.
Anisoscapha winkleri (Müller): Perreau, 2000: 182.

Genus ***Augustia*** Zariquiey, 1928
Augustia Zariquiey, 1928 [1927]: 152.

Type species. *Augustia Weiratheri* Zariquiey, 1928 by monotypy (habitus in Fig. 122.4).

Diagnosis. (Zariquiey 1928): Size 3.0 mm, bathyscioid facies (Fig. 122.4). Body shape ovoid, convex and attenuated subsequently. Colour reddish-brown, depigmented. Punctation very fine and quite dense. Pubescence yellowish, short and lying.

Head: With little marked occipital carina, without eyes.

Antennae: Thin, reaching half of body; all antennomeres longer than wide; the 1st being shorter than the 2nd and this one longest of all; the 8th cylindrical, almost two and a half times longer than width; the 11th oval, longer than the 10th.

Pronotum: Bell-shaped, very transverse, with maximum width at base, and this as wide as anterior margin of elytra, but narrower than widest area of elytra. Sides little and regularly arcuated; angles acute, with vertices sharp and directed backwards.

Elytra: Ovoid, little convex and little elongated, about 1.40 times longer than wide. Maximum width in anterior quarter, and significantly attenuated towards apexes, these rounded and divergent. Fine and quite dense punctation, not aligned in transverse striolae. Parasutural stria absent.

Legs: Quite long and robust; male protarsi tetrameres, slightly dilated. Protibiae without comb at the apical and outer edges, with well-developed external spurs; mesotibiae slightly spiny, arcuated (not metatibiae), both without apical basket of thorns, but with external spurs.

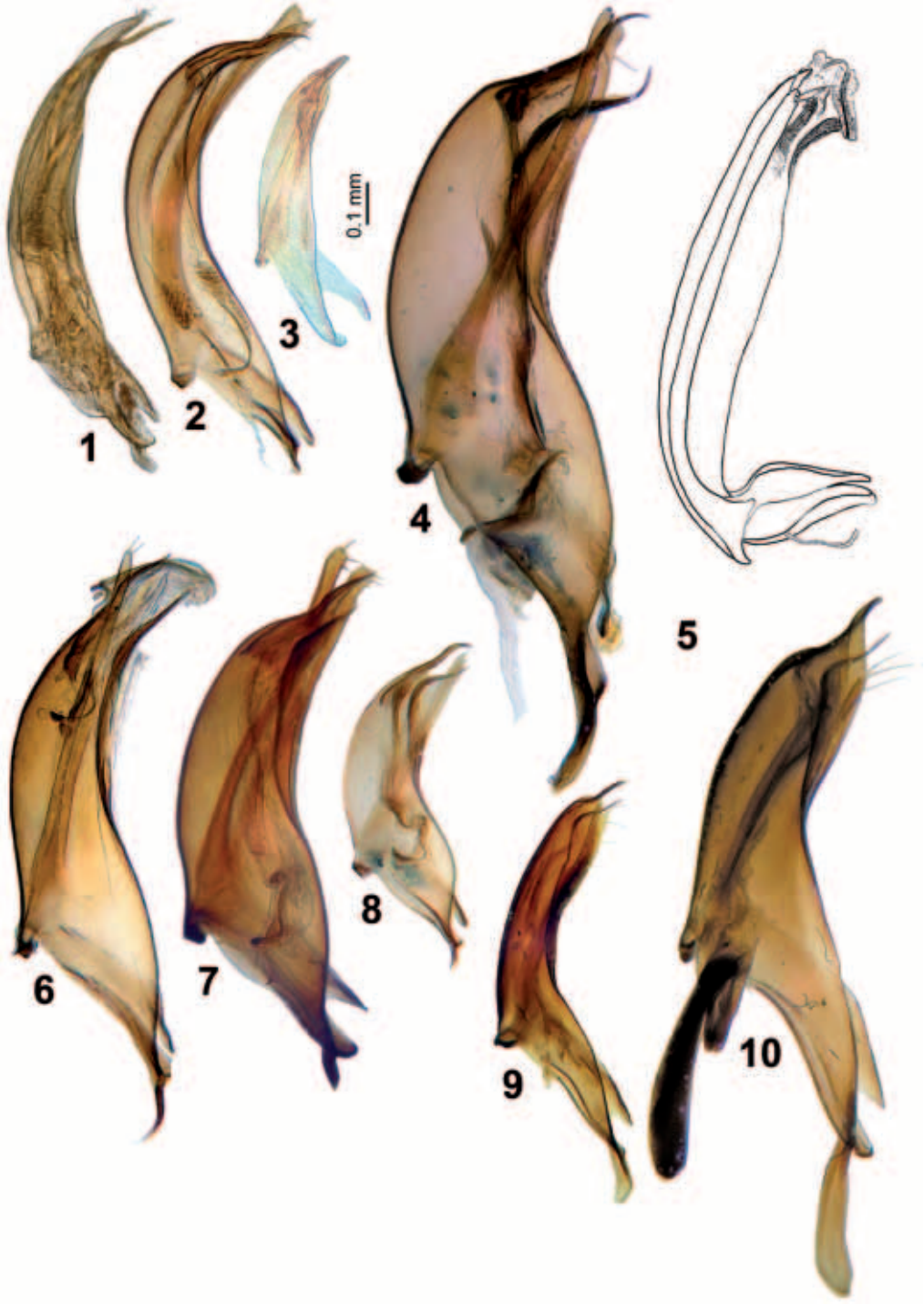
Mesoventral keel: Very high, set immediately behind the articular collar, the anterior edge thin and rounded forming a quarter circle, the ventral edge thickened in the anterior half slightly sinuate; the angle formed by the edges obtuse and not toothed. Posterior prolongation does not reach the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and robust. In lateral view unknown. In dorsal view (Fig. 131.7), quite wide, with sides almost parallel to near apex where it narrows sharply and forms a depressed beak, with arched sides and rounded tip. Basal blade broad and rhomboid, with a developed tongue over middle area of posterior edge.

Endophallus (Fig. 131.7): Bottom of sac of basal part with a short and curved sclerotized centerpiece, at its base a lanceolate structure is fixed. On each side of this piece, a sclerotized and slightly bent bar, wide at the base and sharp at the apex.

Parameres (Fig. 133.4): Somewhat longer than the median lobe and not arcuated; thicker in basal area, then thickness is uniform until apical part, in which no



FIGURES 130.1–130.10: *Anthroherpon* series, *Pholeuonopsis* group. Aedeagus in lateral view of: (**1**) *Albanella scutariensis* (modified from Perreau 2019), (**2**) *Anillocharis stenopterus*, (**3**) *Anisoscapha klimeschi misella*, (**4**) *Blattochaeta matchai*, (**5**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**6**) *Leonhardella* (*Leonhardellina*) *antennaria* ssp., (**7**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**8**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**9**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**10**) *S.* (*Speonesiotes*) *gobanzi.*

club is differentiated. Three setae of similar length and oriented inwards are inserted, one apical, another lower very close and a third one clearly distant from other two. Ventral blade of tegmen shorter and as wide as basal blade of median lobe.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Zariquiey (1928) points out that, by to its morphological characters, *Augustia* belongs to *Leonhardella* series (*sensu* Jeannel 1924a), Division II of «Théléomorphes». It must be placed near *Proleonhardella* by short and lying pubescence; by punctate elytra with rounded apexes, and by short and thick aedeagus, with basal lamina with well-developed tongue. Later, V.B. Guéorguiev (1976) includes him in subtribe Bathysciina, a criterion adopted by Perreau (2000), which also includes him in phyletic series of «*Leonhardella*». Currently, its position in phylogenetic tree is unknown, as molecular studies have not been carried out.

It is a rare species which, unless in error, seems to be known only from the holotype. Several morphological structures are unknown.

Distribution. The only known species has been caught in cavities of the Čvrsnica mountain in Bosnia-Herzegovina.

Species

Augustia weiratheri Zariquiey, 1928
Augustia Weiratheri Zariquiey, 1928 [1927]: 153.
Augustia weiratheri Zariquiey: Pretner, 1974: 9.

Genus ***Blattochaeta*** Reitter, 1910
Bathyscia (*Blattochaeta*) Reitter, 1910: 164.
Blattochaeta Reitter: Jeannel, 1930e: 124.

Type species. *Bathyscia* (*Blattochaeta*) *Marianii* Reitter, 1910 by original designation (for the habitus see that of the similar species *Blattochaeta matchai* in Fig. 122.5).

Diagnosis. Large size, between 4.2–5.5 mm. Facies bathyscioid with oval body shape, wide, short and without narrowing in apical area (Fig. 122.5). Integument bright, dark reddish; punctation well differentiated, fine and spaced in head and pronotum, being deep with nearby points at base of elytra, while they are more spaced and superficial in lateral and apical parts of elytra. Spaces between the points smooth. Pubescence yellowish, more or less abundant depending on area of body, the hairs being longer and more erect in lateral and apical areas of elytra. Depigmented.

Head: Retractable, somewhat longer than wide; occipital carina fine, generally blurred; anophthalmous.

Antennae: Robust, more or less long depending on species, reaching in some cases the middle part of elytra. First antenomere more globose and clearly shorter than the second one; antennomeres of club quite dilated, flattened and longer than wide, although the 8th in some species is somewhat wider than long, and the 11th being the longest.

Pronotum: Short, transverse and semicircular with sides regularly arcuated to base, although in some species somewhat sinuated in basal part; maximum width at base or very close to base, this as wide as the basal area of elytra.

Elytra: Oval, short, between 1.3–1.5 times longer than wide, with maximum width towards half, transverse striolation and parasutural stria lacking, apical areas rounded.

Legs: Quite long and robust; protibiae without comb on apical and external edges; protarsi tetrameres and thin in males. Tibiae with external spurs; tibiae and femora with thin and numerous bristling spines, without apical basket.

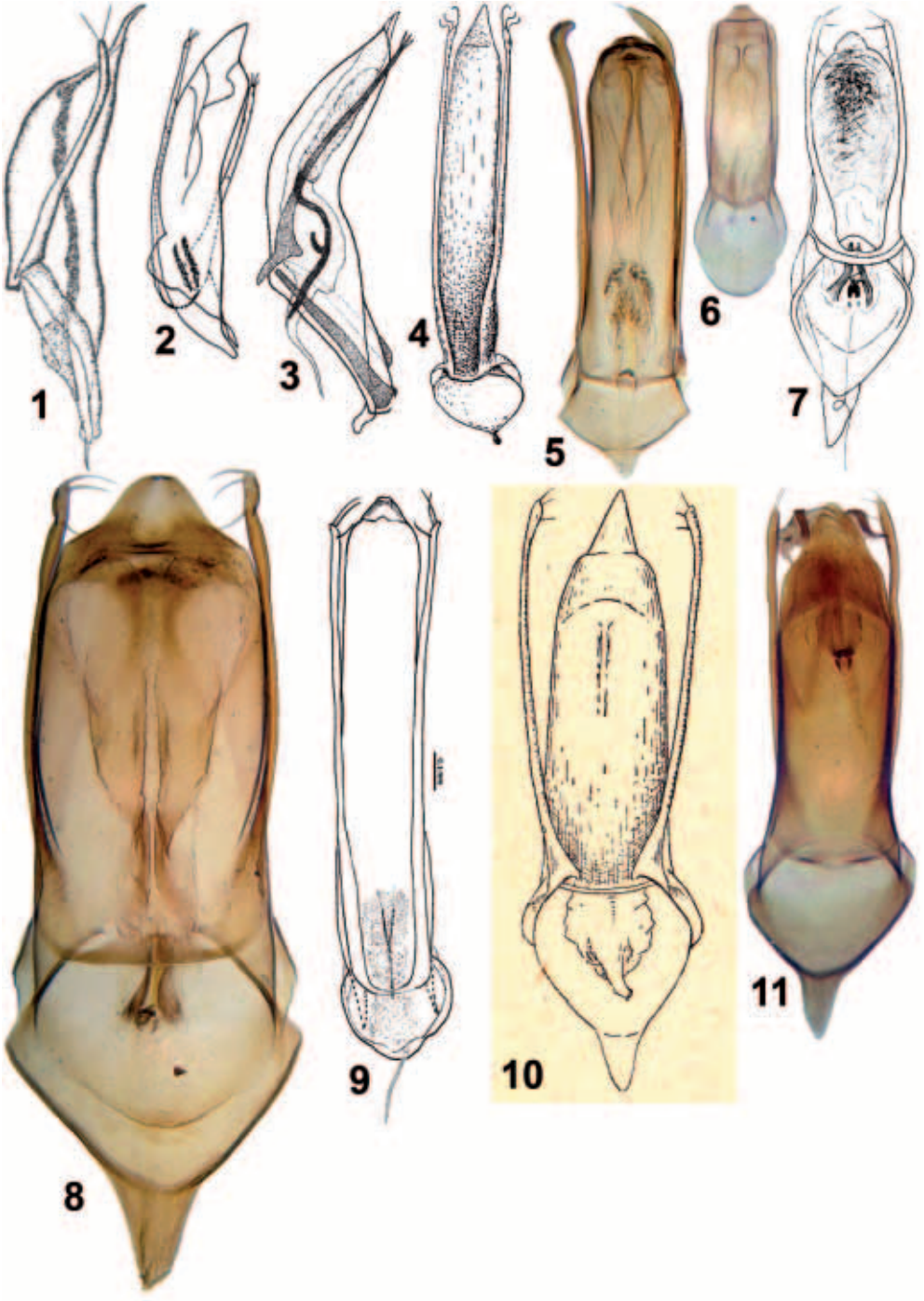
Mesoventral keel (Fig. 126.7): High and robust, subquadrangular; anterior border deeply low-cut at base, straight or convex with blunt or narrowed vertex depending on species. Ventral border quite wide, toothed and with setae, concave or sinuated, with posterior prolongation variable but without reaching the metaventrite. The transverse collar very developed.

Suture of the metaventrite (Fig. 126.7): Throughout its entire length, it is very close to the coxal cavity.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Short, thick, wide and well sclerotized. In lateral view (Fig. 130.4), little arcuated, being the most pronounced arc in dorsal margin; apical area in short beak, curved, narrow and sharp, with apex oriented towards the ventral face. In dorsal view (Fig. 131.8), sides subparallel to apical part that forms a triangular structure with concave or subrectilinear sides, and apex in a wide or narrow arc depending on species. Basal blade in elongated rhombus with a well-developed tongue on middle posterior edge.

Endophallus (Fig. 131.8): With a robust arcuated basal stylus that is flanked by two thick sclerotized and subtriangular nodules. Middle area with sclero-



FIGURES 131.1–131.11: *Anthroherpon* series, *Pholeuonopsis* group. Aedeagus in lateral view of: (**1**) *Tartariella durmitorensis durmitorensis* (modified from Nonveiller & Pavićević 1999), (**2**) *Pseudobathyscidius serbicus* (modified from Karaman 1964), (**3**) *Henrotiella eubeensis* (modified from B.V. Guéorguiev 2007). Aedeagus in dorsal view of: (**4**) *Albanella lonae* (modified from Jeannel 1941), (**5**) *Anillocharis stenopterus*, (**6**) *Anisoscapha klimeschi misella*, (**7**) *Augustia weiratheri* (modified from Zariquiey 1928), (**8**) *Blattochaeta matchai*, (**9**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**10**) *Leonhardella (Leonhardella) angulicollis* (modified from Jeannel 1948), (**11**) *L.* (*Leonhardellina*) *antennaria* ssp.

tized structures and small spines or scales; dorsal apical area with two rather sclerotized wavy thickenings.

Parameres (Fig. 133.5): Thin, as long as or slightly shorter than median lobe. Apical area sinuated with poorly differentiated club, bearing three setae of similar length and thickness, one apical and two lateral or two apical with insertion pores very close and the other lateral and distant. Ventral lamina of tegmen shorter than and as wide as the basal lamina of median lobe.

Spermathecal complex: Spermatheca (Fig. 134.3) sacciform, without differentiated lobes; middle area wider and posterior area narrower, more sclerotized and faintly striated. With spermathecal gland and spermatic duct very thin and short.

Female uroventrite VIII (Fig. 135.3): Apical margin in wide arc; basal margins in smooth arcs with some distant pores at the edge; spiculum very short, broad and truncated apex.

Discussion. Molecular data are not available. By a series of common characters, *Blattochaeta* has been included in phyletic series of «*Leonhardella*» (*sensu* Jeannel 1924a; Perreau 2000) such as: antennae with first antenomere shorter than second one, tetrameres protarsi in male and no protibial combs, median lobe of aedeagus with apical area not sharp and basal lamina with a tongue on posterior middle edge, endophallus with a basal structure similar to a stylus, and parameres armed with three setae. Therefore, *Blattochaeta* has affinities with the genera of that phyletic lineage, such as *Anillocharis*, *Augustia* or *Tartariella* among others.

Distribution. Mostly species of this genus colonize caves in karst areas of central and north-western Montenegro. Only two sub-species of *Blattochaeta marianii* are located outside Montenegro, one in a cave nestled in mountain of Sniježnica, southern Croatia, and other in south-west of Bosnia-Herzegovina near Grab.

Species

Blattochaeta brankojalzici Čeplík, Lakota & Čeplík, 2021
Blattochaeta brankojalzici Čeplík, Lakota & Čeplík, 2021c: 87

Blattochaeta hawelkai Knirsch, 1929
Blattochaeta Hawelkai Knirsch, 1929: 95.
Blattochaeta hawelkai Knirsch: Pretner, 1974: 10.

Blattochaeta marianii (Reitter, 1910)
Blattochaeta marianii brevipennis Jeannel, 1930
Blattochaeta Marianii ssp.*brevipennis* Jeannel, 1930e: 127.
Blattochaeta Marianii brevipennis Jeannel: Pretner, 1974: 10.
Blattochaeta marianii brevipennis Jeannel: Perreau, 2000: 183.

Blattochaeta marianii kusijanovici Polak & Jalžić, 2009
Blattochaeta marianii kusijanovici Polak & Jalžić, 2009: 17.

Blattochaeta marianii marianii (Reitter, 1910)
Bathyscia (Blattochaeta) Marianii Reitter, 1910a: 164.
Pholeuonopsis Marianii Reitter: Jeannel, 1911a: 463.
Blattochaeta Marianii Reitt.: Jeannel, 1914b: 42.
Blattochaeta marianii marianii (Reitter): Perreau, 2000: 183.

Blattochaeta marianii paganettii Jeannel, 1924
Blattochaeta Paganettii Jeannel, 1924a: 263.
Blattochaeta Marianii ssp. *Paganettii* Jeannel, 1930e: 126.
Blattochaeta marianii paganettii Jeannel: Perreau, 2000: 183.

Blattochaeta matchai Jeannel, 1924
Blattochaeta Matchai Jeannel, 1924a: 263.
Blattochaeta matchai Jeannel: Perreau, 2000: 183.

Blattochaeta montenegrina Jeannel, 1930
Blattochaeta montenegrina Jeannel, 1930e: 125.

Blattochaeta peterhlavaci Čeplík, Lakota & Čeplík, 2021
Blattochaeta peterhlavaci Čeplík, Lakota & Čeplík, 2021c: 93

Blattochaeta remyi Jeannel, 1931
Blattochaeta Remyi Jeannel, 1931b: 258.
Blattochaeta remyi Jeannel: Perreau, 2000: 183.

Genus ***Hygrodromus*** Giachino, Casale & Jalžić, 2021
Hygrodromus Giachino, Casale & Jalžić, 2021: 55.

Type species. *Hygrodromus nikolinae* Giachino, Casale & Jalžić, 2021 by original designation (habitus in Fig. 123.1).

Diagnosis. Medium size, 4.1–5.0 mm, pubescent, with pholeounoid body shape (Fig. 123.1); depigmented.

Head: Elongate, not retractile, without occipital carina; clypeus and labrum with dense and long pubescence. Penultimate labial palpomere long and apically dilated; apical palpomere very short and stout. Labrum transverse, with anterior margin slightly concave and lateral margins curved, bearing, in addition to the strong and long pubescence, a set of ten modified thorns. These strong thorns, flattened and apically truncated, start ventrally and are of different lengths. Eight of them are placed along the anterior border (two long, lateral, and six in the central position). Mandibles widened and flattened in the apical half, but not twisted and not toothed on the inner edge. Maxillae short, stipe with the articles bearing tufts of long setae; lacinia reduced, the outer lobe capped by a sort of triangular membranous and fully striated lobe. Maxillary palpi elongate, with the second palpomere thin, the third short and ovoidal. Labium fully covered by a dense and long pubescence, with anterior margin protruding in a wide and short tooth; front edge equipped, on the inner side of the mouth, with a set of six modified thorns, similar to those of the labrum; these thorns are arranged laterally in two groups of three, two long and one short. Ligula sub-trapezoidal, with anterior border markedly concave and bearing a complete range of robust setae; central area of anterior border bearing two short modified thorns. Anophthalmous.

Antennae: Relatively short, inserted on the medium third of head, similar in both sexes and not reaching the elytron apex, shorter than the body length; first antennomere widened, longer than the second; the 11th antennomere as long as the 10th.

Pronotum: Large and sexually dimorphic: elongate, longer than wide in the male; shorter and wider in the female; subrectangular in shape, with its maximum width just at the middle in the male, slightly bell-shaped with its maximum width just before the base in the female. Lateral sides more regularly rounded in the female; rounded anteriorly, subrectilinear basally in the male. Hind angles obtuse but evident; basal margin wider than the base of elytra. Anterior margin protruding in the middle in the male. Pterothorax not pedunculate.

Elytra: Elongate-ovate, moderately attenuate at apex; peculiarly sexually dimorphic elytra. Apex separately rounded in the male; expanded in two large, digitiform expansions in the female. Microsculpture sparse, not forming transversal rows; disc with thin pubescence; parasutural stria absent.

Legs: Very long and slender, with femora thickened basally. Protibiae widened just at apex, without comb but with an incomplete apical basket of spines and without external spurs; inner spurs simple, very small and thin. Male protarsi four-segmented, with three basal tarsomeres dilated. Meso- and metatibiae with inner, simple apical spur and apical basket of very short apical spines; tarsal claws long, slightly widened.

Mesoventral keel: Absent; mesocoxal cavities contiguous.

Metatergal apparatus (Fig. 128.1): Very reduced, short and narrow wings of the metascutum, without apophysis of the alacrista.

Metendosternite (Fig. 129.1): Stout, not «V»-shaped, with robust furcal arms, somewhat longer than the trunk, and short and stout furcal plate. Arms apophysis well-developed. Short furcal trunk, somewhat wider than long, with the sides clearly narrowed in the middle part.

Male genital segment: Shoe-shaped in lateral view.

Median lobe of aedeagus: Small sized, slender. In lateral view (Fig. 129.5), abruptly arcuate before the base; basal lamina bent, without ventral keel. In dorsal view (Fig. 131.9), elongate, with subparallel sides almost to the apex, which is subtriangular and slightly truncate.

Endophallus (Fig. 131.9): Almost unarmed, with only a short, apical, thorny bundle.

Parameres (Fig. 133.6): Shorter than the median lobe, each furnished with three setae at apex, two apical and another one subapical, placed on the inner side; dorsal view, apical area sharp and outward oriented.

Spermathecal complex (Fig. 134.4): Spermatheca small and membranous, bean-shaped, slightly sclerotized and annulated only in the basal part; short and thin spermatic duct, about twice the length of the spermatheca.

Ovipositor: Fully atrophied, genital segment membranous.

Female uroventrite VIII (Fig. 135.4): Apical margin broadly arcuate, spiculum rather long, parallel-sided and subtruncate tip.

Discussion. The single known species of this genus lives in semi-aquatic habitat (Giachino *et al*. 2021); it have mouth parts strongly modified to be able to filter the organic matter of the water that runs through the walls of the caves (Lohaj *et al*. 2012). Presents a series of common body characters with several genera living in the same environments (*Hadesia*, *Nauticiella* and

Kircheria, all from *Anthroherpon* series) such as: shape of mouth parts, insertion of antennae, second antennomere shorter than the first one, feminine genitalia with styli fully atrophied. Tarsal claws dilated and female uroventrite VIII with spiculum.

In other genera, with hygropetricolous way of life, similar modifications of the mouth parts are instead to be considered here as simple convergence phenomena. We quote for such purpose the genera: *Radziella*, *Tartariella*, *Croatodirus*, *Velebitodromus* and *Cansiliella*.

Recent and unpublished molecular data approach *Hygrodromus* to *Speonesiotes* of our *Pholeuonopsis* group (Polak 2022 *pers. comm*.).

Distribution. Known only from the cave Mladenova jama, located in the Pelješac peninsula, Croatia.

Species

Hygrodromus nikolinae Giachino, Casale & Jalžić, 2021
Hygrodromus nikolinae Giachino, Casale & Jalžić, 2021: 58.

Genus ***Leonhardella*** Reitter, 1903
Leonhardella Reitter, 1903a: 209.

Type species. *Leonhardella angulicollis* Reitter, 1903 by monotypy (habitus in Fig. 123.2).

Diagnosis. Elongated and convex body, size between 3.0–4.5 mm, facies pholeuonoid (Fig. 123.2). Reddish-brown colouration; depigmented.

Head: No-retractable; anophthalmous.

Antennae: Thin, elongated, but not reaching the apex of elytra; first antenomere clearly shorter than the second one; the 8th at least twice as long as width; the 11th, in males, longer than the 10th or the 11th antennomere as long as the 10th in both sexes.

Pronotum: Bell-shaped, as long as wide or transverse, narrower than the maximum width of elytra. Base clearly wider than the anterior area; middle area with protruding sides, rounded, being the sides of the basal third strongly concave with sharp angles, oriented outwards.

Elytra: Ovoid, convex and elongated, about 1.5 times longer than wide; pubescence short and lying down, without long, raised or erect setae; shoulders angular, protruding or rounded. Parasutural stria absent.

Legs: Long, thin and straight; protarsi tetramerous and not dilated in male; anterior tibiae without comb at the apical and external edges; tibiae finely spiny and with well-developed external spurs.

Mesoventral keel (Figs 126.8, 126.9): Tall and stout, with straight front edge, rounded or very slightly indented apex and obtuse angle; slightly concave and silky ventral edge; the posterior prolongation reaches the posterior part of the coxal cavity.

Suture of the metaventrite (Fig. 126.8, 126.9): Proximal to the coxal cavity, although in the apical half it delimits a reduced arched area.

Metatergal apparatus (Fig. 128.2): Quite robust, with metascutum wings rather short and broad, triangular in appearance; apophysis of alacrista well-developed and apices not sharp.

Metendosternite (Fig. 129.2): Stout; furcal arms long, twice as long as trunk; well-developed apophysis extends laterally in a narrow band with tapering apex; furcal plane narrows progressively from base of arm to apical part. Furcal trunk slightly longer than wide with divergent median keel in basal part.

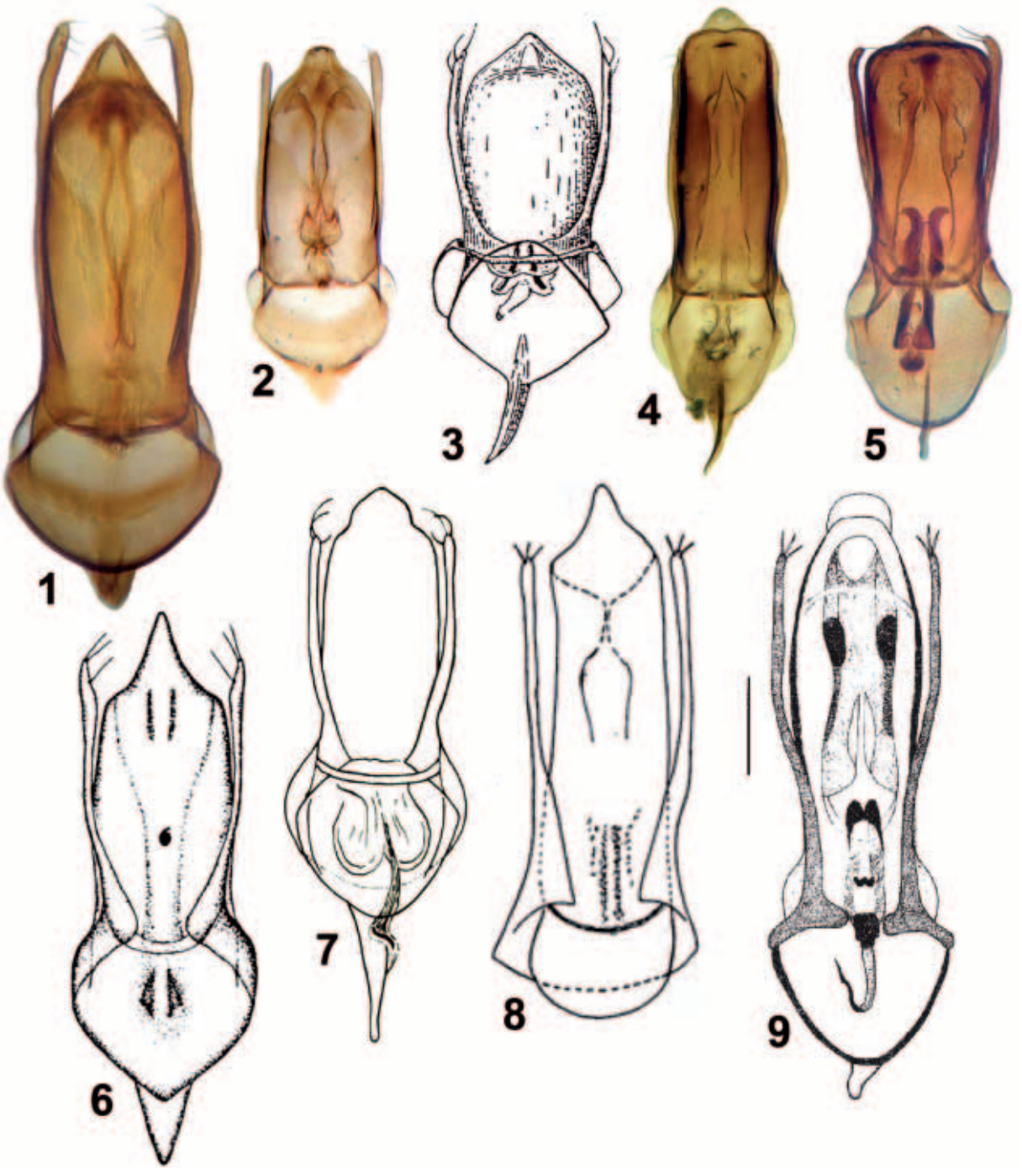
Median lobe of aedeagus: Short and robust or thicker. In lateral view (Fig. 130.6), thick, the ventral side concave in the basal half and convex in the apical half; the dorsal side in a smooth and uniform arc up to the apical area which is sinuous with the apex sharp and oriented towards the dorsal side. In dorsal view (Figs 131.10, 131.11), quite wide with slightly arcuated sides that join to form in the apical area a triangular, flattened, beak structure, with sharp or rounded tip. Basal blade broad and oval, with a marked tongue over the middle area of the posterior edge.

Endophallus (Figs 131.10, 131.11): Bottom of the sac with a short, robust and arcuated stylet, thicker at base, and two laminar structures on the sides. Walls of the basal and middle areas with a number of spinulae; a well-defined reinforcement bands reach the middle area of the sac.

Parameres (Figs 133.7, 133.8): As long as the median lobe, of uniform thickness to the apical area or more thin and shorter than the median lobe. That can be more or less fusiform and with three setae of similar length, oriented inwards.

Spermathecal complex (Fig. 134.5). Spermatheca small, with the areas of the apical lobe and union duct not differentiated and not sclerotized; basal lobe wider, longer and well sclerotized; somewhat widened area where the spermatic ducts and spermathecal gland converge.

Female uroventrite VIII (Fig. 135.5). Apical middle part of posterior margin slightly sunken and less sclerotized; anterior lateral margins straight, spiculum well-developed with rounded apex and a pores field at the base.



FIGURES 132.1–132.9: *Anthroherpon* series, *Pholeuonopsis* group. Aedeagus in dorsal view of: (**1**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**2**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**3**) *Speonesiotes* (*Crivosiella*) *hummleri* (modified from Jeannel 1941), (**4**) *S.* (*Kulzeria*) *muelleri*, (**5**) *S.* (*Speonesiotes*) *narentinus latitarsis,* (**6**) *Tartariella durmitorensis durmitorensis* (modified from Nonveiller & Pavićević 1999), (**7**) *Weiratheria bocki* (modified from Zariquiey 1928), (**8**) *Pseudobathyscidius serbicus* (modified from Karaman 1964), (**9**) *Henrotiella eubeensis* (modified from B.V. Guéorguiev 2007).

Subgenus ***Leonhardella***

Diagnosis. Size between 3.0–4.0 mm; antennae with the 11th antennomere in males, longer than the 10th; elytra with shoulders angular or protruding; apical part of the median lobe of aedeagus in very sharp triangle and narrow base (Fig. 131.10); parameres as long as the median lobe, of uniform thickness to the apical area.

Discussion. In the phylogenetic tree of figure 1H, *Leonhardella* appears as a sister of *Pholeuonopsis* with a support, 74.7/100. In turn, both join with a high support, 100/100, to the separate clades *Proleonhardella* + *Speonesiotes* to form the group *Pholeuonopsis*.

Unpublished molecular data approach *Hygrodromus* to *Speonesiotes* (Polak 2022 *pers. comm*.). These molecular data, absolutely preliminary given the low number of taxa for which they are available, goes in the direction of a confirm, at least partial, of the phyletic series of *Leonhardella*, as proposed by Jeannel (1924a), and which would include the genera: *Leonhardella, Proleonhardella*, *Anisoscapha*, *Anillocharis*, *Pholeuonopsis* and *Blattochaeta*.

Distribution. It colonizes several cavities in the southern area of Bosnia-Herzegovina and a cave in northern Montenegro near the border with Bosnia-Herzegovina.

Species

Leonhardella (***Leonhardella***) ***angulicollis*** Reitter, 1903
Leonhardella angulicollis Reitter, 1903a: 209.
Leonhardella (*Leonhardella*) *angulicollis* Reitt.: Reitter, 1908a: 8.
Leonhardella (s. str.) *angulicollis* Reitter: Jeannel, 1948d: 93.

Leonhardella (***Leonhardella***) ***jeanneli*** Winkler, 1933
Leonhardella angulicollis ssp. *Jeanneli* Winkler, 1933: 76.
Leonhardella (s. str.) *Jeanneli* Winkler: Jeannel, 1948d: 92.
Leonhardella (s. str.) *jeanneli* Winkler: Perreau, 2000: 184.
Leonhardella (*Leonhardella*) *jeanneli* Winkler: Perreau, 2004: 151.

Leonhardella (***Leonhardella***) ***montenegrina*** Jeannel, 1948
Leonhardella (s. str.) *montenegrina* Jeannel, 1948d: 93.
Leonhardella montenegrina Jeannel: Pretner, 1974: 9.

Leonhardella (***Leonhardella***) ***setnikana*** Reitter, 1908
Leonhardella (***Leonhardella***) ***setnikana kyselyi*** Jeannel, 1924
Leonhardella Kyselyi Jeannel, 1924a: 251.
Leonharda Kyselyi Jeannel: Fagniez, 1927: 22.
Leonhardella (s. str.) *setnikana* Subsp. *Kyselyi* Jeannel: Jeannel, 1948d: 91.
Leonhardella (s. str.) *setnikana kyselyi* Jeannel: Perreau, 2000: 185.

Leonhardella (***Leonhardella***) ***setnikana setnikana*** Reitter, 1908
Leonhardella angulicollis Setnikana Reitter, 1908a: 8.
Leonhardella angulicollis subsp. *setnikana* Reitter: Jeannel, 1910a: 39.
Leonhardella angulicollis var. *setnikana* Reitter: Jeannel, 1911a: 455.
Leonhardella Setnikana Subsp. *Setnikana* Reitter, 1908: Jeannel, 1924a: 251.
Leonhardella (s. str.) *setnikana* Subsp. *setnikana* Reitter: Jeannel, 1948d: 91.

Subgenus ***Leonhardellina*** Jeannel, 1948
Leonhardella (*Victorella*) Reitter, 1908a: 7 (*Nom praeocc*. Homonymy with *Victorella* Kent, 1870 – Bryozoa –).
Leonhardella (*Leonhardellina*) Jeannel, 1948d: 90 (*Nomen novum*).

Type species. *Leonhardella antennaria* Apfelbeck, 1907 by subsequent designation (habitus in Fig. 123.3).

Diagnosis. Size between 4.0–4.5 mm. Subgenus with the same facies and general characters as *Leonhardella* s. str.; the most significant differences between both subgenera are the following (Jeannel 1924a; V.B. Guéorguiev 1976): antennae with 11th antennomere as long as the 10th in both sexes; elytra shoulders rounded; apical part of the median lobe of aedeagus in a blunt triangle with a broad base; parameres of the tegmen more thin, and shorter than the median lobe.

Discussion. See Discussion section of the nominotypical subgenus.

Distribution. Almost all taxa live in caves placed in the northern area of Montenegro, most in the karst of the Durmitor National Park. Only *Leonhardella* (*Leonhardellina*) *setniki bielasicensis* lives in caves in southern Bosnia-Herzegovina in Vučja Bara area.

Species

Leonhardella* (*Leonhardellina*) *antennaria Apfelbeck, 1907.

Leonhardella* (*Leonhardellina*) *antennaria acutangula Jeannel, 1948
Leonhardella (*Leonhardellina*) *antennaria* Subsp. *acutangula* Jeannel, 1948d: 95.
Leonhardella antennaria acutangula Jeannel: Pretner, 1974: 9.
Leonhardella (*Leonhardellina*) *antennaria acutangula* Jeannel: Perreau, 2000: 185.

Leonhardella* (*Leonhardellina*) *antennaria antennaria Apfelbeck, 1907
Leonhardella antennaria Apfelbeck, 1907d: 89.
Leonhardella (*Victorella*) *antennaria* Apfelb.: Reitter, 1908a: 8.
Leonhardella antennaria Subsp. *antennaria* Apfelbeck: Jeannel, 1924a: 251.
L. (*Leonhardellina*) *antennaria* Subsp. *antennaria* Apfelbeck: Jeannel, 1948d: 95.
Leonhardella (*Leonhardellina*) *antennaria antennaria* Apfelbeck: Perreau, 2000: 185.

Leonhardella* (*Leonhardellina*) *antennaria brevis Jeannel, 1948
Leonhardella (*Leonhardellina*) *antennaria* Subsp. *brevis* Jeannel, 1948d: 95.
Leonhardella antennaria brevis Jeannel: Pretner, 1974: 9.
Leonhardella (*Leonhardellina*) *antennaria brevis* Jeannel: Perreau, 2000: 185.

Leonhardella* (*Leonhardellina*) *roseni G. Müller, 1937
Leonhardella Setniki Roseni G. Müller, 1937: 109.
L. (*Leonhardellina*) *Roseni* J. Müller: Jeannel, 1948d: 95.
Leonhardella roseni (G. Müller): Pretner, 1974: 9.
Leonhardella (*Leonhardellina*) *roseni* Müller, 1937: Perreau, 2000: 186.

Leonhardella* (*Leonhardellina*) *setniki Reitter, 1907
Leonhardella* (*Leonhardellina*) *setniki bielasicensis G. Müller, 1937
Leonhardella Setniki bielasicensis G. Müller, 1937: 108.
L. (*Leonhardellina*) *Setniki* Subsp. *bjelasicensis* Müller: Jeannel, 1948d: 94.
Leonhardella (*Leonhardellina*) *setniki bielasicensis* Müller: Perreau, 2000: 186.

Leonhardella* (*Leonhardellina*) *setniki setniki Reitter, 1907
Leonhardella Setniki Reitter, 1907a: 321.
Leonhardella (*Victorella*) *antennaria Setniki* Reitt.: Reitter, 1908a: 8.
Leonhardella antennaria subsp. *Setniki* Reitter: Jeannel, 1910a: 39.
L. (*Leonhardellina*) *Setniki* Subsp. *Setniki* Reitter: Jeannel, 1948d: 94.
Leonhardella (*Leonhardellina*) *setniki setniki* Reitter: Perreau, 2000: 186.

Genus ***Pholeuodromus*** Breit, 1913
Pholeuodromus Breit, 1913b 354.

Type species. *Pholeuodromus Leonhardi* Breit, 1913 by monotypy (for the habitus see that of the similar species *Pholeuodromus jeanneli* in Fig. 123.4).

Diagnosis. (Jeannel 1924a; V.B. Guéorguiev 1976): Medium size, lenght between 3.8–4.6 mm. Body shape elliptical, quite wide, of rather bathyscioid facies (Fig. 123.4). Pubescence dense of raised short hairs, accompanied by longer and more erect, scattered, setae.

Antennae: Rather long, exceed half the length of body, with first antennomere clearly shorter than the second one.

Pronotum: As wide as the elytra with sides regularly arcuated, not sinuated in front of the posterior angles. Maximum width in the basal area.

Elytra: Poorly attenuated, regularly arcuated at apex. Shoulders little protruding, do not exceed outwards the posterior angles of pronotum. No parasutural stria.

Legs: Protibiae do not protrude when retracted under the pronotum; male protarsi tetramers; protibiae without comb on apical and external edges.

Mesoventral keel: High and short, with posterior prolongation does not reach the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus, *endophallus*, *parameres*, *spermathecal complex* and *female uroventrite VIII*: Unknown.

Discussion. We have no molecular data available for this genus. We therefore maintain the systematic position assigned to him by Jeannel (1924a) which seems to us, at the moment, the most correct. These are two endogeous species for which there are apparently no data other than the original descriptions: four specimens of *Pholeuodromus jeanneli* and one of *P. leonhardi*. There are no descriptions of their aedeagus.

Distribution. Bosnia-Herzegovina. Collected under sunken stones in forests: Visočica planina and Trebević planina.

Species

Pholeuodromus jeanneli Knirsch, 1929
Pholeuodromus Jeanneli Knirsch, 1929: 90.
Pholeuodromus jeanneli Knirsch: Perreau, 2000: 186.

Pholeuodromus leonhardi Breit, 1913
Pholeuodromus Leonhardi Breit, 1913b 355.
Pholeuonopsis (*Pholeuodromus*) *Breiti* Jeannel, 1924a: 258.
Pholeuodromus breiti (Jeannel): Perreau, 2000: 186.

Note: Jeannel (1924a) changed the name of this species from *leonhardi* to *breiti* because of the primary homonymy created with *Pholeuonopsis* (*Silphanillus*) *leonhardi* Reitter, 1903 when *Pholeuodromus* was considered a subgenus of *Pholeuonopsis*. The elevation of *Pholeuodromus* to genus range by V.B. Guéorguiev (1976) eliminates this homonymy and restores validity to the binomial *Pholeuodromus leonhardi* Breit, 1913.

Genus ***Pholeuonopsis*** Apfelbeck, 1901
Pholeuonopsis Apfelbeck, 1901: 14.
Blattodromus Reitter, 1904b: 153 (Type species: *Pholeuonopsis* (*Blattodromus*) *herculeana* Reitter, 1904).
Serbopholeuonopsis S. Ćurčić & Boškova, 2002: 11 (Type species. *Pholeuonopsis cvijici* S. Ćurčić & Brajković, 2002 = *Pholeuonopsis magdelainei* Jeannel, 1924).

Type species. *Pholeuonopsis ganglbaueri* Apfelbeck, 1901 by monotypy (for the habitus see that of the similar species *Pholeuonopsis grabowskii grabowskii* in Fig. 124.1).

Diagnosis. Medium size, 3.5–5.9 mm, body elliptical and elongated, with pholeuonoid facies (Fig. 124.1), quite wide and not posteriorly narrowed or narrower and elongated body shape. Colour bright reddish-brown. Pubescence short or long, abundant or small in number, lying or raised, accompanied by very long and erect setae on the pronotum and especially in the posterior area of elytra. Microsculpture more or less marked throughout the body.

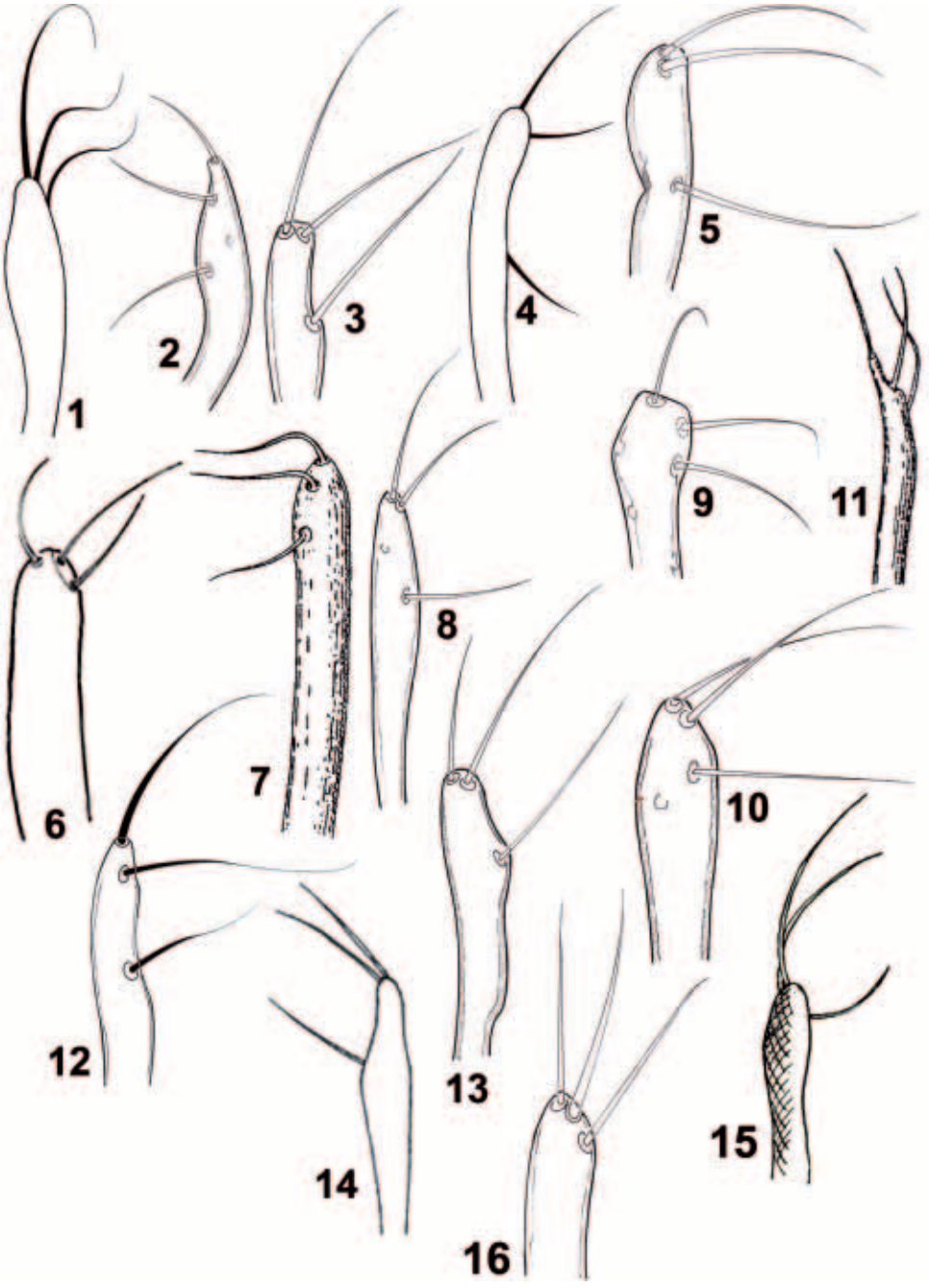
Head: Elongated, longer than wide, with occipital carina indistinct; without omatidi, but often with eyespots; only *Pholeuonopsis* (*Pholeuonopsis*) *zlatiborensis* shows some ommatidia. Punctation well-developed, the points smaller than in pronotum and elytra.

Antennae: Moderately long and robust, exceeding half the length of body. Antennomeres longer than wide and pubescent, dilated at the top and with club quite thick. First antennomere barely once and a half longer than wider or more elongated, being almost twice as long as wide, clearly shorter than the second one. Eighth subglobose or cylindrical, somewhat longer than wide; eleventh ovoid, somewhat longer than the tenth.

Pronotum: Wider than long, generally bell-shaped, with the widest area between the middle and basal part depending on the species. Front lateral margins rounded; sides, in the basal third, between little to very sinuous. Vertices little or very sharp and more or less protruding outward; angles between acute to obtuse. Basal area without impressions or with two-four longitudinal impressions more or less marked. Base narrower than the anterior area of the elytra or almost as wide as the base of elytra or in front of the base strongly narrowed and sinuated. Fine punctate, more or less dense or scattered, accompanied by a cross-linking between the points; in some species without points along the middle part, being smooth and shiny. Dorsal surface pubescent, being weaker in the apical area of the elytra. Prosternum with the basal border truncate at the midline, without protrusion or with a backward prominence within the anterior coxae.

Elytra: If elongated, twice as long as wide, if oval, one and a half times longer than wide. Generally not very convex, with a rounded apex; maximum width towards half and wider than the pronotum. Punctation strong and deep, points large and without order, with or without cross-linking between the points. Anterior half of lateral margins serrated (*P. grabowskii*). Shoulders rounded or protruding exceed the posterior vertices of the pronotum or do not outwardly exceed the angles of pronotum. Parasutural stria absent.

Legs: Long and quite robust; protarsi tetrameres and non-dilated in male; protibiae more or less



FIGURES 133.1-133.16: *Anthroherpon* series, *Pholeuonopsis* group. Apex of the paramere of: (**1**) *Albanella lonae* (redrawn from Jeannel 1941), (**2**) *Anillocharis stenopterus*, (**3**) *Anisoscapha klimeschi misella*, (**4**) *Augustia weiratheri* (redrawn from Zariquiey 1928), (**5**) *Blattochaeta matchai*, (**6**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**7**) *Leonhardella (Leonhardella) angulicollis* (modified from Jeannel 1924a), (**8**) *L.* (*Leonhardellina*) *antennaria* ssp., (**9**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**10**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**11**) *Speonesiotes* (*Crivosiella*) *hummleri* (modified from Jeannel 1941), (**12**) *S.* (*Kulzeria*) *muelleri*, (**13**) *S.* (*Speonesiotes*) *gobanzi*, (**14**) *Tartariella durmitorensis durmitorensis* (modified from Nonveiller & Pavićević 1999), (**15**) *Weiratheria bocki* (modified from Zariquiey 1928), (**16**) *Henrotiella eubeensis* (redrawn from B.V. Guéorguiev 2007).

straight, without comb along the external margin and with a small external apical spur. At rest protrude a little from the sides of the pronotum; meso- and metatibiae straight and relatively narrow, with long and very thin spines; tarsal claws well-developed and somewhat widened.

Mesoventral keel (Fig. 127.4): Well developed, high and subtriangular, with a rounded or toothed vertex and angle obtuse, posterior prolongation does not reach the metaventrite; or hight but very short, only extends along a third of mesoventrite, with a flat surface in front of base of the anterior edge. Normally, anterior border convex and the posterior one concave, this border more or less denticulated and with setae.

Suture of the metaventrite (Fig. 127.4): It runs close to the coxal cavity, only in the upper third it delimits a narrow and very reduced area.

Metatergal apparatus (Fig. 128.3): Slightly variable, with relatively long, narrow and straight, or a little curved metascutum wings, and the alacrista with moderately long basal process.

Metendosternite (Fig. 129.3): Furca in «Y»-shape, variable in position and shape of the laminae, a small anterior lamina in the apical part is observed. Arms as long as or a little longer than the trunk, widened in the apical area, without terminal process or apophysis. Trunk somewhat longer than wide.

Median lobe of aedeagus: More or less long and more or less wide, robust and well sclerotized. In lateral view (Fig. 130.7), arcuated and globose, with apical area very narrow and sharp. In dorsal view (Fig. 132.1), sides more or less arched, subparallel, and sharply narrow in the apical area it forms a developed triangular beak, clearly depressed at the base, with a rounded or sharp tip. Basal blade wide, oval, with a highly developed tongue structure in the posterior middle area.

Endophallus (Fig. 132.1): Basal area with a stylet, rather short, arcuated and widened at the base. Sides of the apical area with some sclerotized, longitudinal, folds. Upper area with two narrow and long reinforcement bands, exceeding the middle area of the lobe.

Parameres (Fig. 133.9): Relatively thin, slightly longer or somewhat shorter than the median lobe; apical area curved inwards, in general with an elongated, little dilated, club bearing three subequal setae (four in *Pholeuonopsis* (*Pholeuonopsis*) *herculeana*); position of insertion of pores variable.

Spermathecal complex: Spermatheca (Fig. 134.6) small, arcuated, rod-shaped or hook-shaped, well sclerotized basal part which is longer and wider; undifferentiated junction duct and apical lobe, both slightly sclerotized almost hyaline; apical area being rounded and clearly narrower. There is a spermathecal gland.

Female uroventrite VIII (Fig. 135.6): Triangular in shape, not wide, with the lateral vertices sharp and curved inwards; the spiculum short and wide with the apex rounded or slightly notched; the posterior edge angulate with the lateral margins largely rectilinear and with numerous fine setae, plus some longer and more robust setae inserted at regular intervals. Also, in some species the posterior edge may describe a regular arc little or no angulate with only thin setae along the lateral margins (Čeplík 2021: Fig. 19).

Subgenus ***Pholeuonopsis***

Diagnosis. Medium size, 3.5–5.9 mm, body elliptical and elongated, with pholeuonoid facies, quite wide and not posteriorly narrowed. First antennomere barely once and a half longer than wider. Base of the pronotum narrower than the anterior area of the elytra. Prosternum with the basal border truncate at the midline, without protrusion. Shoulders of the elytra rounded or protruding exceed the posterior vertices of the pronotum. Mesoventral keel well-developed, high and subtriangular, with vertex more or less sharp and angle obtuse, posterior prolongation does not reach the metaventrite.

Discussion. The genus *Pholeuonopsis* is included in the phyletic lineage of *Leonhardella* (Jeannel 1911, 1924a), and differs from the more morphologically similar genera *Anillocharis*, *Blattochaeta* and *Leonhardella* in body shape, especially in pronotum and elytra, in protarsomeres of males and in shape of different structures of aedeagus (Čeplík 2021). In the phylogenetic tree (Fig. 1H) *Pholeuonopsis* appears as sister group of *Leonhardella* with a support 74.7/100; in turn both join *Proleonhardella* with a high support, 96.9/100; the entire set joins *Speonesiotes* with 100/100 support to form the *Pholeuonopsis* group.

Distribution. Currently belongs to this subgenus 14 species and six cave dwelling and endogean subspecies that have colonized a wide karst area of the Dinaric region, in this case of central and southern Bosnia-Herzegovina, western Serbia and northern Montenegro, Durmitor mountains.

Species

Pholeuonopsis* (*Pholeuonopsis*) *ganglbaueri Apfelbeck, 1901
Pholeuonopsis Ganglbaueri Apfelbeck, 1901: 14.
Pholeuonopsis (s. str.) *Ganglbaueri* Apfelbeck: Jeannel, 1914b: 41.
Pholeuonopsis (s. str.) *ganglbaueri* Apfelbeck: Perreau, 2000: 186.
Pholeuonopsis (*Pholeuonopsis*) *ganglbaueri* Apfelbeck, 1901: Perreau, 2004: 152.

Pholeuonopsis* (*Pholeuonopsis*) *grabowskii Apfelbeck, 1907.

Pholeuonopsis* (*Pholeuonopsis*) *grabowskii grabowskii Apfelbeck, 1907
Pholeuonopsis Grabowskii Apfelbeck, 1907b: 402.
Pholeuonopsis Winkleri Breit, 1913b 352.
Pholeuonopsis (*Silphanillus*) *Leonhardi* Reitter: Jeannel, 1914b: 41.
Pholeuonopsis (s. str.) *Grabowskii* Apfelbeck, 1907: Jeannel, 1924a: 259.
Pholeuonopsis (*s. str.*) *grabowskii grabowskii* Apfelbeck: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *grabowskii grabowskii* Apfelbeck, 1907: Perreau, 2004: 152.

Pholeuonopsis* (*Pholeuonopsis*) *grabowskii lupoglavensis Knirsch, 1928
Pholeuonopsis grabowskii lupoglavensis Knirsch, 1928 [1927]: 103.
Pholeuonopsis (*s. str.*) *grabowskii lupoglavensis* Knirsch, 1928: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *grabowskii lupoglavensis* Knirsch, 1928: Perreau, 2004: 152.

Pholeuonopsis* (*Pholeuonopsis*) *grabowskii ottonis Breit, 1913
Pholeuonopsis Ottonis Breit, 1913b 352.
Pholeuonopsis (*s. str.*) *Ottonis* Breit: Jeannel, 1914b: 41.
Pholeuonopsis (*Pholeuonopsis*) *grabowskii ottonis* (Breit): Pretner, 1969 [1968]: 17.
Pholeuonopsis (*s. str.*) *grabowskii ottonis* Knirsch, 1928: Perreau, 2000: 187.

Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki Jeannel, 1930
Pholeuonopsis (s. str.) *Grabowskii* subsp. *Setniki* Jeannel, 1930b: 228.
Pholeuonopsis (*s. str.*) *grabowskii setniki* Knirsch, 1928: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *grabowskii setniki* Knirsch, 1928: Perreau, 2004: 152.

Pholeuonopsis* (*Pholeuonopsis*) *herculeana Reitter, 1904
Pholeuonopsis (*Blattodromus*) *herculeana* Reitter, 1904b: 153.
Pholeuonopsis herculeanus Reitter: Jeannel, 1910a: 40.
Blattodromus herculeanus Reitt.: Jeannel, 1914b: 42.
Blattodromus herculeus Reitter: Pretner, 1970c: 162.
Pholeuonopsis (s. str.) *herculeanus* Reitter, 1904: Čeplík, 2021: 567.

Pholeuonopsis* (*Pholeuonopsis*) *intermedia Knirsch, 1929
Pholeuonopsis intermedius Knirsch, 1929: 92.
Pholeuonopsis (*s. str.*) *intermedius* Knirsch: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *intermedius* Knirsch, 1929: Perreau, 2004: 152.
Pholeuonopsis (*s. str.*) *intermedia* Knirsch, 1929: Čeplík, 2021: 568.

Pholeuonopsis* (*Pholeuonopsis*) *lupi S. Ćurčić & Pavićević, 2018
Pholeuonopsis lupi S. Ćurčić & Pavićević *in* S. Ćurčić, Pavićević, Vesović, Mulaomerović, Rađa, Antić, Bosco, Marković & Petković, 2018: 542.
Pholeuonopsis (s. str.) *lupi* S. Ćurčić & Pavićević, 2018: Čeplík, 2021: 568.

Pholeuonopsis* (*Pholeuonopsis*) *magdelainei Jeannel, 1924
Pholeuonopsis (s. str.) *Magdelainei* Jeannel, 1924a: 260.
Pholeuonopsis cvijici S. Ćurčić & Brajković, 2002: 43.
Pholeuonopsis magdelainei Jeannel: Rossi & Santamaria, 2010: 600.
Serbopholeuonopsis cvijici S. Ćurčić & M.M. Brajković: S. Ćurčić & Boškova, 2002: 11.
Pholeuonopsis (s. str.) *magdelainei* Jeannel: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *magdelainei* Jeannel, 1924: Perreau, 2004: 152.

Pholeuonopsis* (*Pholeuonopsis*) *perucensis S. Ćurčić, Vrbca, Vesović, Mulaomerović & B. Ćurčić, 2014
Pholeuonopsis perucensis S. Ćurčić, Vrbca, Vesović, Mulaomerović & B. Ćurčić, 2014: 178.
Pholeuonopsis (s. str.) *perucensis* S. Ćurčić *et al.* 2014: Čeplík, 2021: 568.

Pholeuonopsis (***Pholeuonopsis***) ***pfeiferi*** Breit, 1914
Pholeuonopsis Leonhardi ssp. *Pfeiferi* Breit, 1914: 61.
Pholeuonopsis (*Silphanillus*) *Leonhardi* subsp. *Pfeiferi* Breit: Jeannel, 1914b: 42.
Pholeuonopsis (s. str.) *Pfeiferi* Breit, 1914: Jeannel, 1924a: 259.
Pholeuonopsis Pfeiferi Breit: Fagniez, 1927: 22.
Pholeuonopsis (s. str.) *pfeiferi* Breit: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *pfeiferi* Breit, 1914: Perreau, 2004: 152.

Pholeuonopsis (***Pholeuonopsis***) ***romanjensis*** Knirsch, 1929
Pholeuonopsis romanjensis Knirsch, 1929: 92.
Pholeuonopsis (s. str.) *romanjensis* Knirsch: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *romanjensis* Knirsch, 1929: Perreau, 2004: 152.

Pholeuonopsis (***Pholeuonopsis***) ***setipennis*** Apfelbeck, 1907.

Pholeuonopsis (***Pholeuonopsis***) ***setipennis fuchsi*** Zariquiey, 1927
Pholeuonopsis setipennis sbsp. *fuchsi* Zariquiey, 1927: 157.
Pholeuonopsis (s. str.) *setipennis fuchsi* Zariquiey: Perreau, 2000: 187.
Pholeuonopsis (*Pholeuonopsis*) *setipennis fuchsi* Zariquiey, 1927: Perreau, 2004: 152.

Pholeuonopsis (***Pholeuonopsis***) ***setipennis setipennis*** Apfelbeck, 1907
Pholeuonopsis setipennis Apfelbeck, 1907a: 304.
Pholeuonopsis (s. str.) *setipennis* Apfelbeck: Jeannel, 1914b: 41.
Pholeuonopsis (s. str.) *setipennis setipennis* Apfelbeck: Perreau, 2000: 188.
Pholeuonopsis (*Pholeuonopsis*) *setipennis setipennis* Apfelbeck, 1907: Perreau, 2004: 152.

Pholeuonopsis (***Pholeuonopsis***) ***sljivovicensis*** S. Ćurčić, Vrbca, Vesović, Antić, Petković, Bosco & B. Ćurčić, 2015
Pholeuonopsis sljivovicensis S. Ćurčić, Vrbca, Vesović, Antić, Petković, Bosco & B. Ćurčić, 2015: 394.
Pholeuonopsis (s. str.) *sljivovicensis* S. Ćurčić *et al.* 2015: Čeplík, 2021: 568.

Pholeuonopsis (***Pholeuonopsis***) ***tarensis*** S. Ćurčić & Pavićević, 2018
Pholeuonopsis tarensis S. Ćurčić & Pavićević *in* S. Ćurčić, Pavićević, Vesović, Mulaomerović, Rađa, Antić, Bosco, Marković & Petković, 2018: 539.
Pholeuonopsis (s. str.) *tarensis* S. Ćurčić & Pavićević, 2018: Čeplík, 2021: 568.

Pholeuonopsis (***Pholeuonopsis***) ***weiratheri*** (Reitter, 1913)
Silphanillus Weiratheri Reitter, 1913a: 155.
Pholeuonopsis (*Silphanillus*) *Weiratheri* Reitt.: Jeannel, 1914b: 42.
Pholeuonopsis (s. str.) *Weiratheri* Reitter, 1913: Jeannel, 1924a: 260.
Pholeuonopsis weiratheri (Reitter): Pretner, 1974: 10.
Pholeuonopsis (s. str.) *weiratheri* (Reitter): Perreau, 2000: 188.
Pholeuonopsis (*Pholeuonopsis*) *weiratheri* (Reitter, 1913): Perreau, 2004: 152.

Pholeuonopsis (***Pholeuonopsis***) ***zlatiborensis*** S. Ćurčić, Brajković, B. Ćurčić & N. Ćurčić, 2006
Pholeuonopsis zlatiborensis S. Ćurčić, Brajković, B. Ćurčić & N. Ćurčić, 2006: 497.
Pholeuonopsis (s. str.) *zlatiborensis* S. Ćurčić *et al.* 2006: Čeplík, 2021: 568.

Subgenus ***Scotosites*** Knirsch, 1929
Pholeuonopsis (*Scotosites*) Knirsch, 1929: 88.

Type species. *Pholeuonopsis spaethi* Knirsch, 1929 by original designation (habitus in Fig. 124.2).

The description by Knirsch (1929) is, for the time, very precise but, made on a single female specimen, it lacks several important information. Having not been able to examine any specimen of this taxon we limit ourselves to reporting the salient characters of the original description.

Diagnosis. Long 4.2 mm, elliptical, pale yellow. Pubescence long, lying down and dense.

Head: Small, non-retractable, with scattered, fine, and dense punctation. Male unknown.

Antennae: Thin, with moderately dilated club, the second article almost 1/3 longer than the first, which is thickened; the third longer than the first, the eighth cylindrical and twice as long as large.

Pronotum: Slightly transverse, bell-shaped. Base as wide as the base of the elytra. Base wider than the front edge, with sharp and protruding basal angles, but blunt at the vertex. Flat and rounded side edge, not angled, narrowed to the front almost straight, slightly

sinuated posteriorly. Posterior edge weakly bi-sinuated; disc moderately curved to very curved, finely and deeply knurled, weakly and sparsely dotted.

Elytra: Two and 3/4 times longer than wide, slightly wider than the pronotum, with maximum width of the proximal third at the base. Elytral disc equipped with punctation arranged in subtly protruding transverse lines, short, and with long setae of irregular insertion. Humeral angles of the elytra do not pass outwardly the posterior angles of the pronotum.

Legs: Moderately long; the anterior tibia in a resting position not visible from above. Medium and posterior tibiae equipped with some small thorns.

Discussion. According to Knirsch (1929), following by V.B. Guéorguiev (1976), *Scotosites* differs from *Pholeuonopsis* s. str. and *Silphanillus* by pronotum base almost as wide as the base of elytra and by shoulders of elytra do not outwardly exceed the angles of pronotum. We cannot exclude future synonyms with the nominotypical subgenus.

Distribution. The only capture has been made on Mount Volujak (Montenegro).

Species

Pholeuonopsis (***Scotosites***) ***spaethi*** Knirsch, 1929
Pholeuonopsis (*Scotosites*) *Spaethi* Knirsch, 1929: 88.
Pholeuonopsis (*Scotosites*) *spaethi* Knirsch: Perreau, 2000: 188.

Subgenus ***Silphanillus*** Reitter, 1903
Silphanillus Reitter, 1903a: 210.

Type species. *Silphanillus leonhardi* Reitter, 1903 by monotypy (habitus in Fig. 124.3).

Diagnosis. Size 4.0 mm. It presents the same facies and general characteristics as *Pholeuonopsis* s. str.; the most significant differences of this subgenus are (Jeannel 1924a; V.B. Guéorguiev, 1976): Narrower and elongated body shape; antennae exceed half the length of the body, with the first antenomere more elongated, being almost twice as long as wide; pronotum narrower than the elytra with the maximum width in the middle part, base clearly narrower than the elytral base; in front of the base strongly narrowed and sinuated; basal border of the prosternum with a backward prominence within the anterior coxae; shoulders of elytra protruding surpass the posterior angles of pronotum; mesoventral keel hight but very short, only extends along a third of mesoventrite, with a flat surface in front of base of the anterior edge.

Discussion. The characters used for the distinction of the subgenus *Silphanillus* appears more as specialization characters than characters with systematic value. We provisionally maintain this systematic framework pending an overall review of the genus that, also on a molecular basis, clarifies the value of these subgeneric taxa.

Distribution. Monospecific and endogean subgenus collected under buried stones on Mount Vlasulja (Bosnia-Herzegovina), near the border with Montenegro (Jeannel 1924a; Perreau 2000).

Species

Pholeuonopsis (***Silphanillus***) ***leonhardi*** (Reitter, 1903)
Silphanillus Leonhardi Reitter, 1903a: 211.
Pholeuonopsis (*Silphanillus*) *Leonhardi* Rttr.: Breit, 1913b 354.
Pholeuonopsis Leonhardi Reitter: Fagniez, 1927: 22.
Pholeuonopsis (*Silphanillus*) *leonhardi* (Reitter): Perreau, 2000: 188.

Genus ***Proleonhardella*** Jeannel, 1910
Proleonhardella Jeannel, 1910a: 16.
Proleonhardia Jeannel, 1910a: 21 (Type species: *Bathyscia* (s. str.) *Neumanni* Apfelbeck, 1901).
Serboleonhardella S. Ćurčić & Schönmann *in* S. Ćurčić *et al.* 2008: 466 syn. nov. (Type species: *Proleonhardella remyi* Jeannel, 1934).
Bozidaria S. Ćurčić & Pavićević *in* S. Ćurčić *et al.* 2021: 59 syn. nov. (Type species: *Bozidaria serboccidentalis* S. Ćurčić & Pavićević *in* S. Ćurčić *et al.* 2021).

Type species. *Bathyscia* (*Aphaobius*) *Matzenaueri* Apfelbeck, 1907 by original designation (habitus in Fig. 125.1).

Diagnosis. Small-medium size, between 1.3–3.5 mm. Facies bathyscioid, with oval body shape or subglobose, something elongated and convex (Fig. 125.1). Pubescence short, lying down and dense.

Head: Retractable, almost equal length and width, with full occipital carina. Eyes absent.

Antennae: Quite long, with first antennomere slightly to clearly shorter than the second one, they can reach half the length of the body; club well differentiated being all antennomeres longer than wide, ex-

cept the 8th smallest and subglobular or subsquared which can be as long as wide; 11th antennomere slender, ovoid, apically more or less pointed, about as long as the 9th and 10th antennomeres combined.

Pronotum: Short, transverse, almost twice as wide as long and as wide as or somewhat narrower than the maximum width of the elytra. Sides regularly arcuated, little rounded later, with the maximum width near the base; it narrows very little at the level of the posterior angles and is as wide as the base of the elytra.

Elytra: Oval elongated and little to clearly convex, between 1.3 and 1.5 longer than wide, rounded apically. Surface with fine and abundant dotting. Shoulders not protruding although a little angular. Without transverse striae and without parasutural stria— visible stria in *Proleonhardella remyi*—.

Legs: Elongate and not very robust; the male protarsi tetrameres and weakly dilated; protibiae without comb and with external apical spur; meso- and metatibiae without apical baskets.

Mesoventral keel (Figs 127.1–127.3): Short, high or low and angular, with the anterior border convex and the posterior border somewhat convex or straight, both narrow; rounded or somewhat toothed vertex, depending on the species, and obtuse-angled; posterior prolongation not reaching the metaventrite.

Suture of the metaventrite (Figs 127.1–127.3): In the basal half close to the coxal cavity and in the apical half it delimits a narrow and elongated area.

Mesothoracic epiventrite (Figs 127.2, 127.3: White arrow): The mesoventrite-mesoepiventrite suture runs very close to the mesoepiventrite-mesoepimere suture so that the mesoepiventrite is very narrow and elongated. This peculiarity has not been observed in any other Leptodirini although an exhaustive search has not been made; the usual shape of the mesoepiventrite is that of a triangle which may be equilateral.

Metatergal apparatus (Fig. 128.4): Moderately developed, with long and narrow metascutum wings; apophysis of alacrista short with sharp apices.

Metendosternite (Fig. 129.4): In «V». With long and narrow furcal arms, almost two and a half times the length of the trunk, with a thick apical apophysis; posterior lamina of the furcal arm disappears in the narrowing part of the arm; trunk short, but clearly longer than wide and the median keel wide with posterior divergence.

IX uroventrite of the male: Subtrapezoidal (S. Ćurčić *et al*. 2008).

Median lobe of aedeagus: Generally quite long and wide. In lateral view (Fig. 130.8), with globose shape until the strong depression that gives rise to a narrow apical blade, sharp and slightly curved towards the ventral face. In dorsal view (Fig. 131.2), with slightly arcuated sides, subparallels to the abrupt apical narrowing; apical area in shape of triangular lobe with rounded apex. Broad and oval basal blade, with a developed oval tongue in the middle area of the posterior edge.

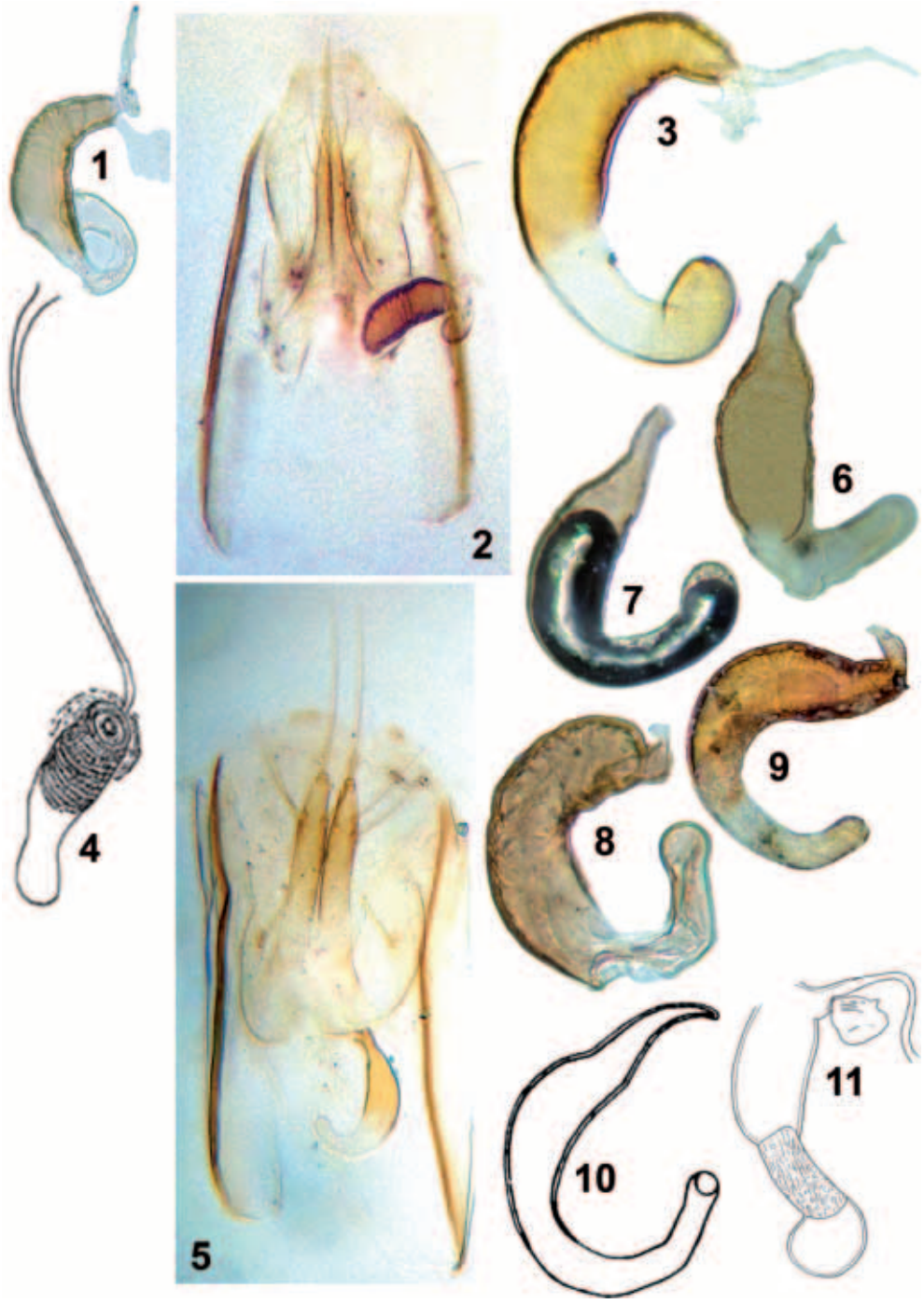
Endophallus (Fig. 132.2): With a well-developed ventral stylus at the bottom of the sac, sometimes bifid, flanked on each side of the apical part by a well-sclerotized accessory piece. Inner walls of the middle area completely covered with very dense short spines. Apical area with two short reinforcement bands reaching the middle part.

Parameres (Fig. 133.10): Thin and subrectilinear, generally longer than the middle lobe and uniform thickness. Apex with an elongated or fusiform club, little dilated, bearing three setae of similar length, sometimes smaller the lower, with equidistant insertion pores, or the ventral pore away from the two apical.

Spermathecal complex: Spermatheca (Fig. 134.7) small, curved or rod-shaped, well sclerotized basal half and more membranous apical half; no differentiation of lobes and the union part, it widens towards the basal third and apically sub-spherical; spermatic duct thin and slightly widening in the area of attachment to the spermatheca; no spermathecal gland observed.

Female uroventrite VIII (Fig. 135.7): Apical margin in a more or less broad arc; spiculum short, triangular in shape and apical part somewhat curved, with the apex rounded or more or less sharp.

Discussion. Is characterised by the small size and bathyscioid facies; short and lying pubescence; antennae quite long with the first antennomere clearly shorter than the second one; pronotum transverse, narrower than the elytra, with arcuated lateral margins; elytra oval without parasutural stria; protarsi tetrameres and slightly widened in males; mesoventral keel short, tall and angular; aedeagus with median lobe quite long, wide, with a shrinkage in the apical area that gives rise to a triangular lobe with the vertex rounded; basal blade with a tongue on the middle posterior edge; endophallus with a robust stylus and the walls of the middle area covered with short spines; parameres shorter than the middle lobe with a slightly dilated apical club with three setae; spermatheca small, curved, no differentiation of lobes and female uroventrite VIII with spiculum short, triangular apex more or less sharp.



FIGURES 134.1-134.11: *Anthroherpon* series, *Pholeuonopsis* group. Spermathecal complex of: (**1**) *Anillocharis stenopterus*, (**2**) *Anisoscapha klimeschi misella*, (**3**) *Blattochaeta matchai*, (**4**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**5**) *Leonhardella (Leonhardella) angulicollis*, (**6**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**7**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**8**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**9**) *S.* (*Speonesiotes*) *narentinus latitarsis*, (**10**) *Tartariella durmitorensis durmitorensis* (modified from Nonveiller & Pavićević 1999), (**11**) *Henrotiella eubeensis* (modified from Perreau 1999).

The genus *Serboleonhardella* was established by S. Ćurčić & Schönmann *in* S. Ćurčić *et al*. (2008), with the type species being *Proleonhardella remyi*. The basic differentiation characters were: larger size, 3.5 mm; ovoid body; 8th antennomere oval; pronotum with somewhat narrowed base and narrower than the elytra; elytra ovoid with parasutural stria. Very inconsistent characters, the most significant being the larger size and the presence of parasutural stria on the elytra. Years later S. Ćurčić *et al.* (2021) in the material examined mention *Proleonhardella* (*Proleonhardella*) *remyi* and also made a key to the genera of the phyletic series of «*Leonhardella*» in which *Serboleonhardella* is not referenced. Between 2008 and 2021, no taxonomic act related to *Serboleonhardella* is carried out. In conclusion, due to the poor consistency of the differentiation characteristics and the absence of any taxonomic act that justifies the existence of this genus, is established the synonymy *Proleonhardella* Jeannel, 1910 = *Serboleonhardella* S. Ćurčić & Schönmann *in* S. Ćurčić *et al.* 2008 syn. nov.

The genus *Bozidaria* S. Ćurčić & Pavićević *in* S. Ćurčić *et al*. (2021) has been reviewed. The article is magnificently illustrated and the description is rigorous so that it is possible to carry out an exhaustive study. It is stated that there are numerous characters that allow *Bozidaria* to be differentiated from *Proleonhardella* – and the other genera of the «*Leonhardella* phyletic series» –; however, there are not many characters and all of them seem more suitable to characterize a species but not a genus. S. Ćurčić *et al*. (2021) point out for these two genera that:

– *Bozidaria*: elliptical and elongated body; shape of antennae elongate, thin, including distal antennomeres; shape of aedeagus long, elongate; shape of basal bulb elongate, narrow; basal projection long.

– *Proleonhardella*: bathyscioid, oval-ovoid and somewhat wider; antennae short with distal antennomeres wide, barely longer than wide; shape of aedeagus mostly wide; shape of basal bulb short and rounded; basal projection short.

In the description of *Proleonhardella* in this text, the genus is characterised by: bathyscioid facies, oval body shape or subglobose, somewhat elongated; antennae quite long, all antennomeres longer than wide, the 8th subglobular and 11th antennomere slender, ovoid, apically more or less pointed; shape of aedeagus quite long and wide; oval basal blade, with a developed oval tongue. The spermatheca and female uroventrite VIII also have the same structure. Without a doubt, all the characters indicated are very similar to those described for *Bozidaria.*

Bozidaria serboocidentalis is more elongated than *Proleonhardella* and this is observed in the body and consequently in the antennae and the aedeagus. All this is reflected in the first point of the dichotomous key where it is seen that only the length of the body differentiates *Bozidaria* from *Proleonhardella*; moreover, the shape of *Bozidaria* is exaggerated when it is said to be similar to a *Pholeuon* (pholeuonoid): «1. Body of bathyscioid form, oval or ovoid, wide and short ..... 2 [*Proleonhardella*] – Body of elliptical or pholeuonoid form ……..... 6 [*Bozidaria*]» (S. Ćurčić *et al*. 2021). *Proleonhardella tarensis*, which is described in the same article, has an elongated body, somewhat more than other species of *Proleonhardella*, also *P. matzenaueri*, although not as much as *Bozidaria serbooccidentalis*. Body shape as a fundamental element of genus characterization has been widely used in classical studies (Reitter, 1881b, 1885a; Jeannel, 1910a, 1911a, 1924a, 1930f, etc.), although it has been postulated that the shape is probably directly related to the selective pressure of the environment, so it should be considered an adaptive character, or set of characters. The rounded (bathys-cioid) and elongated (pholeuonoid, leptodiroid or scaphoid) elements coexist in all clades (see the text on habitus models in the characters section) and coexist in several genera with significantly more marked differences than those that occur between *Proleonhardella* and *Bozidaria*. See the case of *Bathysciella* sensu novo that includes *Bathysciella jeanneli* – with a certain pholeuonoid appearance due to its bell-shaped pronotum –, or *B. mascarauxi* comb. nov. (ex *Phacomorphus* syn. nov.), with its large hemispherical forms, or the small oval such as *B. sioberi* comb. nov. (ex *Phacomorphoides* syn. nov.); or the case of *Troglocharinus* with a continuous gradation of forms between the bathyscioids like *T. mercedesi* and *T. ferreri* markedly pholeuonoid, like the majority of the species (Fresneda *et al*. 2021); or also *Ovobathysciola* sensu novo with the small and markedly bathyscioid species such as *O. gestroi*, the intermediate form with the bell-shaped pronotum of *O. cogonii* comb. nov. (ex *Sardostygia* syn. nov.), or the decidedly pholeuonoid form of *O. sardoa* comb. nov. (ex *Patriziella* syn. nov.). All these cases are diverse in body shape but coincide in genital patterns: these seem to be the basic structures that indicate evolutionary kinship. Consequently, is established the synonymy *Proleonhardella* Jeannel, 1910 = *Bozidaria* S. Ćurčić & Pavićević in S. Ćurčić *et al.* 2021 syn. nov. and the new combination *Proleonhardella serbooccidentalis* (S. Ćurčić & Pavićević *in* S. Ćurčić *et al.* 2021) comb. nov. is proposed.

Molecular study carried out, *Proleonhardella* is in the *Pholeuonopsis* group and is related to *Pholeuonopsis* and *Leonhardella* with a high support 96.9/100 (Fig. 1H).

Subgenus ***Proleonhardella***

Diagnosis. Small or very small size, between 1.3–2.5 mm, exceptionally specimens of *Proleonhardella* (*Proleonhardella*) *remyi* can reach 3.5 mm; antennae with the 8th antennomere generally more than one and a half times longer than wide, if shorter ovoid; pronotum narrower than the elytra, some cases as wide as the elytra, and not or slightly narrowed at the base; mesoventral keel high and longer, posterior apophysis extends to part of the metaventrite.

Discussion. See what is indicated in the genus section.

Distribution. Distributed in Bosnia-Herzegovina, where colonizes caves south of Sarajevo, and west-southwest Serbia near the border with Montenegro, with only one species known from a cave near the town of Seljane.

Species

Proleonhardella (***Proleonhardella***) ***apfelbecki*** Jeannel, 1924
Proleonhardella (s. str.) *Apfelbecki* Jeannel, 1924a: 245.
Proleonhardella (s. str.) *apfelbecki* Jeannel: Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *apfelbecki* Jeannel, 1924: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***epimikes*** sp. nov. (See Appendix New Species)

Proleonhardella (***Proleonhardella***) ***hirtella*** Jeannel, 1934
Proleonhardella hirtella Jeannel, 1934b: 99.
Proleonhardella (s. str.) *hirtella* Jeannel: Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *hirtella* Jeannel, 1924: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***leonhardi*** (Breit, 1913)
Bathyscia (*Proleonhardella*) *Leonhardi* Breit, 1913c 236.
Proleonhardella Leonhardi Breit: Jeannel, 1914b: 18.
Proleonhardella (s. str.) *Leonhardi* Breit, 1913: Jeannel, 1924a: 244.
Proleonhardella (s. str.) *leonhardi* (Breit): Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *leonhardi* Breit, 1913: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***matzenaueri*** (Apfelbeck, 1907).

Proleonhardella (***Proleonhardella***) ***matzenaueri matzenaueri*** (Apfelbeck, 1907)
Bathyscia (*Aphaobius*) *Matzenaueri* Apfelbeck, 1907a: 304.
Bathyscina Matzenaueri Apfelb.: Jeannel, 1908a: 299.
Proleonhardella Matzenaueri Apfelbeck: Jeannel, 1910a: 39.
Proleonhardella (s. str.) *Matzenaueri* Apfelbeck, 1907: Jeannel, 1924a: 245.
Proleonhardella (s. str.) *matzenaueri matzenaueri* (Apfelbeck): Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *matzenaueri matzenaueri* Apfelbeck, 1907: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***matzenaueri ottonis*** G. Müller, 1917
Proleonhardella Matzenaueri Ottonis G. Müller, 1917: 614.
Proleonhardella (s. str.) *Matzenaueri* Subsp. *Ottonis* J. Müller, 1917: Jeannel, 1924a: 245.
Proleonhardella (s. str.) *matzenaueri ottonis* Müller: Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *matzenaueri ottonis* Müller, 1917: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***neumanni*** (Apfelbeck, 1901)
Bathyscia (s. str.) *Neumanni* Apfelbeck, 1901: 15.
Bathyscia (*Aphaobius*) *Neumanni* Apfelbeck, 1901: Jeannel, 1907c: 63.
Proleonhardia Neumanni Apfelbeck: Jeannel, 1910a: 42.
Proleonhardia Neumanni Apfelbeck: Jeannel, 1911a: 493.
Proleonhardella (s. str.) *Neumanni* Apfelbeck, 1901: Jeannel, 1924a: 245.
Proleonhardella (s. str.) *neumanni* (Apfelbeck): Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *neumanni* Apfelbeck, 1901: Perreau, 2004:153.

Proleonhardella (***Proleonhardella***) ***remyi*** Jeannel 1934
Proleonhardella (*Proleonhardella*) *Remyi* Jeannel, 1934b: 98.
Proleonhardella (s. str.) *remyi* Jeannel: Perreau, 2000: 189.

Proleonhardella (*Proleonhardella*) *remyi* Jeannel, 1934: Perreau, 2004: 153.
Serboleonhardella remyi (Jeannel, 1934): S. Ćurčić & Schönmann, 2008: 469.

Proleonhardella (***Proleonhardella***) ***serbooccidentalis*** (S. Ćurčić & Pavićević, 2021) comb. nov.
Bozidaria serbooccidentalis S. Ćurčić & Pavićević *in* S. Ćurčić *et al.* 2021: 63.

Proleonhardella (***Proleonhardella***) ***tarensis*** S. Ćurčić & Pavićević, 2021
Proleonhardella tarensis S. Ćurčić & Pavićević *in* S. Ćurčić *et al.* 2021: 68.

Proleonhardella (***Proleonhardella***) ***weiratheri*** (Reitter, 1913)
Bathyscia (Bathyscia) Weiratheri Reitter, 1913a: 156.
Proleonhardella Weiratheri Reitt.: Jeannel, 1914b: 18.
Proleonhardella (s. str.) *Weiratheri* Reitter, 1913: Jeannel, 1924a: 245.
Proleonhardella weiratheri (Reitter): Pretner, 1974: 9.
Proleonhardella (s. str.) *weiratheri* Reitter: Perreau, 2000: 189.
Proleonhardella (*Proleonhardella*) *weiratheri* Reitter, 1913: Perreau, 2004:153.

Subgenus ***Pholeuonillus*** Breit, 1913
Pholeuonillus Breit, 1913b 355.

Type species. *Bathyscia Adolfi* Reitter, 1911 by original designation (habitus in Fig. 125.2).

Diagnosis. After Breit (1913c), Jeannel (1924a), V.B. Guéorguiev (1976) and S. Ćurčić *et al*. (2008, 2021). Size 3.0 mm. Body shape elliptical and little elongated, with bathyscioid facies (Fig. 125.2).

Head: Retractable, with full occipital carina. Eyes absent.

Antennae: Not reaching the half-length of the body, being antenomere 8th small and subsquared, the 7th widened and the 9th and 10th not elongated.

Pronotum: With maximum width in front of the posterior angles, as wide as the elytra, with sides well arcuated posteriorly and very narrowed at the base.

Elytra: Elliptical, rather long and little convex, apically rounded; punctation showing large and deep points arranged without order; parasutural stria absent.

Legs: Short and quite robust; protibiae without comb. Male protarsi tetrameres.

Mesoventral keel: Short, very low and rounded at vertex.

Discussion. Subgenus with the same facies and general characteristics as the genus *Proleonhardella*; the characterization of this genus are indicated by Jeannel (1924a), V.B. Guéorguiev (1976) and S. Ćurčić *et al*. (2008, 2021).

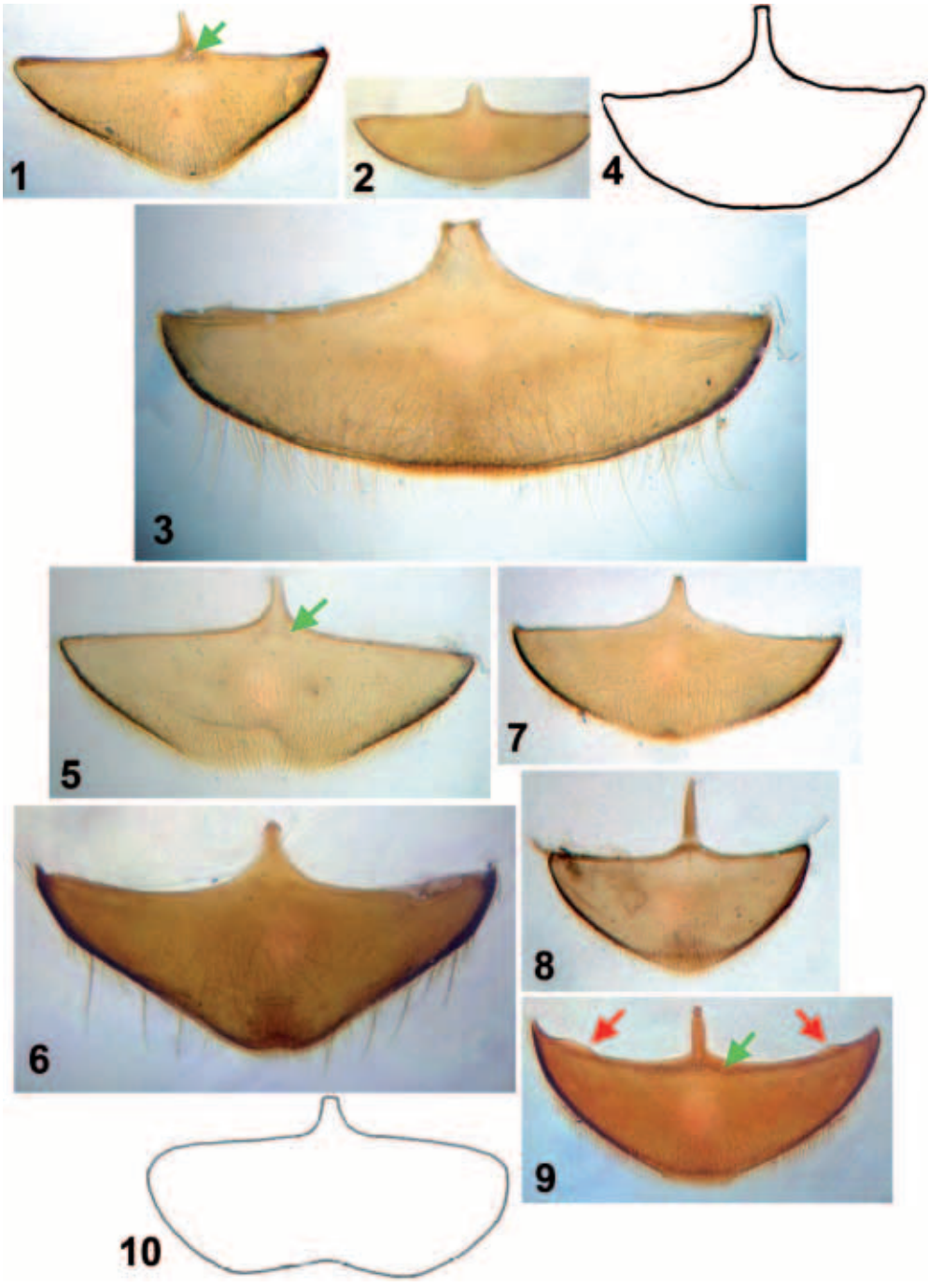
The most relevant differential characters with *Proleonhardella* are medium size; antennae with the 8th antennomere small and subsquared; pronotum with maximum width in front of the posterior angles, as wide as the elytra and very narrow at the base; elytra elliptical with large and deep points, without parasutural stria; mesoventral keel very low and short, with rounded vertex. Following S. Ćurčić *et al*. (2008) raises *Pholeuonillus* to genus status and probably is the sister genus of *Proleonhardella* and *Serboleonhardella*, and belong to a separate phyletic lineage. However, years later S. Ćurčić *et al.* (2021) include *Pholeuonillus* as a subgenus of *Proleonhardella*, and in the key to genera of the phyletic series of «*Leonhardella*», *Pholeuonillus* is not mentioned as a genus. Between 2008 and 2021 there is no taxonomic act in this regard. Like Jeannel (1934), V.B. Guéorguiev (1976) and Perreau (2000), *Pholeuonillus* is conserved with subgenus category.

We do not have molecular data available for *Pholeuonillus* and we cannot confirm or refute what authors have asserted (Jeannel 1924a; V.B. Guéorguiev 1976; S. Ćurčić *et al*. 2008). Certainly, it is evident that the morphological characters used to separate these three genera, are usually morphological characters of specialization towards the subterranean environment rather than characters with phyletic value. The issue will have to be carefully reconsidered in the future, especially on a molecular basis.

Distribution. Mountain of Treskavica in Bosnia-Herzegovina, located in the municipality of Trnovo south of the city of Sarajevo. Endogean, is a taxon that lives under stones.

Species

Proleonhardella (***Pholeuonillus***) ***adolfi*** Reitter, 1911
Bathyscia Adolfi Reitter, 1911b: 50.
Pholeuonillus Adolfi Reitter: Breit, 1913b 355.
Proleonhardella (*Pholeuonillus*) *Adolfi* Reitter: Jeannel, 1924a: 246.
Proleonhardella (*Pholeuonillus*) *adolfi* (Reitter): Perreau, 2000: 188.



FIGURES 135.1-135.10: *Anthroherpon* series, *Pholeuonopsis* group. Female uroventrite VIII of: (**1**) *Anillocharis stenopterus*, (**2**) *Anisoscapha klimeschi misella*, (**3**) *Blattochaeta matchai*, (**4**) *Hygrodromus nikolinae* (modified from Giachino *et al*. 2021), (**5**) *Leonhardella (Leonhardella) angulicollis*, (**6**) *Pholeuonopsis* (*Pholeuonopsis*) *grabowskii setniki*, (**7**) *Proleonhardella* (*Proleonhardella*) *matzenaueri matzenaueri*, (**8**) *Speonesiotes* (*Kulzeria*) *muelleri*, (**9**) *S.* (*Speonesiotes*) *narentinus latitarsis*, (**10**) *Henrotiella eubeensis* (modified from Perreau 1999). Green arrow indicating the «field of pores» at the base of the spiculum; Red arrow indicating the basal lobes.

Genus ***Speonesiotes*** Jeannel, 1910
Speonesiotes Jeannel, 1910a: 15, 38.

Type species. *Adelops narentinus* L. Miller, 1861 by original designation (for the habitus see that of the similar subspecies *Speonesiotes narentinus latitarsis* in Fig. 125.5).

Diagnosis. Size between very small and small, 1.5–3.0 mm. Facies bathyscioid; body oval, wide, short and little convex (Fig. 125.5). Integuments punctate , fine and poorly evident; pubescence yellowish, short and fine. Depigmented.

Head: Wide with fine occipital carina; anophthalmous.

Antennae: Rather long, clearly exceed the base of the pronotum and can reach half of the body or short, thick, do not exceed the base of pronotum; first antennomere shorter, or almost as long as the second; antennomeres of club flattened and fine or wide, narrow at the base and widened at the apex or non-detached and trapezoidal with the base as wide as the apical area; the 8th normally longer than wide or very transverse, twice as wide as long.

Pronotum: Transverse, almost twice as wide as long; with sides regularly arcuated and basal angles directed backwards. Base as wide as base of elytra.

Elytra: Oval, short, between 1.25–1.3 times longer than wide, with maximum width at the base, and apical areas widely arcuated or more or less cuneiform, with sides rectilinear backwards; surface with very fine and close transverse striolae and widely arcuated apical parts or narrowed and usually obliquely truncated; no parasutural stria.

Legs: Long and quite robust; protibiae with a comb of small and regular spines on the outer and apical edges and with a small external apical spur; protarsi tetrameres in male, dilated but narrower than the apex of the protibiae or very little dilated; tibiae finely thorny.

Mesoventral keel (Figs 127.5–127.7): Hight and robust, with rounded vertex and very obtuse angle; anterior edge curved, smooth or somewhat serrated; ventral edge convex, wide, rounded and unsheltered, with several distant setae and without groove. Posterior apophysis does not extend to the metaventrite.

Suture of the metaventrite (Figs. 127.6, 127.7): It forms a continuous arc and delimits a well-manifested area in an arc along the middle part.

Metatergal apparatus (Figs 128.5, 128.6): Wings of metascutum very long and narrow, about ten times as long as wide; apophysis of alacrista well-developed with sharp apexes.

Metendosternite (Figs 129.5, 129.6): «V»-shaped and almost the same in the subgenera *Kulzeria* and *Speonesiotes*, in the former the trunk is somewhat narrower. Formed by long, narrow furcal arms, twice as long as the trunk and the posterior furcal plate is wide at the junction of arms and trunk, not reaching the apical part of the arm; developed apophysis with an embudiform appearance. Trunk one and a half times longer than wide.

Median lobe of aedeagus: Thick, short and wide, about three or four times longer than wide. In lateral view (Fig. 130.9, 130.10), little arcuated, with apical area in narrow beak and apex sharp towards the ventral face. In dorsal view (Fig. 132.3–132.5), sides narrow, subparallel towards the apical area to form a triangular structure with very little sharp apex. Basal blade oval, quite long, with a tongue or extension, or with a very long tongue in general well-developed, at the posterior middle edge.

Endophallus (Fig. 132.3–132.5): With a more or less developed basal armor formed by one or two pairs of elongated pieces, well sclerotized on the dorsal face of the basal region. In some species, in the middle part, they are less sclerotized pieces and small spines grouped or dispersed. With or without hyaline ampoule in the basal area. There is no apical armor, but there is a pair of sigmoid reinforcement bands that can reach the middle area. Although each subgenus has its own model of endophallus.

Parameres (Fig. 133.12, 133.13): Thin, shorter than the median lobe, arcuated in the middle area and sinuous in the apical, with a little differentiated club, sometimes irregular, bearing three rather long setae of similar length, with the insertion points equidistant, or two apical, close, and one internal, basal, further away.

Spermathecal complex: Spermatheca (Fig. 134.8, 134.9) small and in wide arc; area corresponding to the basal lobe well sclerotized, much wider and slightly longer than the area corresponding to the joining duct and apical lobe which is more membranous, apical lobe elongated and of equal width; thin spermiduct, somewhat dilated in the part of union to the spermatheca and there is spermathecal gland.

Female uroventrite VIII (Fig. 135.8, 135.9). Apical margin in arc, with the middle part somewhat protruding; basal margins with a few lobes little marked towards the ends and in the middle a rather long, narrow spiculum, with the apex rounded or slightly strangulated.

Subgenus ***Crivosiella*** Jeannel, 1924
Speonesiotes (*Crivosiella*) Jeannel, 1924a: 280.

Type species. *Speonesiotes* (*Crivosiella*) *Hümmleri* Jeannel, 1924 by original designation (for the habitus see that of the similar species *Speonesiotes* (*Crivosiella*) *brachycerus* in Fig. 125.3).

Diagnosis. Size very small, between 1.5–2.0 mm. Same facies and general characteristics as *Speonesiotes* s. str.; the most significant differences between both subgenera are (Jeannel 1924a; V.B. Guéorguiev 1976): a body general shape short and little convex (Fig. 125.3). Antennae short, thick, do not exceeding the base of the pronotum; club wide and flattened; antennomeres non-detached and trapezoidal with the base as wide as the apical area; the 8th antennomere very transverse, twice as wide as long. Elytra with fine transverse striolation and widely arcuated apical parts. Mesoventral keel (Fig. 127.5) with the characteristics indicated in the description of the genus, but with a smooth and more prominent anterior edge. Median lobe of aedeagus (Fig. 132.3) short and wide, no obvious protrusion in the apical area; basal blade with a very long tongue. Endophallus with long and well-developed basal pieces (Fig. 132.3); basal and middle areas with spines on the walls. Parameres shorter than the median lobe, with the apical part tapering towards the apex and bearing three setae, one apical and the other two latero-internal with equidistant insertion pores (Fig. 133.11).

Discussion. Based on the characters of the aedeagus, *Crivosiella* most likely belongs to the phyletic line of *Pholeuonopsis* and is almost certainly the sister group of *Speonesiotes* s. str. The lack of molecular data does not allow to confirm its taxonomic rank that is, prudently, maintained at the subgeneric level.

Distribution. Crivosiella is known from Montenegro, two species in the northwest near the border with Bosnia-Herzegovina and a third (*S. montenegrinus*) in a cave near Podgorica.

Species

Speonesiotes (***Crivosiella***) ***brachycerus*** Jeannel, 1924
Speonesiotes (*Crivosiella*) *brachycerus* Jeannel, 1924a: 287.

Speonesiotes (***Crivosiella***) ***huemmleri*** Jeannel, 1924
Speonesiotes (*Crivosiella*) *Hümmleri* Jeannel, 1924a: 287.
Speonesiotes (*Crivosiella*) *huemmleri* Jeannel: Perreau, 2000: 195.

Speonesiotes (***Crivosiella***) ***montenegrinus*** Karaman, 1967
Speonesiotes montenegrinus Karaman, 1967: 63.
Speonesiotes (*Crivosiella*) *montenegrinus* Z. Karaman: Pretner, 1970b: 349.

Subgenus ***Kulzeria*** Zariquiey, 1928
Speonesiotes (*Kulzeria*) Zariquiey, 1928 [1927]: 157.

Type species. *Adelops Dorotkana* Reitter, 1881 by subsequent designation (for the habitus see that of the similar species *Speonesiotes* (*Kulzeria*) *muelleri* in Fig. 125.4).

Diagnosis. Size between 2.0–2.6 mm. Same facies and general characteristics as *Speonesiotes* s. str.; the most significant differences between both subgenera are (V.B. Guéorguiev, 1976): the antennae thin, slightly exceeding the base of pronotum; the 8th antennomere oval, barely longer than wide; elytra more or less cuneiform, with sides rectilinear backwards, apical areas narrowed and usually obliquely truncated; male protarsi very little dilated; mesoventral keel (Fig. 127.6) with the characteristics indicated in the description of the genus, but with a serrated earlier edge and all of it in a larger and more regular arc.

Median lobe of aedeagus: In lateral view (Fig. 130.9), slightly curved and the junction of the ventral and dorsal sides forming a short, very narrow beak in the apical region, somewhat curved towards the ventral side. In dorsal view (Fig. 132.4), elongate and sinuous sides with a median projection in the apical area in triangular arc, more developed than in the subgenus *Speonesiotes*.

Endophallus (Fig. 132.4): Different from the other two subgenera, the basic difference being the presence of the hyaline ampoule in the basal area and the thinner basal parts more thinly, although the basal stylet is more evident.

Parameres (Figs 132.4, 133.12): Thin and sinuous, distinctly shorter than the median lobe, with a slightly curved apical part in which three setae are inserted, one apical, one pre-apical and close to the apex, and a third distant and latero-internal.

Discussion. *Kulzeria*, belongs by the characters of the aedeagus to the line of the *Pholeuonopsis* group and is

most likely the sister group of *Speonesiotes* s. str. The lack of molecular data for the other subgenera of *Speonesiotes* does not allow us to confirm its taxonomic rank here. It is, therefore maintained at the subgeneric level.

Distribution. *Kulzeria* colonises several cavities mainly along the western belt of Montenegro, but also some caves of southern Bosnia-Herzegovina and the surroundings of Mitrovici in Croatian Dalmatia.

Species

Speonesiotes* (*Kulzeria*) *dorotkanus (Reitter, 1881)
Speonesiotes* (*Kulzeria*) *dorotkanus dorotkanus (Reitter, 1881)
Adelops Dorotkana Reitter, 1881a: 215.
Bathyscia Dorotkana Reitter: Reitter, 1885a [1884]: 19.
Bathyscia Dorotkana grepcensis Paganetti-Hummler, 1903: 27.
Speonesiotes Dorotkanus rotundipennis G. Müller, 1934: 179.
Bathyscia (*Aphaobius*) *Dorotkana* Reitt.: Paganetti-Hummler, 1903: 26.
Bathyscina dorotkanus Reitt.: Jeannel, 1908a: 299.
Speonesiotes dorotkanus Reitter: Jeannel, 1910a: 39.
Speonesiotes (*Albanella*) *dorotkanus* Reitter: Jeannel: 244.
Speonesiotes (*Kulzeria*) *dorotkanus* Reitter: Zariquiey, 1928 [1927]: 157.
Speonesiotes (*Kulzeria*) *dorotkanus dorotkanus* (Reitter): Perreau, 2000: 195.

Speonesiotes* (*Kulzeria*) *dorotkanus noesskei Zariquiey, 1928
Speonesiotes dorotkanus subsp. *Noesskei* Zariquiey, 1928 [1927]: 158.
Albanella apicenotata Knirsch, 1928 [1927]: 104.
Speonesiotes (*Albanella*) *dorotkanus Noesskei* Zariquiey: Jeannel, 1928: 297.
Speonesiotes (*Kulzeria*) *dorotkanus* subsp. *Noesskei* R. Zar: Jeannel, 1941: 119.
Speonesiotes dorotkanus noesskei Zariquiey: Pretner, 1974: 10.
Speonesiotes (*Kulzeria*) *dorotkanus noesskei* Zariquiey: Perreau, 2000: 195.

Speonesiotes* (*Kulzeria*) *koritoensis Winkler, 1935
Speonesiotes* (*Kulzeria*) *koritoensis brevicornis Jeannel, 1941
Speonesiotes (*Kulzeria*) *koritoensis* subsp. *brevicornis* Jeannel, 1941: 116.

Speonesiotes* (*Kulzeria*) *koritoensis koritoensis Winkler, 1935
Speonesiotes (s. str.) *koritoensis* Winkler, 1935: 235.
Speonesiotes (*Kulzeria*) *koritoensis* Winkler: Jeannel, 1941: 116.
Speonesiotes (*Kulzeria*) *koritoensis koritoensis* Winkler: Perreau, 2000: 196.

Speonesiotes* (*Kulzeria*) *koritoensis planaensis Jeannel, 1941
Speonesiotes (*Kulzeria*) *koritoensis* subsp. *planaensis* Jeannel, 1941: 116.

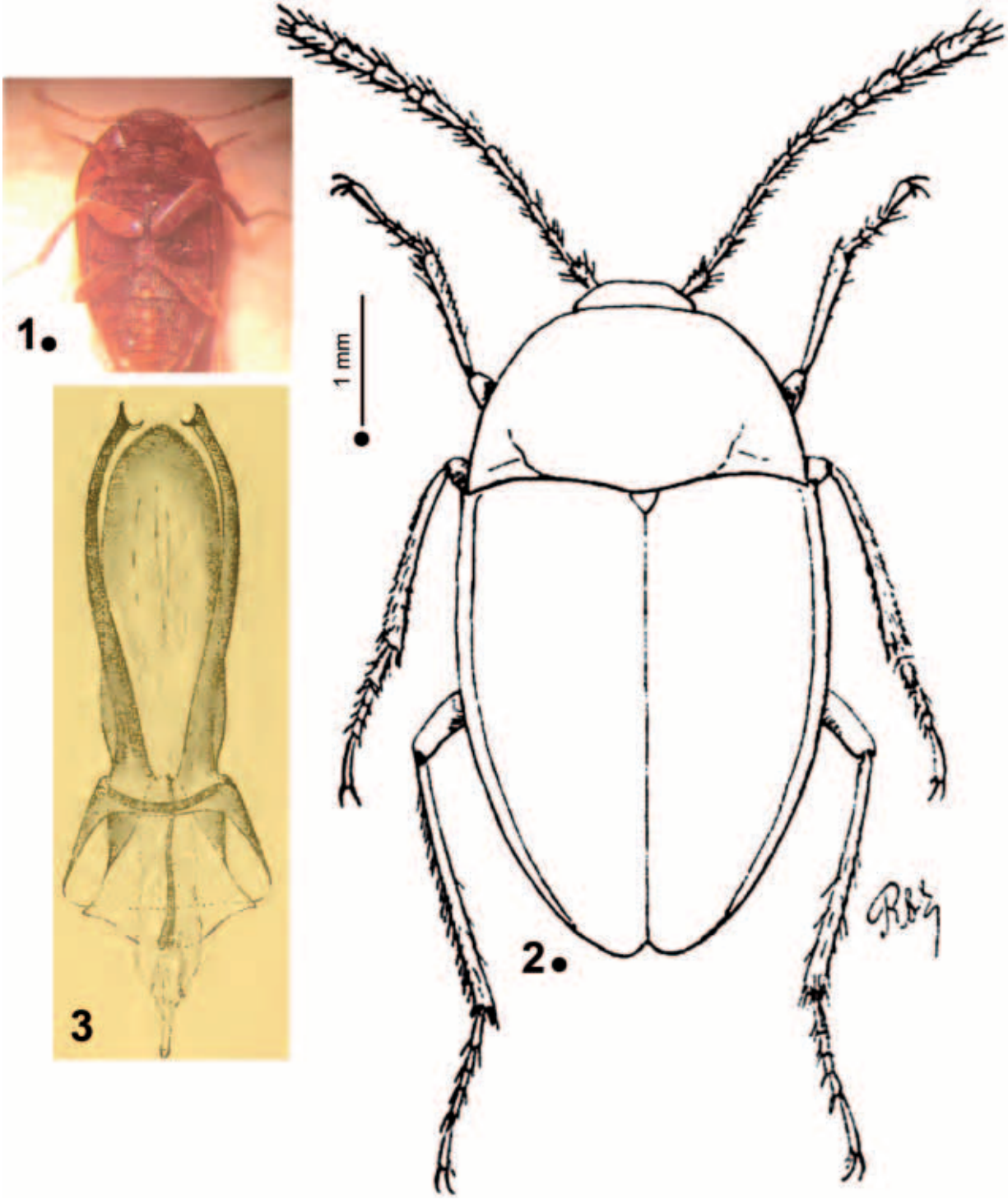
Speonesiotes* (*Kulzeria*) *laticollis G. Müller, 1934
Speonesiotes Dorotkanus laticollis G. Müller, 1934: 179.
Speonesiotes (*Kulzeria*) *laticollis* J. Müller: Jeannel, 1941: 117.

Speonesiotes* (*Kulzeria*) *matchai Fagniez, 1922
Speonesiotes (*Albanella*) *Matchai* Fagniez, 1922: 105.
Speonesiotes (*Kulzeria*) *Matchai* Fagniez: Jeannel, 1941: 119.
Speonesiotes (*Kulzeria*) *matchai* Fagniez: Perreau, 2000: 196.

Speonesiotes* (*Kulzeria*) *muelleri Jeannel, 1941
Speonesiotes (*Kulzeria*) *Mülleri* Jeannel, 1941: 116.
Speonesiotes muelleri Jeannel: Pretner, 1974: 10.
Speonesiotes (*Kulzeria*) *muelleri* Jeannel: Perreau, 2000: 196.

Subgenus ***Speonesiotes***

Diagnosis. Size small to very small, 1.8–3.0 mm. Fairly long antennae, extending well beyond the base of the pronotum and reaching halfway up the body; first antennomere shorter, or almost as long as the second; club antennomeres flattened and fine the 8th normally longer than wide. Elytra oval, short, between 1.25–1.3 times longer than wide, with maximum width at the base and apical areas widely arcuated or more or less cuneiform, with sides rectilinear backwards. Male protarsi dilated but narrower than the apex of the protibiae. Basal blade of the median lobe of aedeagus oval, quite long, with a tongue or extension (Fig. 130.10). Endophallus with a more or less developed basal armor formed by one or two pairs of elongated pieces, well sclerotized on the dorsal face of the basal region, without hyaline ampoule in the basal area (Fig. 132.5). Parameres thin with the apical area curved inwards and three setae, two apical with the in-



FIGURES 136.1–136.3: *Incertae sedis* in *Pholeuonopsis* group. Habitus of: (**1**) *Hoffmannella makarensis* (ventral view), (**2**) *Antrodulus occultus* (modified from Knirsch 1927). Aedeagus in dorsal view of: (**3**) *H. makarensis* (modified from G. Müller 1917).

sertion pores close together and one preapical, distant (Fig. 132.5, 133.13). The Female uroventrite VIII (Fig. 135.9) with two lobes on its basal margins similar to those in *Adelopsella*, and a «pore field» at the base of the spiculum.

DISCUSSION. In the phylogenetic tree (Fig. 1H) the subgenus *Speonesiotes* is recovered sister to the subgenus *Kulzeria* with a support of 93.7/100; both form a supported clade together with the subclade of *Proleonhardella*+ *Pholeuonopsis*+*Leonhardella* (100/100) to form the *Pholeuonopsis* group. In spite of the good node support of these two subgenera, there is a long genetic distance between them; the entire genus should be completely revised to determine the true taxonomic rank of the currently recognised subgenera.

DISTRIBUTION. The genus *Speonesiotes* colonises many caves in Bosnia-Herzegovina, Croatia and Montenegro. In Croatia the genus is found in Dalmatia, in Bosnia-Herzegovina in the southwest and in Montenegro in areas close to Bosnia-Herzegovina.

Species

Speonesiotes* (*Speonesiotes*) *gobanzi (Reitter, 1898)
Bathyscia Gobanzi Reitter, 1898: 339.
Bathyscia (*Aphaobius*) *Gobanzi* Reitt.: Ganglbauer, 1904: 652.
Speonesiotes Gobanzi Reitter: Jeannel, 1910a: 39.
Speonesiotes (s. str.) *Gobanzi* Reitter, 1898: Jeannel, 1924a: 289.
Speonesiotes (s. str.) *gobanzi* (Reitter): Perreau, 2000: 196.
Speonesiotes (*Speonesiotes*) *gobanzi* Reitter, 1898: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *insularis (Apfelbeck, 1907)
Bathyscia (*Aphaobius*) *insularis* Apfelbeck, 1907c: 319.
Speonesiotes insularis Apfelbeck: Jeannel, 1910a: 39.
Speonesiotes (s. str.) *insularis* Apfelbeck, 1907: Jeannel, 1924a: 289.
Speonesiotes (*Speonesiotes*) *insularis* Apfelbeck, 1907: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *issensis (G. Müller, 1903)
Bathyscia (*Aphaobius*) *issensis* G. Müller, 1903c: 194.
Bathyscina issensis J. Müller: Jeannel, 1908a: 299.
Speonesiotes issensis J. Müller: Jeannel, 1910a: 39.
Speonesiotes (s. str.) *issensis* J. Müller, 1903: Jeannel, 1924a: 289.
Speonesiotes (*Speonesiotes*) *issensis* Müller, 1903: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *narentinus (L. Miller, 1861)
Speonesiotes* (*Speonesiotes*) *narentinus latitarsis (Apfelbeck, 1919)
Bathyscia (Speonesiotes) latitarsis Apfelbeck, 1919: 272.
Bathyscia (*Bathysciola*) *latitarsis* Apfelbeck: Apfelbeck, 1920: 93.
Speonesiotes (s. str.) *narentinus* Subsp. *latitarsis* Apfelbeck: Jeannel, 1924a: 288.
Speonesiotes narentinus subsp. *latitarsis* Apfelb.: Winkler, 1925: 142.
Speonesiotes (*Speonesiotes*) *narentinus latitarsis* Apfelbeck, 1919: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *narentinus narentinus (L. Miller, 1861)
Adelops narentinus L. Miller, 1861: 266.
Adelops pruinosus Schaufuss, 1862b: 145.
Bathyscia (*Aphaobius*) *eurycnemis* Reitter, 1904a: 26.
Speonesiotes narentinus hirsutus Jeannel, 1910a: 38.
Adelops Narentina Mil.: Abeille de Perrin, 1878: 154.
Bathyscia narentina Mill.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *narentina* Mill.: Reitter, 1885a [1884]: 19.
Bathyscina narentinus Mill.: Jeannel, 1908a: 299.
Speonesiotes narentinus L. Miller: Jeannel, 1910a: 38.
Speonesiotes (s. str.) *narentinus* Subsp. *narentinus* L. Miller: Jeannel, 1924a: 288.
Speonesiotes (s. str.) *narentinus* Miller: Jeannel, 1941: 119.
Bathyscia pruinosa Schauf.: Schaufuss, 1881: xcvii.
Bathyscia (*Aphaobius*) *narentina* ssp. *eurycnemis* Reitter: Jeannel, 1907c: 63.
Speonesiotes narentinus subsp. *eurycnemis* Reitter: Jeannel, 1911a: 442.
Speonesiotes narentinus subsp. *hirsutus* Jeannel: Jeannel, 1911a: 442.
Speonesiotes (s. str.) *narentinus narentinus* (Miller): Perreau, 2000: 197.
Speonesiotes (*Speonesiotes*) *narentinus narentinus* Miller, 1861: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *narentinus simplicipes Jeannel, 1924
Speonesiotes (s. str.) *narentinus* Subsp. *simplicipes* Jeannel, 1924a: 288.
Speonesiotes (*Speonesiotes*) *narentinus simplicipes* Jeannel, 1924: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *paganettii (Ganglbauer, 1902)
Bathyscia (*Aphaobius*) *Paganettii* Ganglbauer, 1902: 45.
Aphaobius Paganettii Ganglb.: Weber, 1902: 17.
Bathysciina Paganettii Ganglb.: Jeannel, 1908a: 299.
Speonesiotes Paganettii Ganglbauer: Jeannel, 1910a: 39.
Speonesiotes (s. str.) *Paganettii* Ganglbauer, 1902: Jeannel, 1924a: 289.
Speonesiotes (s. str.) *paganettii* (Ganglbauer): Perreau, 2000: 198.
Speonesiotes (*Speonesiotes*) *paganettii* Ganglbauer, 1902: Perreau, 2004: 154.

Speonesiotes* (*Speonesiotes*) *pretneri G. Müller, 1934
Speonesiotes Pretneri G. Müller, 1934: 178
Speonesiotes (s. str.) *Pretneri* Müller: Jeannel, 1941: 124.
Speonesiotes (s. str.) *pretneri* Müller: Perreau, 2000: 198.
Speonesiotes (*Speonesiotes*) *pretneri* Müller, 1934: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *rambouseki Jeannel, 1941
Speonesiotes (s. str.) *Rambouseki* Jeannel, 1941: 123.
Speonesiotes (s. str.) *rambouseki* Jeannel: Perreau, 2000: 198.
Speonesiotes (*Speonesiotes*) *rambouseki* Jeannel, 1941: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *remyi Jeannel, 1941
Speonesiotes* (*Speonesiotes*) *remyi divinensis Jeannel, 1941
Speonesiotes (s. str.) *Remyi* subsp. *divinensis* Jeannel, 1941: 122.
Speonesiotes (s. str.) *remyi divinensis* Jeannel: Perreau, 2000:198.
Speonesiotes (*Speonesiotes*) *remyi divinensis* Jeannel, 1941: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *remyi remyi Jeannel, 1941
Speonesiotes (s. str.) *Remyi* subsp. *Remyi* Jeannel, 1941: 121.
Speonesiotes (s. str.) *remyi remyi* Jeannel: Perreau, 2000: 198.
Speonesiotes (*Speonesiotes*) *remyi remyi* Jeannel, 1941: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *remyi winkleri Jeannel, 1941
Speonesiotes (s. str.) *Remyi* subsp. *Winkleri* Jeannel, 1941: 121.
Speonesiotes (s. str.) *remyi winkleri* Jeannel: Perreau, 2000:198.
Speonesiotes (*Speonesiotes*) *remyi winkleri* Jeannel, 1941: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *schweitzeri Jeannel, 1941
Speonesiotes (s. str.) *Schweitzeri* Jeannel, 1941: 124.
Speonesiotes (s. str.) *schweitzeri* Jeannel: Perreau, 2000:198.
Speonesiotes (*Speonesiotes*) *schweitzeri* Jeannel, 1941: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *septentrionalis Winkler, 1935
Speonesiotes (s. str.) *septentrionalis* Winkler, 1935: 235.
Speonesiotes (*Speonesiotes*) *septentrionalis* Winkler, 1935: Perreau, 2004: 155.

Speonesiotes* (*Speonesiotes*) *spalacis Jeannel, 1941
Speonesiotes (s. str.) *spalacis* Jeannel, 1941: 122.
Speonesiotes (*Speonesiotes*) *spalacis* Jeannel, 1941: Perreau, 2004: 155.

Genus ***Tartariella*** Nonveiller & Pavićević, 1999
Tartariella Nonveiller & Pavićević, 1999: 322.

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Type species. *Tartariella durmitorensis* Nonveiller & Pavićević, 1999 by original designation (habitus in Fig. 126.1).

Diagnosis. Size between 3.7–4.4 mm. Body elongated and robust; facies pholeuonoid (Fig. 126.1); depigmented. Integuments light brown. Pubescence short and raised.

Head: Large, non-retractable, slightly longer than wide, without occipital keel. Pubescence long and fairly dense, characteristically arranged in the anterior dorsal part of the head, the hairs being longer than in other parts of the body. Punctation finely and evenly distributed. Anophthalmous.

Antennae: Long and slender, reaching two-thirds the length of the body, the first two antennomeres thicker than the following ones. The first is a little shorter than the second; the 11th antennomere flattened and a little longer than each of the previous two.

Pronotum: As long as wide, or slightly longer than

wide. Base rectilinear, as wide as the base of the elytra and wider than the anterior area; maximum width equal in the middle and at the base and clearly narrower than the width of the elytra. Lateral margins sinuous, arcuated towards the middle and more or less protruding, depending on the subspecies, with the anterior one rectilinear or slightly arcuated, the posterior one concave. Posterior angles sharp and protruding outward. Microsculpture very fine and dense; punctation fine and superficial.

Elytra: Ovoid, little convex, 1.5 times longer than wide; maximum width towards the posterior third. Lateral margins more arcuated posteriorly with apexes rounded. Punctation very fine, superficial and irregular; pubescence dense, short and lying. Parasutural stria absent.

Legs: Long, slender; without external spurs. Without combs or baskets, but apical area with a row of long robust bristles. Male protarsomeres tetramerous non-dilated.

Mesoventral keel: Lacking.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and robust. In lateral view (Fig. 131.1), ventrally unarcuated and sinuated, dorsally arcuated to the strong apical depression; apex in narrow lamina, sharp and curved towards ventral face. In dorsal view (Fig. 132.6), wide with sides subparallel and slightly arcuated; very narrow apical part in the shape of an isosceles triangle; apical blade flattened and narrow, the vertex more or less sharp. Basal blade broad and oval, with a marked, narrow and sharp tongue over the median area of the posterior edge.

Endophallus (Fig. 132.6): Without basal stylus; bottom of the sac with two little sclerotized and dentiform structures on sides, and two, very narrow, short, spiny bands in its middle apical area.

Parameres (Fig. 133.14): Shorter than the median lobe, thin and of uniform thickness up to the apical club, which is fusiform, slightly enlarged at the base, concave in the inner median area, and narrow and rounded at the apex. Three long, inwardly directed setae of similar length, two apical with closely spaced insertion pores and one subapical, with a pore more or less distant from the previous two.

Spermathecal complex: Spermatheca (Fig. 134.10) short, sickle-shaped, uniformly sclerotized, with the basal part more dilated in the anterior part and very narrow in the posterior part; the apical part curved, narrow and rounded apex, no different from the joint duct.

Female uroventrite VIII: Unknown.

Discussion. No molecular data available. Nonveiller & Pavićević (1999) pointed out that because of the general shape of the body, but especially because of many similar morphological characters and a great resemblance in the genitalia, the genus *Tartariella* is close to the genus *Leonhardella*. Giachino *et al*. (2021) also pointed out that this tetramerous and hygropetricolous genus is close to *Leonhardella*.

Distribution. Monospecific genus whose specimens are found in deep areas on very damp walls, but not immersed in water. It inhabits the «Jama na Vjetrenim brdima» cave and the «Zelenovirska pecina» cave, both on Mount Durmitor, in Montenegro.

Species

Tartariella durmitorensis Nonveiller & Pavićević, 1999
Tartariella durmitorensis durmitorensis Nonveiller & Pavićević, 1999
Tartariella durmitorensis durmitorensis Nonveiller & Pavićević, 1999: 322.

Tartariella durmitorensis zephyrensis Nonveiller & Pavićević, 1999
Tartariella durmitorensis zephyrensis Nonveiller & Pavićević, 1999: 324.

Genus ***Weiratheria*** Zariquiey, 1928
Weiratheria Zariquiey, 1928 [1927]: 155.

Type species. *Weiratheria Bocki* Zariquiey, 1928 by monotypy (habitus in Fig. 126.2).

Diagnosis. (from Zariquiey 1928): Size 2.5 mm. Facies bathyscioid, with body shape ovoid, wide and slightly narrowed posteriorly (Fig. 126.2). Colour dark reddish. Pubescence golden, fine, short and recumbent, with the exception of two rows of long, raised setae, one along the outer edge of the elytra, and the other along the median apical area.

Head: With marked faint occipital carina, without eyes.

Antennae: Short, reaching only to the base of the pronotum or slightly beyond,. First antennomere very slightly shorter than the second. Antennomeres 4th, 5th and 6th of similar length and width; club clearly thickened, with the antennomere 8th ovoid, slightly longer than wide. 11th antennomere almost as long as the sum of the lengths of 9th and 10th antennomeres, the latter being slightly longer than wide.

Pronotum: Transverse and only slightly convex, almost twice as wide as long, with the sides evenly arched, not narrowed behind and slightly sinuate in the basal area. Maximum width at the base, which is as wide as the anterior area of the elytra. Basal angles acute, with rounded apices, slightly protruding backwards. Surface of disc shiny, with microsculpture consisting of an abundant punctation of very fine dots.

Elytra: Ovoidal, stocky, without parasutural stria.

Legs: Short and fairly robust; protibiae without a comb on the apical and outer margins; an irregular series of robust spines is present on outer margin. Protarsi tetramerous and only slightly dilated. Mesotibiae slightly arched, metatibiae straight, both with strong spines on the outer margin.

Mesoventral keel: High and short, with a rounded apex and obtuse angle; the posterior extension does not reach the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Wide and short. Lateral view unknown. In dorsal view (Fig. 132.7), sides subparallel up to near the apex, then narrow sharply to form a triangular structure with subrectilinear sides and a slightly pointed apex. Basal lamella of median lobe well developed with arched posterior margin and a long, pointed tongue.

Endophallus (Fig. 132.7): Middle basal area with bilobed, hyaline ampulla and a long stylet or flagellum, with wider, recurved basal area.

Parameres (Fig. 133.15): Narrow, slightly arched and shorter than the median lobe. Apical club very poorly differentiated, bearing three fairly long setae of similar length: two apical with insertion pores close together and the third more distant and inserted on the inner margin. Ventral blade of tegmen as long and slightly wider than basal blade of median lobe.

Female: Unknown.

Discussion. Zariquiey (1928) pointed out that *Weiratheria*, with its tetramerous male protarsi, without an apical comb, should be included in the «Théléomorphes» of group II of Jeannel (1924a). *Weiratheria* having the 1st antennomere shorter than the 2nd, a stylus in the basal armour of the endophallus, in addition to a similar shape in the apical area of the median lobe and a tongue in the basal lamina. It should belong to the *Leonhardella* phyletic series, close to *Proleonhardella*. V.B. Guéorguiev (1976) also included it in the Bathysciina subtribe, as did Perreau (2000), who placed it close to *Proleonhardella* and in the «*Leonhardella*» phyletic series. Its position in the phylogenetic tree is currently unknown, as no molecular studies have been carried out.

Distribution. Monospecific genus only known from a small unnamed cave near Katun on Kućі plateau, northeast of Podgorica, Montenegro (Perreau 2000).

Species

Weiratheria bocki Zariquiey, 1928
Weiratheria Bocki Zariquiey, 1928 [1927]: 156.
Weiratheria bocki Zariquiey: Perreau, 2000: 190.

3.2.6 *Incertae sedis* in ***Pholeuonopsis*** group

3.2.6.1 Genus ***Pseudobathyscidius*** Karaman, 1964
Bathyscidius (*Pseudobathyscidius*) Karaman, 1964: 30.
Pseudobathyscidius Karaman 1964: V.B. Guéorguiev, 1976: 102.

Type species. *Bathyscidius* (*Pseudobathyscidius*) *serbicus* Karaman 1964 by original designation (habitus in Fig. 126.3).

Diagnosis. Small size, between 1.8–2.0 mm. Body short, regular oval-shaped, very convex and neither laterally compressed nor posteriorly narrowed; bathyscioid facies (Fig. 126.3). Fine microsculpture, reticulate on the elytra but not transversely aligned.

Head: Retractable, with blurred occipital carina; anophthalmous.

Antennae: Short, slender, slightly exceeding the base of the pronotum; first antennomere shorter than the second one.

Pronotum: Very convex and transverse, sides regularly arched with the greatest width at the base, which is not sinuate.

Elytra: Oval, slightly longer than wide, widest at base; lateral margins regularly curved to the apex, the latter rounded; no parasutural stria.

Legs: moderately short and robust; protarsi tetramerous and undilated in both sexes; protibiae without external spurs, but with a comb on the lateral and apical margins; meso- and metatibiae with apical basket.

Mesoventral keel (Fig. 127.8): High; the anterior border convex, the apex rounded and the angle obtuse; the posterior border process extends over much of the metaventrite.

Suture of the metaventrite, *metatergal apparatus*, and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and fairly stocky. In lateral view (Fig. 131.2), thick, slightly arched, with a short, thick and pointed apex. In dorsal view (Fig. 132.8), the sides are subparallel to a short apical area that narrows sharply and forms a triangular structure with a blunt tip. Basal lamina short, posterior margins arched.

Endophallus (Fig. 132.8): No «Y»-piece in the basal area, but on the dorsal wall of this area there are sclerotized stems arranged in pairs and small scaly spots on the sides.

Parameres: Shorter than the median lobe; thick in the basal third, thin and straight in the two apical thirds; apical area not thickened, armed with three short setae inserted at the apex. Ventral lamina of tegmen slightly wider and about as long as the basal lamina.

Female: Unknown.

Discussion. The only known specimen is the male described by Karaman (1964), who established *Pseudobathyscidius* as a subgenus of *Bathyscidius*. V.B. Guéorguiev (1976) elevated this subgenus to the rank of genus, while Giachino (2006), on the basis of morphological similarities and male genitalia, proposed the synonymy of *Pseudobathyscidius* with *Bathyscidius*. A little later, Perreau (2008) discussed at length the possible phyletic relationships between the different genera in this group, while highlighting the serious damage suffered by the only known specimen of this species. Perreau (2008) stated: «….The only known specimen of *Pseudobathyscidius serbicus* Karaman is in a very bad state of conservation, the aedeagus is broken, and pieces are missing. There remains the parameres, disconnected, the internal sac of the median lobe except the very basal part and pieces of the external part of the median lobe. The endophallus has a basal sclerotized piece which has an indefinably «Y»-shape in some way similar to that of *Sphaerobathyscia*. The basal parts of the tegmen and the median lobe are destroyed, precluding any direct observation of their lengths…». Perreau (2008) also stressed that this synonymy is unlikely and followed the criteria of V.B. Guéorguiev (1976), when he pointed out as important separating characters the differences that exist in the shape of the less laterally compressed body, the absence of transverse striolae in the elytra, the shorter posterior process of the mesoventral keel and, above all, the thicker and more curved shape of the aedeagus, in lateral view; the basal lamina of the median lobe shorter and the basal area of the endophallus with sclerotized pieces. As mentioned above, Perreau (2019) provided a cladistic analysis on a morphological basis of Bathysciotina (sensu V.B. Guéorguiev, 1976) and placed the genera *Bathyscidius*, *Pavicevicia* and *Ravasinia* in the same clade. Similarly, Polak & Jalžić (2019) proposed that *Pseudobathyscidius* is a good genus and is independent of *Bathyscidius*. For all these reasons, *Pseudobathyscidius* will be treated here as a valid genus. Apparently, *Pseudobathyscidius* shows affinities with *Bathyscidius*, mainly due to its external morphological features, however its endophallus armed with sclerotized structures distances it from the genera *Bathyscidius*, *Pavicevicia* and *Ravasinia* with which it was associated.

The aedeagus is very similar to that of the genera in the *Pholeuonopsis* group of the *Anthroherpon* series: it is extremely similar to the aedeagus of *Anisoscapha* (Figs 131.6, 132.8).

– Like all the genera in this group, *Pseudobathyscidius* has an equal extension of the apex of the median lobe, both laterally and dorsally.

– Like *Anisoscapha*, it lacks the prolongation of the basal lamina present in *Speonesiotes, Tartariella, Leonhardella, Augustia, Pholeuonopsis, Proleonhardella* and *Weiratheria*.

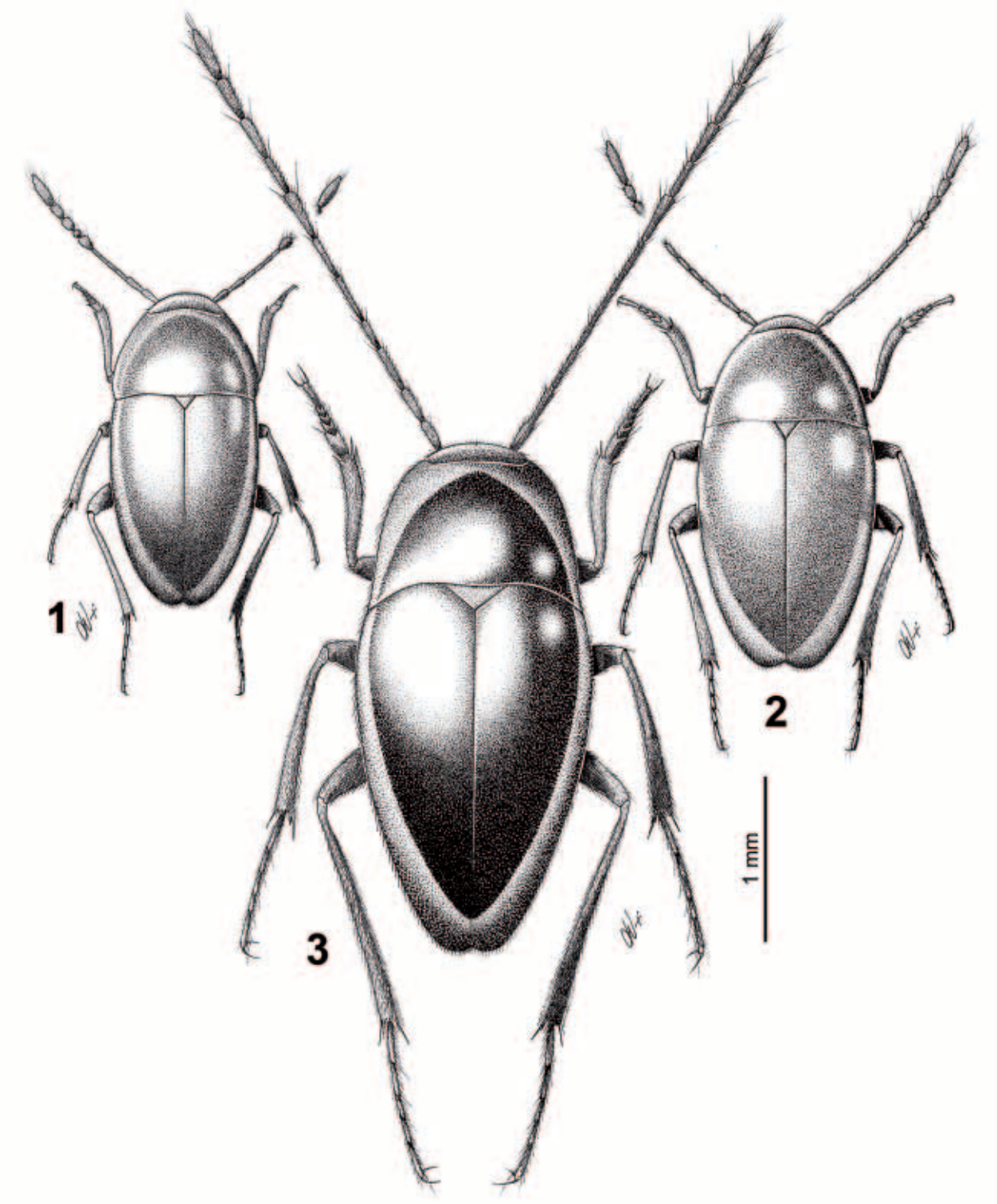
– It shares with *Anisoscapha* and *Speonesiotes* the existence of two symmetrical sinuous pieces in the apical region of the endophallus; its shape is closer to that of *Anisoscapha*.

– It shares with *Speonesiotes*, *Tartariella*, *Leonhardella, Augustia* and some *Proleonhardella*, the existence of two parallel sclerotized phanerae in the basal region of the endophallus, a stylet in *Anisoscapha*, *Pholeuonopsis* or *Weiratheria.*

– *Pseudobathyscidius* has protibiae with a comb on the lateral and apical margins and without external spurs, like *Speonesiotes,* although in this genus the most apical spine is thickened with the appearance of an external apical spur; in *Anisoscapha* the protibiae have no comb on the external and apical margins, with only an external spur, as in the other genera of the *Pholeuonopsis* group.

Numerous morphological characteristics suggest to place *Pseudobathyscidius* in the *Pholeuonopsis* group of the *Anthroherpon* series, but this is not the case when we look at their distributions. *Pseudobathyscidius* is considerably separated from the range of the genera in the *Pholeuonopsis* group, since it is found eastwards, near the border with Bulgaria. A marked hiatus between the two distributions is evident, occupying the whole of central Serbia.

In order to clarify all these doubts about the phylo-



FIGURES 137.1–137.3: *Boldoria* series. Habitus of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii.*

genetic relationships of *Pseudobathyscidius*, it will be essential to collect fresh specimens and carry out a molecular study.

DISTRIBUTION. The only known specimen was caught around the Zajecar district in central Serbia.

Species

Pseudobathyscidius serbicus (Karaman 1964)
Bathyscidius (*Pseudobathyscidius*) *serbicus* Karaman 1964: 30.
Pseudobathyscidius serbicus Karaman: V.B. Guéorguiev, 1974a: 841.

3.2.6.2 Genus ***Henrotiella*** Perreau, 1999
Henrotiella Perreau, 1999: 399.

TYPE SPECIES. *Henrotiella eubeensis* Perreau, 1999 by original designation (habitus in Fig. 126.4).

DIAGNOSIS. (from Perreau 1999): Size between 1.8–1.9 mm. Body of bathyscioid shape, oval and very convex (Fig. 126.4). The sides of the body are regularly arched, with the sides of the pronotum and elytra in perfect continuity with each other. The entire body is covered with a very fine, short golden pubescence.

Head: With blunt or blurred occipital carina, without eyes.

Antennae: First antennomere is much shorter than the second one. Club antennomeres 8th, 9th and 10th transverse and 11th as long as the preceding two.

Pronotum: Transverse, with the greatest width at the base; disc with extremely fine punctation.

Elytra: Very convex, devoid of parasutural stria and transverse striolae. With maximum width at the anterior fifth.

Legs: Males protarsi tetramerous and not dilated. Front tibiae without comb on the outer edge; meso- and metatibiae without apical basket. Unarmed tibial spurs.

Mesoventral keel (Fig. 127.9): High, well-developed, slightly toothed in lateral view, pubescent and not extended on the metaventrite. In ventral view, in shape of a triangle-shaped, wide at the base and thinned in front, bordered on the lateral margins.

Suture of the metaventrite and *metatergal apparatus*: Unknown.

Metendosternite (Fig. 129.7): «V»-shape, with the furcal trunk extremely reduced and furcal arms very thin and spread apart. Apophysis of the arms well-developed.

Median lobe of aedeagus: Of peculiar shape. The ventral valves, which close the apical ostium, are very elongated extending beyond the apex of the median lobe. In lateral view (Fig. 131.3) it is slightly arched, with a very large basal blade, equipped with a dorsal digitiform expansion. In dorsal view (Fig. 132.9) it is elongated and rounded at the apex.

Endophallus (Fig. 132.9): Formed by a complex structure, consisting of an evident basal «Y»-piece, similar to a single lamella, by an «M»-shaped median phanera and by two sclerotized, parallel, apical lamellae.

Parameres (Fig. 133.16): Thin, as long as, or a little bit shorter than the median lobe; without apical club and equipped with three apical setae of equal length.

Spermathecal complex: Spermatheca (Fig. 134.11) elongated, showing two sclerotized lobes separated by a membranous area. The basal lobe is about twice the size of the apical one. Ductus distally sclerotized, before insertion into the spermatheca.

Female uroventrite VIII (Fig. 135.10): Strongly transverse, with slightly cleft distal edge and short and stocky ventral spiculum.

DISCUSSION. As no molecular data on *Henrotiella* are available, its attribution is based solely on morphology. The morphological description of Perreau (1999) was improved by B.V. Guéorguiev (2007) in particular for the description of the endophallus and the figure of the metendosternite. B.V. Guéorguiev (2007), taking up the hypothesis of Perreau (1999), likened *Henrotiella* to the «Théléomorphes» of Division II of Jeannel (1924a) and, in particular, to the genera *Augustia* and *Weiratheria*. The molecular data available on the tribe Leptodirini demonstrate beyond doubt that the phenomenon of tetramerism in male protarsi is distributed along the phylogenetic tree in different clades, which have appeared independently on different occasions. As a result, all hypotheses of phyletic groupings based on this character and, in particular, the so-called «Théléomorphes» (*sensu* Jeannel, 1924a) fall by the wayside. The phyletic affinities of *Henrotiella* will probably be sought, when molecular data will be available, in certain genera (not necessarily with tetramerous protarsi) that are geographically closer, rather than in taxa from Bosnia-Herzegovina or Montenegro. However, the structure of the aedeagus with an extension of the basal lamina and an extension of the tip exactly coincides with the generalised pattern in the *Pholeuonopsis* group of the *Anthroherpon* series in the genera: *Albanella, Anillocharis, Augustia, Blattochaeta, Leonhardella, Pholeuonopsis, Proleonhardella, Speonesiotes, Tar-*

tariella or *Weiratheria*; their relationship with this clade is also plausible according to biogeographical criteria: the Dinarids extend across Epirus and Central Greece to the island of Euboea.

Distribution. Greece, Euboea island, Karystos, Ayia Triada cave.

Species

Henrotiella eubeensis Perreau, 1999
Henrotiella eubeensis Perreau, 1999: 400.

3.2.7 *Incertae sedis* in series ***Anthroherpon***

3.2.7.1 Genus ***Hoffmannella*** G. Müller, 1912
Bathyscia (*Hoffmannella*) G. Müller, 1912: 300.
Bathysciola (*Hoffmannella*) J. Müller: Jeannel, 1914b: 13.
Hoffmannella Müller, 1912: Jeannel, 1924a: 51.

Type species. *Bathyscia* (*Hoffmannella*) *makarensis* G. Müller, 1912 by original designation (habitus in Fig. 136.1).

Diagnosis. (from G. Müller 1912): Size about 2.0 mm. Body shape wide, oval, somewhat narrowed backwards and quite convex; bathyscioid facies (Fig. 136.1). Depigmented.

Head: With complete occipital carina; anophthalmous.

Antennae: Short and thin, with the first antennomere thicker and as long as the second; the 11th somewhat thicker and less than twice the length of the 10th, with the articles of the club slightly thickened.

Pronotum: Transverse, sides regularly arched that widening towards the base, which is the area with the maximum width and as wide as the anterior area of the elytra.

Elytra: Short, with maximum width in the basal area; apical area narrowed in the proximity of the apices; visible, numerous and not ordered stippling; arched and well-defined parasutural stria.

Legs: Short, rather slender. Males protarsi of five tarsomeres very slightly dilated; tibiae almost unarmed; protibiae with two external spurs and no comb on the apical and external edges; meso- and metatibiae with external spurs and without apical baskets.

Mesoventral keel: High, in form of a triangular sheet; in lateral view, the anterior edge is slightly convex, rounded vertex and straight ventral edge with the posterior extension reaching the posterior edge of the metaventrite; in ventral view, ventral edge anteriorly narrow, then, widening, with the edges on the sides delimiting a sulcus.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus (Fig. 136.3): Short and slightly arched. In dorsal view, arched sides narrowing progressively towards the apex in a slightly narrowed arc. Basal lamina well-developed, longer and as wide as the ventral lamina of tegmen.

Endophallus (Fig. 136.3): Basal region with a fairly robust and voluminous stylet, as well as thick teeth and some spines or scaly structures.

Parameres: Slightly arched and slightly thickened, narrowed in the apical area with the apex armed with two very short and robust setae, resembling two conical teeth.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Several clues, both morphological and biogeographical, suggest that *Hoffmannella* should be included in the *Anthroherpon* series, although its position in this series is certainly enigmatic. The fundamental differentiating feature of this genus is the armoring of the apical part of the parameres of the aedeagus with two short, very robust setae. There are no molecular data to enable us to assign this genus a position in the phylogenetic tree. Their relationships are somewhat uncertain. Jeannel (1924a) highlighted some characters of the external morphology and the aedeagus, and concluded that *Hoffmannella* is a genus close to *Speocharis* (= *Quaestus*): close to *Quaesticulus adnexus*. An error in the location of the specimens is possible, but the collector, Adolf Hoffman (Wien), is not known to have collected in Spain; moreover, he gives precise details of the discovery between 17 and 23 May 1913 on the slopes of Biokovo (Nonveiller 1999). It is possible that V.B. Guéorguiev (1976) and Newton (1998) followed R. Jeannel's criterion in placing *Hoffmannella* in the subtribe Pholeuonina or Pholeuina. Perreau (2000) placed it in the *Spelaeochlamys* series. But the ranges of *Hoffmannella* and *Quaestus* or *Spelaeochlamys* are considerably apart, and the ranges of hundreds of species belonging to other series are interspersed between them. *Hoffmannella* should probably be included in the *Anthroherpon* series; an endophallus with a stylet in its basal region is found in several genera distributed throughout the same region of *Hoffmannella*: *Weiratheria* or *Anisoscapha* (*Pholeuonopsis* group). However, it bears a striking resemblance to the aedea-

gus of *Leptomeson* (*Anthroherpon* group). The bathyscioid aspect of *Hoffmannella* contributed, along with other morphological elements, to its inclusion in the *Quaestus* or *Spelaeochlamys* series; but we now know that several of the possible forms of Leptodirini can be found in each of the clades: *Speonesiotes* and *Pholeuonella* (bathyscioids from basal cladogenesis) as well as *Anthroherpon* and *Hadesia* (leptodiroids/ scaphoids originating from derived cladogenesis).

In conclusion, given its biogeographical range and the aedeagus structures reported in relation to the above genera, we propose to include *Hoffmannella* in the *Anthroherpon* series, as an «*incertae sedis*» genus possibly close to *Leptomeson*, until molecular data are available to determine its phylogenetical position.

Distribution. Croatia. Monospecific genus located near the town of Makarska in the Biokovo mountains near the Adriatic coast, in central Dalmatia.

Species

Hoffmannella makarensis (G. Müller, 1912)
Bathyscia (*Hoffmannella*) *makarensis* G. Müller, 1912: 300.
Bathysciola (*Hoffmannella*) *makarensis* J. Müller: Jeannel, 1914b: 13.
Hoffmannella makarensis J. Müller, 1912: Jeannel, 1924a: 52.

3.2.7.2 Genus ***Antrodulus*** Knirsch, 1927
Antrodulus Knirsch, 1927a: 11.

Type species. *Antrodulus occultus* Knirsch, 1927 by original designation (habitus in Fig. 136.2).

Diagnosis. Medium size, 4.5–5.5 mm. Bathyscioid facies (Fig. 136.2). Ovoid body, colour dark reddish-brown shiny, compressed and covered above with long and dense pubescence.

Head: Small, measured from anterior part of upper labrum to limit of occipital carina, as long as wide, densely punctate and very finely furrows; anophthalmous.

Antennae: Slender, reaching the basal quarter of the elytra. 1st antennomere nearly twice as long as wide and shorter than the 2nd; 3rd about as long as the first but longer than the 4th; the 5th almost as long as the 2nd; 6th only a little shorter than the 3rd; 7th almost twice as long as the previous; 8th small and subquadrate, as wide as long; 9th shorter than the 7th and of equal length to the 11th; 10th shorter than the 11th.

Pronotum: Transverse, nearly twice as wide as long, wider at the base and the base as wide or slightly narrower than the anterior margin of the elytra, curved forward, on the sides nearly semicircular and in the proximal third just noticible straight. Posterior edge, on both sides, clearly sinuate. Basal angles acute, projecting slightly backward.

Elytra: Rather broad, at base only slightly narrower than in the middle third. Sides posteriorly individually rounded. Shoulders almost right-angled, only very slightly curved. Without transverse striolation and no parasutural stria. Pygidium not visible from above.

Legs: Long and thin, with apical end of the fore tibia only slightly exceeding the anterior edge of the pronotum. Protarsi tetramerous and not dilated in males. Mesotibiae slightly arched and metatibiae straight.

Metaventrite: Metacoxae far apart; the metaventral process is enlarged accordingly, posterior part serrated and flat, with short and broad apophysis, blunt at the ends.

Mesoventral keel: Biangular, similar to that of the genus *Blattochaeta*; the ventral margin is not evenly extending but describe a curve in an «S»-shaped, more strongly anteriorly than posteriorly; rounded vertex or with curved teeth, depending on the species. Not exceeding the metaventrite.

Aedeagus, *spermathecal complex* and *female uroventrite VIII*: Unknown.

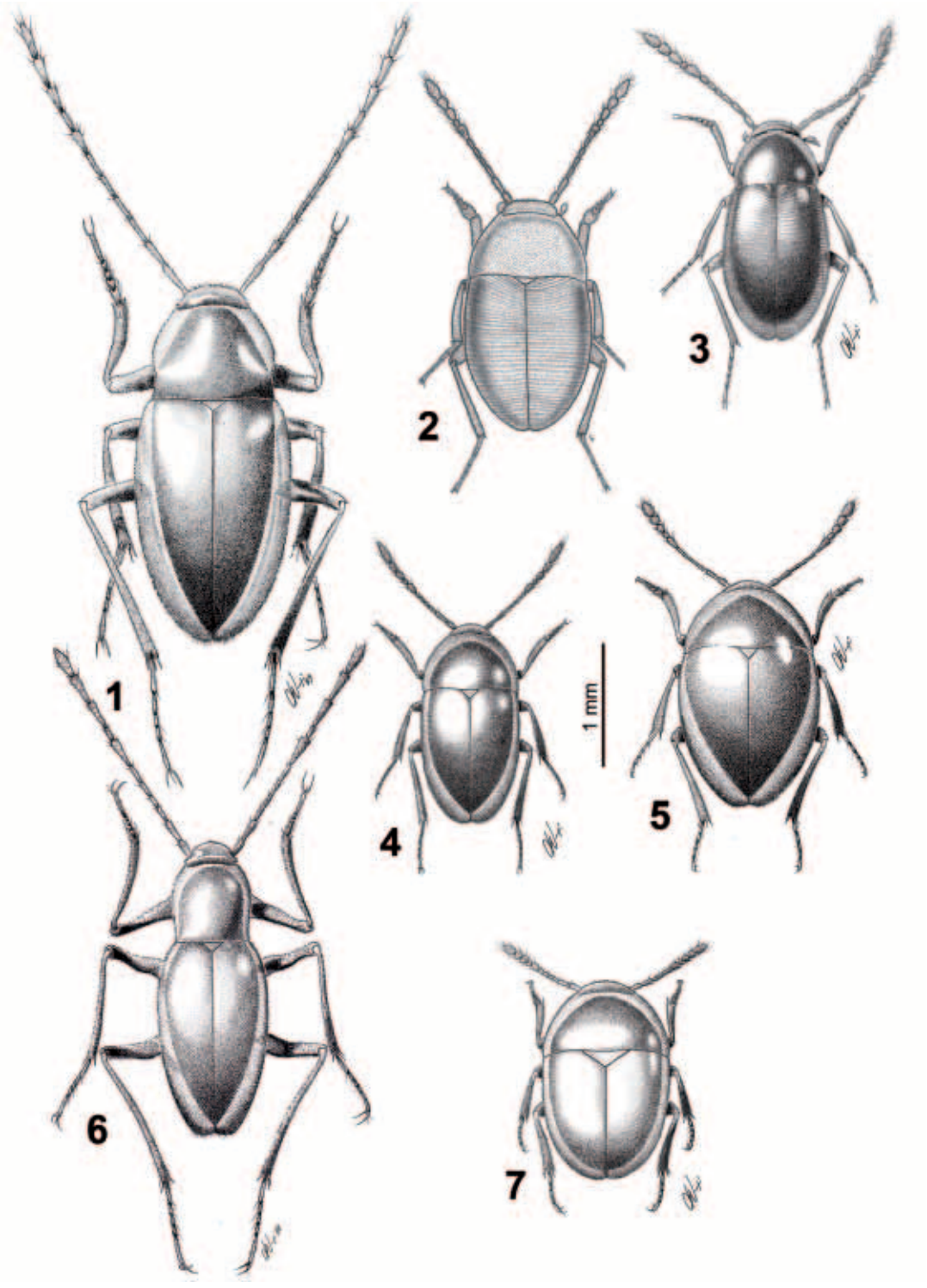
Discussion. Only two species are known and so far no further specimens were collected apart from the material of the original descriptions. However, the description of the species is based only on external characters. The poor information on these species limits the information useful for a taxonomic classification. In a cautious classification the characters known seem to suggest that they are part of the *Anthroherpon* series.

Distribution. Bosnia-Herzegovina, from unnamed cave in Prenj-planina and an endogean site in Crna Gora, south of Prenj-planina.

Species

Antrodulus aequibasalis Knirsch, 1929
Antrodulus aequibasalis Knirsch, 1929: 87.

Antrodulus occultus Knirsch, 1927
Antrodulus occultus Knirsch, 1927a: 11.



FIGURES 138.1–138.7: *Boldoria* series. Habitus of: (**1**) *Insubriella paradoxa,* (**2**) *Miettiella vespertilio* (modified from Piva 2016), (**3**) *Monguzziella grottoloi,* (**4**) *Pavaniola ghidinii ghidinii,* (**5**) *Ragazzonia vestae vestae,* (**6**) *Viallia alfanoi*, (**7**) *Cryptobathyscia gavardensis*.

3.2.8 Series ***Boldoria***

Diagnosis. Size between 1.4–3.3 mm. Depigmented and anophthalmous.

Antennae: Club developed with all antennomeres longer than wide, except the 8th.

Elytra: With transverse striolation and without parasutural stria.

Mesoventral keel: Prolonged on the metaventrite, with a non-toothed vertex, except the genus *Cryptobathyscia* (*incertae sedis*).

Metendosternite: «V»-shaped, with not-triangular furcal arms.

Legs: Males protarsi pentameres; protibiae with complete apical baskets; polidentated and pectinate tibial spurs.

Discussion. This clade appears to include the following genera: *Cacciamalia*, *Viallia*, *Monguzziella*, *Ghidinia*, *Insubriella*, *Ragazzonia*, *Miettiella*, *Boldoria*, *Pavaniola* and as «*incertae sedis*» *Cryptobathyscia*. According to Vailati (2017) a number of genera, might be related to the genus *Cacciamalia*. This in turn would mean that it is likely that is placed in a series related to the *Anthroherpon* series. There are no molecular data available for this groups so we focus here in the position of *Cacciamalia*, as the supossingly most closely related genus which is included in the molecular analysis. In Tree-1 (Fig. 1H), *Cacciamalia* is sister of *Anthroherpon* series with a support of 85.8/42; in Tree-2 (Fig. 2) it is sister of *Hartigiella* with a support of 80.4/57 and the set with *Anthroherpon* + *Epiroella* (this last genus at the base of the complete *Anthroherpon* series) with support 86.1/57. This positions needs further confirmation by analysis including more molecular data of other genera in the series.

Key to genera

1. 11th antennomere very elongated with very sharp apex; with sinuate sides, narrowering towards the basal third, the length more than three times the width; the 9th antennomere very elongated, length more than three times width (except some species of *Cacciamalia*).....2
- 11th antennomere of a different shape, elongated oval, pyriform or rhomboid; the length is less than three times the width; 9th antennomere is the shortest, length less than three times width (except some species of *Viallia*, where the 11th is rhomboid).....4

2. Subpholeuonoid facies. First antennomere somewhat longer than the second. Pronotum with sinuated sides. Mesoventral keel low (Fig. 139.4), with posterior apophysis prolonged over the entire metaventrite, but without exceeding it..... *Insubriella*
- Bathyscioid facies. First antennomere shorter than the second. Pronotum with sides not sinuated. Mesoventral keel high (Figs 139.2, 139.3), with posterior apophysis exceeds the entire metaventrite.....3

3. Median lobe of aedeagus, in lateral view (Fig. 144.2), with the apex thinned and bent upwards like a goose beak; in dorsal view (Fig. 146.2), not lanceolate and in the apical centre with a small protrusions. Endophallus (Fig. 146.2) with atrophic basal «Y»-piece; no phanerae in the median and apical regions. Female uroventrite VIII with an almost non-existent spiculum (Fig. 149.2).....*Cacciamalia*
- Median lobe of aedeagus, in lateral view (Fig. 144.3), with thinned apex, from straight to slightly bending upwards; in dorsal view (Fig. 146.3), with the apical area lanceolated, triangular, and in the centre without protruting parts. Endophallus (Fig. 146.3) with basal «Y»-piece well sclerotized; median region with phanerae central sclerotized; apical region with two sclerotized reinforcing bands, sub-parallel and sinuated. Female uroventrite VIII spiculum short, with the apex rounded or bilobed (Fig. 149.3) .....*Ghidinia*

4. 11th antennomere with the maximum width in the middle, rhomboid; the 8th, 9th and 10th antennomeres at least two and a half times longer than wide. Pholeuonoid or bathyscioid facies. Median lobe of aedeagus, in dorsal view (Fig. 147.4), regularly ogive-shaped not pointed, without protruding parts in the mid-apical part. Endophallus (Fig. 147.4) with atrophic basal «Y»-piece; middle region without phanerae and apical region without reinforcing bands. Female uroventrite VIII spiculum not developed, only a slight and largely obtuse protrusion (Fig. 149.9) .....
.....*Viallia*
- 11th antennomere with the maximum width towards the base, elongated oval or pyriform; the 9th and 10th antennomeres less than twice as long as wide, the 8th generally transverse or slightly longer than wide. Facies always bathyscioid. Median lobe of aedeagus, in dorsal view (Figs 146.1, 146.5, 147.1–147.3), in the apical centre with or without protrusion. Endophallus (Figs 146.1, 146.5, 147.1–147.3) with basal «Y»-piece more or less developed, generally with a sclerotized structure in the middle region and apical region with or without reinforcing bands. Female uroventrite VIII

spiculum short (Figs 149.1, 149.8) or non-existent (Fig. 149.6) 5

5. 11th antennomere pyriform. Median lobe of aedeagus (Figs 146.5, 147.1, 147.3) with wide apical part and a small central prominence at the apex. Apical region of the endophallus (Figs 146.5, 147.1, 147.3) with reinforcing bands well or poorly defined 6
- 11th antennomere elongated oval. Median lobe of aedeagus (Figs 146.1, 147.2) with narrow apical part, lanceolate shape, without central protrusion at the apex. Apical region of the endophallus (Figs 146.1, 147.2) without reinforcing bands 8

6. Mesoventral keel with posterior apophysis beyond the entire metaventrite (Fig. 140.4). Endophallus (Fig. 147.3) with large basal «Y»-piece; median region with phanera large, complex, with sclerotized arms and surrounded by spiny structures; apical region with two symmetrical sclerotized reinforcing bands diverging towards the apex .....*Ragazzonia*
- Mesoventral keel with posterior apophysis prolonged, reaching only a short part on the metaventrite (Figs 140.1, 140.2). Endophallus (Figs 146.5, 147.1) with poorly defined basal «Y»-piece; median region if there is phanera otherwise, just like reinforcing bands of the apical region 7

7. Mesoventral keel moderately high (Fig. 140.1). Endophallus (Fig. 146.5) in the median region with a phanera complex, large and well sclerotized, shape bat-like appearance; apical region with reinforcing bands poorly defined. Parameres clearly shorter than the median lobe. Female uroventrite VIII with spiculum small and rounded apex (Fig. 149.5) ....*Mietiella*
- Mesoventral keel particularly low (Fig. 140.2). Endophallus (Fig. 147.1) in the median region without sclerotized phanerae, only membranous structures covered by very small spinulae; apical region with two weakly sclerotized reinforcing bands, sinuous and divergent. Parameres as long or nearly as long as the median lobe. Female uroventrite VIII without spiculum (Fig. 149.6) .....*Monguzziella*
8. Endophallus (Fig. 146.1) in the median region with a phanerae sclerotized, exceeded by a bilobed structure. Parameres with short three setae (Fig. 147.6) ....*Boldoria*
- Endophallus (Fig. 147.2) in the median region with a phanerae sclerotized, surrounded by silky-spiny and toothed structures. Parameres with very long and flagelliform three-four setae (Fig. 147.11) .....*Pavaniola*

Note. *Cryptobathyscia* is not included in the key, but the main differentiating characteristics are listed in the following: Antennae with the 1st antennomere slightly shorter than the 2nd, the 11th pyriform and the 8th, 9th and 10th antennomeres transverse; elytra with transverse striolation; mesoventral keel (Fig. 140.6) with vertex equipped with a weak tooth, ventral profile slightly sinuated, ventral edge flattened and rhombic; endophallus (Fig. 147.5) with two small sclerotized plates in the middle region; basal blade of the median lobe with a short, narrow and sharp tongue in the posterior middle part.

Genus ***Boldoria*** Jeannel, 1924
Bathysciola (*Boldoria*) Jeannel, 1924a: 117.

Type species. *Bathysciola* (*Boldoria*) *aculeata* Jeannel, 1924 by original designation (habitus in Fig. 137.1).

Diagnosis. Small size, 1.7–2.0 mm, bathyscioid body, elliptical and elongated (Fig. 137.1).

Antennae: Reach, lying backwards the basal third of the elytra. First antennomere much shorter than the second one; the 8th slightly longer than wide; the 11th lanceolate, and as long as the sum of the previous two plus half of the 8th one.

Pronotum: Evenly regularly rounded sides; maximum width just before the base which is slightly narrowed.

Elytra: With fine, but well marked, transverse striolae; without parasutural stria.

Legs: Males protarsi short and not very dilated, narrower than the apex of the protibia. Tibiae with inner polidentated spurs at the apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 139.1): High, with arched front edge but not very prominent forward, with a straight ventral profile, the angle slightly obtuse, almost straight, and rounded vertex. Posterior apophysis beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 141.1): Small and very short, with apophysis of the alacrista wide from half to one third of the length and the apexes sharp.

Metendosternite (Fig. 143.1): «V»-shaped, with non-triangular furcal arms. Arms long and narrow, two and a half times the length of the trunk with the posterior plate of similar width throughout; well-developed apophysis. Trunk short, twice as long as wide.

Median lobe of aedeagus: As long as a third of the body, stout. In lateral view (Fig. 144.1) appears obtusely bent, robust, with the apex not very thinned and

almost straight, very little flex down. In dorsal view (Fig. 146.1) it shows parallel lateral sides and ogival and pointed apex.

Endophallus (Fig. 146.1): Well-sclerotized and complex basal «Y»-piece. Median phanerae consisting of a sclerotized central plate exceeded by a bilobed structure; this structure shows two arms turned proximally and, distally, with two symmetrical and parallel bundles of spinules. Other sclerotized apical structures absent.

Parameres (Fig. 147.6): Robust, slightly shorter than the median lobe. Bearing three setae approximately of same length, two properly apical and one slightly more backward.

Spermathecal complex: Spermatheca (Fig. 148.1) with the proximal lobe slightly elongated and the distal spherical and more voluminous. Spermiduct with short part distally sclerotized for a short part and somewhat widened in the proximal part at its junction with the spermatheca.

Female uroventrite VIII (Fig. 149.1): Spiculum small, reduced to a small triangular tongue, little developed in length, with a rounded apex.

Discussion. In accordance to Vailati (2017), *Boldoria* differs from *Cacciamalia* by the apex of the median lobe of aedeagus symmetrical and downward facing. From *Cacciamalia, Viallia* and *Monguzziella*, it differs also by the presence of the basal «Y»-piece of the endophallus. From *Ghidinia* it differs by the apex of the median lobe of aedeagus not subtriangular. From *Ghidinia* and *Insubriella* it differs by the 8th antennomere being short, slightly longer than wide; while from *Ragazzonia* and *Pavaniola* it differs in the length of 11th antennomere, which is shorter in *Ragazzonia* and *Pavaniola*, and by the shape of the median phanera of endophallus. From *Pavaniola* differs also by the shorter parameres setae.

Distribution. Italy. Brescian Prealps, appears to be common and can be found in sites of a fairly limited geographical distribution rang in the the Palosso and Doppo mountains.

Species

Boldoria aculeata (Jeannel, 1924)
Bathysciola (*Boldoria*) *aculeata* Jeannel, 1924a: 117.
Boldoria (*Boldoria*) *aculeata* Jeannel, 1924: Ghidini, 1937: 62.
Boldoria s. str. *aculeata* Jeannel: Pavan & Ronchetti, 1950: 101.
Boldoria aculeata (Jeannel, 1924): Vailati, 1988: 231.

Genus ***Cacciamalia*** Vailati, 2017
Cacciamalia Vailati, 2017: 19.

Type species. *Boldoria* (s. str.) *glacialis* Vailati, 1975 by original designation (for the habitus see that of the similar species *Cacciamalia allegrettii* in Fig. 137.2).

Diagnosis. Medium size, 1.9–2.8 mm, bathyscioid body, elongated elliptical, more or less ogival posteriorly (Fig. 137.2).

Antennae: Slender and particularly elongated in males; stretched backwards, reaching from the middle to the distal quarter of the elytra. 1st antennomere, much shorter than the 2nd; the 8th elongated, from one and half times to more than two and half times longer than wide; the 11th extremely elongated, with sinuated sides, narrowed towards the proximal third, long from almost to longer than the sum of the previous three ones.

Pronotum: With regularly rounded sides, but also with a whiff of a slight sinuosity just in front of the basal angles, which are acute. Maximum width at the base.

Elytra: Generally wide, with maximum width not far from the base and with thick and well marked transversal striolae. Without parasutural stria.

Legs: Male protarsi moderately dilated, slightly narrower than or at most as wide as the apex of the protibia. Tibial apex with polidentate inner spurs; meso- and metatibiae with complete spiny apical baskets.

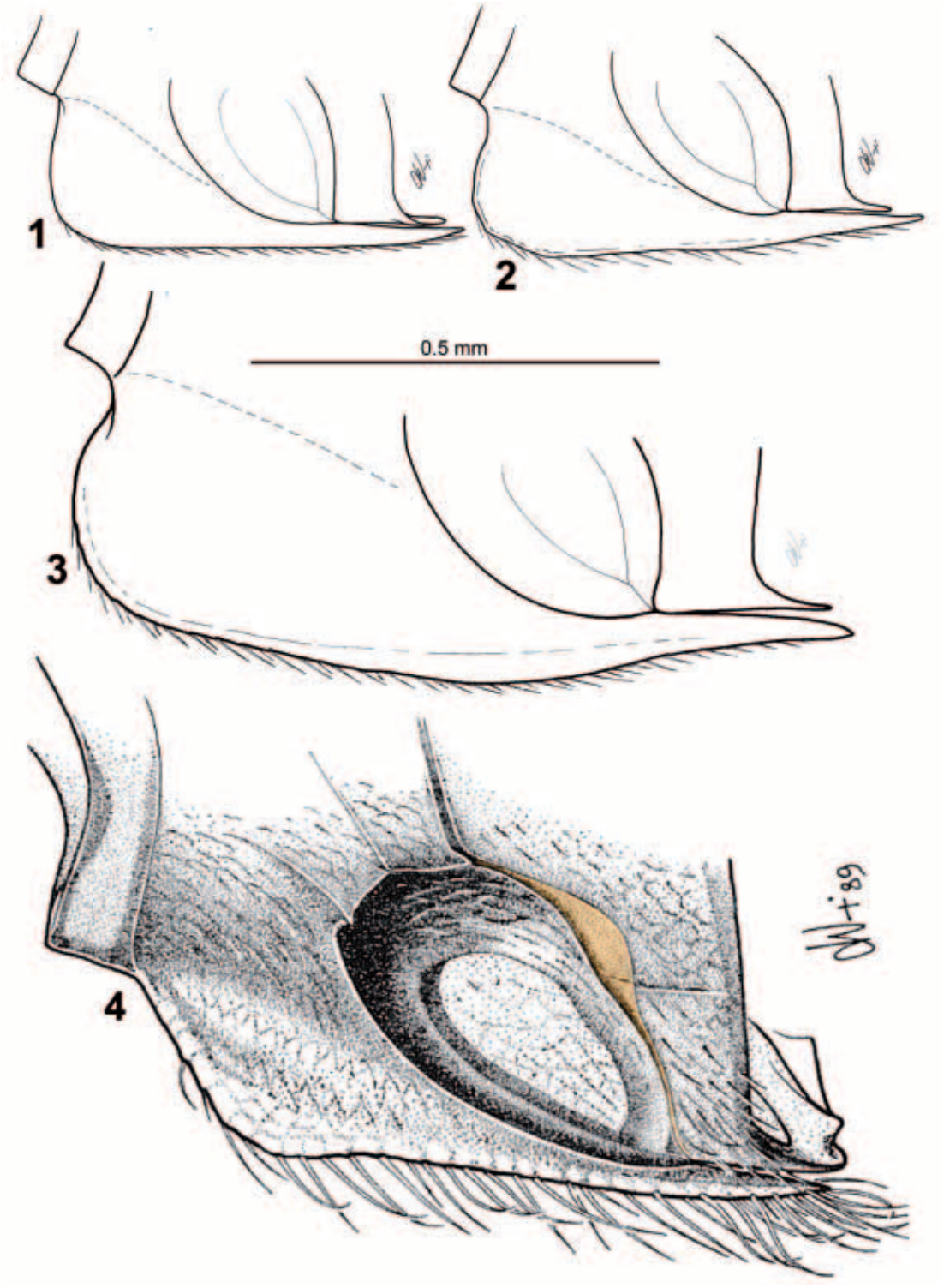
Mesoventral keel (Fig. 139.2): High, rounded, particularly prominent forward, with the ventral profile from straight to slightly curved and sinuous and rounded vertex; posterior apophysis exceeds the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 141.2): Very small and short apophysis of the alacrista with rounded or not very sharp apexes.

Metendosternite (Fig. 143.2): «V»-shaped, with non-triangular furcal arms; arms very long and narrow, slightly more than three times the length of the trunk, with well-developed apophysis; posterior plate of similar width along the entire length of the arm, with almost straight flange. Short furcal trunk, as long as widest area and median keel with elongated posterior divergence.

Median lobe of aedeagus: Relatively small, from a quarter to a third of the body length, stocky. In lateral view (Fig. 144.2), regularly curved, robust, with the apex thinned and bent upwards forming a structure of



FIGURES 139.1–139.4: *Boldoria* series. Pterothorax in lateral view of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii,* (**4**) *Insubriella paradoxa*.

a goose beak-likke appearance. In dorsal view (Fig. 146.2), with the sides parallel or slightly converging in the distal half; apex of ogival shape and equipped with a more or less pronounced apical tongue, truncated obliquely.

Endophallus (Fig. 146.2): Endophallus with atrophic basal «Y»-piece, little sclerotized and not vey apparent. The sclerotized median phaneres are also missing, replaced by membranous, sometimes spinulous bundles that extend to the apex.

Parameres (Fig. 147.7): Slim, slightly shorter than the median lobe; in dorsal view sinuate to the basal third, showing three short setae, two clearly apical and one situated slightly more backward.

Spermathecal complex: Spermatheca (Fig. 148.2) small, with the proximal part reniform, particularly curved and the distal part spherical, not very bulky; thin spermatic duct, somewhat dilated at the junction to the spermatheca, in the area where the spermathecal gland ends.

Female uroventrite VIII (Fig. 149.2): In the shape of a narrow half moon, spiculum absent, maximally reduced towards a median callous thickening just insinuated.

Discussion. In the phylogenetic tree (Fig. 1H) *Cacciamalia* appears, isolated as a separate phyletic series, as sister of *Anthroherpon* series with a low support 85.8/42.

Cacciamalia differs from all the other genera of the series *Boldoria* by the shape of antennae, with the last article being extremely elongated, much longer than the sum of the previous two e.g. sometimes as long as the sum of the previous three; the 11th antennomere with sinuated sides and narrowed in the basal third. In addition it differs in the shape of the median lobe of aedeagus, which equipped at the apex with a more or less apparent and asymmetrical tongue, peculiarly transversaly truncated and facing upwards with a goose beak-like structure. Perreau (2000) includes all species of this genus in the «*glacialis*» group of the genus *Boldoria*.

Distribution. Italy. Brescian Prealps: M. Guglielmo, medium and high altitude in the Val Trompia, the mountains between Val Trompia and Val Sabbia-Idro lake. In the Gardesane Prealps at medium-high altitude of Val Sabbia on the side facing to the west, M. Pizzocolo-Spino-Marmera group, medium and high altitude Val Vestino, Val d'Ampola; Southern Rhaetian Alps: Caffaro valley and lower Giudicaria.

Species

Cacciamalia allegrettii (Jeannel, 1930)
Bathysciola (*Boldoria*) *Allegrettii* Jeannel, 1930e: 224.
Boldoria (*Boldoria*) *Allegrettii* Jeannel, 1930: Ghidini, 1937: 57.
Boldoria s. str. *Allegrettii* Jeannel: Pavan & Ronchetti, 1950: 101.
Boldoria allegrettii (Jeannel): Vailati, 1979b: 133.
Boldoria (*Boldoria*) *allegrettii* (Jeann.): Alberti & Vailati, 1983: 207.
Cacciamalia allegrettii (Jeannel, 1930): Vailati, 2017: 20.

Cacciamalia antonellae (Vailati, 1988)
Boldoria antonellae Vailati, 1988: 162.
Cacciamalia antonellae (Vailati, 1988): Vailati, 2017: 20.

Cacciamalia glacialis (Vailati, 1975)
Cacciamalia glacialis filicornis (Vailati, 1979)
Boldoria (*Boldoria*) *glacialis filicornis* Vailati, 1979a: 7.
Boldoria glacialis filicornis Vailati: Vailati, 1983: 133.
Cacciamalia glacialis filicornis (Vailati, 1979): Vailati, 2017: 20.

Cacciamalia glacialis glacialis (Vailati, 1975)
Boldoria (*s. str.*) *glacialis* Vailati, 1975a: 26.
Boldoria (*Boldoria*) *glacialis* Vailati: Vailati, 1977: 69.
Boldoria glacialis Vailati: Vailati, 1983: 133.
Boldoria glacialis glacialis Vailati, 1975: Vailati, 1988: 172.
Cacciamalia glacialis glacialis (Vailati, 1975): Vailati, 2017: 20.

Cacciamalia glacialis monguzzii (Vailati, 1988)
Boldoria glacialis monguzzii Vailati, 1988: 180.
Cacciamalia glacialis monguzzii (Vailati, 1988): Vailati, 2017: 20.
Cacciamalia glacialis rosai (Vailati, 1988)
Boldoria glacialis rosai Vailati, 1988: 184.
Cacciamalia glacialis rosai (Vailati, 1988): Vailati, 2017: 20.

Cacciamalia viallii (Pavan, 1938)
Boldoria (s. str.) *Viallii* Pavan, 1938: 162.
Boldoria viallii Pavan, 1939: Vailati, 1977: 73.
Cacciamalia viallii (Pavan): Vailati, 2017: 20.

Genus ***Ghidinia*** Pavan, 1939
Ghidinia Pavan, 1939b: 106.

Type species. *Ghidinia Morettii* Pavan, 1939 by monotypy (habitus in Fig. 137.3).

Diagnosis. Medium-large size, 2.7–3.3 mm, bathysciod body, elliptical and somewhat elongated, strongly ogival posteriorly (Fig. 137.3).

Antennae: Long and slender; almost reaching, stretched backwards, the apex of the elytra. Length ratio of the first two antennomeres variable. The 1st antennomere can be just shorter, equal or just longer than the 2nd; the 8th elongated, from slightly less to more than four times longer than wide; the 11th lanceolate with sinuated sides in the basal third, as long as the sum of the previous one plus half of the 9th.

Pronotum: Bell-shaped, with the maximum width at the base; sides slightly sinuated before the basal angles, which are acute.

Elytra: Particularly ogival posteriorly, with the maximum width at the basal third. Without parasutural stria and with dense and numerous transverse striolae, superficial but clearly visible.

Legs: Males protarsi well-dilated, about as wide as the apex of the protibia. Tibiae with inner polidentate spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 139.3): High, widely rounded and somewhat prominent forward; obtuse angle and rounded vertex. Ventral profile from straight to slightly sinuous. Posterior apophysis beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 141.3): Small and short. Longitudinal furrow of apophysis of the alacrista from one fifth to half the length and the apical area very narrow with very sharp apexes.

Metendosternite (Fig. 143.3): «V»-shaped, with non-triangular furcal arms. Similar to *Boldoria* and *Cacciamalia,* but with a larger apophysis and a longer trunk.

Median lobe of aedeagus: Relatively large, almost a third of the body lenght. In lateral view (Fig. 144.3), ventral face widely curved and dorsal face with a slight depression towards the apical quarter, with thinned apex, from right slightly bent upwards. In dorsal view (Fig. 146.3) with the sides parallel or slightly sinuated and a subtriangular, stout, more or less sharp apex.

Endophallus (Fig. 146.3): Basal «Y»-piece well sclerotized. Median phanerae consisting of a sclerotized central plate and a structure with arms turned proximally, all surrounded by silky-spiny bundles. Distally there are two sclerotized listels, sub-parallel and sinuate.

Parameres (Fig. 147.8): Slender, much shorter than the median lobe. At the apex with three setae of different length, one of which is very small.

Spermathecal complex: Spermatheca (Fig. 148.3) with proximal lobe, of kidney-shaped, very elongated and curved; distal lobe spherical and voluminous; hyaline union duct narrower than each of the lobes. Ductus distally not sclerotized.

Female uroventrite VIII (Fig. 149.3): Spiculum small, short, but distinct apically, which can be rounded or bilobed.

Discussion. According to Vailati (2017) work, *Ghidinia* differs from *Cacciamalia* by the apex of the median lobe of aedeagus being symmetrical and downward facing. While from all the other genera of the *Boldoria* series it differs by the apex of the median lobe of aedeagus, subtriangular, ogival or truncate in all the other genera. From *Cacciamalia, Viallia* and *Monguzziella* it differs also by the presence of the basal «Y»-piece of the endophallus. From all the other genera of the *Boldoria* series, excluding *Insubriella*, *Ghidinia* differs by the 8th antennomere which is about four times as long as wide. From *Insubriella*, *Ghidinia* differs by the first two antennomeres of approximately equal length, the first much longer than the second one in *Insubriella*. Perreau (2000) classified the genus as being a part of the phyletic series *Boldoria*, the current species of *Ghidinia* were part of the genus *Boldoria* «*moretti* group».

Distribution. Italy. Bergamasque Prealps: Sebino (Bergamo area). Western Brescian Prealps: North, in the Mt. Guglielmo massif; South, around Punta dell'Orto Mt. and surroundings of Vesalla.

Species

Ghidinia aguinensis Vailati, 1974
Ghidinia aguinensis Vailati, 1974: 36.
Boldoria aguinensis (Vailati, 1974): Vailati, 1988: 194.

Ghidinia morettii Pavan, 1939
Ghidinia morettii morettii Pavan, 1939
Ghidinia Morettii Pavan, 1939b: 106.
Ghidinia morettii s. str. Pavan: Vailati, 1975b: 138.
Boldoria morettii morettii (Pavan, 1939): Vailati, 1988: 200.

Ghidinia morettii morettii Pavan, 1939: Vailati, 2017: 23.
Ghidinia morettii vesallae Vailati, 1974
Ghidinia morettii vesallae Vailati, 1974: 42.
Boldoria morettii vesallae (Vailati, 1974): Vailati, 1988: 206.

Ghidinia vailatii Cavadini, 1988
Ghidinia vailatii Cavadini, 1988: 21.
Boldoria vailatii (Cavadini, 1988): Vailati, 1988: 210.

Genus ***Insubriella*** Vailati, 1990
Insubriella Vailati, 1990: 214.

Type species. *Insubriella paradoxa* Vailati, 1990 by original designation (habitus in Fig. 138.1).

Diagnosis. Medium-large body, 2.7–3.2 mm, tending to pholeuonoid, elongated and posteriorly attenuated (Fig. 138.1).

Head: Retractile; occipital carina poorly marked.

Antennae: Long, thin, reaching, streched backwards, the apical quarter of the elytra. 1st antennomere much longer than the 2nd; the 8th antennomere cylindrical, elongated, more than four times longer than wide; the 11th lanceolate, slightly restricted to the basal third and as long as the sum of the previous plus a quarter of the 9th one.

Pronotum: Transverse but narrow, with sinuate sides, more or less abruptly constricted in the basal third and with acute basal angles. In the middle it is as wide as it is at the base in males, slightly wider in females.

Elytra: Elongated, with dense, regular and well-marked transverse striolae; without parasutural stria.

Legs: Male protarsi long and well-dilated, about as wide as the apex of the protibia. Tibiae with inner polidentated spurs at apex; meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 139.4): Low, rounded front edge but not distinctively pointing forward, elusive. Ventral profile without toothed vertex, but slightly hollow in the anterior part. Posterior apophysis prolonged over the entire metaventrite without exceeding it.

Suture of the metaventrite (Fig. 139.4): Arch-shaped, which is sinuousidal in the basal third and delimits a wider area in the middle part.

Metatergal apparatus (Fig. 141.4): Small, short and sharp apophysis of the alacrista. Longitudinal furrow of the apophysis from one fifth to half the length.

Metendosternite (Fig. 143.4): «V»-shaped, with non-triangular furcal arms; arms narrow and long, slightly longer than twice the length of the trunk, with well-developed apical apophysis; short and narrow furcal trunk clearly longer than wide.

Median lobe of aedeagus: Less than a third of the body lenght, stout and robust. In lateral view (Fig. 145.1) regularly curved, very robust in the basal half, more thinned towards the apex which is curved upwards in a goose beak-shaped structure. In dorsal view (Fig. 146.4) with sides parallel; apex ogival and pointed, with a pronounced apical tongue.

Endophallus (Fig. 146.4): With well-developed and sclerotized basal «Y»-piece. Median phanerae consisting of a sclerotized central plate with two arms facing proximally and distally. There are two sub-parallel sclerotized distal listels, equipped with spinulos bundles at the base.

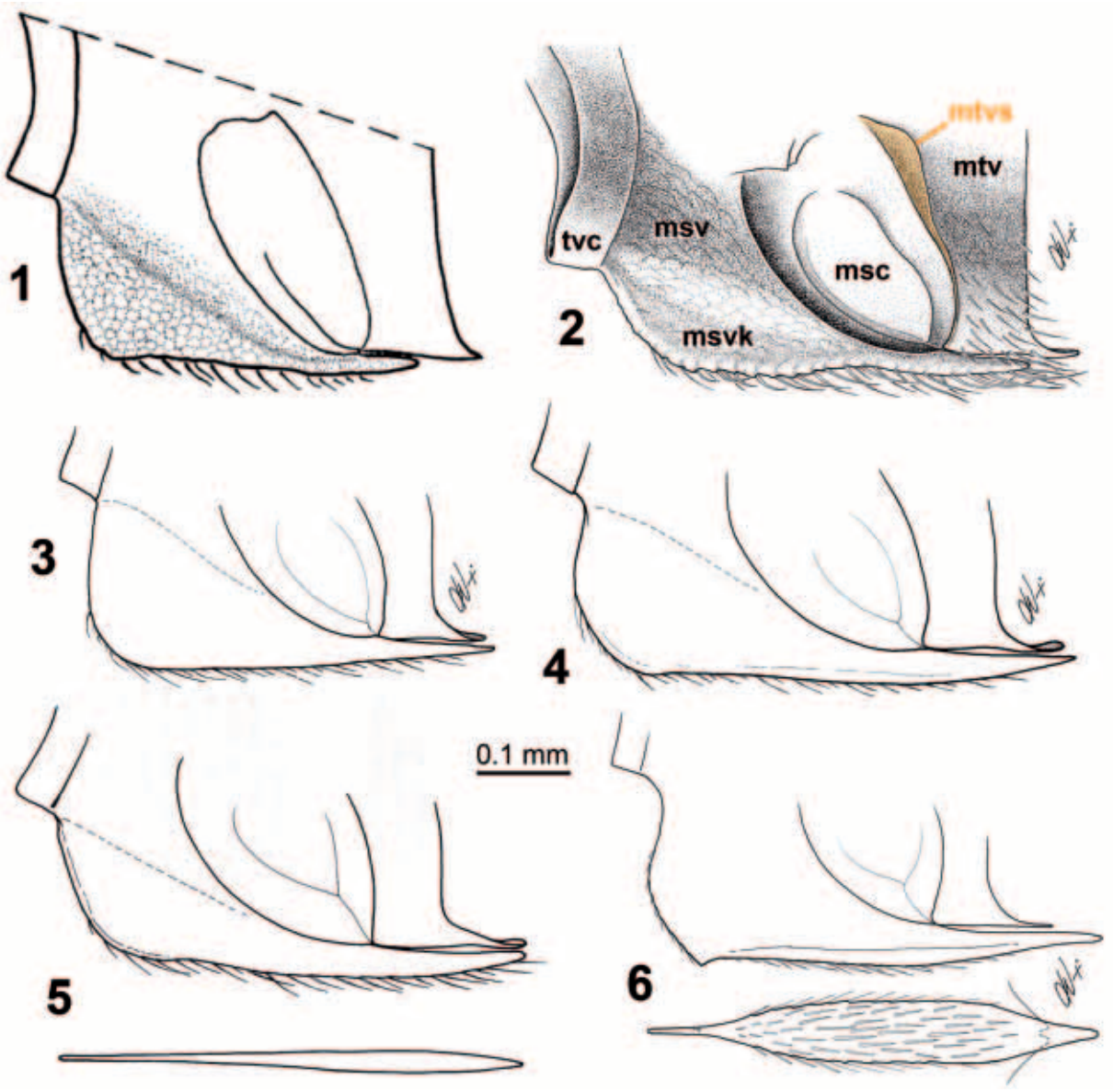
Parameres (Fig. 147.9): Of average strength, not reaching the apex of the median lobe; bearing two apical setae of equal length, one particularly robust and sclerotized, and a third one, shorter, slightly farther back.

Spermathecal complex: Spermatheca (Fig. 148.4) large, asymmetric, with the proximal lobe developed in length and the distal lobe spherical and more voluminous. Thin spermiduct, not or very slightly widened in the area of junction to the spermatheca, the area where the spermathecal gland is situated.

Female uroventrite VIII (Fig. 149.4): Spiculum very small, with apex truncate and sub squared.

Discussion. According to Vailati (2017), *Insubriella* differs from *Cacciamalia* by the apex of the median lobe of aedeagus being symmetrical and downward facing. From *Cacciamalia, Viallia* and *Monguzziella*, it differs also by the presence of the basal «Y»- piece of the endophallus. From *Ghidinia* it differs by the apex of the median lobe of aedeagus not being subtriangular. From all the other genera of the *Boldoria* series, excluding *Ghidinia*, it differs by the 8th antennomere being about four times as long as wide; while from *Ghidinia* it differs by the 1st antennomere much longer than the 2nd, the first two antennomeres of approximately equal length in *Ghidinia*.

Distribution. Italy. Brescian Prealps. Known from few sites on the mountainous territory of Bione and Casto.



FIGURES 140.1–140.6: *Boldoria* series. Pterothorax in lateral view of: (**1**) *Miettiella vespertilio* (modified from Piva 2016), (**2**) *Monguzziella grottoloi,* (**3**) *Pavaniola ghidinii ghidinii,* (**4**) *Ragazzonia vestae vestae,* (**5**) *Viallia alfanoi* (lateral and ventral view), (**6**) *Cryptobathyscia gavardensis* (lateral and ventral view). Abbreviations: **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

Species

Insubriella paradoxa Vailati, 1990
Insubriella paradoxa Vailati, 1990: 216.

Genus ***Miettiella*** Piva, 2016
Miettiella Piva, 2016: 63.

Type species. *Miettiella vespertilio* Piva, 2016 by original designation (habitus in Fig. 138.2).

Diagnosis. Small size, 1.9–2.1 mm, bathyscoid body, elliptical and convex (Fig. 138.2).

Head: Retractile, with occipital carina blurred.

Antennae: Relatively elongated, clavate, stretched

backwards it is almost reaching the basal third of the elytra. 1st antennomere shorter than the 2nd; the 8th a half times longer than wide; the 11th pyriform, wide, always shorter than the sum of the previous two.

Pronotum: Wide, convex, with regularly rounded sides and with the maximum width at the base.

Elytra: Short and wide, widely rounded and with maximum width around the midline; with evident transverse striolae and without parasutural stria.

Legs: Males protarsi well-dilated, slightly wider than the apex of the protibia. Tibiae with inner polidentate spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.1): Moderately high, no forward extension. Front profile slightly rounded, obliquely elusive. Ventral profile straight or slightly sinuous. Posterior apophysis free, prolonged only for a short part on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 141.5): Small and short, with apophysis of the alacrista fairly short.

Metendosternite (Fig. 143.5): «V»-shaped; furcal arms non-triangular, narrow and long, almost two and a half times the length of the trunk, with well-developed apical apophysis; short furcal trunk almost as long as wide.

Median lobe of aedeagus: Small, about a third of the body lenght, stout, wide. In lateral view (Fig. 145.2), slightly curved, robust, with short apical part, slightly bent down. In a dorsal view (Fig. 146.5), with slightly sinuate sides and a broad, rounded apex ending with a very small rounded tongue.

Endophallus (Fig. 146.5): With small and poorly defined basal «Y»-piece. Median phanera complex, large and well sclerotized, reproducing the shape of a bat.

Parameres (Piva 2016): Slender, shorter than the median lobe, bearing three setae of different length at the apex.

Spermathecal complex: Spermatheca (Fig. 148.5) with the proximal lobe elongate with sulcated walls, the middle part very short, almost non-existent, and the distal lobe small and spherical. There is a spermathecal gland that flows into the spermatheca close to the spermatic duct.

Female uroventrite VIII (Fig. 149.5): Spiculum small, short and with a rounded apex.

Discussion. According to Vailati (2017), *Miettiella* differs from *Cacciamalia* by an apex of the median lobe of aedeagus that is symmetrical and downward facing. From *Cacciamalia, Viallia* and *Monguzziella*, it differs also by the presence of the basal «Y»-piece of the endophallus. From *Ghidinia* it differs by the apex of the median lobe of aedeagus which is not subtriangular. From *Ghidinia* and *Insubriella* it differs by the 8th antennomere being short, sligthly longer than wide; while from *Ragazzonia* differs by the length of 11th antennomere, shorter in *Ragazzonia*, and by the shape of the median phanera of endophallus.

Distribution. Italy. Western Venetian Prealps: currently known from a single site in the upper Veronese Lessini mountains.

Species

Miettiella vespertilio Piva, 2016
Miettiella vespertilio Piva, 2016: 64.

Genus ***Monguzziella*** Vailati, 1993
Monguzziella Vailati, 1993: 262.

Type species. *Monguzziella grottoloi* Vailati, 1993 by original designation (habitus in Fig. 138.3).
Diagnosis. Small sized body, 1.8–2.1 mm, bathyscioid shape, but elongated and with narrowed frontpart (Fig. 138.3), covered by dense and relatively long pubescence.

Antennae: Relatively short, when stretched backwards reaching almost the middle of the elytra. 1st antennomere shorter than the 2nd; the 8th transverse; the 11th pyriform, long as the sum of the previous one plus half of the 9th one.

Pronotum: Transverse, narrower than the base of the elytra. Lateral sides regularly rounded, not sinuate but narrowed at the base, with the maximum width at the basal third.

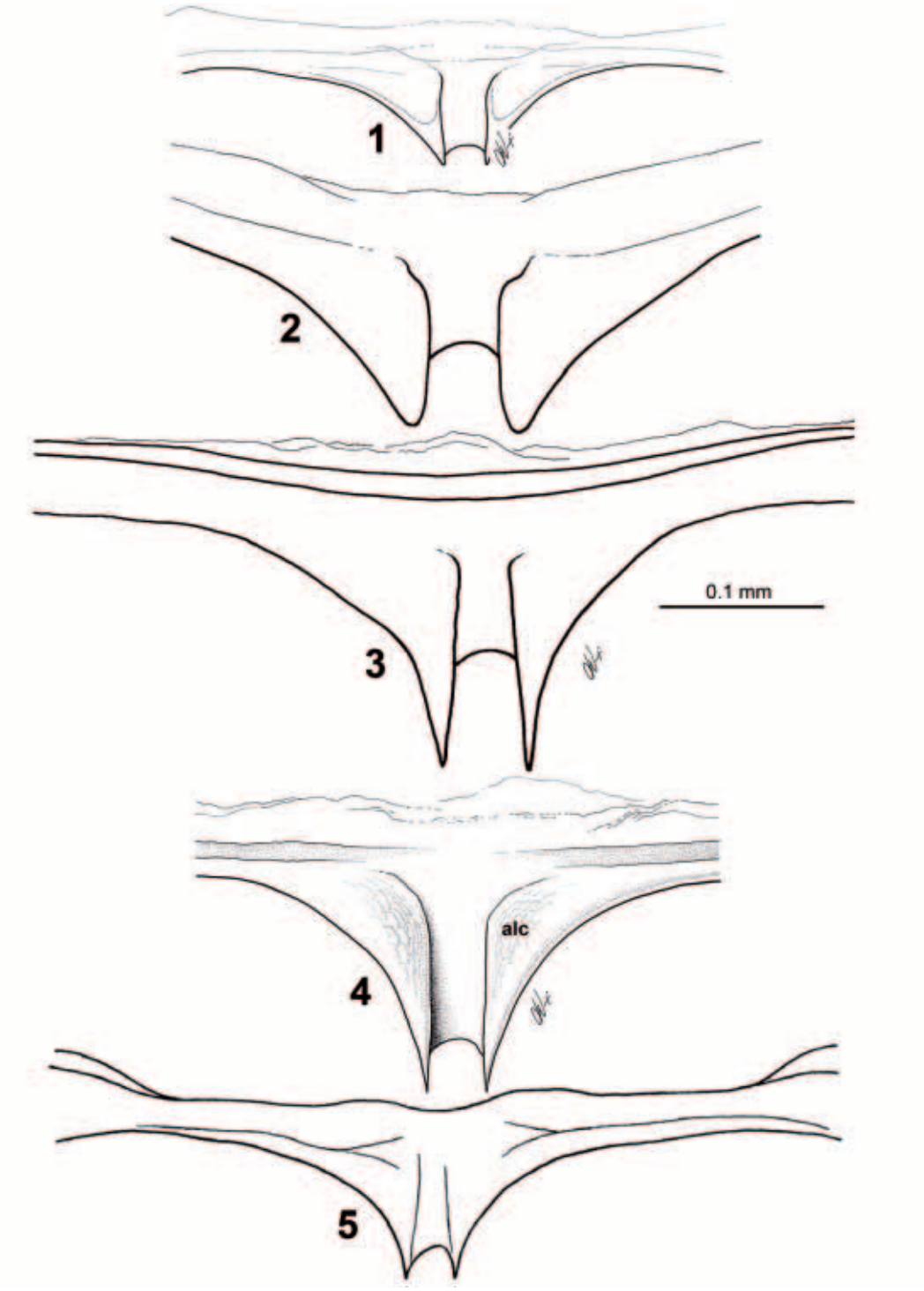
Elytra: With evident, but superficial, transversal striolae; without parasutural stria.

Legs: Males protarsi moderately dilated, slightly over 2/3rd of the apex of the protibia. Tibiae with inner polidentate spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.2): Particularly low, with non-prominent front profile, ventrally elusive, rounded and toothless, with roughly serrated profile. Posterior apophysis prolonged above the metaventrite, of which it does not reach the posterior border.

Suture of the metaventrite (Fig. 140.2): Forms a sinuousidal arch, demarking a well defined area along the three apical quarters, in the basal quarter it runs very close to the coxal cavity.

Metatergal apparatus (Fig. 142.1): Small and short, with the longitudinal furrow of the apophysis of



FIGURES 141.1–141.5: *Boldoria* series. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii*, (**4**) *Insubriella paradoxa,* (**5**) *Miettiella vespertilio* (modified from Piva 2016). Abbreviations: **alc**, alacrista.

the alacrista as wide as a half of the length; apophysis apexes sharp.

Metendosternite (Fig. 143.6): «V»-shaped, with non-triangular furcal arms; arms very long and narrow, about two and a half times the length of the trunk, with the apical apophysis developed; furcal trunk short, a little longer than wide, although somewhat widened at the junction part of the arms.

Median lobe of aedeagus: About a third of the body lenght, stout and robust. In lateral view (Fig. 145.3) robust, regularly curved, with very short, narrow and straight apical part. In dorsal view (Fig. 147.1) with parallel sides and with an apparent preapical constriction; rounded apex, laterally dilated and flattened, with a short and rounded apical tongue.

Endophallus (Fig. 147.1): Basal «Y»-piece present, small, simple and weakly sclerotized. Middle region without particularly sclerotized phanerae, but showing membranous structures covered by very small spinulae. Distally two weakly sclerotized, sinuous and divergent listels emerge.

Parameres (Fig. 147.10): Long, reaching the apex of the median lobe, thinned to the distal quarter. Bearing two very small apical setae and another one ventral, more towards the back.

Spermathecal complex (Fig. 148.6): Short spermatheca, with highly voluminous and elongated the proximal lobe, and spherical and smaller the distal one; very long and very thin spermatic duct, somewhat widened in the area of union to the spermatheca, in this area the spermathecal gland empties.

Female uroventrite VIII (Fig. 149.6): Front edge without spiculum.

Discussion. According to Vailati (2017), *Monguzziella* differs from *Cacciamalia* by the apex of the median lobe of aedeagus being symmetrical and downward facing. From all the other genera of the *Boldoria* series, excluding *Cacciamalia* and *Viallia*, it differs also by the absence of the basal «Y»-piece of the endophallus. While from *Viallia* it differs in the apex of the median lobe of aedeagus, not ogival and with apical tongue. From *Viallia*, *Ghidinia*, *Insubriella*, *Boldoria* and *Pavaniola* differs by the shape of the antennae, with the last segment pyriform.

Distribution. Italy. Western Venetian Prealps: Tonezza-Folgaria and Vigolana highlands, Lavarone-Luserna plateau, Carega, Group-Piccole, Dolomiti-Pasubio and Veronesi Lessini mountains (Piva 2016).

Species

Monguzziella grottoloi Vailati, 1993
Monguzziella grottoloi Vailati, 1993: 263.

Genus ***Pavaniola*** Vailati, 2017
Pavaniola Vailati, 2017: 26.

Type species. *Bathysciola* (*Boldoria*) *Ghidinii* Lona, 1937 by original designation (habitus in Fig. 138.4).

Diagnosis. Small size, 1.5–1.9 mm, bathyscioid body, elliptical, elongated (Fig. 138.4).

Antennae: Reach, if lying backwards the basal third of the elytra. 1st antennomere always shorter than the 2nd one; the 8th from transverse to just longer than wide; the 11th lanceolate and as long as, or slightly less, than the sum of the two previous ones.

Pronotum: With regularly rounded sides, with maximum width at the base.

Elytra: With regular and well marked transverse striolae; without parasutural stria.

Legs: Male protarsi short and slightly to moderately dilated, always much narrower than the apex of the protibia. Tibiae with inner polidentate spurs at the apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.3): High, rounded front edge, but with little or no distinct extension forward, with a straight ventral profile. Posterior apophysis beyond the entire metaventrite.

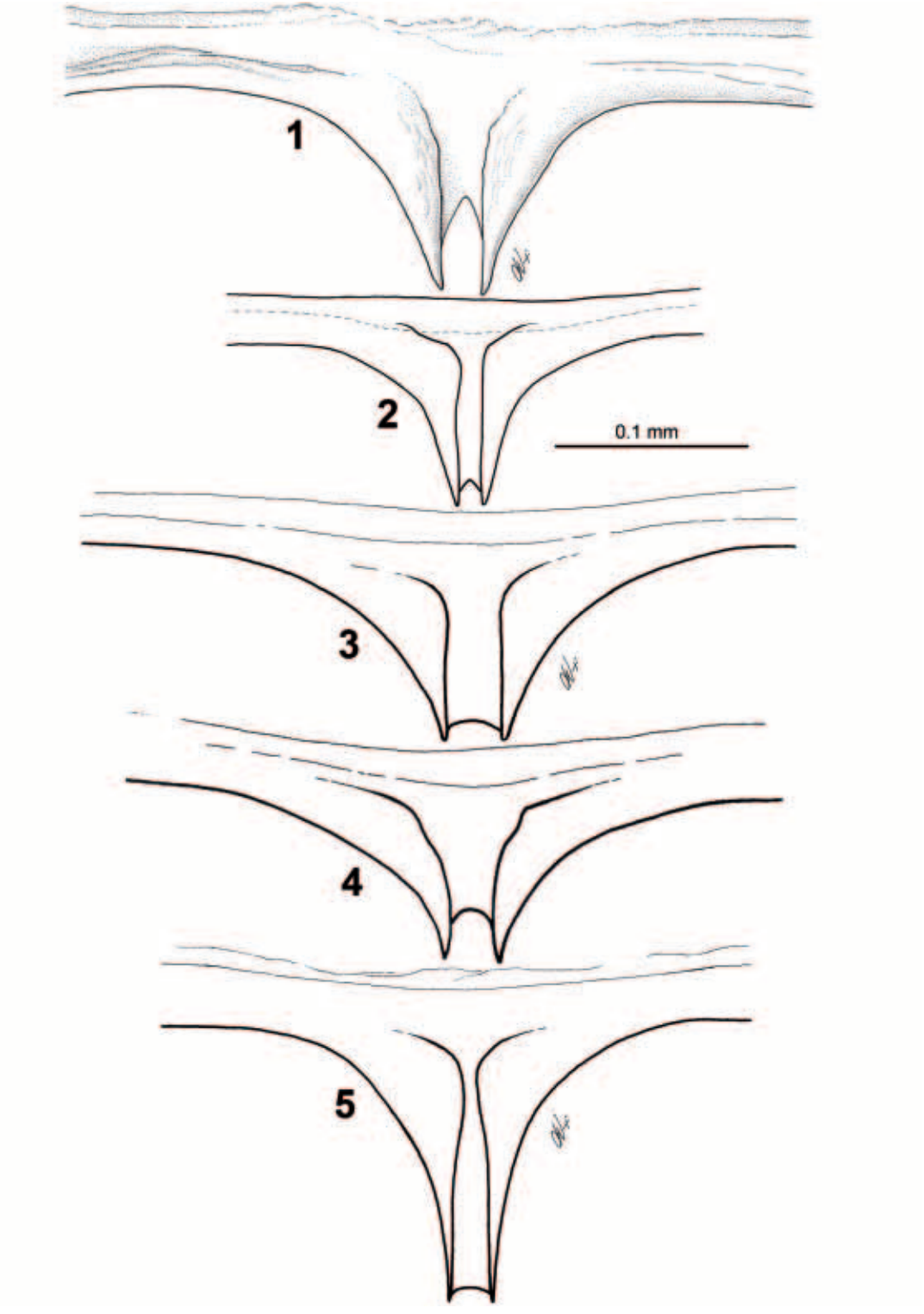
Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 142.2): Small and particularly short, with the apophysis of the alacrista from as wide as long, to a fifth of the length; sharp apophysis apexes.

Metendosternite (Fig. 143.7): «V»-shaped, with non-triangular furcal arms. Arms very long and narrow, two and a half times the length of the trunk; posterior furcal plate very narrow especially in the apical part of the arm; terminal process or apophysis well-developed. Trunk one and a half times longer than wide; median keel diverges little posteriorly.

Median lobe of aedeagus: Small, stout, length from a quarter to a little less than a third of the body. In lateral view (Fig. 145.4) it appears obtusely folded, robust, with the distal half slightly sinuate, with apex not too thin and slightly flexed down. In dorsal view (Fig. 147.2) with parallel sides, apex ogival and pointed, but not sharp.

Endophallus (Fig. 147.2): Basal «Y»-piece well sclerotized and simple. Median phanerae consisting of



FIGURES 142.1–142.5: *Boldoria* series. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Monguzziella grottoloi,* (**2**) *Pavaniola ghidinii ghidinii,* (**3**) *Ragazzonia vestae vestae,* (**4**) *Viallia alfanoi*, (**5**) *Cryptobathyscia gavardensis*.

a sclerotized central plate, surrounded by silky-spiny and toothed structures; distally there are silky membranous structures. Sclerotized apical structures are absent.

Parameres (Fig. 147.11): Robust, much shorter than the median lobe, usually bearing four setae at apex (three in *Pavaniola regalini*), always particularly long and flagelliform.

Spermathecal complex: Spermatheca (Fig. 148.7) small, with the proximal lobe of variable length, generally small, reniform; distal lobe spherical and more voluminous; median part very short and hyaline; spermatic duct somewhat dilated in the area where it joins to the spermatheca.

Female uroventrite VIII (Fig. 149.7): Spiculum small, reduced to a stout little tongue, short; apex enlarged and bilobed.

Diiscussion. According to Vailati (2017), *Pavaniola* differs from *Cacciamalia* by the apex of the median lobe of aedeagus being symmetrical and downward facing. From *Cacciamalia, Viallia* and *Monguzziella*, it differs also by the presence of the basal «Y»-piece of the endophallus. From *Ghidinia* it differs by the apex of the median lobe of aedeagus not subtriangular. From *Ghidinia* and *Insubriella* it differs by the short 8th antennomere, from transverse to just longer than wide; while from *Boldoria* differs by the length of the 11th antennomere, which is longer in *Boldoria*, and by the longer setae of the parameres. Vailati (2017) established three groups for *Pavaniola* species based on their morphological characteristics are described by Vailati (1988). While Perreau (2000) includes the current species of this genus in the «*ghidinii* group».

Distribution. Italy. Bergamasque Prealps: between lower Val Seriana and Val Cavallina, and in the Sebino (Bergamo area). Brescian Prealps: mountains between Iseo lake and the media and lower Val Trompia; foothills near the city of Brescia; group of Palosso mountain and median Val Sabbia.

Species

«*comottii* group» *sensu* Vailati, 2017
Pavaniola comottii (Vailati, 1988)
Boldoria (s. str.) sp.: Regalin, 1983 [1981]: 148; 149.
Boldoria comottii Vailati, 1988: 260.
Pavaniola comottii (Vailati, 1988): Vailati, 2017: 27.

«*ghidiini* group» *sensu* Vailati, 1988
Pavaniola ghidinii (Lona, 1937)

Pavaniola ghidinii blesioi (Vailati, 1988)
Boldoria (*B*.) nov. sp.: Vailati, 1977: 73.
Boldoria ghidinii blesioi Vailati, 1988: 254.
Pavaniola ghidinii blesioi (Vailati, 1988): Vailati, 2017: 27.

Pavaniola ghidinii ghidinii (Lona, 1937)
Bathysciola (*Boldoria*) *Ghidinii* Lona, 1937: 92.
Boldoria Ghidinii F. Lona, 1937: Ghidini, 1937: 61.
Boldoria (s. str.) *Ghidinii* Lona: Pavan & Ronchetti, 1950: 102.
Boldoria ghidinii ghidinii (Lona, 1937): Vailati, 1977: 73.
Pavaniola ghidinii ghidinii (Lona, 1937): Vailati, 2017: 27.

Pavaniola ghidinii kahleni (Vailati, 1988)
Boldoria ghidinii kahleni Vailati, 1988: 258.
Pavaniola ghidinii kahleni (Vailati, 1988): Vailati, 2017: 27.

Pavaniola ghidinii polavenensis (Pavan, 1939)
Boldoria (*Boldoria*) *polavenensis* Pavan, 1939a: 126.
Boldoria (s. str.) *polavenensis* Pavan: Pavan & Ronchetti, 1950: 102.
Boldoria ghidinii polavenensis Pavan, 1939: Vailati, 1988: 250.
Pavaniola ghidinii polavenensis (Pavan, 1939): Vailati, 2017: 27.

Pavaniola longitarsis (Pavan, 1941)
Boldoria (s. str.) *longitarsis* Pavan, 1941: 214.
Boldoria longitarsis Pavan, 1941: Vailati, 1977: 73.
Pavaniola longitarsis (Pavan, 1941): Vailati, 2017: 27.

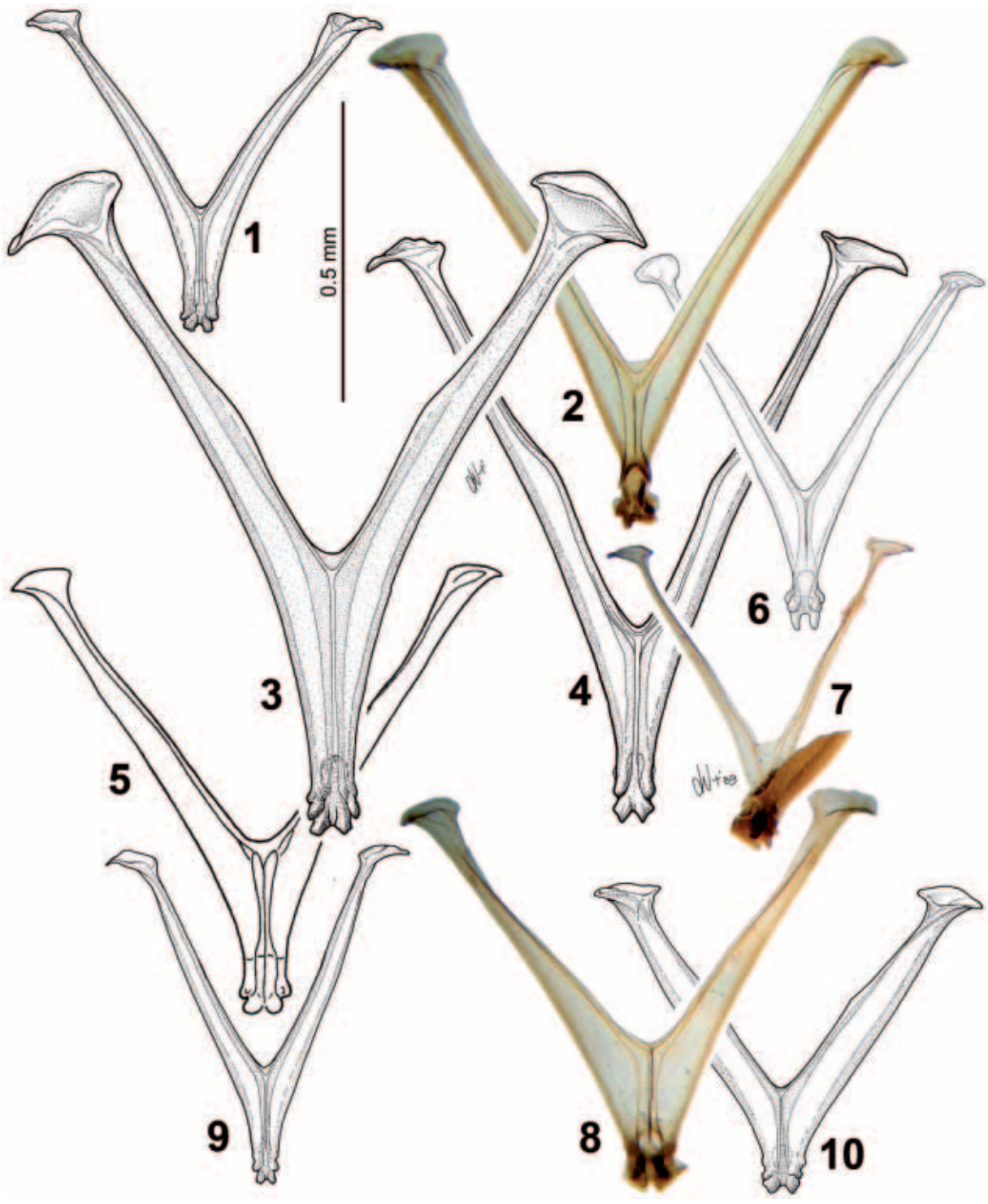
«*regalini* group» *sensu* Vailati, 2017
Pavaniola regalini (Vailati, 1988)
Boldoria regalini Vailati, 1988: 236.
Pavaniola regalini (Vailati, 1988): Vailati, 2017: 27.

Genus ***Ragazzonia*** Vailati, 2017
Ragazzonia Vailati, 2017: 24.

Type species. *Bathysciola* (*Boldoria*) *breviclavata* G. Müller, 1931 by original designation (for the habitus see that of the similar species *Ragazzonia vestae vestae* in Fig. 138.5).

Diagnosis. Medium size, 1.8–2.3 mm, bathyscioid body, elliptical and stout, globose (Fig. 138.5).

Antennae: Short, reaching backwards to the basal fifth or at most the basal quarter of the elytra; strongly clavate. 1st antennomere stocky, much shorter than the



FIGURES 143.1–143.10: *Boldoria* series. Metendosternite of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia glacialis glacialis,* (**3**) *Ghidinia morettii morettii,* (**4**) *Insubriella paradoxa,* (**5**) *Miettiella vespertilio* (modified from Piva 2016), (**6**) *Monguzziella grottoloi,* (**7**) *Pavaniola ghidinii ghidinii,* (**8**) *Ragazzonia vestae vestae,* (**9**) *Viallia alfanoi*, (**10**) *Cryptobathyscia gavardensis*.

2nd one; the 8th from transverse to just longer than wide; the 11th pyriform and wide, always shorter than the sum of the previous two.

Pronotum: Wide, convex, with regularly rounded sides and the maximum width at the base.

Elytra: Globose, widely rounded and with maximum width at the basal quarter. Spaced and rough, but well marked, transversal striolae; without parasutural stria.

Legs: Males protarsi well-dilated, as wide as or wider than the apex of the protibia. Tibiae with inner polidentated spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.4): Moderately high, with a rounded and slightly prominent vertex, and a straight or slightly sinuate ventral profile. Posterior apophysis beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 142.3): Small and short, with the apophysis of the alacrista little developed in length.

Metendosternite (Fig. 143.8): «V»-shaped, with non-triangular furcal arms. Arms long and narrow, two times the length of the trunk; furcal posterior plate widest at the junction of the arms and trunk; apical apophysis well-developed and at the end part of the arm a short anterior plate and a narrow posterior plate are observed. Trunk as long as the widest area; median keel diverges posteriorly.

Median lobe of aedeagus: Large, about half the length of the body, stout. In lateral view (Fig. 145.5) it is folded in an obtuse way, robust, with the apex from right to sharply down flexed. In dorsal view (Fig. 147.3) with slightly sinuous sides, rounded apex, somewhat depressed in the middle (*Ragazzonia breviclavata*) or ending with a very small tongue.

Endophallus (Fig. 147.3): With large and well-sclerotized basal «Y»-piece. Median phanera large, complex, with sclerotized arms facing proximally and are surrounded by spiny structures. Distally with two symmetrical sclerotized listels diverging towards the apex.

Parameres (Fig. 147.12): Slender, much shorter than the median lobe; apex showing three setae of different length.

Spermathecal complex: Spermatheca (Fig. 148.8) with the proximal lobe elongated, the median part somewhat short and hyaline and distal lobe from sub-spherical to elongated, but less voluminous; on it the surface striated. Ductus distally sclerotized for a short distance.

Female uroventrite VIII (Fig. 149.8): Spiculum small, stout, reduced in length and with the apex from rounded or sharp to wide and square.

Discussion. According to Vailati (2017), *Ragazzonia* differs from *Cacciamalia* by the apex of the median lobe of aedeagus being symmetrical and downward facing. From *Cacciamalia, Viallia* and *Monguzziella*, it differs also by the presence of the basal «Y»-piece of the endophallus. From *Ghidinia* it differs by the apex of the median lobe of aedeagus not being subtriangular. From *Ghidinia* and *Insubriella* it differs by the 8th antennomere being short and transverse; while from *Miettiella* differs by the length of the 11th antennomere, wich is longer in *Miettiella*. In Perreau (2000) the current species of *Ragazzonia* is classified as being part of the «*breviclavata* group» in the genus *Boldoria*.

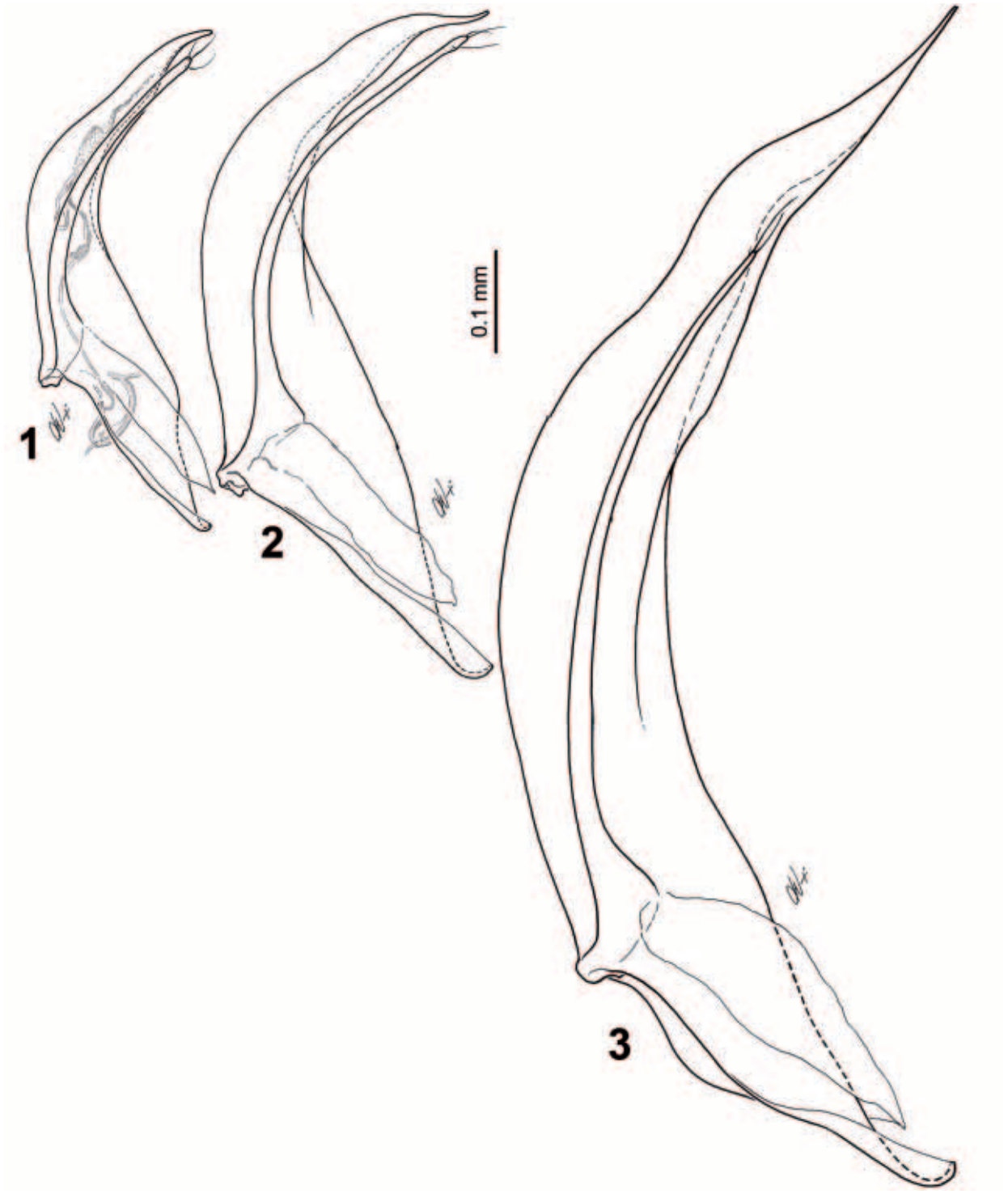
Distribution. Italy. Brescian Prealps: M. Guglielmo, middle Val Trompia, mountains between Val Trompia and Val Sabbia up to the foothills in the surroundings of Idro lake. Gardesane Prealps: middle Val Sabbia and Idro lake left side, mountain group of M. Pizzocolo-Spino-Marmera, middle and upper Val Vestino, Val d'Ampola. Southern Rhaetian Alps: Caffaro valley and lower Giudicaria; in the northern part follows the distribution area of the genus *Cacciamalia*.

Species

Ragazzonia breviclavata (G. Müller, 1931)
Bathysciola (*Boldoria*) *breviclavata* G. Müller, 1931a: 197.
Boldoria (*Boldoria*) *breviclavata* Müller, 1931: Ghidini, 1937: 59.
Boldoria (s. str.) *breviclavata* Müller: Pavan & Ronchetti, 1950: 101.
Boldoria breviclavata Müller, 1931: Vailati, 1988: 226.
Ragazzonia breviclavata (Müller, 1931): Vailati, 2017: 24.

Ragazzonia trumplina (Vailati, 1988)
Boldoria trumplina Vailati, 1988: 222.
Ragazzonia trumplina (Vailati, 1988): Vailati, 2017: 24.

Ragazzonia vestae (Ghidini, 1936)
Ragazzonia vestae meridionalis (Vailati, 1988)
Boldoria vestae meridionalis Vailati, 1988: 218.
Boldoria breviclavata vestae (Ghidini): Vailati, 1977: 66.
Ragazzonia vestae meridionalis (Vailati, 1988): Vailati, 2017: 24.



FIGURES 144.1–144.3: *Boldoria* series. Aedeagus in lateral view of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii*.

Ragazzonia vestae vestae (Ghidini, 1936)
Boldoria Vestae Ghidini, 1936: 104.
Boldoria (*Boldoria*) *Vestae* Ghidini: Ghidini, 1937: 57.
Boldoria (s. str.) *Vestae* Ghidini: Pavan & Ronchetti, 1950: 101.
Boldoria (*Boldoria*) *breviclavata vestae* (Ghidini): Vailati, 1977: 66.
Boldoria vestae vestae Ghidini, 1936: Vailati, 1988: 213.
Ragazzonia vestae vestae (Ghidini, 1936): Vailati, 2017: 24.

Genus ***Viallia*** Pavan, 1950
Viallia Pavan, 1950: 56.

Type species. *Viallia Alfanoi* Pavan, 1950 by original designation (habitus in Fig. 138.6).

Diagnosis. Medium sized body, 2.2–2.6 mm, from bathyscioid (elliptical or ovoid) to pholeuonoid body (Fig. 138.6), covered by relatively long and thick pubescence.

Antennae: Rather long, when stretched backwards, reaching from the basal third to the apical fifth of the elytra. 1st antennomere, much shorter than the 2nd; the 8th, from slightly longer to two and half times longer than wide; the 11th lanceolated, widened in the middle, rhomboid in shape, and slightly longer than the previous one.

Pronotum: In the only pholeuonoid species (*V. alfanoi*) much narrower than the elytra. In the other species wide at the base, with the sides regularly rounded, but also slightly sinuate just before the basal angles.

Elytra: With slightly to well marked transversal striolae, with particularly long pubescence; without parasutural stria.

Legs: Male protarsi short and not very dilated, more dilated in the bathyscioid forms, but narrower than the apex of the protibia. Tibiae with inner polidentated spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.5): Lower and anteriorly elusive in the pholeuonoid specie. High, widely rounded and very forward prominent in species with bathyscioid facies; in these the ventral side, slightly arched, results in a ventral view flattened, wide, in the shape of a long rhombus. Posterior apophysis beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 142.4): Small and short, with the longitudinal furrow of the apophysis of the alacrista from as wide as long, to as wide as a quarter of the length.

Metendosternite (Fig. 143.9): «V»-shaped, with not-triangular furcal arms. Arms long and narrow, almost three times the length of the trunk, with the posterior plate of similar width throughout; well-developed, hooked apophysis. Narrow furcal trunk, twice as long as the widest part of the trunk.

Median lobe of aedeagus: Relatively small, length less than a third of the body, stocky. In lateral view (Fig. 145.6) is moderately curved, with a long basal blade, and with the distal half flattened and dorsally sinuate. In dorsal view (Fig. 147.4) with wide basal blade and sides converging towards the apex, that is regularly ogive-shaped but not pointed. Apex ventrally bent.

Endophallus (Fig. 147.4): With atrophic basal «Y»-piece, slightly sclerotized and poorly evident; without any sclerotized median phanera, but centrally supplied by membranous and silky-spinulos bundles.

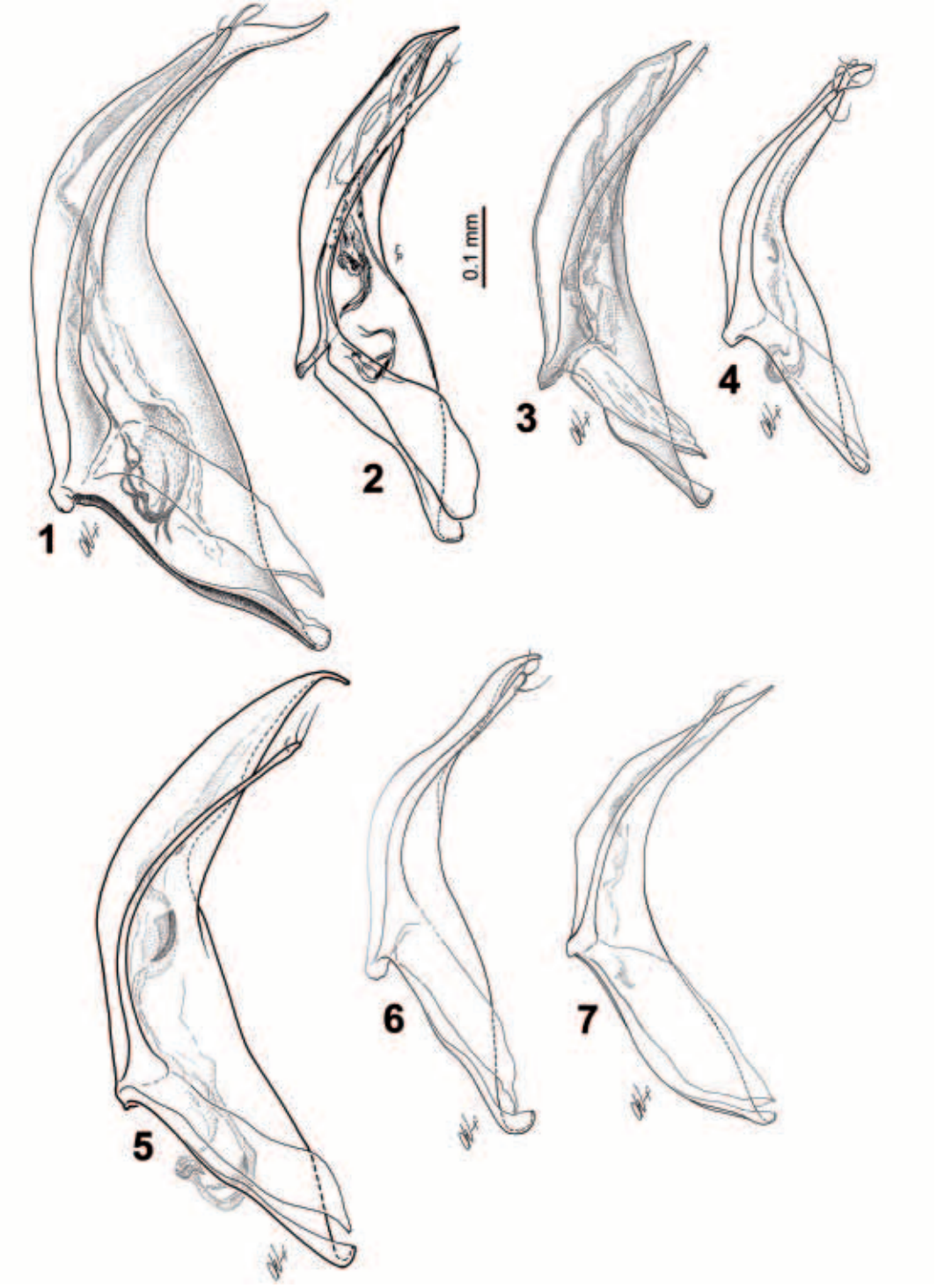
Parameres (Fig. 147.13): Of «normal» strength, shorter than the median lobe; bearing two apical setae of equal length and a more backward preapical one.

Spermathecal complex: Spermatheca (Fig. 148.9) strongly asymmetrical, with voluminous proximal lobe and a very small distal lobe; both thin and slightly sclerotized. Part of attachment of the spermatic duct to the basal lobe slightly enlarged.

Female uroventrite VIII (Fig. 149.9): Spiculum little or not developed, the anterior margin with a slight and largely obtuse prominence.

Discussion. Following Vailati (2017), *Viallia* differs from *Cacciamalia* by the apex of the median lobe of aedeagus symmetrical and downward facing. From all the other genera of the *Boldoria* series (including *Cacciamalia*) differs by the shape of antennae, with the last article lanceolate, vaguely rhomboid in shape and only slightly longer than the previous one; by the 8th antennomere always longer than wide. From all the genera of the *Boldoria* series, excluding *Cacciamalia* and *Monguzziella*, it differs also by the absence of the basal «Y»-piece of endophallus. While from *Monguzziella* it differs by the apex of the median lobe of aedeagus, ogival and without apical tongue. Vailati (1988) established two groups for the species of the genus *Viallia*.

Distribution. Italy. Bergamasque Prealps: Imagna valley, middle Brembana valley, low and middle Seriana valley, Monte Pora.



FIGURES 145.1–145.7: *Boldoria* series. Aedeagus in lateral view of: (**1**) *Insubriella paradoxa,* (**2**) *Miettiella vespertilio* (modified from Piva 2016), (**3**) *Monguzziella grottoloi,* (**4**) *Pavaniola ghidinii ghidinii,* (**5**) *Ragazzonia breviclavata,* (**6**) *Viallia alfanoi*, (**7**) *Cryptobathyscia gavardensis*.

Species

«***alfanoi* group**» *sensu* Vailati, 1988
Viallia alfanoi Pavan, 1950
Viallia Alfanoi Pavan, 1950: 56.
Viallia alfanoi Pavan, 1950: Vailati, 1988: 134.

«***mismae* group**» *sensu* Vailati, 1988
Viallia cappai Vailati, 1988
Boldoria (s. str.) *cappai* Focarile, 1965 (*in litt*.): 42.
Viallia cappai Vailati, 1988: 150.

Viallia grottoloi Vailati, 1988
Viallia grottoloi Vailati, 1988: 144.

Viallia mismae (Inzaghi & Regalin, 1982)
Boldoria (s. str.) *mismae* Inzaghi & Regalin, 1982: 31.
Viallia mismae (Inzaghi & Regalin, 1982): Vailati, 1988: 140.

3.2.9 *Incertae sedis* in series ***Boldoria***

3.2.9.1 Genus ***Cryptobathyscia*** Vailati, 1980
Cryptobathyscia Vailati, 1980: 58.

Type species. *Cryptobathyscia gavardensis* Vailati 1980 by original designation (habitus in Fig. 138.7).

Diagnosis. Small size, 1.6–1.7 mm, bathysciod body, stout, but not globular, elliptical (Fig. 138.7).

Antennae: Short, just reaching in females, or exceding in the males, lying backwards, the base of the pronotum. First antennomere just shorter than the second one; the antennomeres 8th, 9th and 10th transverse; the 11th pyriform and less longer than the sum of two previous ones.

Pronotum: With regularly rounded sides, with maximum width just before the base.

Elytra: With slightly marked transverse striolae; without parasutural stria.

Legs: Males protarsi short and slightly dilated, always much narrower than the apex of the protibia. Tibiae with inner trifids spurs at apex. Meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 140.6): High, rounded front edge, prominent forward, not elusive, provided with a weak tooth. Ventral profile slightly sinuate; ventral edge flattened and rhombic, bordered at sides but without groove. Posterior apophysis long, beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 142.5). Small and short, with the apophysis of the alacrista well-developed. Longitudinal furrow anteriorly narrowed; posteriorly as wide as a sixth of the length of the elytra.

Metendosternite (Fig. 143.10): «V»-shaped, with not-triangular furcal arms. Arms are wider than the typical «non-triangular» arms in the genera of the *Boldoria* series, although there is a small protrusion in the middle area of the anterior furcal suture.

Median lobe of aedeagus: Large, elongated, length a third of the body. In lateral view (Fig. 145.7) it appears regularly curved, robust, with the distal part straight and the apex thin and not flexed down. In dorsal view (Fig. 147.5) with slightly converging sides, apex ogival and showing a small and sharp, apical tongue. Basal blade very long, as long as the half of the full median lobe and in the posterior middle part with a short prolongation similar to a short and narrow lobe.

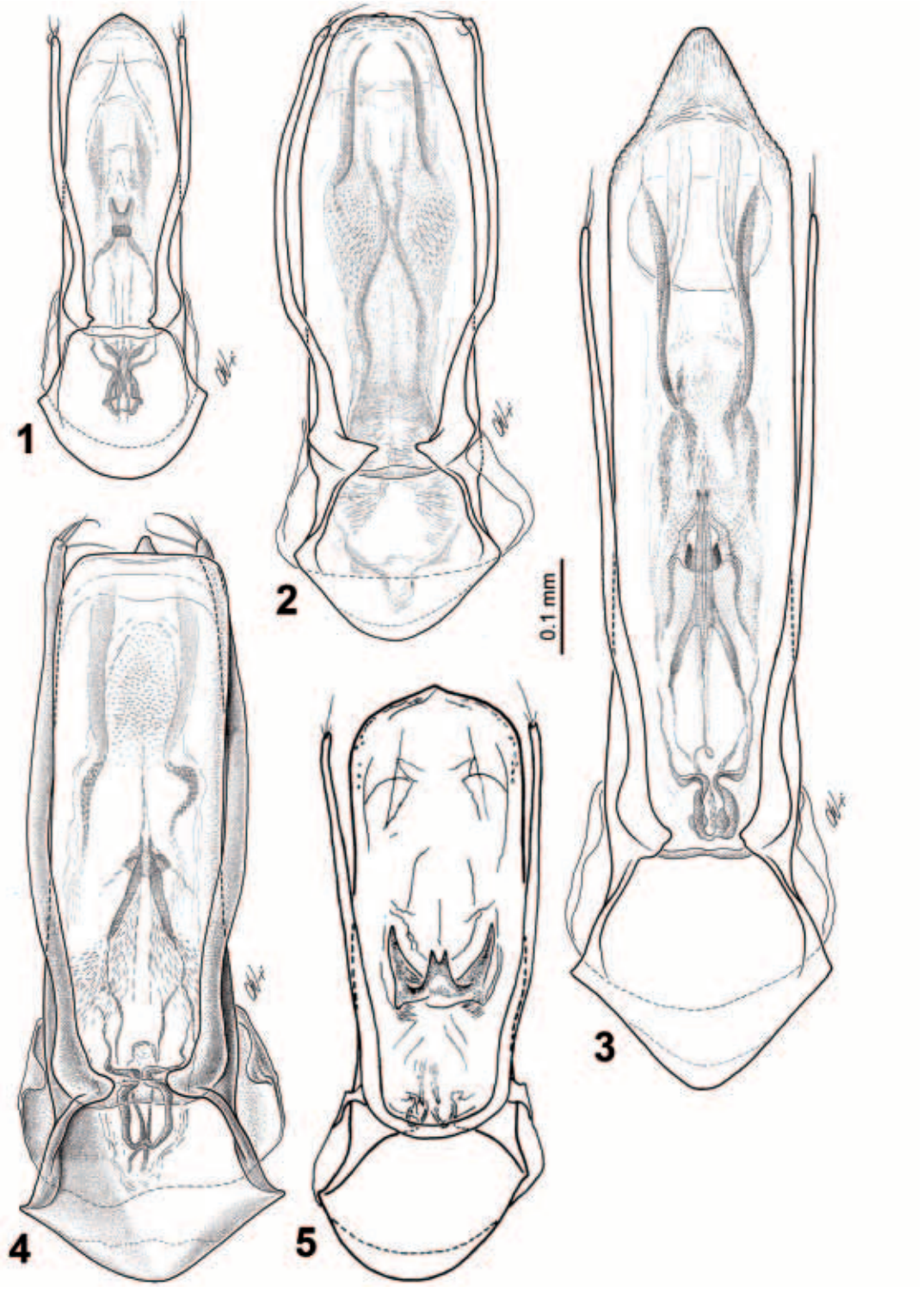
Endophallus (Fig. 147.5): Basal «Y»-piece present. Median phanerae consisting of two small sclerotized plate, close by they are surrounded by hyaline structures in shape of symmetrical arms, spread apart. Sclerotized apical structures formed by two longitudinal slats, slightly sclerotized, arcuated, bearing at the base two silky bundles.

Parameres (Fig. 147.14): Slender, much shorter than the median lobe, bearing three setae at apex: two apical and one subapical. Ventral blade of tegmen very long and wide.

Spermathecal complex (Fig. 148.10): Spermatheca large, with the proximal lobe small, elongate; distal lobe subspherical and voluminous; hyaline junction duct as long as wide; spermiduct thin and slightly dilated in the area where it joins the proximal lobe; the spermathecal gland is not visible.

Female uroventrite VIII: Unknown.

Discussion. Vailati (2017) noted that it was inappropriate and not without doubts from the beginning, that it is supported to include the genus *Cryptobathyscia* into «*Boldoria* phyletic series» (*sensu* Vailati 1988). This taxon, which today appears morphologically and taxonomically somewhat isolated, is therefore excluded from this group on ground of insufficient evidence. Vailati (2017) already recalled that for an assessment of its systematic position it is necessary to wait for the revision of the Italian species of the heterogeneous genus *Bathysciola* as then understood by the authors. Although this revision, at least for alpine species, with probable phyletic relations to the *Dellabeffaella* series, has been completed by Giachino and



FIGURES 146.1–146.5: *Boldoria* series. Aedeagus in dorsal view of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii,* (**4**) *Insubriella paradoxa,* (**5**) *Miettiella vespertilio* (modified from Piva 2016).

Vailati (2019) their classification on a purely morphological base is still very difficult. For a more profound evaluation, it will be necessary to wait until molecular data are available, that are not easily obtainable given the rarity of the taxon. Perreau (2000) included this genus in the phyletic series *Boldoria*.

Distribution. Italy. Brescian Prealps: media Sabbia valley and surroundings of Gavardo (right border of Garda lake).

Species

Cryptobathyscia gavardensis Vailati 1980
Cryptobathyscia gavardensis Vailati, 1980: 60.

3.2.10 *Incertae sedis* in ***Leptodirus-Anthroherpon*** clade

Even though this is not the only group with a slightly uncertain taxonomic position it seems appropriate to consider the group with respect to the finding the molecular analysis as presented in this work. When focussing on the genera *Hartigiella, Epiroella* and *Cacciamalia,* the Tree-1 (Fig. 2) indicates that:

Hartigiella is sister to the *Leptodirus* series (63.1/31), *Epiroella* is sister to the clade formed by the *Leptodirus* + *Hartigiella* + *Speonomidius* + *Neobathyscia* series (40/19) and *Cacciamalia* is sister to the *Anthroherpon* series (85.8/42).

On the other hand in Tree-2 (Fig. 2):

Hartigiella is sister *to Cacciamalia* (80.4/57); the clade is sister to *Epiroella* (86.1/57) and the whole set sister to the *Anthroherpon* series (36.9/49).

These two topologies show that the identified relationships are strongly dependent on the evolutionary model applied and the uncertainty of the taxonomic classification is evident also in the equally low support values observed.

Overall is appears as if the three genera, *Hartigiella, Epiroella* and *Cacciamalia,* are part of a fairly complex clade, which is genetically distant to its sister group. In any case so far the *Cacciamalia* is the only genus so far classified as part of the *Boldoria* series, a series so far composed by 9 to 10 genera. In this sense *Hartigiella* and *Epiroella*, as like to be related to this could represent the «tip of an iceberg» of a yet to be discovered clade.

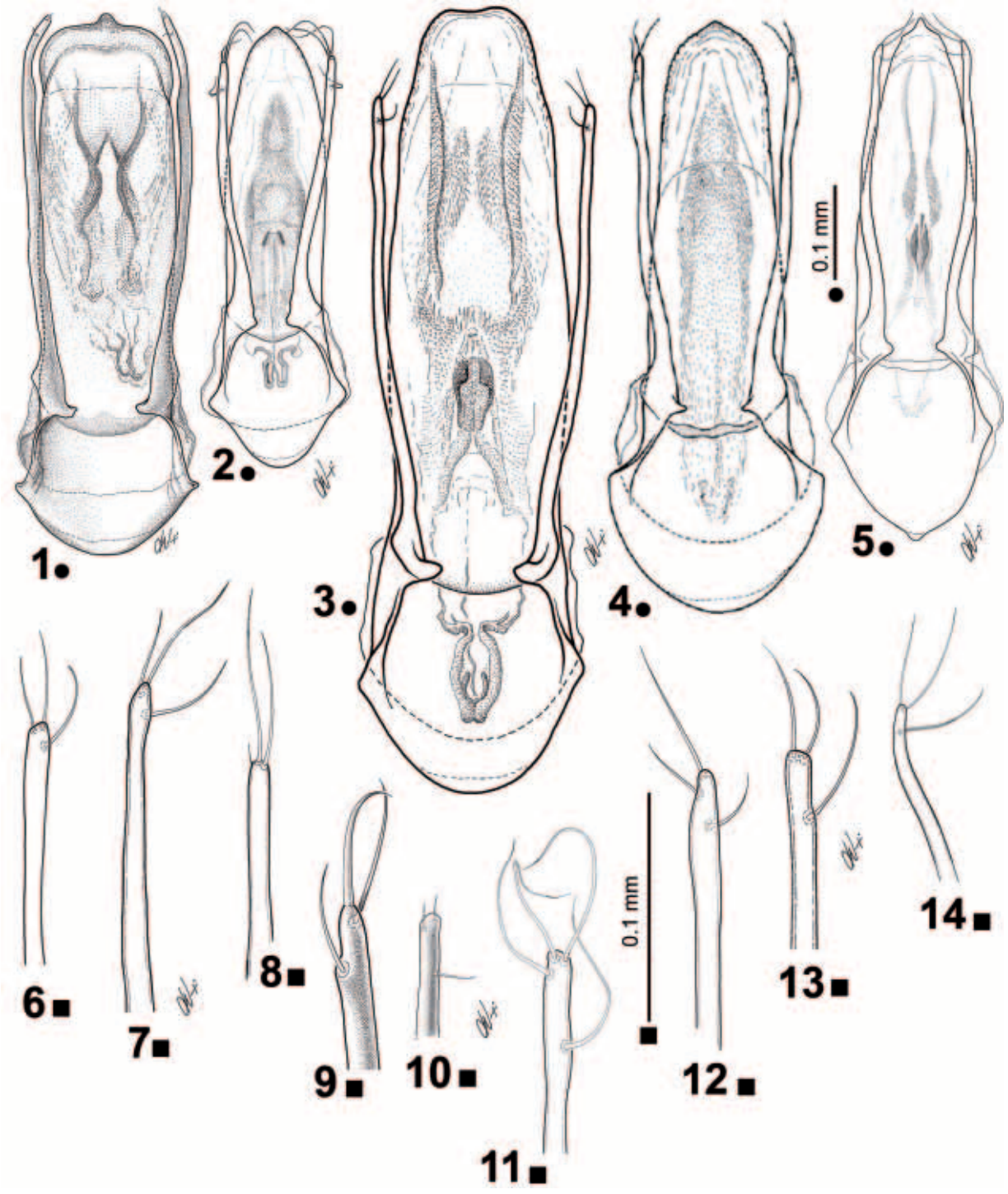
These three genera are seen as being derived in the most basal cladogenesis of one of the basal clades of the *Leptodirina sensu novo*. Due to this the species of these clade are considered «ancient» in the sense that they are derived at an early stage of the evolutionary process in cave beetles, however, the proposed large evolutionary distance is causes difficulties discovering their relationship as the morphological characters as are the molecular sequences are too distant to allow a good «resolution» in the in phylogenetic analysis. They will be incorporated as genera *incertae sedis* within the large *Leptodirus-Anthroherpon* clade.

3.2.10.1 Genera ***Epiroella*** **and** ***Hartigiella***

The history and composition of this group is complex, and originally it was considered by morphological analysis that the *Epiroella* are part of the genus *Phaneropella*, before this the was divided into four distinct subgenera: *Phaneropella*, *Epiroella*, *Hittitia* and *Uludagites*. This classification, however, should be reconsidered, at least on a morphological basis as suggested by Casale and co-workers (Casale *et al*. 2013). In fact, these authors (Casale *et al*. 2013) discuss about the need to reclassify all subgenera, and make them genera , with this they appear to form acoherent phyletic lineage with an Anatolian-Balkan distribution This was the case at least at the time the species were described (Casale et al. 1991). Casale *et al*. (2013) limited themselves to raise the taxon *Epiroella* to the rank of genus, for which they describe a new species, postponing the elevation to genus of *Hittitia* and *Uludagites*.

Nowadays, molecular data of five generic-level taxa belonging to the established phyletic lineage of *Phaneropella* (*sensu auctorum*): *Epiroella* (with the species *E. acharnanis*), *Hittitia* stat. nov. (with the species *H. schuelkei* comb. nov. and *Zoiana kociani* comb. nov.), *Uludagites* stat. nov. (with the species *U. minuta* comb. nov.) and *Phaneropella* (with the species *P. lesinae*) are available. However, the molecular analysis allowed a reclassification of *Phaneropella lesinae* as belonging to the *Catopsinus* series and sister to *Besuchetiola* and *P. kociani* comb. nov. In turn *P. kociani* comb. nov. is the type species of the genus *Zoiana* nov. and sister to *Georgiana* gen. nov., also of the *Catopsinus* series.

The examination of the phylogenetic trees (Fig. 2) hint towards some interesting, but also controversial issues. On one hand the series of *Hittitia*, consisting of *Hittitia* stat. nov. and *Uludagites* stat. nov., is established with very high support (98.9/100) but also has a Northern-Anatolian distribution, which links them, to the *Drimeotus* + *Catopsinus* series, albeit with a very low support, 36.6/39.



FIGURES 147.1–147.14: *Boldoria* series. Aedeagus in dorsal view of: (**1**) *Monguzziella grottoloi,* (**2**) *Pavaniola ghidinii ghidinii,* (**3**) *Ragazzonia breviclavata*, (**4**) *Viallia alfanoi*, (**5**) *Cryptobathyscia gavardensis*. Apex of the paramere of: (**6**) *Boldoria aculeata*, (**7**) *Cacciamalia allegrettii,* (**8**) *Ghidinia morettii morettii,* (**9**) *Insubriella paradoxa*, (**10**) *Monguzziella grottoloi,* (**11**) *Pavaniola ghidinii ghidinii,* (**12**) *Ragazzonia breviclavata*, (**13**) *Viallia alfanoi*, (**14**) *Cryptobathyscia gavardensis*.

In the molecular analysis the *Epiroella* series in Tree-1 (Fig. 1I) is located at the base of the clade formed by the *Leptodirus* + *Hartigiella* series and *Speonomidius* + *Neobathyscia* series,which it is found to be related to, however, with very low support (49/19); while in Tree-2 (Fig. 2) the relationship is with the *Anthroherpon* series also with very low support (36.9/49). This is probably due to the almost complete lack of molecular data from the genera of Greece: two species from two differnt genera currently DNA data are available, out of over 50 genera consisting of 150 species which are in addition currently revised by Giachino and Vailati (*in prep*.)

Genus ***Epiroella*** Casale, Giachino, Vailati & Rampini, 1991
Phaneropella (*Epiroella*) Casale, Giachino, Vailati & Rampini, 1991: 202.
Epiroella Casale, Giachino, Vailati & Rampini, 1991: Casale, Giachino & Vailati 2013: 20.

Type species. *Phaneropella muelleriana* Paoletti, 1975 by original designation (habitus in Fig. 150.1).

Diagnosis. Small size, 1.1–1.7 mm, with bathyscioid shape (Fig. 150.1); with short, slightly convex and pubescent body. Depigmented.

Head: retractable, with complete, but blunted occipital carina in the middle, with reduced or no eyes.

Antennae: Short, just reaching or scarcely exceeding the base of the pronotum if stretched backwards, with the 1st antennomere as long as, or just shorter than the 2nd.

Pronotum: Broad, very transverse, convex, covered with a short and procumbent pubescence. Maximal width at the base, as wide as the base of the elytra. Lateral side not sinuated, long and regularly curved up to the anterior angles and less down curved towards the posterior angles.

Elytra: Relatively stout, ovoid, convex, regularly tapered in the posterior half, slightly dehiscent at the apex, with transversely aligned, weak, punctation; parasutural stria present or absent.

Legs: Short and thick. Males protarsi tetrameres and not dilated; protibiae slightly enlarged, provided with two robust spurs, without comb at apex; mesotibiae weakly arcuated and provided with thin spines on the external margin; metatibiae straight; meso- and metatibiae without apical basket. Metafemora not toothed in male.

Mesoventral keel (Fig. 150.2): High, with subretilinear or slightly curved anterior edge, with more or less apparent, or absent, tooth. Slightly sinuousidal ventral margin, with posterior apophysis prolonged over part of metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 150.3): With the wings of the metascutum elongated, each wing two and a half times as long as wide; apophysis of the alacrista prominent and the apices sharp.

Metendosternite (Fig. 150.4): «V»-shaped; furcal arms one and a half times longer than trunk, with thick apical apophysis; posterior furcal lamina with straight or slightly arched posterior edge; furcal trunk wider than long, middle keel on trunk diverging posteriorly.

Median lobe of aedeagus: Short and slightly curved in lateral view (Fig. 150.5). In dorsal view (Fig. 150.6), with sides progressively narrowing, and quite sinuous shaped, towards the apex, which is widely rounded or sub-truncated. Basal blade poorly developed.

Endophallus (Fig. 150.6): Basal «Y»-piece large, with very developed lateral branches. There is a complex median phanera in shape of inverted «V» or «U» or, again, of leaf-shape, which extends into the apical half of the median lobe with a weakly sclerotized flagellum, apically surrounded by two short and sclerotized lateral reinforcing bands.

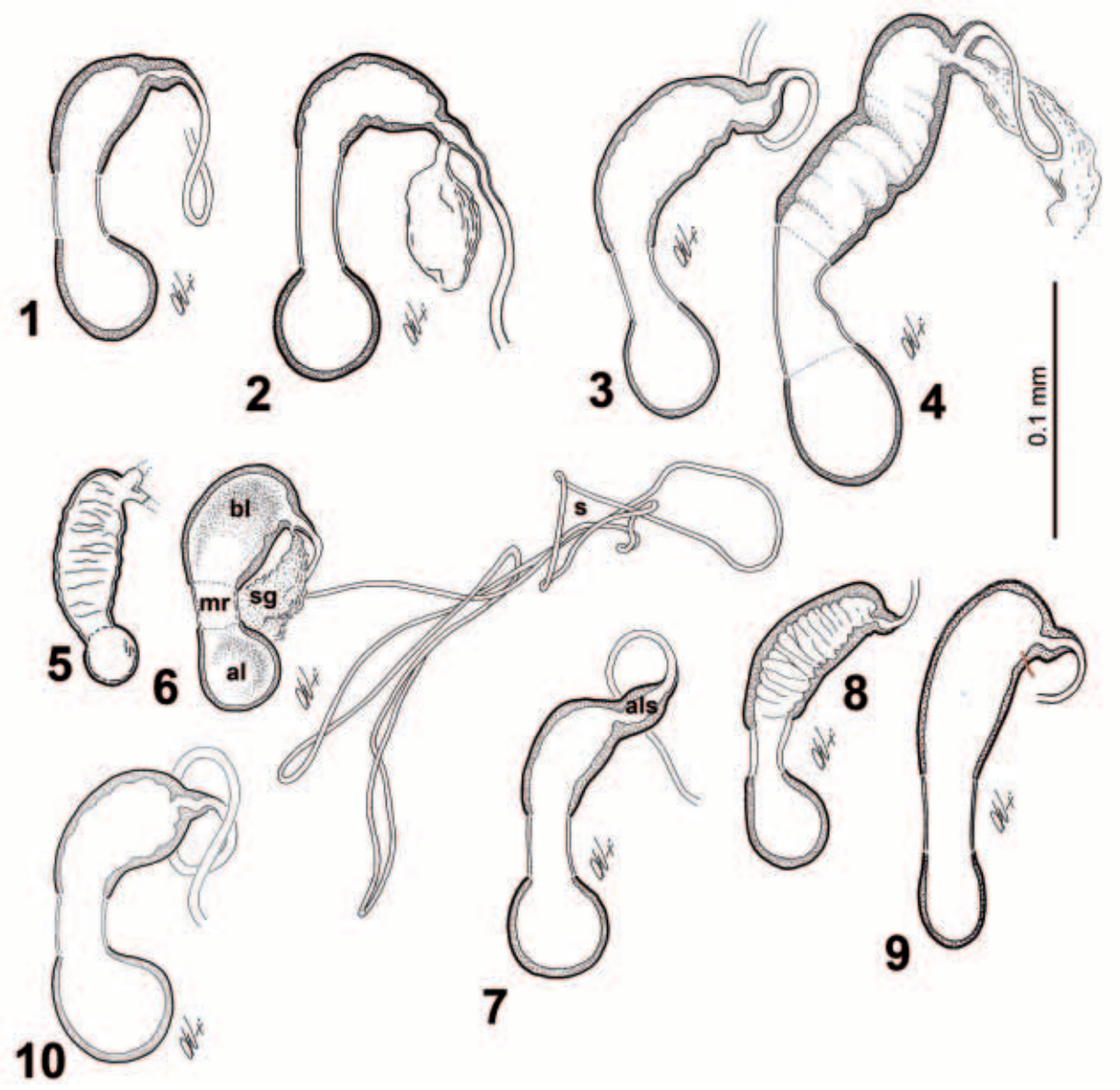
Parameres (Fig. 150.7): Thin, shorter or as long as the apex of the median lobe, bearing three subequal setae, two apical and one subapical internal one.

Spermathecal complex: Spermatheca (Fig. 150.8) sclerotized or not and elongated; saccular small and hyaline, sometimes with spherical distal lobe, wider than the elongated basal lobe and the short, hyaline junction part. Ductus dilated and sclerotized or not at the level of its insertion into the spermatheca; spermathecal gland hyaline, shapeless.

Female uroventrite VIII (Fig. 150.9): Short and broad, with spiculum short, tapering towards the apex that is somewhat rounded or truncate, not pointed.

Discussion. In addition to what has been pointed out in the discussion series section, it is important to note that *Epiroella* it differs from *Phaneropella* by the absence of eyes and parasutural stria, by the endophallus with a well-developed basal «Y»-piece and an otline of median flagellum, and for the well sclerotized and elongated spermatheca.

Distribution. Greece, Epirus.



FIGURES 148.1–148.10: *Boldoria* series. Spermathecal complex of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii,* (**4**) *Insubriella paradoxa,* (**5**) *Miettiella vespertilio* (modified from Piva 2016), (**6**) *Monguzziella grottoloi,* (**7**) *Pavaniola ghidinii ghidinii,* (**8**) *Ragazzonia vestae vestae*, (**9**) *Viallia alfanoi*, (**10**) *Cryptobathyscia gavardensis*. Abbreviations: **al**, apical lobe; **bl**, basal lobe; **mr**, median region; **s**, spermiduct; **sg**, spermathecal gland.

Species

Epiroella acharnanis Casale, Giachino & Vailati, 2013
Epiroella acharnanis Casale, Giachino & Vailati, 2013: 17.

Epiroella epirota (Giachino, 1989)
Muelleriella epirota Giachino, 1989: 33.
Phaneropella (*Epiroella*) *epirota* (Giachino, 1989): Casale, Giachino, Vailati & Rampini, 1991: 207.
Epiroella epirota (Giachino, 1989): Casale, Giachino & Vailati, 2013: 20.

Epiroella muelleriana (Paoletti, 1975)
Phaneropella pindica Müller: Paoletti, 1975: 1 (*Nomen nudum*).
Phaneropella muelleriana Paoletti, 1975: 2.
Muelleriella bonzanoi Casale, 1984: 2.
Phaneropella (*Epiroella*) *muelleriana* Casale, Giachino, Vailati & Rampini, 1991: 206.
Epiroella muelleriana (Casale, Giachino, Vailati & Rampini, 1991): Casale, Giachino & Vailati, 2013: 20.

Genus ***Hartigiella*** G. Müller, 1935
Bathysciola (*Hartigia*) G. Müller, 1928: 188 (*Nom. praeocc.* Homonymy with *Hartigia* Schiødte, 1838 – Hymenoptera –, *Hartigia* Desvoidy, 1863 – Diptera – and *Hartigia* Rondani, 1871 – Hymenoptera –).
Bathysciola (*Hartigiella*) G. Müller, 1935: 62 (*Nomen Novum*).
Hartigiella Müller, 1935: Vailati, 2017: 22.
Type species. *Bathysciola* (*Hartigia*) *baldensis* G. Müller, 1928 by original designation (habitus in Fig. 151.1).

Diagnosis. Medium sized, 2.4–2.8 mm, bathyscioid body, oval and posteriorly attenuated (Fig. 151.1).

Antennae: Slender and long, if strechted backwards, reachinguo to the half of elytra in males. 1st antennomere much shorter than the 2nd one; 8th more than twice as long as time longer than wide; 11th lanceolate and similar, although less elongated, the one of *Cacciamalia*, i. e, with sinuous sides, narrowed in the proximal third, as long as the previous one plus half of the 9th.

Pronotum: With regularly rounded sides, with the maximum width at the base or just above it; sharp, backward-facing rear vertices and acute angles.

Elytra: Ovoid, without parasutural stria and with regular and well marked transverse striolae.

Legs: Male protarsi pentameres, particularly developed in length, as long as, or also longer than the protibiae; very dilated, with the first tarsomere much wider than the protibiae. Tibiae with inner polidentate spurs at apex; meso- and metatibiae with complete spinous apical baskets.

Mesoventral keel (Fig. 151.2): High, widely rounded and prominent forward. Rounded vertex and obtuse angle. Ventral profile slightly curved. Posterior apophysis long, beyond the entire metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 151.3): Somewhat reduced, with longitudinal furrow of alacrista as wide as long and with sharp tips.

Metendosternite (Fig. 151.4): «V»-shaped, with not-triangular furcal arms. Furcal arms very thin and distinctly longer than the trunk, with a short and thick apophysis; posterior lamina of the furca narrow along the arm and arched posterior edge. Furcal trunk twice as long as wide at base and median keel with elongated posterior divergence.

Median lobe of aedeagus: Just over a third of the body long, stout. In lateral view (Fig. 151.5) it appears obtuse folded, with the apex thinned and curved downwards. In dorsal view (Fig. 151.6) with subparallel sides in basal half and therefore converging towards the apex. Apex regularly pointed and terminated by a very small, rounded, apical tongue.

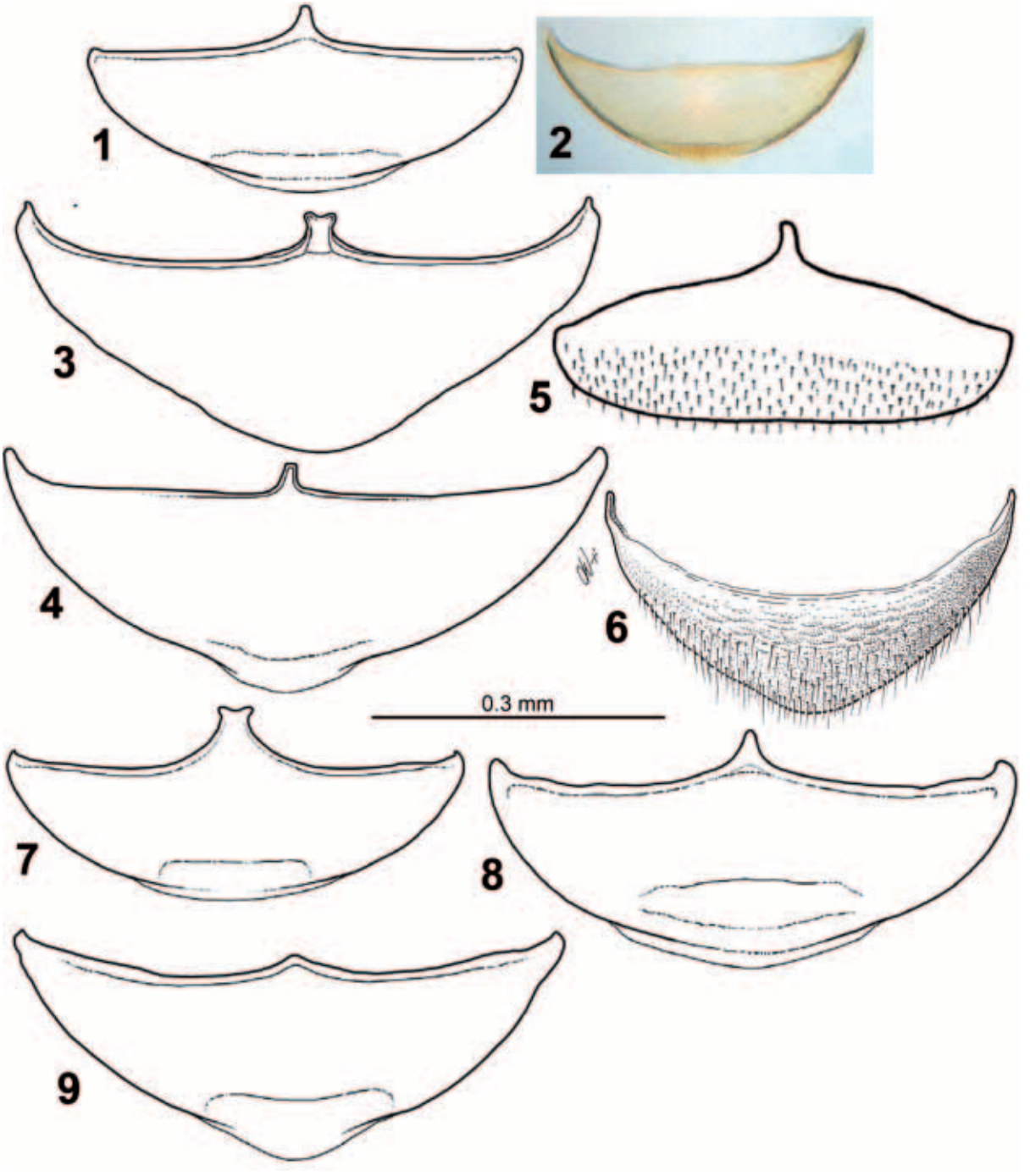
Endophallus (Fig. 151.6): With well-developed and sclerotized basal «Y»-piece. Median phanerae consisting of a sclerotized «butterfly-shape» central plate surrounded by fibrous hyaline structures. Distally there are two subparallel sclerotized bars, among which there are some long spines and two structures with surface spangled with small teeth.

Parameres (Fig. 151.7): Long and extremely slender, shorter than the median lobe. Without differentiated club with three setae: one apical and two preapical. The most proximal one very small.

Spermathecal complex: Spermatheca (Fig. 151.8) with a voluminous, pyriform, elongated proximal lobe and spherical and smaller distal lobe; hyaline union duct, as long as the apical lobe and narrower; thin spermatic duct, not dilated at its junction with the spermatheca.

Female uroventrite VIII (Fig. 151.9): Spiculum small, stout, little developed in length, with a pointed apex.

Discussion. In Tree-1 (Fig. 1I), *Hartigiella* appears as sister to the *Leptodirus* series with low support, 63.1/31. In Tree-2 (Fig. 2) it is placed sister to *Cacciamalia* also with fairly low support, 80.4/57, with this set sister to the *Epiroella* + *Anthroherpon* series with support of 86.1/57. The supports are low and the genetic distances are large in these two trees. However, in either analysis *Hartigiella* is always placed inside the large *Leptodirus*- *Anthroherpon* clade; this clade is one of the most basal and within it the genera *Cacciamalia*, *Epiroella* and *Hartigiella* are thought to be derived from very basal cladogenesis, as originating right at the dawn of the Leptodirina radiation as a whole. Since these three genera can occur together or separately, and also exhibit a substantial genetic distance amonst them, these three series have been considered in the analysis, with one representative for each genus. It seems that they have to be placed at the



FIGURES 149.1–149.10: *Boldoria* series. Female uroventrite VIII of: (**1**) *Boldoria aculeata*, (**2**) *Cacciamalia allegrettii,* (**3**) *Ghidinia morettii morettii,* (**4**) *Insubriella paradoxa,* (**5**) *Miettiella vespertilio* (modified from Piva 2016), (**6**) *Monguzziella grottoloi,* (**7**) *Pavaniola longitarsis,* (**8**) *Ragazzonia vestae vestae,* (**9**) *Viallia cappai*.

base of *Leptodirus-Anthroherpon* group, however, it is not possible to specifying which one exactly. *Hartigiella* that has always been considered very basal based on morphology and being similar to the genera of *Boldoria* group – this has recently been pointed out by Vailati (2017) –. In accordance with Tree-1 and Tree-2 *Hartigiella* is found outside the *Boldoria* group and placed in a separate serie as sister group of *Leptodirus-Anthroherpon* series. Undoubtedly, to be sure of the position of *Hartigiella*, molecular studies on unexamined clades of the *Boldoria* group or the undescribed genera from Greece are needed (Giachino & Vailati, *in prep*.) which also include morphological characteristics and geographic distribution. On the other hand, the disproportionate length of the mesoventral keel, which even exceeds the metaventrite, seem to correspond to the keels of the genera of the *Boldoria* series, although this particularity is also found in *Neobathyscia mancinii*, *Pholeuonidius halbherri* or *Rhaetiella pinkeri* of the *Neobathyscia* series.

Distribution. Italy. Gardesane Prealps, the whole massif of Baldo mountain, Stivo mountain and up to Bondone mountain.

Species

Hartigiella baldensis (G. Müller, 1928)
Bathysciola (*Hartigia*) *baldenis* G. Müller, 1928: 188.
Bathysciola (*Hartigia*) *baldenis* var. *lagarinensis* Tamanini, 1934: 37.
Bathysciola (*Hartigiola*) *baldensis* Müller: Ruffo, 1938: 98.
Bathysciola (*Hartigiella*) *baldensis* Müller: Conci, 1951: 56.
Boldoria (*Boldoria*) *baldensis baldensis* (Müller): Vailati, 1976: 37.
Boldoria baldensis (Müller, 1928): Vailati, 1988: 188.
Boldoria (sottog. *Hartigia* Müll.) *baldensis* var. *lagarinensis* Tamanini, 1934: 37.
Bathysciola (*Hartigiella*) *baldensis* subsp. *lagarinensis* Taman.: Conci, 1951: 56.
Boldoria (*Boldoria*) *baldensis lagarinensis* Tamanini: Vailati, 1976: 42.
Hartigiella baldensis (Müller, 1928): Vailati, 2017: 20.

3.2.10.2 Series ***Leptostagus***

In this series the genera *Leptostagus*, *Petkovskiella, Elladoherpon* and *Albanodirus* with an uncertain position on the phylogenetic tree are combined preliminarily, possibly until new and more molecular data become available. In our analysis this set of genera was found to be related to the phyletic series of *Leptodirus,* as it was already assumed by V.B. Guéorguiev (1976), followed by Perreau (2000, 2004) and Giachino *et al*. (2016). The group is characterised by the second antennomere elongated, not short as typical in *Anthroherpon*, although in general their appearance is very similar to *Leptostagus*. The genera of the *Leptodirus* series are distributed all the way from the karst of Trieste (Italy) to Bosnia-Herzegovina following the mountainous areas of the Balkan Peninsula, including the Dalmatian coast and islands, while those of the *Anthroherpon* series are distributed from the middle of Croatia to that of Albania, and in some areas of Croatia/Bosnia-Herzegovina where these two series have an overlapping geographical distribution. The *Leptostagus* series however is distributed from Albania towards the east, covering Greek Macedonia and the Republic of North Macedonia. Although the morphology seems to indicate a more or less close evolutionary relationship with the *Leptodirus* series, its distribution makes a close relationship with the *Anthroherpon* series more plausible. In the absence of molecular data, its position is uncertain, somewhere in the large clade of the *Anthroherpon-Leptodirus-Neobathyscia-Speonomidius-Epiroella-Hartigiella* series although its exact position cannot be determined with certainty.

Key to genera

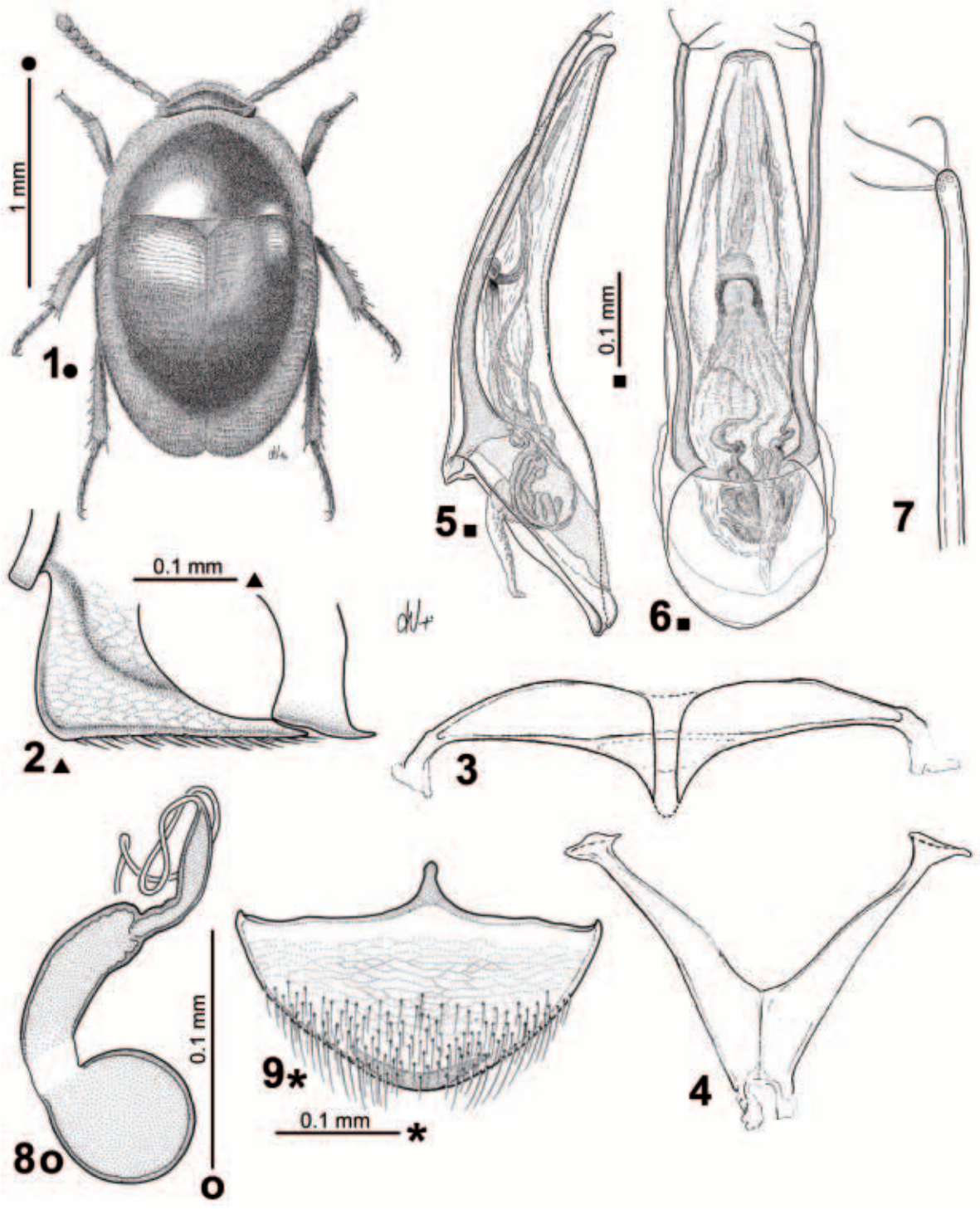
1. Large sized between 7.1–7.3 mm .....*Albanodirus*
- Medium sized between 3.4–4.3 mm….....2

2. Parameres bearing five setae (Fig. 153.11) ....*Petkovskiella*
- Parameres bearing three setae (Figs 153.9, 153.10) 3

3. Parameres with a rounded apical membranous lobe (Fig. 153.9) .....*Elladoherpon*
- Parameres without a rounded apical membranous lobe (Fig. 153.10).....*Leptostagus*

Genus ***Albanodirus*** Giachino & Vailati, 1998
Albanodirus Giachino & Vailati, 1998b [1995]: 113.

Type species. *Albanodirus trezzii* Giachino & Vailati, 1998 by original designation (habitus in Fig. 152.1).



FIGURES 150.1–150.9: Genus *Epiroella*. *Epiroella muelleriana*: (**1**) Habitus, (**3**) Metatergal apparatus, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere. *Epiroella acharnanis*: (**2**) Mesoventral keel, (**8**) Spermatheca, (**9**) Female uroventrite VIII. Figs **1**, **3–7** modified from Casale & Giachino (1989); Figs **2**, **8**, **9** modified from Casale *et al*. (2013).

Diagnosis. Large size, 7.1–7.3 mm. Body shape leptodiroid, very elongated, convex and narrowed anteriorly (Fig. 152.1). Colour bright reddish somewhat darker on the head and pronotum, lighter on the elytra. Pubescence very reduced, null or almost null in head and pronotum, short and very sparse on the elytra, although some longer and raised setae are interspersed. Integument with a very superficial and irregular punctation, barely visible, in head and pronotum; Punctation on elytra dense, with thick, shallow and close spots.

Head: Large, little elongated, not retractable and without occipital carina. Progressively narrowed in the posterior area; as, or almost as, wide as the pronotum; anophthalmous.

Antennae: Inserted approximately half the length of the head, very thin and very long, far extending well beyond the apex of the elytra, with the first antennomere dilated in the apical part and slightly longer than the second; 9th antennomere slightly longer than 10th and both shorter than 11th, which is the longest of all.

Pronotum: Small, elongated, 1.5–1.7 times longer than wide, with maximum width in the anterior third (in female towards the middle). Sides of the anterior half regularly arched, sinuous or concave in the posterior half. Posterior vertices sharp and outward-facing; posterior angles right; base as wide as the elytral base.

Elytra: Globose, pseudophysogastric, elongated oval, 1.6–1.7 times longer than broad overall. Maximum width towards the apical third; apical area narrowed and laterally concave; anterior area with a visible lateral ridge; apices not very acute. No parasutural stria.

Legs: Very long and slender, club-shaped; femora distinctly enlarged distally. Protibiae without comb and without external spurs, but with an internal trifid spur. Protarsi of males pentamerous and undilated. Claws long, not dilated. Numerous hairs in the apical area of the tibiae.

Mesothorax: Elongated and narrowed towards the front, although it does not form a true «peduncle» as in *Anthroherpon*.

Mesoventral keel (Giachino *et al*. 2016): Very low and very short, widely obtuse, with a small, sharp tooth.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Robust. In lateral view (Fig. 153.1) only slightly arched, with the dorsal surface straight in the basal two thirds and arched downwards in the apical third; apex not pointed and curved towards the dorsal surface. In dorsal view (Fig. 153.4), the sides are sinuous, concave towards the middle and convex in the apical third; the apex is bilobed with the lobes little not very prominent, rounded and with a marked slit between them. Basal blade short, posterior part, in dorsal view, in a wide arc; straight, narrow and pointed in lateral view. Ventral blade of tegmen shorter and of similar width to basal blade.

Endophallus (Fig. 153.4): There is no basal armour or differentiated parts, only a weakly scaly part and poorly defined reinforcement bands in the apical region.

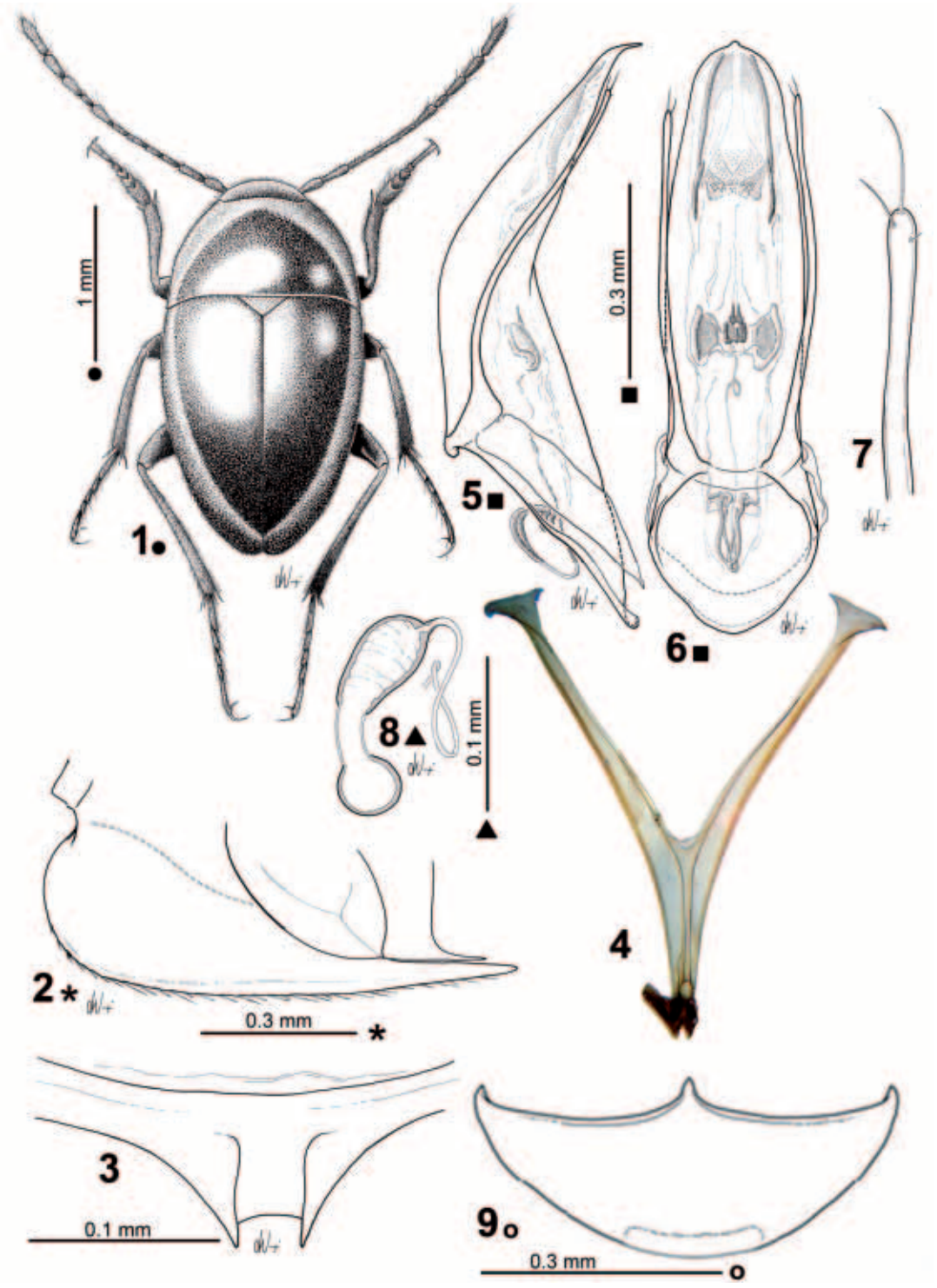
Parameres (Fig. 153.8): Thin, a little shorter than the median lobe, without a differentiated club, bearing three relatively long, subequal setae with proximate and equidistant insertion, one apical, one dorsal and one ventral.

Spermathecal complex (Fig. 154.1): With a large, well-sclerotized apical lobe. There are no difference between the union duct and the basal lobe, both of which are only slightly sclerotized. A large spermathecal gland drains into the spermiduct near the junction with the basal lobe.

Female uroventrite VIII (Fig. 154.4): Posterior margin arched, very slightly sharp in the middle apical area; spiculum short with more or less sharp apex.

Discussion. Without doubt, on superficial external examination, *Albanodirus* is very reminiscent of certain species of the genus *Anthroherpon*, due to the general shape of the body, physogastric elytra, the very elongated legs and antennae, and the almost pedunculated mesothorax. However, its affinities with *Leptodirus* are much greater: similar insertion of the antennae (near the middle of the length of the head), simple and non-enlarged claws, distally dilated femora, non-pedunculated mesothorax and similar type of protibial apical armature. There are also significant differences in the shape of the aedeagus, although the size and insertion of the setae are similar to those of *Leptodirus*, and in the genital segment of the male. Therefore, and until confirmed by molecular studies, we associate the genus *Albanodirus* with the phyletic series *Leptodirus* (*sensu* Jeannel 1924a) (Giachino & Vailati 1998; Giachino *et al*. 2016).

Distribution. The three species of *Albanodirus* known to date are all distributed in a band of Albanian mountain ranges between the Drin Nero valley to the east and the confluent Mat and Fan rivers to the West. This is a geologically complex area that includes major massifs such as Mali i Deiës, Mali i Shënjtit and Oroshit, and the Lurës mountains.



FIGURES 151.1–151.9: *Hartigiella baldensis*: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Metatergal apparatus, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere, (**8**) Spermatheca, (**9**) Female uroventrite VIII. Figs **1–3**, **5–9** modified from Vailati (2017).

Species

Albanodirus gobettii Giachino, Vailati & Casale, 2016
Albanodirus gobettii Giachino, Vailati & Casale, 2016: 140.

Albanodirus ivanpetrovi Giachino, Vailati & Casale, 2016
Albanodirus ivanpetrovi Giachino, Vailati & Casale, 2016: 141.

Albanodirus trezzii Giachino & Vailati, 1998
Albanodirus trezzii Giachino & Vailati, 1998b [1995]: 114.
Albanodirus beroni Giachino & Vailati, 2001: 100.

Genus ***Elladoherpon*** Casale, 1983
Elladoherpon Casale, 1983: 261.

Type species. *Elladoherpon inopinatum* Casale, 1983 by original designation (habitus in Fig. 152.2).

Diagnosis. Medium size, between 3.4–3.8 mm. Body leptodiroid (Fig. 152.2), elongated, with the anterior part narrowed and the posterior part convex, a little globular in the centre. Tegument shiny, yellowish with lighter appendages. Microsculpture generally fine, without order. Pubescence yellowish, short, scattered and recumbent.

Head: Longer than wide, not retractile, without a complete occipital carina and narrower than the anterior area of the pronotum; punctation fine, distant and a little deeper on the forehead; anophthalmous.

Antennae: Very long and slender, as long as the body in males, slightly shorter and not reaching the apex of the elytra in females. All the antennomeres, except the 1st, cylindrical, clearly longer than wide; the first slightly shorter than the second; the 7th and 11th antennomeres of similar length are the longest.

Pronotum: Cordate, elongate, 1.3–1.4 times longer than wide. Sides evenly arched in the anterior part and concave in the posterior part, which is the narrowest. Maximum width in the anterior third. Posterior vertices not very prominent and slightly acute; angles between straight or slightly obtuse. Median part with an elongated, well-defined depression that fades in the anterior and posterior parts. Punctation small, with spaced dots; pubescence with short, flat- lying hairs.

Elytra: Elongated oval, subglobose, convex, much longer than wide (1.8 in males; 1.6 in females). Narrowed anteriorly and attenuated in the apical parts; wider and globular in females. Punctation slightly denser and stronger than on pronotum; pubescence slightly longer; without parasutural stria.

Legs: Very long and slender. Protibiae slightly arched in the apical area, more evident in females, meso- and metatibiae straight; protibiae without a comb, with a large trifid inner spur. Protarsi of males pentamerous and enlarged, formerly a little narrower than the apical area of the protibia; tetramerous and slender in females. Femora straight, enlarged in the basal area.

Mesoventral keel (Casale 1983): Almost non-existent, reduced to a very small prominence in the median part of the mesoventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Casale 1983): Very small, only a very small smooth transverse band.

Metendosternite: Unknown.

Median lobe of aedeagus: Small, only slightly sclerotized. In lateral view (Fig. 153.2), evenly curved and smooth, with a narrowed apical part and rounded apex. In dorsal view (Fig. 153.5), lateral margins regularly arched to apical part, gradually narrowing to is blunt and very slightly sinuate apex. Basal blade well developed, arched posteriorly, slightly longer than the ventral blade of the tegmen but narrower.

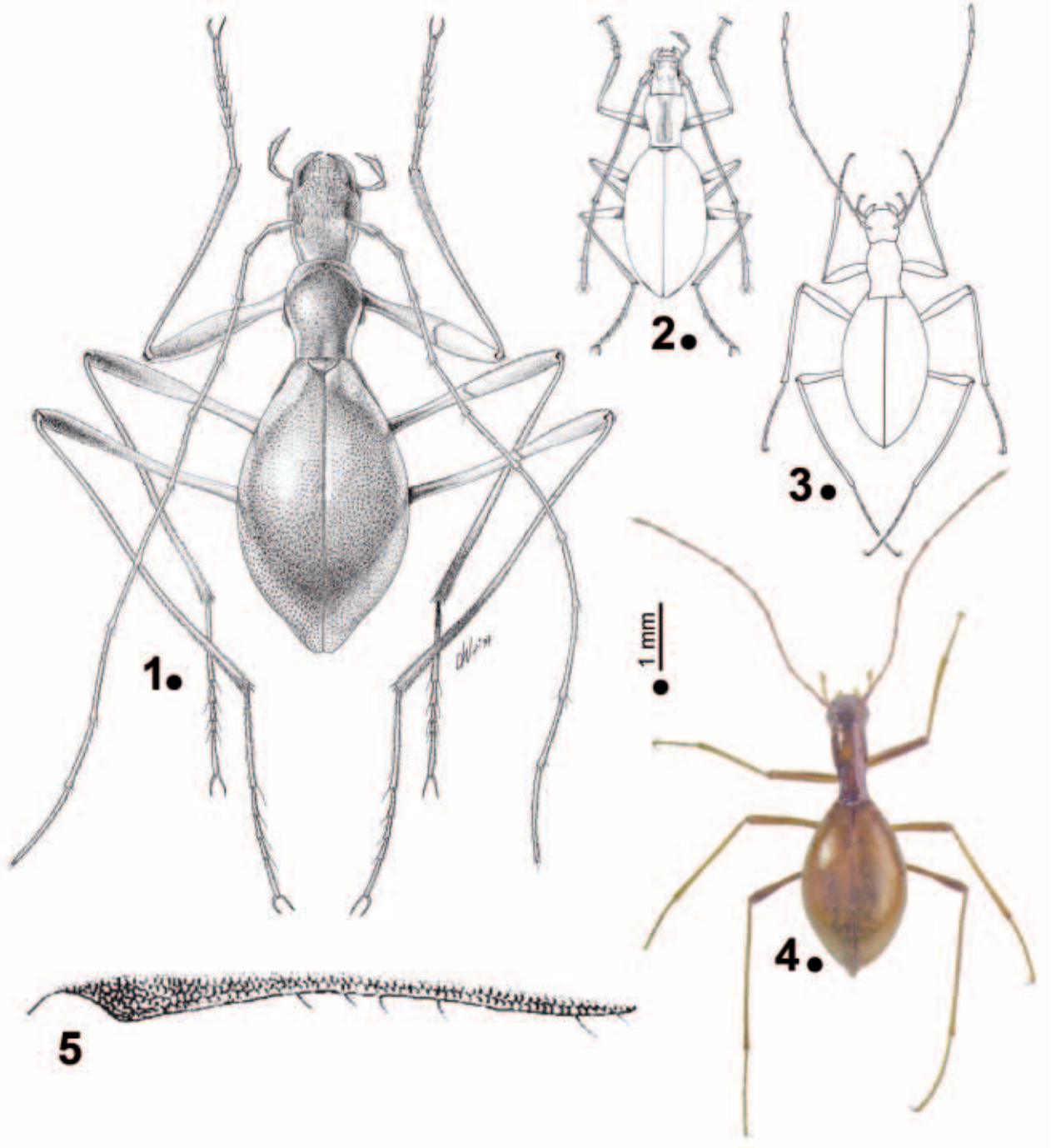
Endophallus (Fig. 153.5): Without basal structures, with two narrow bands of scales along the lateral areas of the sac and a group of small spines in the median region.

Parameres (Fig. 153.9): Quite thick and long, reaching the apex of the median lobe; apical area slightly curved, with three setae inserted near the apex and a rounded apical membranous lobe.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. *Elladoherpon* presents morphological characters comparable to those of the genera *Parapropus* and *Astagobius*; the geographical area colonised, the «southern Dinaric part», as indicated by V.B. Guéorguiev (1977); it presents a good number of affinities with several north-Egeidian genera (Casale 1983). Undoubtedly, molecular analysis which have not yet been carried out will make it possible to establish whether this genus is closer to the genera *Parapropus* and *Astagobius* or to *Leptostagus* and *Petkovskiella* with which it also shares many characters.

Distribution. Greece, Macedonia. Captured in a small, cold, damp pit on the slopes of mount Vermio (Casale 1983).



FIGURES 152.1–152.5: *Leptostagus* series. Habitus of: (**1**) *Albanodirus trezzii* (modified from Giachino *et al*. 2016), (**2**) *Elladoherpon inopinatum* (modified from Casale 1983), (**3**) *Leptostagus babunae,* (**4**) *Petkovskiella stygia*. Mesoventral keel in lateral view of: (**5**) *P. stygia* (modified from S. Ćurčić *et al.* 2005).

Species

Elladoherpon inopinatum Casale, 1983
Elladoherpon inopinatum Casale, 1983: 263.

Genus ***Leptostagus*** Karaman, 1954
Leptostagus Karaman, 1954b: 72.

Type species. *Leptostagus babunae* Karaman, 1954 by original designation (habitus in Fig. 152.3).
Diagnosis. Average size between 3.5–3.8 mm. Body narrow and elongated, with leptodiroid facies (Fig. 152.3). Colour bright reddish-brown. Pubescence yellowish, with short, spares, flat-lying hairs. Punctation poorly differentiated, with very fine dots.

Head: Elongated, longer than wide, not retractable, a little convex and a little narrower than the pronotum; without occipital carina; anophthalmous.

Antennae: Long and slender, inserted on the posterior third of the head, as long as the body; first antennomere three times shorter than the second; 11th antennomere as long as the 10th.

Pronotum: Subrectangular, slightly convex, with median area sometimes flattened, between 1.9–2.0 times as long as wide. Maximum width towards the anterior third, narrowing in the posterior part. Lateral margins almost entirely splayed, regularly arched from a little in front of the median part to the anterior base, being concave in the posterior third; base slightly convex. Dorsal surface well punctate; pubescence very short and scattered.

Elytra: Physogastric, convex, moderately elongated, between 1.6–1.7 times as long as wide. Maximum width towards the middle. Lateral margins flanged and regularly rounded, tapering gradually towards the rear, with rounded apical areas. Punctation formed by wide, deep dots; pubescence short, dense and recumbent. Parasutural stria lacking.

Legs: Very long and slender, covered with fine pubescence. Protibiae with inner margin of apical area slightly concave, without comb of short outer apical spines. Males protarsi pentamerous, with first tarsomere moderately dilated. Meso- and metatibiae straight; femora narrowed before distal part.

Mesoventral keel (Karaman 1954b): Very low, with obtuse angle and rounded vertex. Ventral margin slightly concave, with a few scattered setae.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Fairly long and robust. In lateral view, ventral margin slightly sinuate, dorsal margin convex in middle area, apical area narrow and somewhat concave, with acute apex. In dorsal view (Fig. 153.6), subparallel, with sides slightly arcuate in basal three quarters, then evenly narrow in apical quarter, with rounded apex. Basal blade short and only slightly enlarged, with an arched posterior margin, almost as wide as the ventral blade of the tegmen, which is also short.

Endophallus (Fig. 153.6): Without a defined armour, only a few sclerotized parts in basal and apical medial areas.

Parameres (Fig. 153.10): Long and slender, shorter than median lobe. Club very slightly thickened, curved and apically pointed, with three medium-length setae and insertion pores close to the tip.

Spermathecal complex: Spermatheca (Fig. 154.2) small, weakly sclerotized and irregular sac-shaped of similar thickness, without distinct regions. Spermatic duct short; spermathecal gland well defined.

Female uroventrite VIII (Fig. 154.5): Apical margin narrowed arcuate, ventral side with numerous setae; arcuate sides of basal margin joined to form short, narrow spiculum with acute tip.

Discussion. *Leptostagus* has the facies of *Anthroherpon*, although it is included in the *Leptodirus* series by V.B. Guéorguiev (1976). As already indicated, it is very close both morphologically and geographically to *Petkovskiella* and *Elladoherpon* (Casale 1983). Molecular analysis will be conclusive as to their position and phylogenetic relationships.

Distribution. Known from a cave in the north of the Republic of North Macedonia, Damjanica cave nestled near Nezhilovo in the municipality of Čaška.

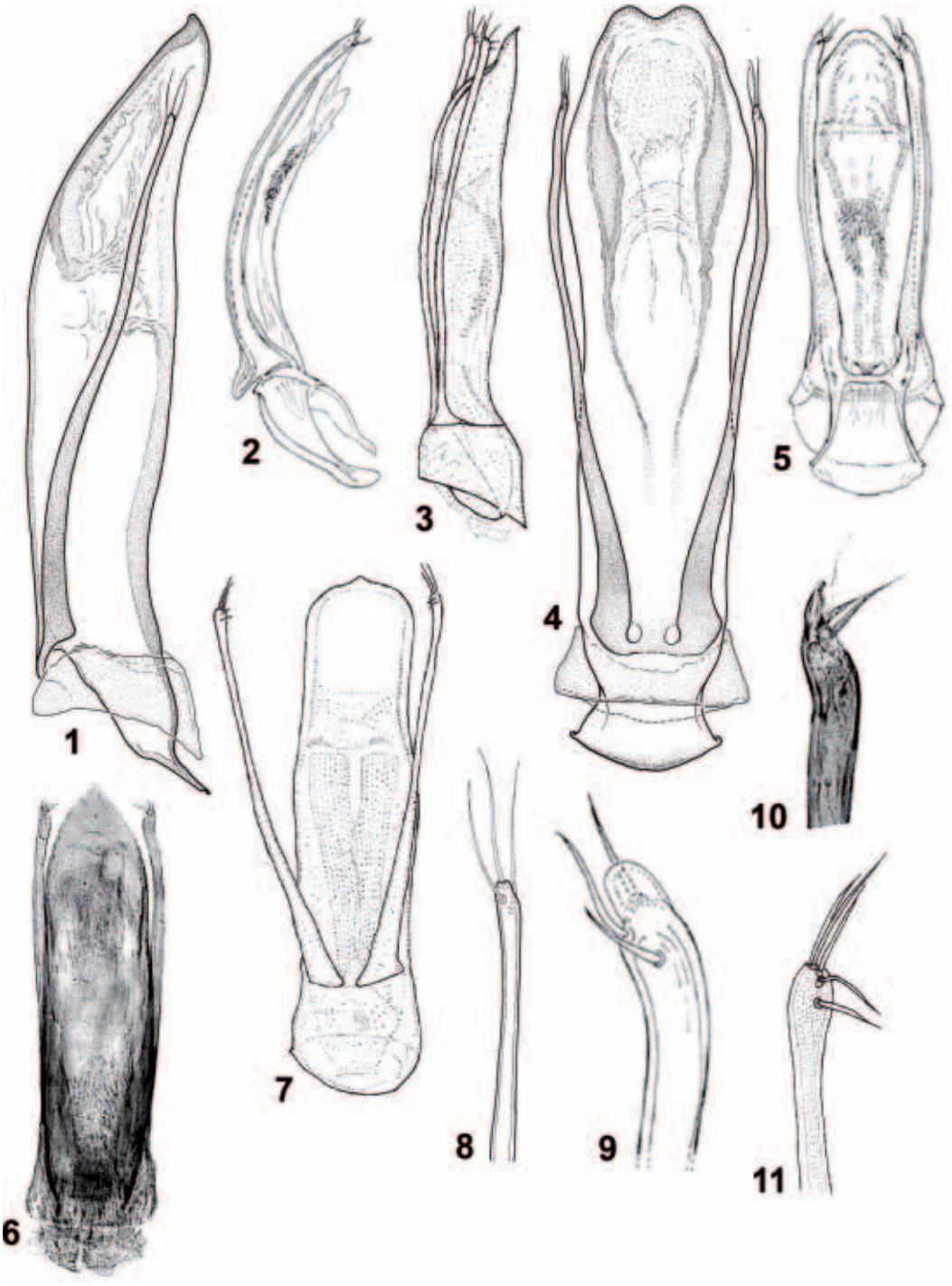
Species

Leptostagus babunae Karaman, 1954
Leptostagus babunae Karaman, 1954b: 74.

Genus ***Petkovskiella*** V.B. Guéorguiev, 1976
Petkovskiella V.B. Guéorguiev, 1976: 128.

Type species. *Leptostagus stygius* Karaman, 1954 by original designation (habitus in Fig. 152.4).

Diagnosis. Average size 3.6–4.3 mm. Body narrow and elongated, with leptodiroid facies (Fig. 152.4). Reddish-brown in colour, with slightly lighter antennae and tarsi. Pubescence yellowish, made up of short or long, scattered and flat-lying hairs; pubescence not very differentiated, with very fine dots.



FIGURES 153.1–153.11: *Leptostagus* series. Aedeagus in lateral view of: (**1**) *Albanodirus trezzii,* (**2**) *Elladoherpon inopinatum*, (**3**) *Petkovskiella stygia*. Aedeagus in dorsal view of: (**4**) *Albanodirus trezzii,* (**5**) *Elladoherpon inopinatum*, (**6**) *Leptostagus babunae*, (**7**) *Petkovskiella stygia*. Apex of the paramere of (**8**) *A. trezzii,* (**9**) *E. inopinatum,* (**10**) *Leptostagus babunae*, (**11**) *P. stygia*. Figs **2**, **5**, **9** modified from Casale (1983); Figs **3**, **7**, **11** modified from S. Ćurčić *et al.* (2005); Figs **6**, **10** modified from Perreau & Pavićević (2008); Figs **1**, **4**, **8** modified from Giachino *et al*. (2016).

Head: Elongated, a little longer than wide, not retractable, a little convex and as wide as the pronotum; occipital carina absent; anophthalmous.

Antennae: Long and slender, inserted on the posterior third of the head, longer than the body; first antennomere as long as the second; the 11th antennomere as long as the 10th.

Pronotum: Subrectangular, slightly convex with the median area sometimes flattened, between 1.8–2.0 times as long as wide. Maximum width towards the anterior third, narrowing in the posterior area. Lateral margins evenly arched from a little before the median part to the anterior margin, being concave in the posterior third; flanges in this part. Base of pronotum slightly convex; dorsal surface with very fine punctation; pubescence very short and scattered.

Elytra: Elongate, ovate and moderately convex, between 1.7–1.8 times as long as wide. Maximum width towards the middle; lateral margins regularly rounded and progressively narrowed towards the rear, with rounded apical areas. Punctation shallow and fairly dense; pubescence well developed, dense and recumbent. Parasutural stria absent.

Legs: Very long and slender, covered with fine pubescence. Protibiae with inner margin of apical area slightly concave, without comb of short outer apical spines, nor basket, nor inner spurs. Males protarsi pentamerous, with first tarsomere moderately dilated; meso- and metatibiae straight; femora narrowed before distal areas. Tarsal claws simple, long and slightly enlarged.

Mesoventral keel (Fig. 152.5): Very low, formed by a small prominence in the anterior area of the mesoventrite with an obtuse angle and a vertex between rounded and slightly pointed, and a long, slightly concave ventral margin, with a few scattered setae.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Fairly long and robust. In lateral view (Fig. 153.3), slightly sinuate ventrally and convex in the dorsal median part, the apical part narrow and slightly concave, with an acute apex. In dorsal view (Fig. 153.7), the sides are parallel, slightly widened in the basal two-thirds and narrowed in the apical third; this area does not narrow at the apex and a small prominence is formed in the middle. Basal blade of median lobe short, slightly enlarged with posterior margin arched, almost as wide as ventral blade of tegmen, which is also short.

Endophallus (Fig. 153.7): With two longitudinal bands along the basal and medial areas, and above some discreete sclerotized areas towards the middle.

Parameres (Fig. 153.11): Long and slender, slightly shorter than the median lobe. The apical club is slightly thickened and bears five medium-length setae , three at the apex, and the other two inserted in the inner margin with insertion pores nearby.

Spermathecal complex: Spermatheca (Fig. 154.3) small, without clearly differentiated regions, weakly sclerotized and sac-shaped with the apical area widest. Spermatic duct short, thin in the anterior part and thicker in the posterior part; spermathecal gland well defined, with a very short duct terminating at the junction of the spermiduct to the basal part of the spermatheca.

Female uroventrite VIII (Fig. 154.6): Apical margin in broad, regular arc, ventral surface with numerous setae and short, broad spiculum with rounded tip.

Discussion. Genus geographically close to the genera *Leptostagus* and *Parapropus*, these genera also share many external morphological characters and very similar male genitalia. V.B. Guéorguiev (1976) included them in the subtribe Leptodirina and Casale (1983) brought it closer to *Elladoherpon*, but until molecular studies show their relationships, it is difficult to indicate their phylogenetic proximity.

Distribution. It is known from two caves in the Republic of Northern Macedonia, one towards the centre, the Zmejeviza cave, near Kapra, south of Mount Jama (Perreau 2000) and the other, to south, the small Manastirska Propast pit, municipality of Prilep, on Mount Dautica (S. Ćurčić *et al*. 2005).

Species

Petkovskiella stygia (Karaman, 1954)
Leptostagus stygius Karaman, 1954b: 76.
Petkovskiella stygia (Karaman): V.B. Guéorguiev, 1976: 128.
Petkovskiella henrikenghoffi S. Ćurčić & B. Ćurčić, 2005: 310.

3.2.10.3 Series ***Magdelainella***

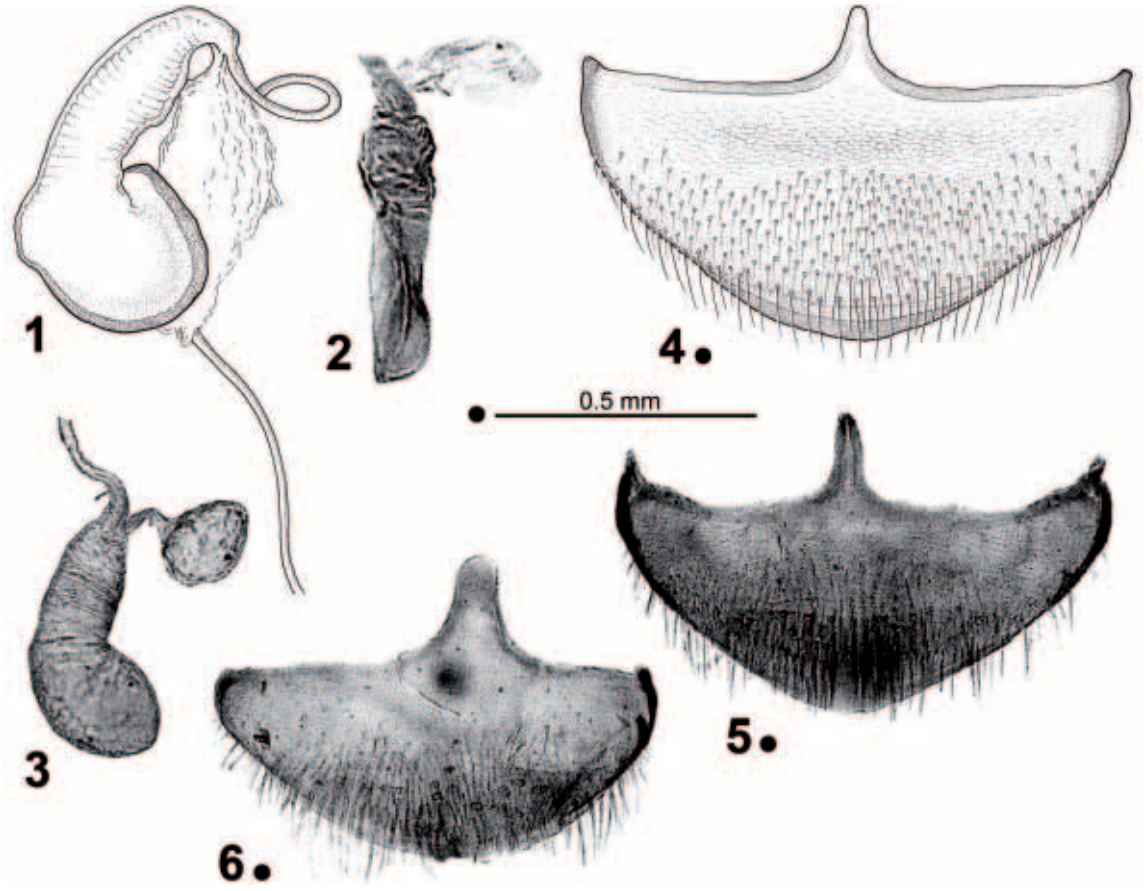
Diagnosis. Small size, between 1.8–2.5 mm. Bathyscioid facies and depigmented species.

Head: Anophthalmous or with macules in the ocular area.

Antennae: First antennomere shorter than or as long as the second.

Pronotum: As wide as or slightly wider than the maximum width of elytra.

Elytra: With or without parasutural stria.



FIGURES 154.1–154.6: *Leptostagus* series. Spermatheca of: (1) *Albanodirus trezzii,* (**2**) *Leptostagus babunae*, (**3**) *Petkovskiella stygia*. Female uroventrite VIII of: (4) *A. trezzii,* (**5**) *L. babunae*, (**6**) *P. stygia*. Figs **2**, **3**, **5**, **6** modified from Perreau & Pavićević (2008); Figs **1**, **4** modified from Giachino *et al*. (2016).

Legs: Protibiae without comb on apical and outer margin, with external spurs. Meso- and metatibiae without apical basket. Protarsi pentamerous in males and tetramerous in females.

Mesoventral keel: High and triangular, the posterior process extends over the metaventrite, but does not reach the posterior margin.

Endophallus: Median area without, or with 1–3 pairs of small sclerotized pieces or groups of phanera and in the basal area with a flagellum, a stylet or something similar.

Parameres: As long as or almost as long as the median lobe and armed with three setae.

Spermatheca: With short, non-hyaline, union duct; spermathecal gland undifferentiated. Spermiduct with a small sclerotized piece, or with a larger expansion, at its junction with the copulatory bursa.

Discussion. The genera *Magdelainella*, *Derveniella*, and *Knirschiella* are very similar in both external morphological characters and genitalia, so their validity or independence needs to be confirmed by molecular studies, as well as its phylogenetic relationship with the other series. S. Ćurčić *et al*. (2004a, 2004b, 2009) assumed, without molecular data, that these genera constitute a complex of probably Mesogean age and origin, their species having differentiated during the Alpine orogeny due to drastic palaeoclimatic events, which affected large areas of the Balkan Peninsula.

Key to genera

1. Elytra with longitudinal carinae. In lateral view, the middle area of the median lobe of aedeagus not glo-

bose (Fig. 155.5); endophallus with three groups of phanera (Fig. 156.1). Parameres with a shorter, globose club and with the insertion pore of the subapical setae close to the pores of the apical setae (Fig. 156.4). Spermatheca with the basal lobe more developed than the apical (Fig. 156.7) .....*Derveniella*
- Elytra without longitudinal carinae. Aedeagus in lateral view with central area of median lobe globose (Figs 155.6, 155.7); endophallus with 1–2 pairs of phanerae (Figs 156.2, 156.3). Parameres with a more elongated or poorly developed club and with the insertion pore of the subapical seta distant from the pores of the apical seta (Figs 156.5, 156.6). Spermatheca with basal lobe as or less developed than apical (Figs 156.8, 156.9) 2

2. 11th Antennomere distinctly longer than 9th and 10th antennomeres. Elytra without parasutural stria. Mesotibiae without external sinuosity. Female protarsi slightly dilated.....*Knirschiella*
- 11th Antennomere as long as or slightly shorter than 9th and 10th antennomeres. Elytra with parasutural stria. Mesotibiae with external sinuosity. Female protarsi not dilated .....*Magdelainella*

Genus ***Derveniella*** Pavićević & Perreau, 2008
Magdelainella (*Derveniella*) Pavićević & Perreau, 2008: 194.
Derveniella Pavićević & Perreau: S. Ćurčić, Makarov & B. Ćurčić, 2009: 762.

Type species. *Magdelainella* (*Derveniella*) *stevanovici* Pavićević & Perreau, 2008 by original designation (habitus in Fig. 155.1).

Diagnosis. Small size, 2.0 mm. Bathyscioid facies, body short, ovoid, distinctly convex and only slightly narrowed towards the rear (Fig. 155.1). Tegument shiny dark reddish. Pubescence short and recumbent.

Head: Sub-squared, fairly robust, without occipital carina; without eyes.

Antennae: Short, almost reaching the base of the pronotum; first antennomere as long and a little more robust than the second; 4th to 6th and 8th to 10th antennomeres transverse, the 11th as long as the sum of the lengths of the 9th and 10th.

Pronotum: Transverse, 1.7 times wider than long, as wide as the elytra and with regularly arched lateral margins; maximum width at the base which does not narrow. Posterior vertices rounded, very little directed backwards and the basal angle between straight and slightly obtuse. Disc of pronotum with sparse punctation made up of small dots and a few larger ones, smooth surface between the dots.

Elytra: Short and wide, 1.2 times as long as wide, with margins regularly curved towards the apex, the latter rounded; maximum width at the base. Transverse striolae, fine and regularly spaced, in addition to two very faint longitudinal grooves. Parasutural stria lacking.

Legs: Short, fairly stout; male protarsi pentamerous, well expanded, a little wider than the apical margin of the protibiae. Protibiae without comb; mesotibiae thick and curved, with a marked external sinuosity over the entire apical third in both sexes; metatibiae not very arched and, in both, with a few long spines on the outer margins.

Mesoventral keel (Fig. 155.3): High and triangular with the anterior margin convex and the ventral margin narrow, somewhat sinuate, with setae. Posterior process not extending beyond the metaventrite; vertex with a small prominence and an obtuse angle.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

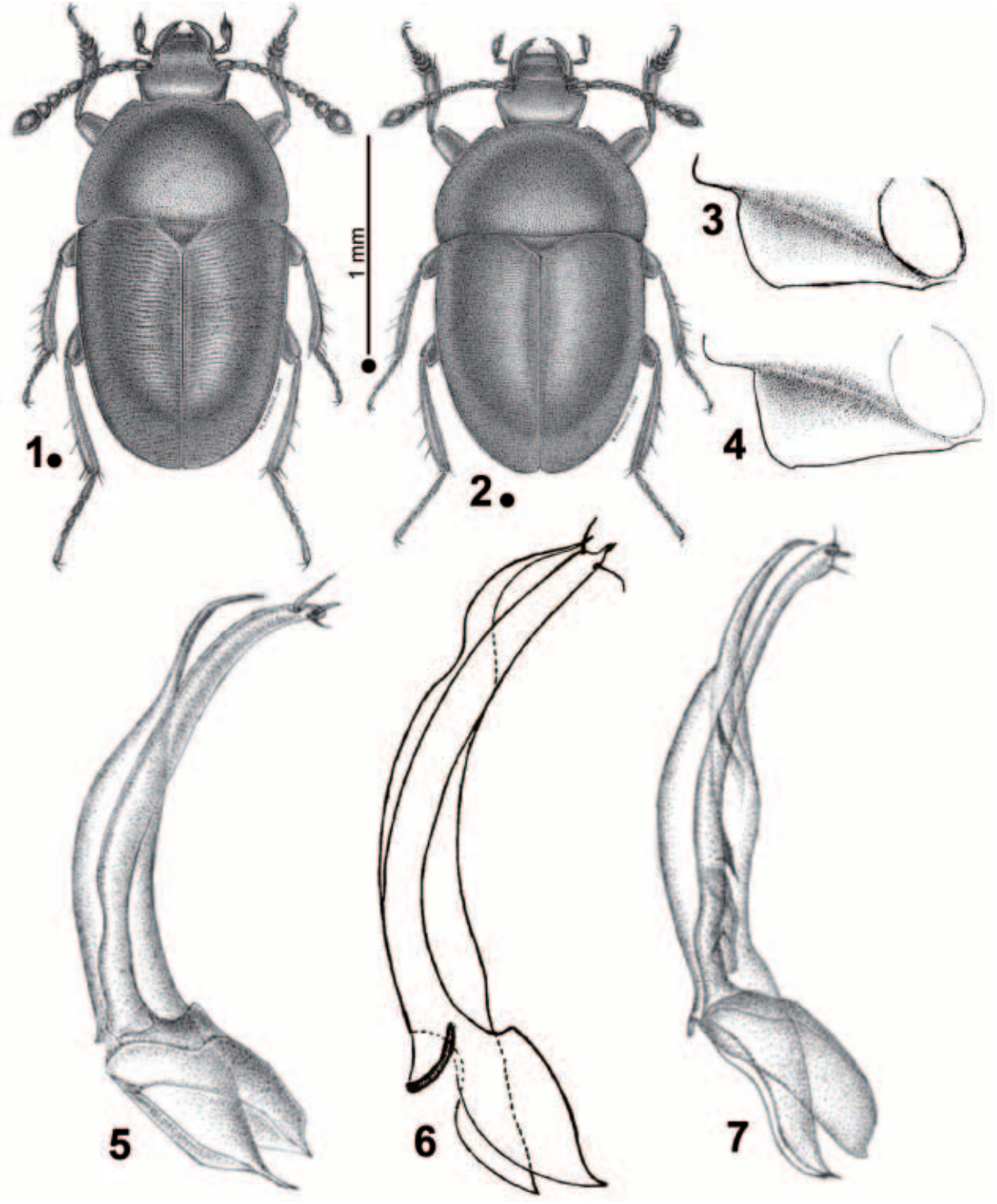
Median lobe of aedeagus: In lateral view (Fig. 155.5), only slightly arched with the basal three quarters of similar thickness and the apical fourth very curved and narrow with an acute apex facing ventrally. In dorsal view (Fig. 156.1), sides arched and slightly narrowed in the basal third, with the apical part shaped like an arrow with a pointed tip. Basal blade, in ventral view, only slightly arched with subrectilinear posterior margin.

Endophallus (Fig. 156.1): Basal area with sparsely sclerotized structure in the form of an elongate vessel. The median region with three successive groups of spines of different thicknesses. The apical region with two reinforcing bands densely covered with inverted spines and a triangular phanera between them in its basal region.

Parameres (Fig. 156.4): In lateral view, thick with the apical area narrower and somewhat angular, as long as the median lobe. Ventrally, with a differentiated club bearing three setae, two small apical ones with the insertion pores close together and a third internal preapical one, not far apart and slightly longer. Ventral blade of tegmen shorter and slightly wider than basal lamina.

Spermathecal complex: Spermatheca (Fig. 156.7) small, arched and well sclerotized; apical and basal lobes dilated, junction duct short but well differentiated. Apical lobe spherical and basal lobe of the same diameter, the latter more elongated and oblong. No spermathecal gland observed.

Female uroventrite VIII (Fig. 156.10): Broad, with posterior margin arched and rounded prominence in



FIGURES 155.1–155.7: *Magdelainella* series. Habitus of: (**1**) *Derveniella stevanovici,* (**2**) *Magdelainella nonveilleri*. Mesoventral keel in lateral view of: (**3**) *D. stevanovici,* (**4**) *M. serbica*. Aedeagus in lateral view of: (**5**) *D. stevanovici,* (**6**) *Knirschiella ravasinii* (redrawn after G. Müller 1922), (**7**) *M. serbica*. Figs **1–5**, **7** modified from Pavićević & Perreau (2008)

median area; anterior margin sinuously arched. Spiculum triangular, with acute, slightly elongated apex.

Discussion. *Derveniella* is closely related to *Magdelainella*, a genus with which it shares a similar structure of the median lobe of aedeagus, particularly evident in lateral view: only slightly arched, although the median part in this genus is not globose, but it has the fourth apical very narrow and very curved with the apex pointed and oriented towards the ventral face. It is also distinguished by thicker mesotibiae, with a more pronounced external sinuosity in the apical third, by elytra with only two tiny longitudinal carinae; by the anterior edge of the mesoventral keel more rounded, by thicker parameres with two apical and one preapical setae and above all by the structures of the endophallus (Pavićević & Perreau 2008). *Derveniella* inhabits the southeastern region of Serbia and *Magdelainella* has colonized the central part of the Balkan Peninsula. No molecular studies have been carried out to establish the position of these genera in the phylogeny.

Distribution. *Derveniella* colonises endogean habitats of the Svrljiške and Suva mountains, as well as the area around Dimitrovgrad, in southeastern Serbia.

Species

Derveniella stevanovici (Pavićević & Perreau, 2008)
Magdelainella (*Derveniella*) *stevanovici* Pavićević & Perreau, 2008: 196.
Derveniella stevanovici (Pavicevic & Perreau, 2008): S. Ćurčić, Makarov & B. Ćurčić, 2009: 762.

Genus ***Knirschiella*** V.B. Guéorguiev, 1976
Magdelainella (*Knirschiella*) V.B. Guéorguiev, 1976: 127.
Knirschiella V. B. Guéorguiev, 1976: S. Ćurčić, Brajković, B. Ćurčić, Schönmann, Makarov, Mitić & Tomić, 2004: 119.

Type species. *Bathysciola Ravasinii* G. Müller, 1922 by original designation.

Diagnosis. (from G. Müller 1922a): Small size, between 1.8–2.2 mm. Broad, ovoid body, bathyscioid facies. Brownish colouration. Pubescence yellowish, formed of short, sparse, flat-lying hairs.

Head: Rather broad, without occipital carina; anophthalmous.

Antennae: Short, reaching the base of pronotum; first antennomere as long as the second; 11th antennomere distinctly longer than the sum of the lengths of the 9th and 10th.

Pronotum: wide and very convex; maximum width at base and as wide as elytra, sides evenly arched.

Elytra: Short, overall ovoid and rather convex; maximum width towards the basal area; lateral margins evenly rounded and not narrowing in the apical area, apex rounded; elytral sculpture with more or less diffuse dots between strong microreticulation. Punctation forming well-defined transverse striolae in the basal half and blurred in the apical half; absence of longitudinal carinae and parasutural stria.

Legs: Short and rather robust; protibia with external spurs but without a comb on the apical and external margins; protarsomeres pentamerous in males, with the first tarsomere distinctly wider than the apical area of the protibia; mesotibiae thin and regularly curved. Females with tetramerous and slightly dilated protarsomeres.

Mesoventral keel: High and triangular; anterior and ventral margin straight and rectilinear extending across the mesoventrite without reaching the posterior margin; apex arched, a small prominence on the underside; angle obtuse.

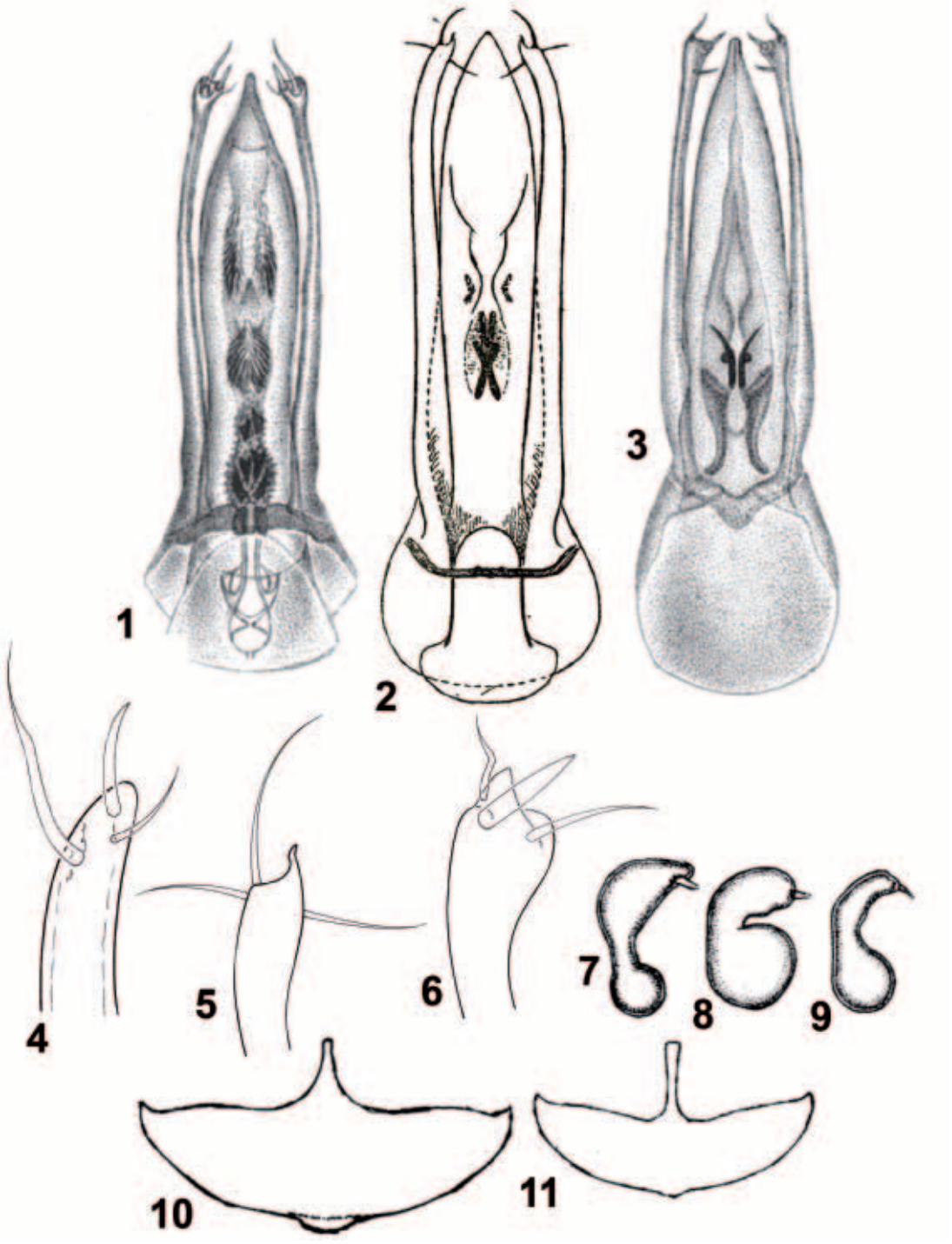
Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Moderately long and slightly arched, similar to that of *Magdelainella serbica*, according to Jeannel (1924a). In lateral view (Fig. 155.6), slightly arched, the apical area tapering and curving towards the ventral side. In dorsal view (Fig. 156.2), sides slightly arched and narrowly towards the apical area. Basal lamina well developed with rounded apical margin, longer and as wide as ventral lamina of tegmen.

Endophallus (Fig. 156.2): Armature rather complex, similar to that of *Magdelainella serbica*; median part with a pair of coarse teeth, two elongate laterodorsal folds beneath the teeth joining at the base in a loop-shaped transverse piece. Basal area with a sclerotized band along the dorsal median area which, at the bottom of the sac, ventrally surrounds a long flagellum or stipe.

Parameres (Fig. 156.5): As long as the median lobe, briefly arcuate and rather thick, with the apical area in a slightly dilated oblong club and laterally a short pointed protuberance, with three rather long setae of equal length turned inwards, two apical and one subapical.

Spermathecal complex and *female uroventrite VIII*: Unknown.



FIGURES 156.1–156.11: *Magdelainella* series. Aedeagus in dorsal view of: (**1**) *Derveniella stevanovici,* (**2**) *Knirschiella ravasinii* (modified from G. Müller 1922), (**3**) *Magdelainella serbica*. Apex of the paramere of: (**4**) *D. stevanovici,* (**5**) *K. ravasinii* (redrawn from G. Müller 1922), (**6**) *M. serbica*. Spermatheca of: (**7**) *D. stevanovici,* (**8–9**) *M. serbica*. Female uroventrite VIII of: (**10**) *D. stevanovici,* (**11**) *M. serbica*. Figs **1**, **3**, **7–11** modified from Pavićević & Perreau (2008); Figs **4**, **6** redrawn from Pavićević & Perreau (2008).

Discussion. Jeannel (1924a) noted that *Magdelainella ravasinii* is characterised by the sculpture of the elytra, by the last antennomere longer than the sum of the lengths of the previous two, and by the separation of its range from the one of the other *Magdelainella* species. V.B. Guéorguiev (1976) taking into account the criteria of Jeannel (1924a) established the subgenus *Knirschiella*, followed by Pavićević & Perreau (2008). Although earlier, S. Ćurčić *et al*. (2004b) established a new genus status for *Knirschiella*, which they maintained in 2009, with the characteristic somewhat enlarged protarsi of females. No molecular studies have been conducted to establish the phylogenetic position of this genus. This is a very rare species for which no material is available to illustrate the habitus, and no publications have been found in which it is represented.

Distribution. Endogean monospecific genus. Specimens have been collected under stones in the Tomor Mountains, in the central area of Albania.

Species

Knirschiella ravasinii (G. Müller, 1922)
Bathysciola Ravasinii G. Müller, 1922a: 88.
Magdelainella Ravasinii Müller: Jeannel, 1924a: 76.
Magdelainella (*Knirschiella*) *ravasinii* Müller: V.B. Guéorguiev, 1976: 127.
Knirschiella ravasinii (Müller): S. Ćurčić, Brajković, B. Ćurčić, Schönmann, Makarov, Mitić & Tomić, 2004: 119.

Genus ***Magdelainella*** Jeannel, 1924
Magdelainella Jeannel, 1924a: 73.
Kosaniniella S. Ćurčić, Brajković & B. Ćurčić, 2004: 115 syn. nov. (Type species: *Kosaniniella javorensis* S. Ćurčić, Brajković, B. Ćurčić, Schönmann, Makarov, Mitić & Tomić, 2004b = *Magdelainella Hussoni* Jeannel, 1934).

Type species. *Bathyscia serbica* Müller, 1904 by original designation (for the habitus see that of the similar species *Magdelainella nonveilleri* in Fig. 155.2).

Diagnosis. Small size between 1.8–2.5 mm. Body short, between rounded and slightly elongated, regularly oval, very convex, not subsequently narrowed; bathyscioid facies (Fig. 155.2). Tegument bright brownish, shiny, uniformly pubescent, with short, more or less flat-lying yellowish hairs. Sculpture formed by fine stippling and microreticular meshes, regular on the elytra.

Head: Retractable. Sub-square, fairly robust, with occipital carina between well-marked and absent. Without eyes or with small macules in the ocular area.

Antennae: Short, reaching little or no farther than the base of pronotum. First antennomere shorter or as long as the second. Club differentiated, although antennomeres slightly flattened; antennomeres 3 to 6 of similar length and width; the 8th globose and transverse; the 9th and 10th transverse and as thick as the 11th, the 11th between slightly longer or slightly shorter than the 9th and 10th together.

Pronotum: Transverse, 1.8–2.0 times wider than long; maximum width at or near the base, which narrows slightly. Lateral margins more widely arched in basal third; posterior vertices acute or rounded, with acute basal angles more or less projecting backwards. Base as wide as the anterior area of the elytra and maximum width towards the basal quarter, as wide as or very slightly wider than the maximum base of the elytra (in females slightly narrower). Punctation very fine and very small, randomly distributed on an obviously microreticulate background.

Elytra: Short, oval and convex, 1.1–1.2 longer than wide, with maximum width towards the anterior third, not narrowed afterwards with rounded apices. Transverse striolation formed by numerous fine, closely spaced striae, plus 4–5 more or less pronounced longitudinal carinae sometimes absent, depending on the species. Punctation formed by small dots. Parasutural stria parallel to the suture, generally poorly defined, with about 5 to 8 dots present between the base and the median part of the elytra.

Legs: Short and stout; protibiae with external spurs but without a comb on the apical and external margins; with three external apical spines and one internal, apical one. Protarsi pentamerous in the male, more or less dilated depending on the species. Mesotibiae slender, usually with a slight sinuosity in the fifth of their length. Meso- and metatibiae without an apical basket of spines, but with long, and robust spines on the outer edges.

Mesoventral keel (Fig. 155.4): High, triangular, with anterior margin between straight and slightly convex, ventral margin narrow, usually a little sinuous and with setae. The long process does not extend beyond the entire metaventrite; this margin slightly sinuous, bearing setae. Apex more or less sharped depending on the species. Angle between straight and slightly obtuse.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Between short and mod-

erately long. In lateral view (Fig. 155.7), fairly long, slightly but evenly arched, with the median area globose as well as the dorsal and ventral margins, convex. Apical fourth part sinuous, narrow, with the apex very acute and curved towards the ventral side. In dorsal view (Fig. 156.3), sides only slightly arched and narrow regularly towards a more or less compressed apical area; apex more or less sharply pointed depending on the species. Basal blade well developed with a rounded apical margin, longer and as wide as the ventral blade of the tegmen.

Endophallus (Fig. 156.3): Median area with a pair of well-developed simple or bifid teeth. Under the teeth, there are two lateral laminar folds with lamellae, absent in *M. orientalis*. Basal area with a «U»-shaped sclerotized structure, or without a ribbed structure and a more or less developed flagellum-like structure (Jeannel 1924). In Pavićević & Perreau (2008) the structures of the basal region of the endophallus are not observed.

Parameres (Fig. 156.6): Thin or more or less stout, generally as long as the median lobe, shallowly arched or slightly sigmoid and dilated or not in the apical area; in dorsal and ventral view, with a rounded or straight apex and a small lateral protuberance in the shape of a pointed triangle, bearing three short, inwardly directed setae, the length, thickness and insertion of which dependon the species, but being normally two apical and one more remote, subapical. Ventral lamina of the tegmen as long and as wide as the basal lamina of the median lobe.

Spermathecal complex: Spermatheca (Figs 156.8, 156.9) small, short, usually arcuate and well sclerotized. Lobes well differentiated with the apical lobe spherical, generally more developed and differentiated than the basal lobe, the latter being of variable thickness. Short, non-hyaline, junction duct sclerotized like the lobes, generally poorly differentiated as it only forms the constriction between the two lobes. Undifferentiated spermathecal gland and spermiduct, at the base, normally with a sclerotized piece.

Female uroventrite VIII (Fig. 156.11): Generally narrow, the shape of the apical border and the spiculum variable, although is the latter normally long and narrow.

Discussion. A genus whose position is uncertain until a molecular examination of one of its species is carried out, making it possible to establish its phylogenetic position. Jeannel (1911a) was unable to assign a clear position to the species that would become part of this genus; this author in 1924 established the genus *Magdelainella* and placed it in the «Euryscapes», Division I, close to the *Spelaeochlamys* and *Speocharis* phyletic lineages, which is highly debatable. V.B. Guéorguiev (1976) included it in the subtribe Pholeuonina and Perreau (2000), following the two previous authors, placed them in the subtribe Pholeuina and the phyletic series *Quaestus*, particularly for the structures of the endophallus with a stylet or flagellum at the bottom of the sac. But the distribution range of *Magdelainella* and the species of the *Spelaeochlamys* series is considerably distant, and the distribution range of hundreds of species belonging to other series comes between them. Without molecular data, its position in the phylogenetic tree cannot be considered. S. Ćurčić *et al*. (2009) in the revision of the genus *Magdelainella*, discussed only the validity and taxonomic position of species already included in the genus *Magdelainella* or already in the genus *Kosaniniella* syn. nov. in addition to elevating *Derveniella* to the genus rank.

As shown in the figures provided by Pavićević & Perreau (2008) – S. Ćurčić *et al*. (2009) in their review of the genus included only illustrations of the species described in this article, not of all those they purport to review – the median lobe of aedeagus of *M. serbica*, *M. hussoni*, *M. nonveilleri* and *M. orientalis* are extremely similar in both their lateral and dorsal views, responding to the same model (Pavićević & Perreau 2008: (Figs. 6–9, 11–14); this is considerably peculiar among the Leptodirini and strongly suggests that this is a monophyletic clade. There are minor differences in the size or degree of curvature of the apical part, those by which entomologists differentiate the different morphospecies within the same general structural pattern.

Their endophallus also follows the same model, with two parentheses-shaped basal phaneres whose lower end diverges at the base of the median region, two teeth or pairs of teeth, of varying size and complexity at the upper end of the basal phaneres, and two bands of apical reinforcement in the upper region; the hyaline, inconspicuous structures of the basal region (Jeannel 1924a: Fig. 89) are not repeated in Pavićević & Perreau (2008). In *M. orientalis* there are no parenthetical basal phanera, but there are the teeth, which in this case are particularly developed: this could probably be a derived state with loss of structures or derived from basal cladogenesis. The distribution of these four species is contiguous (Pavićević & Perreau 2008: Fig. 42), with those of *M. orientalis* and *M. nonveilleri* on one side of the part, and those of *M. serbica* and *M. hussoni*, overlapping, on the other; the whole delimits

a specific part with no apparent disjunctions. For all this evidences, consequently, is established the synonymy *Magdelainella* Jeannel, 1924 = *Kosaniniella* S. Ćurčić, Brajković & B. Ćurčić, 2004 **syn. nov.** In contrast, *Derveniella* is well characterised by its endophallus, the basal area of which has a sparsely sclerotized structure, the median region three successive groups of spines of different thickness and the apical region two reinforcing bands densely covered with inverted spines and a triangular phanera in between in its basal region. It is distributed further south in a considerably separate area (Suva mountains, southeast Serbia) from *Magdelainella*. Its consideration as a genus or subgenus of *Magdelainella* is debatable, and without molecular data it is complex to make a decision. In this article, the arrangement of Pavićević & Perreau (2008) is adopted with the consideration of *Derveniella* as its own genus by S. Ćurčić *et al*. (2009).

In the illustrations by S. Ćurčić *et al*. (2009) of *Magdelainella studenicae* – the aedeagus in dorsal view (Fig. 3) and the apex of the parameres (Fig. 5) – , an extreme resemblance to *M. serbica* is observed: identical structure of the endophallus and general shape of the median lobe, and thickened , straight apex of the parameres. It is suspected that this is the same species. Perreau (2022, *pers. comm*.) agrees with this assessment. It has not been possible to study material of *M. studenicae* and therefore synonymy with *M. serbica* is not established.

Distribution. In this genus, most species are endogean, some found in caves and pits. Distributed in an area comprising part of the central and western Balkan peninsula corresponding to central, eastern, western and south-western Serbia, several isolated localities in central and south-eastern Bosnia-Herzegovina and north-eastern Montenegro.

Species

Magdelainella hussoni Jeannel, 1934
Magdelainella Hussoni Jeannel, 1934b: 97.
Magdelainella zivojindjordjevici S. Ćurčić, Brajković, B. Ćurčić & Schönmann, 2004a: 65.
Magdelainella nikolateslai S. Ćurčić, Brajković, B. Ćurčić & Schönmann, 2004a: 69.
Kosaniniella javorensis S. Ćurčić, Brajković & B. Ćurčić *in* S. Ćurčić, Brajković, B. Ćurčić, Schönmann, Makarov, Mitić & Tomić, 2004b: 117.
Kosaniniella hussoni (Jeannel, 1934): S. Ćurčić, Makarov & B. Ćurčić, 2009: 763.

Magdelainella nonveilleri Pavićević & Perreau, 2008
Magdelainella (*Magdelainella*) *nonveilleri* Pavićević & Perreau, 2008: 192.
Kosaniniella nonveilleri (Pavićević & Perreau, 2008): S. Ćurčić, Makarov & B. Ćurčić, 2009: 764.

Magdelainella orientalis Pavićević & Perreau, 2008
Magdelainella (*Magdelainella*) *orientalis*: Pavićević & Perreau, 2008: 192.
Kosaniniella orientalis (Pavićević & Perreau, 2008): S. Ćurčić, Makarov & B. Ćurčić, 2009: 764.

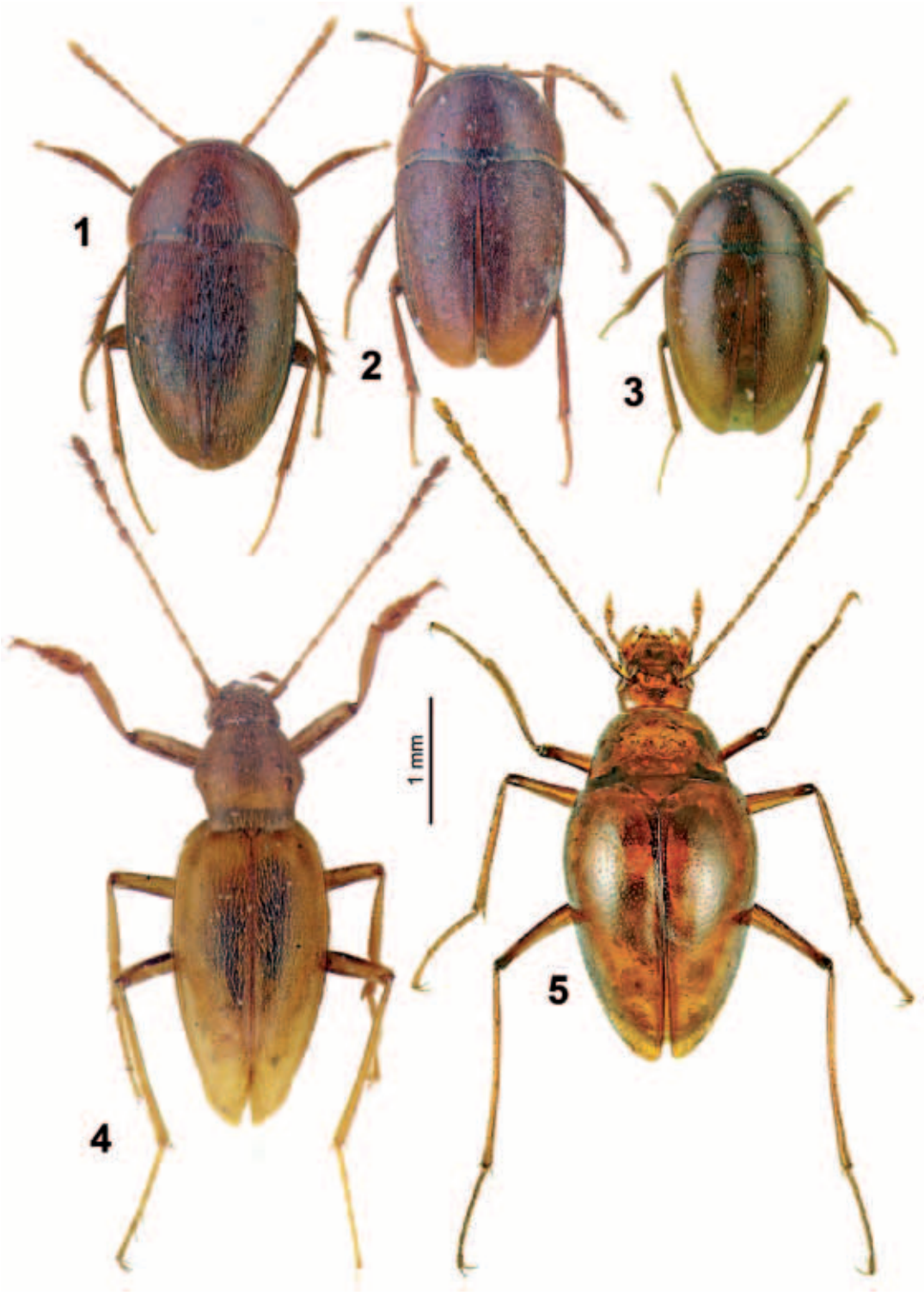
Magdelainella serbica (G. Müller, 1904)
Bathyscia serbica G. Müller, 1904b: 41.
Magdelainella serbica J. Müller, 1904: Jeannel, 1924a: 75.
Magdelainella (*Magdelainella*) *serbica* (Müller): Perreau, 2000: 284.
Bathyscia (*Bathysciola*) *Noesskei* Apfelbeck, 1919: 271.
Magdelainella Winkleri Jeannel, 1934b: 97.
Magdelainella bozidarcurcici S. Ćurčić & Brajković, 2003: 97.
Magdelainella mucanjensis S. Ćurčić, Brajković, B. Ćurčić & Schönmann, 2004a: 67.
Magdelainella milojebrajkovici S. Ćurčić & B. Ćurčić, 2005, in S. Ćurčić, B. Ćurčić, Makarov, Mitić & Mihajlova, 2005: 314.

Magdelainella studenicae S. Ćurčić, Makarov & B. Ćurčić, 2009
Magdelainella studenicae S. Ćurčić, Makarov & B. Ćurčić, 2009: 758.

Incertae sedis

Magdelainella kauti (Apfelbeck, 1907)
Bathyscia (*Bathyscia*) *Kauti* Apfelbeck, 1907a: 305.
Magdelainella Kauti Apfelbeck, 1907: Jeannel, 1924a: 76.
Magdelainella (*Magdelainella*) *kauti* (Apfelbeck): Perreau, 2000: 284.

Note. Jeannel (1924a) in his «Monographie des Bathysciinae» and Perreau (2000) in his Catalogue include the species *kauti* in the genus *Magdelainella* on the basis of certain morphological structures, but its position is uncertain until the characteristics of the male genitalia are known.



FIGURES 157.1–157.5: *Cytodromus* series, *Ovobathysciola* group. Habitus of: (**1**) *Batinoscelis lostiae* **comb. nov.**, (**2**) *Latellana fortesculpta* **comb. nov.**, (**3**) *Ovobathysciola majori,* (**4**) *O. sardoa* **comb. nov.**, (**5**) *O. cogonii* **comb. nov.**

3.3 Clade ***Cytodromus-Quaestus***

3.3.1 Series ***Cytodromus***

Diagnosis. Habitus variable, from bathyscioid to pholeuonoid and very different sizes, ranging from 1.2 mm in some species of *Salfia* stat. nov. or *Bathysciola* to 5.0 mm in some species of *Cytodromus*. Depigmented.

Head: Last article of the maxillary palps short and conical. Anophthalmous.

Antennae: With 11 articles inserted on the middle third of the head, with the first antennomere as long as the second and thicker.

Legs: Protarsi pentamerous in males, tetramerous in females, with the exception of the males of the genus *Speophyes* of the *Diaprysius* group, which are tetramerous. Protibiae without a comb, but with two or three well-developed external spurs. Meso- and metatibiae without apical baskets. Claws fine, thin and narrow.

Mesoventral keel: May be fused to the metaventrite (*Ovobathysciola majori*), high and well developed (*Speophyes lucidulus*) or absent, in which case the mesocoxal cavities are confluent (*Isereus*). No posterior extension on the metaventrite.

Metatergal apparatus: May have very long (*Ovobathysciola cogoni* comb. nov.) or very short (*Galliana* gen. nov.) alacristae, with all lengths in between; there may be sexual dimorphism in the shape of the apophyses (*Salfia* stat. nov.).

Endophallus: Armed with bands or articulated parts and a well-defined phanera at the bottom of the sac, generally in the shape of a «Y», more rarely in the shape of an inverted «T» (*Ovobathysciola*); this phanera lacking in *Speophyes*.

Parameres: Armed with three (*Speophyes* or *Ochsiella* stat. nov.) or up to a dozen setae of very different lengths (*Diaprysius* group), or even with some modified ones (*Parabathyscia*). No penicillum, with the exception of a few species of *Batinoscelis*.

It should be noted that the diversity is such that it does not allow a precise characterisation of the series.

Discussion. The *Cytodromus* series is sister of the clade made up of the *Nanobathysciola*, *Quaestus* and *Spelaeochlamys* series, with 79.7/90 support. Molecular studies have established that the *Cytodromus* series is made up of five groups: *Cytodromus*, *Isereus*, *Parabathyscia*, *Ovobathysciola* and *Diaprysius* in total with very high joint support (99.9/100) (Fig. 1G).

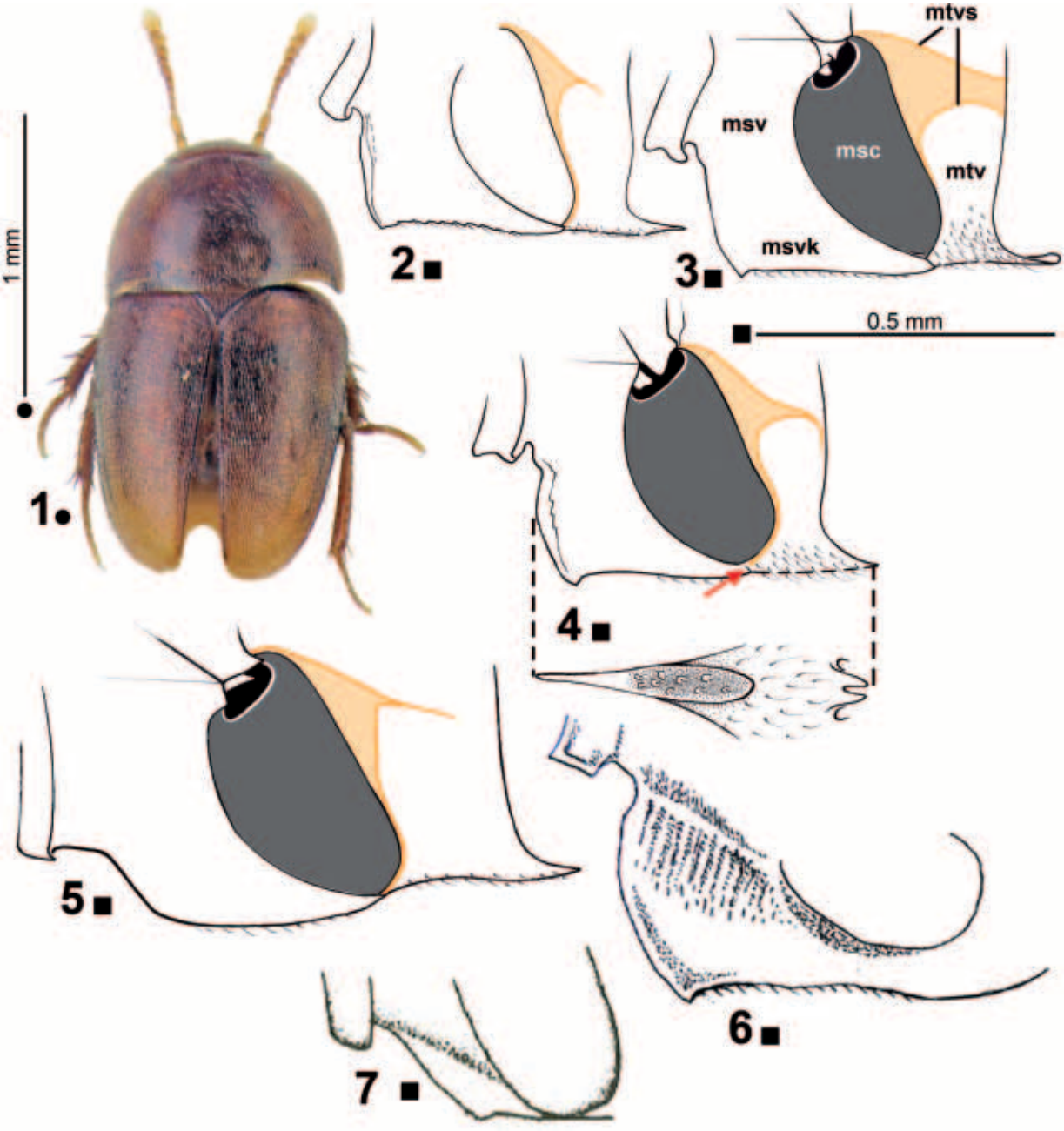
Key to groups

1. Apical area of parameres (Fig. 179.4) with a membranous lobe and three unequal setae, two of which modified, very thick, lanceolate or falciform. Endophallus (Fig. 178.2) with very short apical reinforcing bands; between them, two very sclerotized phanera in the shape of an inverted «V».....*Parabathyscia* group
- Apical area of parameres without membranous lobe and with three (Figs 163.5, 179.6, 186.8) or more (Fig. 170.4) non-falciform setae. Endophallus with short or long reinforcing bands (Figs 162.10, 169.6, 178.3, 186.4); among these, no sclerotized phanera in the shape of an inverted «V» 2

2. Median lobe of aedeagus, in lateral view (Figs 177.3, 185.2), with a depression towards the apical third of the dorsal surface and then, in general, sinuous to the apex. Apical area of parameres (Figs 179.5, 186.8) with three regular setae, sometimes the stoutest at apex (Fig. 179.8) 3
- Median lobe of aedeagus, in lateral view (Figs 162.3, 169.1–169.4), without depression towards the apical third of dorsal surface and apical area not sinuous; if depression present (Figs 162.1, 162.7), apex of parameres with more than three setae. Apical area of parameres with three (Figs 163.4–163.6, 163.9, 170.5, 170.6) or more than three setae (Figs 163.3, 163.8, 170.1–170.4) 4

3. Mesoventral keel low, with broadly rounded margin (Fig. 182.4), angular or reduced to a short pointed arista (Figs 182.5, 182.6). Endophallus (Figs 186.1–186.5) with long, more or less thick, well-sclerotized phanera extending from the middle to the basal region; the rather long reinforcing bands rest on ligules whose inner part is sclerotized .....*Cytodromus* group
- High mesoventral keel with rounded apex (Figs 173.1, 173.2, 173.4), or very low, arched terminal part (Figs 173.3, 173.6). Endophallus (Figs 178.3, 178.4, 179.1, 179.2) with long, thin, hyaline phanera extending from the middle to the apical region; very short reinforcing bands resting on membranous ligules *Isereus* group

4. Elytra without transverse striolae. Endophallus (Figs 169.5–169.9) with a «Y»-shaped piece in the basal region. Apical area of parameres (Figs 170.1–170.4) with more than three setae; if three setae are present (Fig. 170.5), they are always inserted in series with large insertion pores, but if the pores are small (Fig. 170.6), in this case the male protarsi are tetramerous.....*Diaprysius* group



FIGURES 158.1–158.7: *Cytodromus* series, *Ovobathysciola* group. Habitus of: (**1**) *Salfia ruffoi* **comb. nov.** Pterothorax in lateral view of: (**2**) *Batinoscelis lostiae* **comb. nov.**, (**3**) *Latellana fortesculpta* **comb. nov.**, (**4**) *Ovobathysciola majori* (and ventral view), (**5**) *O. sardoa* **comb. nov.**, (**6**) *O. cogonii* **comb. nov.** (modified from Casale 2019), (**7**) *S. damryi* **comb. nov.** (modified from Giachino, 1990). Red arrow pointing to the suture between meso- and metaventrite. Abbreviations: **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture.

- Elytra with or without transverse striolae. Endophallus with (Fig. 162.8) or without (Figs 162.10, 163.1, 163.2) a «Y»-shaped piece in the basal region. If there is no striolation and the endophallus presents «Y»-shaped piece in the basal region, then the apex of the parameres (Figs 163.4–163.7, 163.9) has three setae, and if there are four (Fig. 163.3), the insertion pores are small and usually accompanied by a penicillum .. ..*Ovobathysciola* group

3.3.1.1 ***Ovobathysciola*** group

Diagnosis. Small to medium-sized species; habitus variable, from bathyscioid (with inclined head) to pholeuonoid (with non-inclined head); antennae short to elongated; integument pubescent or glabrous; legs slightly and more or less elongated; protarsi of the male pentamerous not or variously, dilated; polydentate tibial spurs; meso- and metatibiae with incomplete apical basket.

Mesoventral keel (Figs 158.2–158.7): Slightly to very high, toothed or not at apex of anterior margin, not extending onto metaventrite. Not thickened, or thickened and dilated posteriorly; ventral side sometimes flattened with bordered margins.

Suture of the metaventrite (Figs 158.2–158.5): Two sutures that join before the posterior suture of the metaventrite and delimit a triangular area with a narrow, acute apex or the two sutures remain independent until the posterior suture of the metaventrite.

Metatergal apparatus (Figs 159.1–159.3, 160.1–160.4): With the apophysis of the alacrista from shorter to longer than half the elytra. In the Sardinian species of *Salfia* stat. nov. there is marked sexual dimorphism with the posterior apophysis visibly dilated distally in males (Figs 160.3, 160.4).

Metendosternite (Figs 161.1–160.5): Not «V»-shaped, furcal arms triangular, broad at base.

Median lobe of aedeagus: Elongate, with subparallel lateral margins, slightly arched in lateral view (Figs 162.1–162.7), to tip which is straight or decidedly curved (sometimes «S»-shaped) in ventral part. Apex, in dorsal view (Figs 162.8–162.11, 163.1, 163.2), regularly rounded, lanceolate or subtriangular and pointed.

Endophallus (Figs 162.8–162.11, 163.1, 163.2): Structure variable. Sometimes with an internal armature formed of three sclerotized pieces, making it possible to differentiate three regions (basal, medial and apical). With or without a «Y»-shaped basal piece, sometimes, with a characteristic «T»-shaped or inverted «anchor»-shaped phanera in the median region. Sometimes completely devoid of armature.

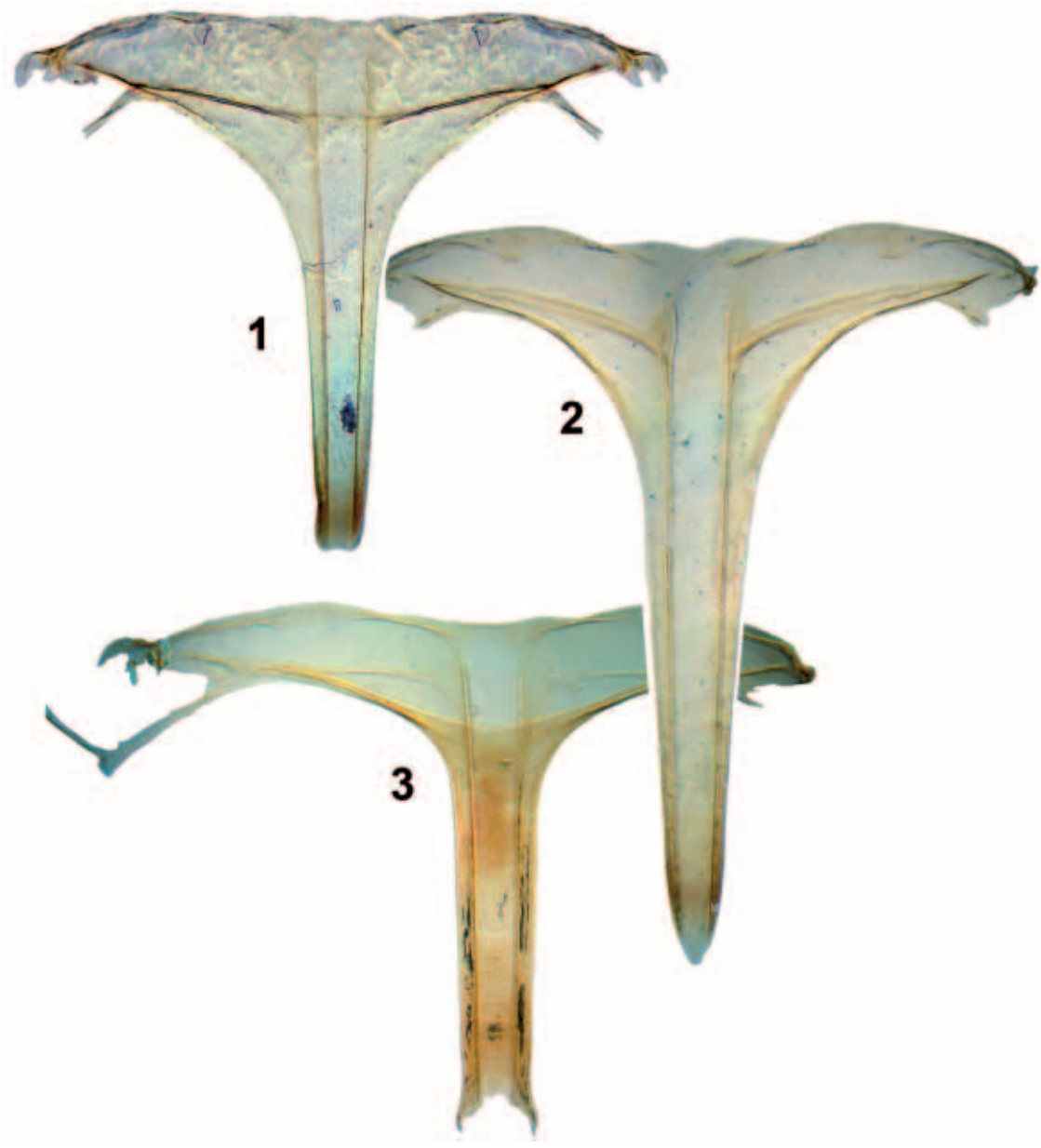
Parameres (Figs 163.3–163.9): About as long as the median lobe. Not enlarged, slightly or clearly enlarged at apex. Three long or short setae at apex of parameres, all at distal end, or two at distal end, one lower. Sometimes four long setae and a subapical penicillum of fine setae are present.

Spermathecal complex (Figs 164.1–164.7): Spermatheca elongate, sometimes «C»-shaped, sclerotized at base and apex, with distal part sub-spherical, hyaline in median part. Basal and apical lobes of the same size or larger for the basal lobe. Expanded part of the spermatic duct present (stretched or rounded) or absent.

Female uroventrite VIII (Figs 165.1–165.6): Distally rounded, with strongly curved proximal margin. Spiculum short, slightly enlarged and blunt or bifid at the apex.

Discussion. A group of genera (*Ovobathysciola* sensu novo, *Batinoscelis* stat. nov., *Salfia* stat. nov. and *Latellana* gen. nov.) well supported molecularly, 100/100 in Tree-1 (Fig. 1G) and, 99.9/100 in Tree-2 (Fig. 2); this group constitutes the basal clade of the *Cytodromus* series, and joins the other groups in the series with very high support, 99.5/100. Furthermore, the relationship between the genera in this group is strongly supported, 100/100. The analysis of the part of the tree relating to the *Ovobathysciola* group, in addition to highlighting the systematic choice that we will have to make on the clade of *Batinoscelis* stat. nov.-*Salfia* stat. nov.- *Latellana* gen. nov. with high support 99.6/100 (a choice to which we will return when we deal with these three genera), led to a reflect in depth on the systematic extension of the genus *Ovobathysciola* sensu novo itself. As shown in the phylogram in figure 1G, created on a molecular basis, this clade also includes taxa that have hitherto been included in other genera such as *Patriziella* and *Sardostygia*.

With regard to the genus *Patriziella,* Sbordoni *et al*. (1982), Rampini & Zoia (1990) and Casale (2004) have already highlighted the difficulties in finding characters that would separate *Patriziella* from *Ovobathysciola*. Apart from the general shape of the body, attributable to greater or lesser specialisation in the subterranean environment, it was above all the homogeneity of the morphology of the aedeagus that raised doubts about the actual validity of these two genera. Their conservation was proposed by Rampini & Zoia (1990) as a «convenience genera». Subsequently, Casale (2014), in the course of a careful revision of the



FIGURES 159.1–159.3: *Cytodromus* series, *Ovobathysciola* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Batinoscelis onnisi* **sp. nov**., (**2**) *Latellana fortesculpta* **comb. nov.**, (**3**) *Ovobathysciola majori*.

genus *Ovobathysciola*, thoroughly rediscussed this problem on the basis of the available data, both molecular (Caccone & Sbordoni 2001) and morphological, chorological, biogeographical and ecological, supporting the value of maintaining the separation between these two genera. In the same contribution, Casale (2014) described five new species of *Ovobathysciola*.

It is precisely the molecular data now available from these five additional species of *Ovobathysciola*, compared to the original three, that now compel us to reconsider the problem of the validity of these two genera.

This problem has now been compounded by the issue of the taxon *Sardostygia cogonii* recently de-

scribed as belonging to a different genus. The author (Casale 2019) highlights the peculiarity of certain characters displayed by *Sardostygia* that seem to differentiate it from both *Ovobathysciola* and *Patriziella*: glabrous dorsal integuments, head without occipital carina (even the occipital carina is almost completely obsolete also in *Patriziella muceddai*) and endophallus devoid of any sclerotized structure. In the same discussion, Casale (2019) cites preliminary molecular data, the same now used for the construction of the phylogenetic tree presented here (Fig. 1G), which would give the new taxon a «highly derived position within the *Ovobathysciola-Patriziella* complex». Again citing I. Ribera (2019 *in litt*.), Casale (2019) stresses the persistence of uncertainties regarding the relationships between the various species in the group.

Analysis of the part of the tree relating to *Ovobathysciola* (Fig. 1G) forces us to choose between two possible systematic approaches:

1. Consider a single genus, *Ovobathysciola*, which also includes the species of *Patriziella* and *Sardostygia*.

2. Subdivide the clade into four distinct genera: *Patriziella* with the species *P. sardoa*, *P. grafittii* and *P. supramontana* (not well supported in some parts); *Ovobathysciola* with the species *O. majori* and a new undescribed species; *Sardostygia* with the species *S. cogonii* and *S. deleddae*; a new genus for the species *O. gestroi* and *O. castrimedusae*.

Between the two options, the most practicable and common-sense one seems to us to be the first which, apart from avoiding excessive fragmentation of the clade, makes it possible to operate on a single genus, well defined in its synapomorphic characters, rather than on a plethora of genera based almost exclusively on a stock of characters adaptive to subterranean life.

There are parallel cases among the Leptodirini of other origins:

– The genus *Troglocharinus*, from the Catalan reliefs, includes species of diverse morphology, formerly belonging to other genera: *Antrocharidius*, *Speophilus* and *Speonomus*. They share the same aedeagus model, particularly the endophallus, but the external morphology varies from those with a pholeuonoid facies (certain *Troglocharinus* and *Antrocharidius* from the Serralades Litorals Catalanes), to those with an elongated bathyscioid shape (ex *Speophilus* from Serralades Prelitorals Catalanes) or clearly bathyscioid (certain ex *Speonomus* from the pre-Pyrenean Catalan reliefs) (Fresneda *et al*. 2021).

KEY TO GENERA

1. Elytra without transverse striolae.....2
- Elytra with transverse striolae 3

2. Parameres with penicillium (Fig. 163.3). Endophallus with a basal «Y»-shaped piece (Fig. 162.8) ....*Batinoscelis* stat. nov.
- Parameres without penicillium (Figs 163.5-163.7). Endophallus without basal «Y»-shaped piece (Fig. 162.10, 163.1, 163.2) .....*Ovobathysciola* sensu novo

3. Metatergal apparatus with the apophysis of the alacrista longer than half of the elytra (Figs 160.3, 160.4). Endophallus with short apical reinforcement bands (Fig. 162.11). Parameres little or not enlarged at apical area, with three or four setae, when there are three, all at apex (Figs 163.8, 163.9)..... .....*Salfia* stat. nov.
- Metatergal apparatus with the apophysis of the alacrista shorter than half the elytra or just reaching it (Fig. 159.2). Endophallus with long apical reinforcement bands (Fig. 162.9). Parameres with widened apical part, generally spoon-shaped, with three setae at apex, two at distal end, one inferior (Fig. 163.4) ....*Latellana* gen. nov.

Genus ***Batinoscelis*** Jeannel, 1924 stat. nov.
Speonomus (*Batinoscelis*) Jeannel, 1924a: 131.

TYPE SPECIES. *Bathyscia lostiae* Dodero, 1904 by original designation (habitus in Fig. 157.1).

DIAGNOSIS. Medium size, 2.2–3.0 mm, bathyscioid shape (Fig. 157.1); body oval and slightly convex. Pubescence golden, short and recumbent.

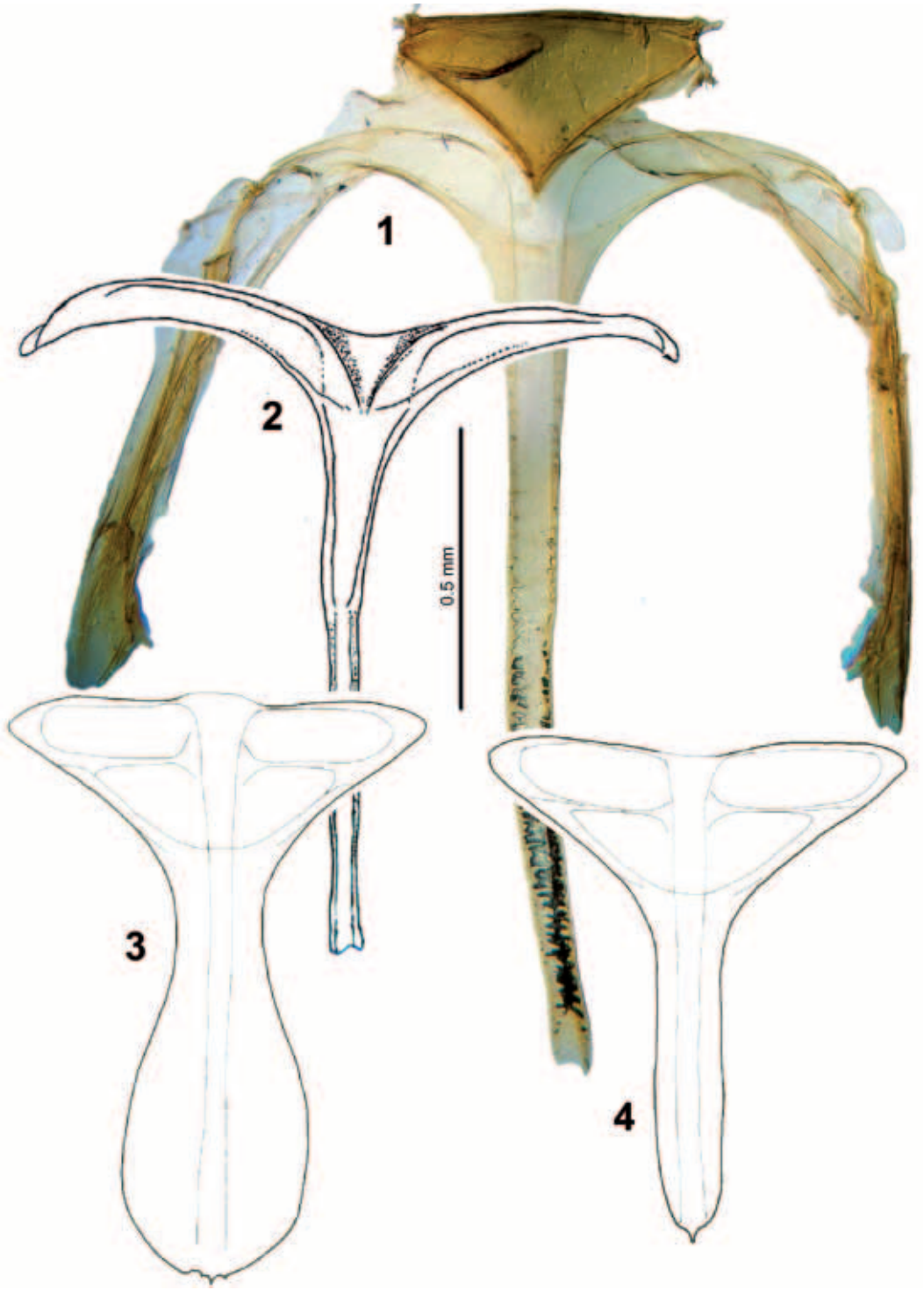
Head: Retractile, with a complete occipital carina; eyes absent.

Antennae: Short to relatively long (just above the base of the pronotum or reaching the middle of the elytra); relative length of antennomeres variable, with the 8th ovoid, as long as wide, and the 9th and 10th as long as wide or slightly longer than wide.

Pronotum: Very transverse, with evenly arched sides and acute angles.

Elytra: Slightly convex and slightly elongated, with a rounded apex; without transverse striolae, the rough, fine dots being arranged in irregular, closely spaced rows; parasutural stria present, between blurred and well marked.

Legs: Short and not very thick; apex of protibiae on inner side with polydentate spurs. Apical baskets of



FIGURES 160.1–160.4: *Cytodromus* series, *Ovobathysciola* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Ovobathysciola sardoa* **comb. nov.**, (**2**) *O. cogonii* **comb. nov.** (modified from Casale 2019), (**3**) *Salfia damryi* **comb. nov.** male, (**4**) idem, female. Figs **3**, **4** modified from Giachino (1990).

meso- and metatibiae incomplete. Meso- and metatibiae cylindrical, armed with robust, bristly spines and robust spurs; male protarsomeres pentamerous and narrower than protibia.

Mesoventral keel (Fig. 158.2): Hight and short, with the vertex more or less dentate. Posterior process not reaching or slightly exceeding the metaventrite; ventral margin smooth or serrated.

Suture of the metaventrite (Fig. 158.2): Upper half of the two sutures in triangular area with a bent junction vertex; basal half of the lower suture bordering the coxal cavity.

Metatergal apparatus (Fig. 159.1): Wings of metascutum short and rather enlarged ; apophysis of the alacrista long and blunt.

Metendosternite (Fig. 161.1): «Y»-shaped. Furcal arms narrow, shorter than furcal trunk, without terminal apophysis; furcal trunk long, twice as long as the widest area, median furcal keel with convergent posterior apices and rounded tips.

Median lobe of aedeagus: Elongate, with subparallel lateral margins, slightly arched in lateral view (Fig. 162.1), up to the tip which is straight or decidedly curved (sometimes «S»-shaped) in the ventral part. In dorsal view (Fig. 162.8), subrectilinear sides up to two-thirds, narrowing regularly in the apical third and ending in a rounded or slightly tapered point; in some species, apical third subtriangular in shape.

Endophallus (Fig. 162.8): With an internal armature formed by three sclerotized pieces, allowing the differentiation of three regions (basal, medial and apical). Presence of a «Y»-shaped piece and a flagellum in the basal area. Short apical reinforcement bands. Apex widened or not.

Parameres (Fig. 163.3): Approximately as long as median lobe. Apex enlarged or not. Apex with three or four long setae and subapical penicillum well developed with fine setae.

Spermathecal complex (Fig. 164.1): Basal and apical lobes of equal size and hyaline union duct, long and narrower than the lobes. Expanded area of the spermatic duct absent.

Female uroventrite VIII (Fig. 165.1): Distal area in regular arc; spiculum short with rounded apex.

Discussion. As indicated in the «Discussion» of the genera *Salfia* stat. nov. and *Latellana* gen. nov. the analysis of the tree in figure 1G, built on molecular data (even if a certain number of species of *Batinoscelis* stat. nov., *Salfia* stat. nov. and *Latellana* gen. nov. are missing, because no fresh material was available to carry out this analysis), leads us to some reflections on the systematic choices made. The first choice could be to consider the entire clade as a single genus; in this case *Batinoscelis* stat. nov.. The second choice could be to consider *Salfia* stat. nov. as synonymous with *Batinoscelis* stat. nov. and to proceed with the description of a second genus (*Latellana* gen. nov.). We have instead opted for a third option, that of considering three distinct genera (*Batinoscelis* stat. nov., *Salfia* stat. nov. and *Latellana* gen. nov.), which seems to us to be more informative from both taxonomic and systematic point of view. The choice of considering three distinct genera, as already discussed in relation to *Salfia* stat. nov. and *Latellana* gen. nov., is also more appropriate from a zoogeographical point of view, as these three genera are probably distributed over the fragmented remains of the ancestral Apennine chain, the fragmentation of which dates back to around the middle Miocene (17 My) (Álvarez 1972; Álvarez *et al*. 1974; Bosellini 2005; Giachino *et al*. 2011).

At present, five species belong to the genus *Batinoscelis* stat. nov., two of which are described here as *B. onnisi* sp. nov. (from the sa Rutta'e Scusi cave (Sardinia, Villasalto, province of South Sardinia) and *B. degiovannii* sp. nov. (from Sardinia, Monte Tonneri, Ogliastra, central-eastern province). Of the five species discussed here, molecular data are available for two, while those for *B. aritzensis* comb. nov., *B. diabolicus* comb. nov. and *B. degiovannii* sp. nov. are lacking.

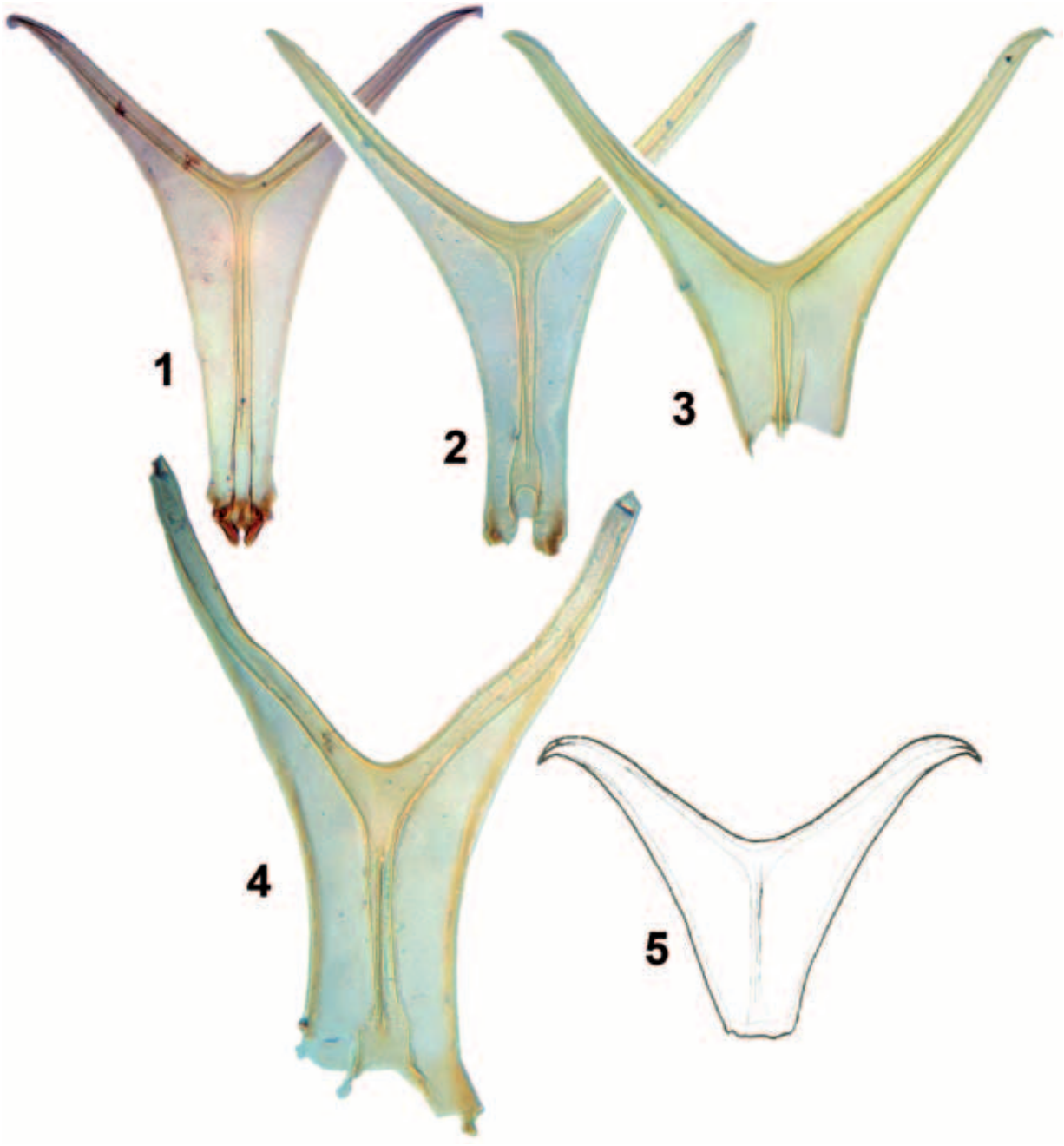
The results of the phylogenetic analysis (Fig. 1G) show that the genus *Batinoscelis* stat. nov. is monophyletic with high support, 100/100, and sister to the genus *Salfia* stat. nov. with low support, 17.5/75, no doubt more molecular data from the species of these two genera will provide us more information.

Distribution. Italy. Sardinia and Tuscany.

Species

Batinoscelis aritzensis (Jeannel, 1911) comb. nov.
Bathysciola Lostiai aritzensis Jeannel, 1911a: 239.
Bathysciola (s. str.) *Lostiai* subsp. *aritzensis* Jeannel: Jeannel, 1914b: 9.
Speonomus (*Batinoscelis*) *aritzensis* Jeannel, 1911a: Jeannel, 1924a: 148.

Batinoscelis degiovannii sp. nov. (See Appendix New Species)



FIGURES 161.1–161.5: *Cytodromus* series, *Ovobathysciola* group. Metendosternite of: (**1**) *Batinoscelis onnisi* **sp. nov**., (**2**) *Latellana fortesculpta* **comb. nov.**, (**3**) *Ovobathysciola majori*, (**4**) *O. sardoa* **comb. nov.**, (**5**) *Salfia doderoi* **comb. nov.** (modified from Giachino 1990).

Batinoscelis diabolicus (Jeannel, 1911) comb. nov.
Bathysciola Lostiai diabolica Jeannel, 1911a: 240.
Bathysciola (s. str.) *Lostiai* subsp. *diabolica* Jeannel: Jeannel, 1914b: 9.
Speonomus (*Batinoscelis*) *diabolicus* Jeannel, 1911: Jeannel, 1924a: 148.

Batinoscelis lostiae (Dodero, 1904) comb. nov.
Bathyscia Lostiae Dodero, 1904a: 58.
Bathysciola Lostiai Dodero: Jeannel, 1910a: 28.
Bathysciola (s. str.) *Lostiai* Dodero: Jeannel, 1914b: 9.
Speonomus (*Batinoscelis*) *Lostiai* Dodero, 1904: Jeannel, 1924a: 147.

Batinoscelis onnisi sp. nov. (See Appendix New Species)

Genus ***Latellana*** nov.
https://zoobank.org/NomenclaturalActs/87DD1638-4640-44B6-8A1A-AF6533D19C0F

Type species. *Bathysciola fortesculpta* Jeannel, 1914 by present designation (habitus in Fig. 157.2).

Description. Medium size, 1.5–2.7 mm, bathyscioid body (Fig. 157.2).

Head: Retractile, with complete occipital carina; eyes absent.

Antennae: Medium length; length of antennomeres variable, although the first is shorter and more robust than the second, 8th to 10th transverse.

Pronotum: Transverse, broadest at base, regularly curved towards anterior angles and less curved towards posterior angle, posterior margin weakly bisinuate. Posterior angles acute.

Elytra: Surface with transverse strioles, sometimes disappearing towards the apex; with or without parasutural stria.

Legs: Apex of tibiae on the inner side with polydentate spurs. Apical baskets of meso- and metatibiae incomplete. Male protarsomeres pentamerous and, depending on the species, narrower to wider than the anterior area of the protibia.

Mesoventral keel (Fig. 158.3): High, with a slightly convex anterior margin and a straight or curved lower margin; the outermost process not extended over the metaventrite; apex at the junction of both margins toothed.

Suture of the metaventrite (Fig. 158.3): This is unique in Leptodirini in that the two sutures remain separate and reach the posterior suture of the metaventrite. The lower suture is arc-shaped and passes very close to the coxal cavity in its lower half.

Metatergal apparatus (Fig. 159.2): Wings of metascutum short and broad, their length slightly shorter than the alacrista; alacrista long, but shorter than, or barely reaching half of elytra; tips acute.

Metendosternite (Fig. 161.2): «Y»-shaped, furcal arms triangular, broad at base and a little shorter or as long as trunk, apical part tapering and without apophysis. Trunk slightly or clearly longer than the widest part.

Median lobe of aedeagus: In lateral view, thin, with subparallel, slightly arched lateral margins, (Figs 162.2, 162.3), up to the tip, which is curved in the ventral part. In dorsal view (Fig. 162.9), apex regularly rounded, slightly truncated or a little pointed.

Endophallus (Fig. 162.9): Endophallus with an internal armature formed of three sclerotized pieces, making it possible to differentiate three regions (basal, medial and apical). «Y»-shaped piece and a flagellum in the basal area. Long apical reinforcement bands.

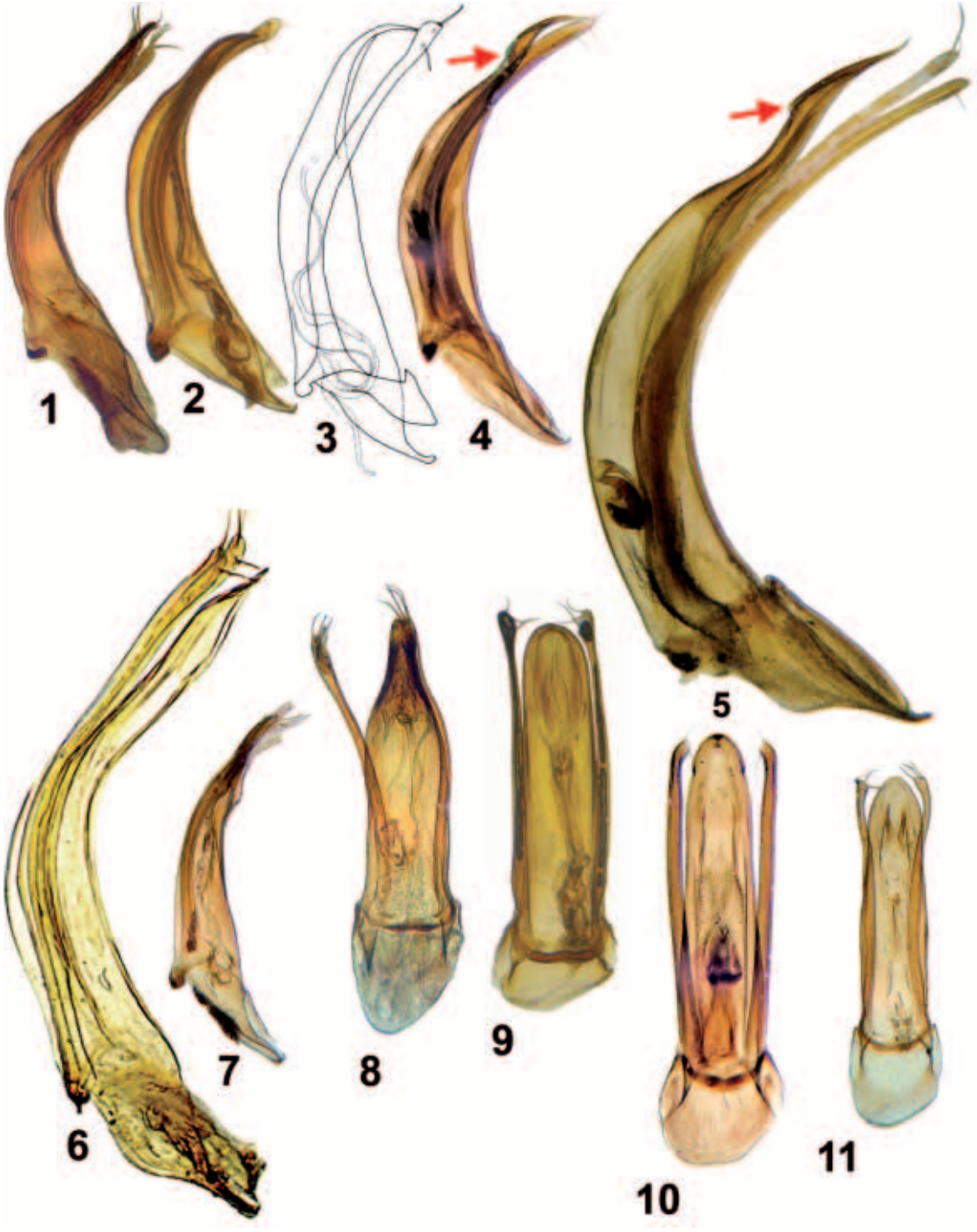
Parameres (Fig. 163.4): As long as or slightly longer than median lobe. Apical area enlarged, usually spoon-shaped. Three setae at the apex of the parameres, the form of insertion depending on the species.

Spermathecal complex (Fig. 164.2): Basal and apical lobes of same size or larger for basal . Lobes well sclerotized and median part long and hyaline or very slightly sclerotized. Presence of an enlarged area of the spermatic duct (stretched or rounded) close to the spermatheca but independent of it. Spermathecal gland present.

Female uroventrite VIII (Fig. 165.2): Distally rounded, with slightly concave proximal margins. Spiculum depending on species short, triangular, enlarged at base and apical area pointed, rounded or truncated.

Etymology. The new genus is dedicated to our colleague Leonardo Latella (Verona, Italy), renowned specialist in Leiodidae Cholevinae. The name is feminine.

Discussion. The phylogenetic tree in figure 1G, based on molecular data, shows that *Latellana* gen. nov. is sister to *Salfia* stat. nov. and *Batinoscelis* stat. nov. with a very high support, 99.6/100; it is important to point out that some species of *Salfia* stat. nov. and *Latellana* gen. nov. are missing, as fresh material was not available, which leads us to some reflections on the systematic choices made.



FIGURES 162.1–162.11: *Cytodromus* series, *Ovobathysciola* group. Aedeagus in lateral view of: (**1**) *Batinoscelis lostiae* **comb. nov.**, (**2**) *Latellana valeriae* **comb. nov.**, (**3**) *L. delayi* **comb. nov.** (modified from Latella & Rampini 1994), (**4**) *Ovobathysciola majori*, (**5**) *O. sardoa* **comb. nov.**, (**6**) *O. cogonii* **comb. nov.** (modified from Casale 2019), (**7**) *Salfia ruffoi* **comb. nov.** Aedeagus in dorsal view of: (**8**) *B. lostiae* **comb. nov.**, (**9**) *L. valeriae* **comb. nov.**, (**10**) *O. majori*, (**11**) *S. ruffoi* **comb. nov.** Figs **2**, **9** modified from Latella *et al.* (2017).

Already Latella *et al*. (2017), while not making formal systematic decisions, pointed out how the «*Bathysciola*» group to which we now assign the name *Latellana* gen. nov. seems taxonomically well characterised by a series of synapomorphic characters compared to *Salfia* stat. nov. and *Batinoscelis* stat. nov. Characters reported in the table (Latella *et al*. 2017: table 2). These characters are reported by us in the diagnosis of this new genus.

There is some variability in size and structures:

– Size small about 1.5 for *Latellana gardinii* comb. nov., to medium size, 2.7 mm for *Latellana sbordonii* comb. nov.

– Antennae: Short, barely extending beyond the base of the pronotum in all species; relative length of antennomeres variable from species to species.

– The median lobe of aedeagus may have the apex, in dorsal view, regularly rounded (*Latellana vignai* comb. nov.) or pointed (*Latellana raveli* comb. nov., *Latellana sbordonii* comb. nov.).

– The apex of the parameres can be small (*Latellana fortesculpta* comb. nov.) or larger, spoon-shaped and dilated (*Latellana raveli* comb. nov.)

– The setae at the apex of the parameres can be long (*Latellana fortesculpta* comb. nov.) or short (*Latellana sbordonii* comb. nov.).

– The basal and apical lobes of the spermatheca may be of the same size (*Latellana magrinii* sp. nov.) or with the basal lobe larger (*Latellana valeriae*).

At present, 16 species belong to the genus *Latellana* gen. nov. Five unpublished species are described here as *Latellana petruzzielloi* sp. nov. – from the Picentini Mounts (Campania, province of Avellino) –, *Latellana petruzziellana* sp. nov. – from the Grotta dei Briganti (Cusano Mutri, Campania) –, *Latellana magrinii* sp. nov. – from the Matese plateau (Campania, Province of Caserta) –, *Latellana benellii* sp. nov. and *Latellana degiovannii* sp. nov. (from Monte Sant'Angelo (near Maranola, Lazio, province of Latina). Of the 16 species covered here, molecular data are available for 10 of them, while those for *Latellana raveli* comb. nov., *Latellana gardinii* comb. nov., *Latellana octaviani* comb. nov., *Latellana magrinii* sp. nov., *Latellana petruzziellana* sp. nov. and *Latellana petruzzielloi* sp. nov. are missing.

Distribution. Italy: Sardinia (Albo Mount), Lazio and Campania (including Capri island).

Species

Latellana benellii sp. nov. (See Appendix New Species)

Latellana degiovannii sp. nov. (See Appendix New Species)

Latellana delayi (Latella & Rampini, 1994) comb. nov.
Bathysciola (*Bathysciola*) *delayi* Latella & Rampini, 1994: 141.
Bathysciola delayi: Moldovan & Juberthie, 1998: 108.

Latellana fabiolae (Latella, Sbordoni & Allegrucci, 2017) comb. nov.
Bathysciola fabiolae Latella, Sbordoni & Allegrucci, 2017: 18.

Latellana fortesculpta (Jeannel, 1914) comb. nov.
Bathysciola (s. str.) *fortesculpta* Jeannel, 1914c: 201.

Latellana gardinii (Zoia & Rampini, 1985) comb. nov.
Bathysciola (*Bathysciola*) *gardinii* Zoia & Rampini, 1985: 161.

Latellana magrinii sp. nov. (See Appendix New Species)

Latellana octaviani (Latella, Sbordoni & Allegrucci, 2017) comb. nov.
Bathysciola octaviani Latella, Sbordoni & Allegrucci, 2017: 21.

Latellana partenii (Ruffo, 1947) comb. nov.
Bathysciola (s. str.) *partenii* Ruffo, 1947: 189.

Latellana petruzziellana sp. nov. (See Appendix New Species)

Latellana petruzzielloi sp. nov. (See Appendix New Species)

Latellana rampinii (Latella, 2002) comb. nov.
Bathysciola rampinii Latella, 2002: 129.

Latellana raveli (Dodero, 1904) comb. nov.
Bathyscia Raveli Dodero, 1904a: 57.
Bathyscia (?) *Raveli* Dodero: Jeannel, 1910a: 47.
Parabathyscia Raveli Dodero: Luigioni, 1923: 3.
Bathysciola (s. str.) *Raveli* Dodero, 1904: Jeannel, 1924a: 108.

Bathysciola (s.str.) *raveli* (Dodero): Perreau, 2000: 228.

Latellana sbordonii (Rampini & Latella, 1993) comb. nov.
Bathysciola (*Bathysciola*) *sbordonii* Rampini & Latella, 1993: 165.

Latellana sisernica (Cerruti & Patrizi, 1952) comb. nov.
Bathysciola sisernica Cerruti & Patrizi, 1952: 92.
Bathysciola (s. str.) *sisernica* Cerruti-Patrizi: Cerruti, 1955: 1.

Latellana valeriae (Latella, Sbordoni & Allegrucci, 2017) comb. nov.
Bathysciola valeriae Latella, Sbordoni & Allegrucci, 2017: 25.

Latellana vignai (Sbordoni & Rampini, 1978) añadir: comb. nov.
Latellana vignai (Sbordoni & Rampini, 1978): 40.

Genus ***Ovobathysciola*** Jeannel, 1924 sensu novo
Ovobathysciola Jeannel, 1924a: 76
Patriziella Jeannel, 1956b: 106 syn. nov. (Type species: *Patriziella sardoa* Jeannel, 1956).
Sardostygia Casale, 2019: 53 syn. nov. (Type species: *Sardostygia cogonii* Casale, 2019).

Type species. *Bathyscia majori* Reitter, 1884 by original designation (habitus in Fig. 157.3).

Diagnosis. Genus comprising bathyscioid (Fig. 157.3) to pholeuonoid (Fig. 157.4) species of small to medium size, 1.7–4.0 mm. Body short ovoid, elongate ovoid or more or less distinctly pholeuonoid; convex, elytra attenuated posteriorly , sometimes dehiscent. Teguments depigmented, shiny or moderately matt on the elytra, testaceous or brown, with slightly lighter appendages. Dorsal surface covered with small dots, not aligned transversely; pubescence short to long, recumbent, , sometimes very reduced (*Ovobathysciola grafittii*, *Ovobathysciola supramontana*), or longer and more obvious (*Ovobathysciola gestroi*, *Ovobathysciola muceddai* comb. nov.), sometimes completely absent (*Ovobathysciola cogonii* comb. nov.)

Head: Short, retractable or not, with a complete occipital carina in most species, missing in the centre in *Ovobathysciola magrinii*, almost completely obsolete in *Ovobathysciola muceddai* comb. nov., absent in *Ovobathysciola cogonii* comb. nov. Last article of maxillary palps of variable length, longer or shorter than half of the penultimate. Anophthalmous.

Antennae: Short (in bathyscioid forms not reaching, just reaching, or exceeding, the basal angles of the pronotum) or elongated (in the pholeuonoid forms reaching or well exceeding half the elytra). First antennomere always much shorter than the second. 8th-10th antennomeres sub-square or transverse, forming an obvious «antennal club», or longer than wide (*Ovobathysciola gestroi*, *Ovobathysciola sardoa* comb. nov., *Ovobathysciola muceddai* comb. nov., *Ovobathysciola nuragica* comb. nov., *Ovobathysciola cogonii* comb. nov.). Antennomere VII subconical, distally dilated and with a well-developed Hamann organ. Antennomere XI ovoid, slightly longer than the previous one.

Pronotum: of different shapes, transverse, with maximum width at or just before the base (in species with bathyscioid facies), narrow at the base (in species with pholeuonoid facies) or bell-shaped. As wide as, or narrower, than the width of the elytra at the base.

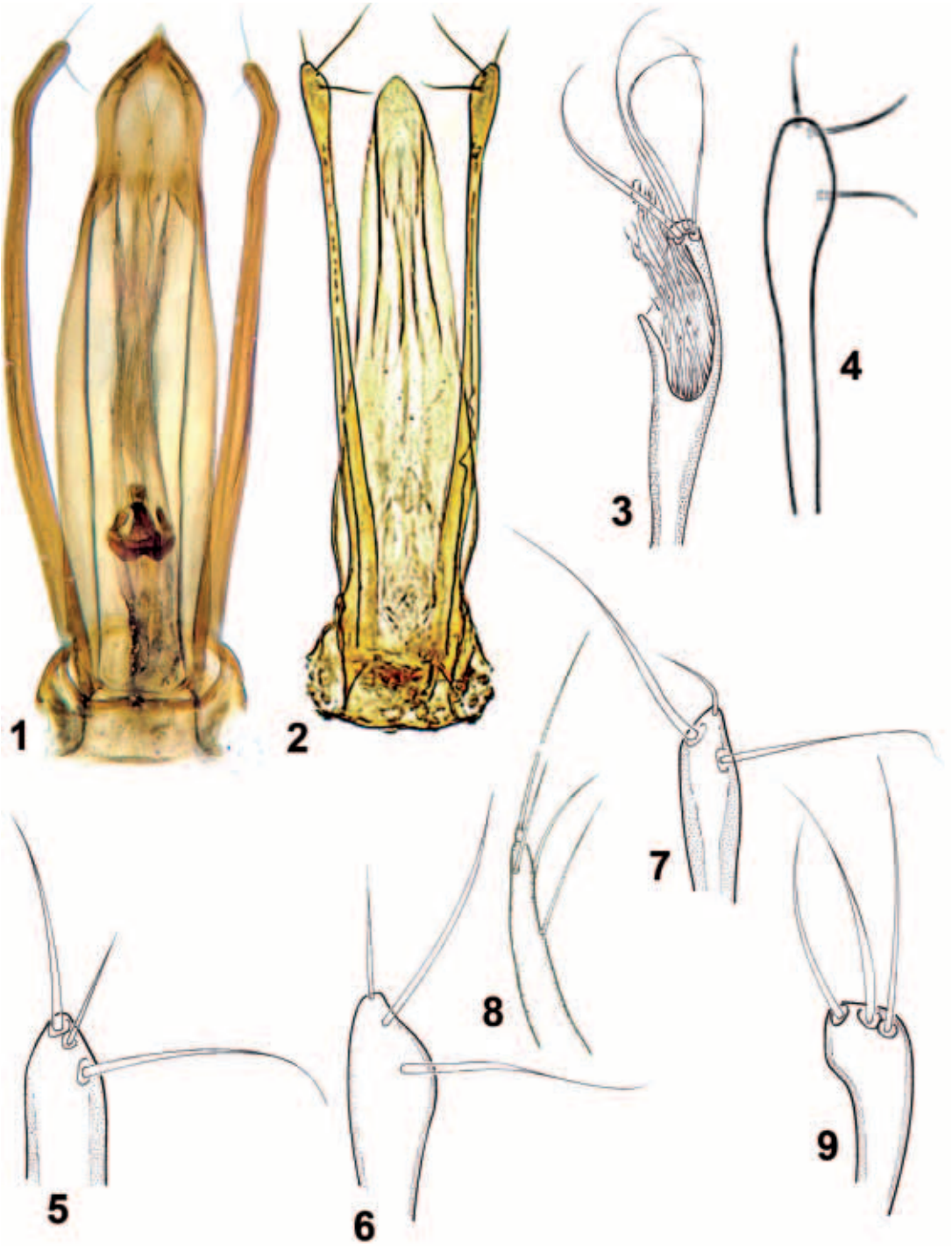
Elytra: Ovoid or elliptical, with parasutural stria present (close and parallel to the suture, complete or partially absent in the basal part or at the apex, sometimes barely distinct) or absent; without transverse striation.

Legs: Relatively slender, more elongate in species with pholeuonoid facies. Protibiae sometimes sinuous or curved outwards, without a comb and with 2-3 external, pre-apical spurs and an internal, polydentate, apical, spur. Meso- and metatibia with an incomplete apical basket. Male protarsi pentamerous, with three basal tarsomeres not or variously dilated.

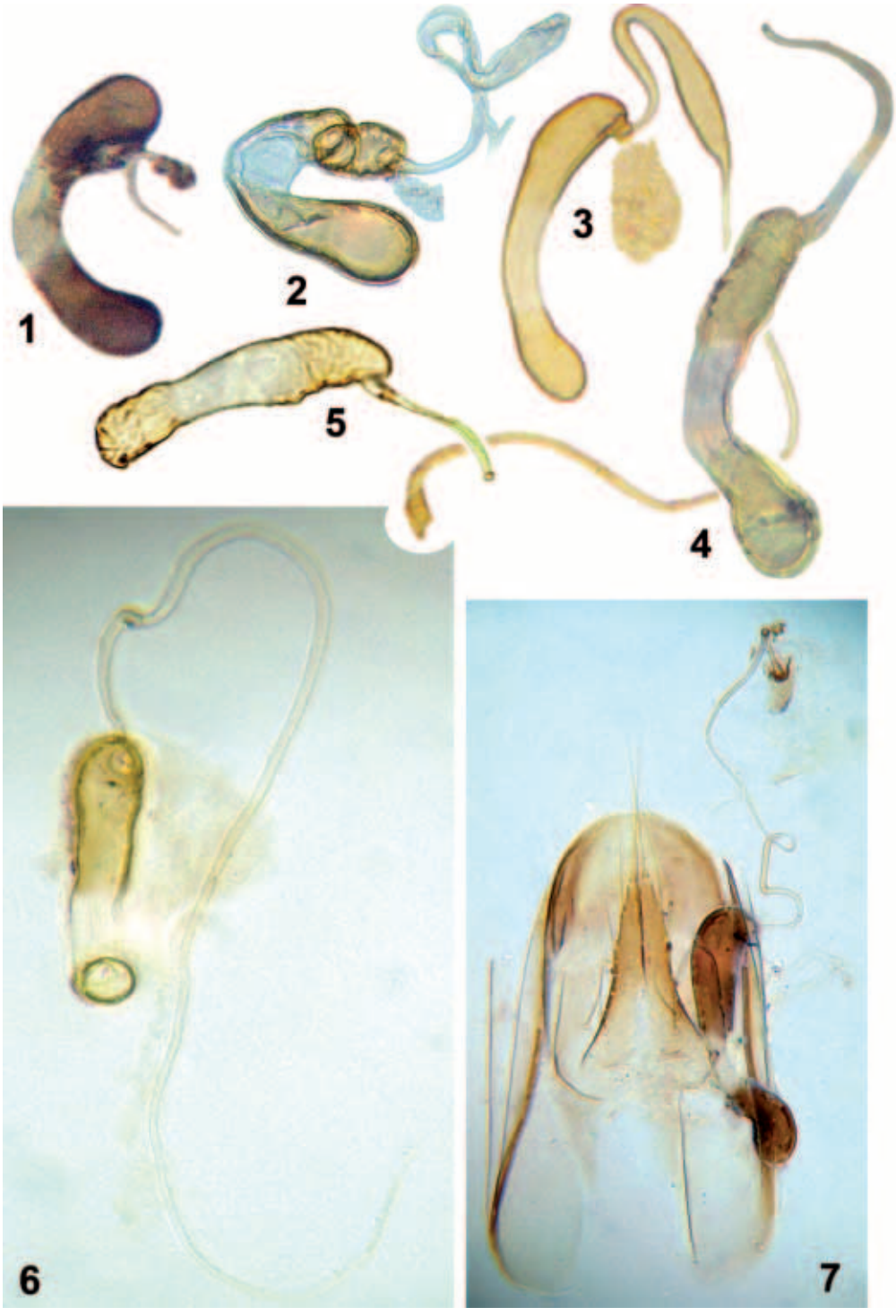
Metaventrite: Not keeled.

Mesoventral keel (Figs 158.4–158.6): Between low and very high; in lateral view, the anterior margin convex and the ventral margin convex, smooth, sinuous or almost straight with small setae; in ventral view, not thickened or narrowed in the first part and widened in the posterior part; the apex toothed or not, the posterior extension not reaching the metaventrite. In the case of *Ovobathysciola majori,* meso- and metaventrite are fused together and the suture is visible on the lateral side (Fig. 158.4).

Sutures of the metaventrite (Figs 158.4, 158.5): The two sutures delimit a triangular area which, when joined, together form a narrow, elongated, curved or straight apex, the tip of which is distant from or very close to the posterior suture of the metaventrite. The lower suture, curved or straight, passes very close to the coxal cavity in the lower part.



FIGURES 163.1–163.9: *Cytodromus* series, *Ovobathysciola* group. Aedeagus in dorsal view of: (**1**) *Ovobathysciola sardoa* **comb. nov.**, (**2**) *O. cogonii* **comb. nov.** (modified from Casale 2019). Apex of the paramere of: (**3**) *Batinoscelis lostiae* **comb. nov.**, (**4**) *Latellana gardinii* **comb. nov.** (modified from Zoia & Rampini 1985), (**5**) *O. majori*, (**6**) *O. cogonii* **comb. nov.** (redrawn from Casale 2019), (**7**) *O. sardoa* **comb. nov.**, (**8**) *Salfia damryi* **comb. nov.** (modified from Giachino 1990), (**9**) *S. ruffoi* **comb. nov.**



FIGURES 164.1–164.7: *Cytodromus* series, *Ovobathysciola* group. Spermathecal complex of: (**1**) *Batinoscelis onnisi* **sp. nov.**, (**2**) *Latellana fortesculpta* **comb. nov.**, (**3**) *Latellana valeriae* **comb. nov.** (modified from Latella *et al*. 2017), (**4**) *Ovobathysciola majori*, (**5**) *O. cogonii* **comb. nov.** (modified from Casale 2019), (**6**) *O. sardoa* **comb. nov.**, (**7**) *Salfia doderoi* **comb. nov.**

Metatergal apparatus (Figs 159.3, 160.1, 160.2): Very developed, with broad or narrow and fairly long metascutum wings; long alacrista apophyses with unsharpened tips, reaching from half to 4/5 the length of the elytra.

Metendosternite (Figs 161.3, 161.4): Broad, not «V»-shaped, with triangular furcal arms, developed and relatively broad at base, as long as trunk and without apical process; posterior furcal plate very narrow almost absent in apical area of arm and broad throughout trunk. Robust furcal trunk longer than or as long as the widest part; median keel divergent.

Median lobe of aedeagus: In lateral view (Figs 162.4–162.6) elongate, curved, with well-differentiated apical region, not curved, with a marked or slightly sinuous depression; in dorsal view (Figs 162.10, 163.1, 163.2), sides arched in the basal area, usually widest, then gradually narrowing, apical region rounded or lanceolate.

Endophallus (Figs 162.10, 163.1, 163.2): Without a «Y»-shaped basal piece or differentiated sclerotized structures, but provided, in the median region, with a characteristic «T»- or inverted «anchor»- shaped phanera (with the exception of *Ovobathysciola cogonii* comb. nov. in which the endophallus is totally unarmed).

Parameres (Figs 163.5–163.7): Elongate, arcuate, thickened or not distally, not reaching, reaching or exceeding the apex of the median lobe. Each with three setae: a ventral subapical, a dorsal subapical, and a shorter apical.

Spermathecal complex (Figs 164.4–164.6): Spermatheca elongate, sometimes «C»-shaped or straight; sclerotized at base and apex, with distal part sub-spherical. Median part or hyaline junction part slightly narrower and a little longer or as long as each of the parts.

Female uroventrite VIII (Figs 165.3–165.5): Distal margin rounded and sides of proximal margin subrectilinear or very curved; spiculum between short and quite long, slightly widened and blunt, rounded or bifid, at apex.

Discussion. As already discussed above and clearly emphasised by Casale (2004, 2014), the only real differences between *Ovobathysciola* and *Patriziella* lie in the shape of the body, which is more or less specialised for life in hypogean environment. The morphologies of the median lobe of aedeagus, parameres, endophallus and spermatheca, as also pointed out by Rampini & Zoia (1990), are exactly the same in both genera.

As can be seen, only the external morphological structures distinguish *Patriziella* from *Ovobathysciola*, their genital structures corresponding to the same model. The same applies to *Sardostygia,* which, like *Patriziella*, are derived elements of the larger *Ovobathysciola* clade. Molecular and morphological arguments suggest that *Ovobathysciola* should be synonymized with *Patriziella* and *Sardostygia*, with the former, which is the earliest described, prevailing . As a result:

– *Patriziella* Jeannel, 1956 syn. nov. = *Ovobathysciola* Jeannel, 1924.

– *Sardostygia* Casale, 2019 syn. nov. = *Ovobathysciola* Jeannel, 1924.

In the tree (Fig. 1G) *Ovobathysciola* sensu novo appears as the basal genus of the group and sister to the genera *Latellana* gen. nov.*, Salfia* stat. nov. and *Batinoscelis* stat. nov. with a support of 100/100.

Distribution. North-western, central, central-eastern and south-eastern Sardinia.

Species

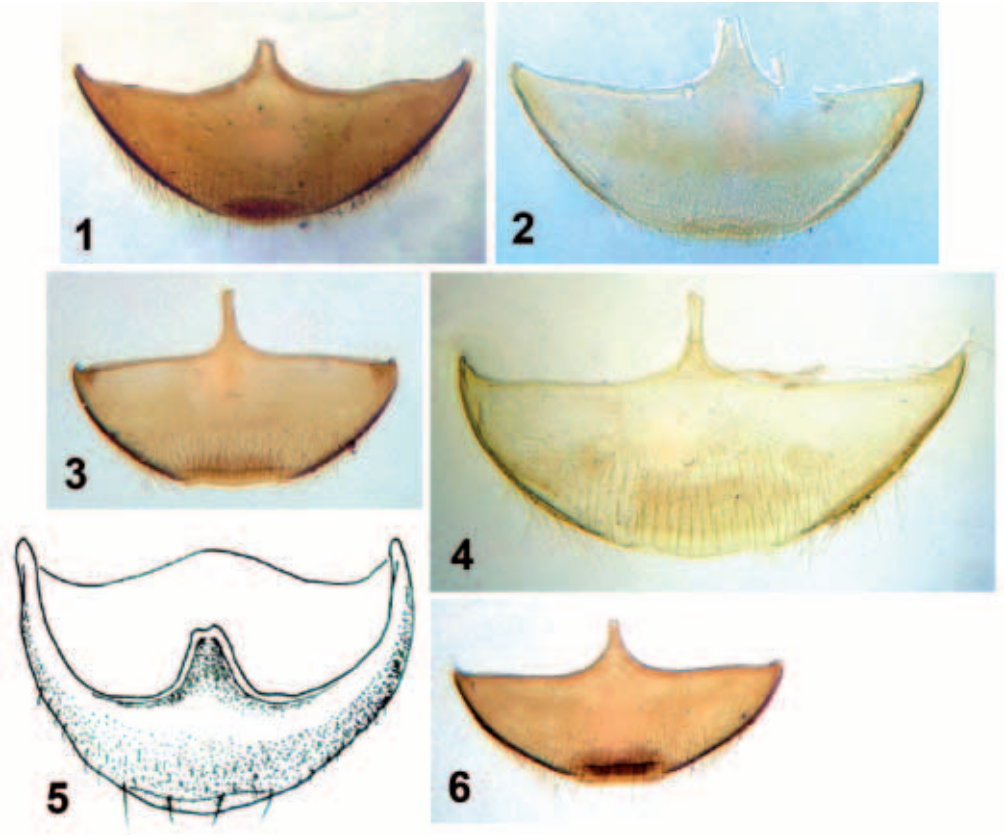
Ovobathysciola castrimedusae Casale, 2014
Ovobathysciola n. sp. Casale *in litt*.: Caccone & Sbordoni, 2001: 124.
Ovobathysciola castrimedusae Casale, 2014: 245.

Ovobathysciola cogonii (Casale, 2019) comb. nov.
Sardostygia cogonii Casale, 2019: 53.

Ovobathysciola deleddae Casale, 2014
Ovobathysciola deleddae Casale, 2014: 253.

Ovobathysciola gestroi (Fairmaire, 1872)
Adelops gestroi Fairmaire, 1872: 54.
Quaestus Gestroi Fairm.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *Gestroi* Fairm.: Reitter, 1885a [1884]: 23.
Bathyscia (*Parabathyscia*) *Gestroi* Fairm.: Jeannel, 1908a: 309.
Bathysciola Gestroi Fairmaire: Jeannel, 1910a: 28.
Bathysciola Gestroi Fairmaire: Jeannel, 1911a: 236.
Bathysciola (s. str.) *Gestroi* Fairmaire: Jeannel, 1914b: 8.
Bathysciola (*Ovobathysciola*) *Gestroi* Fairmaire, 1872: Jeannel, 1924a: 118.
Ovobathysciola gestroi (Fairmaire): Perreau, 2000: 282.

Ovobathysciola grafittii Rampini & Sbordoni, 1980
Ovobathysciola grafittii Rampini & Sbordoni, 1980: 337.



FIGURES 165.1–165.6: *Cytodromus* series, *Ovobathysciola* group. Female uroventrite VIII of: (**1**) *Batinoscelis onnisi* **sp. nov.**, (**2**) *Latellana fortesculpta* **comb. nov.**, (**3**) *Ovobathysciola majori*, (**4**) *O. sardoa* **comb. nov.**, (**5**) *O. cogonii* **comb. nov.** (modified from Casale 2019), (**6**) *Salfia doderoi* **comb. nov.**

Ovobathysciola magrinii Casale, 2014
Ovobathysciola magrinii Casale, 2014: 258

Ovobathysciola majori (Reitter, 1884)
Bathyscia majori Reitter, 1885a [1884]: 24.
Bathysciola Majori Reitter: Jeannel, 1910a: 28.
Bathysciola (s. str.) *Majori* Reitt.: Jeannel, 1914b: 9.
Bathysciola (*Ovobathysciola*) *Majori* Reitter, 1885a [1884]: 118.
Ovobathysciola majori (Reitter, 1885): Casale, 1975: 193.

Ovobathysciola muceddai (Casale, 2004) comb. nov.
Patriziella muceddai Casale, 2004: 13.

Ovobathysciola nuragica (Rampini & Zoia, 1990) **comb. nov.**
Patriziella nuragica Rampini & Zoia, 1990: 369.

Ovobathysciola paeoniae Casale, 2014
Ovobathysciola paeoniae Casale, 2014: 249.

Ovobathysciola sardoa (Jeannel, 1956) comb. nov.
Patriziella sardoa Jeannel, 1956b: 107.

Ovobathysciola supramontana Casale, 2014
Ovobathysciola supramontana Casale, 2014: 265.

Genus ***Salfia*** Tamanini, 1955 stat. nov.
Bathysciola (*Salfia*) Tamanini, 1955b: 4.

Type species. *Bathysciola* (*Salfia*) *ruffoi* Tamanini, 1955 by original designation (habitus in Fig. 158.1).

Diagnosis. Small size, 1.2–2.2 mm, bathyscioid facies; body oval, slightly acuminate posteriorly and rather convex (Fig. 158.1).

Head: Retractile, with a complete occipital carina; eyes absent or reduced to a small white macula.

Antennae: Short, barely extending beyond the base of the pronotum; relative length of the antennomeres

variable; the first shorter than the second and the 8th transverse or slightly longer than wide.

Pronotum: Transverse, sides evenly arched with maximum width near the base; posterior apical areas directed backwards, with acute angles and more or less acute vertices; sinuous posterior margin.

Elytra: Without or with transverse striolae and without o with parasutural stria generally blurred in the proximal third.

Legs: Apex of tibiae on the inner side with polydentate spurs. Apical baskets of the meso- and metatibiae incomplete. Pentamerous and protarsi enlarged in males, degree of dilatation depends on species.

Mesoventral keel (Fig. 158.7): Between low and high, with or without toothed apex; anterior margin oblique and lower margin straight or only slightly curved. Not extended into the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus: Well developed and in some cases dimorphic. Wings of metascutum short and broad ; apophysis of the alacrista longer than half the elytra. Marked sexual dimorphism with the posterior apophysis visibly dilated distally in males (Figs 160.3, 160.4), at least in the Sardinian species (*Salfia damryi* comb. nov., *Salfia kraussei* comb. nov. and *Salfia doderoi* comb. nov.).

Metendosternite (Fig. 161.5): Short, «V»-shaped, triangular in appearance, broad at base; furcal arms short, as long as trunk, with apical area tapering, curved downwards and without apical apophysis; furcal trunk broad, slightly wider than long measured at basal area.

Median lobe of aedeagus: In lateral view, slender, with sub-parallel, slightly arched lateral margins (Fig. 162.7), down to the tip, which is straight or decidedly curved (sometimes «S»-shaped) in the ventral part. In dorsal view (Fig. 162.11), regularly rounded, pointed or lanceolate apex.

Endophallus (Fig. 162.11): With an internal armature formed of three sclerotized pieces, allowing three regions to be differentiated (basal, medial and apical). Presence of a «Y»-shaped piece and a flagellum in the basal area. Short apical reinforcement bands.

Parameres (Fisg. 163.8, 163.9): As long as or slightly longer than median lobe. Apex not or only slightly enlarged. Three or four long or short setae (sometimes sickle-shaped or very reduced) at apex of parameres, all at distal end, except when there are four setae (Fig. 163.8).

Spermathecal complex (Fig. 164.7): Spermatheca well sclerotized and elongated, with the median part or union duct hyaline, long and not narrow. The basal and apical lobes of the same size, or the basal one larger. Spermatic duct with expanded area present (stretched or rounded) or absent, joining at its end a small basal process of the copulatrix sac.

Female uroventrite VIII (Fig. 165.6): Posterior margin broadly arcuate with elongate macule in median area close to margin; sides of anterior margin subrectilinear, meeting in median area to form short, pointed, more or less triangular spiculum.

Discussion. The characters reported in the table of Latella *et al*. (2017: table 2), related to at least two species of *Salfia* stat. nov. (*Salfia sarteanensis*comb. nov. and *Salfia georgii* comb. nov.), as well as the redescription of «*Bathysciola*» *destefanii* (now treated as *Salfia* stat. nov.) (Latella, 2012), have been reported by us in the Diagnosis section of the genus *Salfia* stat. nov., originally described by Tamanini (1955) as a subgenus of *Bathysciola*. On the other hand, Jeannel (1924a: 82), on the subject of *Bathysciola clavicornis*, has already suggested the probable affinity of this species with *Bathysciola damryi* (now *Salfia damryi* comb. nov.) from Sardinia.

The genus *Salfia* stat. nov., as it is understood here (comprising 15 species), will require a thorough taxonomic revision carried out, in the first instance, on a morphological basis. This group of «*Bathysciola*» has not been revised since the monograph by Jeannel (1924a); Giachino (1990) limited himself to reviewing the Sardinian species (*Salfia damryi* comb. nov., *Salfia kraussei* comb. nov. and *Salfia doderoi* comb. nov.) and Pace (1977) to describing three new species and a new subspecies.

At present, 18 species are included in the genus *Salfia* stat. nov. Two new species are described here as *Salfia laudis* stat. nov. – from Monte Sirino (Lagonegro, Lucania) – and *Salfia angelinii* stat. nov. – from Accettura (Lucania) –. Of these species, we have molecular data for only five (*Salfia damryi* comb. nov., *Salfia georgii* comb. nov., *Salfia ruffoi* comb. nov., *Salfia derosasi* comb. nov. and *Salfia sarteanensis* comb. nov.). The other species are attributed, sometimes dubiously, solely on morphological grounds.

In the phylogenetic tree (Fig. 1G) *Salfia* stat. nov. is sister to *Batinoscelis* stat. nov. (see Discussion section of this genus) with a low support of 17.2/75.

Distribution. Italy: Tuscany, Umbria, Marche, Abruzzo, Lazio, Campania, Lucania, Calabria, Sardinia, Sicily.

Species

***Salfia angelinii* sp. nov.** (See Appendix New Species)

Salfia anxanensis (Pace, 1977) comb. nov.
Bathysciola anxanensis Pace, 1977: 208.
Bathysciola (s. str.) *anxanensis* Pace: Perreau, 2000: 233.

Salfia clavicornis (Jeannel, 1924) comb. nov.
Bathysciola clavicornis Jeannel, 1924a: 82.
Bathysciola (s. str.) *clavicornis* Jeannel: Perreau, 2000: 233.

Salfia damryi (Abeille de Perrin, 1881) comb. nov.
Bathyscia Damryi Abeille de Perrin, 1881: IX.
Bathyscia (*Bathyscia*) *Damryi* Ab.: Reitter, 1885a [1884]: 22.
Bathysciola Damryi Abeille: Jeannel, 1910a: 27.
Bathysciola (s. str.) *Damryi* Abeille de Perrin: Jeannel, 1914b: 8.
Bathysciola damryi (Abeille, 1881): Giachino, 1990: 302.
Bathysciola (s. str.) *damryi* (Abeille): Perreau, 2000: 233.

Salfia derosasi (Jeannel, 1914) comb. nov.
Bathysciola (s. str.) *Derosasi* Jeannel, 1914c: 200.
Bathysciola derosasi Dod.: Patrizi, 1956: 303.
Bathysciola (s. str.) *derosasi* Jeannel: Perreau, 2000: 234.

Salfia destefanii (Ragusa, 1881) comb. nov.
Adelops Destefanii Ragusa, 1881: 6.
Bathyscia muscorum Dieck, 1869: Reitter, 1885a [1884]: 24.
Bathyscia Destefanii Rag.: Dodero, 1904b: 121.
Bathysciola Destefanii Ragusa: Jeannel, 1910a: 28.
Bathysciola (s. str.) *Destefanii* Ragusa: Jeannel, 1914b: 8.
Bathysciola (s. str.) *destefanii* (Ragusa, 1881): Latella, 2012: 67.

Salfia doderoi (Giachino, 1990) comb. nov.
Bathysciola doderoi Giachino, 1990: 317.
Bathysciola (s. str.) *doderoi* Giachino, 1990: Perreau, 2000: 234.

Salfia ferdinandi (Jeannel, 1924) comb. nov.
Bathysciola Ferdinandi Jeannel, 1924a: 50.
Bathysciola (s. str.) *Ferdinandi* Jeannel, 1924: Jeannel, 1924a: 101.
Bathysciola (s. str.) *ferdinandi* Jeannel: Perreau, 2000: 234.

Salfia georgii (Cerruti & Patrizi, 1952) comb. nov.
Bathysciola georgii Cerruti & Patrizi, 1952: 93.
Bathysciola (s. str.) *Georgii* Cerruti-Patrizi: Cerruti, 1955: 4.
Bathysciola (s. str.) *georgii* Cerruti & Patrizi: Perreau, 2000: 234.

Salfia hadriatica (Pace, 1977) comb. nov.
Bathysciola (s. str.) *hadriatica* Pace, 1977: 212.

Salfia kraussei (Melichar, 1912) comb. nov.
Bathysciola Kraussei Melichar, 1912: 35.
Bathysciola (s. str.) *Kraussei* Melichar: Jeannel, 1914b: 9.
Bathysciola kraussei Melichar, 1912: Giachino, 1990: 311.
Bathysciola (s. str.) *kraussei* Melichar: Perreau, 2000: 234.

Salfia laudis sp. nov. (See Appendix New Species)

Salfia picena (Pace, 1977) comb. nov.
Bathysciola (s. str.) *picena* Pace, 1977: 205.

Salfia ruffoi (Tamanini, 1955) comb. nov.
Bathysciola (*Salfia*) *Ruffoi* Tamanini, 1955b: 6.
Bathysciola (*Bathysciola*) *ruffoi* Tamanini, 1955: Zoia, 1991: 70.
Bathysciola (*Salfia*) *ruffoi* Tamanini: Perreau, 2000: 241.

Salfia sarteanensis (Bargagli, 1870) comb. nov.
Salfia sarteanensis paganettii (Jeannel, 1924) comb. nov.
Bathysciola sarteanensis Paganettii Jeannel, 1924c: 50
Bathysciola (s. str.) *sarteanensis* Subsp. *Paganettii* Jeannel, 1924: Jeannel, 1924a: 100.
Bathysciola (s. str.) *sarteanensis paganettii* Jeannel: Perreau, 2000: 234.

Salfia sarteanensis sarteanensis (Bargagli, 1870) comb. nov.
Adelops Sarteanensis Bargagli, 1870: 175.
Bathyscia delicata Reitter, 1885b: 375.
Quaestus sarteanensis Barg.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *sarteanensis* Bargagli: Reitter, 1885a [1884]: 22.
Bathyscia sarteanensis Barg.: Dodero, 1900: 417.
Bathysciola sarteanensis Bargagli: Jeannel, 1910a: 27.
Bathysciola (s. str.) *sarteanensis* Bargagli: Jeannel, 1914b: 11.
Bathysciola (s. str.) *sarteanensis* Subsp. *Sarteanensis* Bargagli, 1870: Jeannel, 1924a: 100.

Bathysciola (*Bathysciola*) *sarteanensis sarteanensis* (Bargagli): Perreau, 2000: 235.

Salfia simbruinica (Jeannel, 1911) comb. nov.
Salfia simbruinica aretina (Jeannel, 1924) comb. nov.
Bathysciola (s. str.) *simbruinica aretina* Jeannel, 1924a: 101.
Salfia simbruinica latia (Jeannel, 1924) comb. nov.
Bathysciola (s. str.) *simbruinica latia* Jeannel, 1924a: 102.

Salfia simbruinica simbruinica (Jeannel, 1911) comb. nov.
Bathysciola subterranea ssp. *simbruinica* Jeannel, 1911a: 223.
Bathysciola (s. str.) *subterranea* subsp. *simbruinica* Jeannel: Jeannel, 1914b: 12.
Bathysciola (s. str.) *simbruinica* Subsp. *simbruinica* Jeannel, 1911: Jeannel, 1924a: 101.

Salfia simbruinica trasimenica (Jeannel, 1924) comb. nov.
Bathysciola (s. str.) *simbruinica trasimenica* Jeannel, 1924a: 102

Salfia subterranea (Krauss, 1900) comb. nov.
Bathyscia subterranea Krauss, 1900: 292.
Bathysciola subterranea H. Krauss: Jeannel, 1910a: 27.
Bathysciola (s. str.) *subterranea* H. Krauss: Jeannel, 1914b: 12.

Salfia volsiniensis (Jeannel, 1924) **comb. nov.**
Salfia volsiniensis sibyllina (Pace, 1977) **comb. nov.**
Bathysciola (s. str.) *volsiniensis sibyllina* Pace, 1977: 214.

Salfia volsiniensis volsiniensis (Jeannel, 1924) comb. nov.*Bathysciola* (s. str.) *volsiniensis* Jeannel, 1924a: 101.
Bathysciola (s. str.) *volsiniensis volsiniensis* Jeannel, 1924: Perreau, 2000: 235.

3.3.1.2 ***Diaprysius*** group

Diagnosis. Pholeuonoid or bathyscioid facies. Orange tegument, covered with a fine, short, yellowish pubescence, recumbent and rarely raised. Depigmented.

Head: Epistomal suture darkened and slightly curved; anophthalmous.

Elytra: Punctation without order and without transverse striolae; in general without parasutural stria, although it is more or less developed in *Catalaniana* gen. nov., difuse in *Speophyes* and in some species of *Diaprysius*.

Legs: Male protarsi pentamerous, except in *Speophyes* where they are tetramerous. Tibiae generally pubescent, with two internal pectinated spurs, two simple external ones, and a series of unequal spines between them; protibiae not tapered in the apical part; mesotibiae and metatibiae without apical baskets.

Suture of the metaventrite: Arched and from end to end of the mesocoxal cavity.

Metaventrite: With a bifid protruding process separating the metacoxal cavities.

Male genital segment: Very reduced, open with two long peduncles.

Endophallus: With three differentiated regions and a «Y»-piece in the basal region.

Parameres: With more than three setae; if there are three they are arranged in a series.

Discussion. This is a remarkable clade where in the different generic cladogenesis an alternation of genital structures has occured. In one of the most basal of genera, *Catalaniana* gen. nov., the structure of the endophallus is peculiar with various pieces which look unlike those found in other members of the tribe; the number of setae of the parameres, three in the vast majority of Leptodirini, is multiplied by two or three in *Catalaniana* gen. nov. In the subsequent branching, *Speophyes* emerges and is the only genus of *Diaprysius* group with the male protarsi tetramerous; in the middle region of the endophallus a thin transverse phanera «M»-shaped is present, but the apices of the parameres are decorated with three setae, the same as in *Galliana* gen. nov., which also has an endophallus with unique pieces such as two thin phanerae which are slightly sclerotized and extend from the basal to the apical region. Finally, the most derived genus, *Diaprysius*, exhibits a multiplication of the setae on the parameres, on the other hand the endophallus is what can be described a more «classic» form for this group, with dorsal and ventral phanerae arranged in an usual way, bridging the gap between the genera of the *Speonomus* series, with which, on the other hand, has no kinship. Everything seems to indicate a convulsive cladogenetic process, with the isolation of small populations that have diverged, although it should be noted that, as shown in the genetic distance measures, over a long time. In the phylogenetic tree (Fig. 1G) the group is supported by 99.9/100 and within the *Cytodromus* series, the *Diaprysius* group is the basal one

and joins the *Cytodromus*, *Isereus* and *Parabathyscia* groups with a support of 83.2/93 in Tree-1 (Fig. 1G) and a support of 73.6/82 in Tree-2 (Fig. 2).

Key to genera

1. Parameres with five to 14 setae in the apical part (Figs 170.1–170.4) 2
- Parameres with three setae in the apical part (Figs 170.5, 170.6) 3

2. Pholeuonoid facies (Fig. 166.2). Elytra with the apical region tiped. Antennae long, longer than the elytral suture; club articles longer than wide. Metatergal apparatus (Fig. 168.2) with metascutum very narrow and alacrista apophysis very long. Metendosternite with furcal trunk very long, short arms and no terminal apophysis (Fig. 168.6). Apex of parameres club rounded or narrowed, with two groups of setae, short and long, clearly separated (Fig. 170.4). Spermathecal complex with well-developed nodule in the spermatic duct (Fig. 171.2) .....*Diaprysius*
- Bathyscioid facies (Fig. 166.1). Elytra with the apical region broadly rounded. Antennae short, at most as long as the elytral suture; club articles transverse. Metatergal apparatus (Fig. 168.1) with wider metascutum and clearly shorter alacrista apophysis. Metendosternite (Fig. 168.5) with shorter trunk, longer arms and terminal apophysis. Apex of the parameres in elliptical club, with setae long, sinuous and with insertion pores close to each other (Figs 170.1–170.3). Spermathecal complex with poorly developed nodule in the spermatic duct (Fig. 171.1) .....*Catalaniana* gen. nov.

3. Male protarsi pentamerous. Elytra without parasutural striae. Setae inserted in the apical area of the parameres with pores in the form of large circular cavities (Fig. 170.5). Endophallus (Fig. 169.7) without transverse phanera in the middle region and very short reinforcing bands of the apical region that rest on membranous ligules covered with long setae; among them an axial piece elongated «Y»-shaped with upper arms very short.....*Galliana* gen. nov.
- Male protarsi tetramerous. Elytra with parasutural striae. Setae inserted in the apical part of the parameres with small pores (Fig. 170.6). Endophallus (Fig. 169.8) with a phanera «M»-shaped and transverse in the middle region and the thin and longer reinforcing bands of the apical region rest on membranous ligules of striated tissue; between them there is no axial «Y»-shaped piece .....*Speophyes*

Genus ***Catalaniana*** nov.
https://zoobank.org/NomenclaturalActs/81AB68F9-DA99-4D14-9F16-D66B647A4DC6

Type species. *Bathysciola zariquieyi* Bolívar, 1919 by present designation (habitus in Fig. 166.1).

Description. Size ranging between 1.5-2.2 mm. Bathyscioid facies (Fig. 166.1); body shape short, wide and depressed; integument with a matte appearance and covered with lying pubescence; the whole body marked by irregular scratchy punctation, the same as on the elytra.

Head: With complete occipital carina.

Antennae: Short and thick, barely reaching the base of the pronotum and scarcely longer than the middle of the elytral suture; regular club, in it the segments transverse and a little flattened.

Pronotum: Very transverse and convex, with the lateral margins regularly arched; widest at base and posterior angles acute with blunt vertices.

Elytra: Short, wide and somewhat depressed, with a flat disc; lateral margins subrectilinear and edged; apical areas broadly rounded; there is a parasutural stria not parallel to the suture, non-existent in the periscutellar region; appears separates from the suture up to the middle of the elytra and finally converges strongly towards the suture in the posterior third; no transverse striolae.

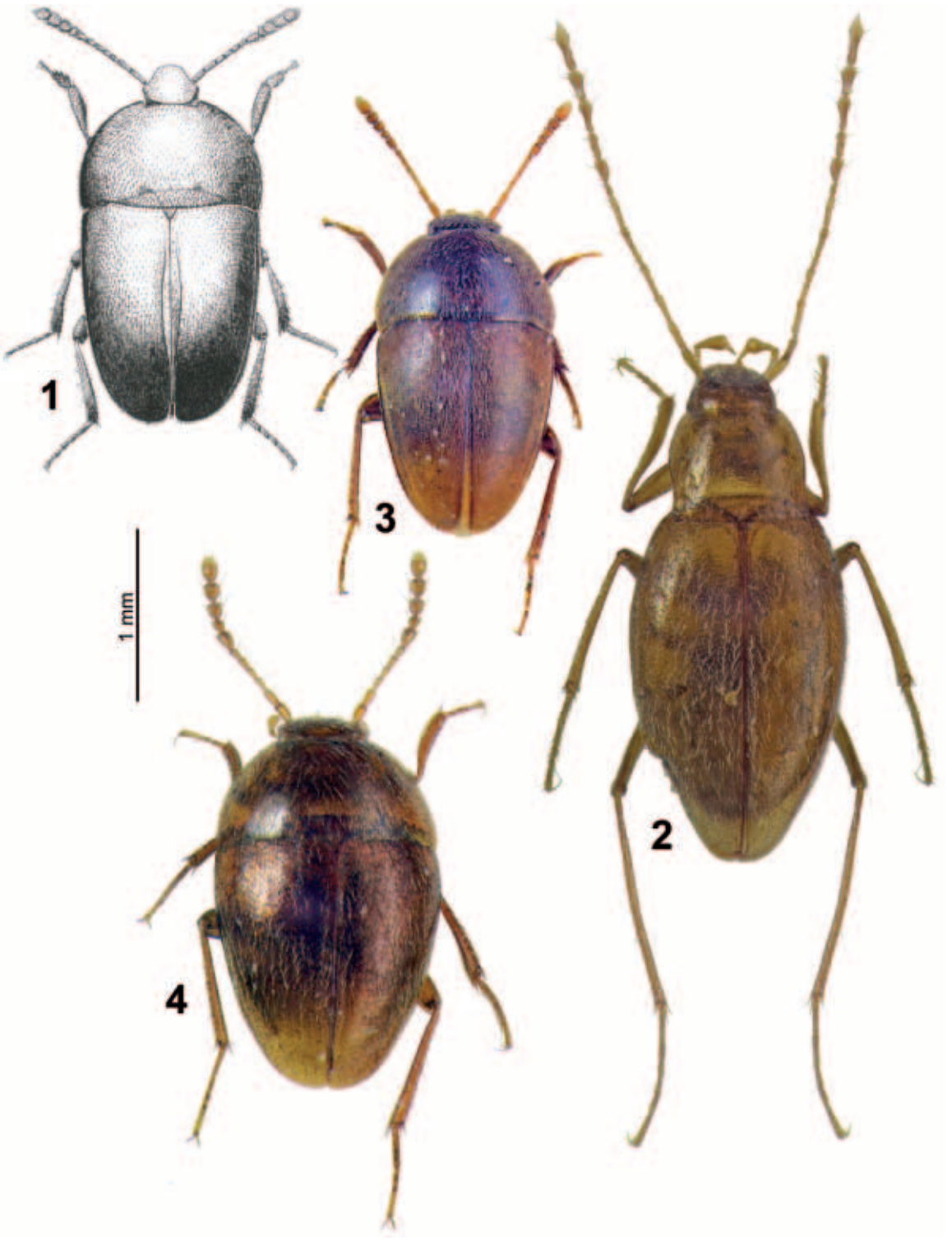
Legs: Short and robust. Male protarsi more or less dilated; mesotibiae curved and metatibiae straight; all tibiae with spines on outer side, very large on mesotibiae.

Mesoventral keel (Fig. 167.1): Low or slightly higher; in the first case the anterior and posterior margins form a continuous arc, with a very obtuse angle; in the second, both margins form a vertex that may or may not be serrated and the angle right.

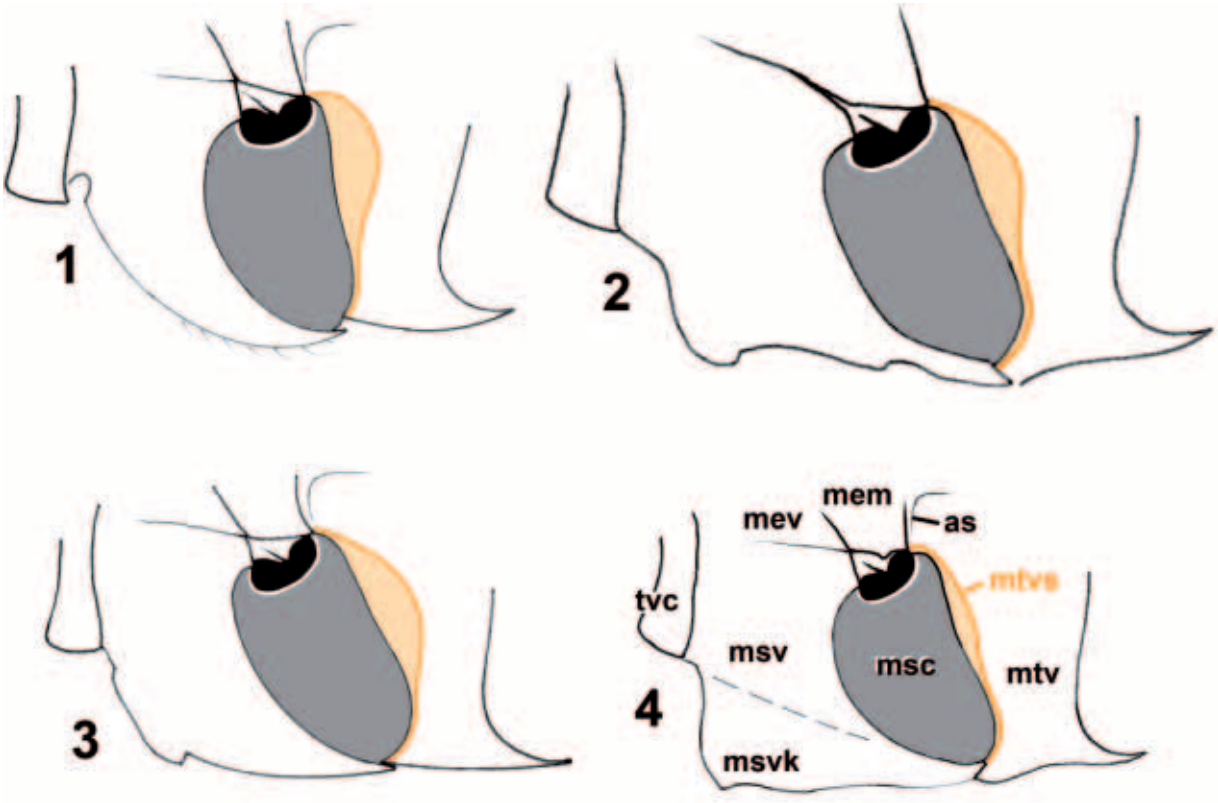
Suture of the metaventrite (Fig. 167.1): In arc and delimits a reduced area between the suture and the mesocoxal cavity, wider in the upper area.

Metatergal apparatus (Fig. 168.1): With the metascutum long and somewhat widened, one wing of the metascutum being somewhat longer than the alacrista; apophysis of the alacrista prolonged and apices sharp.

Metendosternite (Fig. 168.5): «V»-shaped furca. Furcal arms as long as trunk, narrow at apical area which is arched with sharp tip and well-developed terminal apophysis; posterior lamina wide in the middle, then narrows and is preserved until the apex of the arm, the edge arched. Furcal trunk wide and slightly



FIGURES 166.1–166.4: *Cytodromus* series, *Diaprysius* group. Habitus of: (**1**) *Catalaniana zariquieyi* **comb. nov.**, (**2**) *Diaprysius caudatus caudatus*, (**3**) *Galliana linderi linderi* **comb. nov.**, (**4**) *Speophyes lucidulus*.



FIGURES 167.1–167.4: *Cytodromus* series, *Diaprysius* group. Pterothorax in lateral view of: (**1**) *Catalaniana penicillata* **comb. nov.**, (**2**) *Diaprysius serullazi muelleri,* (**3**) *Galliana linderi linderi* **comb. nov.**, (**4**) *Speophyes lucidulus*. Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

wider than long at base; median keel diverges very little posteriorly.

Median lobe of the aedeagus: In lateral view (Fig. 169.1), arched in the two basal thirds, which can be more or less thick, while the apical third is sub-rectilinear or sinuous and regularly narrowed to the apex, which is pointed or slightly prolonged and peaked, oriented towards the ventral face; in the apical third there may be a small depression on the dorsal region. In dorsal view (Fig. 169.5), the apical area is narrower and with subparallel sides, the apex arched or slightly truncated.

Endophallus (Fig. 169.9): With the branches of the «Y»-piece symmetrical and extended along the sides of the sac into the middle region where they come into contact with the appendix of the dorsal bags or curve to disappear near the flagellum of the «Y»-piece; there may be obvious dorsal and ventral phanerae and two large bags covered with spines in which the reinforcing bands rest or a highly sclerotized «U»-shaped piece from which the axial piece originates; in the latter, there appears a bag, densely covered by fine pilosity located between the reinforcing bands, and another, covered with thick spicules, located between the hyaline extensions of the «Y»-piece.

Parameres (Figs 170.1–170.3): Fine and slender, shorter or as long as the median lobe, with a dilated apex in elliptical shaped club, provided with 5-14 long setae, all with apical insertion, except *C. zariquieyi* with a subapical one.

Spermathecal complex: Spermatheca (Fig. 171.1) curved throughout its length; the two sclerotized lobes wider than the junction duct, narrower and hyaline; the basal one being more elongated; the very thin spermatic duct is joining the spermatheca by a small nodule into which also empties the spermathecal gland.

VIII female uroventrite (Fig. 171.5): Posterior edge narrowed regular arc, the spiculum quite long and narrow.

Etymology. Derived from Catalania, Catalunya, region of Europe. The toponym is found for the first time in written form around 1117 in the Latin form Catalania or Catalaunia which appears in the Pisan poem *Liber maiolichinus de gestis pisanorum illustribus*. Feminine.

Discussion. It is the sister genus of the entire *Diaprysius* group clade and is related with very consistent support 99.9/100 (Fig. 1G). It is characterised by the absence of transverse striolae on the elytra and the presence of a parasutural stria not parallel to the suture. Also because the apex of the parameres is armed with more than the usual three setae in most Leptodirini; this character is variable, species-specific. The apex of the parameres of *Catalaniana penicillata* comb. nov. has nine setae, according to the original description – Jeannel, 1924b –, although a specimen with ten is known; in some cases it coincides with those of *Catalaniana madoni* comb. nov. – from eight to 14 for three specimens studied by Coiffait (1959), or 12 according to Jeannel (1923a) –. For *Catalaniana zariquieyi* comb. nov., in the original description, Bolívar (1919) indicated that the apex of the paramere is armed with five setae, two longer and three shorter; in fact this is correct for the two paramers of the holotype, although Jeannel (1924b) stated that the specimens he studied had six setae. It seems that in general the tendency is to assume that there is a multiple of the three main setae present. In addition, the endophallus exhibits important differences between the different species and a common pattern is not evident; it can be proposed that these large morphological differences can be explained by the prolonged period of divergent evolution, as there is also a considerable genetic distance detected.

– *Catalaniana madoni* comb. nov.: The endophallus has between the hyaline prolongations of the «Y»-piece two tiny phanerae located within a membranous sac; there is a highly sclerotized «U»-shaped piece from which the axial piece originates; a bag densely covered by fine pilosity located between the reinforcing bands is also observed.

– *Catalaniana penicillata* comb. nov.: There is a highly sclerotized «U»-shaped piece from which the axial piece originates, which is hyaline; there are no differentiated phanerae in the middle region and the reinforcing bands rest on membranous ligules; between the apical reinforcing bands there is a bag whose tissue is covered with pilosity.

– *Catalaniana zariquieyi* comb. nov.: It has obvious ventral phanerae and the dorsal ones are very reduced and only extend until they come into contact with the «Y»-piece; the apical reinforcing bands rest on membranous ligules whose integument is densely covered with spines; these ligules have a sclerotized pedunculus in their lower region.

Distribution. Spain and France. It is distributed in the northeast of the Iberian Peninsula, from the northern slope of the eastern Pyrenees to the pre-Pyrenean mountains and the Catalan coastal mountains to the south of the massif, in Catalonia.

Species

Catalaniana madoni (Jeannel, 1923) comb. nov.
Bathysciola Madoni Jeannel, 1923a: 104.
Bathysciola (*Bathysciola*) *Madoni* Jeannel: Jeannel, 1924a: 109.

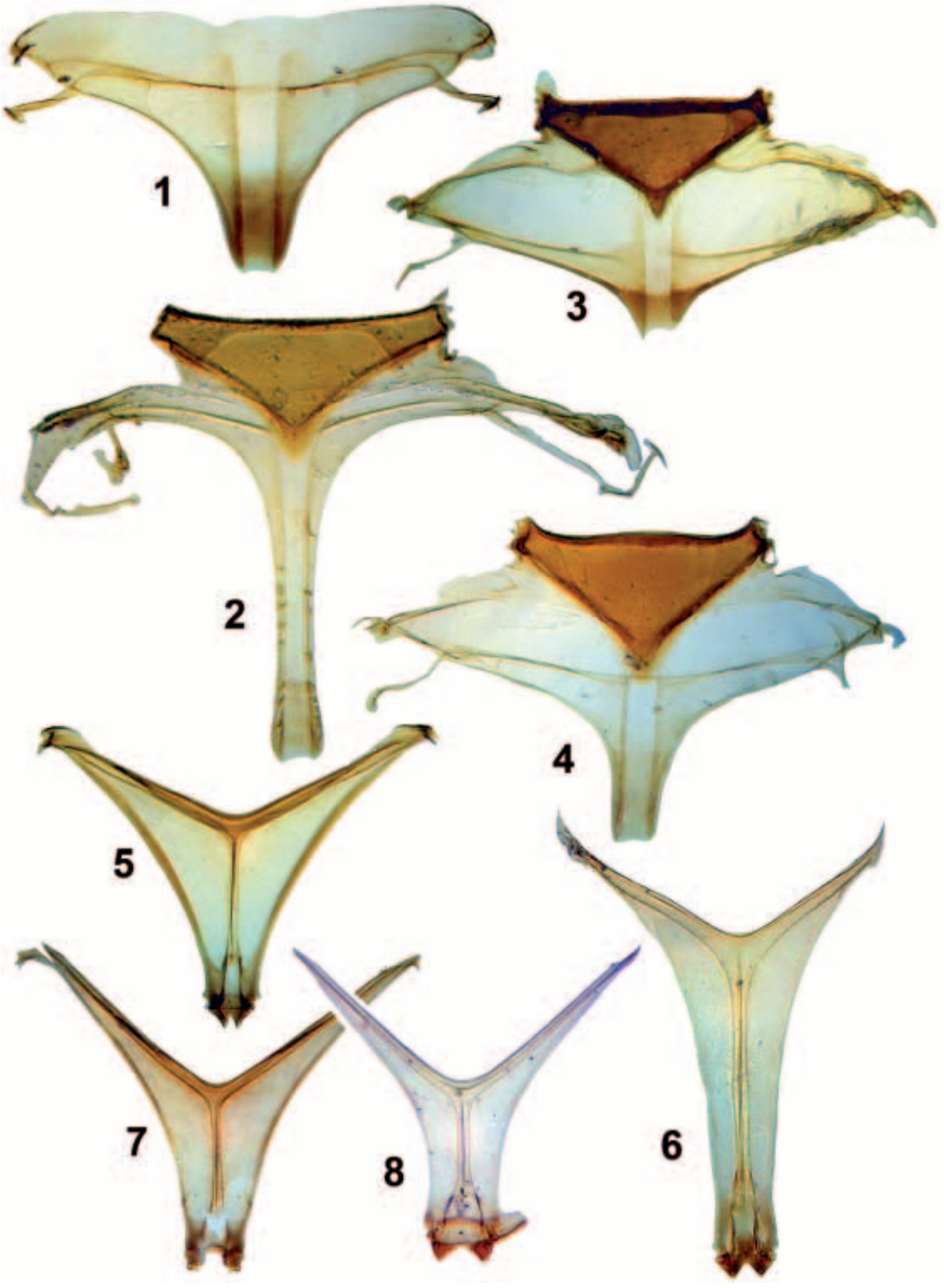
Catalaniana penicillata (Jeannel, 1924) comb. nov.
Bathysciola penicillata Jeannel, 1924a: 11.
Bathysciola (*Bathysciola*) *penicillata* Jeannel: Jeannel, 1924a: 109.

Catalaniana zariquieyi (Bolívar, 1919) comb. nov.
Catalaniana zariquieyi serratensis (Coiffait, 1959) comb. nov.
Bathysciola Zariquieyi subsp. *serratensis* Coiffait, 1959a: 159.
Bathysciola (*Bathysciola*) *zariquieyi serratensis* Coiffait: Perreau, 2000: 229.
Catalaniana zariquieyi zariquieyi (Bolívar, 1919) comb. nov.
Bathysciola (*Bathysciola*) *zariquieyi* Bolívar, 1919: 18.
Bathysciola Zariquieyi Bolívar: Lagar, 1954: 250.

Genus ***Diaprysius*** Abeille de Perrin, 1878
Diaprysius Abeille de Perrin, 1878: 149.

Type species. *Pholeuon caudatum* Abeille de Perrin, 1875 by subsequent designation (habitus in Fig. 166.2).

Diagnosis. Size ranging between 2.6–4.2 mm. Pholeuonoid facies (Fig. 166.2); shape oblong and elongated, narrowed at the two ends, although wide towards the middle and convex. Integument with a shiny appearance and covered with sparse pubescence, long and erect or lying down. Smooth pronotum, with fine and disorderly punctation; on the elytra there is a superficial microreticulum and large,



FIGURES 168.1–168.8: *Cytodromus* series, *Diaprysius* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Catalaniana zariquieyi* **comb. nov.**, (**2**) *Diaprysius sicardi,* (**3**) *Galliana linderi linderi* **comb. nov.**, (**4**) *Speophyes lucidulus*. Metendosternite of: (**5**) *C. zariquieyi* **comb. nov.**, (**6**) *D. sicardi,* (**7**) *G. l. linderi* **comb. nov.**, (**8**) *S. lucidulus*.

irregular points. Females, in general, more robust than the males, with more convex elytra and dehiscent elytral ápices.

Head: Not retracted under the pronotum, prominent and with the occipital carina blurry in the centre.

Antennae: Long, considerably longer than the elytral suture, with the antennomeres of the club thickened at the apex and the 11th very long, almost twice the length of the 10th.

Pronotum: Transverse and convex, about one and a half times as wide as long, always narrower than the elytra; with arched lateral margins in the anterior half and sub-rectilinear or sinuate in the basal area; maximum width in the middle or slightly displaced towards the apex, posterior angles right, with the vertex more or less sharp and facing outwards; base regularly curved from one end to the other, narrower than the basal area of the elytra.

Elytra: Long, the sides in regular curve, with the maximum width in the basal third and strongly acuminate towards the apex; not edged; parasutural stria may be complete, partial, or absent depending on the species.

Legs: Long, with the male protarsi more or less dilated; meso- and metatibiae straight and no tibiae with spines on the external face.

Mesoventral keel (Fig. 167.2): Not very high and short, barely occupying half of the mesoventrite, and triangular in shape, with an obtuse angle and vertex rounded or very slightly pointed; anterior border arched, beaded and the inferior one concave or straight, sometimes serrated, with a narrow edge. Mesoepimere and mesoepiventrite welded, there is no suture between them.

Suture of the metaventrite (Fig. 167.2): It goes from one end to the other of the mesocoxal cavity; the basal half adjacent to the edge of the cavity, with a very reduced and slightly sinuous area; the apical half forms an arc separated from the edge and outlines a larger area.

Metatergal apparatus (Fig. 168.2): With the metascutum long and very narrow, one wing of the metascutum being shorter than the alacrista; the apophysis of the alacrista very long with the apices not pointed.

Metendosternite (Fig. 168.6): Furca in «Y». Furcal arms short and trunk very long; the arms being twice as short as the trunk, they narrow to the apical area where the tip is very pointed and oriented inwards, without terminal apophysis; posterior lamina does not reach the apex of the arm, with an arched edge in the apical area and sub-rectilinear in the basal area. Trunk twice as long as the width at basal area; middle keel diverges slightly posteriorly.

Median lobe of the aedeagus: In lateral view (Fig. 169.2), arched towards the middle, with the ventral border subrectilinear in the apical half, and the dorsal border sinuous, somewhat depressed in the apical half; the tip pointed and arched towards the ventral face. In dorsal view (Fig. 169.6), long and ending in a narrowed or rounded tip; its edges slightly arched towards the apical quarter, forming a slight sinuosity.

Endophallus (Fig. 169.6): In the basal region there is a «Y»-piece with a reduced apical nodule; there are phanerae attached and an evident ventral complex. In the middle region there are ventral and dorsal phanerae, and a long axial piece with a bifid apex and located within a bag of scaly tissue. In the apical region there are two short reinforcing bands.

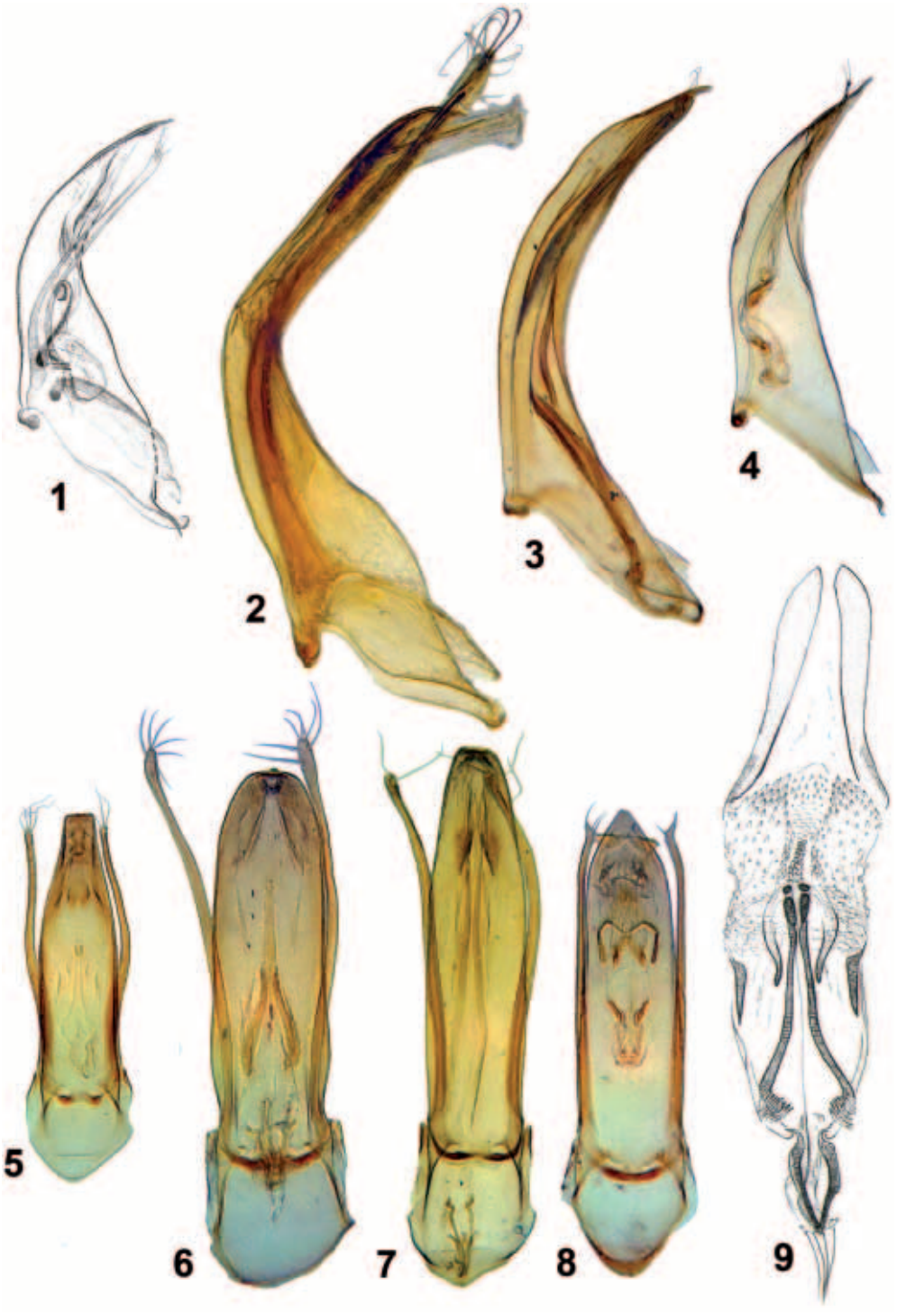
Parameres (Fig. 170.4): Thin and elongated; as long or longer than the median lobe, slightly widened in the apical area forming a slightly dilated club, already rounded or subtruncated at the tip; armed with between six and 12 setae of variable length and arrangement, generally forming two groups of longer and shorter setae separated by a space.

Spermathecal complex (Fig. 171.2): Spermatheca long and narrow, with the two lobes slightly thickened, more sclerotized than the middle region, which is long and hyaline; apical lobe small and spherical and basal one elongated, both about the same thickness, as is the middle region; there is a third ovoid lobe more developed than the other two and unlike the latter sclerotized which joins the spermatheca at the end of the spermatic duct in form of a short cylindrical area; spermatic duct short, less than twice the length of the spermatheca and joins the copulatory bag by a sclerotized basal process; there is a spermathecal gland.

VIII female uroventrite (Fig. 171.6): Elongated and narrow; posterior border with apical area in a slightly concave arc; spiculum short and very fine.

Discussion. It is the most derived genus within its clade (Fig. 1G) and the only one with pholeuonoid morphology. The sister genus is *Galliana* gen. nov., with support 94/100, The nodes between the species of the genus have high support except for the one that joins *Diaprysius mazaurizi* AC149 with the rest of its clade (*D. gezei* RA519 (*D. caudatus* RA522 + *D. caudatissimus* AC148)), 62.7/100.

Diaprysius and *Galliana* gen. nov. both with a very similar spermathecal complex, although it differs in the number of setae of the club of the parameres, this genus general exhibit three. *Diaprysius* concurs



FIGURES 169.1–169.9: *Cytodromus* series, *Diaprysius* group. Aedeagus in lateral view of: (**1**) *Catalaniana zariquieyi* **comb. nov.**, (**2**) *Diaprysius sicardi,* (**3**) *Galliana linderi linderi* **comb. nov.**, (**4**) *Speophyes lucidulus*. Aedeagus in dorsal view of: (**5**) *C. zariquieyi* **comb. nov.**, (**6**) *D. serullazi muelleri,* (**7**) *G. l. linderi* **comb. nov.**, (**8**) *S. lucidulus*. Endophallus of: (**9**) *C. zariquieyi* **comb. nov.**

with *Catalaniana* gen. nov., which is considered the most basal group, by having the apex of the parameres armed with five to 14 setae, in *Diaprysius* between six and 12, depending on the species. In the different species of this genus there is an apparent variability in the number, length and insertion pores of the setae, sometimes even among the specimens of the same species. Although, the character of presenting the setae separated by two groups is constant. Alonso & Lefèbvre (2015) provided a complete study of this taxón in their work.

Distribution. France. The distribution is discontinues, with the two southernmost species *Diaprysius sicardi* and *D. ducailari* isolated from other species by the deep valleys of Vidourle and Gard. The genus thus extends from the edge of the Larzac, around the Lergue and the Buèges to the Rhône valley north of the bassin of the Ardèche, through the departments of Hérault, Gard and from the Ardèche.

Species

Diaprysius caudatissimus (Abeille de Perrin, 1876)
Antrodietus Caudatissimus Abeille de Perrin, 1876: 29.
Antrocharis caudatissima Abeille: Abeille de Perrin, 1878: 153.
Diaprysius caudatissimus (Abeille de Perrin): Reitter, 1885 [1884]: 15.

Diaprysius caudatus (Abeille de Perrin, 1875)
Diaprysius caudatus bettingeri Jeannel, 1914
Diaprysius caudatus Bettingeri Jeannel, 1914d: 241.
Diaprysius caudatus bettingeri Jeannel: Perreau, 2000: 268.
Diaprysius caudatus caudatus (Abeille de Perrin, 1875)
Pholeuon caudatum Abeille de Perrin, 1875c: 214.
Antrodietus Caudatus Abeille de Perrin: Abeille de Perrin, 1876: 29.
Antrocharis (*Diaprysius*) *Caudata* (Abeille de Perrin): Abeille de Perrin, 1878: 153.
Diaprysius caudatus Abeille de Perri): Reitter, 1885 [1884]: 15.

Diaprysius ducailari Jeannel, 1947
Diaprysius Du Cailari Jeannel, 1947a: 86.
Diaprysius ducailari Jeannel: Perreau, 2000: 270.

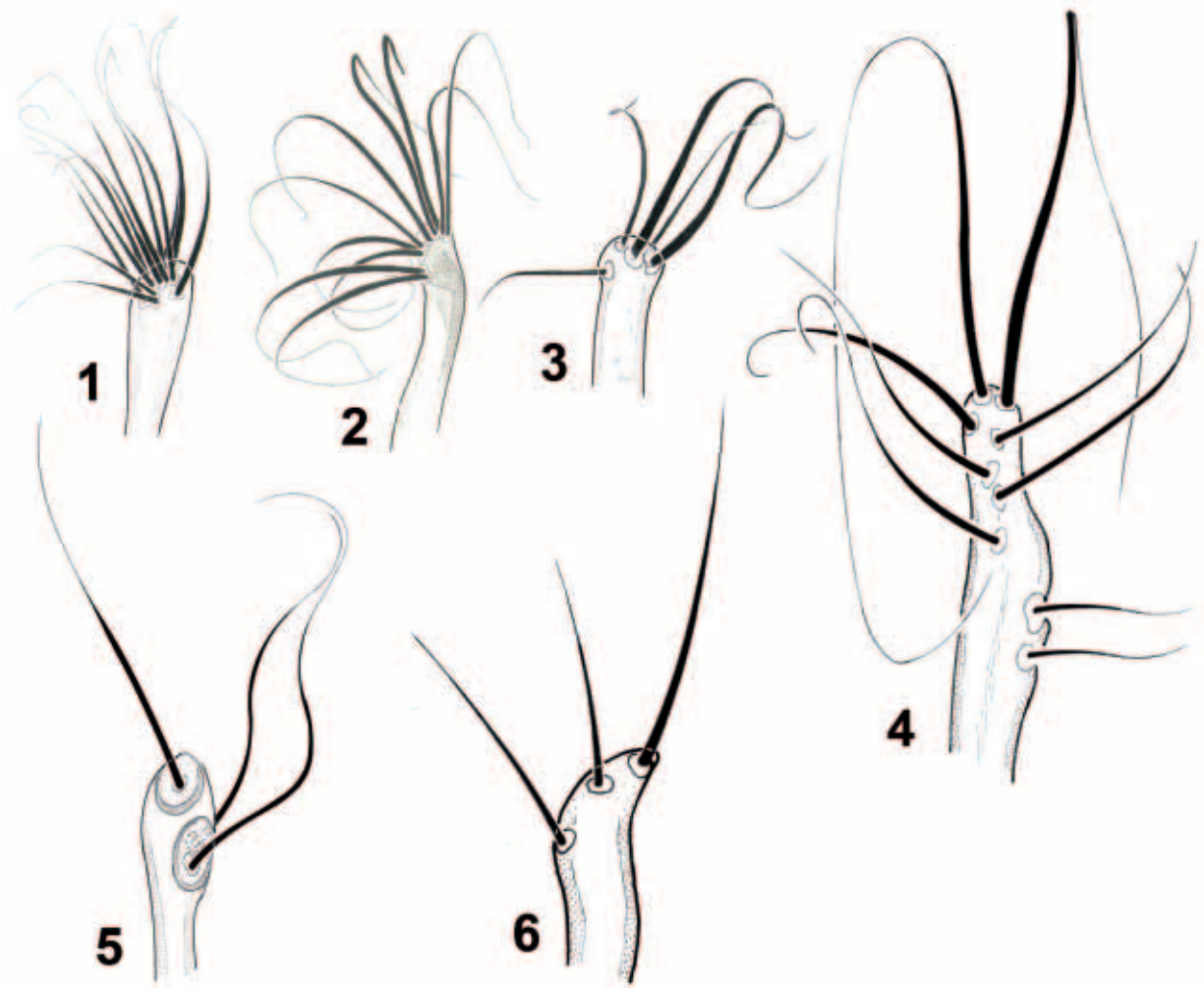
Diaprysius fagei Jeannel, 1914
Diaprysius Fagei Jeannel, 1914d: 241.
Diaprysius fagei Jeannel: Perreau, 2000: 268.

Diaprysius fagniezi Jeannel, 1910
Diaprysius Fagniezi Jeannel, 1910c: 12.
Diaprysius fagniezi Jeannel: Perreau, 2000: 269.

Diaprysius gezei Jeannel, 1936
Diaprysius Gezei Jeannel, 1936: 63.
Diaprysius gezei Jeannel: Perreau, 2000: 269.

Diaprysius mazaurici Mayet, 1903
Diaprysius mazaurici lussanensis Jeannel, 1947
Diaprysius Mazaurici subsp. *lussanensis* Jeannel, 1947a: 87.
Diaprysius mazaurici lussanensis Jeannel: Perreau, 2000: 269.
Diaprysius mazaurici mazaurici Mayet, 1903
Diaprysius Mazaurici Mayet, 1903: 139.
Diaprysius mazaurici mazaurici Mayet: Perreau, 2000: 269.

Diaprysius serullazi Peyerimhoff, 1904
Diaprysius serullazi alberti Jeannel, 1924
Diaprysius Serullazi subsp. *Alberti* Jeannel, 1924a: 193.
Diaprysius serullazi alberti Jeannel: Perreau, 2000: 269.
Diaprysius serullazi argodi Jeannel, 1914
Diaprysius Serullazi Argodi Jeannel, 1914d: 241.
Diaprysius serullazi argodi Jeannel: Perreau, 2000: 269.
Diaprysius serullazi jolyi Jeannel, 1936
Diaprysius Serullazi subsp. *Jolyi* Jeannel, 1936: 63.
Diaprysius serullazi jolyi Jeannel: Perreau, 2000:269.
Diaprysius serullazi magdelainei Jeannel, 1914
Diaprysius Serullazi Magdelainei Jeannel, 1914d: 242.
Diaprysius serullazi magdelainei Jeannel: Perreau, 2000:269.
Diaprysius serullazi muelleri Jeannel, 1910
Diaprysius Serullazi subsp. *Mulleri* Jeannel, 1910g: 85.
Diaprysius serullazi mulleri Jeannel: Perreau, 2000: 269.
Diaprysius serullazi peyerimhoffi Jeannel, 1910
Diaprysius Serullazi subsp. *Peyerimhoffi* Jeannel, 1910c: 12.
Diaprysius serullazi peyerimhoffi Jeannel: Perreau, 2000: 270.
Diaprysius serullazi piraudi Jeannel, 1910
Diaprysius Serullazi subsp. *Piraudi* Jeannel, 1910g: 85.
Diaprysius serullazi piraudi Jeannel: Perreau, 2000: 270.



FIGURES 170.1–170.6: *Cytodromus* series, *Diaprysius* group. Apex of the paramere of: (**1**) *Catalaniana madoni* **comb. nov.**, (**2**) *C. penicillata* **comb. nov.**, (**3**) *C. zariquieyi* **comb. nov.**, (**4**) *Diaprysius sicardi,* (**5**) *Galliana linderi linderi* **comb. nov.**, (**6**) *Speophyes lucidulus.*

Diaprysius serullazi serullazi Peyerimhoff, 1904
Diaprysius Serullazi Peyerimhoff, 1904a: 185.
Diaprysius Serullazi subsp. *Serullazi* Peyerimhoff: Jeannel, 1924a: 193.
Diaprysius serullazi serullazi Peyerimhoff: Perreau, 2000: 270.

Diaprysius sicardi Mayet, 1907
Diaprysius Sicardi Mayet, 1907: 194.
Diaprysius Sicardi subsp. *Andreae* Fagniez, 1922: 106.
Diaprysius Andreae Fagniez: Jeannel, 1924a: 193.
Diaprysius sicardi Mayet: Perreau, 2000: 270.

Genus ***Galliana*** nov.
https://zoobank.org/NomenclaturalActs/89BF3BBF-5C7A-4155-8384-34D6C253FBDC

Type species. *Adelops linderi* Abeille de Perrin, 1875 by present designation (habitus in Fig. 166.3).

Description. Size ranging between 2.0–2.2 mm. Bathyscioid facies (Fig. 166.3); ovoid shape body, short, wide and convex; integument with a shiny appearance and covered with white-yellowish and recumbently pubescence ; body marked by a microreticulum, more strongly printed on the pronotum; fine and

irregular punctation on the pronotum, rough and vaguely aligned across on the elytra. Depigmented. There is no apparent sexual dimorphism in general appearance or in antennae.

Head: With occipital carina complete but slightly marked; anophthalmous.

Antennae: Short, slightly longer than half of the elytral suture, barely reaching the base of the pronotum, with the club thickened, and the articles 8th to 10th transverse and cylindrical.

Pronotum: Transverse and convex, with the lateral margins regularly arched; greatest width at base, which is sinuous and about as wide as base of elytra; acute posterior angles and blunt vertices.

Elytra: Short, wide and convex; lateral margins regularly curved and finely beaded, with rounded apices; maximum width very close to the base and without parasutural stria.

Legs: Short. Male protarsi not dilated; protibiae without spines on outer surface; mesotibiae curved and metatibiae straight, both with spines on the external face that are very large in the intermediate ones.

Mesoventral keel (Fig. 167.3): Not very high and forms an obtuse angle with apex hooked with the blunt or pointed tip; anterior border somewhat sinuous and inferior convex with a narrow ridge.

Suture of the metaventrite (Fig. 167.3): There is a single one in a regular arc that goes from one end to the other of the mesocoxal cavity; the middle part is the most separated and delimits a hemyelliptic area.

Metatergal apparatus (Fig. 168.3): With the metascutum wide and long; a wing of the metascutum slightly longer than the alacrista and triangular appearance; the apophysis of the alacrista prolonged, rather short, and the apexes sharp.

Metendosternite (Fig. 168.7): Furcal arms longer than the trunk, they narrow very sharply in the apical area that is very slightly arched in the form of a small hook; there is no terminal apophysis; posterior lamina narrows in the arms although it is preserved up to the apex; the entire edge arched. Trunk as long as the width of the basal part; middle keel diverges posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 169.3), narrow, elongated, with an almost regular arc with a slight depression toward the apical quarter; the apical area slightly curved towards the ventral face. In dorsal view (Fig. 169.7), the maximum width in the middle part, the apical area slightly narrowed and the apex rounded.

Endophallus (Fig. 169.7): Basal region with a small «Y»-piece with phanerae attached; in the apical nodules of the «Y»-piece arise two phanerae thin and slightly sclerotized extending up to the apical region. Middle region much longer than the other two. In the apical region there are two tiny reinforcing bands that rest on membranous ligules that are covered with long setae; between the reinforcement bands there is a «Y»-shaped axial piece whose upper arms are very short.

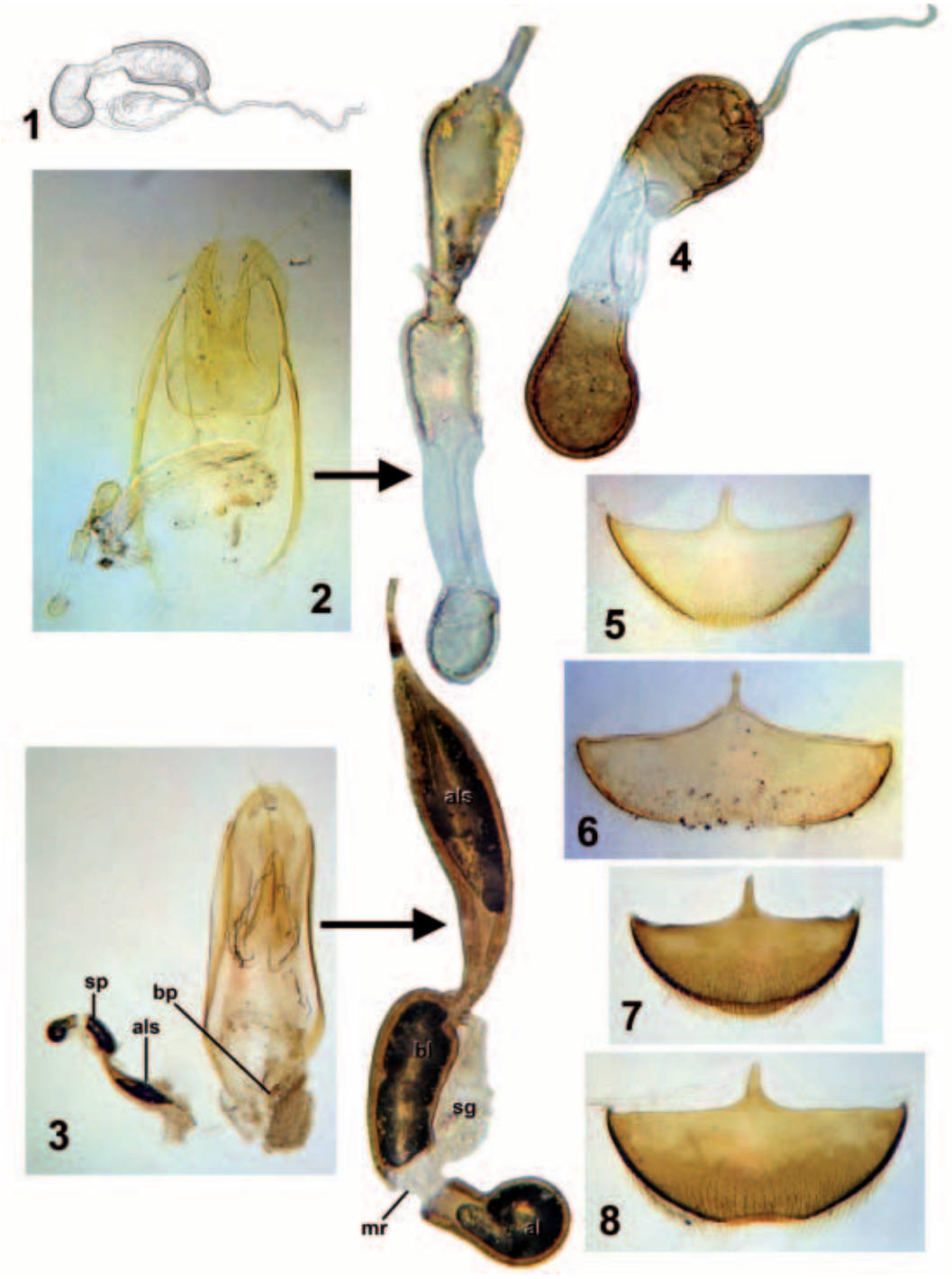
Parameres (Fig. 170.5): Thin and somewhat shorter than the median lobe; with three long sinuous setae inserted in large circular pits on a small apical club.

Spermathecal complex (Fig. 171.3): Spermatheca long and curved, with two well sclerotized lobes, the apical one being spherical and somewhat wider than the basal one, which is elongated; short and hyaline junction duct; short spermatic duct, about twice the length of the spermatheca, in the anterior area with a third lobe well sclerotized with an elongated oval shape and in the posterior area it joins the copulatory bag through a sclerotized basal process; there is a spermathecal gland that empties between the spermatheca and the beginning of the spermatic duct.

Female uroventrite VIII (Fig. 171.7): With the apical area of the posterior margin in a wide arc; the spiculum short, slightly widened at the base and the apex sharp.

ETYMOLOGY. Derived from Gallia, the Roman name given to a region of Western Europe currently occupied by various states. The toponym has been preserved through time only in the extension of lands that today belongs to France. Feminine.

DISCUSSION. *Galliana* gen. nov. is sister of the genus *Diaprysius* with a support of 94/100. It was, based on its external morphology as well as the taxonomic description, initial misclassified and included in the genus *Bathysciola*. Both the study of its genital structures and molecular analysis lead to its segregation from it. Its emergence is attributed to the third cladogenesis of the *Diaprysius* group and is the sister of this genus. Apparently, there is no apparent morphological element that allows us to relate *Galliana* gen. nov. to *Diaprysius*: the first bathyscioid, the other pholeuonoid, and the male genital structures very different. However, it is very characteristic of the *Galliana* gen. nov. + *Diaprysius* clade, that in the spermatic duct of a thick lobe or nodule (Fig. 171.3: als), near the point of insertion with the spermatheca, is present. This peculiarity is also found in *Euryspeonomus* (Fig. 278.4: als), a genus phylogenetically very distant; the function of this lobe is unknown, which is



FIGURES 171.1–171.8: *Cytodromus* series, *Diaprysius* group. Spermathecal complex of: (**1**) *Catalaniana penicillata* **comb. nov.**, (**2**) *Diaprysius serullazi muelleri,* (**3**) *Galliana linderi linderi* **comb. nov.**, (**4**) *Speophyes lucidulus*. Female uroventrite VIII of: (**5**) *C. madoni* **comb. nov.**, (**6**) *D. s. muelleri,* (**7**) *G. l. linderi* **comb. nov.**, (**8**) *S. lucidulus*. Abbreviations: **al**, apical lobe of the spermatheca; **als**, apical lobe of the spermiduct; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **sp**, spermatheca; **sg**, spermathecal gland.

taken here as evidence for a case of evolutionary convergence.

DISTRIBUTION. France. Subterranean environment of the mountainous reliefs of southeastern France, in Ardèche, Gard, Hérault and Isère.

Species

Galliana linderi (Abeille de Perrin, 1875) comb. nov.
Galliana linderi linderi (Abeille de Perrin, 1875) comb. nov.
Adelops Linderi Abeille de Perrin, 1875c: 215.
Adelops Mayeti Abeille de Perrin, 1875c: 215.
Bathyscia (*Bathyscia*) *Linderi* Abeille de Perrin: Reitter, 1885 [1884]: 34.
Bathysciola linderi Abeille: Jeannel, 1910a: 28.
Bathyscia payolivei Abeille de Perrin, 1905: 209 (*Nomen nudum*).
Bathysciola (*Bathysciola*) *linderi linderi* (Abeille de Perrin): Perreau, 2000: 231.
Galliana linderi mialetensis (Abeille de Perrin, 1881) comb. nov.
Bathyscia mialetensis Abeille de Perrin, 1881: ix.
Bathysciola Linderi subsp. *mialetensis* Abeille: Jeannel, 1910a: 28.
Bathysciola (s. str.) *Linderi* subsp. *mialetensis* Abeille: Jeannel, 1924a: 115.
Bathysciola (*Bathysciola*) *linderi mialetensis* (Abeille de Perrin): Perreau, 2000: 232.
Galliana linderi nemausica (Chobaut, 1903) comb. nov.
Bathyscia nemausica Chobaut, 1903b: 264.
Bathyscia Linderi subsp. *nemausica* Chobaut: Jeannel, 1910a: 28.
Bathysciola Linderi subsp. *nemausica* Chobaut: Jeannel, 1910a: 28.
Bathysciola (*Bathysciola*) *Linderi* subsp. *nemausica* Chobaut: Jeannel, 1914b: 9.
Bathysciola (*Bathysciola*) *linderi nemausica* (Chobaut): Perreau, 2000: 232.

Genus ***Speophyes*** Jeannel, 1910
Speophyes Jeannel, 1910a: 15.

TYPE SPECIES. *Adelops lucidulus* Delarouzée, 1860 by original designation (habitus in Fig. 166.4).

DIAGNOSIS. Size ranging between 1.7-2.5 mm. Bathyscioid facies (Fig. 166.4); shape ovoid, short and convex. Reddish brown colouration, very bright; pubescence very fine and lying. Sculpture formed of very shallow points scattered on the pronotum, the points are quite deep, close and irregular on the elytra. There is no apparent sexual dimorphism in general appearance.

Head: Retractable, with complete occipital carina.

Antennae: Somewhat shorter than the elytral suture, they slightly exceed the posterior edge of the pronotum in males and barely reaching it in females; First and second antennomeres of similar length and thickness; club thick and antennomeres transverse from 8th to 10th, but not flattened, the 11th being somewhat longer than the 10th.

Pronotum: Widest at base which is as wide as the base of the elytra, with sides regularly arched; posterior angles acute with vertices rounded and non-protruding; base, in profile view, sinuous.

Elytra: One and a quarter times as long as broad, widest near base and from here progressively narrowing to rounded apices; parasutural stria very blurred in the anterior third and visible in the posterior two thirds. Pygidium covered by the elytra.

Legs: Short and robust. Protarsi slender, short, tetramerous in both sexes; pentamerous meso- and metatarsi; mesotibiae arched and metatibiae straight; all tibiae with spines on external side.

Mesoventral keel (Fig. 167.4): Quite high and triangular, with anterior border rounded and ridged; ventral border slightly sinuous, with a narrow ridge in the anterior part and widened in the posterior, as well as a slight groove; vertex hooked and right angle.

Suture of the metaventrite (Fig. 167.4): The unique suture runs from end to end of the mesocoxal cavity delimiting a very narrow and elongated area.

Metatergal apparatus (Fig. 168.4): With the metascutum long and wide, being a wing of the metascutum somewhat longer than the alacrista; the apophysis of the alacrista prolonged and the apices not very pointed.

Metendosternite (Fig. 168.8): Furcal arms straight and longer than the trunk, narrow abruptly to the apical area in a very sharp tip; there is no terminal apophysis; posterior lamina narrow and conserved up to the apex, the posterior border being straight in the arm and arched in the region of the trunk. Trunk somewhat longer than the width of the basal part; middle keel diverges widely posteriorly.

Median lobe of the aedeagus: In lateral view (Fig. 169.4), slightly arched with the apical area flattened and sharp. In dorsal view (Fig. 169.8), with parallel sides and slightly arched, the apical area triangular with a slightly pointed apex.

Endophallus (Fig. 169.8): In the basal region, the

«Y»-piece is slim and well-developed, with thick apical nodules and phanerae attached. In the middle region a narrow transverse «M»-shaped phanera and two long bags of striated tissue that extend to the apex of the sac, at the lower end each one forms a sclerotized nodule below the «M». In the apical region two thin and short reinforcing bands.

Parameres (Fig. 170.6): As long as or somewhat shorter than the median lobe, with three setae of unequal length, the longest being the external apical; all of them are inserted serially in a club that is not very differentiated and somewhat bent, with insertion pores quite large.

Spermathecal complex: Spermatheca (Fig. 171.4) short and not curved, with well sclerotized lobes; the apical being spherical and as wide as the basal; junction duct hyaline and as long as length of the apical lobe; spermatic duct very thin and of almost uniform thickness, without nodule; no spermathecal gland is seen.

Female uroventrite VIII (Fig. 171.8): Apical middle area of posterior border in a slightly concave arc; spiculum short and curved, somewhat widened at base with sharp apex.

Discussion. The most striking morphological feature of this genus is that the male protarsi are tetramerous. The tetramery of the male protarsi seems to be a derived state that appears in different unrelated clades, so somehow this character loses the phylogenetic value that has traditionally been attributed to it. *Speophyes* is found in the base of the clade *Diaprysius* + *Galliana* **gen. nov.** with a support of 99.8/100; it is found within a clade whose most basal and terminal representatives present pentamerous protarsi. They are described by Jeannel (1924a) as tetramerous – It indicates what position they occupy in the phylogenetics trees (Figs 15.1–15.2) –:

– Tribu Bathysciae «Théléomorphes»

Division II:

– Not ascribed to any series: *Bathyscia* (series *Bathyscia*), *Phaneropella* (series *Catopsinus*), *Speophyes* (series *Cytodromus*).

– *Hexaurus* phyletic series: *Netolitzkya* (series *Bathyscia*), *Hexaurus* (series *Bathyscia*).

– *Aphaobius* phyletic series: *Aphaobius* (series *Oryotus*), *Oryotus* (series *Oryotus*), *Orostygia* (series *Oryotus*).

– *Aphaotus* phyletic series: *Aphaotus* (series *Neobathyscia*).

– *Leonhardella* phyletic series: *Proleonhardella* (series *Anthroherpon*), *Anisoscapha* (series *Anthroherpon*), *Leonhardella* (series *Anthroherpon*), *Anillocharis* (series *Anthroherpon*), *Pholeuonopsis* (series *Anthroherpon*), *Blattochaeta* (series *Anthroherpon*), *Blattodromus* (series *Anthroherpon*).

Division III:

– Not ascribed to any series: *Bathyscidius* (series *Bathyscia*).

– *Ravasinia* phyletic series: *Ravasinia* (series *Bathyscia*), *Sphaerobathyscia* (series *Leptodirus*).

– *Neobathyscia* phyletic series: *Bathysciotes* (series *Leptodirus*), *Neobathyscia* (series *Neobathyscia*).

– *Speonesiotes* phyletic series with the subgenera: *Albanella* (series *Anthroherpon*), *Crivosiella* (series *Anthroherpon*), *Speonesiotes* s. str. (series *Anthroherpon*).

– Tribu Antroherpona

– *Spelaeobates* phyletic series: *Spelaeobates* (series *Leptodirus*).

All of them, are isolated derived cases distributed along the clades with male pentamerous protarsi. The geographic distribution is consistent with the inclusion of *Speophyes* in the *Diaprysius* clade. Alonso & Lefèbvre (2013) provided a complete study of this taxon.

Distribution. France. Occupies underground sinkholes whose distribution extends from the foothills of Sumène (Gard) to the mountains of Séranne (Hérault), on both sides of the Hérault valley.

Species

Speophyes lucidulus (Delarouzée, 1860)
Adelops lucidulus Delarouzée, 1860: xxvii.
Bathyscia (*Bathyscia*) *lucidula* Delarouzée: Reitter, 1885 [1884]: 26.
Bathyscia lucidula Delarouzée: Mayet & Sicard, 1907: 193.
Speophyes lucidulus Delarouzée: Jeannel, 1910a: 37.

3.3.1.3 ***Parabathyscia*** group

Being the only genus in the group, the characteristics that define it respond to those of the genus itself.

Genus ***Parabathyscia*** Jeannel, 1908
Parabathyscia Jeannel, 1908a: 308.
Bathysciola (*Platybathyscia*) Capra, 1920: 11 (Type species: *Bathyscia grouvellei* Abeille de Perrin, 1882).

Type species. *Bathyscia spagnoli* Fairmaire, 1882 by subsequent designation (habitus in Fig. 172.2).

DIAGNOSIS. Bathyscioid facies; pubescence abundant, lying down; punctation small, irregular throughout the body; depigmented.

Head: Anophthalmous.

Pronotum: Transverse with sides regularly arched, with the maximum width towards the base.

Legs: First article of metatarsi as long as the two following ones.

Mesoventral keel: Not prolonged over the metaventrite.

Median lobe of aedeagus: Sharp, sharply pointed.

Parameres: Thick, armed with three setae, two thick and falciform, and a membranous lobe; in the subgenus *Ligurobathyscia* thin and of the three setae only two are somewhat thicker and the membranous lobe is very reduced.

Endophallus: «Y»-piece with developed arms and two phanerae highly sclerotized in the shape of an inverted «M».

DISCUSSION. The name *Parabathyscia* was established by Jeannel (1908) as a subgenus of *Bathyscia*. Later Jeannel (1911) raised it to the category of genus, a group of species that present unique characteristics in the aedeagus are part of this, these are the pointed shape of the median lobe, parameres thick with unique shape of the three setae in the apical part, two thick and falciform, and a generally well-developed membranous lobe, in addition to the sclerotized structures of the endophallus.

KEY TO SUBGENERA

1. Male protarsi with the third tarsomere asymmetrical. Median lobe of the aedeagus with subparallel sides up to the proximity of the apical area; this area being short and pointed (Fig. 178.1). Slender parameres with a reduced membranous lobe and three short apical setae, one fine and the other two somewhat thicker (Fig. 179.3) .....*Ligurobathyscia*
- Male protarsi with third tarsomere symmetrical. Median lobe of aedeagus with arched sides tapering gradually in the long terminal half and lanceolate in shape (Fig. 178.2). Parameres generally thick, with a well-developed membranous lobe and three apical setae, one long and fine, the other two robust, one lanceolate and the other falciform or both falciform (Fig. 179.4) .....*Parabathyscia*

Subgenus ***Ligurobathyscia*** Zoia, 1986
Ligurobathyscia Zoia, 1986: 333.

TYPE SPECIES. *Parabathyscia brigantii* Zoia, 1980 by original designation (habitus in Fig. 172.1).

DIAGNOSIS. Size ranging between 2.8-4.2 mm. Bathyscioid facies (172.1). Very short and lying pubescence; pronotum smooth, with fine microreticulation; parasutural stria on the elytra very blurred, almost non-existent. In general, the female is larger in size than the male.

Antennae: Short, with 8th to 10th segments transverse.

Legs: Males protarsi dilated but narrower than the apical area of the tibiae; third tarsomere asymmetric.

Mesoventral keel (Fig. 173.1): Keel high with the anterior edge straight in the upper half and arcuate in the lower half; vertex hooked with blunt tip and right angle; ventral edge convex, with the ariste broad and the apophysis not extending over the metaventrite.

Suture of the metaventrite (Fig. 173.1): Arched with a slight depression towards the basal half, the area that delimits in the upper narrow half.

Metatergal apparatus (Fig. 174.1): Wings of the metascutum broad, one of them as long as the apophysis of the alacrista.

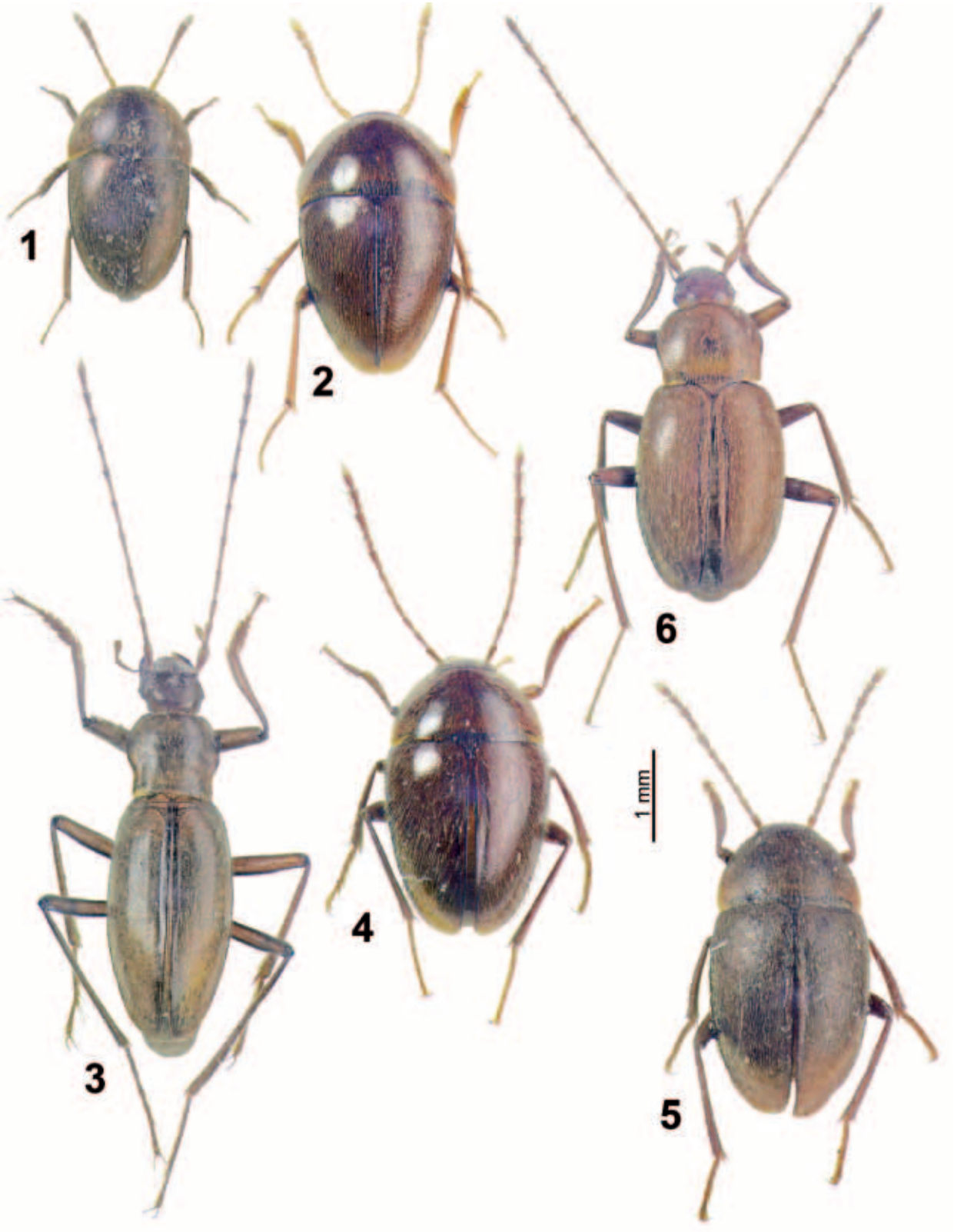
Metendosternite: Unknown.

Median lobe of aedeagus: In lateral view (Fig. 177.1), it is subrectilinear, with a slight depression near the terminal sector that describes a short arc oriented towards the ventral side. In dorsal view (Fig. 178.1), the lateral margins are almost parallel and sharply narrow near the apex, thus the apical area is short and the apex very pointed.

Endophallus (Fig. 178.1): Basal region with the «Y»-piece well-developed and short fibres are attached to its apices. Middle region with two well sclerotized phanerae each consisting of a series of four teeth. Apical region with two very short reinforcing bands (bra) and two phanerae small, with the shape of an inverted «M».

Parameres (Fig. 179.3): Thin and slightly arched with the apical area barely dilated; three short setae are inserted in this area, two somewhat more robust and the middle apical one thiner. At the apex there is a reduced membranous lobe semicircular on the inner side.

Spermathecal complex: Spermatheca (Fig. 180.1) with the two lobes large and well sclerotized; the basal elongated and sacciform and the apical spherical, both of similar thickness; the middle region short and hyaline and the spermatic duct thin, two or three times



FIGURES 172.1–172.6: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Habitus of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii,* (**2**) *P. (Parabathyscia*) *spagnoloi spagnoloi*, (**3**) *Isereus xambeui,* (**4**) *Ochsiella bucheti* **comb. nov.**, (**5**) *Speodiaetus galloprovincialis*, (**6**) *Troglodromus bucheti bucheti*.

longer than the spermatheca; spermathecal gland is observed.

Female uroventrite VIII (Fig. 181.1): Short, twice as wide as long, with the middle of the apical margin slightly sinuous; spiculum very short, triangular.

Discussion. No molecular data are available. It differs from the nominotypical subgenus by various characteristic features of the male genitalia. In *Ligurobathyscia* the median lobe of the aedeagus (Fig. 178.1) has subparallel sides throughout its length and a short and pointed apical area, sharply tapering; parameres (Fig. 179.3) thin with a very reduced membranous lobe at the apex, and the three setae short, two of them dilated and the third fine. In *Parabathyscia* s. str. the median lobe (Fig. 178.2) with arched sides that gradually taper off in the terminal half, this area being long and pointed; moreover, the parameres (Fig. 179.4) are thicker, the membranous lobe of the apex more developed and the setae highly modified, especially the two internal ones that are very thickened, one much longer and falciform, the other shorter, lanceolate or falciform in shape; the third, distal, is thin and arranged in the axial prolongation of the paramere.

Distribution. Italy. Liguria, Sprugola di Capo Corvo and Grotta del Salotto in the vicinity of Paese di Montemarcello – Ameglia, La Spezia –.

Species

Parabathyscia* (*Ligurobathyscia*) *brigantii Zoia, 1980
Parabathyscia brigantii Zoia, 1980a: 54.
Parabathyscia (*Ligurobathyscia*) *brigantii* Zoia: Zoia, 1996: 349.

Subgenus ***Parabathyscia***

Diagnosis. Size ranging between 1.3–3.3 mm. Body generally rounded, wide, pointed backwards and clearly convex (Fig. 172.2). Integument shiny reddish, covered with thin pubescence, short, lying and whitish-yellowish; pronotum smooth, with very scarce punctation; in the elytra the punctation more printed. Female similar to the male, the antennal articles of the club being somewhat more robust and protarsi slender.

Head: Retractable, with the occipital carina complete, although blurred; epistomal suture slightly curved and somewhat darkened.

Antennae: Short, slightly longer than half the suture, with the antennomeres of the club thickened and flattened or not, the 8th transverse or somewhat longer than wide.

Pronotum: Very transverse, almost twice as wide as long with regularly arched sides; maximum width before the base; base somewhat sinuous and as wide as basal area of the elytra; posterior angles right with the vertex sharp and directed backwards.

Elytra: Cuneiform, with lateral margins narrow and rounded apical areas; with or without parasutural striae in this case not parallel to the suture and may be complete or obliterated in the basal region.

Legs: Short but slender. Males protarsi dilated, width depending on species, third tarsomere symmetrical; all tibiae hairy with two pectinate internal spurs, two simple external ones and a series of unequal spines between them; protibiae not attenuated without spines on outer surface; mesotibiae curved and thickened, and metatibiae straight, both with spines on the external face that are very thick in the mesotibiae.

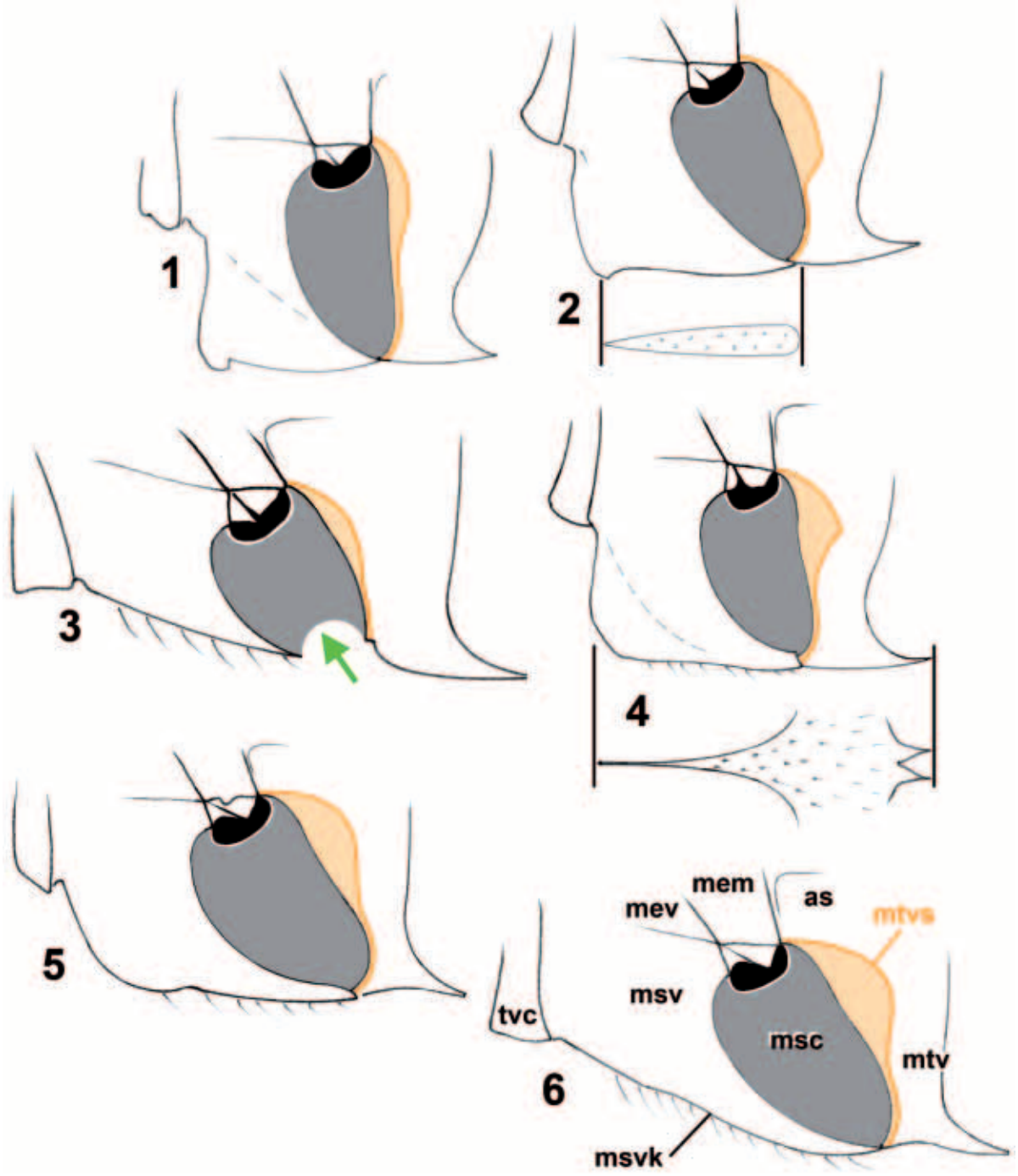
Mesoventral keel (Fig. 173.2): It can be low or high; if it is low, it is not angular and the angle is very obtuse; if it is high, the angle is almost right, with a slightly sharp hooked vertex and a sub-rectilinear and bordered anterior edge; the ventral edge somewhat convex, with the arista broad and flat; in both cases it does not extend over the metaventrite.

Suture of the metaventrite (Fig. 173.2): With a single suture that forms an irregular arc from one end to the other of the mesocoxal cavity; delimits a narrow and elongated area, almost non-existent in the basal part.

Metatergal apparatus (Fig. 174.2): With the metascutum long and narrow, being a wing of the metascutum somewhat longer than the alacrista; the apophysis of the alacrista prolonged, these with sharp apices.

Metendosternite (Fig. 176.1): Furcal arms gracile and narrow, straight and pointed in the apical area, somewhat longer than the trunk and without defined terminal apophysis; posterior lamina progressively narrows near the apex, with a straight edge on the arms and then arched. Trunk one and a half times longer than the width of the basal part; the middle keel on the trunk with the posterior divergence slightly open, long and narrow.

Median lobe of aedeagus: Long and quite robust. In lateral view (Fig. 177.2), subrectilinear, slightly curved with a depression or dorsal notch in the terminal sector; the apical area long and curved towards the ventral side. In dorsal view (Fig. 178.2), sides arched and sinuous in the basal part then gradually tapering along the terminal half; with a sharp apex,



FIGURES 173.1–173.6: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Pterothorax in lateral view of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii,* (**2**) *P.* (*Parabathyscia*) *spagnoloi devillei* (and ventral view), (**3**) *Isereus xambeui,* (**4**) *Ochsiella bucheti* **comb. nov.** (and ventral view), (**5**) *Speodiaetus galloprovincialis*, (**6**) *Troglodromus bucheti caussicola*. Green arrow pointing to the mesocoxal cavities in contact. Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

it resembles an arrowhead. Basal lamina long.

Endophallus (Fig. 178.2): With well-developed and robust «Y»-piece, junction node and terminal lobes; there is no evident ventral complex; between the arms of the «Y»-piece a long flagellum is inserted that runs through the middle region. Fibres originate from the apices of the «Y»-piece extending along the middle region to its apical part, where two paired phanerae meet so that both of them form an inverted «V» arranged symmetrically on both sides of the axis; they may be modified or accompanied by large spines or teeth. In the apical region there are two very short reinforcing bands and between them two phanerae strongly sclerotized that form an inverted «V».

Parameres (Fig. 179.4): Shorter than the median lobe, with a differentiated club and the shape depends on the species. At the apex there is a more or less developed membranous lobe that is armed with three setae, two of them internally modified by thickening the structure, one much longer and falciform, the other shorter and lanceolate or falciform in shape; the third distal, thin and arranged in the axial extension of the paramere.

Spermathecal complex (Fig. 180.2): With two lobes very large and well sclerotized; the basal sacciform and the apical markedly spherical and much broader; the junction duct very short and hyaline; the spermatic duct thin, two or three times longer than the spermatheca and without basal process.

VIII female uroventrite (Fig. 181.2): A little wider than long, the posterior margin with a slight arched projection in the middle; the spiculum short, narrow and truncated.

Discussion It is the sister genus of the *Cytodromus* and *Isereus* groups of the *Cytodromus* series and was found to be related to them with a support of 82.5/99 (Fig. 1G). The support of nodes formed by the species is high except those concerning:

– *Parabathyscia oodes* AN908 with the two subspecies of *Parabathyscia spagnoloi* which is somewhat doubtful, with widely varying support of 34.8/100. The long genetic distance plus the support of 99.9/100 suggests that *P. spagnoloi devillei* AF1 and *P. spagnoloi spagnoloi* RA508 should be considered *bona species*; however, there are other subspecies of the complex that have not been studied, so no taxonomic change is proposed here.

– *Parabathyscia gracilicornis* AH187 with *Parabathyscia remyi* AH188 whose support is 66.5/100; between these two Corsican species a long genetic distance was found.

The endophallus with the middle region occupied by long and hyaline phanerae and the spermatheca with hypertrophied lobes are characters that correspond exactly to those that have been described for the genera of the *Cytodromus* series. The mesoventral keel with the arista of the lower edge broad and flat, the two inverted «V»-shaped phanerae at the apical region of the endophallus, and the modified setae at the apex of the parameres are peculiarities unique to *Parabathyscia* within the clade of the *Cytodromus* series. Zoia (1986) provided a complete taxonomic study of the Italian species.

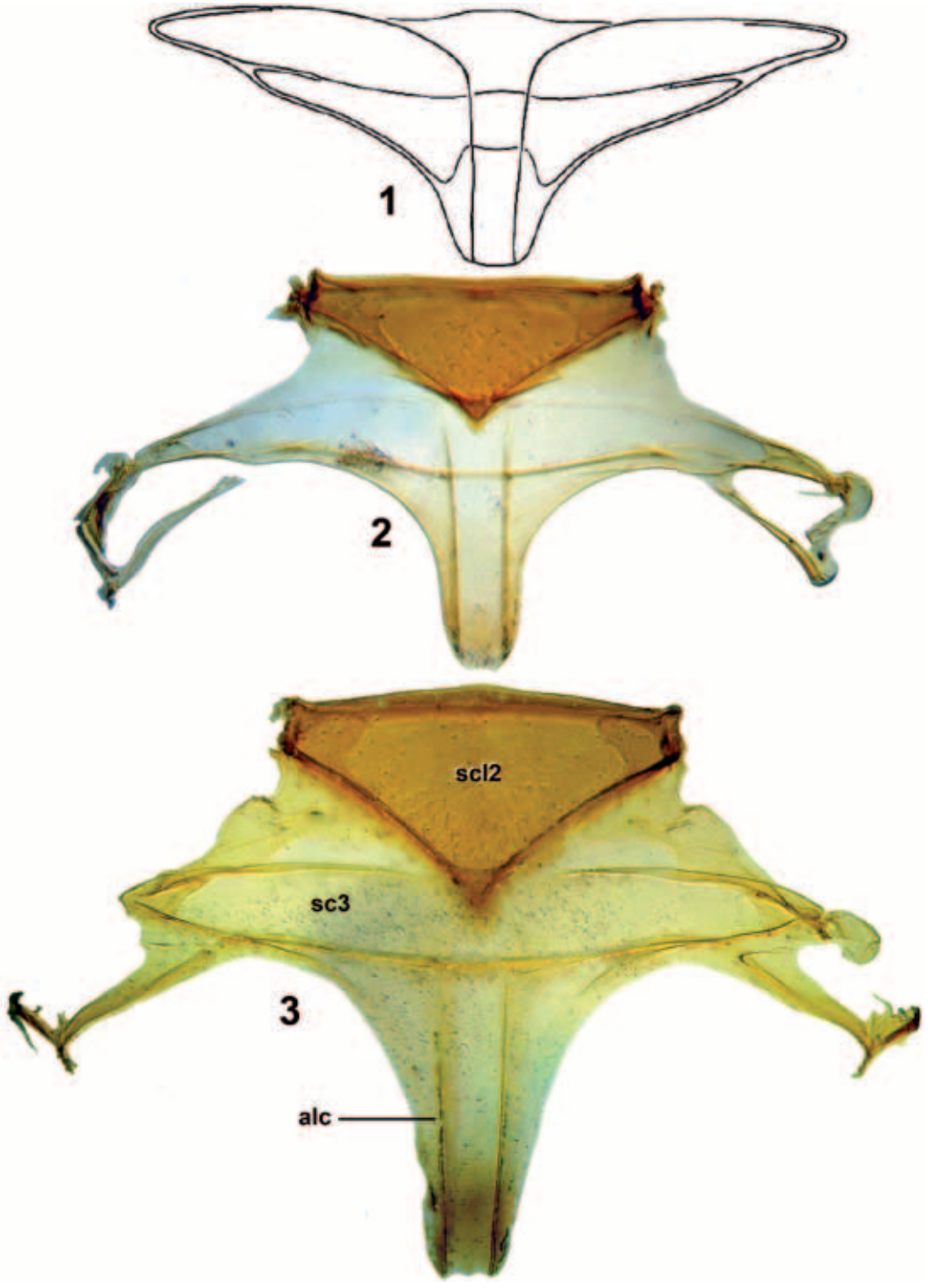
Distribution. With musciculous, endogean and subterranean species show a wide geoographical distrinbution range since they are distributed in the Ligurian and Alpes-Maritimes between the extreme southeast of France and the province of Savona with some isolated locations in Toscana and Emilia; in the western alpine sector and northern Apennine in Italy; in the centre and southern end of the Italian peninsula south of Toscana: Latio, Campania and Calabria; and in isolated stations in the south of the United Kingdom, north coast of France from Bretagne to Calais and Montagne Noire in Haut-Languedoc; Corsica.

Species

Parabathyscia* (*Parabathyscia*) *andreinii (Jeannel, 1914)
Bathysciola (*Parabathyscia*) *Andreinii* Jeannel, 1914c: 201.
Parabathyscia (*Parabathyscia*) *Andreinii* Jeannel: Jeannel, 1924a: 125.
Parabathyscia (*Parabathyscia*) *andreinii* Jeannel: Zoia, 1980b: 165.

Parabathyscia* (*Parabathyscia*) *apuana Jeannel, 1924
Parabathyscia* (*Parabathyscia*) *apuana apuana Jeannel, 1924
Parabathyscia (*Parabathyscia*) *apuana* Jeannel, 1924a: 55.
Parabathyscia* (*Parabathyscia*) *apuana lunensis Zoia, 1986
Parabathyscia apuana lunensis Zoia, 1986: 406.

Parabathyscia* (*Parabathyscia*) *avetonensis Jeannel, 1924
Parabathyscia (*Parabathyscia*) *apuana* subsp. *avetonensis* Jeannel, 1924a: 57.
Parabathyscia (*Parabathyscia*) *avetonensis* Jeannel, 1924: Zoia, 1986: 395.



FIGURES 174.1–174.3: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii* (modified from Zoia 1980), (**2**) *P. (Parabathyscia*) *dematteisi dematteisi*, (**3**) *Isereus colasi*. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Parabathyscia* (*Parabathyscia*) *calabra Pace, 1975
Parabathyscia (*Parabathyscia*) *calabra* Pace, 1975 [1974]: 109.

Parabathyscia* (*Parabathyscia*) *caprai Zoia, 1978
Parabathyscia (*Parabathyscia*) *caprai* Zoia, 1978: 97.

Parabathyscia* (*Parabathyscia*) *corsica (Abeille de Perrin, 1875)
Adelops corsicus Abeille de Perrin, 1875c: 216.
Bathyscia (*Bathyscia*) *corsica* (Abeille de Perrin): Reitter, 1885[1884]: 21.
Parabathyscia corsica (Abeille de Perrin): Jeannel, 1910a: 29.
Parabathyscia Wollastoni corsica (Abeille de Perrin): Jeannel, 1911a: 274.
Bathysciola (*Parabathyscia*) *Wollastoni corsica* (Abeille de Perrin): Jeannel, 1914b: 14.
Parabathyscia (*Parabathyscia*) *corsica* (Abeille de Perrin): Jeannel, 1924a: 125.

Parabathyscia* (*Parabathyscia*) *dematteisi Ronchetti & Pavan, 1953
Parabathyscia* (*Parabathyscia*) *dematteisi casalei Zoia, 1986
Parabathyscia (*Parabathyscia*) *dematteisi casalei* Zoia, 1986: 355.
Parabathyscia* (*Parabathyscia*) *dematteisi dematteisi Ronchetti & Pavan, 1953
Parabathyscia (*Parabathyscia*) *dematteisi* Ronchetti & Pavan, 1953: 51.
Parabathyscia (*Parabathyscia*) *dematteisi dematteisi* Ronchetti & Pavan: Zioa, 1986: 352.

Parabathyscia* (*Parabathyscia*) *doderoi (Fairmaire, 1882)
Bathyscia doderoi Fairmaire, 1882: 445.
Parabathyscia doderoi (Fairmaire): Jeannel, 1910a: 30.
Bathysciola (*Parabathyscia*) *doderoi* (Fairmaire): Jeannel, 1914b: 13.
Parabathyscia (*Parabathyscia*) *doderoi* (Fairmaire): Jeannel, 1924a: 126.

Parabathyscia* (*Parabathyscia*) *doriae (Fairmaire, 1872)
Adelops Doriae Fairmaire, 1872: 55.
Bathyscia (*Bathyscia*) *Doriae* (Fairmaire): Reitter, 1885[1884]: 25.
Parabathyscia Doriai (Fairmaire): Jeannel, 1910a: 29.
Bathysciola (*Parabathyscia*) *Doriai* (Fairmaire): Jeannel, 1914b: 13.
Parabathyscia (*Parabathyscia*) *Doriai* (Fairmaire): Jeannel, 1924a: 126.
Parabathyscia (*Parabathyscia*) *doriai* (Fairmaire): Zoia, 1986: 400.

Parabathyscia* (*Parabathyscia*) *emeryi Jeannel, 1934
Parabathyscia Emeryi Jeannel, 1934a: 97.
Parabathyscia (*Parabathyscia*) *emeryi* Jeannel: Zoia, 1986: 414.

Parabathyscia* (*Parabathyscia*) *finitima Zoia, 1986
Parabathyscia (*Parabathyscia*) *finitima* Zoia, 1986: 382.

Parabathyscia* (*Parabathyscia*) *fiorii (Capra, 1920)
Bathysciola (*Platybathyscia*) *Fiorii* Capra, 1920: 12.
Parabathyscia (*Platybathyscia*) *Fiorii* Capra: Jeannel, 1924a: 128.
Parabathyscia (*Platybathyscia*) *florentina* Jeannel, 1924c: 57.
Parabathyscia (*Parabathyscia*) *fiorii* (Capra, 1920): Zoia, 1986: 379.

Parabathyscia* (*Parabathyscia*) *genuensis Zoia, 1986
Parabathyscia (*Parabathyscia*) *genuensis* Zoia, 1986: 385.

Parabathyscia* (*Parabathyscia*) *gracilicornis Jeannel, 1947
Parabathyscia (*Parabathyscia*) *corsica gracilicornis* Jeannel, 1947c: 67.
Parabathyscia longicornis Jeannel, 1949: 16.
Parabathyscia lamilzai Raffaldi, 2007: 130.
Parabathyscia raffaldii Lemaire, 2008: 84.
Parabathyscia (*Parabathyscia*) *gracilicornis* Jeannel: Zoia, 1986: 391.

Parabathyscia* (*Parabathyscia*) *grouvellei (Abeille de Perrin, 1882)
Bathyscia Grouvellei Abeille de Perrin, 1882: 17.
Bathyscia (*Bathyscia*) *Grouvellei* Abeille de Perrin: Reitter, 1885[1884]: 24.
Parabathyscia Grouvellei Abeille de Perrin: Jeannel, 1910a: 29.
Bathysciola (*Parabathyscia*) *Grouvellei* Abeille de Perrin: Jeannel, 1914b: 13.
Parabathyscia (*Parabathyscia*) *grouvellei* (Abeille): Zoia, 1986: 370.

Parabathyscia* (*Parabathyscia*) *latialis Jeannel, 1911
Parabathyscia* (*Parabathyscia*) *latialis latialis Jeannel, 1911



FIGURES 175.1–175.3: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Ochsiella bucheti* **comb. nov.**, (**2**) *Speodiaetus galloprovincialis*, (**3**) *Troglodromus bucheti ochsi*.

Parabathyscia latialis Jeannel, 1911a: 279.
Bathysciola (Parabathyscia) *latialis* Jeannel: Jeannel, 1914b: 13.
Parabathyscia (*Parabathyscia*) *latialis* Jeannel: Jeannel, 1924a: 127.
Parabathyscia (*Parabathyscia*) *latialis latialis* Jeannel: Zoia, 1986: 414.
Parabathyscia* (*Parabathyscia*) *latialis straneoi Jeannel, 1934
Parabathyscia latialis subsp. *Straneoi* Jeannel, 1934a: 96.
Parabathyscia (*Parabathyscia*) *latialis straneoi* Jeannel: Zoia, 1986: 414.

Parabathyscia* (*Parabathyscia*) *ligurica (Reitter, 1889)
Bathyscia ligurica Reitter, 1889c: 293.
Bathyscia subsp. *Spagnoloi ligurica* (Reitter): Jeannel, 1907c: 64.
Parabathyscia ligurica Reitter: Jeannel, 1910a: 30.
Bathysciola (Parabathyscia) *ligurica* Reitter: Jeannel, 1914b: 13.
Parabathyscia (Parabathyscia) *ligurica* Reitter: Jeannel, 1924a: 126.

Parabathyscia* (*Parabathyscia*) *luigionii Jeannel, 1911
Parabathyscia Luigionii Jeannel, 1911a: 278.
Bathysciola (Parabathyscia) *Luigionii* Jeannel: Jeannel, 1914b: 14.
Parabathyscia (Parabathyscia) *luigionii* Jeannel: Zoia, 1986: 414.

Parabathyscia* (*Parabathyscia*) *mancinii Jeannel, 1924
Parabathyscia (*Parabathyscia*) *Mancinii* Jeannel, 1924a: 125.
Parabathyscia (*Parabathyscia*) *mancinii* Jeannel: Zoia, 1986: 402.

Parabathyscia* (*Parabathyscia*) *meridionalis Jeannel, 1949 stat. nov.
Parabathyscia corsica meridionalis Jeannel, 1949: 15.

Parabathyscia* (*Parabathyscia*) *obruta Zoia, 1986
Parabathyscia (*Parabathyscia*) *obruta* Zoia, 1986: 374.

Parabathyscia* (*Parabathyscia*) *oodes (Jeannel, 1934)
Bathysciola (s. str.) *oodes* Jeannel, 1934a: 94.
Parabathyscia (Parabathyscia) oodes (Jeannel): Zoia, 1986: 351.

Parabathyscia* (*Parabathyscia*) *paganoi Zoia, 1977
Parabathyscia (Parabathyscia) paganoi Zoia, 1977: 6.

Parabathyscia* (*Parabathyscia*) *peragalloi Jeannel, 1911
Parabathyscia Peragalloi Jeannel, 1911a: 278.
Bathysciola (*Parabathyscia*) *Peragalloi* (Jeannel): Jeannel, 1914b: 14.
Parabathyscia (*Platybathyscia*) *Peragalloi* Jeannel: Jeannel, 1924a: 128.
Parabathyscia (*Parabathyscia*) *peragalloi* Jeannel: Zoia, 1986: 372.

Parabathyscia* (*Parabathyscia*) *remyi Jeannel, 1947
Parabathyscia (*Parabathyscia*) *Remyi* Jeannel, 1947c: 68.
Parabathyscia Remyi Jeannel: Jeannel, 1949: 17.
Parabathyscia (*Parabathyscia*) *remyi* Jeannel: Zoia, 1986: 391.

Parabathyscia* (*Parabathyscia*) *rugulosa Jeannel, 1949
Parabathyscia rugulosa Jeannel, 1949: 16.
Parabathyscia (*Parabathyscia*) *rugulosa* Jeannel: Zoia, 1986: 391.

Parabathyscia* (*Parabathyscia*) *sanffilippoi Zoia, 1987
Parabathyscia (*Parabathyscia*) *sanffilippoi* Zoia, 1987: 117.

Parabathyscia* (*Parabathyscia*) *sbordonii Zoia, 1986
Parabathyscia (*Parabathyscia*) *sbordonii* Zoia, 1986: 377.

Parabathyscia* (*Parabathyscia*) *spagnoloi (Fairmaire, 1882)
Parabathyscia* (*Parabathyscia*) *spagnoloi brevipilis (Dodero, 1900)
Bathyscia Spagnoli var. *brevipilis* Dodero, 1900: 417.
Parabathyscia Spagnoli subsp. *brevipilis* Dodero: Jeannel, 1910a: 29.
Bathysciola (*Parabathyscia*) *Spagnoli* subsp. *brevipilis* Dodero: Jeannel, 1914b: 14.
Parabathyscia (*Parabathyscia*) *spagnoli brevipilis* (Dodero): Zoia, 1986: 366.
Parabathyscia* (*Parabathyscia*) *spagnoloi colbranti Laneyrie, 1955
Parabathyscia spagnoloi subsp. *colbranti* Laneyrie, 1955: 26.
Parabathyscia (*Parabathyscia*) *spagnoloi colbranti* Laneyrie: Zoia, 1986: 360.



FIGURES 176.1–176.5: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Metendosternite of: (**1**) *Parabathyscia* (*Parabathyscia*) *dematteisi dematteisi*, (**2**) *Isereus colasi,* (**3**) *Ochsiella bucheti* **comb. nov.**, (**4**) *Speodiaetus galloprovincialis,* (**5**) *Troglodromus bucheti ochsi*.

Parabathyscia* (*Parabathyscia*) *spagnoloi devillei Jeannel, 1911.
Parabathyscia Spagnoloi subsp. *Devillei* Jeannel, 1911a: 281.
Bathysciola (*Parabathyscia*) *Spagnoloi* subsp. *Devillei* Jeannel: Jeannel, 1914b: 14.
Parabathyscia (*Parabathyscia*) *spagnoloi devillei* Jeannel: Zoia, 1986: 362.
Parabathyscia* (*Parabathyscia*) *spagnoloi propinqua Zoia, 1986
Parabathyscia (*Parabathyscia*) *spagnoloi propinqua* Zoia, 1986: 364.
Parabathyscia* (*Parabathyscia*) *spagnoloi spagnoloi (Fairmaire, 1882)
Bathyscia Spagnoli Fairmaire, 1882: 446.
Bathyscia (*Bathyscia*) *Spagnoli* Fairmaire: Reitter, 1885 [1884]: 23.
Bathyscia (Parabathyscia) Spagnoli Fairmaire: Jeannel, 1908a: 309.
Parabathyscia Spagnoli Fairmaire: Jeannel, 1910a: 29.
Parabathyscia (*Parabathyscia*) *spagnoloi spagnoloi* (Fairmaire): Zoia, 1986: 37.

Parabathyscia* (*Parabathyscia*) *spinolai Zoia, 2003
Parabathyscia (*Parabathyscia*) *spinolai* Zoia, 2003: 159.

Parabathyscia* (*Parabathyscia*) *tigullina Binaghi, 1940
Parabathyscia tigullina Binaghi, 1940: 13.
Parabathyscia (*Parabathyscia*) *tigullina* Binaghi: Zoia, 1986: 412.

Parabathyscia* (*Parabathyscia*) *viti Zoia, 1986
Parabathyscia (*Parabathyscia*) *viti* Zoia, 1986: 398.

Parabathyscia* (*Parabathyscia*) *wollastoni (Janson, 1857)
Adelops Wollastoni Janson, 1857: 70.
Bathyscia (*Bathyscia*) *Wollastoni* Janson: Reitter, 1885 [1884]: 26.
Parabathyscia Wollastoni Janson: Jeannel, 1910a: 29.
Bathysciola (*Parabathyscia*) *Wollastoni* Janson: Jeannel, 1914b: 14.
Parabathyscia (*Parabathyscia*) *Wollastoni* Janson: Jeannel, 1924a: 124.
Parabathyscia (*Parabathyscia*) *wollastoni* (Janson): Zoia, 1986: 387.
Adelops muscorum Dieck, 1869: 5.
Bathyscia (*Bathyscia*) *frondicola* Reitter, 1885a [1884]: 25.

3.3.1.4 ***Isereus*** group

Diagnosis Integument red-orange, covered with a flat-lying pubescence – erect in *Ochsiella* –, fine and whitish-yellowish in colour. Thin or thick, irregular punctation all over the body. Depigmented.

Head: Anophthalmous.

Elytra: With irregular punctation and parasutural stria present, sometimes blurred.

Legs: All tibiae hairy, with two pectinate inner spurs, two simple outer ones and a series of spines unequal to each other.

Metaventrite: Forms a protruding bifid process that separates the metacoxal cavities.

Median lobe of aedeagus: Sinuous in the fourth terminal, the basal area reduced.

Endophallus: Three regions; the basal with a «Y»-shaped piece at the bottom of the sac, without stylet; the middle region with sclerotized phanerae concentrated in its distal part and the rest, which is very long, only with phanerae very long, thin, and hyaline; the apical region with very short reinforcement bands.

Spermathecal complex: With both lobes enlarged and the spermatic duct short and thin.

Female uroventrite VIII: Spiculum short and wide.

Discussion. This is the sister group to *Cytodromus* with a support of 100/100 (Fig. 1G). The whole clade, with a support of 99.7/100, is composed of four genera and the nodes are well supported with the exception of the one shared by *Ochsiella* stat. nov. and the two sister genera *Troglodromus* + *Isereus*; *Speodiaetus* is the sister genus of the whole group.

Key to genera

1. Bathyscioid facies (Figs 172.4, 172.5). Pronotum with lateral margins neither sinuous nor narrowed towards the basal half. Segments of club thickened. Mesoventral keel high, with rounded apex (Figs 173.4, 173.5). «M»-shaped metendosternite with the furcal trunk broad and short, as long as or slightly longer than the width of the basal part (Figs 176.3, 176.4) 2
- Pholeuonoid facies (Figs 172.3, 172.6). Pronotum with sinuous lateral margins, narrowed towards the basal half. Segments of club slender, 8th to 10th clearly longer than wide. Mesoventral keel very low, reduced to an arista (Figs 173.3, 173.6). «Y»-shaped metendosternite with a long furcal trunk, much longer than the width of the basal area (Figs 176.2, 176.5).....3



FIGURES 177.1–177.6: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Aedeagus in lateral view of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii* (modified from Zoia 1980), (**2**) *P. (Parabathyscia*) *spagnoloi devillei*, (**3**) *Isereus xambeui*, (**4**) *Ochsiella bucheti* **comb. nov.**, (**5**) *Speodiaetus galloprovincialis*, (**6**) *Troglodromus bucheti ochsi*.

2. Antennae shorter than elytral suture; antennomeres 7th to 10th slightly longer than wide. Female protarsi slightly dilated. Suture of the metaventrite arched, delimiting a narrow, elongated area (Fig. 173.5). Metendosternite with wide furcal arms and a developed terminal apophysis (Fig. 176.4). Apical area of parameres with three setae, one long and two shorter (Fig. 179.7). Upper middle region of endophallus with a complex axial piece, formed by a pair of rounded, sclerotized nodules and a notched rectangular central piece (Fig. 179.1).....*Speodiaetus*
- Antennae longer than elytral suture; antennomeres 7th to 10th clearly longer than wide. Females protarsi gracile. Sutures of the metaventrite meet at an acute vertex and delineate a subtriangular area (Fig. 173.4). Metendosternite with narrow furcal arms and no terminal apophysis (Fig. 176.3). Apical area of parameres with three setae, two of equal length and one shorter (Fig. 179.6). Upper middle region of endophallus with one axial piece formed by phanerae, another two very thin,parenthesis-shaped, and two others more external (Fig. 178.4) .....*Ochsiella* stat. nov.

3. Base of pronotum narrower or as wide as the anterior area (Fig. 172.3). Posterior apical part of the mesoventral keel not reaching the metaventrite, the mesocoxal cavities touching (Fig. 173.3). Metendosternite with furcal arms as long as the trunk, the apical area in a small arc, with slightly sharp vertices; the trunk twice as long as the width of the basal part (Fig. 176.2). Apical part of the parameres enlarged, the three setae with almost in the same length (Fig. 179.5). Basal region of the endophallus with a ventral complex from which a flagellum appears that extends to the middle region; middle region with a pair of axially positioned phanerae that together form an inverted «U» with vertices curved outwards, to which are attached well sclerotized and rounded nodules (Fig. 178.3). Female uroventrite VIII with a central notch on distal edge; spiculum very short and broad, with a truncate or bifid vertex (Fig. 181.3) .....*Isereus*
- Base of the pronotum much wider than the anterior area (Fig. 172.6). Posterior apical part of the mesoventral keel reaching, the metaventrite and the mesocoxal cavities separated (Fig. 173.6). Metendosternite with furcal arms clearly longer than the trunk, with the apical area elongated and sharp; the trunk one and a half times longer than the width of the basal part (Fig. 176.5). Apical part of the parameres not enlarged and curved in lateral view, one of the three setae much longer and more robust (Fig. 179.8). Basal region of endophallus without an evident ventral complex and with a fibre bundle; middle region with two pairs of fine, hyaline phanerae extending throughout this region to apical area where two well-sclerotized elliptical nodules are present (Fig. 179.2). Female uroventrite VIII without central notch on distal edge; spiculum short and broad, with rounded vertex (Fig. 171.6) .....*Troglodromus*

Genus ***Isereus*** Reitter, 1886
Isereus Reitter, 1886b: 100.

Type species. *Trocharanis xambeui* Argod-Vallon, 1885 by monotypy (habitus in Fig. 172.3).

Diagnosis. Size between 3.7-4.7 mm. Pholeuonoid facies, body very long and narrow (Fig. 172.3); integument dull orange, covered with a short,recumbent pubescence; punctation fine, tight and superficial on the pronotum, slightly rough on the elytra; well-printed microreticulum on both pronotum and elytra; sexual dimorphism visible in the tarsal formula, in the enlargement of the protarsi of the males and in the apex of the elytra.

Head: Voluminous, with a complete occipital carina; epistomal suture curved and darkened.

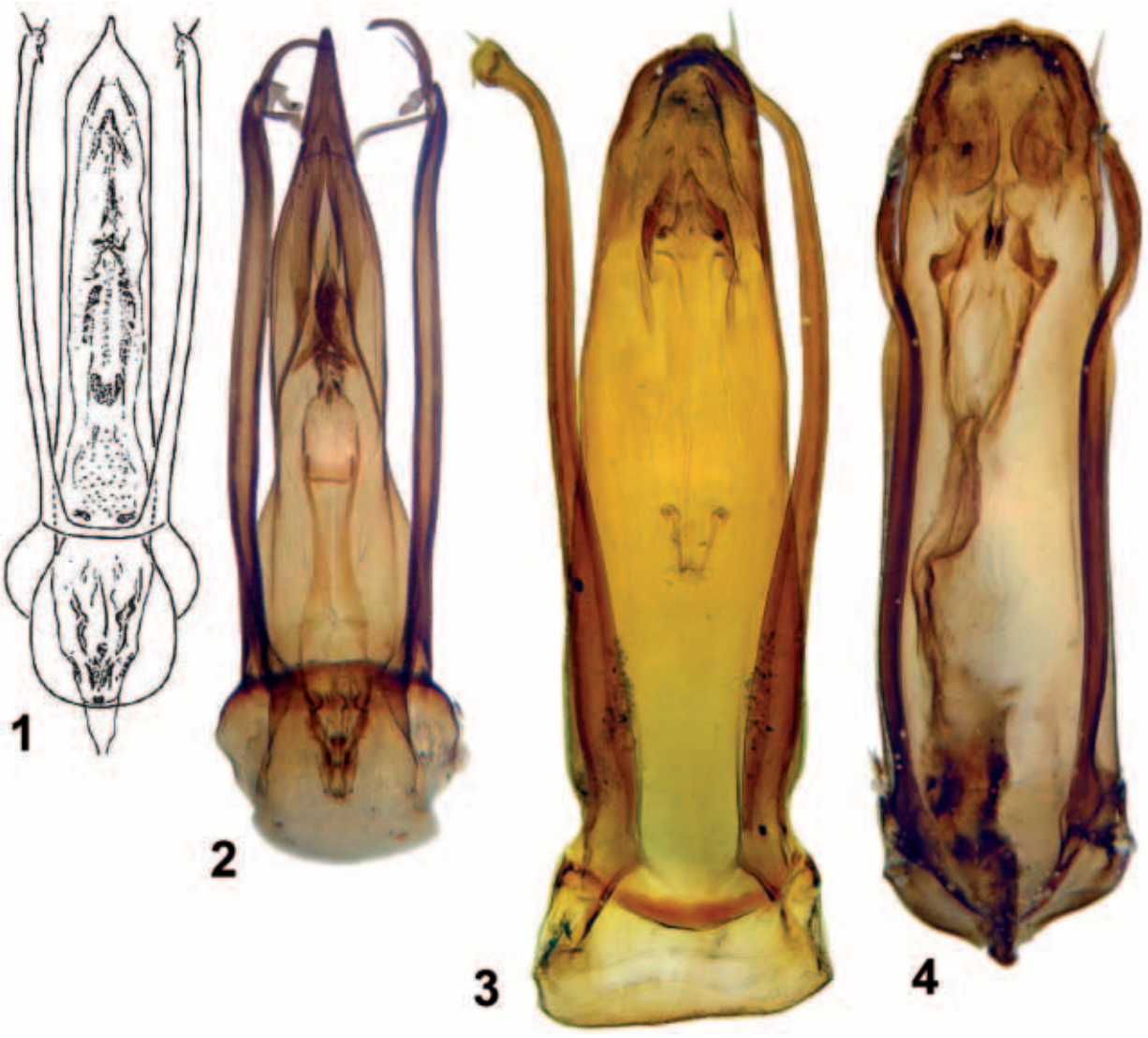
Antennae: Long and slender, much longer than the elytral suture, with all segments longer than wide; First antennomere thicker and as long as the second; segments 7th, 8th, 9th and 10th slightly thickened in the apical area, the 8th being slightly shorter than the segments of the club.

Pronotum: Cordate, base narrower than the anterior area; almost as wide as long, the greatest width towards the anterior third; sides rounded in the anterior part and in the posterior part from strongly sinuous to almost parallel; base rectilinear and posterior angles straight, with rounded vertices.

Elytra: No wider than pronotum, four times as long as wide; parasutural stria deep, well-marked, not parallel to the suture and with signs of a few ribs on the disc; pygidium completely covered by the elytra, the apical areas of which are fused or dehiscent and the vertices rounded, acute or truncated.

Legs: Very long. Femora stout, slightly narrowed at apical area and slightly arched; male protarsi dilated with first protarsomere as wide as apical part of protibia; tibiae very hairy, especially protibiae and mesotibiae; protibiae attenuated in apical area, meso- and metatibiae straight, none with spines on outer side.

Mesoventral keel (Fig. 173.3): Very low, forming a subrectilinear arista of axial position which in its anterior part does not touch the transverse collar (tvc);



FIGURES 178.1–178.4: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Aedeagus in dorsal view of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii* (modified from Zoia 1980), (**2**) *P. (Parabathyscia*) *grouvellei*, (**3**) *Isereus xambeui,* (**4**) *Ochsiella bucheti* **comb. nov.**

posterior extension not reaching the anterior edge of the metaventrite, so the mesocoxal cavities are in contact.

Suture of the metaventrite (Fig. 173.3): A single suture that forms an arc from the apex to the base of the mesocoxal cavity, delimiting a very narrow, elongated area.

Metatergal apparatus (Fig. 174.3): Metascutum long and somewhat enlarged, one wing of the metascutum being as long as the alacrista; apophysis of the alacrista prolonged, the apices not very acute.

Metendosternite (Fig. 176.2): «Y»-shaped, furcal arms and trunk long; arms as long as trunk tapering to apical area which is curved, without defined terminal apophysis; posterior furcal plate retained narrow along arm to apex,edge very slightly arched; trunk twice as long as width of basal area; middle carina of trunk diverging posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 177.3), more or less arched depending on the species; dorsal edge sinuous towards the apical quarter, with the apical area thickened at the base and the vertex acute; ventral margin more or less straight along the basal and middle parts and slightly sinuous in the apical third. In dorsal view (Fig. 178.3), lateral edges convex and non-parallel, vertex more or less pointed, sometimes a lobe. Basal blade reduced.

Endophallus (Fig. 178.3): With three regions. The basal region with very short «Y»-shaped part and a ventral complex with a flagellum emerging and extending into the median region. The median region with a pair of axially positioned phanerae which together form an inverted «U» with the vertices curved outwards; at the vertex of these phanerae there are well-sclerotized rounded nodules; on the outside there are two long and strongly sclerotized phanerae and two other hyaline ones with sharp vertex; on the sides of the endophallus there are two other very fine and elongated phanerae. The apical with two very short reinforcing bands that rest on membranous ligules.

Parameres (Fig. 179.5): As long as or shorter than the median lobe, slender and thickened club-like at their tips; armed with three setae of unequal length, usually the apical half thicker and longer than the others.

Spermathecal complex (Fig. 180.3): Spermatheca elongate with spherical apical lobe; membranous junction duct as long as or slightly longer than apical lobe and slightly shorter than basal lobe; basal lobe well-developed and larger than apical; very long and thin spermatic duct; well-developed spermathecal gland well-developed.

Female uroventrite VIII (Fig. 171.3): With a more or less deep central notch on distal edge; spiculum very short, broad and truncate or bifid.

Discussion. In the phylogenetic tree (Fig. 1G) *Isereus* joins its sister genus *Troglodromus* with the highest support (100/100). *Isereus* is a genus with a pronounced pholeuonoid facies; the body is extremely long, narrow, the pronotum is very narrow in its basal half, the base narrower than the anterior margin. Among the morphological characteristics, the mesoventral keel is very low and reduced to an axial positioned arista which in its anterior part does not touch the transverse collar, being also very short, it does not reach the edge of the metaventrite and therefore the two mesocoxal cavities touch, are joined. This is probably, the plesiomorphic state of the character that is already derived in the various sister or outgroups of Leptodirini, the Ptomaphagini – with a keel that totally separates the two mesocoxal cavities – but which is the same in the external group Cholevini, with the two cavities united although in this case there is no axial arista in the mesoventrite. In *Adelopsella*, *Platycholeus* and the genera of the *Leptodirus* and *Anthroherpon* series, the mesocoxal cavities are also in contact. Alonso (2018) provided a taxonomic and geonomic study of *Isereus*.

Distribution. France. The distribution is discontinuous. *Isereus xambeui* occupies cavities in the Grande-Chartreuse massif in Isère, and the other three species are found in distant massifs almost two hundred kilometers apart in the Maritime Alps: underground cavities in the Val Ferrière near Séranon, in the Montagne de l'Audibergue near la Moulière and the eastern end of the Plateau de Caussols.

Species

Isereus colasi Bonadona, 1955
Isereus colasi Bonadona, 1955a: 119.

Isereus giordani Bonadona, 1981
Isereus giordani Bonadona, 1981: 182.

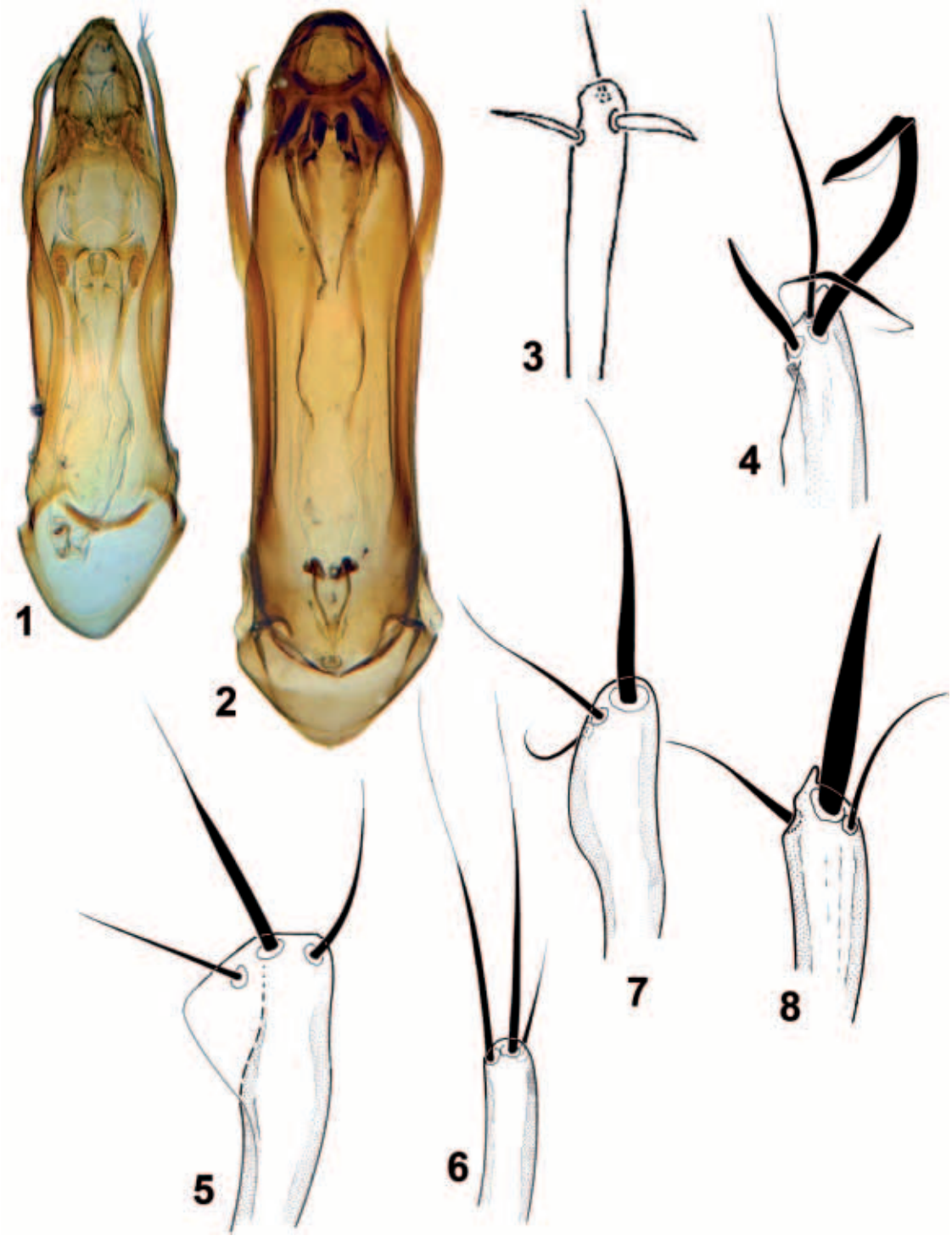
Isereus serullazi Fagniez, 1914
Isereus Serullazi Fagniez, 1914: 408.
Isereus serullazi Fagniez: Deleurance, 1958: 3286.

Isereus xambeui (Argod-Vallon, 1885)
Trocharanis Xambeui Argod-Vallon, 1885: CLXIII.
Isereus xambeui Argod: Reitter, 1886b: 100.
Isereus xambeui (Argod-Vallon): Perreau, 2000: 259.

Genus ***Ochsiella*** Jeannel, 1947 stat. nov.
Speodiaetus (*Ochsiella*) Jeannel, 1947b: 2.

Type species. *Bathyscia Bucheti* Abeille de Perrin, 1905 by original designation (habitus in Fig. 172.4).

Diagnosis. Size between 2.6-3.0 mm. Bathyscioid facies (Fig. 172.4); body elongated-oval, broad and clearly convex. Integument dark reddish, very shiny and covered with a fine, long, dense and erect pubescence. Pronotum with relatively strong and thick punctation; similar in the elytra and in the two points arranged without order. Sexual dimorphism weak, limited to the tarsal formula and the fact that the females are a little more robust and the antennae a little shorter, with the segments of the club a little thicker.



FIGURES 179.1–179.8: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Aedeagus in dorsal view of: (**1**) *Speodiaetus galloprovincialis*, (**2**) *Troglodromus bucheti ochsi.* Apex of the paramere of: (**3**) *Parabathyscia* (*Ligurobathyscia*) *brigantii* (modified from Zoia 1980), (**4**) *P.* (*Parabathyscia*) *spagnoloi devillei*, (**5**) *Isereus xambeui*, (**6**) *Ochsiella bucheti* **comb. nov.**, (**7**) *Speodiaetus galloprovincialis*, (**8**) *Troglodromus bucheti caussicola.*

Head: Voluminous, with the occipital carina obliterated in the central part; epistomal suture straight, slightly impressed and not masked.

Antennae: Slightly longer than the suture, extending beyond the middle of the body; segments not flattened, all longer than wide, those of the club thicker especially in the apical area, the shortest being the 8th.

Pronotum: Transverse with the sides evenly arched forwards; maximum width in the basal area which is as wide as the anterior area of the elytra, but a little narrower than the area of greatest elytral width; posterior angles almost straight with the vertex rounded; the basal edge a little sinuous.

Elytra: Short and wide, one and a half times as long as wide, with the sides and vertices evenly curved ; marginal ridge visible from above; widest a little before the base; parasutural stria entire, deep and arched in the middle area.

Legs: Short but slender. Male protarsi slightly dilated, distinctly narrower than apex of protibiae; apex of protibiae slightly enlarged, without spines on outer side; mesotibiae slightly arched and metatibiae straight, both with spines on outer surface.

Mesoventral keel (Fig. 173.4): High, with broadly rounded vertex and obtuse angle; anterior margin convex and unrimmed; ventrally straight, with narrow arista anteriorly and widened posteriorly; not extending onto metaventrite. Meso- and metaventrite fused, the suture visible laterally.

Sutures of the metaventrite (Fig. 173.4): Two sutures that start from one end of the mesocoxal cavity, extend towards the posterior margin of the metaventrite and converge at a point forming a blunt vertex, delimiting a subtriangular area.

Metatergal apparatus (Fig. 175.1): Metascutum long and narrow, one wing of the metascutum as long as the alacrista; apophysis of the alacrista prolonged, the apices not very sharp.

Metendosternite (Fig. 176.3): «M»-shaped. Furca with long, narrow arms and a short, wide trunk. Arms much longer than the trunk, tapering to the slightly curved, without defined terminal apophysis apical area; suture of the arms delimiting a small anterior lamina towards the apical area, the narrow posterior lamina almost disappearing in the apical area, the edge being straight. Furcal trunk short and wide, as long as the width of the basal area; the mid-trunk keel diverging widely posteriorly.

Median lobe of aedeagus: Arched, with wide basal area. In lateral view (Fig. 177.4), the dorsal margin straight until the fourth terminal, when it inflects and becomes strongly sinuous; apical area long, narrow and pointed, slightly curved towards the ventral side; ventral edge straight throughout the median area. Basal two thirds straight in dorsal view (Fig. 178.4), the apical third arched, narrowing to form a small, narrow, pointed prominence with a blunt apex in the median area. Basal lamina very short.

Endophallus (Fig. 178.4): Three regions. In the basal, the «Y»-piece short, with a sharp apical nodule with a transverse arrangement; no obvious ventral complex; in this region, two pairs of thin, hyaline phanerae extending throughout the middle region to its apical area; axial piece, made up of two phanerae, present at the upper end, another two very thin phanerae parenthesis-shaped, and two more outer ones; in the apical part, two very short reinforcing bands resting on membranous ligules.

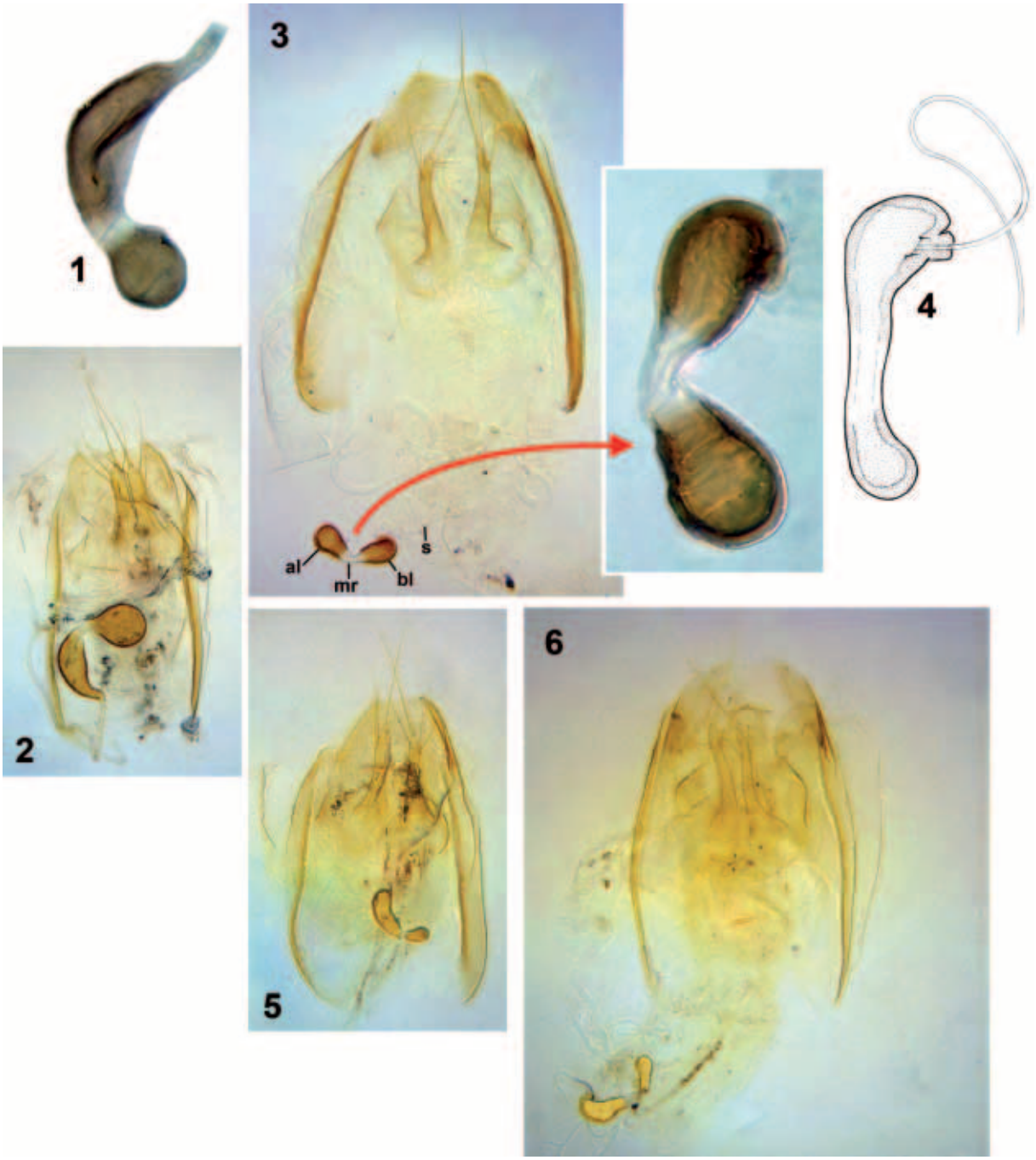
Parameres (Fig. 179.6): Slender, shorter than median lobe, apical area arched, distal end not clubbed; three contiguous setae inserted at apex, two longer and equal, the third shorter.

Spermathecal complex: Spermatheca (Fig. 180.4) elongated, with the two lobes well differentiated; the basal one larger and more dilated than the apical one, which is spherical; the spermatic duct short and thin.

Female uroventrite VIII (Fig. 181.4): Middle area of posterior margin lobe-shaped; spiculum triangular, short, broad and rounded at vertex.

Discussion. In the phylogenetic tree (Fig. 1G) *Ochsiella* is more closely related to the genera *Isereus* and *Troglodromus*, which it joins with a support of 86.6/100, than to *Speodiaetus*, the basal genus of the clade and in which it has been included as a subgenus; *Ochsiella* is also related to the previous three with a high support (99.7/100). All this indicates the close relationship that exists between the genera of the *Isereus* group.

It is a special animal within its clade. In the metaventrite, there are two sutures which start at one end of the mesocoxal cavity, extend towards the posterior edge of the metaventrite and converge at a point forming a vertex and delimiting a subtriangular area; this is the characteristic conformation of the *Quaestus* clade of Cantabrian distribution: *Breuilia*, *Espanoliella*, etc., (a group of genera with which it has no phylogenetic relationship) a conformation also shared with the corsican *Batinoscelis* stat. nov. As this character is also found in Ptomaphagini, it seems likely that the existence of two sutures may be the plesiomorphic character. In derived groups, they have been reduced to a single trace of suture, which may disappear. There seems to be a general tendency towards the fusion of body



FIGURES 180.1–180.6: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Spermathecal complex of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii* (modified from Zoia 1980), (**2**) *P. (Parabathyscia*) *spagnoloi devillei*, (**3**) *Isereus colasi,* (**4**) *Ochsiella bucheti* **comb. nov.**, (**5**) *Speodiaetus galloprovincialis*, (**6**) *Troglodromus bucheti caussicola.* Abbreviations: **al**, apical lobe; **bl**, basal lobe; **mr**, middle region; **s**, spermiduct.

plate which, once being completed, may even involve the blurring of the junction lines: the group tends towards the reduction of body plates. Its evolutionary significance is uncertain, although it is thought that it could be advantageous in preventing dehydration in animals like these, which are frankly stenohygrobics: sutures could be a weak point in the body's watertightness. The configuration of the parameres is also peculiar, with two long setae and a third smaller one; the virtually undilated male protarsi is also an anomaly for this clade.

Distribution. France: Alpes-Maritimes. Caves on the left bank of the Vésubie valley near Figaret-d'Utelle.

Species

Ochsiella bucheti (Abeille de Perrin, 1905) comb. nov.
Bathyscia Bucheti Abeille de Perrin, 1905: 208.
Bathyscia (*Speophyes*) *Bucheti* Abeille de Perrin: Jeannel, 1914b: 17.
Speodiaetus Bucheti Abeille: Jeannel, 1924a: 204.
Speodiaetus (Ochsiella) Bucheti Abeille de Perrin: Jeannel, 1947b: 2.

Genus ***Speodiaetus*** Jeannel, 1908
Speodiaetus Jeannel, 1908a: 296.

Type species. *Adelops galloprovincialis* Fairmaire, 1860 by monotypy (habitus in Fig. 172.5).

Diagnosis. Size between 3.0-3.4 mm. Bathyscioid facies (Fig. 172.5); body oval, short, broad and obviously convex. Integument dull reddish covered with short, dense, recumbent pubescence – a few short, raised setae on the sides of the elytra (Alonso 2017) – Integument of pronotum and elytra marked by a microreticulum; punctation thick, sparsely marked and arranged without order. No obvious sexual dimorphism; differences in the antennae slightly longer in the males, with pentamerous and slightly more dilated protarsi.

Head: Voluminous, with the occipital carina blurred in the centre; epistomal suture slightly curved and darkened.

Antennae: As long as two thirds of the suture, not extending beyond the middle of the body; segments of the club slightly thickened and all the same length.

Pronotum: Very transverse, almost twice as wide as long, wider near the base and slightly narrower than the elytra; sides evenly arched from base to anterior margin; base straight; posterior vertices not projecting backwards; angles rounded and acute.

Elytra: Elongated, although broad and very convex, one and a half times longer than broad; marginal ridge visible from above and apex in a regular curve; maximum width in the median part; a deep parasutural stria not parallel to the suture. Pygidium covered by elytra.

Legs: Short but fairly stout; protarsi of males not greatly enlarged, clearly narrower than apex of protibia, also slightly enlarged in female; protibiae slightly enlarged at apical area, without spines on outer surface; mesotibiae slightly curved and metatibiae straight, both with fine spines on outer surface.

Mesoventral keel (Fig. 173.5): Low, with broadly rounded vertex and very obtuse angle; with slightly curved anterior margin and slightly sinuous ventral margin, with narrow arista; not extending into metaventrite.

Suture of metaventrite (Fig. 173.5): A single suture forming an arc from one end of the mesocoxal cavity to the other; delimiting a narrow, elongated area, slightly wider in the anterior area.

Metatergal apparatus (Fig. 175.2): Metascutum long and narrow, one wing of the metascutum as long as the alacrista; the apophysis of the alacrista prolonged and the apices not very sharp; similar to that seen in *Ochsiella*, although the apophyses of the alacrista somewhat broader and shorter.

Metendosternite (Fig. 176.4): «V»-shaped. Furcal arms wide, with the same width throughout, about one and a half times longer than the trunk, with a developed terminal apophysis; posterior lamina retaining the same width as far as the apical area, with a subrectilinear border . Trunk, although wide, slightly longer than the width of the basal area; middle keel of the trunk diverging posteriorly.

Median lobe of aedeagus: Short and thick. In lateral view (Fig. 177.5), the dorsal surface smoothly and regularly arched, the apical area slightly depressed and slightly curved towards the ventral surface, the vertex sharp; the ventral surface more arched, the median area with a marked obtuse angle. margins sinuous in the basal two thirds in dorsal view (Fig. 179.1) the apical third narrowing to a blunt or subtruncate arc. Basal lamina short.

Endophallus (Fig. 179.1): Three regions. In the basal region, the «Y»-shaped piece with very divergent arms and the existence of ventral complex is not appreciated, but rather a bundle of fibres. The middle region with sclerotized phanerae only at its upper end, in the lower part which is longer; there are fine hyaline phanerae which originate in the «Y»-shaped piece, a

pair of fine phanerae and another larger pair on the outside with a sclerotized nodule at their upper end; the axial piece is complex, with a pair of strongly sclerotized and rounded nodules and a central, rectangular notched piece. The apical region has very short reinforcing bands.

Parameres (Fig. 179.7): Very slender and shorter than the median lobe; in dorsal view, distal end not club-shaped, but slightly curved inwards with a small membranous lobe; at the apex are inserted three setae of unequal length with contiguous insertion pores; the apical outer seta longer and slightly more robust than the other two, which are almost equal.

Spermathecal complex (Fig. 180.5): Spermatheca elongate, with both lobes well differentiated, the basal much larger than the apical, which is spherical; hyaline junction area shorter than apical lobe; spermatic duct short and thin.

Female uroventrite VIII (Fig. 171.5): Posterior median margin regularly arched, with a dark oval mark; spiculum short and rather broad, with the vertex truncate.

Discussion. As previously indicated, the genus *Speodiaetus* is at the base of the clade of the *Isereus* group with a support of 99.7/100 (Fig. 1G). The most striking feature is the dilatation of the female protarsi, whose width is almost similar to that of the male. On the other hand, the endophallus shows the median region with the sclerotized phanerae displaced apically , while the rest of the middle region is occupied by long,hyaline phanerae and the apical nodules of the «Y»-shaped piece; in the apical region the reinforcement bands are very short; the reduced dorsal sinuosity of the median lobe of aedeagus, very marked in *Ochsiella*, is also characteristic, as well as the hypertrophied basal lobe of the spermatheca that make this taxon a representative model of the *Isereus* clade.

Distribution. France. Bouches-du-Rhône and Var. Species found in the subterranean environment of the Parc Naturel Régional de la Sainte-Baume and other mountainous areas as far as the Mediterranean coast.

Species

Speodiaetus galloprovincialis (Fairmaire, 1860)
Adelops galloprovincialis Fairmaire, 1860: 631.
Bathyscia (*Bathyscia*) *galloprovincialis* Fairmaire: Reitter, 1885a [1884]: 23.
Speodiaetus galloprovincialis Fairmaire: Jeannel, 1908a: 289.

Genus ***Troglodromus*** Sainte Claire Deville, 1901
Troglodromus Sainte Claire Deville, 1901: 59.

Type species. *Cytodromus bucheti* Sainte Claire Deville, 1898 by original designation (habitus in Fig. 172.6).

Diagnosis. Size between 3.2-3.8 mm. Pholeuonoid facies (Fig. 172.6); body long, robust, wide and convex. Tegument orange, moderately shiny and covered with a short, flat-lying pubescence. Thick, dense punctation on the pronotum and slightly more superficial on the elytra; no microreticulum. Females slightly more robust, with shorter antennae than males.

Head: Voluminous, with the occipital carina blurred in the centre; epistomal suture curved and darkened.

Antennae: Long and slender, much longer than the elytral suture, with all segments longer than wide; antennomeres 7, 8, 9 and 10 slightly enlarged in the apical area; the 8th slightly shorter and thinner than the others.

Pronotum: Transverse with greatest width in anterior third; subquadrate, as wide as long or slightly wider than long; sides distinctly rounded anteriorly and between sinuous and parallel posteriorly; posterior angles straight with rounded vertices; base generally subrectilinear, narrower than anterior area of elytra.

Elytra: Elongated, one and a half times as long as wide, with the greatest width in the median part and without a margin; apices together form a regular curve; parasutural stria well marked and arched on the sides of the suture.

Legs: Long and slender; protarsi of males dilated; usually first protarsomere as wide as apical part of protibia; protibiae slightly attenuated in the apical area, also slightly arched outwards; meso- and metatibiae straight, all with a few very fine spines on the outer surface.

Mesoventral keel (Fig. 173.6): Very low, formed by an axially positioned arista that touches the transverse collar in its anterior part, forming a wide arc in the posterior third; not extended over the metaventrite.

Suture of the metaventrite (Fig. 173.6): With a single suture that forms an arc from one end to the end of the mesocoxal cavity; it delimits a wide area in the anterior middle part and a very narrow one in the posterior part.

Suture of the metaventrite (Fig. 173.6): Single suture forming an arc from one end of the mesocoxal cavity to the other; it delimits a wide area in the me-

dian anterior part and a very narrow one in the posterior part.

Metatergal apparatus (Fig. 175.3): Metascutum long and slightly enlarged, one wing of the metascutum being as long as the alacrista; apophysis of the alacrista prolonged and the apices not very acute; very similar to that seen in *Isereus*, only the membrane lateral to the alacrista slightly narrower towards the apical part.

Metendosternite (Fig. 176.5): «Y»-shaped. Furcal arms clearly longer than the trunk, tapering towards the apical area, which is elongated, narrow, pointed and with a very open arch; no terminal apophysis; posterior lamina progressively narrowing towards the vertex, the edge slightly arched in the middle. Trunk one and a half times longer than the width of the basal area; middle keel of the trunk diverging posteriorly.

Median lobe of aedeagus: Long and robust. In lateral view (Fig. 177.6), slightly arched, terminal third of dorsal face sinuous with a slight depression; the terminal area arched ventrally, the tip pointed. In dorsal view (Fig. 179.2), broad with parallel sides to the distal end, then tapering slightly and ending with a broadly rounded apex. Basal region reduced.

Endophallus (Fig. 179.2): Three regions. In the basal region, a short «Y»-shaped piece with a sharp apical nodule of transverse arrangement; no obvious ventral complex but a bundle of fibres; in addition, in this region, two pairs of thin, hyaline phanerae extending throughout the median region to its apical area bearing two well-sclerotized elliptical nodules on either sides of the axis of symmetry of the endophallus.

Apical region with two very short reinforcing bands resting on membranous ligules.

Parameres (Fig. 179.8): Slightly shorter than the median lobe, arched inward in the apical third and without a thickened vertex; armed with three setae, one much thicker and longer at the median apical insertion, the other two thinner and shorter on either side.

Spermathecal complex (Fig. 180.6): Spermatheca with both lobes well sclerotized, of larger calibre than median region which is hyaline; apical lobe spherical, the basal much larger; spermatic duct very thin and short.

Female uroventrite VIII (Fig. 181.6): Spiculum very short, wide, triangular in shape with rounded vertex.

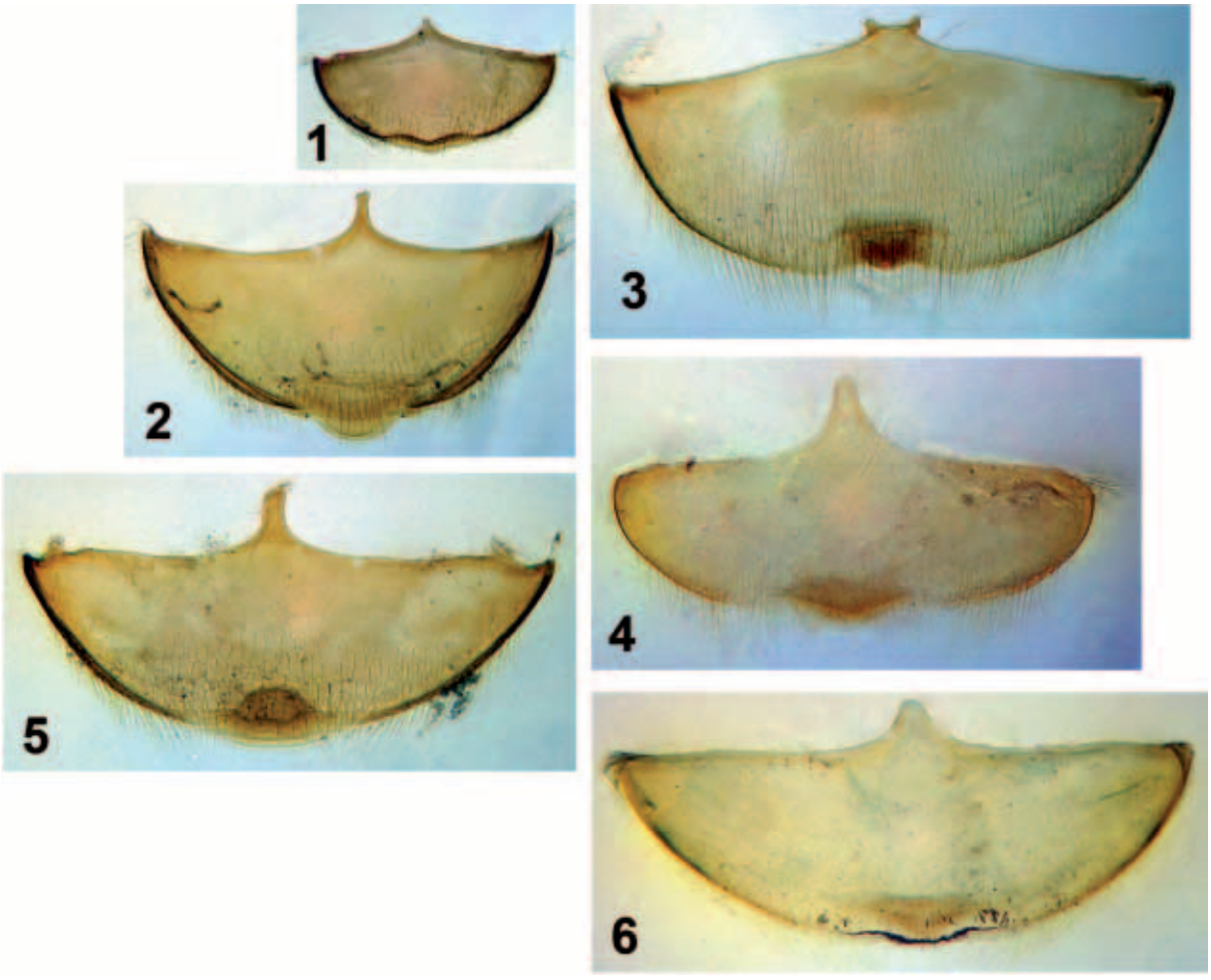
Discussion. Sister genus to *Isereus,* in the phylogenetic tree (Fig. 1G) the two genera are in the highest branch of the *Isereus* clade with support of 100/100. Both have pholeuonoid facies, less pronounced in *Troglodromus*, specimens of this genus are also less elongate and broader and the pronotum less narrow in its basal half; in addition, aedeagus is characterised by parameres armed with one large apical seta and two smaller ones located on either side.

Distribution. France. Alpes-Maritimes and Var: underground cavities in the Siagne and Loup valleys, reliefs between the Loup valley and the Var valley, with the Cheyron massif and the Baou de Vence, Plateau de Caussols, Montauroux, Canaux, Aspremont, Séranon, Roquefort and Roquefort-les-Pins massifs.

Species

Troglodromus bonadonai Jeannel, 1947
Troglodromus bonadonai Jeannel, 1947b: 3.

Troglodromus bucheti (Sainte Claire Deville, 1898)
Troglodromus bucheti boissyi Bonadona, 1955
Troglodromus Bucheti Boissyi Bonadona, 1955b: 108.
Troglodromus bucheti boissyi Bonadona: Perreau, 2000: 262.
Troglodromus bucheti bonafonsi Sainte Claire Deville, 1901
Troglodromus Bonafonsi Sainte Claire Deville, 1901: 72.
Troglodromus Bucheti Bonafonsi Deville: Jeannel, 1908a: 289.
Troglodromus bucheti bonafonsi Sainte Claire Deville: Perreau, 2000: 262.
Troglodromus bucheti bucheti (Sainte Claire Deville, 1898)
Cytodromus Bucheti Sainte Claire Deville, 1898: 196.
Troglodromus Bucheti Sainte Claire Deville: Sainte Claire Deville, 1901: 59.
Troglodromus Bucheti subsp. *Bucheti* Sainte Claire Deville: Jeannel, 1924a: 206.
Troglodromus bucheti bucheti (Sainte Claire Deville): Perreau, 2000: 262.
Troglodromus bucheti carboneli Sainte Claire Deville, 1902
Troglodromus Bucheti ssp. *Carboneli* Sainte Claire Deville, 1902: 709.
Troglodromus Bucheti subsp. *Gaveti* sous-race *Carboneli* Fagniez: Jeannel, 1947b: 10.
Troglodromus bucheti carboneli Sainte Claire Deville: Perreau, 2000: 262.
Troglodromus bucheti caussicola Jeannel, 1947
Troglodromus Bucheti subsp. *paenitens* sous-race *caussicola* Jeannel, 1947b: 10.



FIGURES 181.1–181.6: *Cytodromus* series, *Parabathyscia* and *Isereus* groups. Female uroventrite VIII of: (**1**) *Parabathyscia* (*Ligurobathyscia*) *brigantii*, (**2**) *P. (Parabathyscia*) *spagnoloi devillei*, (**3**) *Isereus colasi,* (4) *Ochsiella bucheti* **comb. nov.**, (**5**) *Speodiaetus galloprovincialis*, (**6**) *Troglodromus bucheti caussicola.*

Troglodromus bucheti caussicola Jeannel: Laneyrie, 1967: 628.

Troglodromus bucheti chobauti Fagniez, 1914

Troglodromus Bucheti Chobauti Fagniez, 1914: 411.

Troglodromus Chobauti Fagniez: Jeannel, 1924a: 208.

Troglodromus bucheti chobauti Fagniez: Perreau, 2000: 262.

Troglodromus bucheti colasi Bonadona, 1948

Troglodromus Bucheti subsp. *Colasi* Bonadona, 1948: 29.

Troglodromus bucheti colasi Bonadona: Perreau, 2000: 262.

Troglodromus bucheti gaveti Sainte Claire Deville, 1901

Troglodromus Gaveti Sainte Claire Deville, 1901: 59.

Troglodromus Bucheti Gaveti Sainte Claire Deville: Jeannel, 1908a: 289.

Troglodromus bucheti gaveti Sainte Claire Deville: Deleurance, 1957: 2318.

Troglodromus bucheti giordani Bonadona, 1982

Troglodromus bucheti giordani Bonadona, 1982: 126.

Troglodromus bucheti infernalis Jeannel, 1947

Troglodromus Bucheti subsp. *paenitens* sous-race *infernalis* Jeannel, 1947b: 10.

Troglodromus bucheti infernalis Jeannel: Laneyrie, 1967: 628.

Troglodromus bucheti laetus Bonadona, 1955

Troglodromus bucheti laetus Bonadona, 1955b: 108.

Troglodromus bucheti ochsi Jeannel, 1947
Troglodromus Bucheti subsp. *Ochsi* Jeannel, 1947b: 8.
Troglodromus bucheti ochsi Jeannel: Perreau, 2000: 263.
Troglodromus bucheti orientalis Jeannel, 1947
Troglodromus Bucheti subsp. *paenitens* sous-race *orientalis* Jeannel, 1947b: 10.
Troglodromus bucheti orientalis Jeannel: Laneyrie, 1967: 628.
Troglodromus bucheti philippi Laneyrie, 1955
Troglodromus bucheti philippi Laneyrie, 1955: 24.
Troglodromus bucheti poenitens Sainte Claire Deville, 1902
Troglodromus Bucheti ssp. *poenitens* Sainte Claire Deville, 1902: 708.
Troglodromus Bucheti subsp. *parvulus* Jeannel, 1924a: 206.
Troglodromus bucheti poenitens Sainte Claire Deville: Perreau, 2000: 263.

Troglodromus perroti Bonadona, 1948
Troglodromus perroti colbranti Bonadona, 1948
Troglodromus Perroti subsp. *Colbranti* Bonadona, 1948: 32.
Troglodromus perroti perroti Bonadona, 1948
Troglodromus perroti Bonadona, 1948: 31.

3.3.1.5 ***Cytodromus*** group

Diagnosis. Integument orange covered with golden pubescence, short, fine, lying down and quite dense on the elytra. Irregular punctation, fine on the pronotum and granular on the elytra.

Elytra: Parasutural stria not parallel to the suture.

Legs: All tibiae hairy, with two internal pectinate spurs, two simple external ones, and a series of unequal spines between them; pro- and metatibiae with spines on the external face.

Mesoventral keel (Figs 182.4-182.6): Low or very low, with the apex rounded or forms a small sharp protuberance; it does not extend over the metaventrite.

Suture of the metaventrite (Figs 182.4-182.6): A single suture that forms an arc from end to end of the mesocoxal cavity; delimits a narrow and long area.

Median lobe of aedeagus (Figs 185.1-185.3): In lateral view with a marked depression towards the apical third.

Endophallus (Figs 186.1-186.5): With three defined regions, with long phanerae that extend from the middle to the basal region and reinforcing bands that rest on pieces with the interior area sclerotized.

Parameres (Figs 186.6-186.9): With three simple apical setae.

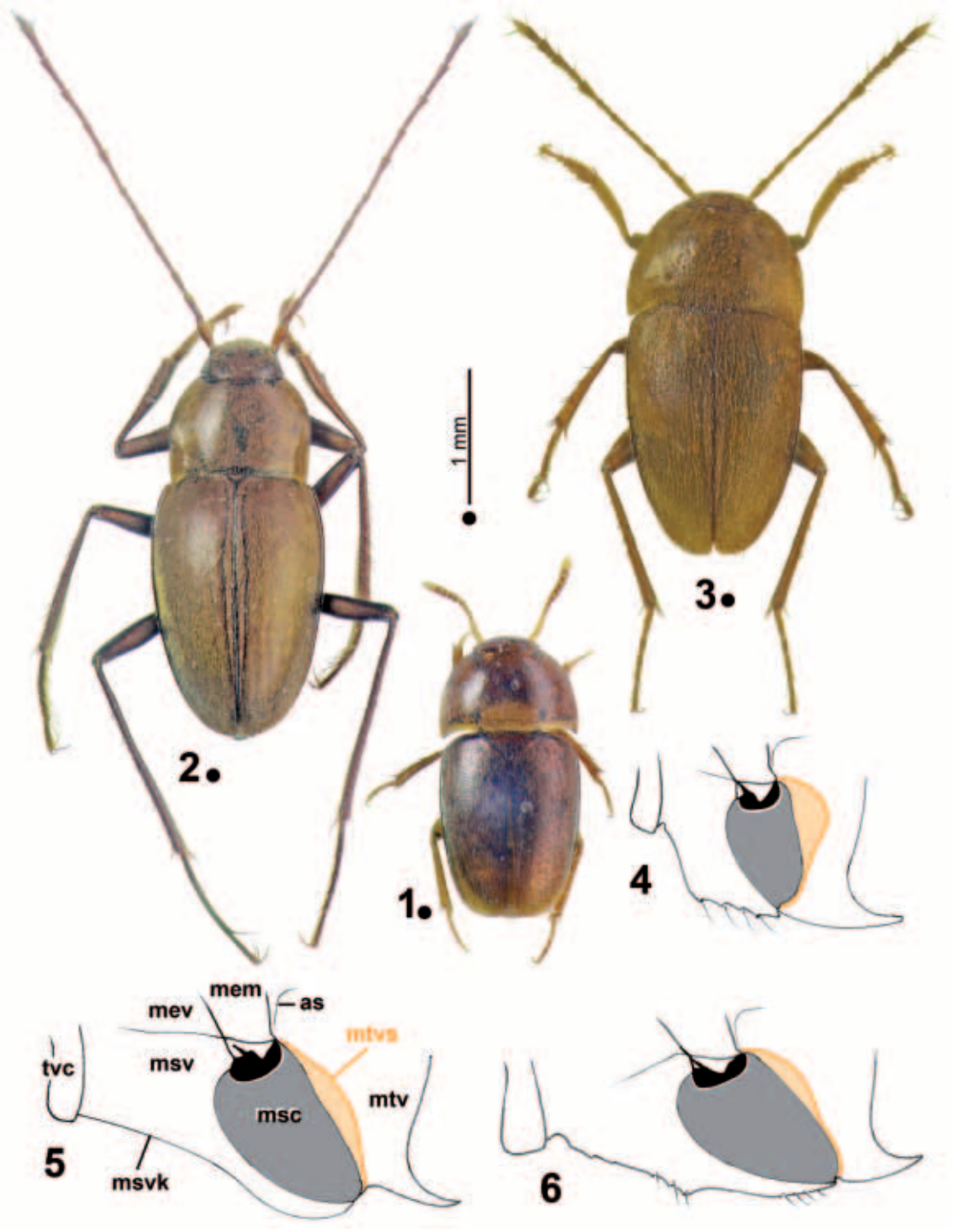
Spermathecal complex (Figs 187.1-187.3): Spermatheca with basal lobe highly developed and short spermiduct.

Discussion. The characters shared by the three genera – *Bathysciola*, *Cytodromus* and *Royerella* – that form the clade *Cytodromus* group are described above and all three genera show a joint support of 83.7/100. In the phylogenetic tree (Fig. 1G) this group constitutes the most derived branch of the series *Cytodromus*, with *Isereus* being the sister group, existing between both the support 100/100.

Key to genera

1. Pholeuonoid facies (Fig. 182.2), with lateral margins in the basal area of the sinuous pronotum. Antennae much longer than the elytral suture, with gracile club segments, 8th to 10th longer than wide. Trochanters of the forelegs with a small spine. Metendosternite (Figs 184.3, 184.4) with trunk and furcal arms long, in these the furca delimits a small anterior lamina narrow and long in the basal part and a reduced terminal apophysis is observed .....*Cytodromus*
- Bathyscioid facies (Figs 182.1, 182.3), with the lateral margins of the pronotum regularly arched. Antennae as long as or shorter than the elytral suture, with the club segments thickened, 8th to 10th as wide or wider than long. Trochanters of the forelegs without spine. Metendosternite with trunk and furcal arms short (Figs 184.1, 184.2) or long (Fig. 184.5), in these the furca does not delimit an anterior lamina and there is no terminal apophysis 2

2. Mesoventral keel (Fig. 182.6) very low, with a small pointed projection towards the middle. Metendosternite (Fig. 184.5) with arms and furcal trunk long. Median lobe of aedeagus, in dorsal view (Fig. 186.5), with broadly rounded apex; in lateral view (Fig. 185.3), without thickening prior to dorsal depression. Parameres (Fig. 186.9) with two apical setae and one of preapical insertion. Middle region of the endophallus (Fig. 186.5) with two large long plates that have at their upper end highly sclerotized lobes and two small phanerae also highly sclerotized on the outside. Female uroventrite VIII (Fig. 188.3) with the spiculum widened at the base and the apex truncated .....*Royerella*
- Mesoventral keel (Fig. 182.4) low, but well defined, with the apex more or less rounded. Metendosternite



FIGURES 182.1–182.6: *Cytodromus* series, *Cytodromus* group. Habitus of: (**1**) *Bathysciola brevicollis,* (**2**) *Cytodromus dapsoides,* (**3**) *Royerella tarissani henroti*. Pterothorax in lateral view of: (**4**) *Bathysciola champsauri,* (**5**) *C. ambiguus,* (**6**) *R. t. henroti.* Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

(Figs 184.1, 184.2) with arms and furcal trunk short. Median lobe of aedeagus, in dorsal view (Figs 186.1-186.3), with the apex more or less pointed; in lateral view (Fig. 185.1), with a thickening prior to the dorsal depression. Parameres (Figs 186.6, 186.7) with the three setae of apical insertion. Middle region of the endophallus (Figs 186.1-186.3) with a large axial piece of triangular-shape apparently formed by two symmetrical pieces and on both sides two folded phanerae that together form a «W», also, below these structures there are two strongly sclerotized nodules and two phanerae thin, external and parenthesis-shaped. Female uroventrite VIII (Fig. 188.1) with spiculum narrow and more or less long.....*Bathysciola*

Genus ***Bathysciola*** Jeannel, 1910
Bathysciola Jeannel, 1910a: 9.

TYPE SPECIES. *Bathyscia aubei*, Kiesenwetter, 1850 by original designation (for the habitus see that of the similar species *B. brevicollis* in Fig. 182.1).

DIAGNOSIS. Size ranging between 1.2-2.4 mm. Bathyscioid facies (Fig. 182.1); body shape short, broad, sides sub-parallel and moderately convex. Integument matte and marked by an apparent microreticulum. Females may be slightly smaller although, in general, there is no marked sexual dimorphism in body shape, external differences in antennae and protarsi.

Head: Retractable, with the occipital carina inconspicuous but complete; epistomal suture slightly curved and darkened.

Antennae: Short, a little longer than the middle of the elytral suture, and slightly exceeding the base of the pronotum; antennomeres very short, those of the club thickened, being from the 8th to the 10th wider than long.

Pronotum: Aspect of a quarter of a sphere, between 1.4-1.6 times as wide as long, with the maximum width very close to the base, which is as wide as the anterior area of the elytra; lateral margins regularly arched, posterior angles nearly right, with sharp vertex; sinuous base.

Elytra: Long, 1.3-1.5 times as long as wide, widest at the base or very close from it; the two apices separated and widely arched; there is parasutural stria more or less impressed depending on the species.

Legs: Short and robust; males protarsi more or less dilated depending on the species, generally narrower than the apical area of the protibiae; tibiae flattened, not cylindrical; protibiae not attenuated; mesotibiae and metatibiae somewhat curved.

Mesoventral keel (Fig. 182.4): Short and low, but well defined, with the apex broadly arched or more reduced; the ventral edge in some species slightly toothed.

Suture of the metaventrite (Fig. 182.4): In arc and delimits a quite wide area.

Metatergal apparatus (Figs 183.1, 183.2): Short with the metascutum small and the apophysis of the alacrista long.

Metendosternite (Figs 184.1, 184.2): Furcal arms and trunk short. Arms somewhat longer than the trunk and tapered towards the apical area, which is slightly curved and the tips more or less pointed, without terminal apophysis; posterior furcal lamina progressively narrows but is preserved to apical area, with posterior border regularly concave. Trunk as long as the widest part or slightly longer; middle keel on trunk diverges slightly posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 185.1), more or less strongly arched, depending on the species, and towards the apical quarter with a thickening prior to a marked dorsal depression. In dorsal view (Figs 186.1-186.3), triangular in shape with arched sides, decreasing towards the apex, which is more or less pointed depending on the species.

Endophallus (Figs 186.1-186.3): With three defined regions. In the basal region there is a «Y»-piece and ventral complex from which a long flagellum emerges. The middle region with a large axial piece of triangular shape apparently formed by two symmetrical pieces; on both sides there are two bent phanera «M»-shaped whose whole forms a «W» with the axial piece in the middle; just below these structures there are two strongly sclerotized nodules and two external phanerae fine and curved that form a kind of parenthesis; the dorsal phanerae extend to the «Y»-piece in the basal region. The apical region with reinforcing bands that rest on ligules that have sclerotized inner rims.

Parameres (Figs 186.6, 186.7): Fine and as long as or somewhat shorter than the median lobe; the apex is very slightly thickened and with three setae of apical insertion that may be alike or of different length and thickness.

Spermathecal complex: Spermatheca (Fig. 187.1) short, with both lobes sclerotized and dilated, the basal one much more dilated; spermatic duct short, between two and three times the length of the spermatheca; there is a spermathecal gland.

Female uroventrite VIII (Fig. 188.1): Broad and short, with the spiculum more or less long and thin.



FIGURES 183.1–183.4: *Cytodromus* series, *Cytodromus* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Bathysciola aubei,* (**2**) *B. brevicollis*, (**3**) *Cytodromus dapsoides,* (**4**) *Royerella tarissani ferrierensis*. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Discussion. In the phylogenetic tree (Fig. 1G) the complex of species of the genus *Bathysciola* appears with a support of 93.4/100 and is a sister of the genera *Cytodromus* and *Royerella* with a support of 83.7/100. Jeannel (1924a) divided the genus *Bathysciola* into eight sections. Following the conception of R. Jeannel, several new species were discovered adding up to about 80, present in Sardinia, Croatia, Slovenia, Spain, France, Georgia, Italy, Israel, Lebanon, Russia, Sicily and Turkey. Thus, under the name of *Bathysciola*, a large number of taxa were grouped, which indicates its polyphyly, this in terms suggests that a major revision of the genus will be needed to resolve the relationships; this has already been proposed by many other authors such as Jeannel (1910a, 1910b, 1910c, 1910d, 1910e), Newton (1998), Giachino (1988, 1998), Giachino *et al*. (1998), Fresneda & Salgado (2000, 2006), Perreau (2000) or Fresneda *et al*. (2007). A few taxa have already been allocated newly by incorporating them in other genera or describing new genera for them (Giachino & Vailati 2019). In the fourth section of the work of Jeannel (1924a) it is proposed that for the for the genus *Bathysciola,* that *Bathysciola aubei* is the nominotypical species of the genus,. In this study, the genus has been reduced to the species of the «*aubei* group», section IV *in pars* by Jeannel (1924a) which is also supported by Giachino & Vailati (2019) and is reflected in the molecular phylogeny. From section IV various species have been newly allocated or described a separate genera such as the genera *Catalaniana* gen. nov. (belongs to the *Diaprysius* group), *Latellana* gen. nov. (belongs to the *Ovobathysciola* group) and the subgenus *Salfia* stat. nov. is re-evaluated as a genus of the *Ovobathysciola* group. The study of the abundant materials from Piedmont and Liguria (Italy) has made it possible to identify a number of new species, which are described in the Appendix New Species.

Distribution. France. Alpes-Maritimes, Drôme, Gard, Isère, Provence and Var. Italy. Piemonte Liguria and Emilia.

Species

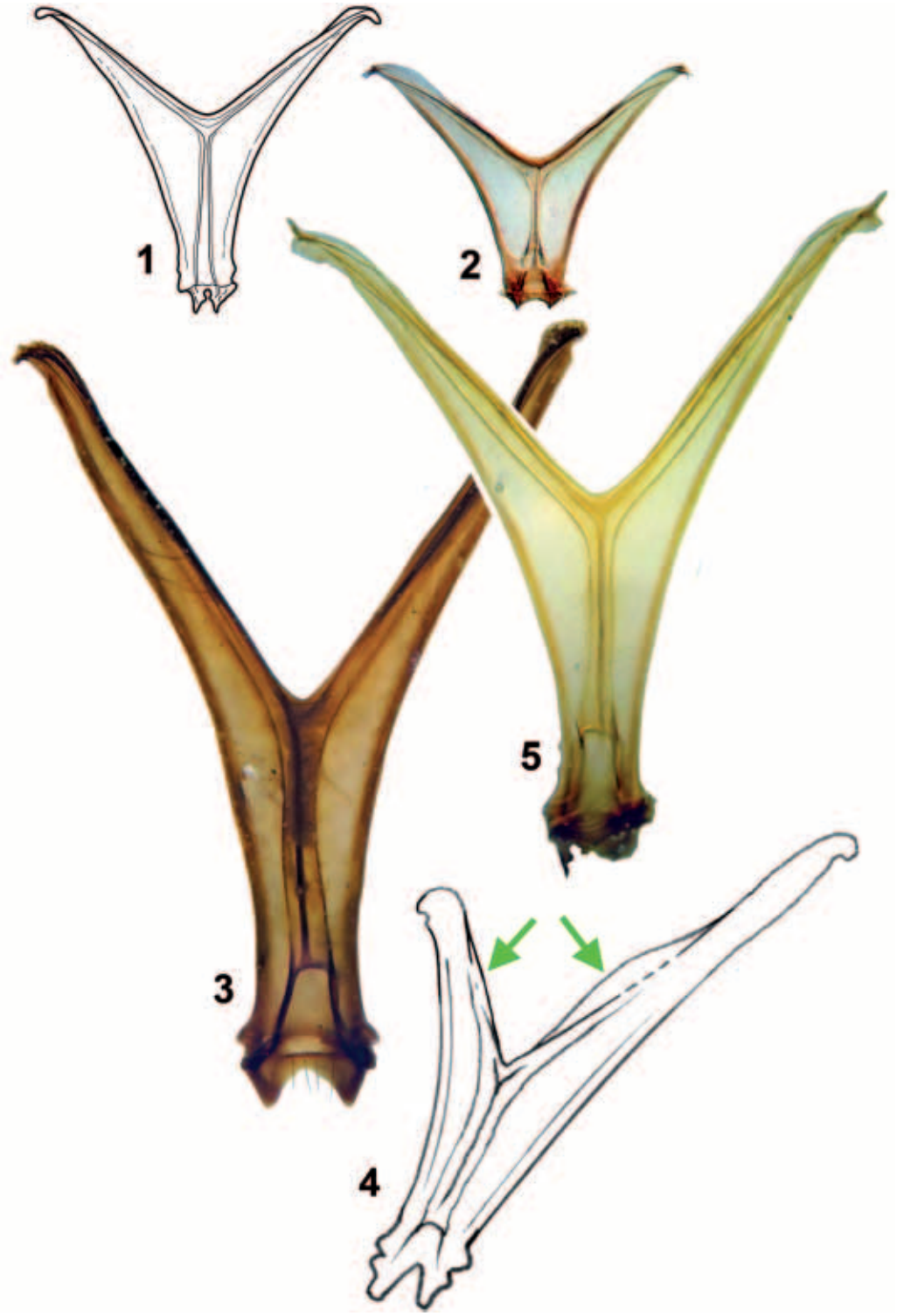
Bathysciola aubei (Kiesenwetter, 1850)
Bathysciola aubei aubei (Kiesenwetter, 1850)
Bathyscia Aubei Kiesenwetter, 1850: 223.
Adelops Aubei Kiesenwetter: L. Miller, 1855: 508.
Bathyscia (*Bathyscia*) *Aubei* Kiesw.: Reitter, 1885 [1884]: 25.
Bathysciola Aubei Kiesenwetter: Jeannel, 1910a: 27.
Bathysciola Nerusorum Fagniez, 1922: 317.
Bathysciola Aubei var. *Nerusorum* Fagniez: Jeannel, 1924a: 104.
Bathysciola aubei aubei Kiesenwetter: Bonadona, 1985: 3.
Bathysciola (s. str.) *aubei aubei* (Kiesenwetter): Perreau, 2000: 224.
Bathysciola aubei degenerata Bonadona, 1985
Bathysciola aubei ssp. *degenerata* Bonadona, 1985: 3.
Bathysciola (s. str.) *aubei degenerata* Bonadona: Perreau, 2000: 225.
Bathysciola digna orientalis Avon & Courtial, 2008b: 13 (Unjustified new replacement name).

Bathysciola aubei digna Bonadona, 1985
Bathysciola aubei ssp. *digna* Bonadona, 1985: 3.
Bathysciola (s. str.) *aubei digna* Bonadona: Perreau, 2000: 225.
Bathysciola digna caussolensis Avon & Courtial, 2008b: 10 (Unavailable name).
Bathysciola digna occidentalis Avon & Courtial, 2008b: 16 (Unavailable name).
Bathysciola digna verdonensis Avon & Courtial, 2008b: 16 (Unavailable name).
Bathysciola digna medius Avon & Courtial, 2008b: 18 (Unavailable name).
Bathysciola aubei orta Bonadona & Giordan, 1988: 241.

Bathysciola balestrae sp. nov. (See Appendix New Species)

Bathysciola brevicollis (Abeille de Perrin, 1882)
Bathyscia brevicollis Abeille de Perrin, 1882: 19.
Bathyscia (*Bathyscia*) *brevicollis* Ab.: Reitter, 1885 [1884]: 25.
Bathysciola Aubei subsp. *brevicollis* Abeille de Perrin: Jeannel, 1910a: 27.
Bathysciola brevicollis Abeille: Fagniez, 1927: 30.
Bathysciola brevicollis launei Avon & Courtial, 2008b: 48 (Unavailable name).
Bathysciola brevicollis nocei Avon & Courtial, 2008b: 49 (Unavailable name).
Bathysciola bonadonai Giachino, 1988: 264: Lemaire, 2021: 4.

Bathysciola brianconnetensis Ochs, 1949
Bathysciola brianconnetensis Ochs, 1949: 37.
Bathysciola brianconnetensis lauvensi Avon & Courtial, 2008b: 33 (Unavailable name).



FIGURES 184.1–184.5: *Cytodromus* series, *Cytodromus* group. Metendosternite of: (**1**) *Bathysciola aubei,* (**2**) *B. brevicollis*, (**3**–**4**) *Cytodromus henroti henroti,* (**6**) *Royerella tarissani ferrierensis.* Green arrow pointing to an internal protuberance.

Bathysciola brianconnetensis valferrierei Avon & Courtial, 2008b: 35 (Unavailable name).
Bathysciola brianconnetensis cheironi Avon & Courtial, 2008b: 36 (Unavailable name).
Bathysciola brianconnetensis josyi Avon & Courtial, 2008b: 40 (Unavailable name).

Bathysciola casalei Giachino, 1988
Bathysciola casalei Giachino, 1988: 258.

Bathysciola champsauri (Peyerimhoff, 1904)
Bathyscia Aubei subsp. *Champsauri* Peyerimhoff, 1904b: 215.
Bathysciola Aubei Champsauri Peyerimhoff: Jeannel, 1910a: 27.
Bathysciola (s. str.) *Champsauri* Peyerimhoff: Jeannel, 1924a: 106.

Bathysciola chestai sp. nov. (See Appendix New Species)

Bathysciola courtiali Avon, 2007
Bathysciola courtiali Avon, 2007: 33.
Bathysciola courtiali andrei Avon & Courtial, 2008b: 24 (Unavailable name).

Bathysciola digitata Bonadona, 1985 stat. nov.
Bathysciola aubei ssp. *digitata* Bonadona, 1985: 3.
Bathysciola (s. str.) *aubei digitata* Bonadona: Perreau, 2000: 225.

Bathysciola diva Bonadona & Giordan, 1988
Bathysciola diva Bonadona & Giordan, 1988: 245.

Bathysciola epuraeoides (Fairmaire, 1869)
Adelops epuraeoides Fairmaire, 1869: 231.
Bathyscia epuraeoides Fairmaire: Abeille de Perrin, 1882: 18.
Bathyscia (*Bathyscia*) *epuraeoides* Fairm.: Reitter, 1885 [1884]: 25.
Bathysciola Aubei var. *epuraeoides* Fairmaire: Jeannel, 1910a: 27.
Bathysciola giordani Bonadona, 1985: 5.

Bathysciola foveicollis Peyerimhoff, 1904
Bathysciola foveicollis alberti Faignez, 1927
Bathysciola foveicollis Alberti Fagniez, 1927: 19.
Bathysciola foveicollis argodi Jeannel, 1924
Bathysciola (s. str.) *foveicollis Argodi* Jeannel, 1924a: 105.
Bathysciola foveicollis forme *Argodi* Jeannel: Fagniez, 1927: 10.

Bathysciola foveicollis foveicollis Peyerimhoff, 1904
Bathysciola Aubei subsp. *foveicollis* Peyerimhoff, 1904b: 216.
Bathyscia Aubei-foveicollis Peyerimhoff: Peyerimhoff, 1906b: 112.
Bathysciola (s. str.) *foveicollis* Peyerimhoff: Jeannel, 1924a: 105.

Bathysciola furca Avon, 1994
Bathysciola furca Avon, 1994: 133.

Bathysciola giordania Bonadona, 1985
Bathysciola giordania Bonadona, 1985: 7.

Bathysciola guedeli Jeannel, 1910
Bathysciola Aubei subsp.*Guedeli* Jeannel, 1910f: 52.
Bathysciola (s. str.) *Guedeli* Jeannel: Jeannel, 1924a: 8.
Bathysciola (s. str.) g*uedeli* Jeannel: Perreau, 2000: 227.

Bathysciola guerzoi Giachino, 1988
Bathysciola guerzoi Giachino, 1988: 251.

Bathysciola guillaumensis Avon & Courtial, 2008
Bathysciola guillaumensis Avon & Courtial, 2008a: 83.

Bathysciola lanai sp. nov. (See Appendix New Species)

Bathysciola monregalensis Giachino, 1988
Bathysciola monregalensis Giachino, 1988: 270.

Bathysciola nicaeensis Peyerimhoff, 1905
Bathysciola brevicollis subsp. *nicaeensis* Peyerimhoff, 1906a [1905]: 300.
Bathysciola Aubei var. *brevicollis-nicaeensis* Peyerimh.: Jeannel, 1914b: 8.
Bathysciola nicaeensis Peyerimhoff, 1906: Lemaire, 2016: 363.
Bathysciola turcatiana Bonadona, 1985: 4: Lemaire, 2021: 5.

Bathysciola ochsi Jeannel, 1924
Bathysciola (s. str.) *Ochsi* Jeannel, 1924a: 108.
Bathysciola ochsi Jeannel: Bonadona, 1985: 6.
Bathysciola ochsi rutensis Avon & Courtial, 2008b: 29 (Unavailable name).

Bathysciola oliveroi sp. nov. (See Appendix New Species)

Bathysciola opaca (Reitter, 1885)
Bathyscia (*Bathyscia*) *opaca* (Abeille de Perrin): Reitter, 1885a [1884]: 26.
Bathysciola opaca Reitter: Jeannel, 1910a: 27.

Bathysciola parvula Bonadona & Giordan, 1988
Bathysciola parvula Bonadona & Giordan, 1988: 242.

Bathysciola silvicola Jeannel, 1910
Bathysciola Aubei subsp. *silvicola* Jeannel, 1910f: 51.
Bathysciola (s. str.) *silvicola* Jeannel: Jeannel, 1924a: 107.

Bathysciola solarii (Dodero, 1900)
Bathysciola solarii aemiliana Jeannel, 1924
Bathysciola (s. str.) *Solarii* subsp. *aemiliana* Jeannel, 1924c: 54.
Bathysciola (s. str.) *solarii aemiliana* Jeannel: Perreau, 2000: 228.
Bathysciola solarii solarii (Dodero, 1900)
Bathyscia Solarii Dodero, 1900: 416.
Bathysciola Aubei Solarii Dodero: Jeannel, 1910a: 27.
Bathysciola (s. str.) *Solarii* Dodero: Jeannel, 1924a: 106.
Bathysciola (s. str.) *solarii solarii* (Dodero): Perreau, 2000: 229.

Bathysciola spectata Bonadona & Giordan, 1988
Bathysciola spectata Bonadona & Giordan, 1988: 244.

Bathysciola subalpina (Fairmaire, 1869)
Adelops subalpinus Fairmaire, 1869: 231.
Bathyscia (*Bathyscia*) *subalpina* Fairm.: Reitter, 1885 [1884]: 25.
Bathysciola Aubei subalpina Fairmaire: Jeannel, 1910a: 27.
Bathysciola subalpina Fairmaire: Fagniez, 1927: 20.

Bathysciola turcati Fagniez, 1922
Bathysciola (s. str.) *Turcati* Fagniez, 1922: 106.
Bathysciola turcati Fagniez: Bonadona, 1985: 6.

Bathysciola ubayensis Fagniez, 1922
Bathysciola (s. str.) *Aubei* subsp. *ubayensis* Fagniez, 1922: 107.
Bathysciola ubayensis Fagniez: Fagniez, 1927: 19.

***Bathysciola* unavailable names**

Avon & Courtial (2008), in their review on the *Bathysciola* from Provence-Alpes-Côte d'Azur, proposed different taxon names, that do not comply with segments 16.4.1 and 16.4.2 of the Code of Zoological Nomenclature (ICZN 1999) regarding to the mandatory name-bearing type designation. Consequently, all the names of the taxa described are to be considered unavailable. In the case of subspecies, they have been incorporated into the synonymy list of each of the nominotypical subspecies, and the species are listed below:
Bathysciola aubierensis Avon & Courtial, 2008: 38 (Unavailable name).
Bathysciola bonadonius Avon & Courtial, 2008: 26 (Unavailable name).
Bathysciola magalii Avon & Courtial, 2008: 45 (Unavailable name).
Bathysciola pseudodigitata Avon & Courtial, 2008: 21 (Unavailable name).

***Bathysciola* incertae sedis**

Bathysciola ovoidea (Fairmaire, 1869)
Adelops ovoideus Fairmaire, 1869: 231.
Bathyscia (*Bathyscia*) *ovoidea* Fairm.: Reitter, 1885 [1884]: 22.
Bathysciola ovoidea Fairmaire: Jeannel, 1910a: 28.

This is an enigmatic species whose typical locality are the «Alpes-Maritimes» and for which Jeannel (1924a) added a second locality: the Bormida di Spigno on the edges of the Ligurian Alps and the Ligurian Apennines. Either locality lies in the distribution area of *Bathysciola* and not in the corresponding *Galliana linderi* comb. nov. *Bathysciola ovoidea* is related to *Bathysciola linderi* forming section VIII described by Jeannel (1924a).

Genus ***Cytodromus*** Abeille de Perrin, 1876
Cytodromus Abeille de Perrin, 1876: 30.
Eskualdunella Coiffait, 1950b: 65 (Type species: *Eskualdunella Delespierrei* Coiffait, 1950 = *Pholeuon dapsoïdes* Abeille de Perrin, 1875).

Type species. *Pholeuon dapsoides* Abeille de Perrin, 1875 by monotypy (habitus in Fig. 182.2).

Diagnosis. Size ranging between 3.5-5.0 mm. Pholeuonoid facies (Fig. 182.2); body shape elliptical and broad or long. Integument shiny, without microreticulum. In general, the female is more robust, convex and larger than the male; antennomeres somewhat thicker and shorter.

Head: Incompletely retractable, occipital carina

entire, although very poorly marked; epistomal suture curved and darkened.

Antennae: Much longer than the elytral suture; all the segments clearly longer than wide and the 7th to 10th dilated in the apical part.

Pronotum: Almost as long as wide; maximum width towards the middle; sides slightly arched, slightly sinuous and raised backwards so that the posterior vertices are deflected, protruding and separated from the disc forming a deep fold; base narrower than the basal area of elytra.

Elytra: Longer than the pronotum, elliptic, with blurred or well-marked shoulders and widest in the middle; marginal rim visible throughout its length and rounded apices extend over the pygidium; whole parasutural stria, separated from the suture in the middle, tangent to it at the apical part of the elytra.

Legs: Long and thin; male protarsi as wide as or slightly wider than the apical area of the protibia and first tarsomere larger than the second; protrochanters with a small spine on posterior margin; very long and falciform claws; protibiae attenuated, meso- and metatibiae straight.

Mesoventral keel (Fig. 182.5): Blurred or poorly defined, very low; forms a continuous ventral border, subrectilinear in the first half and convex in the second and at the junction of these two parts a small sharp protuberance.

Suture of the metaventrite (Fig. 182.5): In a regular arc from the beginning to the end of the mesocoxal cavity; delimits a narrow area.

Metatergal apparatus (Fig. 183.3): With the metascutum long and narrow, one wing of the metascutum being as long as the alacrista; the apophysis of the alacrista prolonged and the apices not very sharp.

Metendosternite (Figs 184.3, 184.4): In «Y», with furcal arms and trunk long. Arms clearly longer than the trunk, narrow to the apical area which is somewhat dilated, with a reduced terminal apophysis; an anterior rim of the furca in each arm delimits an anterior lamina, narrow and long in the basal part, while the posterior lamina progressively narrow but are preserved until the apex of the arm, being the border slightly wavy in the anterior part and arched in the middle and posterior parts. Furcal trunk twice as long as width of basal part; the mid-trunk keel diverges widely posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 185.2), regularly arched; the dorsal face of the apical third with a more or less marked depression and then strongly sinuous; the apex very fine and sharp is prolonged and oriented towards the dorsal face. In dorsal view (Fig. 186.4) triangular in shape; decreases towards the apex which is more or less pointed depending on the species. Ventral lamina reduced.

Endophallus (Fig. 186.4): With three regions. In the basal there is a complete and well-developed «Y»-piece and a ventral complex inside this there is a short stylet. In the middle there is an axial piece of triangular shape, two phanerae parenthesis-shaped that have a denticle towards the top, two small phanerae sclerotized inside the parenthesis and two more are very fine that form another external parenthesis. In the apical there are reinforcing bands that rest on long sclerotized nodules that are ridged and have a lobe at their lower end.

Parameres (Fig. 186.8): Fine and somewhat shorter than the median lobe; the apex more or less thickened, with three setae, one longer than the others; these three setae have an apical insertion or two have an apical insertion and the other is internal, shorter, at the base of the club.

Spermathecal complex (Fig. 187.2): Spermatheca long, with both lobes sclerotized and dilated, the basal one much more dilated; spermatic duct four to five times longer than the spermatheca; there is spermathecal gland.

Female uroventrite VIII (Fig. 188.2): Spiculum widened towards the apex; the apex truncated.

Discussion. Both morphologically and molecularly, *Cytodromus* is closely related to *Royerella* with support of 100/100 (Fig. 1G), they are sister genera which frequently coexists in the same environment. This part of the clade is in turn sister to *Bathysciola* with a support of 83.7/100. It seems certain that in this case as well as in the *Diaprysius* clade there is an alternating appearance of pholeuonoid and bathyscioid forms in this geographical area, in which they are derived forms from *Bathysciola* that is by definition actually bathyscioid. A similar case of this coexisting body shapes in a clade then is present in the *Isereus* group, here for instance the: *Isereus* shows a pholeuonoid body shape and *Ochsiella* stat. nov. one that is bathyscioid. If it is observed the sister group *Isereus* of this clade, it is also formed by elements of the two forms: *Isereus* (pholeuonoid) and *Ochsiella* stat. nov. (bathyscioid) among others.

Distribution. France. Species distributed in the greater area of the Isère, on both banks of the Bourne, in numerous caves of the Vercors and Royans massifs (Alonso & Lefèbvre 2012).



FIGURES 185.1–185.3: *Cytodromus* series, *Cytodromus* group. Aedeagus in lateral view of: (**1**) *Bathysciola aubei,* (**2**) *Cytodromus dapsoides,* (**3**) *Royerella villardi villardi.*

Species

Cytodromus ambiguus Laneyrie, 1963
Cytodromus ambiguus Laneyrie, 1963: 114.

Cytodromus dapsoides (Abeille de Perrin, 1875)
Pholeuon dapsoides Abeille de Perrin, 1875a: clxxx.
Cytodromus dapsoides Abeille de Perrin: Abeille de Perrin, 1876: 30.
Eskualdunella delespierrei Coiffait, 1950b: 65.

Cytodromus henroti Jeannel, 1948
Cytodromus henroti conandi Laneyrie, 1961
Cytodromus henroti conandi Laneyrie, 1961: 429.
Cytodromus henroti gallorum Réveillet, 1974
Cytodromus henroti gallorum Réveillet, 1974: 664.
Cytodromus henroti henroti Jeannel, 1948
Cytodromus Henroti Jeannel, 1948b: 77.
Cytodromus henroti Jeannel: Réveillet, 1974: 665.
Cytodromus henroti henroti Jeannel: Perreau, 2000: 258.

Genus ***Royerella*** Jeannel, 1910
Royerella Jeannel, 1910a: 9.

TYPE SPECIES. *Adelops tarissani* Bedel, 1878 by original designation (habitus in Fig. 182.3).

DIAGNOSIS. Size ranging between 3.5-4.0 mm. Bathyscioid facies. Body shape oval, wide and depressed, slightly convex (Fig. 182.3). Matt integument with a well-printed microreticulum. Female of the same shape and size as the male.

Head: Incompletely retractable, always visible from above, and occipital carina complete but blurred in the centre; epistomal suture sinuous and darkened.

Antennae: Long, as long as the elytral suture; all the segments longer than wide; the club segments being thickened and the 8th being the shortest, two and a half times as long as wide.

Pronotum: Very transverse, almost twice as wide as long, with sides regular and fully arched or subparallel in the basal part; widest on the verge of the base, the latter is as wide as the base of the elytra; acute posterior angles and pointed vertices projecting backwards; sinuous base.

Elytra: Long and wide, between 1.4-1.5 times longer than wide, with a narrow rim and slightly corrugated; apices rounded and slightly ruptured and cover completely the pygidium; almost complete parasutural stria, blurred in the vicinity of the scutellum and separated in the middle area.

Legs: Long and slender. Male protarsi dilated, as wide as or wider than the apical area of the protibia; protibiae not attenuated, mesotibiae somewhat curved and metatibiae straight.

Mesoventral keel (Fig. 182.6): Very low and towards the middle a small spiny protuberance.

Suture of the metaventrite (Fig. 182.6): It delimits an area very narrow and arched that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 183.4): Robust, with the metascutum long and narrow being a wing of the metascutum somewhat longer than the alacrista; the apophysis of the alacrista prolonged and the apices not very pointed.

Metendosternite (Fig. 184.5): Furcal arms and trunk long. Arms somewhat longer than the trunk, narrow towards the apical area which is very slightly curved and dilated; anterior and posterior borders of the furcal arms join and are prolonged into a filiform structure apically pointed; no terminal apophysis defined; the posterior lamina of the furca narrows progressively but is preserved up to the apical area, with a straight edge in the anterior area and a smooth arc in the middle and posterior areas. Trunk nearly twice as long as width of the basal part; the middle keel of the trunk diverges posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 185.3) the apical third more or less sinuous depending on the species, with a marked depression at the beginning of the apical part and the apex sharp oriented slightly towards the ventral side. In dorsal view (Fig. 186.5) broad in the basal and middle parts; arched sides that narrow very little in the apical part and the apex broadly rounded. Small basal lamina.

Endophallus (Fig. 186.5): With three distinct regions. In the basal region there is «Y»-piece, ventral complex and a fine and short stylet. In the middle there are two large and long plates that have very sclerotized lobes on their upper end and two small phanerae also very sclerotized on their external part; these, together with two fine phanerae more external still, extend to the well-developed «Y»-piece. In the apical region there are reinforcing bands that rest on membranous ligules whose inner edge is strongly sclerotized.

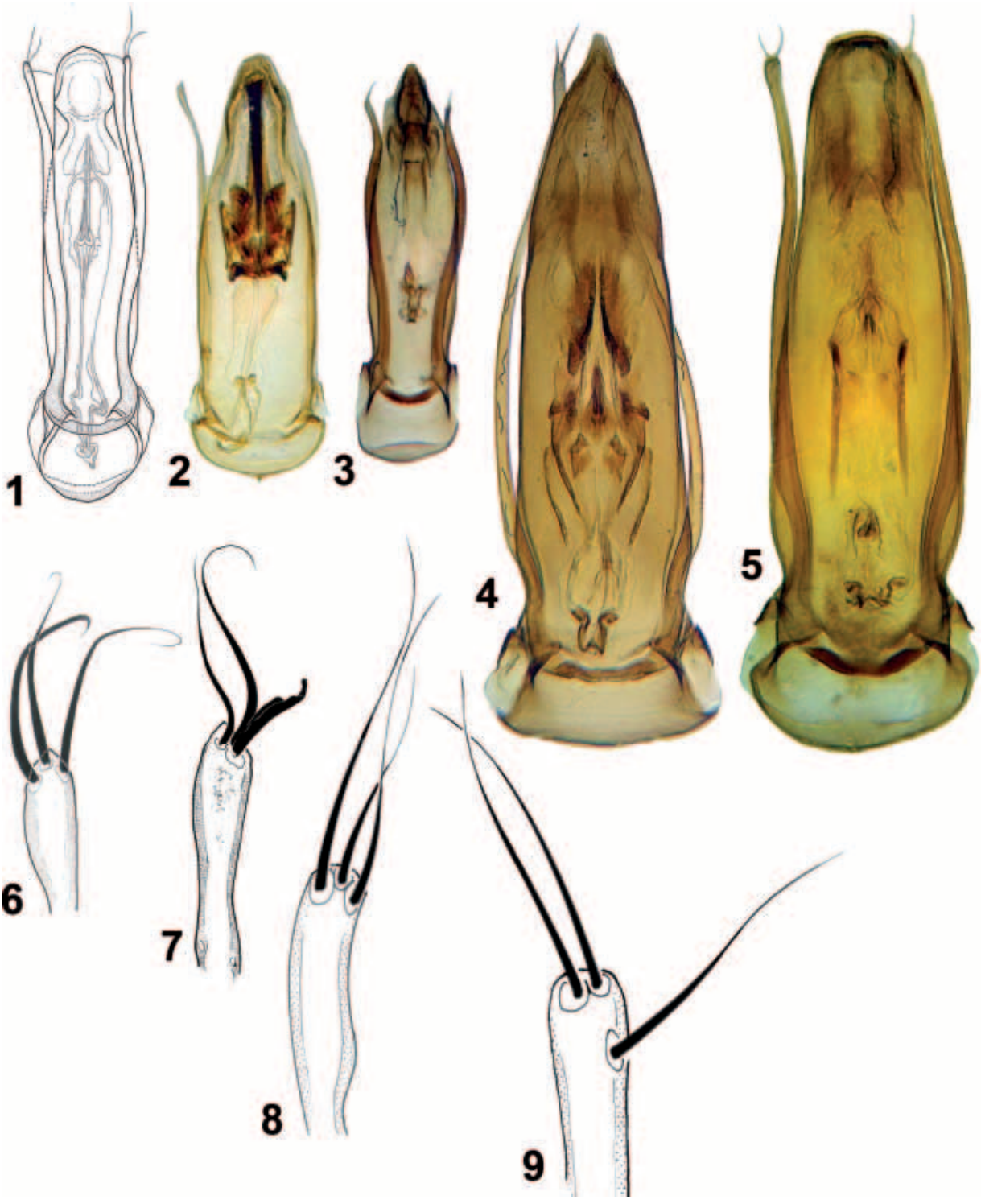
Parameres (Fig. 156.9): Fine and somewhat shorter than the median lobe; apical part somewhat widened in a palette in which three setae long and subequal are inserted, two apical and one of preapical insertion.

Spermathecal complex (Fig. 187.3): Spermatheca long, with both lobes sclerotized and dilated, the basal one slightly more dilated; hyaline junction canal as long as the apical lobe; spermatic duct short and near the junction to the spermatheca drain a diffuse spermathecal gland.

Female uroventrite VIII (Fig. 188.3): Median posterior border slightly concave; spiculum short, widened at the base and apex between rounded or truncated.

DISCUSSION. This genus is morphologically close to *Cytodromus*. It could be a case of sympatric divergence, since they coexist in the same geographical area and apparently in the same environment: species of both genera can be observed together, although it is probable that they exploit different ecological niches. Molecular phylogeny demonstrates a close relationship between these two sister genera by a very high support of 100/100 (Fig. 1G).

DISTRIBUTION. France. Drôme and Isère. Caves in the Vercors, Royans, Coulmes, Cirque de Choranche, Plateau de Presles and Forêt de Lente massifs. Switzerland, Canton of Berne.



FIGURES 186.1–186.9: *Cytodromus* series, *Cytodromus* group. Aedeagus in dorsal view of: (**1**) *Bathysciola aubei,* (**2**) *B. brevicollis*, (**3**) *B. turcati*, (**4**) *Cytodromus dapsoides,* (**5**) *Royerella tarissani lentensis*. Apex of the paramere of: (**6**) *B. aubei,* (**7**) *B. turcati*, (**8**) *Cytodromus henroti henroti,* (**9**) *R. villardi villardi.*

Species

Royerella argodi Fagniez, 1917
Royerella Argodi Fagniez, 1917: 91.
Royerella Tarissani Argodi Fagniez: Jeannel, 1952b: 47.
Royerella argodi Fagniez: Réveillet, 1980:178.

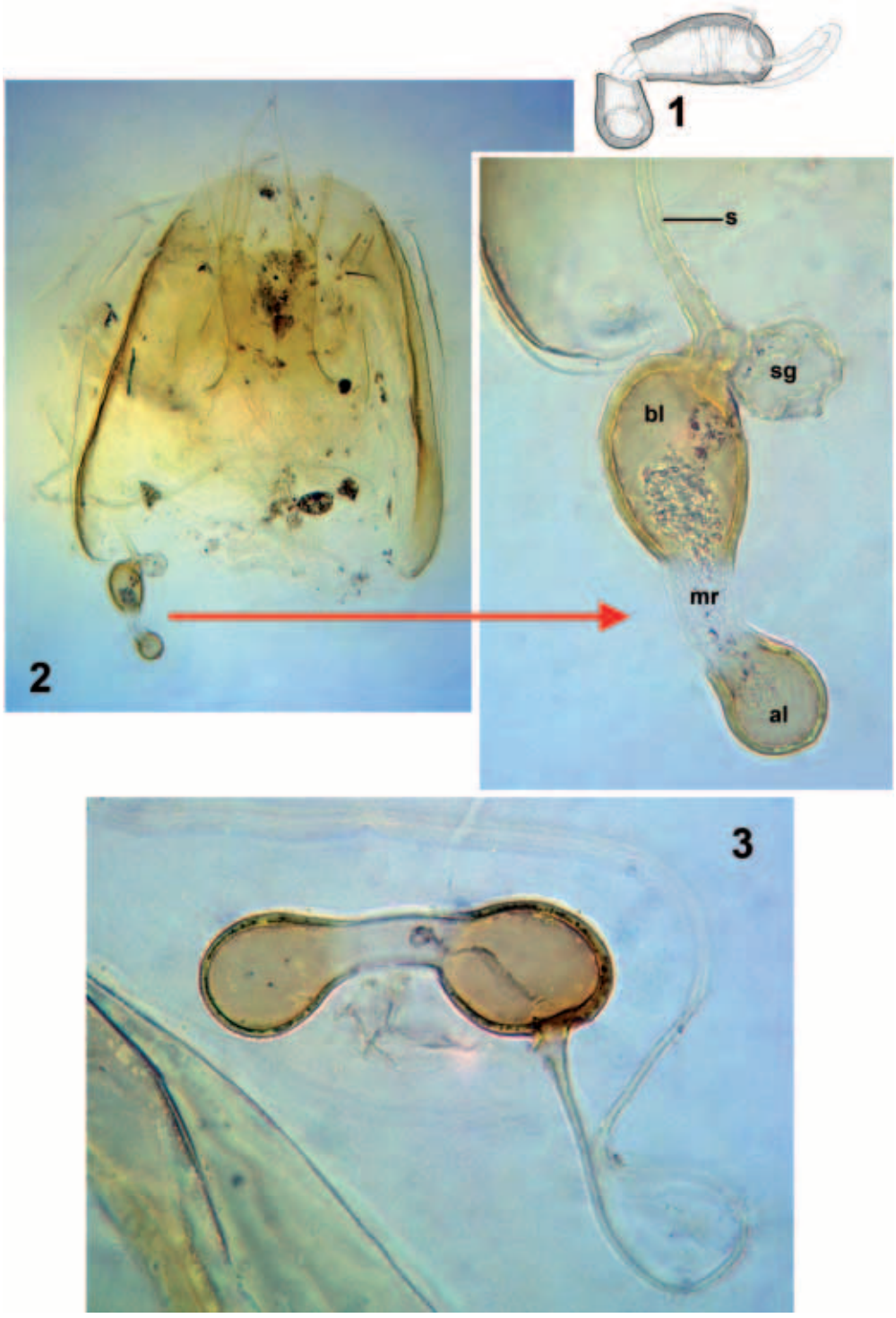
Royerella cularensis Jeannel, 1952
Royerella cularensis Jeannel, 1952b: 48.

Royerella tarissani (Bedel, 1878)
Royerella tarissani bettingeri Bettinger, 1923
Royerella tarissani var. *Bettingeri* Bettinger, 1923: 112.
Royerella tarissani bettingeri Bettinger: Réveillet, 1980: 178.
Royerella tarissani ferrierensis Fagniez, 1917
Royerella Tarissani race *ferrierensis* Fagniez, 1917: 91.
Royerella tarissani ferrierensis Fagniez: Réveillet, 1980: 178.
Royerella tarissani gaveti Laneyrie, 1955
Royerella tarissani gaveti Laneyrie, 1955: 28.
Royerella tarissani henroti var. *gaveti* Laneyrie: Réveillet, 1980: 178.
Royerella tarissani henroti Jeannel, 1948
Royerella (s. str.) *Henroti* Jeannel, 1948b: 76.
Royerella tarissani henroti Jeannel: Réveillet, 1980: 178.
Royerella tarissani hustachei Fagniez, 1917
Royerella Tarissani race *Hustachei* Fagniez, 1917: 91.
Royerella tarissani hustachei Fagniez: Réveillet, 1980: 178.
Royerella tarissani lentensis Fagniez, 1917
Royerella Tarissani race *lentensis* Fagniez, 1917: 91.
Royerella tarissani lentensis Fagniez: Réveillet, 1980: 177.
Royerella tarissani rivularis Bettinger, 1923
Royerella Tarissani var. *rivularis* Bettinger, 1923: 111.
Royerella tarissani rivularis Bettinger: Réveillet, 1980: 178.
Royerella tarissani tarissani (Bedel, 1878)
Adelops Tarissani Bedel, 1878: LXXIV.
Bathyscia (Bathyscia) Tarissani Bedel: Reitter, 1885 [1884]: 23.
Royerella Tarissani Bedel: Jeannel, 1910a: 35.
Royerella (s. str.) *Tarissani* subsp. *Tarissani* Bedel: Jeannel, 1924a: 200.
Royerella tarissani tarissani Bedel: Réveillet, 1980: 177.
Royerella tarissani vertacomicora Fagniez, 1917
Royerella Tarissani race *vertacomicora* Fagniez, 1917: 91.
Royerella tarissani vertacomicora Fagniez: Réveillet, 1980: 178.

Royerella villardi (Bedel, 1884)
Royerella villardi matheyi Jeannel, 1922
Royerella Villardi subsp. *Matheyi* Jeannel, 1922b: 203.
Royerella villardi matheyi Jeannel: Besuchet, 1986: 157.
Royerella villardi sermeti Jeannel, 1948
Royerella Villardi subsp. *Sermeti* Jeannel, 1948c: 466.
Royerella Villardi subsp. *Sermeti* sous-race *Strinatii* Jeannel: Jeannel, 1955c: 25.
Royerella villardi sermeti Jeannel: Strinati, 1955: 11.
Royerella villardi villardi (Bedel, 1884)
Bathyscia Villardi Bedel, 1884: LIII.
Bathyscia (*Bathyscia*) *Villardi* Bedel: Reitter, 1885 [1884]: 23.
Royerella Villardi Bedel: Jeannel, 1910a: 35.
Royerella (s. str.) *Villardi* subsp. *Villardi* Bedel: Jeannel, 1924a: 201.
Royerella Villardi subsp. *Villardi* sous-race *longicornis* Jeannel, 1955c: 25.
Royerella villardi. villardi Jeannel: Besuchet, 1986: 157.
Royerella villardi. longicornis Jeannel: Besuchet, 1986: 157.

3.3.2 Subclade series ***Spelaeochlamys***, ***Nanobathysciola*** gen. nov. and ***Quaestus***

The Leptodirini belonging to the sister series *Quaestus*, *Nanobathysciola* and *Spelaeochlamys* constitute independent clades with acceptable and similar supports in the analyzes carried out; the more basal clade *Spelaeochlamys* is sister of *Nanobathysciola* gen. nov. and *Quaestus* series with support (94.7/95) (Fig. 1F), and these two share a node with 68.3/85. The support is not very high but their relationship is supported by well-defined geographic distributions: 1. the *Quaestus* series in the Cantabrian mountains, 2. the *Nanobathysciola* series on both slopes of the Pyrenées mountains and 3. the *Spelaeochlamys* series in the Mediterranean coast of the Iberian peninsula. The three areas form a continuum from the eastern reliefs of Galicia to the Alicante mountains. The clade formed by these three series is sister to the *Cytodromus* series with support 79.7/90.



FIGURES 187.1–187.3: *Cytodromus* series, *Cytodromus* group. Spermathecal complex of: (**1**) *Bathysciola aubei,* (**2**) *Cytodromus dapsoides,* (**3**) *Royerella villardi villardi.* Abbreviations: **al**, apical lobe; **bl**, basal lobe; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

KEY TO SERIES

1. Endophallus with «Y»-piece in the basal region ... .series *Nanobathysciola*
- Endophallus without «Y»-piece in the basal region, with stylet or unarmed.....2

2. Mesoventral keel high and short, the posterior apophysis reaches, or very slightly exceeds the meso-coxal cavities (Figs 190.1-190.3). Apical part of the furcal arms of the metendosternite narrow and straight or very slightly dilated and arched (Figs 190.9-190.11). Spermatheca with poorly differentiated basal lobe (Figs 191.10-191.12). Species distributed along a strip near the Mediterranean coast, between the south of Tarragona (Ebro river) and Alicante..... .....series *Spelaeochlamys*
- Mesoventral keel high and long, in some species of *Quaestus* somewhat shorter but, at least, always reaching the middle of the metaventrite (Figs 193.3, 193.4, 197.1-197.6, 204.1-204.11). Apical part of the furcal arms of the metendosternite wider, with the apex arched (Fig. 194.3, 194.4, 198.4-198.6, 206.1-206.7). The spermatheca with the basal lobe generally well differentiated (Figs 195.5, 195.6, 200.7-200.12, 209.1-209.9). Species distributed along the Cantabrian coast, between western Guipúzcoa (Deva River) and the provinces of Lugo and Oviedo, except for a small enclave in the Sierra de Guadarramas e - ries .....*Quaestus*

3.3.3 Series ***Spelaeochlamys***

DIAGNOSIS. Bathyscioid or bathyscioid-elongated with bell-shaped pronotum. Reddish colouration and integument entirely covered by fine, lying, dense, whitish-yellowish pubescence. Pronotum smooth and elytra with rough or granular punctation. Depigmented.

Head: With occipital carina. Epistomal suture slightly curved and darkened. Last segment of maxillary palps short and conical. Anophthalmous.

Antennae: With 11 antennomeres, shorter than the elytral suture and dilated from the 7th article. Females with shorter antennae than males.

Elytra: Without parasutural stria.

Legs: Proportionally long and slender; male protarsi pentameres, slightly dilated, with adhesive setae on ventral side; females tetrameres protarsi not dilated. All tibiae hairy, with two internal spurs pectinate, two simple external ones and a series of unequal spines between them; unattenuated protibiae without combs; meso- and metatibiae practically straight.

Mesoventral keel: Not prolonged over the metaventrite and the vertex rounded or hooked.

Metaventrite: With a bifid protruding process that separates the metacoxal cavities.

Suture of the metaventrite: Exists in *Anillochlamys* and *Paranillochlamys*; absent in *Spelaeochlamys*.

Metendosternite: Furcal arms narrow, straight or very slightly sinuous and the apex sharp or slightly thickened and curved; lacks the anterior lamina of the furca.

Male genital segment: Very small, ring-shaped with two long pedunculus.

Median lobe of aedeagus: The shape varies depending on the genus, but the basal lamina is longer than the ventral lamina of the tegmen and has a more or less distinct keel or tongue in the middle of the apical part.

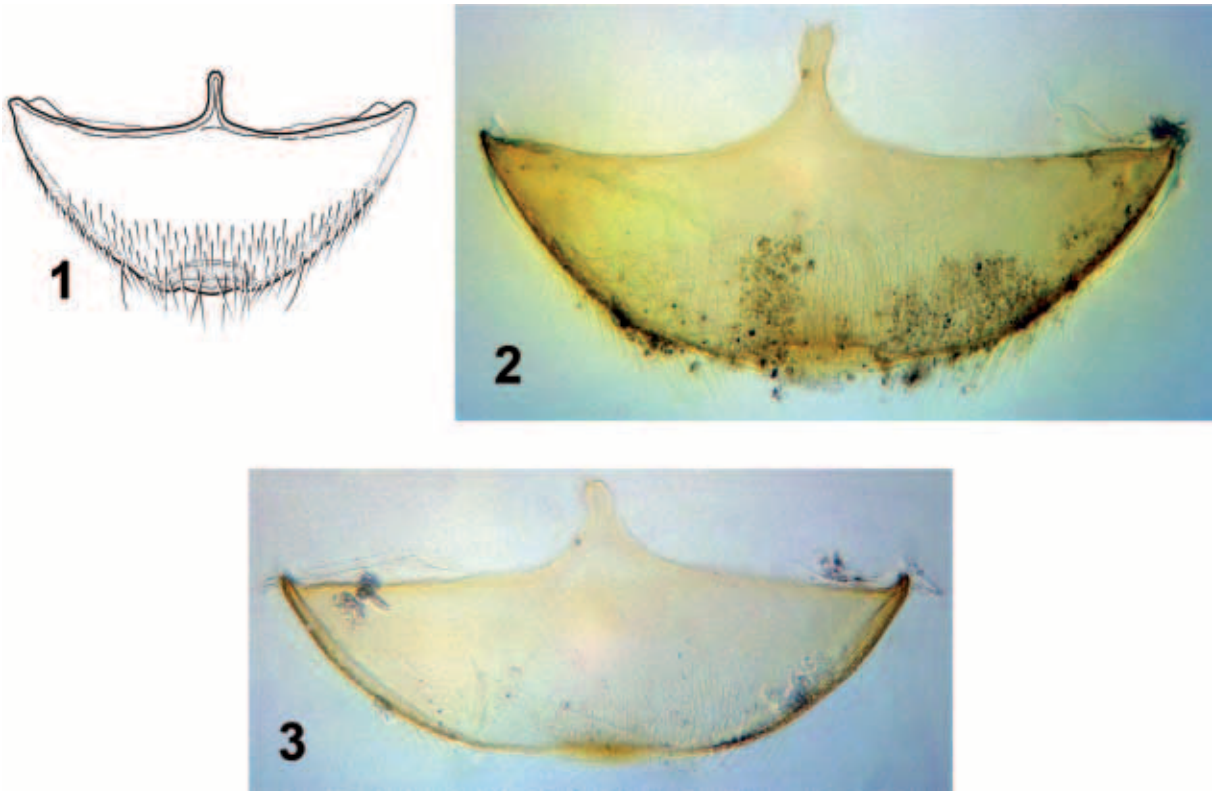
Tegmen: Basal lamina usually with a keel, generally short.

Parameres: As long as or slightly longer than the median lobe, with three setae on the club, two adjoining and one separated.

Endophallus: With a very short stylet in *Anillochlamys* and *Spelaeochlamys*, and a very long one in *Paranillochlamys*. Stylet surrounded by squamous or spinous tissue and, in addition, two reinforcing bands covered with scales, spines, pilosity, or a combination of these structures.

Spermathecal complex: Spermatheca short, longer than wide; in general, three regions are differentiated, two lobes and the junction duct, with the basal lobe being poorly differentiated and the apical lobe more dilated and rounded; the spermatic duct, in general, somewhat widened in the interface to the basal lobe of the spermatheca and without a connecting piece to the copulatory bag.

DISCUSSION. It is the sister group to the entire clade *Quaestus* series + *Nanobathysciola* series (Fig. 1F) with a support of 94.7/95, in terms the series is with 100/100 highly supported . The *Spelaeochlamys* clade is consisting of three genera that are strictly subterranean and live on the Mediterranean coast of Spain, from the Tivissa and Montsant mountains, to the north of the Ebro river in Tarragona, to the south into theprovince of Alicante, in what would be the remains of the old Catalan range (Salgado & Fresneda 2004a). Together with the genera *Ovobathysciola* and *Patriziella* from Sardinia, they are part of Laneyrie's «group II» (Laneyrie 1967, 1969), association refused by the phylogenetic study. This clade was therefore



FIGURES 188.1–188.3: *Cytodromus* series, *Cytodromus* group. Female uroventrite VIII of: (**1**) *Bathysciola aubei,* (**2**) *Cytodromus dapsoides,* (**3**) *Royerella argodi.*

placed inside the «Supraflagellates» as defined by Giachino *et al*. (1998). In the opinion of Español (1975) the section *Anillochlamys* (= *Spelaeochlamys* series) includes the Iberian genera *Anillochlamys*, *Paranillochlamys*, *Spelaeochlamys* and *Typhlochlamys*, which, were considered closely related to *Ovobathysciola* and *Patriziella* from the island of Sardinia. However, according to this author, the genus *Typhlochlamys* did not seem to be linked to the two Tyrrhenian genera, but he considered it to be an intermediate link between *Anillochlamys* and *Spelaeochlamys*; a geographical neighbor of both, and he pointed out the possibility that future surveys in still unexplored areas from Sardinia could discover the tyrrhenid homologue of the Iberian *Typhlochlamys*,. The morphological study points in this direction, although the molecular study has revealed that the coincidence in morphological structures with the Sardinian Leptodirini is due to evolutionary convergence.

Key to genera

1. Very long stylet that extends through much of the endophallus (Fig. 191.5). Metendosternite robust, with the furcal trunk wider and longer (Fig. 190.10) ....*Paranillochlamys*
- Very short stylet (Figs 191.4, 191.6). Metendosternite more gracile, with furcal trunk narrower and shorter (Figs 190.9, 190.11) 2

2. Body elliptical, elongated, with the posterior lateral margins of the pronotum sinuous (Fig. 189.3). The vertex of the mesoventral keel forms a hooked tooth (Fig. 190.3) and metaventrite without suture (Fig. 190.3). Metatergal apparatus with very narrow metascutum and alacrista absent (Fig. 190.8). Metendosternite with the apical area of the furcal arms straight and sharp (Fig. 190.11). Apical area of the median lobe of

aedeagus widened, with subparallel sides (Fig. 191.6). Spiculum of the VIII uroventrite of the female short, very wide and truncated (Fig. 191.15) ....*Spelaeochlamys*

- Body ovoid, almost hemispherical, with the posterior lateral margins of the pronotum in a continuous arc (Fig. 189.1). Vertex of the mesoventral keel rounded and metaventrite with an arched suture (Fig. 190.1). Metatergal apparatus with wide metascutum and with alacrista (Fig. 190.6). Metendosternite with the apical area of the furcal arms not very pointed and somewhat curved (Fig. 190.9). Apical part of the median lobe of aedeagus with a regular curve towards the apex (Fig. 191.4). Spiculum of the VIII uroventrite of the female longer and narrower (Fig. 191.13).....*Anillochlamys*

Genus ***Anillochlamys*** Jeannel, 1909
Anillochlamys Jeannel, 1909b: 471.

Type species. *Bathyscia tropica* Abeille de Perrin, 1881 by original designation (habitus in Fig. 189.1).

Diagnosis. Size ranging between 1.6-2.5 mm. Body shape bathyscioid (Fig. 189.1), short, wide, almost hemispherical and very convex.

Antennae: Proportionally short, with the first and second antennomeres robust, longer than wide, and the 11th longer and wider than the 10th.

Pronotum: Proportionally large, very transverse, narrowed forwards and somewhat wider than the elytra taken as a whole; lateral margins regularly arched and maximum width at the base; posterior angles acute.

Elytra: Short, with maximum width at the base or in middle; very fine marginal edge, always visible, sharp and dehiscent apices.

Legs: Tibiae with spaced spines on the external face.

Mesoventral keel (Fig. 190.1): High, with the anterior border slightly convex and strongly beaded; lower edge sinuous with the arista and vertex rounded.

Suture of the metaventrite (Fig. 190.1): Describes an arc that is well separated from the edge of the mesocoxal cavity in the first half of its course, then runs contiguous and parallel to the edge, the area being very narrow.

Metatergal apparatus (Fig. 190.6): Wings of the metascutum wide and elongated, apophysis of the alacrista long and pointed.

Metendosternite (Fig. 190.9): Furcal arms longer than its trunk, from the base to the apex they narrow progressively and are straight; apex slightly dilated and curved, without terminal apophysis; posterior lamina of the furca is continuous almost up to the apical part, with the posterior edge almost straight. Trunk short, the length equal to the width of the basal part; middle keel on trunk diverges posteriorly, conspicuous short keel.

Median lobe of aedeagus: In lateral view (Fig. 191.1), sinuous and abruptly pointed at its distal end; in dorsal view (Fig. 191.4), with subparallel sides and the widened apical part ends in a more or less narrow arc and in some species is prolonged into a small lobe.

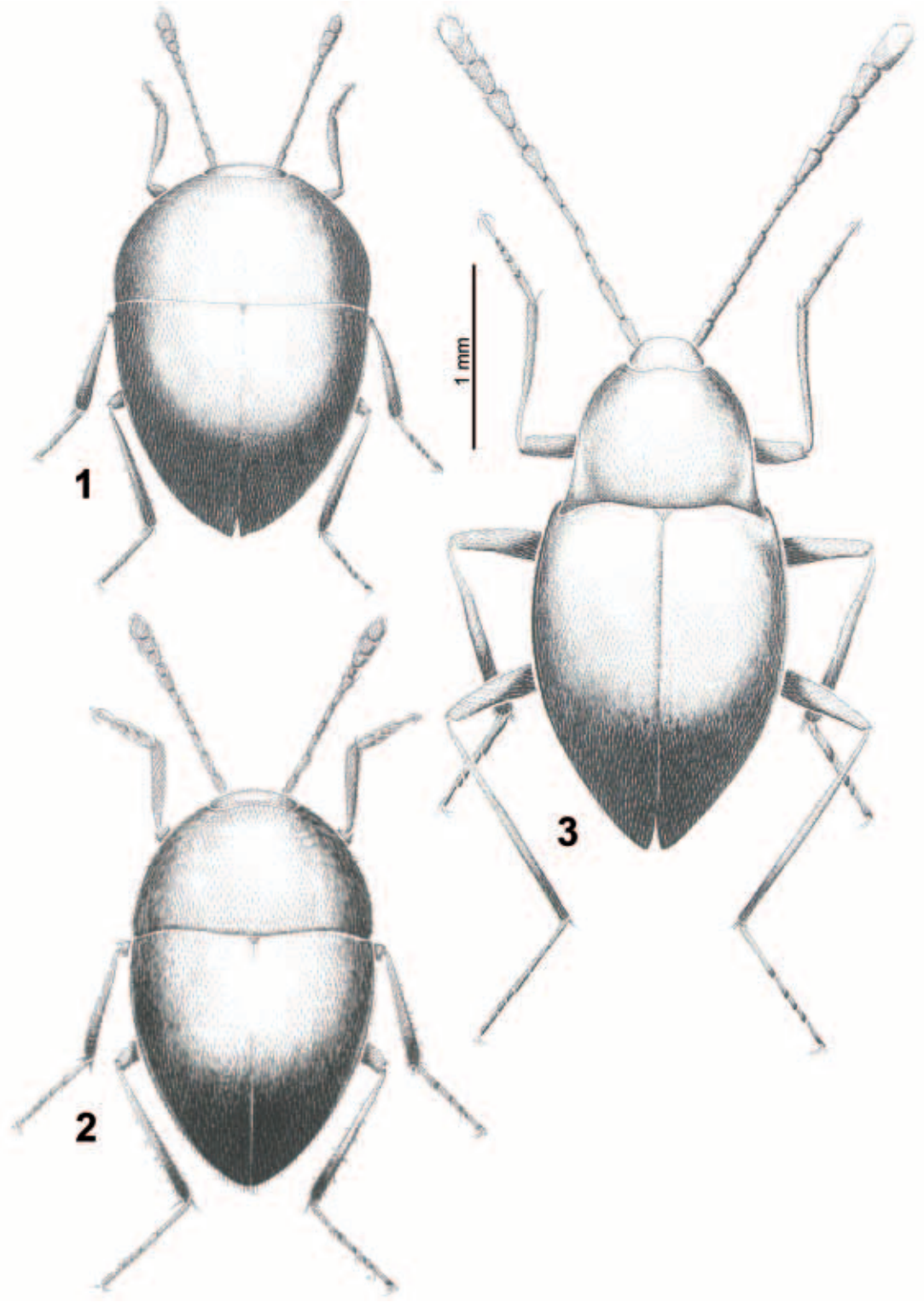
Endophallus (Fig. 191.4): With a tooth or stylet more or less complex, wrapped in a scaly, spiny or hairy sac; there are two reinforcing bands that can be densely covered with scales, spines or hair.

Parameres (Fig. 191.7): The apex armed with three subequal setae, one of them with a preapical insertion, and a more or less developed apical membranous prolongation. Basal lamina of tegmen with a conspicuous short keel in the middle of the apical part.

Spermathecal complex: Spermatheca (Fig. 191.10) little curved and little sclerotized; basal lobe more or less differentiated, apical thick and rounded and middle region or junction duct hyaline; there is a spermathecal gland inserted in the anterior thickening of the spermatic duct near the point of union with the spermatheca; spermatic duct two or three times longer than the spermatheca, attaches directly to the copulatory bag.

Female uroventrite VIII (Fig. 191.13): Spiculum can be short and spatuliform, short, very wide and truncated or long, thin and sharp.

Discussion. The genus *Anillochlamys*, although it is close to *Spelaeochlamys*, is clearly different body shape and is also divergent with respect to other characters such as the mesoventral keel, suture of the metaventrite, metatergal apparatus, metendosternite and aedeagus. In *Anillochlamys* the body is short and almost hemispherical, the mesoventral keel has a rounded vertex, the suture of the metaventrite delimits a well-defined area, the wings of the metascutum of the metatergal apparatus are wide and the apophysis of the alacrista well-developed, the apex of the furcal arms slightly dilated and curved outwards, the the median lobe of aedeagus, in dorsal view, has more or less sinuous lateral margins and the apical end is never wider than the rest of the structure; in lateral view, the distal third or fourth is strongly sinuous. The endophallus differs in that it occupies the entire length of the median lobe and does not protrude to the outside in the resting position; it is characterised by presenting



FIGURES 189.1–189.3: *Spelaeochlamys* series. Habitus of: (**1**) *Anillochlamys tropica,* (**2**) *Paranillochlamys velox,* (**3**) *Spelaeochlamys ehlersi.* Figs **1–3** modified from Salgado *et al*. (2008).

a bag formed by different portions of the structure and densely covered in thorns and hair; in the middle part there are two triangular pieces located on both sides of the axis of symmetry that act as a stylet. The parameres are somewhat shorter than the median lobe, with the apex armed with three subequal setae and a small membranous lamina is usually observed. On the other hand, in the genus *Spelaeochlamys* the body is elongated and somewhat elliptical, the keel has a toothed vertex, the suture of the metaventrite borders the entire mesocoxal cavity without delimiting an area, the wings of the metascutum are narrow and there are no apophysis of the alacrista, furcal arms of the metendosternite are very long, pointed and straight in the apical area and the median lobe of aedeagus, in dorsal view, has the apex widened preapically and appearance of a club with a very conspicuous distal tip; in lateral view, it is slightly curved and has a narrower basal portion and a long, slender terminal fourth curved dorsally. The endophallus has pointed scales on the integument and always a more or less dense penicillum at its distal end. The parameres, as long as or somewhat longer than the median lobe, have the apex armed with two setae with a distal insertion and another preapical, and there is no membranous lamina. The relationship with the genus *Paranillochlamys* is somewhat more distant (Fig. 1F), although in this genus the shape of the body is more oval, the vertex of the mesoventral keel forms a tooth, the apical area of the arms of the furca is straight and sharp at the apical part, and although the median lobe is similar to *Anillochlamys*; however, the endophallus of *Paranillochlamys* has a well-differentiated stylet almost as long as the median lobe. In the phylogenetic tree (Fig. 1F) the genus *Anillochlamys* is sister to the genus *Spelaeochlamys* with a fairly high support of 91/100.

Distribution. Spain. Comprises eight species that are distributed throughout the Spanish Levant, from Castelló de la Plana (south of the Ebro river) to the confines of the province of Alicante (Fresneda & Salgado 2017).

Species

Anillochlamys aurouxi Español, 1965
Anillochlamys aurouxi Español, 1965c: 98.
Anillochlamys (s. str.) *aurouxi* Español: Perreau, 2000: 298.

Anillochlamys bueni Jeannel, 1909
Anillochlamys Bueni Jeannel, 1909b: 472.
Bathysciola (*Anillochlamys*) *Bueni* (Jeannel): Jeannel, 1914b: 5.
Anillochlamys bueni Jeannel: Comas, 1983: 246.
Anillochlamys avariae Comas, 1977a: 21.
Anillochlamys (s. str.) *bueni* Jeannel: Perreau, 2000: 299.

Anillochlamys cullelli Lagar, 1978
Anillochlamys cullelli Lagar, 1978: 18.
Anillochlamys (s. str.) *cullelli* Lagar: Perreau, 2000: 299.

Anillochlamys lencinai Salgado & Fresneda, 2006
Anillochlamys lencinai Salgado & Fresneda, 2006: 22.

Anillochlamys moroderi Bolívar, 1923
Anillochlamys moroderi Bolívar, 1923: 423.
Anillochlamys negrei Comas, 1992: 69.
Anillochlamys (s. str.) *moroderi moroderi* Bolívar: Perreau, 2000: 299.

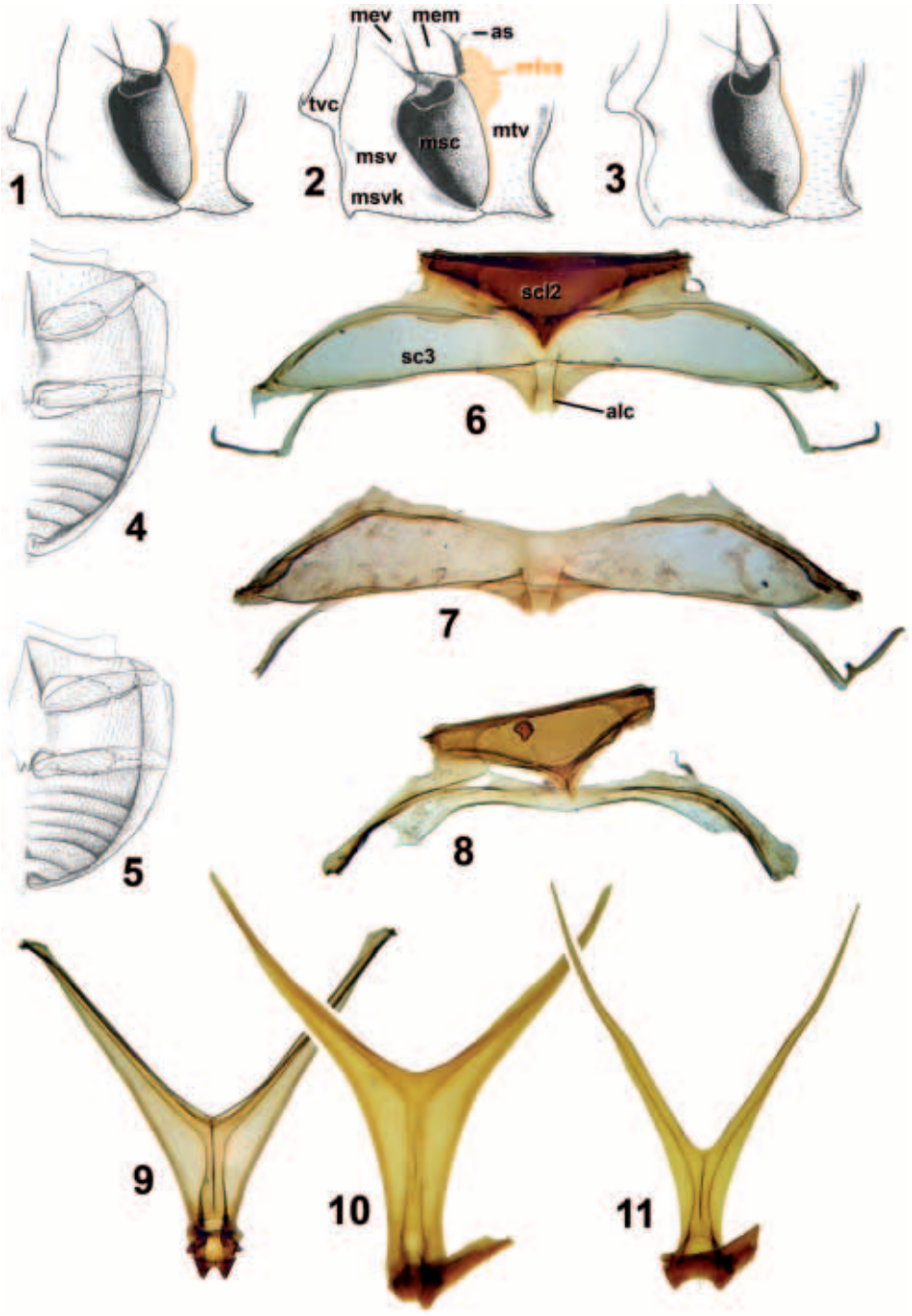
Anillochlamys sendrai Salgado & Fresneda, 2006
Anillochlamys sendrai Salgado & Fresneda, 2006: 20.

Anillochlamys subtruncata Jeannel, 1930
Anillochlamys Moroderi subsp. *subtruncatus* Jeannel, 1930a: 90.
Anillochlamys Baguenai Jeannel, 1930a: 91.
Anillochlamys (s. str.) *moroderi subtruncatus* Jeannel: Perreau, 2000: 299.

Anillochlamys tropica (Abeille de Perrin, 1881)
Bathyscia tropica Abeille de Perrin, 1881: ix.
Bathyscia (*Bathyscia*) *tropica* Ab.: 1885 [1884]: 37.
Adelops hispanicus Ehlers, 1893, *in* Uhagón, 1893: 125.
Anillochlamys tropicus (Abeille): Jeannel, 1909b: 472.
Anillochlamys tropicus var. *apicalis* Jeannel, 1909b: 472.
Bathysciola (*Anillochlamys) tropica* (Abeille): Jeannel, 1914b: 5.
Anillochlamys (s. str.) *tropicus* (Abeille): Perreau, 2000: 299.

Genus ***Paranillochlamys*** Zariquiey, 1940
Paranillochlamys Zariquiey, 1940: 529.

Type species. *Paranillochlamys velox* Zariquiey, 1940 by monotypy (habitus in Fig. 189.2).



FIGURES 190.1–190.11: *Spelaeochlamys* series. Pterothorax in lateral view of: (**1**) *Anillochlamys tropica,* (**2**) *Paranillochlamys velox,* (**3**) *Spelaeochlamys ehlersi.* Pterothorax and abdomen, ventral view of: (**4**) *P. catalonica*, (**5**) *P. urgellesi*. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**6**) *A. tropica*, (**7**) *P. velox*, (**8**) *S. ehlersi*. Metendosternite of: (**9**) *A. tropica*, (**10**) *P. velox*, (**11**) *S. ehlersi*. Figs **1**–**5** modified from Salgado *et al*. (2008). Abbreviations: Pterothorax: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar. Metatergal apparatus: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

DIAGNOSIS. Size ranging between 1.9-3.0 mm. Body shape bathyscioid, oval and convex (Fig. 189.2).

Antennae: With the first and second antennomeres long and narrow.

Pronotum: Transverse, slightly narrowed forward and as wide as the base of the elytra; lateral margins regularly arched and widest at base; posterior angles right.

Elytra: Taper regularly towards the apex and may well exceed the tip of the pygidium, widest at the base; not sharp or dehiscent; marginal edge fine, almost negligible.

Legs: Tibiae with very small and fine spines, spaced apart on the external face.

Mesoventral keel (Fig. 190.2): High, with anterior border slightly sinuous and beaded; lower edge somewhat convex with arista broad and rounded or flat; the angle formed by the edges almost right and the vertex in the form of a hooked tooth.

Suture of the metaventrite (Fig. 190.2): It describes an arc widely separated from the edge of the mesocoxal cavity in the first half of its course, then runs contiguous and parallel to the edge, without delimiting an area.

Metatergal apparatus (Fig. 190.7): Wings of the metascutum wide and elongated, and the apophysis of the alacrista not very prominent.

Metendosternite (Fig. 190.10): More robust than in *Anillochlamys* and *Spelaeochlamys*. Furcal arms somewhat longer than the trunk, both narrow progressively towards the apex, which is straight, sharp and without terminal apophysis; width of posterior lamina narrows sharply to apex, with posterior border concave. Trunk long, one and a half times longer than wide; median keel diverges posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 191.2) slightly arched, the dorsal part slightly arched or with pronounced sinuosity. In dorsal view (Fig. 191.5), subparallel sides in the basal two thirds, then arched and ending in a apex more or less pointed or very sharp.

Endophallus (Fig. 191.5): Armor consisting of a long ventral stylet, which at high magnification is seen to be formed by two sclerotized pieces perfectly differentiated in their three basal quarters and as if enveloped by a fine sheath of chitin; in the apical region there are two hairy reinforcing bands and, between them it can be found a membranous bag covered with thick spines.

Parameres (Fig. 191.8): Thick, particularly towards the basal area, and ending in three twisted setae, two adjacent and one separated; the apex with a minute membranous prolongation, not defined in *P. velox*. Basal lamina of tegmen with a keel, inconspicuous in *P. velox*.

Spermathecal complex (Fig. 191.11): Formed by a small and curved spermatheca, with the two lobes slightly thickened and slightly sclerotized, apically rounded; spermatic duct, which is about two or three times longer than the spermatheca, is inserting directly into the copulation bag and widens before the point of insertion, an area where the spermathecal gland empties; in *P. catalonica* it is formed a small nodule.

Female uroventrite VIII (Fig. 191.14): Spiculum short and wide or short and narrow, with a sharp or slightly dilated tip.

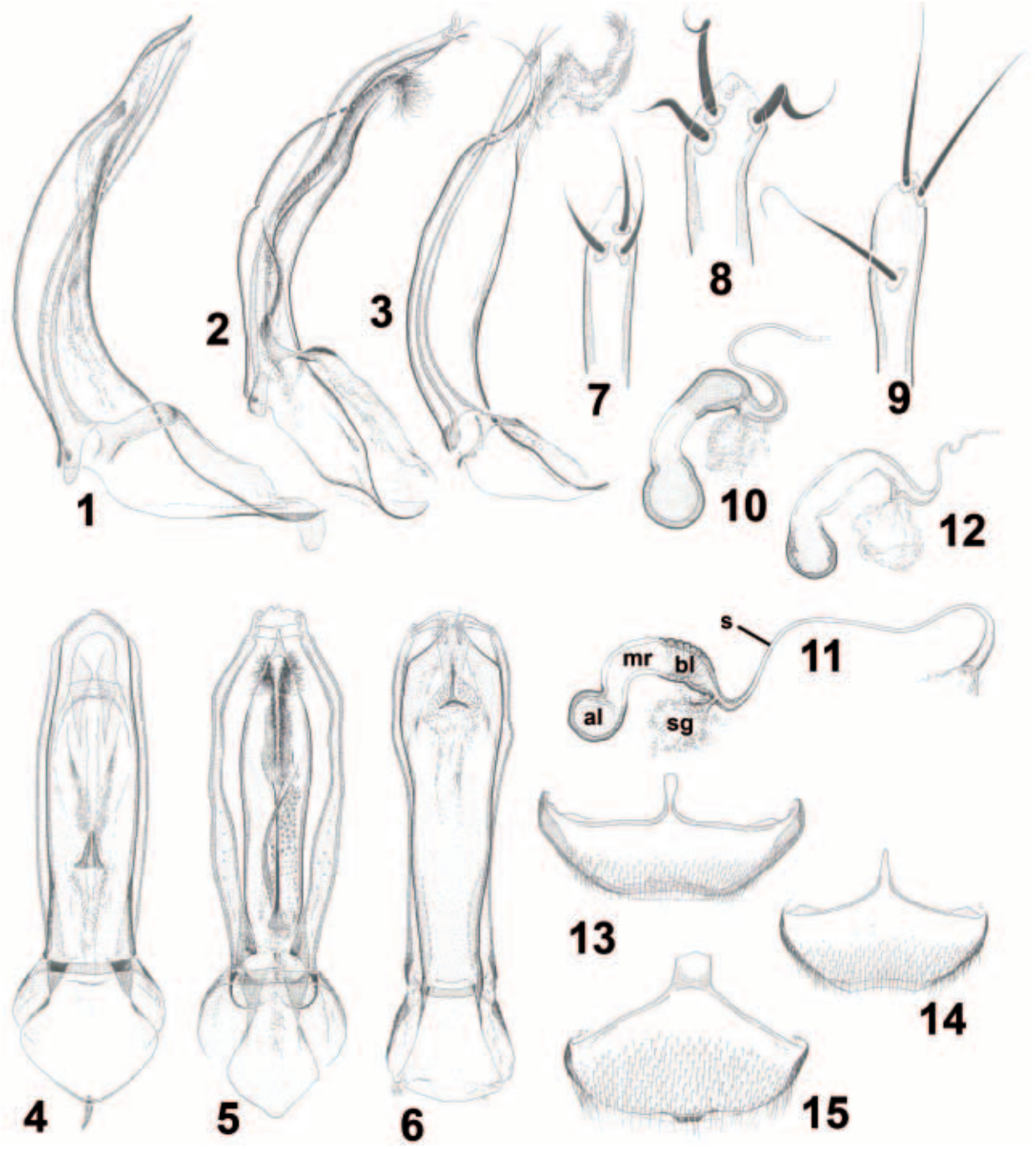
DISCUSSION. Described as a genus (Zariquiey 1940), it was later relegated to subgenus of *Anillochlamys* (Comas 1977a). The presence of an extremely long stylet, as well as other details of the endophallus, characterise this genus; the uniformity of genital pattern and an area of distribution well separated from the one of *Anillochlamys* supports the conservation of this taxon as a genus in accordance with the classification characteristics proposed by Fresneda (1998) and Salgado & Fresneda (2004a). *Paranillochlamys* should be placed close to *Anillochlamys* but clearly distinct from it due to the characteristics found in the aedeagus, body shape, robust form of the metendosternite with straight and sharp furcal arms in the apical area and its long trunk and mesoventral keel with the vertex provided with a hooked tooth. It also shares elements with the *Quaestus* and the *Speonomidius* series (Salgado 2000), especially due to the presence of a long stylet in the endophallus. In the phylogenetic tree (Fig. 1F) *Paranillochlamys* appears as a sister of *Anillochlamys* + *Spelaeochlamys* with a support of 100/100.

DISTRIBUTION. Spain. This genus covers three species that are distributed throughout the Catalan coastal mountains, north and south of the Ebro river, all of them in the province of Tarragona (Fresneda & Salgado 2017).

Species

Paranillochlamys catalonica (Jeannel, 1913)
Anillochlamys catalonica Jeannel, 1913: 454.
Bathysciola (*Anillochlamys*) *catalonica* Jeannel: Jeannel, 1914b: 5.

Anillochlamys (*Paranillochlamys*) *catalonicus* (Jeannel): Comas, 1983: 246.



FIGURES 191.1-191.15: *Spelaeochlamys* series. Aedeagus in lateral view of: (**1**) *Anillochlamys tropica,* (**2**) *Paranillochlamys velox,* (**3**) *Spelaeochlamys ehlersi.* Aedeagus in dorsal view of: (**4**) *A. tropica,* (**5**) *P. velox,* (**6**) *S. ehlersi.* Apex of the parameres of: (**7**) *A. tropica,* (**8**) *P. velox,* (**9**) *S. ehlersi.* Spermathecal complex of: (**10**) *A. tropica,* (**11**) *P. velox,* (**12**) *S. ehlersi.* Female uroventrite VIII of: (**13**) *A. tropica,* (**14**) *P. velox,* (**15**) *S. ehlersi.* Figs **1**–**15** modified from Salgado *et al*. (2008). Abbreviations: **al**, apical lobe; **bl**, basal lobe; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

Paranillochlamys catalonicus (Jeannel): Salgado & Fresneda, 2004a: 373.

Paranillochlamys urgellesi (Español, 1965)
Anillochlamys urgellesi Español, 1965: 452.
Paranillochlamys urgellesi (Español): Salgado & Fresneda, 2004a: 373.

Paranillochlamys velox Zariquiey, 1940
Paranillochlamys velox Zariquiey, 1940: 532.
Paranillochlamys velox montadai Lagar, 1963: 68.
Anillochlamys (*Paranillochlamys*) *velox* (Zariquiey): Comas, 1983: 246.

Genus ***Spelaeochlamys*** Dieck, 1870
Spelaeochlamys Dieck, 1870: 93.
Typhlochlamys Español, 1975: 121 (Type species: *Typhlochlamys bardisai* Español, 1975).

Type species. *Spelaeochlamys ehlersi* Dieck, 1870 by monotypy (habitus in Fig. 189.3).

Diagnosis. Size ranging between 1.8-2.3 mm. Body shape bathyscioid, elongated, somewhat elliptical, slightly convex and attenuated towards the back (Fig. 189.3).

Antennae: Longer than the elytral suture in one species and shorter in the other; first and second antennomeres long and thin.

Pronotum: Bell-shaped, a little longer than wide or strongly transverse, very narrowed forward and somewhat narrower than the basal part of the elytra; lateral margins sinuous, very converging towards the front and widest at the base; acute posterior angles with sharp vertices that may diverge or even appear somewhat raised.

Elytra: Widest towards the middle, apices attenuated and more or less dehiscent; they can have a convex appearance in the basal third or be slightly convex; marginal ridge very fine and visible in the three anterior quarters. Females with elytra slightly more convex than males.

Legs: Tibiae without spines on the external face.

Mesoventral keel (Fig. 190.3): High, with the anterior border somewhat sinuous and ridged; lower edge also sinuous and slightly toothed, it has a pointed arista in its anterior half and broadly rounded in its posterior part; angle formed by the edges almost right with vertex hooked.

Suture of the metaventrite (Fig. 190.3): It is contiguous to the mesocoxal cavity, without delimiting an area.

Metatergal apparatus (Fig. 190.8): Wings of the metascutum very narrow and elongated, there are no apophysis of the alacrista.

Metendosternite (Fig. 190.11): Furcal arms very narrow, slightly wavy and long, at least twice as long as the trunk, with the apical area straight, pointed and without terminal apophysis; width of posterior lamina greatly reduced towards the apex. Trunk short and narrow, twice as long as width at base, and mid-keel diverging posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 191.3), slightly curved, with the basal portion reduced and the terminal fourth of the median lobe long, thin and very curved towards the back. In dorsal view (Fig. 191.6), robust, with sinuous margins and widened preapically, then abruptly narrowing to the apex, which can be more or less pointed.

Endophallus (Fig. 191.6): It is characterised by a sac covered on the inside with scales which there is a very small stylet; there are also two reinforcing bands that may have pointed scales on the integument and always a more or less dense penicillum at the distal end; all the specimens studied presented the endophallus partially evaginated; the two reinforcing bands emerge outside through the apical pore of the median lobe.

Parameres (Fig. 191.9): More or less thick and rectilinear up to the apex or with curved or sinuous terminal sector; apex armed with two setae of distal insertion and another preapical, the three subequal and long setae, also with a depression more or less marked. Basal lamina of tegmen with a well-developed keel in the middle of the apical part.

Spermathecal complex: Spermatheca (Fig. 191.12) little curved and little sclerotized, with basal lobe undifferentiated and apical lobe thick; there is a spermathecal gland inserted in a thickening or nodule of the spermatic duct near the point of union with the spermatheca; spermatic duct about three times longer than the spermatheca and inserts directly into the dorsal part of the copulatory bag.

Female uroventrite VIII (Fig. 191.15): Spiculum short, very wide and truncated at the apex.

Discussion. The genus *Spelaeochlamys* is similar to the genus *Anillochlamys* and they are likely to be closely related to each other, but is can be easily distinguished by the particular body shape, the metatergal apparatus, the metendosternite, and the characteristics of the aedeagus. It represents the group with the most strongly modified species of the entire series, especially *S. ehlersi*. When Comas (1977b) studied *S. ehlersi verai*, he found that it had certain characteris-

tics that did not allow it to be differentiated from the genus *Typhlochlamys*, which led him to suspect that it could be a synonym of *Spelaeochlamys*. The detailed study of the genital structures confirmed this later (Salgado & Fresneda 2004a); although, the molecular study could not be completed, as it was not possible to capture specimens of *Typhlochlamys* as the caves in which the species are known to occur were completely dry. *Spelaeochlamys* differs from *Anillochlamys* and *Paranillochlamys* by its elliptical, elongated and slightly convex body (subhemispherical or ovoid and strongly convex in the other two genera), and especially by various characters of the metatergal apparatus, the metendosternite and genitalia already indicated in the description of the genera. In the phylogenetic tree (Fig. 1F) *Spelaeochlamys* is sister to *Anillochlamys* with a support of 91/100.

Distribution. Spain. Has three taxa, which are distributed in various caves of the interior mountains of the province of Alicante. *Spelaeochlamys* mark the southern limit of the distribution area of the Iberian Leptodirini (Fresneda & Salgado 2017).

Species

Spelaeochlamys bardisai (Español, 1975)
Typhlochlamys bardisai Español, 1975: 123.
Typhlochlamys escolai Comas, 1978b: 161.
Spelaeochlamys bardisai (Español): Salgado & Fresneda, 2004a: 379.

Spelaeochlamys ehlersi Dieck, 1870
Spelaeochlamys ehlersi ehlersi Dieck, 1870
Spelaeochlamys Ehlersi Dieck, 1870: 94.
Spelaeochlamys ehlersi ehlersi Dieck: Salgado & Fresneda, 2004a: 381.
Spelaeochlamys ehlersi verai Comas, 1977
Spelaeochlamys verai Comas, 1977b: 217.
Spelaeochlamys ehlersi verai Comas: Salgado & Fresneda, 2004a: 381.

3.3.4 Series ***Nanobathysciola***

The triangular phanerae of the median region is the only synapomorphy of the clade; it should also be noted that they are the smallest Leptodirini of those that populate Western Europe: between 1.1 mm-1.4 mm of *Bathysciola ovata.* Being the only genus in the series, the characteristics that define it respond to those of the genus. The species of the *Nanobathysciola* series, due to their distribution on both slopes of the Pyrenean mountains, represent a link between the Cantabrian species of the *Quaestus* series and the Levantine species of the *Spelaeochlamys* series. The sister series of *Nanobathysciola* is *Quaestus*, is support by values of 68.3/85, which in turn is linked to the *Spelaeochlamys* series with a support of 94.7/95 (Fig. 1F).

Genus ***Nanobathysciola*** nov.
https://zoobank.org/NomenclaturalActs/9689E7B7-AE0F-44AB-955A-8A4277FB3F46

Type species. *Bathyscia ovata* Kiesenwetter, 1850 by present designation (habitus in Fig. 192.1).

Diagnosis. Length: 1.1-1.4 mm. Bathyscioid facies (Fig. 192.1); body ovoid, convex, attenuated backwards and without pronotum-elytral angle; colouration between reddish and dark-reddish; integument entirely covered by a pubescence thin, recumbent, dense and yellowish; depigmented.

Head: With marked occipital carina; epistomal suture slightly curved and darkened; last article of maxillary palps short and conical; anophthalmous.

Antennae: Of 11 segments; shorter than the length of the elytral suture, with dilated club segments, the 8th, 9th and 10th segments being clearly transverse.

Pronotum: Transverse, with highly arched lateral margins; posterior angles of the pronotum acute, vertices are prolonged in a triangular point above the elytra; base as wide as the anterior part of the elytra and sinuous; with irregular punctation.

Elytra: Short, somewhat longer than the pronotum and narrowed posteriorly, widest at the base; irregular punctation, lacking transverse striolae, although in some cases there are dots in the basal region of the elytra which are somewhat aligned transversely,but without forming striolae; there is no parasutural stria.

Legs: Short and quite robust, with males protarsi pentamerous more or less dilated depending on the species; tetramerous in females, always gracile.

Male genital segment: Very reduced, in the form of a ring, with two long pedunculus.

Mesoventral keel (Figs 192.2, 192.3): High and long, with a posterior prolongation resting on the metaventrite, with a well-developed anterior border, straight or slightly convex, the angle slightly or very obtuse, and the apex rounded or toothed.

Suture of the metaventrite (Figs 192.2, 192.3): With the anterior half of the suture separated from the edge of the mesocoxal cavity, which delimits a small arched area; the posterior half close to the edge of the cavity.

Metatergal apparatus (Fig. 192.5): Reduced, with

the metascutum very wide and without sutures, the alacrista without apical nodule and the basal apophysis very short with sharp apices.

Metendosternite (Fig. 192.6): Furcal arms short and narrow, although slightly longer than the trunk, with arched apical area and pointed apex, without a defined terminal apophysis; posterior lamina maintains the same width to the apex, with slightly arched edge. Trunk short, as long as the widest area at the base and mid-keel not diverging posteriorly.

Median lobe of aedeagus: In lateral vision (Figs 192.7, 192.8), regularly curved from the base to the apical third, in this area with a more or less marked depression, the final area being sinuous, with the apex thickened, curved and with a pointed tip. In dorsal view, with subparallel or sinuous sides in the apical third, where it gradually tapers off to end with a rounded tip and a tiny terminal axial lobe.

Endophallus (Figs 192.9, 192.10): With three regions. In the basal region there is «Y»-piece and flagellum. In the middle region, the armor of the axial piece is made up of two pieces whose union forms a «U» that also has a thin stylet in the middle; there are some phanerae very reduced and welded with each other, which can be triangular or basically forming a rounded nodule; there are also dorsal and ventral phanerae. In the apical region, the reinforcing bands rest on membranous ligules whose integument is covered with long spines.

Parameres (Fig. 192.11, 192.12): Somewhat shorter than the median lobe, with a more or less sharp apex and an undifferentiated club; three setae of similar length with very close insertion pores are inserted in the apical area.

Spermathecal complex (Fig. 192.13): Spermatheca short, rectilinear and robust, with two lobes differentiated of hemispherical shape, both joined by a middle region slightly sclerotized and cylindrical. Spermatic duct very short, as long as or somewhat longer than the spermatheca; at the point of insertion with it there is a nodule and it is the location where the spermathecal gland opens; this is also the point of contact with the copulatory bag, a basal process in the form of a sclerotized tubular piece is observed.

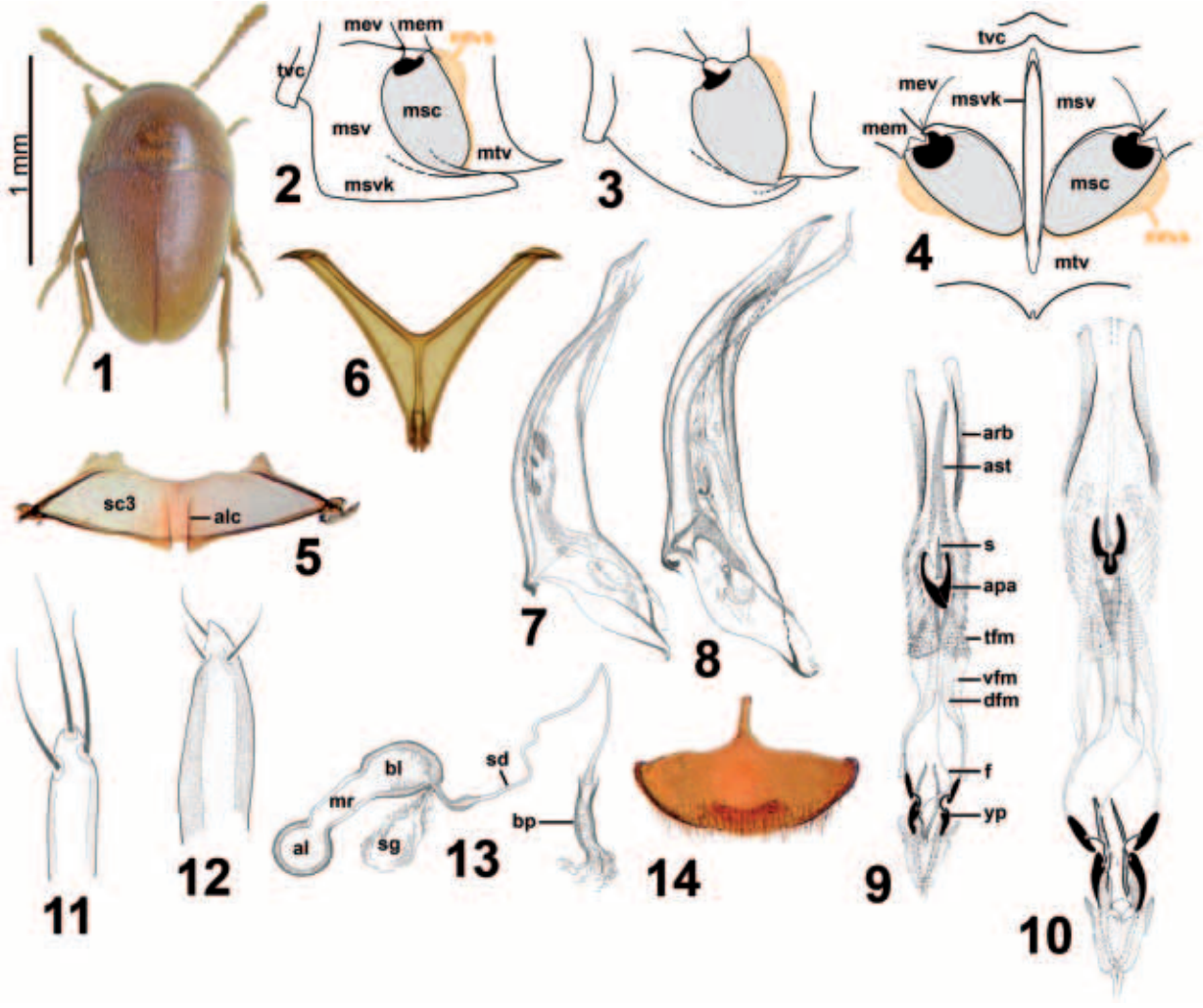
Female uroventrite VIII (Fig. 192.14): Spiculum long, thin and with a rounded apex.

Etimology. From the Greek νάνος, dwarf. In relation to the tiny size of the species. The second part of the name refers to the fact that this group of species was included in the genus *Bathysciola*, a diminutive of *Bathyscia* that incorporates the Greek term βαθυς, depth. Feminine.

Discussion. *Bathysciola ovata* together with *B. asperula*, *B. minuscula*, *B. simonis* and *B. talpa*, form the section VII of the genus *Bathysciola* as proposed by Jeannel (1924a), or the «groupe *ovata*» of Perreau (2000). However, Fresneda *et al*. (2010a) on the base of the type series of *B. ovata*, they reviewed the complex and designated several synonyms and elevating *B. catalana* to the category of species; in Fresneda *et al*. (2010b) described *B. aldensis*, and in Fresneda & Bourdeau (2012) the last species of the group, named *B. faillei*. Thus, there are currently eight species described for this group of species, for all of them the taxonomic state was justified both by morphology and moleculs. Referring to this set Salgado *et al*. (2008) realised that «…this group brings together characters that point to an ancient diversification – with respect to the Pyrenean infraflagellates – and the possibility is contemplated that their phylogenetic relationships must be sought beyond the Pyrenean massif.»

Ribera *et al*. (2010) placed the section VII of the Bathysciola-group among the «Supraflagellates» as were the lineages of *Spelaeochlamys* and *Quaestus*, despite the fact that they exhibit clearly a synapomorphy of the «Infraflagellates» (endophallus with «Y»-piece) and inwhich they had always been included.. This questions the higher-order division of the tribe by Jeannel (1955a) into «Infraflagellates» and «Supraflagellates», representing an ancient cladogenesis in this group. In classifications of the tribe it has been assumed (Jeannel 1924a) that evolution always progresses from simple to ever more complex structures: e.g.from an unarmed endophallus in the most basal groups towards simple ones with one or two regions, squamous clusters and stylet, which then gave rise to even more complex structures with three defined regions, «Y»-piece and numerous other differentiated structures in the most «evolved» groups –. The position of the species of the group with a complex endophallus and three defined regions as the sister of all the «Supraflagellates» with simple endophallus and with two regions suggest that the degree of complexity of the structures may not support a directed evolution from simple to compley, as in this clade the simple sacs are likely to represent a derived state and that the complex ones are more basal

The following character states in this combination define the group of the Franco-Iberian Leptodirini: Irregular elytral punctation, no transverse striolae, no



FIGURES 192.1–192.14: *Nanobathysciola* series. Habitus of: (**1**) *Nanobathysciola ovata* **comb. nov.** Pterothorax in lateral view of: (**2**) *N. ovata* **comb. nov.**, (**3**) *N. asperula* **comb. nov.** Pterothorax in ventral view of: (**4**) *N. ovata* **comb. nov.** Metatergal apparatus, ventral view of the metanotum and axillaria of: (**5**) *N. ovata* **comb. nov**. Metendosternite of: (**6**) *N. ovata* **comb. nov.** Aedeagus in lateral view of: (**7**) *N. ovata* **comb. nov.**, (**8**) *N. asperula* **comb. nov.** Endophallus of: (**9**) *N. ovata* **comb. nov.**, (**10**) *N. asperula* **comb. nov.** Apex of the paramere of: (**11**) *N. ovata* **comb. nov.**, (**12**) *N. faillei* **comb. nov.** Spermathecal complex of: (**13**) *N. ovata* **comb. nov.** Female uroventrite VIII of: (**14**) *N. ovata* **comb. nov.** Figs **7**–**13** modified from Fresneda & Salgado (2006). Abbreviations: Pterothorax: **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar. Metatergal apparatus: **alc**, alacrista; **sc3**, metascutum. Endophallus: **apa**, armature of the axial piece; **bra**, apical reinforcing band; **ast**, apical stylet; **fdm**, dorsal phanerae of the median region; **f**, flagellum; **s**, stylet; **tfm**, triangular phanerae of the median region; **fvm**, ventral phanerae of the median region; **py**, «Y»-shaped piece. Spermathecal complex: **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **sd**, spermiduct; **sg**, spermathecal gland.

parasutural stria, mesoventral keel prolonged over the metaventrite, suture of the metaventrite separated in the anterior half of the edge of the mesocoxal cavity delimiting a small arched area, spermatic duct as long as the spermatheca with nodule and tubular basal process, apex of the parameres sharp with only three setae, endophallus of defined three regions and the presence of «Y»-piece and triangular phanerae of the median region.The existence of triangular phanerae of the median region is a synapomorphy and below there are the characters listed which allow to separate them from other lineages:

– The type of elytral punctation is found in all the representatives of the *Spelaeochlamys* and *Quaestus* lineages, and in various genera or species present in different clades of the Pyrenean radiation of the *Speonomus* complex: *Aranzadiella* and *Nafarroa* (Basque district clade), *Gesciella* (*Antrocharis* clade), *Pseudospeonomus* (*Parvospeonomus* clade), *Speonomites velox* and *S. nitens* (*Speonomites* clade).

– The absence of parasutural stria is found in the great majority of species of the clade *Quaestus* with western distribution, in the clades *Spelaeochlamys* and *Speonomidius*, and in practically all the genera of the *Speonomus* clade (Salgado *et al*. 2008). However, not present in *Bathysciola aubei*, type species of *Bathysciola*.

– The mesoventral keel prolonged over the metaventrite is found in all representatives of the *Quaestus* lineage, developed more or less strongly (Salgado 1996a).

– The short spermatic duct is found in all representatives of the *Quaestus* lineage though exhibiting different degrees of development (Salgado *et al*. 2008).

– The apex of the parameres with only three setae (Figs 192.11, 192.12) is also found in the *Bathysciola* of the «*aubei*» group (clade of the western Alps and foothills surrounding the Lyon gulf), in the genera of the *Antrocharis* clade (north slope of the central Pyrenees) including *Baronniesia*; also, although with different variations in the arrangement of the setae (Salgado *et al*. 2008), in *Breuilites*, *Cantabrogeus*, *Espanoliella*, *Leonesiella*, *Oresigenus* and *Quaestus* – except *Asturianella* – (Cantabrian clade) and *Spelaeochlamys* (Ibero-Mediterranean clade).

– The presence of «Y»-piece in the endophallus is found in all representatives of the *Speonomus* group from the Pyrenees as defined by Ribera *et al*. (2010), with the exception of *Pseudospeonomus*, *Bellesia* (*Bathysciella* clade) and *Josettekia* (clade of the Basque biospeleological district).

– The endophallus with three clearly defined regions is a characteristic of most groups of «Infraflagellates».

Some differences were observed between two groups of species in the genus *Nanobathysciola* gen. nov., one formed by *N. ovata* comb. nov., *N. catalana* comb. nov., *N. minuscula* comb. nov., group of «*N. ovata*» and another for *N. aldensis* comb. nov., *N. asperula* comb. nov., *N. faillei* comb. nov., *N. simonis* comb. nov. and *N. talpa* comb. nov., group of «*N. asperula*». In the species of the «*ovata* group» the mesoventral keel (Fig. 192.2) is high and forms a right angle or is at least somewhat obtuse with a pointed or toothed apex; the anterior border is straight, somewhat convex or even sinuous; there is a process that extends to the middle of the metaventrite; in the endophallus (Fig. 192.9) the apical reinforcing bands rest on two membranous bands covered with spines, and also in the middle region there are two short triangular phanerae with a thickened inner margin and provided with thick thorns of transverse disposition; the parameres are fine and sinuous. In contrast, in the «*asperula* group» the mesoventral keel is low and regularly rounded, with a short extension whose tip rests on the metaventrite (Fig. 192.3); in the endophallus (Fig. 192.10) the apical reinforcement bands do not rest on any differentiated structure and in addition in the middle region there are two rounded phanerae very close or united by their internal margin, these appear to be homologous to those that occupy the same area in the species of the «*ovata* group»; the parameres are more robust and arched, with the tip strongly bent towards the median lobe. Not only morphological aspects support the monophyly of these two groups, but also the topology of the phylogenetic tree as shown in figure 1F. Both groups – the «*asperula*» and the «*ovata*» form their own subclade and these are united by a node with high support, 100/100.

Distribution. They are distributed throughout Spain and France, with a very extended distribution area, perhaps one of the geographically largest ranges xof all Leptodirini. They stretch from one end of the Pyrenean massif to the other, between the Aude river basin (Aude department) to the east and the Gave de Larrau to the west (Pyrénées-Atlantiques); across the Pyrenees towards its southern slopes in two instances: in the eastern part of the mountain range marking the descend into Ripoll (Girona) and in the central part of the massif it follows the basins of the Noguera Ribagorçana and Ésera rivers, meeting in the bank of the latter its southernmost location in the town of Campo (Huesca). To the north they populate the Garonne river basin up to its mouth in the Atlantic ocean in Bordeaux (Gironde), but

they are also found in the Massif Central (Lot and Tarn-et-Garonne), as well as from three isolated localities in the western Alps and nearby foothills: from the right bank of the river Rhône near Lyon (Rhône) from the foothills located between the rivers Drac and Romanche, and the Isère, very close to Grenoble (Isère), and the upper basin of the river Ubaye, a tributary from the western bank of the river Durance, in the heart of the Alpine massif (Alpes-de-Haute-Provence) (Kiesenwetter 1850; Fairmaire 1858; Saulcy 1872; Abeille de Perrin 1872a, 1875b, 1901b; Normand 1907a; Hustache 1913; Bolívar 1919; Jeannel 1909, 1924a; Fagniez 1927; Español 1956; Coiffait 1959a; Vanderbergh 2002; Fresneda & Salgado 2006, 2017; Salgado *et al*. 2008; Fresneda *et al*. 2010a, 2010b; Fresneda & Bourdeau 2012). Species of this genus can be found in any sheltered or hidden environmental niches: in the forest environment among moss, dead leaves or under stones and also in underground caves.

Species

«***ovata*** group»
Nanobathysciola catalana (Coiffait, 1959) comb. nov.
Bathysciola ovata catalana Coiffait, 1959a: 164.
Bathysciola (s. str.) *ovata catalana* Coiffait Perreau, 2000: 230
Bathysciola (*Bathysciola*) *catalana* Coiffait, 1959: Fresneda, Fery & Faille, 2010b: 100.

Nanobathysciola minuscula (Abeille de Perrin, 1901) comb. nov.
Bathyscia minuscula Abeille de Perrin, 1901: 68.
Bathysciola minuscula (Abeille de Perrin): Jeannel, 1910a: 46.
Bathysciola (*Bathysciola*) *ovata minuscula* (Abeille de Perrin): Jeannel, 1924a: 113.

Nanobathysciola ovata (Kiesenwetter, 1850) comb. nov.
Bathyscia ovata Kiesenwetter, 1850: 223.
*Adelops ovatus (*Kiesenwetter): L. Miller, 1855: 508.
Bathyscia (*Bathyscia*) *ovata* Kiesw.: Reitter, 1885 [1884]: 34.
Bathysciola ovata (Kiesenwetter): Jeannel, 1910a: 28.
Bathysciola ovata var. *gabasensis* Hustache, 1913: 86.
Bathysciola (s. str.) *ovata gabasensis* Hustach: Jeannel, 1924a: 231.
Bathysciola ovata aragonica Coiffait, 1959a: 164.
Bathysciola (*Bathysciola*) *ovata* (Kiesenwetter, 1850): Fresneda, Fery & Faille, 2010b: 96.

«***asperula*** group»
Nanobathysciola aldensis (Fresneda, Perreau & Vanderbergh, 2010) comb. nov.
Bathysciola aldensis Fresneda, Perreau & Vanderbergh, 2010c: 427.

Nanobathysciola asperula (Fairmaire, 1857) comb. nov.
Adelops asperulus Fairmaire, 1858 [1857]: 731.
Adelops subasperatus Saulcy, 1872: 22.
Bathyscia (*Bathyscia*) *asperula* (Fairmaire): Reitter, 1885 [1884]: 34.
Bathyscia Schioedtei subasperata (Saulcy): Jeannel, 1907b: 423.
Bathyscia asperula intermedia Jeannel, 1909a: 19.
Bathysciola asperula intermedia Jeannel: Jeannel, 1910a: 28
Bathysciola asperula (Fairmaire): Jeannel, 1910a: 28.
Bathysciola asperula subasperata (Saulcy): Secq, B. & M., 1996: 13.

Nanobathysciola faillei (Fresneda & Bourdeau, 2012) comb. nov.
Bathysciola faillei Fresneda & Bourdeau, 2012: 23

Nanobathysciola simonis (Abeille de Perrin, 1875) comb. nov.
Adelops Simonis Abeille de Perrin, 1875b: cxcix.
Bathyscia (*Bathyscia*) *Simonis* (Abeille de Perrin): Reitter, 1885 [1884]: 34.
Bathysciola asperula Simoni (Abeille de Perrin): Jeannel, 1910a: 28.
Bathysciola (s. str.) *asperula simonis* (Abeille de Perrin): Perreau, 2000: 230

Nanobathysciola talpa (Normand, 1907) comb. nov.
Bathyscia talpa Normand, 1907a: 121.
Bathyscia asperula talpa Normand: Jeannel, 1909a: 19.
Bathysciola asperula talpa Normand: Jeannel, 1910a: 28.
Bathysciola talpa Normand: Coiffait, 1959a: 164.
Bathysciola (s. str.) *talpa* (Normand): Perreau, 2000: 231

3.3.5 Series ***Quaestus***

Diagnosis. Bathyscioid facies. Reddish colouration and integument entirely covered by thin pubescence, recumbent, dense and whitish-yellowish; punctation of pronotum and elytra always irregular; non transverse striolae on elytra; depigmented.

Head: With occipital carina; epistomal suture

slightly curved and darkened; last article of maxillary palps short and conical; anophthalmous.

Legs: Male protarsi pentamerous and tetramerous in females.

Male genital segment: Very reduced, in the form of a ring with two long pedunculus.

Mesoventral keel: High and long with rounded vertex.

Metaventrite: With a bifid protruding process or apophysis separating the metacoxal cavities.

Metendosternite: Lacking the anterior furcal plate.

Parameres: With three, four or five setae in the apical part, generally three, and never penicillum.

Endophallus: With two regions.

Spermatheca: With the basal lobe generally well differentiated.

Discussion. The series is high supported with values of 100/100. In search of a taxonomic system that is reflecting the evolutionary processes of the Leptodirini only morphological characters were attempted to be identified that have a universal phylogenetic value. However, to date it becomes clear that there are no such universal phylogenetic characters. It turned out that many structures have not changed or seem to have changed in a similar manny simultaniously even in clearly distant clades. Just the endophallus was identified as being useful for establishing the generic relationship in the *Speonomus* series, which is in accordance with the molecular analysis. in the *Quaestus* series the situation is very different, with high variability in the structures of the endophallus, as well as in the median lobe, tegmen parameres and spermathecal complex. So here the valuable characters are different once, which poses a risk for the study, or at least require a very high level of taxonomic expertise to distinguish which parameters are important in which group and how to deal with species from transitional areas, taxonomically as well as geographically. For instance, in *Quaestus* the detailed molecular analysis indicate that the genitalia are very plastic and not suitable for analysis trying to establish the evolutionary relationship and that a number of other characters are found to present synapomorphies, such as the stylet with a basal bowl in *Quaestus*. The genus *Speocharinus*, the only one with subpholeuonoid facies and for which no molecular data are available, has been included in this series in *Quaesticulus* group. The reasons herefore are presented in detail in the group section (3.3.5.3).

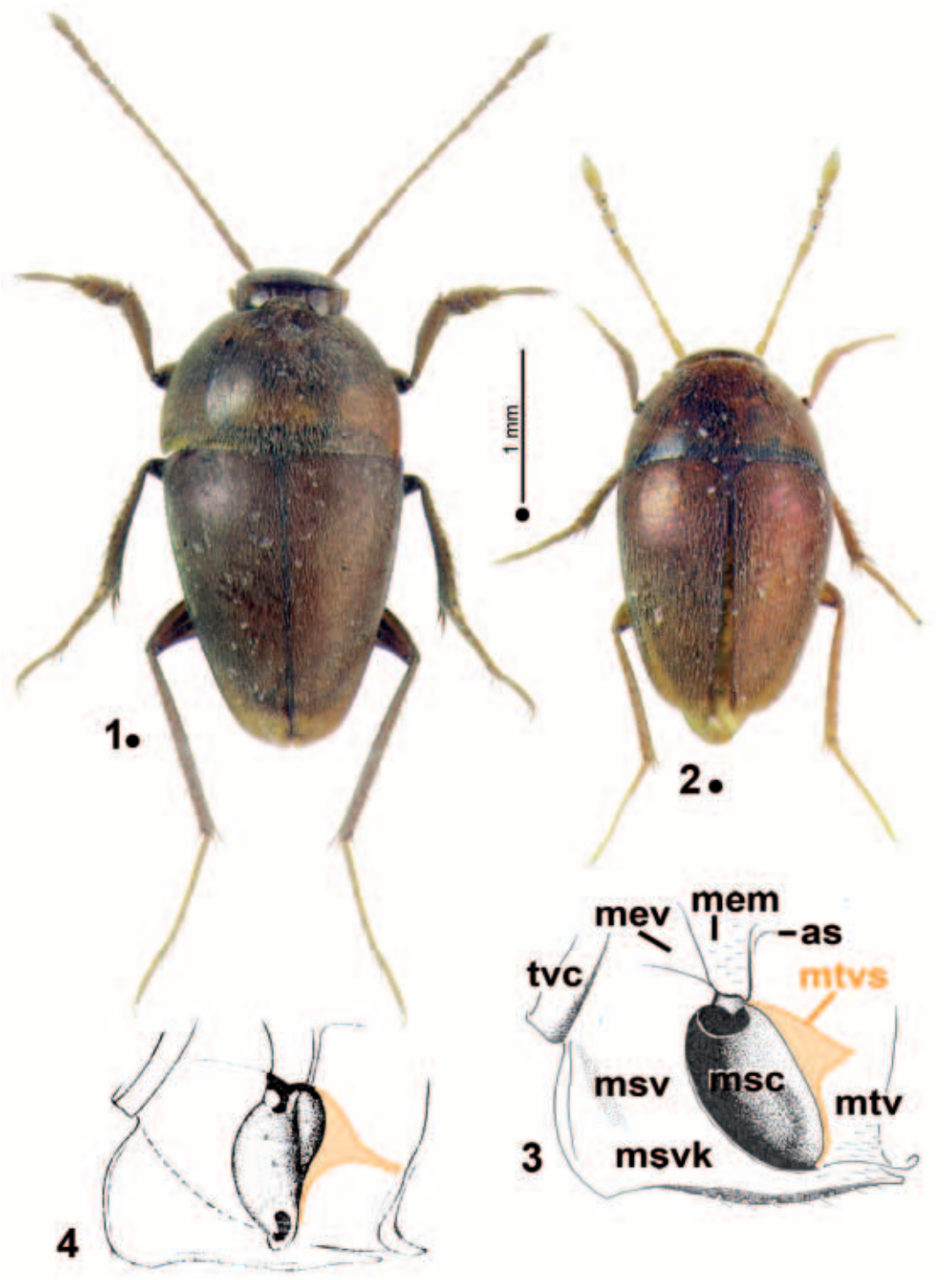
Genera groups

An identification key for this group has so far not been proposed. The genera e.g. the groups their of are characterised by a certain combination of characters, but each of them separately can be found in more than one of the different groups of genera:

– *Breuilia* group: Apical part of the elytra truncated or subtruncated. Parasutural stria absent; short and blurry towards basal third in *Breuilites*. The sutures of the metaventrite form a triangle with a pointed apex (Figs. 193.3, 193.4). Mesoventral keel with the ventral edge widened in the middle part (Figs. 193.3, 193.4), with a groove in *Breuilia*. Endophallus without stylet (Figs. 195.1, 195.2). Parameres with three (Fig. 195.4) or five (Fig. 195.3) setae in the apical part. Spermatheca (Figs. 195.5, 195.6) slightly elongated with undifferentiated basal lobe. Short spermatic duct, about twice as long as the spermatheca. Spiculum of the female uroventrite VIII long and narrow (Figs. 195.7, 195.8).

– *Quaestus* group: Apical part of the elytra arched. Parasutural stria absent or only a few dots in the basal part visible; it is blurred in *Leonesiella* and *Schaufussia* gen. nov. Sutures of the metaventrite in an arc or triangle with a more or less sharp vertex (Figs. 197.1-197.6). Mesoventral keel with a narrow edge (Figs. 197.1-197.6), in some cases widened in the middle area, but always without a groove. Endophallus with stylet, generally long, and basal plate or cup (Figs. 199.1-199.7); it is short and without a cup in *Leonesiella* (Fig. 199.1) and *Schaufussia* gen. nov. (Fig. 199.6), in these cases without developed spines. Slender parameres with three setae, the lower one generally far from the two apical ones (Figs. 200.2, 200.4) – only *Quaestus incognitus* with four setae (Fig. 200.5) –. Spermatheca with both lobes visible, the apical one smaller (Figs. 200.7-200.12); spermatic duct, generally long (Figs. 200.8-200.11), short in *Leonesiella* (Fig. 200.7) and *Schaufussia* gen. nov. (Fig. 200.12), and without a sclerotized piece at the junction with the copulatory bag. Spiculum of female VIII uroventrite short and narrow (Figs. 201.2-201.6), *Leonesiella* wide (Fig. 201.1).

– *Quaesticulus* group: Apical part of the elytra arched. Elytra with parasutural stria, more or less blurred in the basal third. Mesoventral keel high and long, the ventral edge narrow (Figs. 204.10, 204.11), only slightly widened in the middle area of *Quaesticulus autumnalis* comb. nov., but without groove. Sutures of the metaventrite form a triangle with a more or less sharp apex (Figs. 204.10, 204.11). Endophallus



FIGURES 193.1–193.4: *Quaestus* series, *Breuilia* group. Habitus of: (**1**) *Breuilia triangulum,* (**2**) *Breuilites eloyi.* Pterothorax in lateral view of: (**3**) *B. triangulum,* (**4**) *B. eloyi.* Figs **3**, **4** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

(Fig. 207.8, 207.9) with short stylet, without basal plate, and with small spines and scales – never found to exhibit developed spines – very long apical reinforcing bands. Parameres thin, with no or little differentiated club and the three setae with apical insertion. Spermatheca (Figs. 209.8, 209.9) with two well-differentiated lobes, the basal being somewhat larger than the apical. Short and narrow spiculum of the female uroventrite VIII (Figs. 210.9, 210.9).

– *Espanoliella* group: Apical part of the elytra arcuate or tapered. Elytra with well marked parasutural stria. Sutures of the metaventrite in a triangle with a more or less acute vertex (Figs. 204.1-204.5). High and long mesoventral keel, with a wide ventral edge and a marked sulcus (Figs. 204.1-204.5). Endophallus with short stylet, without basal plate and with more or less developed spines (Figs. 207.1, 207.2, 208.1); without stylet in genus *Espanoliella*, in this case with developed spines (Fig. 208.2). Parameres robust, three setae long, shapes – in many cases robust or thickened – and very diverse insertion points (Figs. 208.5-208.7); in general the insertion pores well marked. Spermatheca (Figs. 209.1-209.3) with the two lobes differentiated, the basal being larger. Short spermatic duct, 2-4 times the length of the spermatheca, somewhat longer in *Espanoliella*. Spiculum of the female uroventrite VIII long and narrow (Figs. 210.1-210.3).

– *Cantabrogeus* group: Apical part of the elytra arched. Elytra with well marked parasutural stria, blurred in *Fresnedaella*. Antennae long or very long, with all segments clearly longer than broad. Sutures of the metaventrite delineate a triangular or subtriangular area (Figs. 204.6-204.9), with the apex well defined in *Fresnedaella* (Fig. 204.7). Tall and long mesoventral keel (Figs. 204.6, 204.8, 204.9) – somewhat shorter in *Fresnedaella* (Fig. 204.7) – narrow ventral edge, in some cases widened in the middle area, and no sulcus. Endophallus with a stylet without a basal plate (Figs. 208.3, 208.4); without stylet the genus *Fresnedaella* (Fig. 207.5). Parameres more or less robust, with a differentiated apical club in which three fine and long setae are inserted (Figs. 208.8-208.11). Spermatheca (Figs. 209.4-209.7) with two globose and well differentiated lobes, the basal one being larger in general; spermatic duct short, 2-4 times the length of the spermatheca. Spiculum of the female uroventrite VIII very short and narrow (Figs. 210.4-210.6), somewhat broadened in *Luquesia* gen. nov. (Fig. 210.7).

3.3.5.1 ***Breuilia*** group

Diagnosis. Size ranging between 1.8-3.7 mm. Bathyscioid body shape. Apical part of the elytra truncated or subtruncated.

Antennae: The 11th antennomere somewhat longer than the 10th, with a widened appearance.

Legs: All tibiae hairy, with two pectinate internal spurs, two simple external ones and a series of unequal spines between them; protibiae of constant width, mesotibiae somewhat curved and metatibiae straight with two large spines.

Mesoventral keel: High, with an obtuse angle, rounded vertex and widened ventral edge, with furrow in *Breuilia*.

Sutures of the metaventrite (Figs. 193.3, 193.4): They form a triangle with a acute vertex.

Metatergal apparatus (Figs. 194.1, 194.2): Apophysis of the alacrista long.

Endophallus (Figs. 195.1, 195.2): Of two regions, without stylet.

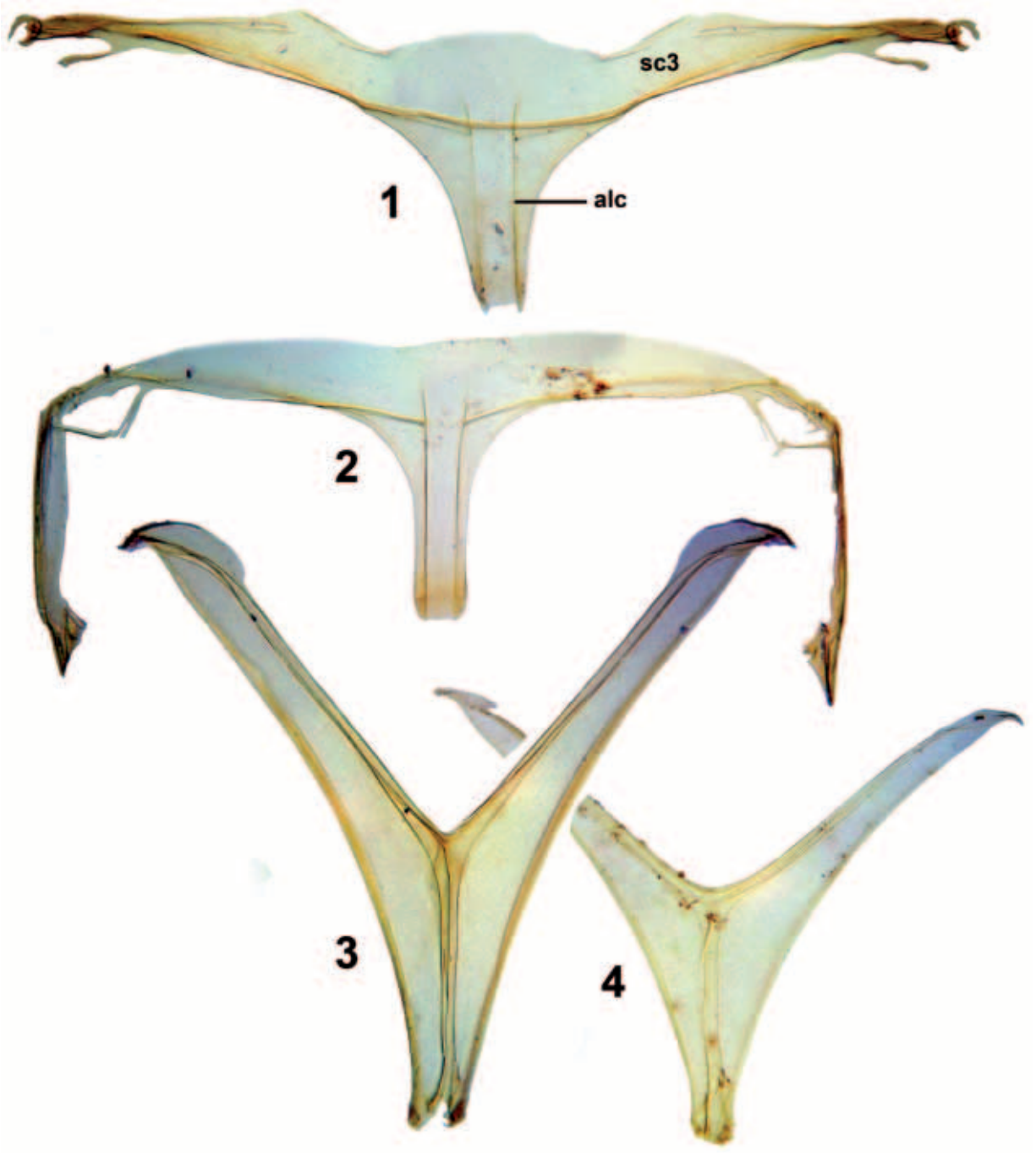
Spermatheca (Figs. 195.5, 195.6): With undifferentiated basal lobe, anterior part of the same size as the middle part.

Discussion. The most basal cladogenesis of the *Quaestus* group is found to have resulted in the split into the sister genera *Breuilia* and *Breuilites*, which represents the most basal group of the entire clade that is formed by the other genera of the *Quaestus* series; in the analysis of the phylogenetic tree (Fig. 1F) they are united by a very high support of 100/100.

Distribution. Spain. The two genera of this group present completely independent geographical distribution areas (Salgado 1976; Fresneda & Salgado 2017). *Breuilites* is found in a restricted area, localised in Sierra del Sueve, however, the distribution of *Breuilia* seems much wider, reaching from the Picos de Europa to the coast in the provinces of Asturias and Cantabria.

Key to genera

1. Size greater than 2.5 mm. Body elongated, strongly ogival towards the posterior end (Fig. 193.1). Antennae very long and thin, with the 8th article at least three times as long as wide. Male protarsi very dilated. Mesoventral keel with slightly hooked apex and a groove on the ventral edge (Fig. 193.3). Furcal arms of the metendosternite long, with apical apophysis (Fig. 194.3). Median lobe of aedeagus with the apical part in a pointed vertex (Fig. 195.1). Endophallus with



FIGURES 194.1–194.4: *Quaestus* series, *Breuilia* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Breuilia triangulum,* (**2**) *Breuilites eloyi.* Metendosternite of: (**3**) *B. triangulum,* (**4**) *B. eloyi.* Abbreviations: **alc**, alacrista; **sc3**, metascutum.

highly developed and grouped spines at the bottom (Fig. 195.1). Parameres flattened, with five apical setae of unequal length (Fig. 195.3) .....*Breuilia*
- Size less than 2.3 mm. Body not elongated and not narrowed backwards (Fig. 193.2). Short antennae with the 8th article transverse or slightly longer than wide. Male protarsi narrow. Mesoventral keel with a rounded tip and no groove on the ventral edge. Furca with long arms, without apical apophysis (Fig. 194.4). Median lobe of aedeagus with a slightly narrowed apical area (Fig. 195.2). Endophallus with two groups of very poorly developed spines and scales on the bottom (Fig. 195.2). Parameres cylindrical, with three apical setae of equal length (Fig. 195.4) .....*Breuilites*

Genus ***Breuilia*** Jeannel, 1909
Breuilia Jeannel, 1909b: 467.

Type species. *Adelops triangulum* Sharp, 1873 by original designation (habitus in Fig. 193.1).

Diagnosis. Size large, between 2.6-3.7 mm. Body shape convex and strongly ogival to the back (Fig. 193.1); body shape of females and males identical. Sculpture of the pronotum composed of dots very small and inconspicuous, the dots of the elytra being larger.

Head: With complete occipital carina.

Antennae: Long and slender, all antennomeres longer than wide, the first and second being of equal length; segments of the club not thickened.

Pronotum: Similar to a quarter of a sphere, very convex, with the sides regularly converging towards the apical edge; maximum width at the base, which is almost rectilinear and the posterior angles are right, with a pointed vertex.

Elytra: Cuneiform, with apices truncated and separated; no parasutural stria.

Legs: Long and slender; male protarsi with first tarsomere much wider than the apex of tibia; protibiae without spines on external face.

Mesoventral keel (Fig. 193.3): High, with the anterior border arched and flanged; the lower edge widened in the middle where there is a narrow longitudinal groove; the edges form an obtuse angle with the vertex slightly sharp; the apophysis extends over the metaventrite for its entire length to the bifid process.

Sutures of the metaventrite (Fig. 193.3): Two sutures that extend towards the edge of the metacoxal cavity and estent up to a point around the middle of the metaventrite to delimit a triangular area with a pointed vertex.

Metatergal apparatus (Fig. 194.1): Wings of the metascutum narrow and elongated, with anterior margins membranous; the apophysis of the alacrista long, very prolonged.

Metendosternite (Fig. 194.3): Furcal arms long, slightly more than one and a half times the length of the trunk, with the apical area pointed, arched and at the apex a terminal apophysis membranous similar to an aileron; posterior lamina of similar width along the arm, with a posterior lateral ridge consistent and posterior border almost straight. Trunk one and a half times longer than the widest area at the furcal base and the mid-keel does not diverge posteriorly.

Median lobe of aedeagus: Long, robust and slightly curved, as long as a quarter of the length of the body. In lateral view, somewhat curved towards the ventral side. In dorsal view (Fig. 195.1), it narrows progressively to the apex forming a sharp tip. Basal lamina long, narrows in the middle and widens at the end and is finely ridged.

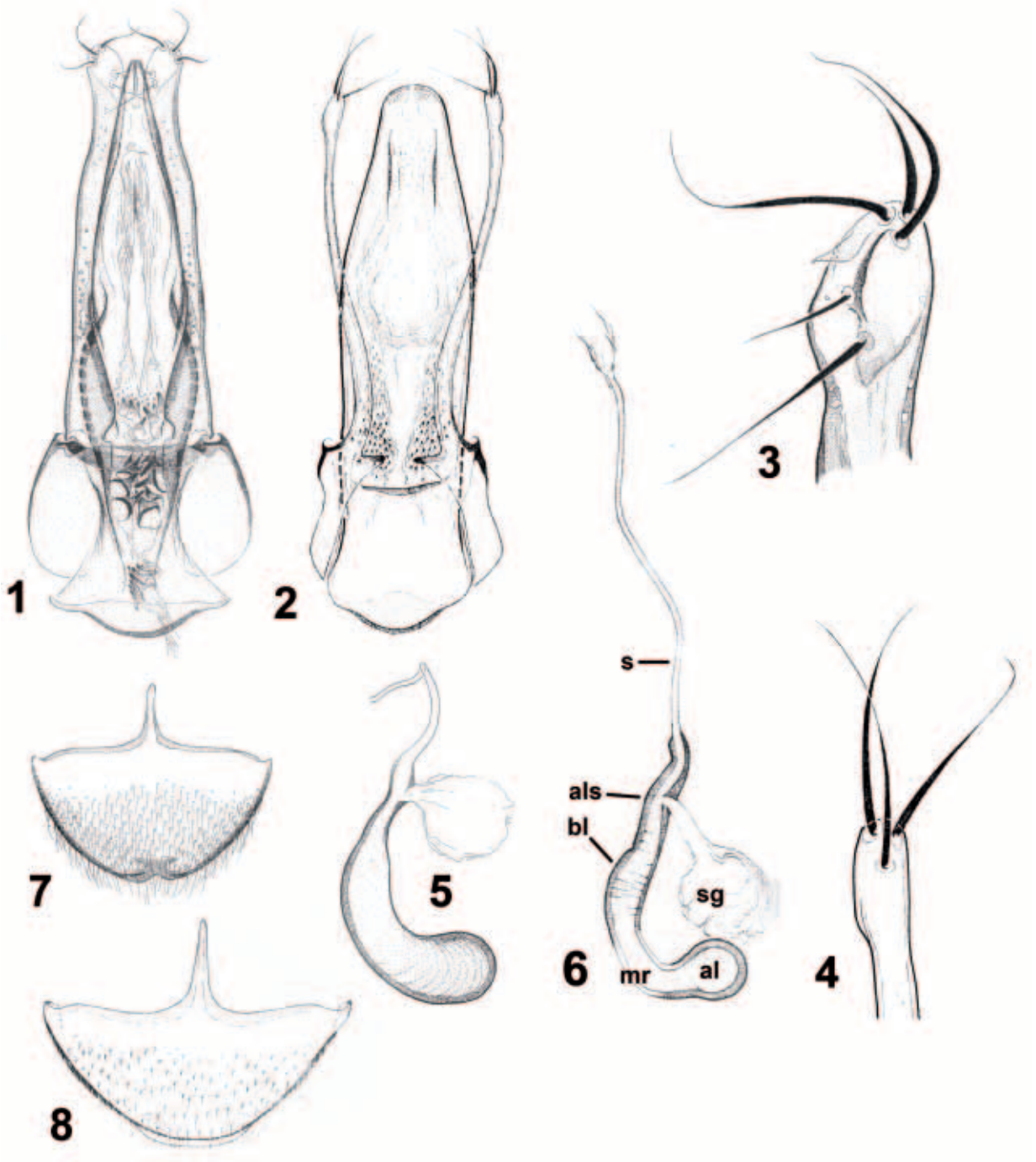
Endophallus (Fig. 195.1): It lacks a stylet and contains several spines short and thick grouped together; at the bottom of the sac there is a small group of smaller spines.

Parameres (Fig. 195.3): Robust and laterally flattened, they slightly exceed the apex of the median lobe and five setae of unequal length are inserted in their terminal part, three apical and two proximal; club poorly differentiated with a small peak in the apical area of the inner margin.

Spermathecal complex (Fig. 195.5): Spermatheca elongated and uniformly sclerotized; apical lobe greatly dilated, no difference between junction canal and basal lobe; spermatic duct not widened anteriorly and rather short, about three times as long as the spermatheca; spermathecal gland well-developed.

Female uroventrite VIII (Fig. 195.7): With a small recess in the middle of the posterior margin and the spiculum short, narrow and somewhat curved in the apical area.

Discussion. *Breuilia* differs significantly from *Breuilites* in the apical part of the furcal arms of the metendosternite, in the peculiar structure of the male copulatory organ (Jeannel 1909, 1911a; Bellés *et al*. 1978; Salgado 1980a, 1993b, 1994a), and in the shape of the spermatheca. The differences in some of the external morphological characters are also very evident, so that it can be very easily distinguished from *Breuilites* as it is also much larger in size, the male protarsus are very widened, the antennae different in shape and length, the shape of the elytra, and the ab-



FIGURES 195.1–195.8: *Quaestus* series, *Breuilia* group. Aedeagus in dorsal view of: (**1**) *Breuilia triangulum,* (**2**) *Breuilites eloyi.* Apex of the paramere of: (**3**) *B. triangulum,* (**4**) *B. eloyi.* Spermathecal complex of: (**5**) *B. triangulum,* (**6**) *B. eloyi.* Female uroventrite VIII of: (**7**) *B. triangulum,* (**8**) *B. eloyi.* Figs **1–8** modified from Salgado *et al*. (2008). Abbreviations: **al**, apical lobe; **als**, apical spermiduct lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

sence of a parasutural striae, the mesoventral keel with a longitudinal groove, and the shape of the suture of the metaventrite. In the phylogenetic tree (Fig. 1F) *Breuilia* appears as sister genus of *Breuilites* with a very high support of 100/100.

Distribution. Spain. Hypogeous Iberian endemism that has a wide dispersion and can be found from the northern foothills of the Picos de Europa to the coast; the area is comprised between the provinces of Asturias, in its eastern part, and Cantabria, in its western part (Salgado 1976; Fresneda & Salgado 2017).

Species

Breuilia triangulum (Sharp, 1872)
Adelops triangulum Sharp, 1872: 268.
Bathyscia (*Bathyscia*) *triangulum* (Sharp): Reitter, 1885 [1884]: 35.
Breuilia triangulum (Sharp): Jeannel, 1909b: 467.

Genus ***Breuilites*** Salgado, 1980
Breuilites Salgado, 1980b: 158.

Type species. *Breuilites eloyi* Salgado, 1980 by original designation (habitus in Fig. 193.2).

Diagnosis. Size ranging between 1.8-2.2 mm. Body ovoid, slightly elongated posteriorly (Fig. 193.2). Sculpture of the pronotum composed of extremely fine points slightly visible; integument of the elytra with a rough appearance and without punctation.

Head: Occipital carina obliterated in the centre.

Antennae: Short, somewhat longer than the middle of the elytral suture, the segments longer than wide except the 8th; club clearly thickened with the 11th article strongly dilated.

Pronotum: Slightly convex and transverse, less than twice as wide as long, with the sides regularly arched and not narrowed backwards; maximum width at the base.

Elytra: About two and a half times as long as the pronotum, widest near the base, then narrowing gradually towards the apex which is very slightly truncated; parasutural stria short and very little marked towards the basal third.

Legs: Short and slender; male protarsi very slightly dilated, almost filiform like those of females; protibiae with spines on external face.

Mesoventral keel (Fig. 193.4): High and long, the apophysis extends over the entire metaventrite; anterior border convex, vertex rounded and the lower border wide in the middle, without groove and with a slight inflection in the anterior part.

Sutures of the metaventrite (Fig. 193.4): Two sutures that extend until contacting the edge of the metacoxal cavity and converge at a point that almost reaches the posterior margin of the metaventrite, forming an acute angle with the vertex elongated, narrow and pointed.

Metatergal apparatus (Fig. 194.2): With metascutum wings narrow, elongated, anterior edges membranous, and apophysis of the alacrista long with blunt apices.

Metendosternite (Fig. 194.4): Furcal arms slightly longer than the trunk, narrowed towards apical area with apex pointed and slightly arched, without terminal apophysis; the posterior lamina is conserved up to the apex, although it decreases progressively, with a posterior lateral ridge little consistent and a posterior border soft arched. Trunk longer than widest area at furcal base and mid-keel not diverging posteriorly.

Median lobe of aedeagus: In lateral view, little arched and very long, almost a third of the length of the body. In dorsal view (Fig. 195.2) wide, with subparallel sides up to the middle area and then progressively narrows towards the apical area, which appears only slightly narrowed and with a well-marked ovoid areola in the middle.

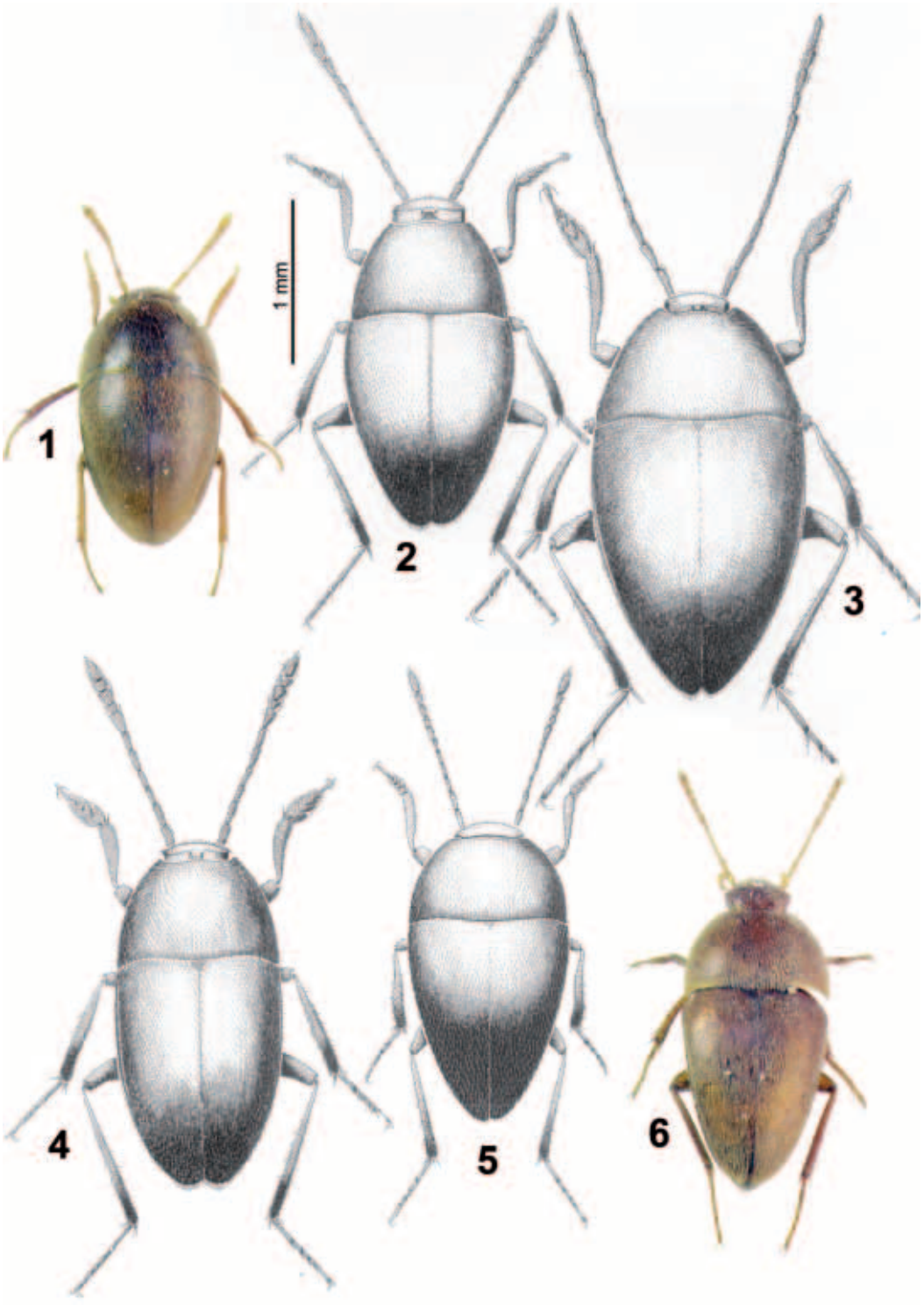
Endophallus (Fig. 195.2): In the middle basal part there is a small central group or two lateral groups of squamosities arranged in a more or less regular way, the basal ones being more robust.

Parameres (Fig. 195.4): Narrow, with a very poorly differentiated apical club, and three long and equal setae inserted at the apex, with the insertion pores close together.

Spermathecal complex (Fig. 195.6): Spermatheca elongated, with the apical lobe thickened and spherical, basal lobe not differentiated; spermatic duct short and thin, about twice the length of the spermatheca; well-developed spermathecal gland.

Female uroventrite VIII (Fig. 195.8): Spiculum moderately long, thin and sharp.

Discussion. This genus was in the phylogenetic analysis found to be sister to *Breuilia* with a support of 100/100, although with a considerable genetic distance (Fig. 1F). The characters that allow to differentiate the two genera have been indicated in the key to the genera, in the diagnosis of *Breuilites* as well as in the discussion section on *Breuilia*. With respect to the structures of the endophallus *Breuilites* is therefore seemingly morphologically more similar to the group



FIGURES 196.1-196.6: *Quaestus* series, *Quaestus* group. Habitus of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Q. jaspei* **comb. nov.**, (**4**) *Q. avicularis*, (**5**) *Q. incognitus*, (**6**) *Schaufussia pachecoi* **comb. nov.** Figs **2–5** modified from Salgado *et al*. (2008).

I of Laneyrie (1967) and Dupré (1992), which is defined by having the endophallus unarmed or only covered with scales. Of the various genera that correspond to this group – group I of Laneyrie (1967) –, the closest morphologically would be *Ceuthophyes*, as it is the only one that shows small groups of squamosities on the endophallus. However, the molecular study shows that these similarities can be acribed to convergent evolutionary development.

Distribution. Spain. Iberian hypogeous endemism that is located in several caves of the western central part of the Sierra del Sueve in Asturias (Fresneda & Salgado 2017).

Species

Breuilites eloyi Salgado, 1980
Breuilites eloyi Salgado, 1980b: 160.

3.3.5.2 ***Quaestus*** group

Diagnosis. Size ranging between 1.5 and 4.5 mm. Bathyscioid facies; integument with a matt appearance.

Elytra: Rounded apex; without parasutural striae or with only a few points in the basal area of the elytra, or blurred in *Leonesiella* and *Schaufussia* gen. nov.

Legs: Tibiae hairy, with two pectinate internal spurs, two simple external ones, a series of unequal spines between them and spines on the external face; protibiae without a comb, not tapered; mesotibiae somewhat curved and metatibiae straight, the two with large spines.

Mesoventral keel: High, with broadly rounded vertex, without tooth; arista of the lower edge narrow or wide, without groove, and short – *Speogeus* – or long posterior prolongation, in this case reaching the posterior margin of the metaventrite (Salgado 1996a).

Metaventrite: With a suture delimiting an arched area, describes a curve in its first half and then runs parallel to the edge of the mesocoxal cavity and forms an arc; or with two sutures which are delimiting by triangular area with a more or less pointed vertex.

Metatergal apparatus: With short and narrow wings of the metascutum (Fig. 198.2), wider in *Leonesiella* (Fig. 198.1) and *Schaufussia* gen. nov. (Fig. 198.3); alacrista apophysis short (Figs. 198.1, 198.2), long only in *Schaufussia* gen. nov. (Fig. 198.3).

Metendosternite: With the middle keel of the trunk diverging posteriorly; apex of furcal arms arched and ogival, without apophysis (Figs. 198.4, 198.5); this blurry or poorly defined in *Schaufussia* gen. nov. (Fig. 198.6).

Endophallus: With two regions; usually includes a long stylet (Fig. 199.7), very short in *Leonesiella* (Fig. 199.1), with (Figs. 199.2-199.5, 199.7) – in *Quaestus* – or without (Figs. 199.1, 199.6) – in *Leonesiella* and *Schaufussia* gen. nov. – bowl or basal plate.

Parameres: Terminal part with three setae (Figs. 200.1-200.4), or in exceptional cases four (Fig. 200.5) – for instance in *Quaestus incognitus* –.

Spermathecal complex (Figs. 200.8-200.11): Spermatheca small; normally with three parts: apical lobe, basal lobe and union duct, the latter generally more hyaline; spermatic duct short and without a sclerotized piece that opens out into the copulatory bag.

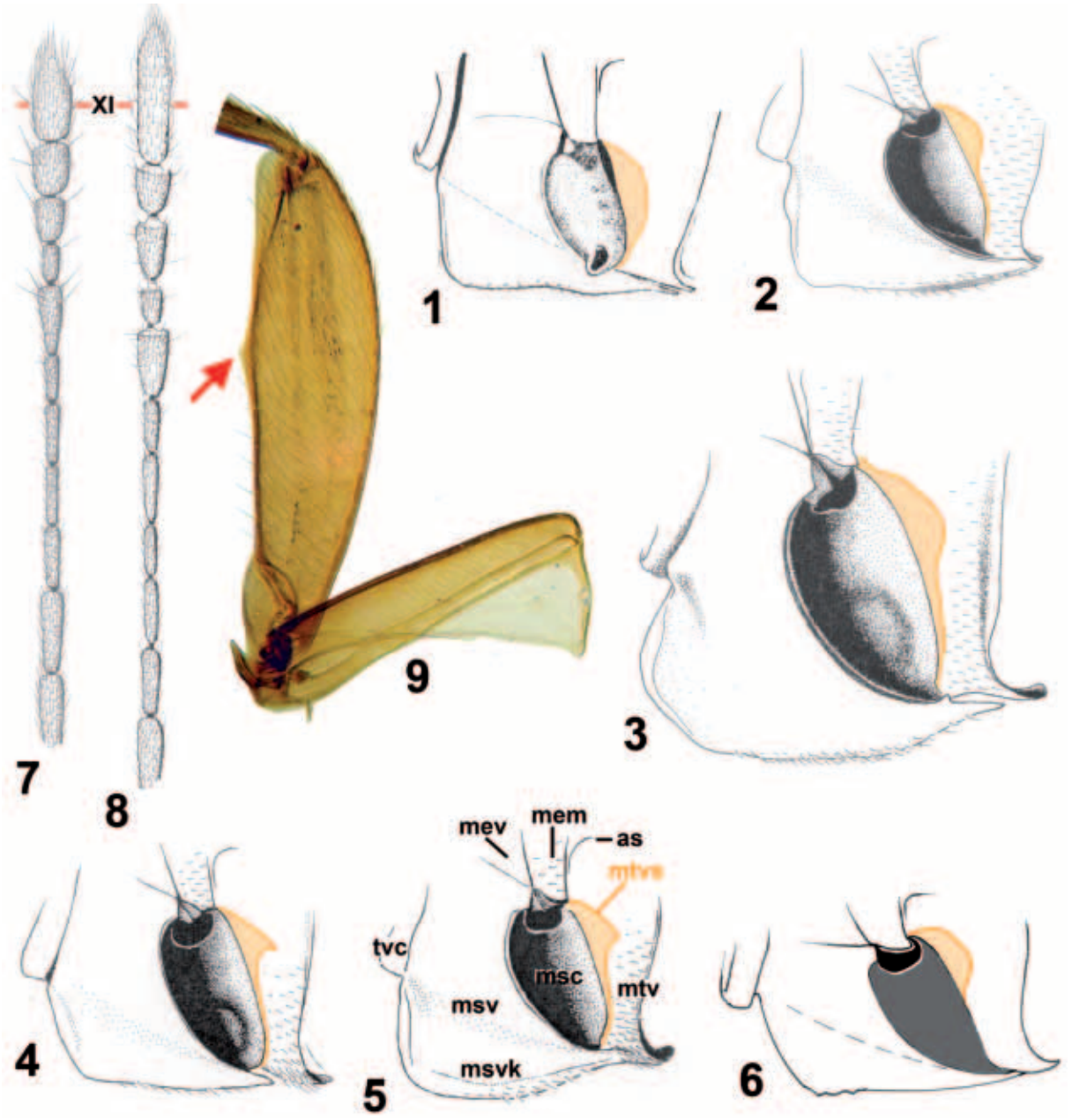
Female uroventrite VIII (Figs. 201.2-201.5): Always with a spiculum in the middle posterior area, although there may be specific forms in the species of some genera, both in the form of the spiculum and of the uroventrite.

Discussion. In order to resolve the contradictory results or support for the taxonomic classification due to the analysis by molecular data and/or the morphological characteristics leave several options to interpret. The one reflecting the most likely scenario is the one that requires meast taxonomic changes, and with this is reducing as far as possible the description of new genera and synonyms. In any case, our approach has let us to question some of the shared characters as being difficult to interpret, however, there are other, hence more complex solutions:

– Including *Schaufussia pachecoi* comb. nov. in the genus *Quaestus* would imply synonymising *Leonesiella*, a genus that is very well characterised by general morphology and genitalia, as well as its geographic distribution; on the other hand *Schaufussia bustilloi* comb. nov., *Schaufussia mariscali* stat. nov. comb. nov., *Schaufussia pachecoi* comb. nov. and *Schaufussia sinuatipenis* sp. nov. share a synapomorphy (See description of *Schaufussia* gen. nov.)

– Preserving the subgenus *Asturianella* implies describing a genus for *Quaestus recordationis* without characters so far identified to distinguish it from the other *Quaestus* which may justify such a change; as a consequence the new genus would have to be included in the subgenus *Asturianella*, however these species all unified by the character of having four setae at the apex of the parameres, the only character that separates *Asturianella* from all the others.

– In a further scenario, preserving the genus *Oresigenus* implies the description of at least six genera



FIGURES 197.1–197.9: *Quaestus* series, *Quaestus* group. Pterothorax in lateral view of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Q. jaspei* **comb. nov.**, (**4**) *Q. avicularis*, (**5**) *Q. incognitus*, (**6**) *Schaufussia pachecoi* **comb. nov.** Antennae of: (**7**) *Q. incognitus*, (**8**) *Q. mermejaensis*. Metafemur of: (**9**) *S. pachecoi* **comb. nov.** Red arrow pointing to the femoral tooth. Figs **1–5, 7, 8** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

and there are no characters to justify this: only the size and the slightly bell-shape pronotum differentiate *Oresigenus* from the rest, since the remaining characters are coherent with the definition of *Quaestus*.
The lack of resasonable alternative interpretation of the findings let us to propose to maintain the genera *Leonesiella* and *Quaestus*, to synonymise the genus *Oresigenus*, the subgenera *Asturianella* and *Speogeus* with the genus *Quaestus*, and to establish the new genus *Schaufussia* gen. nov. for four species.

In the phylogeny (Fig. 1E, 1F), this clade is sister to the clade that includes the groups *Espanoliella*, *Cantabrogeus*, and *Quaesticulus* with a support of 94.2/100.

DISTRIBUTION. Spain. The *Quaestus* group is strictly bound to the subterranean environment exclusively around the mountains of the Cantabrian coast, as well as in areas of the western and centre of the Cantabrian mountains range, between the provinces of Lugo, Orense and Oviedo and in the lower basin of the Besaya river (Cantabria).

KEY TO GENERA

1. Variable sutures of the metaventrite (Figs. 197.2-197.5), usually forming a triangle, subtriangular in *Quaestus asturicus*. Metendosternite with a long furcal trunk (Fig. 198.5). Endophallus with a long or very long stylet, always with a developed cup or basal piece and very long apical reinforcing bands (Figs. 199.2-199.5). Parameres, in general, with the apical part dilated; the subapical seta distant from the two apical ones, except *Quaestus asturicus* and *Quaestus incognitus* with three apical ones (Fig. 200.5). Spermatheca with two well-differentiated lobes, the basal one much larger; long spermatic duct (Figs. 200.8-200.11) .....
.....*Quaestus*
- Sutures of the metaventrite arched (Figs. 197.1, 197.6). Metendosternite with the furcal trunk as long as it is wide or slightly longer (Figs. 198.4, 198.6). Endophallus with short or very short stylet, without basal piece, and apical reinforcement bands normally shorter and closer together (Figs. 199.1, 199.6). Parameres without a differentiated club, the three setae with the insertion pores nearby (Figs. 200.1, 200.6). Spermatheca with the two lobes of similar width and poorly differentiated; short spermatic duct (Figs. 200.7, 200.12) 2

2. Male metafemora without prominence in the middle part of the posterior margin. Mesoventral keel narrow in the middle part (Fig. 197.1). Alacrista apophysis of the metatergal apparatus rather short (Fig. 198.1). Furcal arms of the metendosternite with an arcuate apex and no terminal apophysis (Fig. 198.4). Apical area of the median lobe of aedeagus slightly narrowed (Fig. 199.1). Endophallus with a very reduced stylet, like two small glued blades, and very little developed groups of spines (Fig. 199.1). Spermatic duct in the area of junction with the basal lobe of the spermatheca slightly enlarged (Fig. 200.7). Spiculum of the Female uroventrite VIII with a wide basal area, triangular in shape and a sharp apex (Fig. 201.1).....*Leonesiella*
- Male metafemora with a small prominence towards the middle area of the posterior margin (Fig. 197.9). Mesoventral keel widened in the middle part (Fig. 197.6). Long apophysis of the alacrista of the metatergal apparatus (Fig. 198.3). Furcal arms of the metendosternite with slightly arched apex, somewhat more dilated and with a diffuse terminal apophysis (Fig. 198.6). Apical part of the median lobe of aedeagus narrowed (Fig. 199.6). Endophallus with a short but robust stylet and more developed groups of spines (Fig. 199.6). Spermatic duct in the part of union to the basal lobe of the spermatheca strongly enlarged (Fig. 200.12). Spiculum of the female uroventrite VIII long, narrow and with a sharp apex (Fig. 201.6).....*Schaufussia* gen. nov.

Genus ***Leonesiella*** Salgado, 1996
Leonesiella Salgado, 1996a: 152.

TYPE SPECIES. *Speocharis bergidi* Salgado, 1983 by original designation (habitus in Fig. 196.1).

DIAGNOSIS. Size ranging between 1.5-1.8 mm. Body shape ovoid, markedly convex (Fig. 196.1). Pubescence short. Pronotum smooth, with very little punctation; on elytra rough punctation. Females somewhat more robust than males with slightly more convex elytra.

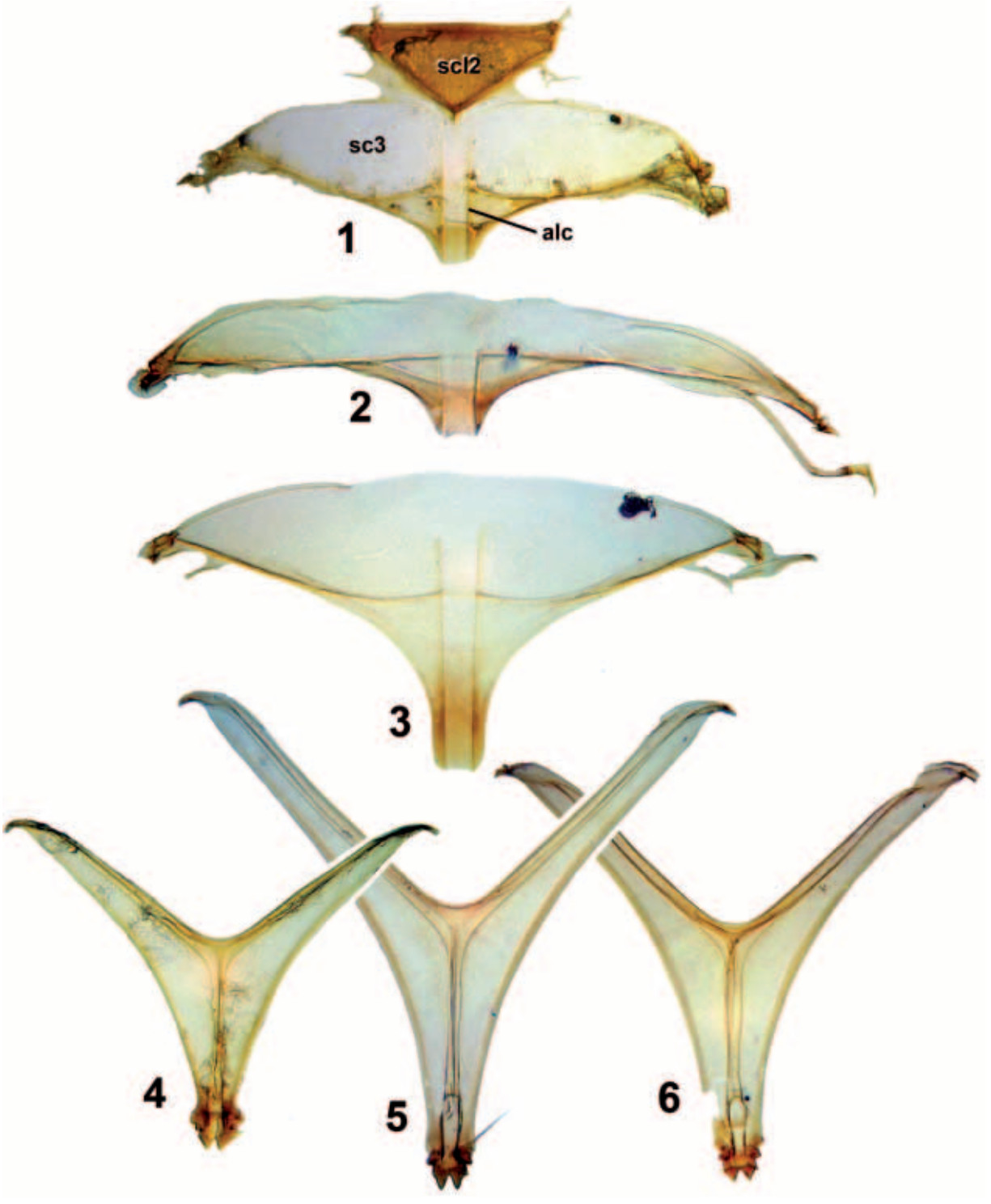
Head: With complete occipital carina.

Antennae: Short, slightly longer than the middle of the elytral suture; the club well differentiated with the 8th, 9th and 10th segments transverse.

Pronotum: Very transverse, as wide as the elytra, with the lateral margins regularly arched.

Elytra: Short and wide, with maximum width very close to the base and the margins regularly curved to the rounded apices; tips dehiscent; parasutural stria very short and very blurred, only fairly distantly spaced dots in the anterior medial area.

Legs: Short and slender; male protarsi very slightly dilated; mesotibiae somewhat curved and metatibiae straight.



FIGURES 198.1–198.6: *Quaestus* series, *Quaestus* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Schaufussia pachecoi* **comb. nov.** Metendosternite of: (**4**) *L. bergidi,* (**5**) *Q. arcanus,* (**6**) *S. pachecoi* **comb. nov.** Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Mesoventral keel (Fig. 197.1): High, with two edges rectilinear and narrow, the previous one with a slight ledge; vertex highly arched and apex of posterior apophysis reaches the suture of the metaventrite.

Suture of the metaventrite (Fig. 197.1): Describes an arc from one end to the other of the mesocoxal cavity and a well-defined area.

Metatergal apparatus (Fig. 198.1): Wings of metascutum broad and about twice as long as wide; the apophysis of the alacrista moderately developed with rounded apices.

Metendosternite (Fig. 198.4): Furcal arms somewhat longer than trunk, both narrow progressively towards the apex, which is sharp then curves into an arc and lacks a terminal apophysis; width of posterior lamina decreases sharply towards apex with concave edge in middle part. Trunk short, as long as wide, with the middle keel on the trunk diverging posteriorly.

Median lobe of aedeagus: In lateral view, curved from the base to the apex, with curvature that is accentuated especially in the centre of the ventral face. In dorsal view (Fig. 199.1), the apical area is arched with a slightly prominent apex.

Endophallus (Fig. 199.1): Basal armor formed by a very small stylet, with a rudimentary structure that resembles two glued sheets and an elongated group of spinules and scales, the lower ones somewhat more developed than the upper ones; in addition, in the apical area, another group of scales can be seen that surrounds the two reinforcement bands, very closely located.

Parameres (Fig. 200.1): Slender and uniform in thickness, as long as or slightly shorter than the median lobe, without distinct club and with three setae of medium length, almost equal and inserted apically.

Spermathecal complex (Fig. 200.7): Spermatheca elongated and basal and apical lobes slightly dilated, almost of equal width; basal one elongated extends into a widened area of the spermatic duct; apical lobe spherical and small; hyaline middle region well differentiated and spermatic duct short, between one and two times the length of the spermatheca.

Female uroventrite VIII (Fig. 201.1): Spiculum long, wide at the base and sharp at the apex, triangular in shape.

Discussion. The molecular study (Fig. 1E), places *Leonesiella* as a sister to the genus *Quaestus* with no or very low support, 5/55, however, but both genera join with very high confidence with *Schaufussia* gen. nov. due to the high support of 99.9/100. The taxonomic classification of *Leonesiella* is supported by a number of external morphological characters that allows to clearly distinguish it from other genera of the group, to mention are the: the model of the endophallus, the shape of the spermatheca, and a geographical distribution distinct form all other representatives of the *Quaestus* series. *Leonesiella* could be mistaken for species of the genus *Notidocharis* and *Uhagoniella* gen. nov., as well as with *Quaesticulus adnexus* or with *Quaesticulus canis* comb. nov., due to its external morphology mainly because of the size, body shape and the similarity of the antennal segments, especially of the club structure (Salgado 1983a, 1983b); however, it clearly differs from *Notidocharis* and *Uhagoniella* gen. nov. in the following characters: lack of eyes, transverse elytral striation and by exhibiting a long mesoventral keel. The differences to the other two genera are found in the short parasutural stria that are very blurred and a suture of the metaventrite that is regularly arched from one end to the other end of the mesocoxal cavity. However, the differences with all these genera become very apparent in the characters of the aedeagus and in those of the spermatheca.

Distribution. Spain. It is the westernmost genus of the *Quaestus* series. It extends through the western foothills of the Montes Aquilanos and Sierra de la Lastra, in the province of León, Sierras de Avellaneira and Sierra de la Lastra, in the province of Orense, Sierras del Caurel and Sierra de Ancares, in the province of Lugo, and in the Sierra del Rañadoiro and Montes de Muniellos, in the province of Asturias (Fresneda & Salgado 2017).

Species

Leonesiella bergidi (Salgado, 1983)
Speocharis (*Speocharis*) *bergidi* Salgado, 1983a: 277.
Quaestus (*Quaestus*) *bergidi* (Salgado): Perreau, 1993: 322.
Leonesiella bergidi (Salgado): Salgado, 1996a: 153.

Genus ***Quaestus*** Schaufuss, 1861
Quaestus Schaufuss, 1861a: 424.
Speocharis Jeannel, 1909: 463 (unjustified replacement name).
Oresigenus Jeannel, 1948a: 73 syn. nov. (Type species: *Oresigenus jaspei* Jeannel, 1948).
Speogeus Salgado, 1985: 262 syn. nov. (Type species: *Speocharis avicularis* Salgado, 1985).
Asturianella Salgado & Fresneda, 2004b: 36 syn. nov. (Type species: *Quaestus incognitus* Salgado & Fresneda, 2004).

Type species. *Quaestus arcanus* Schaufuss, 1861 by subsequent designation (habitus in Fig. 196.2).

Diagnosis. Size ranging between 1.8-4.5 mm. (the smallest *Q. sellai* – 1.75 mm –. Body shape wide and oval (Fig. 196.2). Pubescence short. Pronotal integument with a well-printed microreticulum, on the elytra rugose. Females, in general, somewhat more robust than males and with elytra slightly more convex.

Head: With complete occipital carina.

Antennae: Slender, as long as the elytral suture; the first two segments almost equal and the segments of the club very slightly thickened; the 11th antennomere fine and very long, longer than the second or 7th and almost three times the length of the 10th (Fig. 197.8), short in *Quaestus incognitus* (Fig. 197.7).

Pronotum: Transverse and arched, usually continuous in a regular curve with the elytra.

Elytra: Rounded at the apex and without parasutural stria.

Legs: Longs and slender; male protarsi with the first four tarsomeres with a different degree of dilation depending on the species; mesotibiae almost straight and metatibiae straight.

Mesoventral keel (Fig. 197.2-197.5): High, with a rounded vertex, ventral edge without a groove and generally narrow, posterior prolongation reaches the metaventrite, although in some species it only reaches the middle of the metaventrite.

Suture of the metaventrite (Fig. 197.2-197.5): Variable in shape, either in an arch or in a triangle with the vertex more or less pointed.

Metatergal apparatus (Fig. 198.2): Wings of the metascutum narrow and very long; apophysis of the alacrista rather short.

Metendosternite (Fig. 198.5): Furcal arms a little longer than the trunk, with the apical area sharp and curved into an arc, it lacks a terminal apophysis; posterior lamina retains the same width almost to the apex, with the edge concave in the middle. Trunk long, clearly longer than wide, with middle keel on the trunk diverging posteriorly.

Median lobe of aedeagus: In lateral view, long and more or less arched. In dorsal view (Figs. 199.2-199.5), wide with sub-parallel or slightly arched sides and the final part progressively narrowing, with a tip that exhibits various morphologies in the different species. The basal plate of the aedeagus as long as or slightly shorter than the plate of the tegmen.

Endophallus (Fig. 199.7): It is characterised by presenting two regions. The apical, longer than the basal, with two reinforcing bands that extend to basal region. The basal with a stylet inserted on the internal dorsal region of the sac; this stylet long, usually as long as the length of the median lobe, and runs through both regions of the sac; it always has a sub-rectangular or cup-shaped plate at the base. Also in the basal region there is a tissue that is surrounding the basal area of the stylet which is covered with scales or spicules and in the apical region there is another tissue that is in the same way covered with very fine scales or in other case even with large spines arranged in two groups of axial position. In the middle part there are usually two phanerae symmetrically arranged and hyaline.

Parameres (Figs. 200.2-200.5): In general, with the club slightly dilated and three setae inserted into it, two apical and the other more or less distant, with a preapical insertion; only in *Quaestus asturicus* the three setae are apical and *Q. incognitus* have four setae. With the ventral plate of the tegmen generally a little wider than long and with rounded sides

Spermathecal complex (Figs. 200.8-200.11): Spermatheca small with two lobes sclerotized and differentiated (Perreau, 1989), one proximal or basal, very large and oval or rounded, the other distal or apical, much smaller and rounded; both separated by a very short junction canal, usually hyaline or very slightly sclerotized. Spermatic duct short and more or less widened in the area where it joins the spermatheca; spermathecal gland well differentiated and generally has the shape of a bag oblong or spherical.

Female uroventrite VIII (Figs. 201.2-201.5): Spiculum narrow and between fairly long and very short.

Discussion. The genus *Quaestus* was described by Schaufuss (1861a) and the name reestablished by Perreau (1993), considering *Speocharis* synonymy of the former. Certainly, it is the broadest and most conflictive genus in the phyletic series *Quaestus* (*sensu* Perreau 2000), which is why it has been the subject of intense review work. The contributions of Jeannel (1909b, 1910a, 1911a, 1914a-b, 1924a), Laneyrie (1967), V.B. Guéorguiev (1976), Bellés *et al*. (1978), Español (1958), Salgado (1978b, 1980a, 1985, 1993b, 2000), Dupré (1992), Newton (1998) and Perreau (2000) deserve to be highlighted. In addition to the various characters indicated in the description of the genus, with some very specific characters that define the genus clearly, such as the endophallus stylet, generally very long and always with a basal plate; the spermatheca little sclerotized, small and the basal lobe developed; the elytra without parasutural stria, although sometimes there are some poorly marked

points in the anterior area; the mesoventral keel reaches the posterior edge of the mesoventrite. It is necessary to highlight some special cases, such as:

– A specific feature is that the mesoventral keel in the various *Speogeus* species, which are found to be part of a number of different *Quaestus* subclades, which has the posterior apophysis not exceeding the middle part of the metaventrite.

– That there are three setae inserted at the apex of the parameres, except in *Quaestus* (*Asturianella*) *incognitus* which has four setae.

– That *Oresigenus* might be a derived species, although it is found to be part of the main *Quaestus* clade, which is distinct to the shape of its pronotum, which is somewhat bell-shaped and the size considerably larger.

Considering special cases and the phylogenetic relationship as established by the tree as shown in Fig. 1E, there is a overlap betweeen the *Quaestus* typical characters in all cases justifiying the synonymy of *Oresigenus* Jeannel, 1948 syn. nov., *Speogeus* Salgado, 1985 syn. nov. and *Asturianella* Salgado & Fresneda, 2004 syn. nov. with *Quaestus* Schaufuss, 1861.

The characters mentioned above are summarised in the following:

– The existence of a long stylet in the endophallus is very striking; in 29 species of the genus it is nearly as long as the entire endophallus, this character state is considered derived. The stylet is shorter, around half the length of the endophallus, in *Quaestus arcanus* and *Q. acuminatus* and is even shorter in *Q. littoralis*; that this characteristic is a derivation of the usual structure becomes apparent when considering that these three species are belonging to three independent subclades within the main *Quaestus* clade:

– *Quaestus arcanus* which has a short stylet is the sister species of *Q. breuili* + *Q. perezi* with support of 98.5/99, in which the stylets are found to be long.

– *Quaestus littoralis* also with short stylet is the sister species of *Q. suevensis* + *Q. variabilis* with support 100/100, here aswell the two others have long stylets.

– *Quaestus amicalis dilatatus* AF22 (from type locality) – *Speogeus* – is the sister species of *Q. luctuosus* AF18 (from type locality) with a support of 98.8/100; *Q. amicalis amicalis* AI1078 appears in another clade and is sister species to *Q. riberai* AF77 (from type locality) with a support of 98.6/100 (Fig. 1E). Consequently, *Q. amicalis dilatatus* must be transferred to the rank of bona species: *Quaestus dilatatus* as it was proposed by Salgado (1984). The characters identified by Salgado (1984) as the dilatation of the protarsi and the width of the tenth antennomere, are specific and allow *Q. dilatatus* to be separated from *Q. amicalis*. The shorter mesoventral keel and metaventrite pit of *Q. dilatatus* distinguish this species from its sister species *Q. luctuosus*, which has a long mesoventral keel and metaventrite without a pit.

– *Quaestus jeannei pongai* AI1075 was found to be sister species to *Q. nuptialis* AI1079 (from type locality) (Fig. 1E) with a low support of 60/82) but not from *Q. jeannei jeannei* as suggested, which in our analysis was found to be part of another clade. Subsequently, the subspecies *pongai* must be considered a valid species: *Quaestus pongai* (Salgado, 1982). It was observed that the male protarsi are much wider than the maximum width of the tibiae, the antennae longer than half the body length and as the squamous parts of endophallus is not very apparent in *Q. pongai* and with this a specific characters that allow to differentiate this species from *Q. jeannei*. In this the male protarsi are of the same width as the tibia, the antennae shorter and the scaliness of the endophallus more apparent. In the molecular phylogeny approach the genus *Quaestus* is found to be sister to *Leonesiella* and both are linked with a high level of confidence to the *Schaufussia* gen. nov. by a support of 99.9/100.

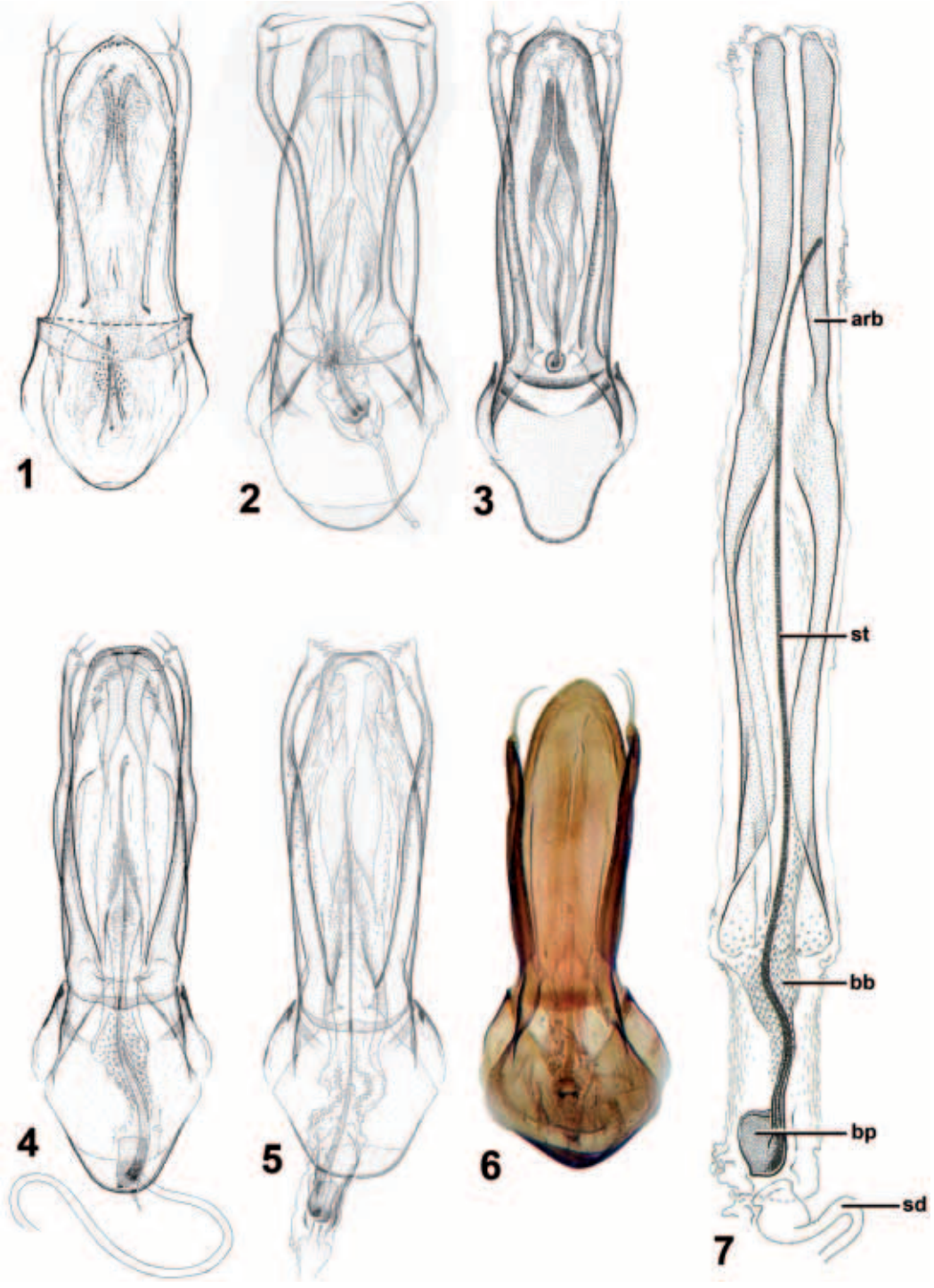
Distribution. Spain. It occupies a large area of dispersion in the Cantabrian mountains range, between the Pinzales and Noreña rivers (Asturias) and the lower basin of the Besaya River (Cantabria), the most western location being the Cueva Benito, in Collada de Atrás, Pola de Siero, with *Quaestus diegoi*, and the most eastern distribution around the Cueva de Cudón nº 2, in Miengo, with *Q. arcanus* (Salgado 1976, 1989b; Fresneda & Salgado 2017).

Species

Quaestus acuminatus Salgado, 1999
Quaestus (*Quaestus*) *acuminatus* Salgado, 1999a: 211.

Quaestus amicalis (Salgado, 1984)
Speocharis amicalis Salgado, 1984: 262.
Speogeus amicalis amicalis (Salgado): Salgado, 1989b: 81.
Quaestus (*Speogeus) amicalis amicalis* (Salgado): Perreau, 1993: 322.

Quaestus arcanus Schaufuss, 1861
Quaestus arcanus Schaufuss, 1861a: 425.
Bathyscia (*Bathyscia*) *arcana* (Schaufuss): Reitter, 1885 [1884]: 35.



FIGURES 199.1–199.7: *Quaestus* series, *Quaestus* group. Aedeagus in dorsal view of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Q. jaspei* **comb. nov.**, (**4**) *Q. avicularis*, (**5**) *Q. incognitus*, (**6**) *Schaufussia pachecoi* **comb. nov.** Endophallus of: (**7**) *Q. nietoi*. Figs **1–5, 7** modified from Salgado *et al*. (2008). Abbreviations: **arb**, apical reinforcement band; **bb**, basal sac; **bp**, basal plate; **sd**, spermiduct; **st**, stylet.

Speocharis arcanus (Schaufuss): Jeannel, 1910a: 30.
Quaestus (*Quaestus*) *arcanus* Schaufuss: Salgado, 2000: 57

Quaestus asturicus Fresneda & Salgado, 2001
Quaestus (*Quaestus*) *asturicus* Fresneda & Salgado, 2001: 104.

Quaestus avicularis (Salgado, 1985)
Speocharis (*Speogeus*) *avicularis* Salgado, 1985: 263.
Speogeus avicularis (Salgado): Salgado, 1989b: 81.
Quaestus (*Speogeus*) *avicularis* Salgado: Perreau, 1993: 322.

Quaestus breuili (Jeannel, 1909)
Speocharis breuili Jeannel, 1909b: 464.
Quaestus (*Quaestus*) *breuili* (Jeannel): Perreau, 1993: 322.

Quaestus diegoi (Salgado, 1989)
Speogeus diegoi Salgado, 1989b: 78.
Quaestus (*Speogeus*) *diegoi* (Salgado): Perreau, 1993: 322.
Speocharis (*Speogeus*) *diegoi* (Salgado): Salgado, 1996a: 155.

Quaestus dilatatus (Salgado, 1984) stat. nov.
Speocharis amicalis dilatatus Salgado, 1984: 263.
Speogeus amicalis dilatatus (Salgado): Salgado, 1989b: 81.
Quaestus (*Speogeus*) *amicalis dilatatus* (Salgado): Perreau, 1993: 322.

Quaestus espanoli (Salgado, 1978)
Speocharis espanoli Salgado, 1978a: 15.
Quaestus (*Quaestus*) *espanoli* (Salgado): Perreau, 1993: 322.

Quaestus incognitus Salgado & Fresneda, 2004
Quaestus (*Asturianella*) *incognitus* Salgado & Fresneda, 2004b: 39.

Quaestus jaspei (Jeannel, 1948) comb. nov.
Oresigenus jaspei Jeannel, 1948a: 73.
Oreosigenus enolensis Bolívar: Escolà, 1978: 485 (*Nomen nudum*).
Speocharis (*Oresigenus*) *jaspei* Jeannel: Bellés *et. al*., 1978: 61.
Quaestus (*Oresigenus*) *jaspei* (Jeannel): Perreau, 1993: 322.

Quaestus jeannei (Coiffait, 1965)
Speocharis jeannei Coiffait, 1965: 292.
Speocharis jeannei sotoensis Salgado, 1982: 52.
Quaestus (*Quaestus*) *jeannei jeannei* (Coiffait): Perreau, 1993: 322.

Quaestus jubilationis Salgado & Fresneda, 2010
Quaestus (*Speogeus*) *jubilationis* Salgado & Fresneda, 2010: 100.

Quaestus littoralis Salgado, 1999
Quaestus (*Speogeus*) *littoralis* Salgado, 1999b: 82.

Quaestus longicornis (Salgado, 1989)
Speocharis longicornis Salgado, 1989a: 127.
Quaestus (*Quaestus*) *longicornis* (Salgado): Perreau, 1993: 322.

Quaestus luctuosus (Salgado, 1984)
Speocharis luctuosus Salgado, 1984: 260.
Quaestus (*Quaestus*) *luctuosus* (Salgado): Perreau, 1993: 322.

Quaestus mermejaensis Salgado & Fresneda, 2004
Quaestus (*Speogeus*) *mermejaensis* Salgado & Fresneda, 2004b: 41.

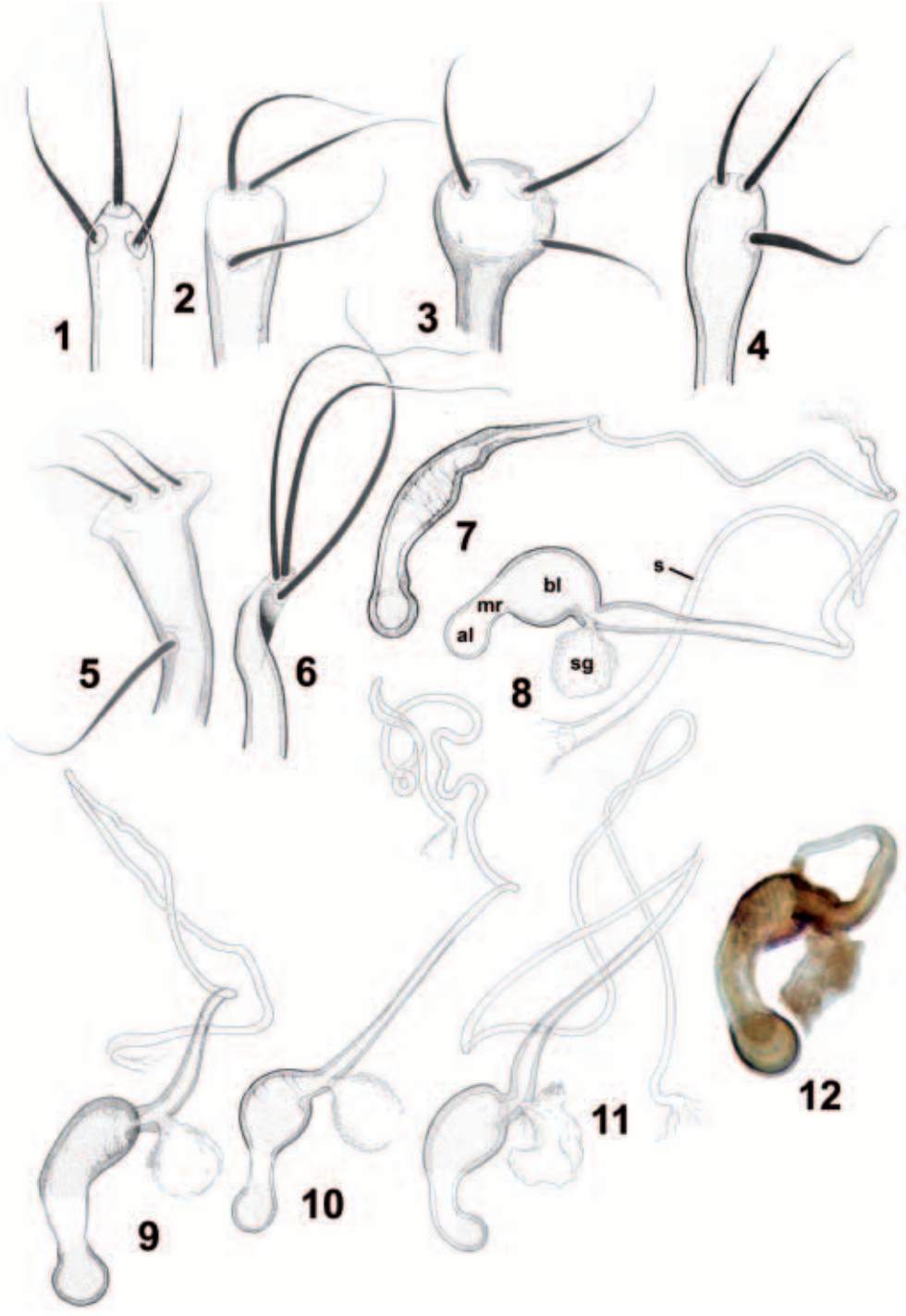
Quaestus nietoi (Salgado, 1988)
Speocharis nietoi Salgado, 1988: 61.

Quaestus nuptialis (Español, 1973)
Speocharis nuptialis Español, 1973: 88.
Speocharis (*Speocharis*) *sajambrensis* Salgado, 1980a: 153.
Quaestus (*Quaestus*) *nuptialis* (Español): Perreau, 1993: 322.

Quaestus occidentalis (Jeannel, 1911)
Speocharis occidentalis Jeannel, 1911a: 301.
Speocharis obermaieri Bolívar, 1923: 427.
Quaestus (*Quaestus*) *occidentalis* (Jeannel): Perreau, 1993: 322.

Quaestus olajensis (Salgado, 1978)
Speocharis olajensis Salgado, 1978a: 12.
Quaestus (*Quaestus*) *olajensis* (Salgado): Perreau, 1993: 322.

Quaestus perezi (Sharp, 1872)
Adelops perezi Sharp, 1872: 269.
Bathyscia (*Bathyscia*) *perezi* (Sharp): Reitter. 1885: 37.
Speocharis perezi (Sharp): Jeannel, 1910a: 30.
Speocharis clermonti Jeannel, 1913: 455.



FIGURES 200.1–200.12: *Quaestus* series, *Quaestus* group. Apex of the paramere of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Q. jaspei* **comb. nov.**, (**4**) *Q. avicularis*, (**5**) *Q. incognitus*, (**6**) *Schaufussia pachecoi* **comb. nov.** Spermathecal complex of: (**7**) *L. bergidi,* (**8**) *Q. arcanus,* (**9**) *Q. jaspei* **comb. nov.**, (**10**) *Q. avicularis*, (**11**) *Q. incognitus*, (**12**) *S. pachecoi* **comb. nov.** Figs **1–11** modified from Salgado *et al*. (2008). Abbreviations: **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

Quaestus (*Quaestus*) *perezi* (Sharp): Perreau, 1993: 322.

Quaestus pongai (Salgado, 1982) stat. nov.
Speocharis jeannei pongai Salgado, 1982: 53.
Quaestus (*Quaestus*) *jeannei pongai* (Coiffait): Perreau, 1993: 322.

Quaestus pseudoccidentalis (Salgado, 1980)
Speocharis pseudoccidentalis Salgado, 1980c: 269.
Quaestus (*Quaestus*) *pseudoccidentalis* (Salgado): Perreau, 1993: 322.

Quaestus recordationis (Salgado, 1982)
Speocharis recordationis Salgado, 1982: 54.
Quaestus (*Quaestus*) *recordationis* (Salgado): Perreau, 1993: 322.

Quaestus riberai Fresneda & Salgado, 2022
Quaestus riberai Fresneda & Salgado, 2022: 28.

Quaestus sajaensis Salgado, 1998
Quaestus (*Quaestus*) *sajaensis* Salgado, 1998: 258.

Quaestus sellai (Bolívar, 1923)
Speocharis sellai Bolívar, 1923: 426.
Speocharis sellai henrici Jeannel, 1924a: 61.
Quaestus (*Quaestus*) *sellai* (Bolívar): Perreau, 1993: 322.

Quaestus spinulosus Salgado, 1998
Quaestus (*Quaestus*) *spinulosus* Salgado, 1998: 261.

Quaestus suevensis (Salgado, 1991)
Speocharis suevensis Salgado, 1991: 122.
Quaestus (*Quaestus*) *suevensis* (Salgado): Perreau, 1993: 322.

Quaestus valenzuelai Fresneda & Salgado, 2022
Quaestus valenzuelai Fresneda & Salgado, 2022: 29.

Quaestus variabilis (Salgado, 1991)
Speocharis variabilis Salgado, 1991: 126.
Quaestus (*Quaestus*) *variabilis* (Salgado): Perreau, 1993: 322.

Genus ***Schaufussia*** nov.
https://zoobank.org/NomenclaturalActs/F4AB9C43-CAC4-4204-B2CF-2AB30D2492A6

Type species. *Speocharis pachecoi* Bolívar, 1915 by present designation (habitus in Fig. 196.6).

Description. Size ranging between 2.2-2.6 mm. Body shape moderately convex, oval and elongated, narrowing regularly towards the apical area (Fig. 196.6). Integument matte and pubescence long, with fine, dense and spaced punctation, in the pronotum very fine and superficial; integument of pronotum and elytra with a microreticulum. Males of the same shape and size than the females.

Head: With the occipital carina obliterated in the central area.

Antennae: Reach two thirds of the elytral suture; the 11th antennomere twice as long as the 10th and broadened into a blade; the 8th to the 10th antennomeres as long as wide or very slightly longer. Females with antennae slightly shorter and more robust.

Pronotum: Transverse with widest area at the base which is only very slightly wider than the base of the elytra; lateral margins regularly arched, with posterior angles acute and apex slightly projecting and blunt; the base is subrectilinear.

Elytra: Elongated and oval with maximum width very close to the base; both elytra loosely united, but generally separated; there is a parasutural stria, although very blurred.

Legs: Relatively long and slender; males protarsi almost as wide as widest extension of protibia and first tarsomere slightly longer than wide; mesotibiae somewhat arched and metatibiae straight. Characteristic of this genus are the mesofemora with a sinuate posterior margin and the metafemora with a small prominence towards the middle of the posterior margin.

Mesoventral keel (Fig. 197.6): High and long, with two slightly convex edges, the anterior and the posterior slightly serrated in the front area and widened in the middle, without a groove.

Suture of the metaventrite (Fig. 197.6): In the first half it describes an arc that delimits a small area and subsequently runs parallel to the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 198.3): Wings of the metascutum very broad and elongated, twice as long as wide; alacrista apophysis long with apices blunt.

Metendosternite (Fig. 198.6): Furcal arms, slightly longer than the furcal trunk (ft), narrow towards the apex, which is slightly arched and somewhat dilated, showing a diffuse terminal apophysis; posterior lamina with the same width all along the arm and the posterior border in a regular arc. Trunk somewhat longer than the area of widest basal extension and the median keel with a slight posterior divergence.

Median lobe of aedeagus: Long. In lateral view, with an arched profile, bent at an obtuse angle towards

the middle and apical area slightly curved towards ventral side. In dorsal view (Fig. 199.6), lateral margins arched, with apical area pointed.

Endophallus (Fig. 199.6): In the basal region there are two phanerae attached one at each side of the stylet at its base, this part is enveloped or flanked by two bundles of squamous tissues; the stylet is quite robust and rather short, it extends up to a third of the length of the sac and is surrounded by bags of tissue all over covered with spicules or thick lateral spines or on its apical part, it does not have a basal plate; the mid-apical region with two long reinforcing bands.

Parameres (Fig. 200.6): Thin, somewhat recurved in the apical area and much shorter than the median lobe; they end in a little differentiated club in which there are three setae inserted apically, which are very long, almost equal in length and with very close insertion pores.

Spermathecal complex (Fig. 200.12): Spermatic duct short, about three to four times longer than the spermatheca, and at the base where the spermatheca is is attached it is widened and a well-developed spermathecal gland empties into that area; both lobes are poorly differentiated and only slightly sclerotized, as is the middle region, with the apical lobe being spherical and similar in size to the basal one.

Female uroventrite VIII (Fig. 201.6): With the median apical margin strongly notched and the spiculum quite long, narrow and with a sharp tip.

Etymology. Genus dedicated to the German entomologist Ludwig Wilhelm Schaufuss (born 24.08.1833, Greiz – dies 16.07.1890, Dresden), the first entomologist to discover hypogeous Leptodirini around the Cantabrian coast and is author of the genera description of *Quaestus* and *Quaesticulus*.

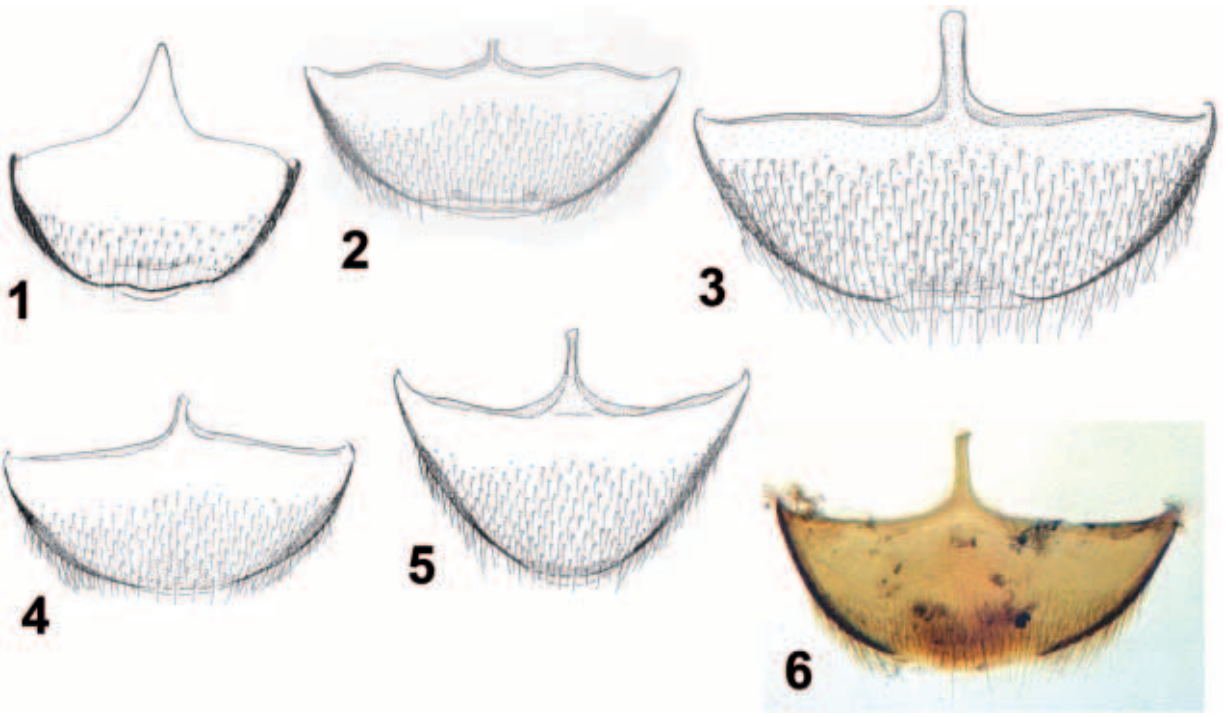
Discussion. The genus presents all the characters described for the *Quaestus* series. The molecular study (Fig. 1E) places *Schaufussia* gen. nov. as a sister group to the large clade *Leonesiella* + *Quaestus* with very high support of 99.9/100. *Schaufussia bustilloi* comb. nov. and *S. pachecoi* comb. nov. were considered to belong to the subgenus *Quaesticulus* because they presented the following characteristics: parasutural striae very blurred, mesoventral keel high and long, stylet of the endophallus short without basal plate, and short spermatic duct (Perreau 1993; Salgado 2001b, Salgado *et al*. 2008). However, Salgado & Fresneda (2009) already pointed out the isolation of these two species in relation to the other representatives of the subgenus, since they present a more western distribution within the subgenus *Quaesticulus* and are the only ones within that subgenus that are found in Asturias. It is true that the stylet of the endophallus is similar in *Schaufussia* gen. nov. and *Quaesticulus*, but in the first the spermatheca has both lobes poorly differentiated, slightly thickened and slightly sclerotized, like the middle region, and in *Quaesticulus* the two lobes are apparent, much larger than the middle region and considerably more sclerotized; in addition, the suture of the metaventrite describes an arc in *Schaufussia* gen. nov. while it is triangular in *Quaesticulus*.

Schaufussia mariscali (Salgado, 1979) comb. nov. is reinstalled as a species close to *Schaufussia pachecoi* comb. nov. with which it shares a very similar shape of the aedeagus, although there are also striking differences in their external morphologies:

– *Schaufussia mariscali* comb. nov. is in general somewhat smaller, around 2.0 mm; the male protarsi are narrower than the distal end of the protibia and elongated in shape; the antennae are shorter and more robust, with the 8th and 10th antennomeres transverse; the parameres are shorter, robust, with the terminal sector curved towards the median lobe; the endophallus encompasses two plates, parallel and slightly sclerotized that are attached to the base of the stylet.

– *Schaufussia pachecoi* comb. nov. is of more than 2.0 mm in size; male protarsi slightly wider than distal end of protibia and heart-shaped; antennae are somewhat longer, but mostly more slender, with the 8th antennomere longer than wide and the 10th as long as wide; the parameres are comparatively longer and more gracile and have a straight terminal sector; endophallus without laminae attached to the base of the stylet, with the terminal sector straight; endophallus without lamina attached to the base of the stylet.

Distribution. Spain, Asturias and Leon. It is the genus with the westernmost dispersion of the entire *Quaestus* clade. It extends from the limestone of the Luna river basin (León) as the easternmost area to the Sierra de Tineo as the westernmost. It is known from more than 70 caves located in a wide belt of carboniferous limestone that extends from the basins of the Geras and Luna rivers to Puerto Ventana (province of León); while in the province of Asturias it is widely dispersed throughout the basins of the Narcea, Nalón, Teverga, Trubia and Somiedo rivers, from their headwaters to the coast (Fresneda & Salgado 2017).



FIGURES 201.1–201.6: *Quaestus* series, *Quaestus* group. Female uroventrite VIII of: (**1**) *Leonesiella bergidi,* (**2**) *Quaestus arcanus,* (**3**) *Q. jaspei* **comb. nov.**, (**4**) *Q. avicularis*, (**5**) *Q. incognitus*, (**6**) *Schaufussia pachecoi* **comb. nov.** Figs **1–5** modified from Salgado *et al*. (2008).

Species

Schaufussia bustilloi (Salgado & Fresneda, 2009) comb. nov.
Quaestus (*Quaesticulus*) *bustilloi* Salgado & Fresneda, 2009: 3.

Schaufussia mariscali (Salgado, 1979) comb. nov.
Speocharis mariscali Salgado, 1979: 387.

Schaufussia pachecoi (Bolívar, 1915) comb. nov.
Speocharis pachecoi Bolívar, 1915: 401.
Quaestus (*Quaestus*) *pachecoi* (Bolívar): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *pachecoi* (Bolívar): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *pachecoi* (Bolívar): Salgado, 2001: 196.

Schaufussia sinuatipenis sp. nov. (see Appendix of new species)

3.3.5.3 ***Quaesticulus*** group

DIAGNOSIS. Species of small size between 1.5-3.0 mm.

Antennae: Antennomeres in general, short and thick, the 11th article being somewhat longer than the 10th, with a widened appearance.

Elytra: Parasutural stria well marked.

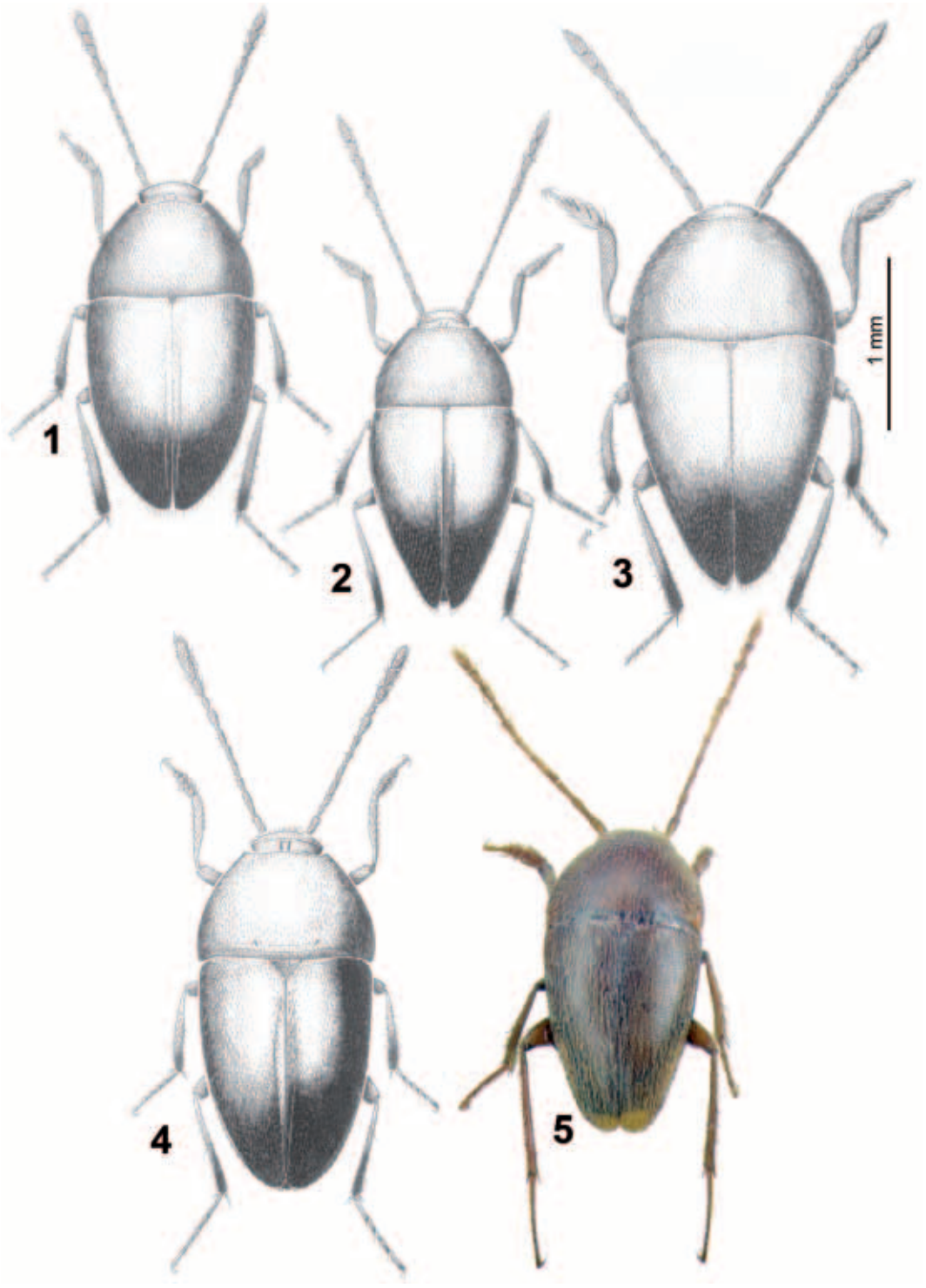
Legs: Males protarsi dilated, but always narrower than the apical part of the protibia.

Mesoventral keel: Tall and long, with the angle obtuse and a narrow ventral edge (Fig. 204.10), only slightly widened in the middle area of *Quaesticulus autumnalis* comb. nov., but without furrow, and the vertex somewhat prominent in *Speocharinus* (Fig. 204.11).

Sutures of the metaventrite: They form a triangle with a more or less pointed vertex (Figs. 204.10, 204.11).

Metatergal apparatus (Fig. 205.7): With the wings of the metascutum wide and the apophysis of the alacrista long.

Metendosternite (Fig. 206.7): Small, with the furcal arms narrow, somewhat longer than the trunk and



FIGURES 202.1–202.5: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Habitus of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *A. oxypterus* **comb. nov.**, (**3**) *Espanoliella tibialis,* (**4**) *Cantabrogeus luquei,* (**5**) *Fresnedaella lucius*. Figs **1–4** modified from Salgado *et al*. (2008).

the apices hooked and sharp, without apical apophysis.

Endophallus (Figs. 207.8, 207.9): With short stylet, without basal plate, and small spines and scales; very long apical reinforcing bands.

Parameres: As long or slightly shorter than the median lobe, without terminal club (Fig. 208.12) or somewhat distinct, and the three setae long and fine with apical insertion; four setae in *Speocharinus* (Fig. 208.13)

Spermatheca (Figs. 209.8, 209.9): With the two lobes well-differentiated, the basal being somewhat larger than the apical.

Female uroventrite VIII: Spiculum short or long and narrow (Figs. 210.8, 210.9).

Discussion. In the phylogenetic tree (Fig. 1F) the *Quaesticulus* group is sister and basal to the groups of *Cantabrogeus* and *Espanoliella* which are sister groups themselves and join the *Quaesticulus* group with a support of 88.4/99. The genus *Speocharinus*, the only one with pholeuonoid facies and for which no molecular data are available, has been included in this series in *Quaesticulus* group. The reason for its inclusion is the presence of several common characters, such as: head with occipital carina; stippling of the pronotum and elytra disorderly, without transverse striation but with parasutural stria; metaventrite with two sutures delimiting a triangular area; mesoventral keel tall and long; endophallus with stylet and spermatheca with two distinct lobes. A final classification e.g. a confirmation of the described taxonomic groupsing of the genus has to postphoned until molecular analysis can be carried out, morphological characters alone are very difficult to interpret and only give hints but lack solid evidence.

Distribution. Spain, Cantabria. The caves of the three species of *Quaesticulus* extend through limestone found between around the right basin of the Saja River, being their westernmost distribution limit, and the left basin of the Miera River, to the east. *Speocharinus* is only found near the area of Astrana in Cantabria.

Key to genera

1. Bathyscioid shape (Fig. 203.3), with the lateral margins of the pronotum regularly arched. Parameres with three apical setae (Fig. 208.12) .....*Quaesticulus*
- Elongated (Fig. 203.4), with slightly bell-shape pronotum. Parameres with four apical setae (Fig. 208.13) .....*Speocharinus*

Genus ***Quaesticulus*** Schaufuss, 1861
Quaesticulus Schaufuss, 1861a: 426.
Sajadytes Salgado, 1992: 101 (Type species: *Speocharis* (*Sajadytes*) *canis* Salgado-Costas, 1992).

Type species. *Quaesticulus adnexus* Schaufuss, 1861 by monotypy (habitus in Fig. 203.3).

Diagnosis. Size ranging between 1.5-2.7 mm. Facies bathyscioid (Fig. 203.3), with body oval or elliptical, and always clearly convex. Pronotum smooth, without apparent microreticulum,fine and scattered punctation; on elytra with somewhat rough punctation. Females somewhat more robust than males.

Head: with complete occipital carina.

Antennae: Normally short, half the length of the elytral suture, or somewhat longer, about three-fourths the length of the suture; the 11th antennomere is the longest, twice as long as the 10th, and the club segments are generally transverse, especially the 8th.

Pronotum: Transverse with regularly arched sides; maximum width at the base, which is sinuous.

Elytra: Short and wide or elongated; maximum width at the base; the apices regularly curve and the parasutural stria present, although in some case more or less blurred in the basal third.

Legs: Short or very short, but slender; males protarsi not or slightly dilated and therefore clearly narrower than the apical end of the tibiae; tibiae hairy, with two bifid internal spurs, two simple external ones and a series of unequal spines between them; protibiae unattenuated, mesotibiae somewhat curved and thickened and metatibiae straight, all with spines on the external face. In *Quaesticulus adnexus* the metafemora of the male have a small tubercle in the middle of the posterior margin.

Mesoventral keel (Fig. 204.10): High and long, with the anterior border almost rectilinear and moniliform, and the ventral border, generally narrow, somewhat convex with a rounded edge; the angle right and the vertex rounded; the posterior apophysis long and reaches the bifid process of the metaventrite.

Sutures of the metaventrite (Fig. 204.10): Two sutures, each starting from one end of the mesocoxal cavity, the basal in its first half follows the edge of the cavity, then both extend towards the posterior edge of the metaventrite and converging at a point, forming a triangular area with a vertex more or less sharp.

Metatergal apparatus (Fig. 205.7): Wings of the metascutum rather broad and elongated, about twice as long as wide; the apophysis of the alacrista long.

Metendosternite (Fig. 206.7): Furcal arms slightly



FIGURES 203.1–203.4: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Habitus of: (**1**) *Hypogesia minos* **comb. nov.**, (**2**) *Luquesia pasensis* **comb. nov.**, (**3**) *Quaesticulus adnexus*, (**4**) *Speocharinus llosesi*.

longer than the furcal trunk, with apex curved and sharp, without terminal apophysis; posterior lamina progressively narrows towards the apex of the arm. Trunk as long as the part of greatest basal width and the median keel with a slight posterior divergence. This genus has the smallest metendosternite in this clade.

Median lobe of aedeagus: In lateral view, it can be slightly or very arched. In dorsal view (Fig. 207.8), the sides of the basal two-thirds of the length a regular

smooth arc, then narrow regularly or somewhat more abruptly and forming an apex blunt or rounded.

Endophallus (Fig. 207.8): With two regions. In the basal part there is a membranous sac covered with spinules and scales poorly developed arranged in an oval shape, in addition to a stylet short and thin, without a basal plate; in the mid-apical region there are two reinforcing bands that are very long.

Parameres (Fig. 208.12): Slender, as long or somewhat shorter than the median lobe and the apex not or slightly thickened; the three setae with apical insertion, very long, sinuous and of similar length.

Spermathecal complex (Fig. 209.8): Spermatheca short, with a middle region very reduced and the two lobes considerably large and sclerotized, the basal one being somewhat more developed; spermatic duct short, about three or four times the length of the spermatheca, and thin throughout its length, only slightly widened at the point of insertion into the spermatheca; spermathecal gland small, but well manifested.

Female uroventrite VIII (Fig. 210.8): Spiculum short, narrow and sharp.

Discussion. In the phylogenetic tree (Fig. 1F), *Quaesticulus* appears as a sister of the clade *Espanoliella* and *Cantabrogeus* groups with support 88.4/99. *Quaesticulus adnexus* is the smallest species in the large clade of the *Quaestus* series, along with *Leonesiella bergidi*. In this genus there are species with elytral suture well marked and others that present it blurred – *Quaesticulus canis* comb. nov. – In any case *Quaesticulus* is well characterised by its morphological characters and the structures of the male and female genitalia: the metendosternite is the smallest of its clade, with the trunk and the arms of the furca shorter; the stylet of the endophallus is short, slender, without a basal plate; the three setae of the parameres have apical insertion; the spermatheca has a very short middle region and the two lobes are very large, the basal one being more developed; the ridge of the ventral edge of the mesoventral keel is narrow – somewhat widened in the middle part in *Quaesticulus autumnalis* comb. nov. – the sutures of the metaventrite converge to one point forming a triangular area; males protarsi very slightly dilated; the 11th antennomere is at least twice as long as the 10th and the 8th to 10th antennomeres are transverse or nearly transverse.

Of the three species, the basal one is *Quaesticulus adnexus*, which joins the sister species *Q. canis* comb. nov. and *Q. autumnalis* comb. nov. with a support 60.4/97 (Fig. 1F).

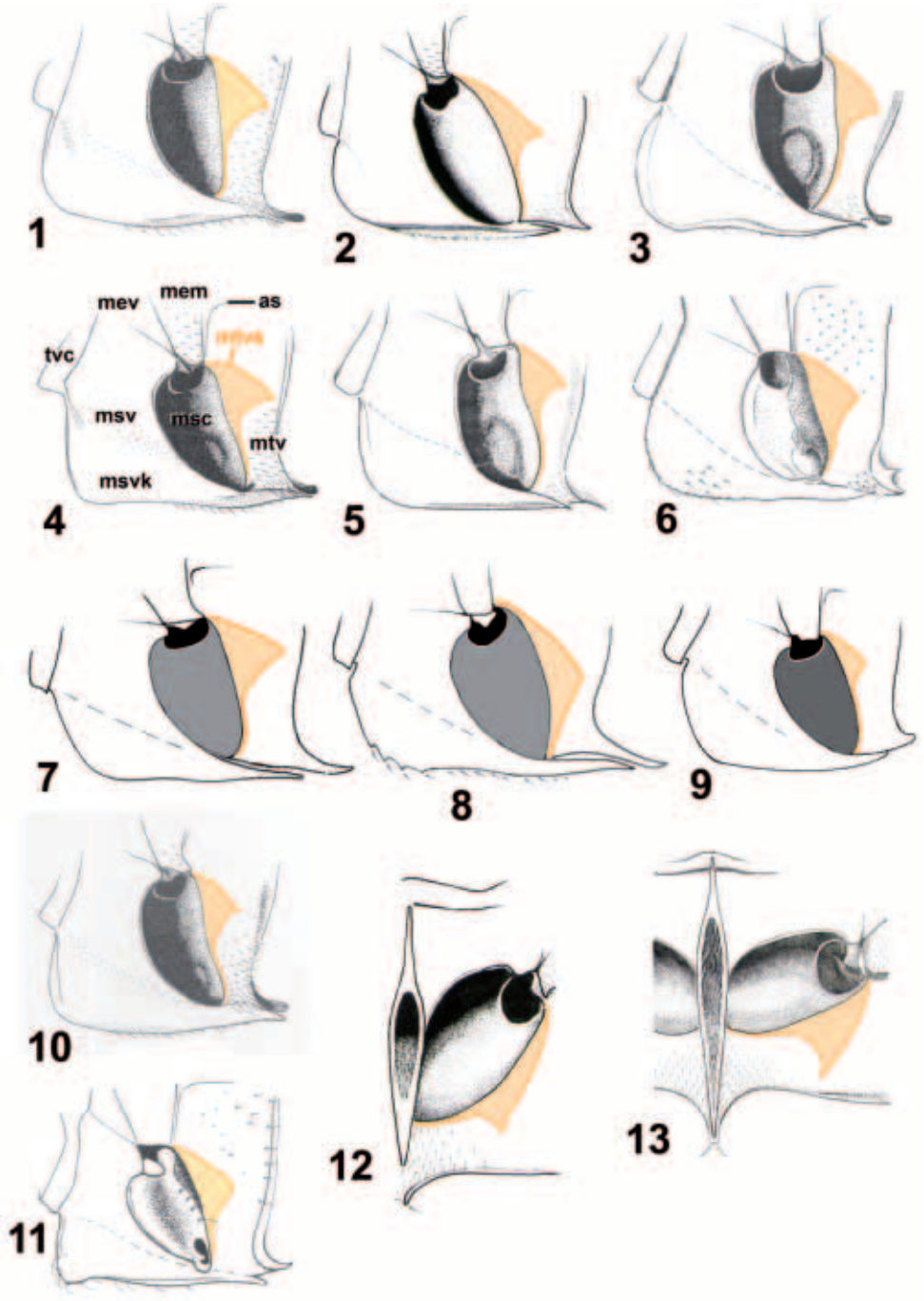
Distribution. Spain, Cantabria. *Quaesticulus adnexus* is found in the karstic areas between the Nansa and Miera river basins; *Q. autumnalis autumnalis* comb. nov. is distributed in cavities nestled in the limestone of the Montes de Ucieza and Sierra Quintana between the middle-low basins of the Pas, Besaya and Saja rivers; *Q. autumnalis brevicornis* comb. nov. in two caves in the northern foothills of Sierra Quintana; *Q. canis* comb. nov. in three cavities close to each other that are located in a small Jurassic karst in the Cabuérniga valley, close to the upper basin of the Saja river (Fresneda & Salgado 2017).

Species

Quaesticulus adnexus Schaufuss, 1861
Quaesticulus adnexus Schaufuss, 1861a: 427.
Bathyscia (*Bathyscia*) *adnexa* (Schaufuss): Reitter, 1885a [1884]: 38.
Speocharis adnexus (Schaufuss): Jeannel, 1910a: 30.
Quaestus (*Quaestus*) *adnexus* (Schaufuss): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *adnexus* (Schaufuss): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *adnexus* (Schaufuss): Salgado, 2001: 19.

Quaesticulus autumnalis (M. de la Escalera, 1898) comb. nov.
Quaesticulus autumnalis autumnalis (M. de la Escalera, 1898) comb. nov.
Bathyscia autumnalis M. de la Escalera, 1898: 37.
Speocharis autumnalis (Escalera): Jeannel, 1910a: 31.
Quaestus (*Quaestus*) *autumnalis* (Escalera): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *autumnalis* (Escalera): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *autumnalis* (Escalera): Salgado, 2001: 196.
Quaesticulus autumnalis brevicornis (Jeannel, 1924) comb. nov.
Speocharis autumnalis brevicornis Jeannel, 1924a: 62.
Quaestus (*Quaestus*) *autumnalis brevicornis* (Jeannel): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *autumnalis brevicornis* (Jeannel): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *autumnalis brevicornis* (Jeannel): Salgado, 2001: 196.

Quaesticulus canis (Salgado, 1992) comb. nov.
Speocharis (*Sajadytes*) *canis* Salgado, 1992: 102.



FIGURES 204.1–204.13: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Pterothorax in lateral view of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *A. luquei* **comb. nov.**, (**3**) *A. noltei* **comb. nov.**, (**4**) *A. oxypterus* **comb. nov.**, (**5**) *Espanoliella jeanneli,* (**6**) *Cantabrogeus luquei,* (**7**) *Fresnedaella lucius*, (**8**) *Hypogesia minos* **comb. nov.,** (**9**) *Luquesia pasensis* **comb. nov.**, (**10**) *Quaesticulus adnexus*, (**11**) *Speocharinus llosesi*. Pterothorax in ventral view of: (**12**) *A. luquei* **comb. nov.**, (**13**) *A. noltei* **comb. nov.** Figs **1–6, 10–13** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

Quaestus (*Sajadytes*) *canis* (Salgado): Perreau, 1993: 322.
Quaestus (*Quaesticulus*) *canis* (Salgado): Salgado, 2001: 196.

Genus ***Speocharinus*** Español & Escolà, 1977
Speocharinus Español & Escolà, 1977: 25.

Type species. *Speocharis llosesi* Español & Escolà, 1977 by monotypy (habitus in Fig. 203.4).

Diagnosis. Size of 3.0 mm. Facies sub-pholeuonoid (Fig. 203.4), with body very elongated, narrowed backwards and forwards, convex. Pronotum smooth and shiny, covered with small and dense punctation; the elytra with a dense, irregular and somewhat rough punctation. Female somewhat more robust than the male.

Head: with complete occipital carina.

Antennae: Long, with the first six segments thin, longer than wide, the 7th being the most robust and the last three thick. Female with the 7th antennomere shorter and strongly thickened.

Pronotum: Slightly transverse, somewhat bell-shaped, narrowed in the posterior third, where the lateral margins appear regularly arched; widest at base as wide as basal area of elytra; acute angles and sharp vertices, facing backwards and outwards.

Elytra: One and a half times as long as wide, with the greatest width in the basal quarter; there is a deep parasutural stria.

Legs: Long and quite robust, with the male protarsi slightly enlarged, somewhat narrower than the apical area of the protibiae; in both sexes there are long setae on protarsi and mesotarsi; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; protibiae unattenuated, mesotibiae curved and thickened, and anterior half of the metatibiae arched, all with spines on the external side.

Mesoventral keel (Fig. 204.11): High, with the vertex rounded and prominent; anterior border straight and moniliform, and inferior border sinuous, narrow, without groove and with arista sharp; the posterior apophysis extends to the bifid process of the metaventrite.

Sutures of the metaventrite (Fig. 204.11): Two sutures that start from one end of the mesocoxal cavity, extend towards the posterior edge of the metaventrite and converge, delimiting a triangular area with a rounded vertex in the middle of the length of the metaventrite.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: In lateral view, dorsal face with a regular arc and the ventral curved at an obtuse angle, with the middle area and the apical third of uniform width, and the apex narrow and sharp. In dorsal view (Fig. 207.9), subparallel sides, the width being fairly uniform up to the apical area, where it becomes progressively narrower.

Endophallus (Fig. 207.9): It encloses in the basal part a stylet which is sinuous, well-differentiated and of medium length without basal plate; towards the middle part a small group of scaly poorly-developed spines is observed; reinforcing bands well-defined and narrow run through the entire apical and middle area.

Parameres (Fig. 208.13): Thin and somewhat shorter than the median lobe; club undifferentiated, armed with four long setae of similar length, three apical and one preapical with the insertion pore somewhat distant.

Spermathecal complex (Fig. 209.9): Spermatheca with apical lobe spherical, somewhat narrower and smaller than the basal lobe; between these two the junction duct, short and less sclerotized than the lobes; spermatic duct thin, about three times longer than the spermatheca and widens slightly in the initial area, where the spermathecal gland empties.

Female uroventrite VIII (Fig. 210.9): Spiculum well-developed, narrow, with a rounded apex and somewhat widened.

Discussion. For this species it was not possible to generate molecular data hence the approximated taxonomic/systematic position is derived from morphology only. The short stylet without basal plate in the basal part of the endophallus, the spines scaly and poorly developed and the existence of apical reinforcement bands, relate this genus to *Quaesticulus*. The presents of four setae (3 apical + 1 preapical) is particular but does not seem of high importance for taxonomic classification; as it has been shown in *Quaestus incognitus* (ex-*Asturianella*), defined by this same peculiarity, it could be a derived state within a clade that universally has three setae. The presence of long setae in the pro- and mesotarsi of both sexes is an exclusive character within the Cantabrian fauna, but a homoplasy with two species of Pyrenean Leptodirini, *Perriniella bofilli* and *P. faurai*. Inititally it was though that it is basal to the *Quaesticulus* clade, since as this one it exhibits similarities in structures like the antennae, the mesoventral keel, the aedeagus with a similar median lobe and endophallus with stylet, scales, small spines and long apical reinforcement bands, and the spermatheca with two well differentiated lobes. The



FIGURES 205.1–205.7: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *Espanoliella tibialis,* (**3**) *Cantabrogeus luquei,* (**4**) *Fresnedaella lucius*, (**5**) *Hypogesia minos* **comb. nov.**, (**6**) *Luquesia pasensis* **comb. nov.**, (**7**) *Quaesticulus adnexus***.** Abbreviations: **alc**, alacrista; **sc3**, metascutum.

incorporation of these species in this clade is also supported by their geographical distribution.

Distribution. Spain, Cantabria. Known for two vertical abysses, Morterón I and II del Hoyo Salzoso; the first represents a the typical locality. Both abysses are close to each other and located in the Los Trillos depression (Español & Escolà 1977), in the Astrana area. The species is rare with very few sightings. Based on the available data, it appears that *Speocharinus llosesi* is found around 300 m depth and above in both caves; in the upper parts *Hypogesia minos* comb. nov. it is more common. Even inhabiting the same caves system, but the two species are not found to occur together in the same places.

Species

Speocharinus llosesi (Español & Escolà, 1977)
Speocharis (*Speocharinus*) *llosesi* Español & Escolà, 1977: 26.
Speocharinus llosesi (Español & Escolà): Bellés, Comás, Escolà y Español, 1978: 61.

3.3.5.4 ***Espanoliella*** group

Diagnosis. Size range between 2.1 and 3.0 mm. The basic character that allows to differentiate the representatives of these clades from the main *Quaestus* clade are a well defined parasutural stria.

Mesoventral keel: High and long, the posterior apophysis reaching up to the posterior border of the metaventrite; vertex rounded and the ventral border wide, with a groove.

Metaventrite: Two sutures are observed, each starting from the ends of the mesocoxal cavity, extending towards the posterior edge of the metaventrite and converging at a point more or less far from the edge, delimiting an interior triangular area whose vertex is pointed or rounded.

Metatergal apparatus: Long apophysis of the alacrista.

Metendosternite: With the furcal arms narrow, somewhat longer than the trunk; the posterior margin of the posterior furcal lamina with a smoothly concave and pointed, arcuate or hooked apices, without apical apophysis.

Endophallus: Two regions, with or without short stylet without basal plate; in general with one or two groups of robust spines in basal position or in the middle part.

Parameres: Robust, with three apical setae of very different lengths, forms and insertion very diverse; in general the insertion pores well marked and may be apical or distributed along the terminal sector of the paramere.

Spermathecal complex: Spermatheca with two differentiated lobes, the basal being larger. Short spermatic duct, 2-4 times the length of the spermatheca – somewhat longer in *Espanoliella* – somewhat widened in the area where it joins the basal lobe, the area where the spermathecal gland opens, and also somewhat widened in the terminal area at the union with the copulatory bag in *Espanoliella*.

Female uroventrite VIII: Spiculum long and narrow.

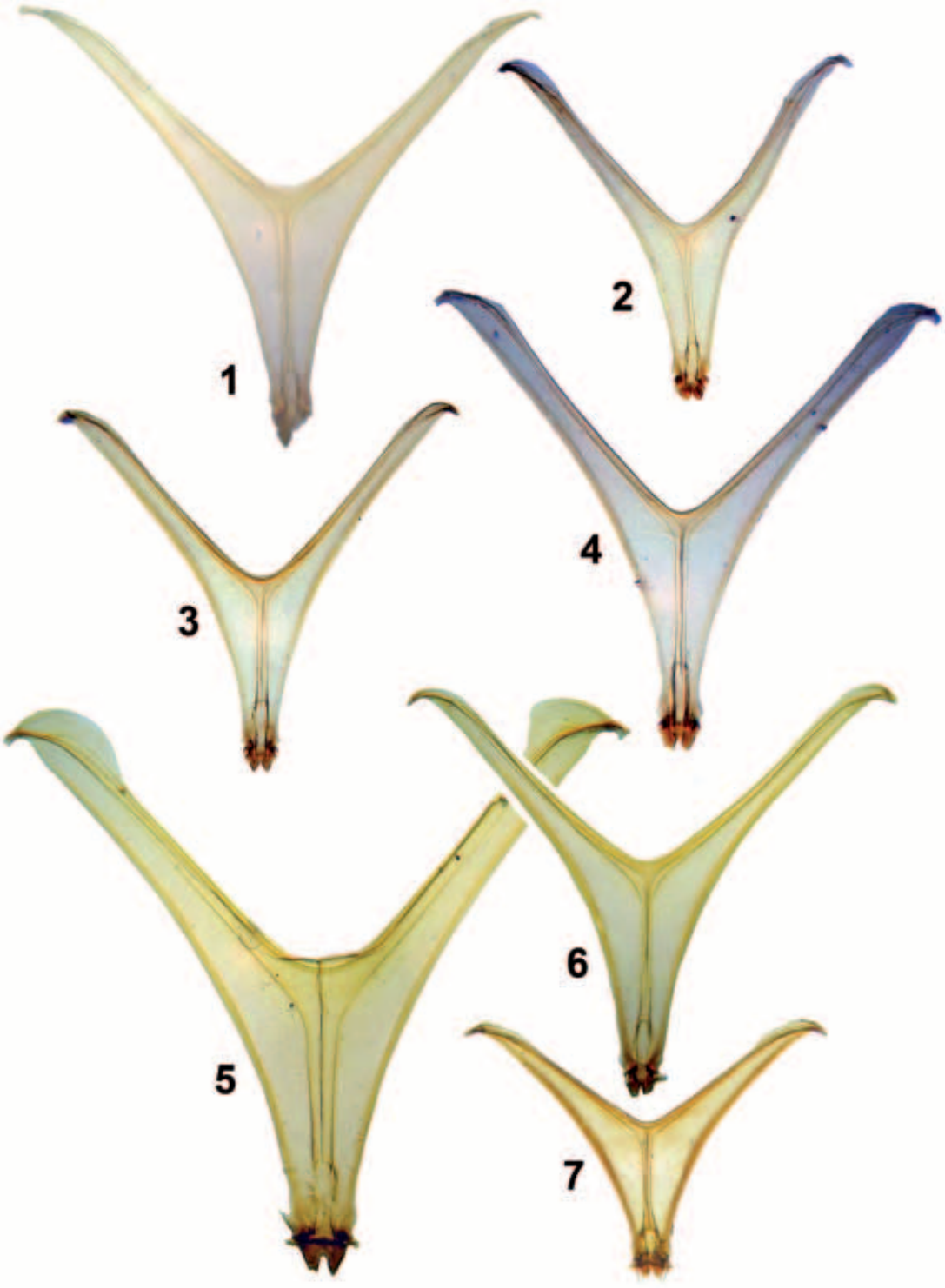
Discussion. The *Espanoliella* group is very well supported with 100/100 (Fig. 1F). It is the sister group of *Cantabrogeus* consisting of: *Cantabrogeus*, *Fresnedaella*, *Hypogesia* gen. nov. and *Luquesia* gen. nov., His clade has a support of 98.7/100. Preserving the subgenus *Samanolla* would have left the description of two distinct genera without valid characters supporting this formal separation. Furthermore, *Amphogeus filicornis* comb. nov. then would have been incorporated into *Samanolla* – despite the absence of common characters – or alternatively to be described as a third genus for this species.

The following differentiating characters are to be highlighted for the other groups of the clade of the *Quaestus* series: elytra with a well-marked parasutural stria; mesoventral keel long with a broad midventral margin and a groove; endophallus without stylet or with a short stylet and no basal plate, usually with several groups of stout spines; robust parameres, with three setae, in many cases with very peculiar adaptations. However, there are some highly significant peculiar characters present in some of the species of this group.

Distribution. Spain. The representatives of this clade colonise a large karstic area in the middle and eastern areas of the Cantabrian mountains range, bordering the eastern region of Cantabria, Northern Burgos and Álava up to areas close to the mouth of the river Deva (Gipuzkoa), with a species located in a small and very isolated massif in the Sierra de Guadarrama (Madrid).

Key to genera

1. Endophallus without stylet (Fig. 207.3). Parameres with three setae, the inner and lower setae much more robust and thickened at the base, normally inserted in



FIGURES 206.1–206.7: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Metendosternite of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *Espanoliella tibialis,* (**3**) *Cantabrogeus luquei,* (**4**) *Fresnedaella lucius*, (**5**) *Hypogesia minos* **comb. nov.**, (**6**) *Luquesia pasensis* **comb. nov.**, (**7**) *Quaesticulus adnexus*.

a well-developed fossa, with the apical part forked or hook-shaped (Fig. 208.7). Longer spermatic duct, about six times the length of the spermatheca and the part of attachment to the copulatory bag widened (Fig. 209.3).....*Espanoliella*
- Endophallus with stylet (Figs. 207.1, 207.2), rudimentary in *Amphogeus luquei* comb. nov.. Parameres with three setae, the lower one is not always the most developed, with the base not dilated and the apical part «normal», e.g without specific structures (Fig. 208.5, 208.6). Short spermatic duct 2-4 times the length of the spermatheca and not widened in the part of union to the copulatory bag (Fig. 209.1, 209.2).....
.....*Amphogeus* stat. nov.

Genus ***Amphogeus*** Salgado, 2000 stat. nov.
Quaestus (*Amphogeus*) Salgado, 2000: 54.
Samanolla Salgado, 2000: 54 syn. nov. (Type species: *Speocharis oxypterus* Bolívar, 1917).

Type species. *Bathyscia cantabrica* Uhagón, 1881 by original designation (habitus in Fig. 202.1).

Diagnosis. Size ranging between 2.1-3.1 mm (*Amphogeus sharpi* comb. nov. 2.1 mm; *Amphogeus filicornis* comb. nov. 3.1 mm). Bathyscioid facies (Fig. 202.1, 202.2); body generally oval-elongated and narrowed to the rear; always exhibit convexity. Pronotum smooth, with very smalldots, on the elytra with a rough spotted pattern . Female, in general, more convex and larger than the male.

Head: Retractable, with the occipital carina complete, sometimes blurred in the middle area.

Antennae: Thin, of variable length and with the first two segments equal or nearly the same, the 11th being generally the longest and most robust; female's antennomeres somewhat shorter and thicker.

Pronotum: Transverse with sides regularly arched and sharp vertices, sometimes divergent; maximum width at the base.

Elytra: Elongated, elliptical, with the apical areas rounded or pointed, sometimes divergent, and the parasutural stria clearly visible.

Legs: Short and slender; males protarsi always dilated but of variable width, from narrower to wider than the apical end of the tibiae; male metafemora in some species with a small tubercle on rear margin; tibiae hairy, with two internal pectinate spurs, two simple external ones, and a series of unequal spines between them; protibiae not tapered and without spines on the outer side; mesotibiae straight or slightly curved, and metatibiae straight, both with thick spines on the outer side.

Mesoventral keel (Figs. 204.1-204.4): Tall, with a rounded vertex; front edge between arcuate and rectilinear, fringed; ventral edge wide, with a more or less long groove in the middle area (Figs. 204.12, 204.13); the posterior apophysis long and reaches the bifid process of the metaventrite.

Sutures of the metaventrite (Figs. 204.1-204.4): Two sutures that each start from one end of the mesocoxal cavity, extend towards the posterior edge of the metaventrite and converge at a point, delimiting a triangular area with a generally sharp and narrow vertex.

Metatergal apparatus (Fig. 205.1): With the metascutum elongated and rather narrow; the apophysis of the alacrista long.

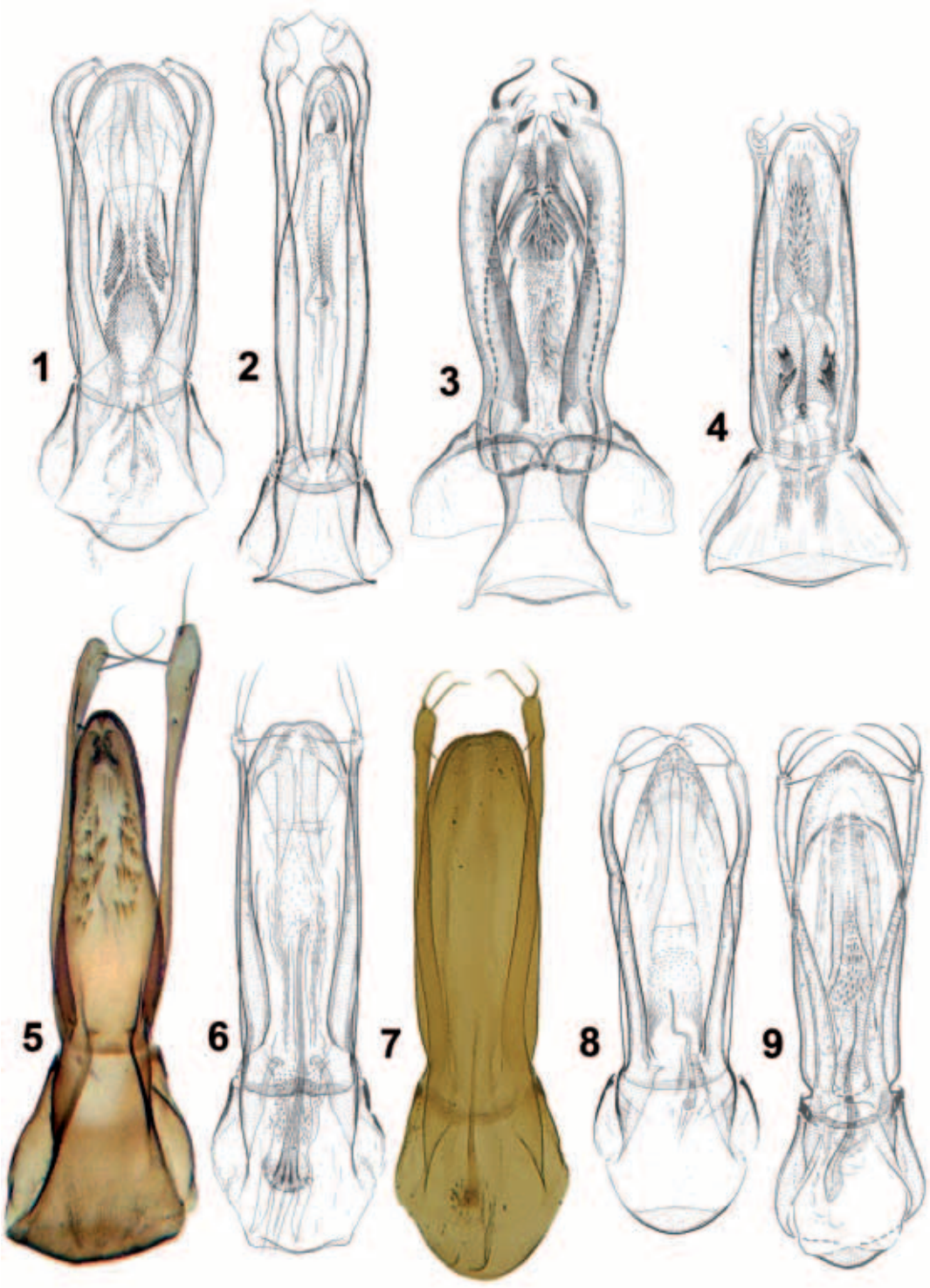
Metendosternite (Fig. 206.1): With the median keel of the trunk shorter than the anterior keel of the furcal arms; with the apex of the arms curved and ogival, without terminal apophysis; the posterior lamina decreases in width towards the apex of the arms. Trunk almost twice as long as the area of greatest width at the base and the median keel with a slight posterior divergence.

Median lobe of aedeagus: In lateral view, long, arched and narrowed towards the apical part; in some species along the ventral midpart eventually a keel is present. In dorsal view (Figs. 207.1, 207.2), the sides are arcuated or subrectilinear, then narrow and the apical area very variable, but never very pointed, sometimes widely arcuate. Basal lamina of the median lobe as long or slightly longer than the tegmen lamina.

Endophallus (Figs. 207.1, 207.2): With stylet, very rudimentary in *Amphogeus luquei* comb. nov., and always without basal plate; phanerae more or less developed depending on the species; apical reinforcement bands visible, long or short.

Parameres (Figs. 208.5, 208.6): Long and robust, as long as or longer than the median lobe; apical area with or without a club, and in this area there are three setae with different shapes, generally the middle one shortest or most robust, and the two apical ones with the insertion pores closest. Ventral lamina of the tegmen broader than long.

Spermathecal complex (Figs. 209.1, 209.2): Spermatheca short, with the middle region reduced and little sclerotized; the lobes of greater caliber than the middle region, the apical being spherical and the basal globose and somewhat more dilated, only elongated in *Amphogeus cantabricus* comb. nov.; short and thin spermatic duct, between three and four times longer than the spermatheca, dilated in the part of union with the spermatheca, part in which ends a well-developed spermathecal gland.



FIGURES 207.1–207.9: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Aedeagus in dorsal view of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *Amphogeus oxypterus* **comb. nov.**, (**3**) *Espanoliella tibialis,* (**4**) *Cantabrogeus luquei,* (**5**) *Fresnedaella lucius*, (**6**) *Hypogesia minos* **comb. nov.**, (**7**) *Luquesia pasensis* **comb. nov.**, (**8**) *Quaesticulus adnexus,* (**9**) *Speocharinus llosesi*. Figs **1–4, 6, 8, 9** modified from Salgado *et al*. (2008).

Female uroventrite VIII (Figs. 210.1, 210.2): Spiculum long and slender; the apical midmargin may be arched or lobed.

Discussion. The genus as such is only very weakly supported with values of 55.5/59, however the node formed with the sister genus *Espanoliella* show a support of 100/100 (Fig. 1F). There is also a set of characters common to all the species of the clade: the elytra with a well-marked parasutural stria; the high and long mesoventral keel, with a wide ventral edge and a more or less long groove in the middle area; the metaventrite with two sutures that delimit a triangular area; the apophysis of the alacrista of the metatergal apparatus long; the spermatheca with the basal lobe globose and somewhat more dilated than the apical one; the spermatic duct short; the spiculum of the female uroventrite VIII long and thin and, in addtion a short stylet without a basal plate in the endophallus is present. In some of the species of this genus there are very unique characteristics exhibited:

– *Amphogeus oxypterus* comb. nov. is an extremely special species concerning its external morphology, with various distinguished morphological characteristics, such as: the elytra with very pointed and divergent apices, the median lobe of aedeagus with a longitudinal keel along the median area of the ventral side, and the female uroventrite VIII with the apical margin, trilobed. However, the genus also exhibits characters typical for the group, which is also reflected in the phylogenetic tree (Fig. 1F), in which it is located well inside the group, and being sister to the two subspecies of *Amphogeus filicornis* comb. nov. with a considerable genetic distance between them and linking them with high a support of 99.8/100. Taking into account its position in the phylogenetic tree, the high support and the morphological specific characters, it is proposed here to synonymise the subgenus *Samanolla* with *Amphogeus*: *Samanolla* Salgado, 2000 syn. nov. = *Amphogeus* Salgado, 2000.

– *Amphogeus luquei* comb. nov., formerly included in the genus *Espanoliella*, is found in the clade *Amphogeus* stat. nov. and not amongst the four species of the genus *Espanoliella*; its relationship with the clade of *Amphogeus sharpi* comb. nov. has low support, 31.6/58 (Fig. 1F). This species presents some very special characters, such as the median lobe of aedeagus with a longitudinal keel along the mid-part of the ventral side, like *A. oxypterus* comb. nov.; the endophallus, although very similar to *Espanoliella* due to its strongly developed spines, it shows a reduced stylet, as well as parameres and setae of totally different conformation, with the apical median seta shorter but very thick and robust. For this reason it is excluded from the genus *Espanoliella* and included in *Amphogeus* stat. nov., both because of its location on the phylogenetic tree and the characters it has in common with the species of this genus, nevertheless the two genera are sisters within the *Espanoliella* group. Considering the phylogenetic relationship of *A. luquei* and the information stated above, the species is placed in the genus *Amphogeus* stat. nov.: *Amphogeus luquei* comb. nov.

– *Quaestus filicornis filicornis* AC91 is sister to *Q. filicornis seeboldi* AF13 (from type locality) with a support of 92.6/100 (Fig. 1F); the considerable genetic distance between these two taxa suggests it is more coherent if they are considered both as *bona species*. In the framework of this taxonomic classification *Amphogeus filicornis* comb. nov. and *Amphogeus seeboldi* comb. nov. have been taken from the *Quaestus* and were included in the list of *Amphogeus* species. *Amphogeus filicornis* comb. nov. has the elytra nearly twice as long as wide, the antennal segments longer and thinner, and the club apex of the parameres pointed. *Amphogeus seeboldi* comb. nov. exhibits an elytra almost two and a half times longer than wide, the antennal segments shorter and thicker, and the apex of the club of the parameres more rounded.

– In the *Amphogeus sharpi* comb. nov. complex there is a considerable genetic distance between the five subspecies when observing the phylogenetic tree (Fig. 1F), in addition each one is well characterised by the structures of the endophallus and each of these models is known from various geographical localities, except for *Amphogeus sharpi monacatus* comb. nov. which is known only from a single locality. This pair of species was also transferred to the genus *Amphogeus* stat. nov. Although the signals derived from the various trees do not give a clear indication of the nature of these species, in some cases, however, the following taxa would be eligible to be considered *bona species*: *Amphogeus nigricans* stat. nov. comb. nov., sister to the entire complex with a support of 100/100, *Amphogeus intermedius* stat. nov. comb. nov. with support of 95.4/58 and *Amphogeus sharpi* comb. nov. with a support of 95.5/58. The complex includes *Amphogeus escalerai* comb. nov., as sister to the subspecies *bolivari* and *monacatus* with a support of 99.2/58; consequently it is elevated to the rank of species *Amphogeus bolivari* stat. nov. comb. nov., and as a subspecies of this *Amphogeus bolivari monacatus* stat. nov. comb. nov., is supported by 100/100, even though the genetic distance appears to be small. These taxonomic changes are listed in the species list.



FIGURES 208.1–208.13: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Endophallus of: (**1**) *Amphogeus noltei* **comb. nov.**, (**2**) *Espanoliella jeanneli,* (**3**) *Cantabrogeus luquei,* (**4**) *Luquesia pasensis* **comb. nov.** Apex of the paramere of: (**5**) *A. cantabricus* **comb. nov.**, (**6**) *A. oxypterus* **comb. nov.**, (**7**) *E. tibialis,* (**8**) *C. luquei,* (**9**) *Fresnedaella lucius*, (**10**) *Hypogesia minos* **comb. nov.**, (**11**) *Luquesia pasensis* **comb. nov.**,(**12**) *Quaesticulus adnexus,* (**13**) *Speocharinus llosesi*. Figs **1–8, 10, 12, 13** modified from Salgado *et al*. (2008).

– *Quaestus cisnerosii cisnerosii* AI524 (from type locality) is a sister of *Q. cisnerosii vasconicus* AF12 (from type locality) with 99.9/100 support (Fig. 1F); the considerable genetic distance between the two taxa makes it seem more coherent to consider them both as *bona species*. *Amphogeus cisnerosii* comb. nov. and *Amphogeus vasconicus* comb. nov. have been included in the genus *Amphogeus*. *Amphogeus cisnerosii* comb. nov. is characteristed by the protarsi of the male as wide as the apex of the tibia, the 10th antennal article longer than it is wide, the parasutural stria well marked in the middle of the elytra, more blurred in the far anterior and posterior parts, and the lower seta of the club of the parameres somewhat shorter than the other two, which are equal. *Amphogeus vasconicus* comb. nov. likewise has the male protarsi slightly wider than the apex of the tibia, the 10th antennal article almost transverse, the parasutural stria well marked along the entire elytra and the inferior seta of the club of the parameres longer than the other two setae, that are the same. These two taxa are an interesting case study for evolutionary and biogeographical reasons: they have very restricted and small distribution areas separated by more than 200 km in a straight line by azoic territories of Leptodirini in the Duero tertiary basin and the Iberian System range.

Distribution. Spain. A genus widely distributed throughout the Cantabrian karstic area, from the banks of the river Deva (Gipuzkoa) as the eastern limit and in the northeast around Burgos, the right basin of the river Besaya and the areas close to Santillana del Mar as the western limits. In addition to the only enclave outside the Cantabrian area is located in the Sierra de Guadarrama (Madrid), with *Amphogeus cisnerosii* comb. nov.

Species

Amphogeus angustitarsis (Español, 1950) comb. nov.
Speocharis cantabricus angustitarsis Español, 1950: 107.
Speocharis angustitarsis Español: Coiffait, 1965: 291.
Speocharis begoniae Nègre, 1965: 93.
Quaestus (*Quaestus*) *angustitarsis* (Español): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *angustitarsis* (Español): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *angustitarsis* (Español): Salgado, 2001: 196.

Amphogeus bolivari (Jeannel, 1913) comb. nov.
Amphogeus bolivari bolivari (Jeannel, 1913) comb. nov.
Speocharis escalerai bolivari Jeannel, 1913: 456.
Quaestus (*Sajadytes*) *sharpi bolivari* (Jeannel): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *sharpi bolivari* (Jeannel): Salgado, 2001: 196.
Amphogeus bolivari monacatus (Salgado, 1994) comb. nov.
Speocharis sharpi monacatus Salgado, 1994b: 16.
Quaestus (*Sajadytes*) *sharpi monacatus* (Salgado): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *sharpi monacatus* (Salgado): Salgado, 2001: 196.

Amphogeus cantabricus (Uhagón, 1881) comb. nov.
Bathyscia cantabrica Uhagón, 1881: 118.
Speocharis cantabricus (Uhagón): Jeannel, 1910a: 31.
Quaestus (*Quaestus*) *cantabricus* (Uhagón): Perreau, 1993: 322.
Quaestus (*Amphogeus*) *cantabricus* (Uhagón): Salgado, 2000: 54.

Amphogeus cisnerosii (Pérez-Arcas, 1872) comb. nov.
Adelops cisnerosii Perez-Arcas, 1872: 127.
Bathyscia (*Bathyscia*) *cisnerosi* (Pérez-Arcas): Reitter, 1885 [1884]: 37.
Speocharis cisnerosi (Pérez-Arcas): Jeannel, 1910a: 31.
Quaestus (*Quaestus*) *cisnerosi* (Pérez-Arcas): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *cisnerosi* (Pérez-Arcas): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *cisnerosi* (Pérez-Arcas): Salgado, 2001: 196.

Amphogeus escalerai (Jeannel, 1909) comb. nov.
Speocharis escalerai Jeannel, 1909b: 465.
Breuilia mimetica Jeannel, 1924a: 71.
Espanoliella mimetica (Jeannel): Guéorguiev, 1976: 127.
Quaestus (*Quaestus*) *escalerai* (Jeannel): Perreau, 1993: 322.
Quaestus (*Amphogeus*) *escalerai* (Jeannel): Salgado, 2000: 58.

Amphogeus filicornis (Uhagón, 1881) comb. nov.
Bathyscia filicornis Uhagón, 1881: 113.
Speocharis filicornis (Uhagón): Jeannel, 1910a: 31.
Speocharis gracilicornis Jeannel, 1911a: 312.

Speocharis gracilicornis debilis Bolívar, 1917: 208.
Quaestus (*Quaestus*) *filicornis* (Uhagón): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *filicornis* (Uhagón): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *filicornis* (Uhagón): Salgado, 2001: 196.

Amphogeus intermedius (Salgado, 1994) stat. nov. comb. nov.
Speocharis sharpi intermedius Salgado, 1994b: 16.
Quaestus (*Sajadytes*) *sharpi intermedius* (Salgado): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *sharpi intermedius* (Salgado): Salgado, 2001: 196.

Amphogeus luquei (Salgado & Fresneda, 2005) comb. nov.
Espanoliella luquei Salgado & Fresneda, 2005: 88.

Amphogeus nigricans (Jeannel, 1924) stat. nov. comb. nov.
Speocharis sharpi nigricans Jeannel, 1924a: 64.
Quaestus (*Sajadytes*) *sharpi nigricans* (Jeannel): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *sharpi nigricans* (Jeannel): Salgado, 2001: 196.

Amphogeus noltei (Coiffait, 1965) comb. nov.
Speocharis noltei Coiffait, 1965: 292.
Quaestus (*Quaestus*) *noltei* (Coiffait): Perreau, 1993: 322
Quaestus (*Sajadytes*) *noltei* (Coiffait): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *noltei* (Coiffait): Salgado, 2001: 196.

Amphogeus oxypterus (Bolívar, 1917) comb. nov.
Speocharis oxypterus Bolívar, 1917: 207.
Quaestus (*Quaestus) oxypterus* (Bolívar): Perreau, 1993: 322
Quaestus (*Samanolla) oxypterus* (Bolívar): Salgado, 2000: 54

Amphogeus seeboldi (Uhagón, 1881) comb. nov.
Bathyscia seeboldii Uhagón, 1881: 115.
Speocharis seeboldii (Uhagón): Jeannel, 1910a: 31.
Quaestus (*Quaestus*) *filicornis seeboldii* (Uhagón): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *filicornis seeboldii* (Uhagón): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *filicornis seeboldii* (Uhagón): Salgado, 2001: 196.

Amphogeus sharpi (Martínez de la Escalera, 1898) comb. nov.
Bathyscia sharpi Martínez de la Escalera, 1898: 37.
Speocharis Sharpi (Martínez de la Escalera): Jeannel, 1910a: 31.
Quaestus (*Quaestus*) *sharpi* (Martínez de la Escalera): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *sharpi sharpi* (Escalera): Salgado, 2000: 58
Quaestus (*Quaesticulus*) *sharpi sharpi* (Escalera): Salgado, 2001: 196

Amphogeus vasconicus (Piochard de la Brûlerie, 1872) comb. nov.
Adelops vasconicus Piochard de la Brûlerie, 1872: 448.
Bathyscia flaviobrigensis Uhagón, 1881: 121.
Bathyscia utzortensis Reitter, 1885a [1884]: 36.
Speocharis vasconicus (Piochard de la Brûlerie): Jeannel, 1910a: 30.
Speocharis dissimilis Coiffait, 1965: 291.
Quaestus (*Quaestus*) *vasconicus* (Piochard de la Brûlerie):Perreau, 1993: 322.
Quaestus (*Sajadytes*) *vasconicus* (Piochard de la Brûlerie): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *vasconicus* (Piochard de la Brûlerie): Salgado, 2001: 196.

Genus ***Espanoliella*** V.B. Guéorguiev, 1976
Espanoliella V.B. Guéorguiev, 1976: 126.

Type species. *Breuilia tibialis* Jeannel, 1909 by original designation (habitus in Fig. 202.3).

Diagnosis. Size range between 2.2-2.9 mm. Bathyscioid facies (Fig. 202.3); body generally ovoid elongated, narrowed and acuminate backwards, always clearly convex. Pronotum smooth, with very little punctation but on elytra with rough punctation. Female, in general, more convex andlarger than the male, with the apical part of the elytra less pointed.

Head: Voluminous and retractable with the occipital carina complete, although blurred.

Antennae: They usually exceed half the length of the body; segments of the club slightly thickened and longer than broad. Female with antennal segments somewhat shorter and broader.

Pronotum: Transverse with regularly arched sides and sharp vertices; maximum width at the base.

Elytra: Elongated, cuneiform or elliptical, with lateral sides well-marked; parasutural stria well visible.

Legs: Short and slender; male protarsi highly dilated about one and a half times as wide as apical end

of tibiae; metafemora robust; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; protibiae not tapered, without spines on external surface; mesotibiae wide, conical and curved, and metatibiae straight, both with short and thick spines on the external face.

Mesoventral keel (Fig. 204.5): High, with rounded vertex; anterior border between slightly arched to rectilinear and ridged; ventral broad, with a well-marked groove along the middle; the posterior apophysis is long and reaches the bifid process of the metaventrite.

Sutures of the metaventrite (Fig. 204.5): Two sutures, each starting from one end of the mesocoxal cavity, then both extend towards the posterior border of the metaventrite and converging at a point, delimiting a triangular area with a vertex generally sharp and narrow.

Metatergal apparatus (Fig. 205.2): With the wings of the metascutum elongated and rather wide, and the apophysis of the alacrista prolonged.

Metendosternite (Fig. 206.2): With the median keel of the trunk shorter than the anterior keel of the furcal arms, with the apex curved and sharp outwards, without apophysis; posterior lamina decreased in width towards the apex of the arms. Trunk almost twice as long as the widest area at base, and mid-keel with slight posterior divergence.

Median lobe of aedeagus: In lateral vision, long, arched and narrowed towards the apical part. In dorsal view (Fig. 207.3), the first two thirds of the sides are arched, then it narrows and the apical area is highly variable, already widely arched, already slightly sharpened or already very acuminate, and in *Espanoliella jeanneli* the apex is dilated. The basal lamina longer, narrowed in the middle area and much longer than the lamina of the tegmen, in most species.

Endophallus (Fig. 207.3): Without stylet. There are groups of spines, thick and highly sclerotized. Without apical reinforcing bands.

Parameres (Fig. 208.7): Long and robust, as long as or longer than the median lobe; in the apical part three setae are inserted in very variable forms: one can be modified in the form of a short or thick spine, straight or with a hooked apex, bifid. Ventral lamina of the tegmen wider than long.

Spermathecal complex (Fig. 209.3): Spermatheca short, with the middle region reduced and little sclerotized; the lobes are larger in caliber than the middle region, the basal one being more dilated than the apical one; spermatic duct long, about six times longer than the spermatheca, dilated in the area where it joins the spermatheca and in the area of junction with the copulatory bag; spermathecal gland sacciform, well-developed.

Female uroventrite VIII (Fig. 210.3): Spiculum long and narrow; the mid-apical margin of the uroventrite arched or subrectilinear.

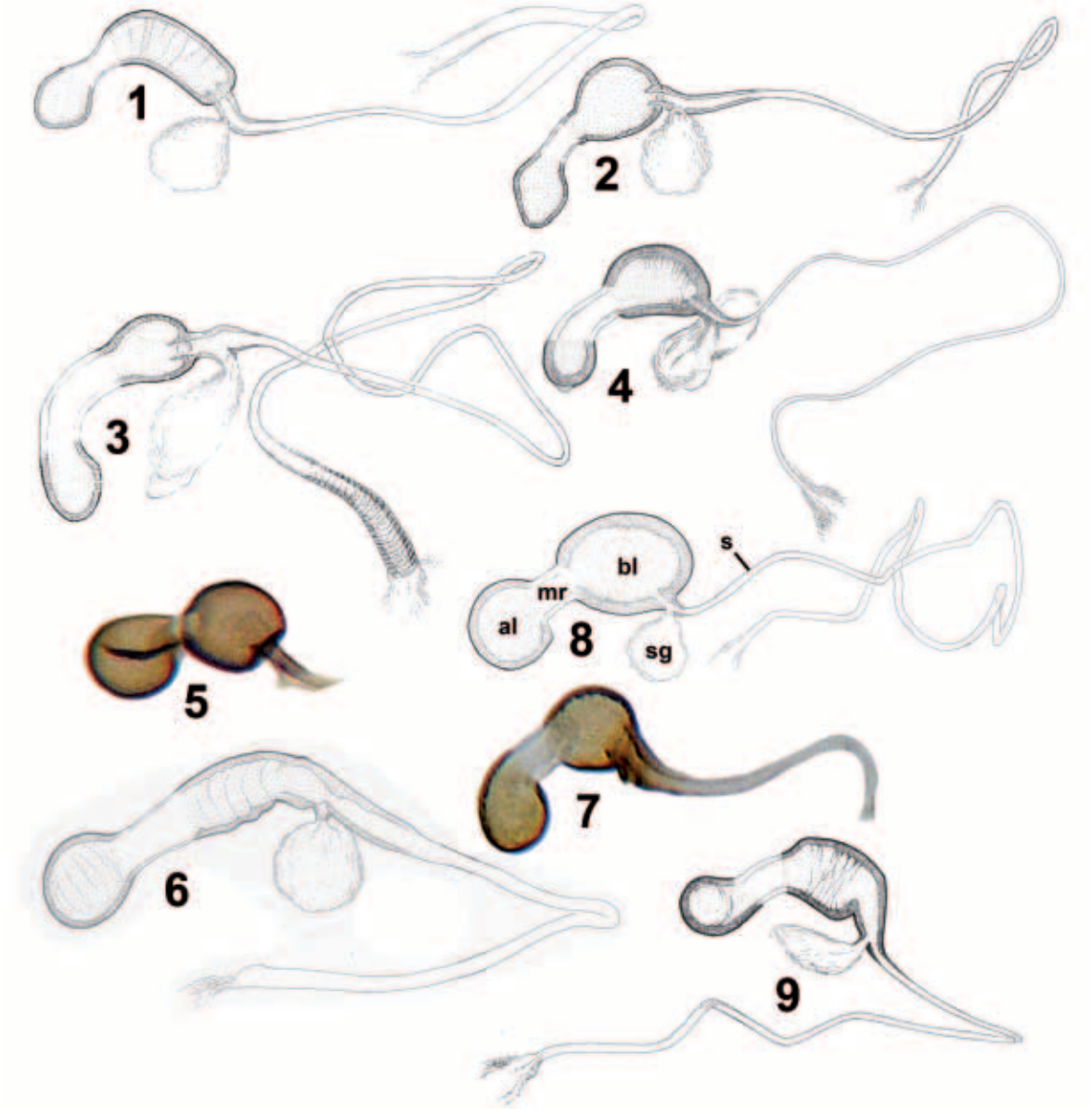
Discussion. The genus *Espanoliella*, established by V.B. Guéorguiev (1976), brought together a group of six species, which Salgado (1978) later reduced to four, and established the synonyms of *Breuilia mimetica* with *Quaestus escalerai* and *Espanoliella cendreroi* with *Espanoliella tibialis*. The molecular study indicates (Fig. 1F) that this group is phylogenetically coherent for the four species and with the exclusion of *E. luquei* it became a monophyletic group; it was foun to be a sister of *Amphogeus* with a support of 100/100. The support of the entire clade is 100/100. Salgado & Fresneda (2005) incorporated *E. luquei* into the genus *Espanoliella*, which in the molecular analysis is not belonging to this genus and indeed are also seperated by morphological characteristics of the male genitalia – middle lobe with ventral keel, endophallus with a rudimentary stylet and parameres with a differentiated club and setae of another shape – and the female genitalia – shorter spermatic duct –. In the phylogenetic tree (Fig. 1F) *E. luquei* is incorporated into *Amphogeus* and is the sister species of the clade of *Amphogeus sharpi* comb. nov. and its subspecies, and which also includes *Amphogeus escalerai* comb. nov.

Distribution. Spain. The representatives of the genus colonise a not very extended geographical area, they are found in the small karstic massif of Carranza in western Vizcaya and small massifs close to the coast in the northeastern part of Cantabria (Salgado & Fresneda 2005, 2017; Salgado *et al*. 2008).

Species

Espanoliella cuneus (Jeannel, 1909)
Breuilia cuneus Jeannel, 1909b: 468.
Espanoliella cuneus (Jeannel): Guéorguiev, 1976: 127.

Espanoliella jeanneli (Bolívar, 1917)
Breuilia jeanneli Bolívar, 1917: 209.
Espanoliella jeanneli (Bolívar): Guéorguiev, 1976: 127.



FIGURES 209.1–209.9: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Spermathecal complex of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *A. oxypterus* **comb. nov.**, (**3**) *Espanoliella jeanneli,* (**4**) *Cantabrogeus luquei,* (**5**) *Fresnedaella lucius*, (**6**) *Hypogesia minos* **comb. nov.**, (**7**) *Luquesia pasensis* **comb. nov.**, (**8**) *Quaesticulus adnexus,* (**9**) *Speocharinus llosesi*. Figs **1–4, 6, 8, 9** modified from Salgado *et al*. (2008). Abbreviations: **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

Espanoliella tibialis (Jeannel, 1909)
Breuilia tibialis Jeannel, 1909b: 469.
Breuilia cendreroi Bolívar, 1923: 424.
Espanoliella tibialis (Jeannel): Guéorguiev, 1976: 126.

Espanoliella urdialensis (Bolívar, 1917)
Breuilia urdialensis Bolívar, 1917: 210.
Espanoliella urdialensis (Bolívar): Guéorguiev, 1976: 127.

3.3.5.5 ***Cantabrogeus*** group

Diagnosis. Size range between 2.0-3.5 mm. Body elongated oval.

Antennae: Long or very long, reaching at least half the length of the body, with all antennomeres clearly longer than broad, the 8th antennal segment two or more times as long as wide.

Pronotum: Transverse with sides regularly arched, with the basal part as wide or slightly narrower than the basal part of the elytra.

Elytra: Parasutural stria well marked, arched in the middle region, only blurred or poorly defined in *Fresnedaella*.

Mesoventral keel (Figs. 204.6-204.9): Tall and long – somewhat shorter in *Fresnedaella* – with a rounded vertex; ventral edge narrow without groove.

Suture of the metaventrite: They delimit a triangular or subtriangular area (Figs. 204.6, 204.8, 207.9), with the vertex well-defined in *Fresnedaella* (Fig. 204.7).

Metatergal apparatus (Figs. 205.3-205.6): With the metascutum long and narrow and the apophysis of the alacrista long or very long.

Metendosternite: It presents the furcal arms longer than the trunk with the apices arched or hooked and pointed (Figs. 206.3, 206.4, 206.6) with a terminal apophysis only in *Hypogesia* gen. nov. (Fig. 206.5).

Endophallus: Consiting of two regions; there is a stylet without a basal plate (Figs. 207.4, 207.6, 207.7); without stylet only in the genus *Fresnedaella* (Fig. 207.5).

Parameres (Figs. 208.8-208.11): More or less robust, with a differentiated apical club in which three fine and long setae are inserted.

Spermathecal complex: Spermatheca with two globose and well differentiated lobes (Figs. 209.4, 209.5, 209.7); in *Hypogesia* gen. nov. the basal lobe is elongated (Fig. 209.6). Short spermatic duct, 2-4 times the length of the spermatheca, which widens slightly in the area of junction with the basal lobe, where the spermathecal gland opens.

Female uroventrite VIII (Figs. 210.4-210.7): Spiculum short, narrow or slightly broadened.

Discussion. The clade of the *Cantabrogeus* group have a high support of 98.6/100 on the phylogenetic tree. It consits of the genera *Cantabrogeus*, *Fresnedaella*, *Hypogesia* gen. nov. and *Luquesia* gen. nov.; it was found to be sister to the clade *Espanoliella* group with support of 98.7/100, and both join the *Quaesticulus* group with support of 88.4/99 (Fig. 1F). In this clade the genus *Cantabrogeus* remains independent which is justified by the highly divergent morphology, in addition to a synapomorphy in the endophallus and the presence of an axis of whorled spines. It has been decided to conserve *Fresnedaella*, a sister to the genus *Cantabrogeus* as a morphologically well-characterised genus; this findungs support need of the description of two new genera for the species *Quaestus minos* and *Quaestus pasensis,* that do not share character states with the former two species mentioned, and are species previously considered *Quaesticulus*. Since there are only very few species it would have been a more convinient solution ot use a single name for one single genus, but not a single common character has been found in all of them.

Distribution. Spain. The species of the four genera of this clade colonise in geographically close but totally independent regions. The genera *Cantabrogeus*, *Fresnedaella* and *Luquesia* gen. nov. colonise karst areas from the centre of Cantabria to the coast, between the rivers Pas and Miera; *Hypogesia* gen. nov. inhabits the largest area, its distribution area includes numerous cave systems in the northwest of Cantabria and a few to the northeast of Burgos and west of Vizcaya.

Key to genera

1. Mesoventral keel well-developed (Fig. 204.8), prominent and the beginning of the ventral edge clearly notched; the sutures of the metaventrite defines a wide triangular area with an arcuated vertex and a very obtuse angle (Fig. 204.8). Metatergal apparatus with long and very narrow metascutum (Fig. 205.5). Furcal arms of the metendosternite with a well-developed membranous wing at the apex (Fig. 206.5). Apical middle part of the median lobe of aedeagus wide and slightly sunken (Fig. 207.6). Endophallus with a long stylet, more than half the length of the median lobe, and very robust (Fig. 207.6). Spermatheca with elongated basal lobe and somewhat narrower than the apical one (Fig. 209.6) .....*Hypogesia* gen. nov.
- Mesoventral keel otherwise shaped (Figs. 204.6, 204.7, 204.9); the sutures of the metaventrite defines a smaller triangular area with a more or less sharp vertex and an acute angle (Figs. 204.6, 204.7, 204.9). Metatergal apparatus with clearly wider metascutum (Figs. 205.3, 205.4, 205.6). Furcal arms of the metendosternite without apical membranous wing (Figs. 206.3, 206.4, 206.6). Apical middle part of the median lobe of aedeagus narrower and not sunken (Figs.

207.4, 207.5, 207.7). Endophallus without a stylet (Fig. 207.5) or with a shorter and generally less robust stylet (Figs. 207.4, 207.7). Spermatheca with basal lobe globose and as wide or slightly wider than the apical one (Figs. 209.4, 209.5, 209.7) 2

2. Second article of the antennae longest. Endophallus with robust spines, with (Fig. 208.3) or without stylet (Fig. 207.5). Spiculum of the female uroventrite VIII short, narrow and the apical area slightly curved (Figs. 210.4, 210.5).....3
- 11th antennae article, the longest. Endophallus with small scales and stylet (Fig. 208.4). Spiculum of the female uroventrite VIII very short and somewhat broadened (Fig. 210.7) .....*Luquesia* gen. nov.

3. Male metafemora dilated. Endophallus without a stylet and the apical midpart with two rows of well-developed spines (Fig. 207.5). Parameres widely exceed the apex of the median lobe and the oblong club developed with an apical seta and the lower seta far removed (Fig. 208.9). Spermatheca with the two lobes of similar diameter (Fig. 209.5).....*Fresnedaella*
- Male metafemora not dilated. Endophallus with a stylet and the apical midpart with an axis of whorled spines (Fig. 208.3). Parameres reach or slightly exceed the apex of the median lobe and the club is short with two apical setae (Fig. 208.8). Spermatheca with the basal lobe more developed than the apical (Fig. 209.4) .....*Cantabrogeus*

Genus ***Cantabrogeus*** Salgado, 2000
Cantabrogeus Salgado, 2000: 52.

Type species. *Speocharis luquei* Salgado, 1993 by original designation (habitus in Fig. 202.4).

Diagnosis. Size range between 1.9-2.5 mm. Bathyscioid facies, ovoid and moderately convex body (Fig. 202.4). Pubescence fine, short and golden. Pronotum microreticulate with very fine punctation; on elytra rough punctation and vaguely aligned transversely. Female, in general, somewhat more robust than the male.

Head: With complete occipital carina.

Antennae: As long as the elytral suture, the second antennomere is the longest of all and the segments of the club slightly thickened, all clearly longer than wide.

Pronotum: Transverse, and posterior area as wide as the base of the elytra; regularly arched sides and sinuous base, with somewhat acute posterior angles and pointed vertices.

Elytra: With separately rounded apical areas and both loosely united at the elytral suture; parasutural stria long and very marked, arched in the middle and somewhat blurred in the basal quarter.

Legs: Short and slender; males protarsi dilated and the degree of enlargement depends on the species; first article being longer than wide; all tibiae hairy and with two pectinate internal spurs, two simple external ones and a series of unequal spines between them; protibiae not tapered, without spines on external surface; mesotibiae slightly curved and metatibiae straight, both with thick spines on the external face.

Mesoventral keel (Fig. 204.6): High, with anterior vertex rounded, slightly obtuse angle, almost right, and the posterior apophysis extends over the metaventrite; anterior border edged and the ventral border narrow, straight, without dentitions and without a groove; this keel belongs to group 2C of Salgado (1996a).

Sutures of the metaventrite (Fig. 204.6): The two sutures each start from one end of the mesocoxal cavity, extend toward the anterior border of the metaventrite, and converge at a point near the edge of the metacoxal cavity; they delimit a triangular area with the vertex more or less sharp depending on the species.

Metatergal apparatus (Fig. 205.3): Wings of the metascutum moderately wide and elongated; apophysis of the alacrista (alc) long and prolonged.

Metendosternite (Fig. 206.3): Furcal arms somewhat longer than the furcal trunk, with apex curved and sharp, without terminal apophysis; posterior lamina with the same width along the arm. Trunk somewhat longer than the area of greatest basal width and the median keel with a slight posterior divergence.

Median lobe of aedeagus: In lateral view, more or less strongly curved with the apical area sharp and curved towards the ventral side. In dorsal view (Fig. 207.4), apical area not very sharp; describes an arc or is blunt.

Endophallus (Fig. 208.3): It encompasses the most representative structure of the species of this genus, a longitudinal grouping of thick whorled spines that is found between the long apical reinforcement bands; in addition, the endophallus contains some toothed or spiny basal pieces, more or less developed depending on the species, and a short stylet that is thin in the anterior area and somewhat dilated in the basal area.

Parameres (Fig. 208.8): Little thickened; both end in a slightly dilated club, generally oblong, in which three long setae of similar length and thickness are inserted, two of apical insertion and one preapical internal.

Spermathecal complex (Fig. 209.4): Spermatheca small, with the basal lobe more developed than the

apical, the latter spherical; both are well sclerotized, and between them a short membranous duct is observed. Spermatic duct thin and not very long, about three or four times the length of the spermatheca, slightly wider in a short anterior area that joins the spermatheca; spermathecal gland empties into this area, which is generally well visible (Salgado *et al*. 2008).

Female uroventrite VIII (Fig. 210.4): Spiculum short, narrow and generally somewhat curved in the apical area (Salgado *et al*. 2008).

Discussion. *Cantabrogeus* is a genus that is morphologically well defined and distinguished from the other hypogeous Leptodirini of the Cantabrian karst, which has traditionally been included in the group of «Supraflagellates» by Jeannel (1955a), as it encloses a stylet without a plate in the basal area of the endophallus and basal groups of distinct spines on a whorled axis. The diploid chromosome set consists of 22 chromosomes (Angus *et al*. 2012). Salgado (2000) included this genus in the «*Quaestus* phyletic series» as it presented the following characteristics: a apparent stylet in the endophallus, three setae in the apical club of the parameres, the shape of the mesoventral keel and the general structure of the spermathecal complex. In addition, Salgado (2000) hinted to other basic structures suitable to define an independent genus: a single sclerotized pieces of the endophallus forming a very peculiar whorled structure; the ventral edge of mesoventral keel being narrow, straight and without pit; and the second article of the antennae the longest of all. The results of the phylogenetic analysis (Fig. 1F) show that the genus *Cantabrogeus* is monophyletic with high support, 100/100, and sister to the genus *Fresnedaella*, also with high support (96.1/100). Along, with the species *Luquesia pasensis* comb. nov. they form a very well supported clade with a support of 100/100. It was found that its sister species is *Hypogesia minos* comb. nov. with a 98.9/100 support. Within the genus there is a basal polytomy, including the species *C. fresnedai*, *C. luquei* and a clade formed by the rest of the species. Resolution between these two lineages has high support (100/100). Relationships within the *C. nadali* clade are well supported as well, with *C. cultellus* sister to *C. antimachus*, and the two sister species to *C. nadali*.

Distribution. Spain, Cantabria. The geographical distribution areas of *Cantabrogeus* species comprise a narrow and elongated band between the northernmost species, *C. cultellus*, and the southernmost, *C. nadali*. *Cantabrogeus antimachus* known only from Covallarco Cave, which is located south of the Las Enguinzas massif. *C. cultellus* is present in three remote areas located in between San Salvador and Solares, in Medio Cudeyo, and Pámanes, in Liérganes, all of them in the foothills of the Macizo de Peña Cabarga natural park and located in its northwesternmost end; *C. fresnedai* from La Peña Caborco cave, close to the Caborco spring and stream in Esles; *C. luquei* in two caves nested in a small Jurassic calcareous massif halfway between two large karstic fronts, Entrambasaguas, Riotuerto and Miera, to the east, and Camargo and Sierra de Gándara, to the north; finally, *C. nadali* from a single cave (La Cañuela / La Cayuela) located in the westernmost area of the Sierra del Hornijo, in Bustablado near Arredondo (Fresneda & Salgado 2017).

Species

Cantabrogeus antimachus Salgado & Luque, 2012
Cantabrogeus antimachus Salgado & Luque, 2012 *in* Salgado *et al*. (2012): 33.

Cantabrogeus cultellus Salgado & Luque, 2012
Cantabrogeus cultellus Salgado & Luque, 2012 *in* Salgado *et al*. (2012): 36.

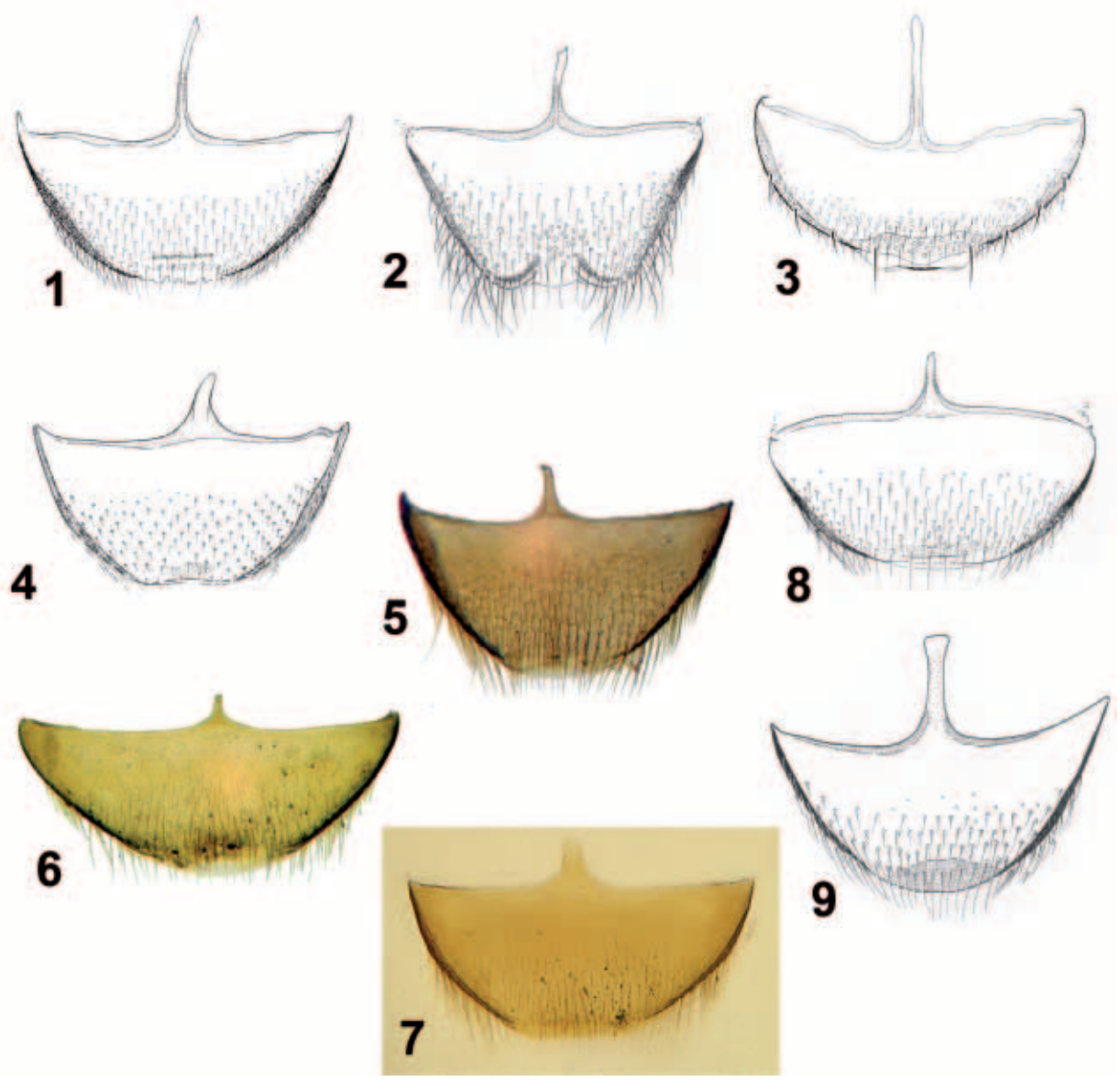
Cantabrogeus fresnedai Salgado & Luque, 2012
Cantabrogeus fresnedai Salgado & Luque, 2012 *in* Salgado *et al*. (2012): 38.

Cantabrogeus luquei (Salgado, 1993)
Speocharis luquei Salgado, 1993a: 31.
Cantabrogeus luquei (Salgado): Salgado, 2000: 52.

Cantabrogeus nadali (Salgado, 1978)
Speocharis nadali Salgado, 1978: 16.
Quaestus (*Quaestus*) *nadali* (Salgado): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *nadali* (Salgado): Salgado, 2000: 58
Cantabrogeus nadali (Salgado): Salgado *et al*., 2008: 222.

Genus ***Fresnedaella*** Salgado, Labrada & Luque, 2011
Fresnedaella Salgado, Labrada & Luque, 2011: 3.

Type species. *Fresnedaella lucius* Salgado, Labrada & Luque, 2011 by original designation (habitus in Fig. 202.5).



FIGURES 210.1–210.9: *Quaestus* series, *Espanoliella*, *Quaesticulus* and *Cantabrogeus* groups. Female uroventrite VIII of: (**1**) *Amphogeus cantabricus* **comb. nov.**, (**2**) *A. oxypterus* **comb. nov.**, (**3**) *Espanoliella jeanneli,* (**4**) *Cantabrogeus luquei,* (**5**) *Fresnedaella lucius*, (**6**) *Hypogesia minos* **comb. nov.**, (**7**) *Luquesia pasensis* **comb. nov.**, (**8**) *Quaesticulus adnexus,* (**9**) *Speocharinus llosesi*. Figs **1–4, 8, 9** modified from Salgado *et al*. (2008).

Diagnosis. Size range between 2.2-2.6 mm. Bathyscioid facies, body cuneiform and elongated (Fig. 202.5). Pubescence dense, quite long, fine, yellowish and recumbent. Integument of the pronotum rough, with well-impressed dots, and the elytra with well-spaced dots. Female not as cuneiform as male, rather elliptical and somewhat more robust.

Head: Wide, half the width of the pronotum, with the occipital carina complete, although poorly marked.

Antennae: Long, exceeding two thirds of the length of the body; all antennomeres longer than wide, the second being the longest of all; antennomeres of the club very slightly thickened.

Pronotum: Clearly transverse, 2.0 times as wide as

long, with slightly arched lateral margins; posterior angles acute and vertices oriented slightly inwards; base sinuous, as wide as the anterior part of the elytra.

Elytra: Elongated, 1.5 times as long as wide, with a very narrow apical area and rounded apices; there is parasutural stria, although blurred in the basal third.

Legs: Quite long and slender; males protarsi strongly dilated, with the first tarsomere longer than wide and wider than the distal end of the protibia; metafemora of male with posterior margin strongly widened in its middle part; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; protibiae not attenuated with spines on the external face; mesotibiae slightly curved and metatibiae straight, both with thick spines on the external face.

Mesoventral keel (Fig. 204.7): Of «type 2C» of Salgado (1996a), with a rounded vertex and a very obtuse angle; anterior border moniliform and a narrow and ventral border slightly sinuate, without a groove; posterior apophysis little elongated, scarcely exceeding half the length of the metaventrite.

Sutures of the metaventrite (Fig. 204.7): Two sutures, each one starting from one end of the mesocoxal cavity, the basal one in its first half follows the border of the mesocoxal cavity, then both are prolonged towards the posterior edge of the metaventrite delimiting a triangular area and converge to form a fairly sharp vertex.

Metatergal apparatus (Fig. 205.4): Wings of the metascutum elongated and moderately wide; the apophysis of the alacrista long.

Metendosternite (Fig. 206.4): Furcal arms longer than the furcal trunk, with curved and sharp apex, without terminal apophysis; posterior lamina narrow with the same width along the arm. Trunk once and a half times longer than the area of greatest basal width and the median keel with posterior divergence.

Median lobe of aedeagus: Very long. In lateral view, apical area strongly curved towards the ventral face and very pointed. In dorsal view (Fig. 207.5), with median lobe narrow, especially in the upper third, whose apex describes a fairly sharp arc. Basal region highly developed and proportionally very large, with the ventral lamina of the tegmen more developed than the basal lamina of the median lobe, in the latter the distal part without prolongation, describes a regular arc.

Endophallus (Fig. 207.5): With two regions. The basal without stylet and no sclerotized pieces are observed, while in the mid-apical region two long lateral rows of robust teeth are observed and towards the apex a small group of tiny scales; there are no reinforcing bands.

Parameres (Fig. 208.9): Long and slender, distinctly longer than the median lobe, with an apex dilated, elongated oval paddle-shaped; the three setae quite long and of similar thickness, two apical with close insertion pores and one basal, clearly distant from the other two.

Spermathecal complex: Spermatheca (Fig. 209.5) short, formed by two spherical lobes, both well sclerotized and much larger in diameter than the middle region, which is hyaline and very short; spermatic duct thin and very short, about twice as long as the spermatheca; spermathecal gland poorly defined.

Female uroventrite VIII (Fig. 210.5): Spiculum short, narrow and slightly curved at the apex.

Discussion. The analysis of the sequences obtained from this genus indicate (Fig. 1F) that *Fresnedaella* is the sister group of the genus *Cantabrogeus* with a support of 96.1/100 and both form a pair that is sister to *Luquesia pasensis* comb. nov., as already described in Salgado *et al*. (2011). This whole clade then is sister to *Hypogesia minos* comb. nov. being the only genus of its clade that lacks a stylet, a character that is also present in some species of *Espanoliella* and the representatives of the *Breuilia* group; in addition, the metatergal apparatus and metendosternite is similar to that of *Cantabrogeus*; the mesoventral keel shows a slightly prolonged posterior apophysis, like the species belonging to the former subgenus *Speogeus*, which is now *Quaestus*, and the second antennomere as the longest of all as it is described for *Cantabrogeus*.

Distribution. Spain. Currently only known from a single cave that is located south of mount Picogeniro at the head of the Carriedano valley around the river Pisueña, in the eastern part of the Cantabrian karst (Salgado *et al*. 2011).

Species

Fresnedaella lucius Salgado, Labrada & Luque, 2011
Fresnedaella lucius Salgado, Labrada & Luque, 2011: 7.

Genus ***Hypogesia*** nov.
https://zoobank.org/NomenclaturalActs/7fd158bf-0117-4b5a-b5ad-04d63f57c928

Type species. *Speocharis minos* Jeannel, 1909 by present designation (habitus in Fig. 203.1).

Diagnosis. Size range between 3.0-3.5 mm. Facies bathyscioid (Fig. 203.1), with body ovoid, clearly narrowed towards the back and very convex. Pronotum smooth, with a very poorly printed microreticulum and very scarce punctation; on elytra rough punctation. Female in general more robust than the male. Depigmented.

Head: With occipital carina complete; anophthalmous.

Antennae: Long, filiform, almost as long as body length; all segments considerably long and club segments practically not thickened. Female with shorter antennae and segments somewhat thicker.

Pronotum: Transverse and very convex, slightly bell-shaped, with the sides very slightly arched in the apical third, then slightly concave, to finish almost straight; posterior angles acute and vertex sharp; maximum width at the base, which is sinuous.

Elytra: Although long,also fairly wide, with a short and well visible parasutural stria along the middle, somewhat blurred in the posterior two-thirds of the elytra.

Legs: Very long and slender, with the males protarsi dilated; the first protarsomere wider than the distal end of the protibia; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; protibiae straight and without spines on the external face; curved and thickened mesotibiae and metatibiae straight, both with thick spines on the external face.

Mesoventral keel (Fig. 204.8): High and large, with vertex broadly rounded and four denticles well-defined on the anterior part of the ventral edge; anterior border arched and moniliform, prominent in the inferior area; ventral edge a little sinuous, with a narrow arista, without a groove or with a diffuse groove in the final area; the posterior apophysis is prolonged to the bifid process of the metaventrite.

Suture of the metaventrite (Fig. 204.8): With a single suture that describes a wide arc somewhat sharp in the central part and encompasses a triangular área.

Metatergal apparatus (Fig. 205.5): Wings of metascutum very narrow and greatly elongated; apophysis of the alacrista very long.

Metendosternite (Fig. 206.5): Furcal arms and furcal trunk long, the arms being somewhat longer, with a curved and pointed apex, and a terminal apophysis with the shape of a well-developed and membranous aileron; posterior lamina wide, remains the same width than in the apical area. Trunk somewhat longer than wide and the mid-keel with a posterior divergence long but not very wide. It has the most robust metendosternite of its group.

Median lobe of aedeagus: Long and very robust. In lateral view, very arched. In dorsal view (Fig. 207.6) with sub-rectilinear sides, with the apical area very little narrowed and in the middle area of the apex slightly sunken.

Endophallus (Fig. 207.6): It does not exhibit peculiar structures in the apical area, with the reinforcing bands not very developed; in the middle part there are scales which are of diffuse distribution and elongated on both sides of the stylet; in the basal part a group of slightly more developed spinules and a fairly long robust stylet without a basal plate, but at the base of the stylet it is a callus or diffuse membranous tissue present that surrounds it.

Parameres (Fig. 208.10): Relatively thin, as long as the median lobe, with a club poorly developed; into the main lobe there are three long setae inserted and they are at an equal level with the very close insertion pores.

Spermathecal complex (Fig. 209.6): Spermatheca very elongated, with apical lobe large and spherical, larger in size than the middle region; basal lobe elongated, almost the same size than the middle region and seemingly with a prolonged narrowing that is to become the spermatic duct which itself is short, about twice the length of the spermatheca; spermathecal gland well-developed.

Female uroventrite VIII (Fig. 210.6): Spiculum very reduced, as long as it is wide and with a pointed apex.

Etymology. *Hypogesia*, a free adaptation of the Greek term – ὑπόγαιον – that designates the environment where this animal is found. Feminine.

Discussion. The genus presents all the characters described for the *Quaestus* series and it is differentiated by several external morphological characters and by unique structures in the male and female genitalia as described above, which justifies it to be clsssified as a genus. In the phylogenetic tree (Fig. 1F) it is basal to the of the clade of the sister genus *Luquesia* gen. nov. to which it is grouped with high support of 98.9/100, and both genera *Fresnedaella* and *Cantabrogeu*s support the the clade witht a suport of 100/100.

Distribution. Spain. The only species of this genus has a wide geographical distribution. It is known from more than 80 caves distributed throughout the karstic parts of Carranza, Vizcaya (Salgado 1977), the northwest of Burgos (Bellés 1977b) and, above all, by an extensive karst of Cantabria comprised between the

upper and middle basins of the rivers Asón, Miera and Pas (Salgado 1976). The type locality is the cave of Cullalvera, in Ramales de la Victoria (Cantabria). The profusion of shapes suggests that it is a very special complex; a detailed morphological study and molecular data could reveal the existence of several species or subspecies, to date indistinguishable as it the characters and molecular data are insufficient for the investigation of variation and the profundity of these possible justifying the description of new species of this genus..

Species

Hypogesia minos (Jeannel, 1909) comb. nov.
Speocharis minos Jeannel, 1909b: 467.
Speocharis mierensis Bolívar, 1911: 570.
Quaestus (*Quaestus*) *minos* (Jeannel): Perreau, 1993: 322.
Quaestus (*Sajadytes*) *minos* (Jeannel): Salgado, 2000: 58.
Quaestus (*Quaesticulus*) *minos* (Jeannel): Salgado, 2001: 196.

Genus ***Luquesia*** nov.
https://zoobank.org/NomenclaturalActs/2FAB4D4B-5CB2-466B-B62C-FDEFE696752C

Type species. *Quaestus pasensis* Salgado, Labrada & Luque, 2010 by present designation (habitus in Fig. 203.2).

Diagnosis. Size range between 2.2-2.5 mm. Facies bathyscioid (Fig. 203.2), with the body convex, uniformly ovoid and posteriorly narrowed. Head with extremely fine and superficial punctation, almost nonexistent. Integument of a very shiny reddish-brown appearance. Pronotum and elytra completely covered with short, fine, scarce and recumbent yellowish pilosity. Pronotum punctation very fine and superficial; on the elytra the punctation is somewhat rough. Female somewhat more convex and, in general, larger than the male; the apical area of the elytra less divergent and pointed. Depigmented.

Head: With complete occipital carina; anophthalmous.

Antennae: Long, exceeding half the length of the body; antennomeres long and cylindrical, all clearly longer than wide, the 11th article being the longest. Female showing antennal segments slightly shorter and broader.

Pronotum: Very transverse, widest at base, about twice as wide as long and as wide as the anterior part of the elytra; lateral margins evenly arched; posterior angles slightly obtuse and vertices blunt, a little prolonged backwards.

Elytra: Elongated, widest near basal quarter, slightly wider than the pronotum; lateral margins evenly curved with rounded tips; with parasutural stria along posterior two-thirds.

Legs: Long and thin; males protarsi with first four tarsomeres dilated, the first being slightly wider than distal part of protibia and also elongated, one and a half times longer than wide; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; protibiae straight, without spines on external surface; mesotibiae somewhat arcuate and metatibiae slightly undulate, both with thick spines on external surface.

Mesoventral keel (Fig. 204.9): As in group 2C of Salgado (1996a), high, lamellar and long since the posterior apex reaches the metaventrite; anterior border slightly arched and slightly prominent, and ventral border straight and narrow; the vertex strongly rounded forms a very obtuse angle.

Sutures of the metaventrite (Fig. 204.9): Two sutures that start from one end of the mesocoxal cavity, extending towards the posterior edge of the metaventrite, one in the basal area with two-thirds of its length very close to the margin of the cavity; then both converging at a point located halfway along its length, delimiting the surface of a small triangle with a little sharp vertex.

Metatergal apparatus (Fig. 205.6): Wings of metascutum narrow and elongated; the apophysis of the alacrista long.

Metendosternite (Fig. 206.6): Furcal arms clearly longer than the furcal trunk, with curved and pointed apex, without terminal apophysis; posterior lamina narrow, maintaining about the same width over the entire length. Trunk much longer than the part of greatest basal width and the median keel with a slight posterior divergence.

Median lobe of aedeagus: In lateral view, broadly arched, forming an obtuse angle near the middle, with the apex narrow and slightly curved towards the ventral side. In dorsal view (Fig. 207.7), with the lateral margins evenly arched and the apex weakly pointed.

Endophallus (Fig. 207.7): With stylet short and thin, with the basal area somewhat dilated and without basal plate and surrounded by small scales at the base that extend through the middle area; in the apical region with reinforcing bands narrow, long and inconspicuous.

Parameres (Fig. 208.11): Slender, as long as or slightly longer than the median lobe, curved to the ventral side with the apical club slightly dilated and sub-rectangular; the three setae quite long, two apical with very close insertion pores and the other preapical with internal lateral insertion, clearly distant from the other two. Ventral lamina of the tegmen broad and rounded, well sclerotized, longer than the basal lamina of the median lobe of aedeagus.

Spermathecal complex (Fig. 209.7): Spermatheca short and bilobed, with the basal lobe ovoid, slightly longer and wider than the apical lobe which is spherical, both lobes well sclerotized; junction canal as long as apical lobe; spermatic duct short and thin, 3-4 times longer than the spermatheca, widened at the beginning, later it joins directly to the dorsal region of the copulatory bag; a spermathecal gland small, round and membranous, usually inconspicuous, opens into the enlarged anterior part of the spermatic duct.

Female uroventrite VIII (Fig. 210.7): Spiculum very short and slightly widened, with sides almost parallel and apex rounded.

Etymology. The genus is dedicated to our good friend, the Cantabrian biospeleologist Carlos González Luque. Feminine.

Discussion. The genus *Luquesia* gen. nov. is sister to *Hypogesia* gen. nov. with a high support of 99.8/100, and this pair in turn is found to be sister genera of the clade *Fresnedaella* and *Cantabrogeus* with 100/100 support (Fig. 1F). The genus presents all the characters described for the *Quaestus* series and is characterised by showing several dicriminatory characters, both in the external morphology and in the male and female genitalia, all of them listed in the description. All antennomers clearly longer than they are wide, with the 11th being the longest; the metatergal apparatus with narrow and elongated metascutum and long alacrista apophysis; endophallus without developed of sclerotized formations, only scales are found as hardend tissue in this area, and or course a short and thin stylet without basal plate. Within its clade the same structure as described for *Fresnedaella* was found forming an, insertion of one of the setae which is clearly displaced, shifted towards the base of the club; in *Cantabrogeus* and *Hypogesia* gen. nov. these insertion pores are located close each other. The new genus differs from it sister genus, *Hypogesia* gen. nov., in a number of characters, such as the short antennae, the narrow male protarsi, the smaller mesoventral keel and metatergal apparatus, the metendosternite without apophysis at the apex of the furcal arms, and in structures of the aedeagus, especially the shorter and thinner stylet.

Distribution. Spain, Cantabria. It is only known from several caves in the Churrón-Millajo Cave karstic system, in the Municipal Districts of Luena and Vega de Pas, located near the karstic region of Ocejo, Montes de Pas (Salgado *et al*. 2010; Labrada *et al*. 2011).

Species

Luquesia pasensis (Salgado, Labrada & Luque, 2010) comb. nov.
Quaestus (*Quaesticulus*) *pasensis* Salgado, Labrada & Luque, 2010: 28.

3.4 Clade ***Oryotus-Drimeotus-Speonomus***

3.4.1 Series ***Karadeniziella***

Analysis of the phylogram in Fig. 1D shows a good correlation (84.9/88) between the genus *Karadeniziella* from the Pontic Alps and an undescribed species belonging to an unpublished genus from the Taygetos mountain, Greece – *Lakedemoniana mizerakisi* gen. nov. sp. nov., (DNA extraction code SMNS-M475) –, and these two together with the genus *Gueorguievella* from the Bulgarian Rhodopes with a support of 82.2/30 (Fig. 1D). If we assess the presumed affinities of *Karadeniziella* and *Gueorguievella* on the basis of a classical zoogeographic approach, such as that proposed by Jeannel (1929), which attributed the Aegean fauna to two distinct phyletic lineages (North Aegean and South Aegean) the affinity between *Karadeniziella* and *Lakedemoniana* gen. nov., the new genus from Mount Taygetos (both South Aegean), seems congruent. On the other hand, the presumed affinity with the genus *Gueorguievella*, whose North Aegean origin is obvious, seems less consistent with the Jeannel's hypothesis. Some authors have already expressed doubts in the past (Giachino & Vailati 1993, 2011) about the validity of the «sillon transégéen» concept in the strict sense (Jeannel 1929) and we do not intend to go into detail here. It should be remembered, however, that this part of the phylogram, developed on a molecular basis, is largely incomplete, as almost all the genera of Leptodirini from the southern part of the Balkan Peninsula and the Aegean islands are missing.

KEY TO GENERA

1. Aedeagus in dorsal view with extended, pointed apex (Fig. 211.7); in lateral view with sinuous distal third and apex bent curved dorsally (Fig. 211.6) ....*Gueorguievella* group
- Aedeagus in dorsal view with rounded apex (Figs. 212.6, 213.5); in lateral view with distal third subrectilinear and the apex curved ventrally (Figs. 212.5, 213.3) .....*Karadeniziella* group

3.4.1.1 ***Gueorguievella*** group

Being the only genus in the group, its defining characteristics correspond to those of the genus diagnosis.

Genus ***Gueorguievella*** Giachino & B.V. Guéorguiev, 2006
Gueorguievella Giachino & B.V. Guéorguiev, 2006: 55.

TYPE SPECIES. *Gueorguievella petrovi* Giachino & B.V. Guéorguiev, 2006 by original designation (habitus in Fig. 211.1).

DIAGNOSIS. Small-sized genus, 1.6-1.9 mm, bathyscioid in shape (Fig. 211.1).

Head: Retractile, with an occipital carina, short and eyeless.

Antennae: Short, weak, barely extending beyond the base of the elytra; club with antennomeres flattened; second segment slightly longer than the first.

Pronotum: Transverse, convex, covered with a short, decumbent pubescence. Maximum width at the base, as wide as the base of the elytra. Lateral sides not sinuate, long and evenly curved to the anterior angles and less curved to the posterior angles. Posterior vertices blunt, barely prominent posteriorly.

Elytra: Oval, robust, with maximum width in the anterior third, distally separated and regularly rounded; elytral disc strongly convex, not transversely striated. Parasutural stria absent.

Legs: Relatively short and thick; protarsi of males pentamerous and strongly dilated. Protibiae without comb, with two polydentate apical outer spurs. Meso- and metatibiae without apical basket.

Mesoventral keel: Raised, with ventral margin concave in lateral view, protruding but not toothed; extended to the posterior quarter of metaventrite (Fig. 211.2). In recently studied specimen, the keel has a straight ventral margin and an arched vertex (Fig. 211.3).

Suture of the metaventrite (Fig. 211.3): Delineates an elongate arcuate area, widest in the upper third.

Metatergal apparatus (Fig. 211.4): Well developed, with the wings of the metascutum short, of regular width, and the apophysis of the alacrista reaching the middle of the length of the elytra.

Metendosternite (Fig. 211.5): «V»-shaped, with non-triangular furcal arms. Furcal trunk short, about half the length of the furcal arms; anterior furcal plate absent. Median furcal keel shorter than the previous suture; furcal plate reduced along the entire length of the arm, which is curved outwards and has no terminal apophysis.

Median lobe of aedeagus: Relatively large, in lateral view (Fig. 211.6) curved, roughly folded in the middle. In dorsal view (Fig. 211.7), thickened and widened, with sides subparallel from base to subapical area. Apex extended into a lanceolate tongue. Basal part short and thickened.

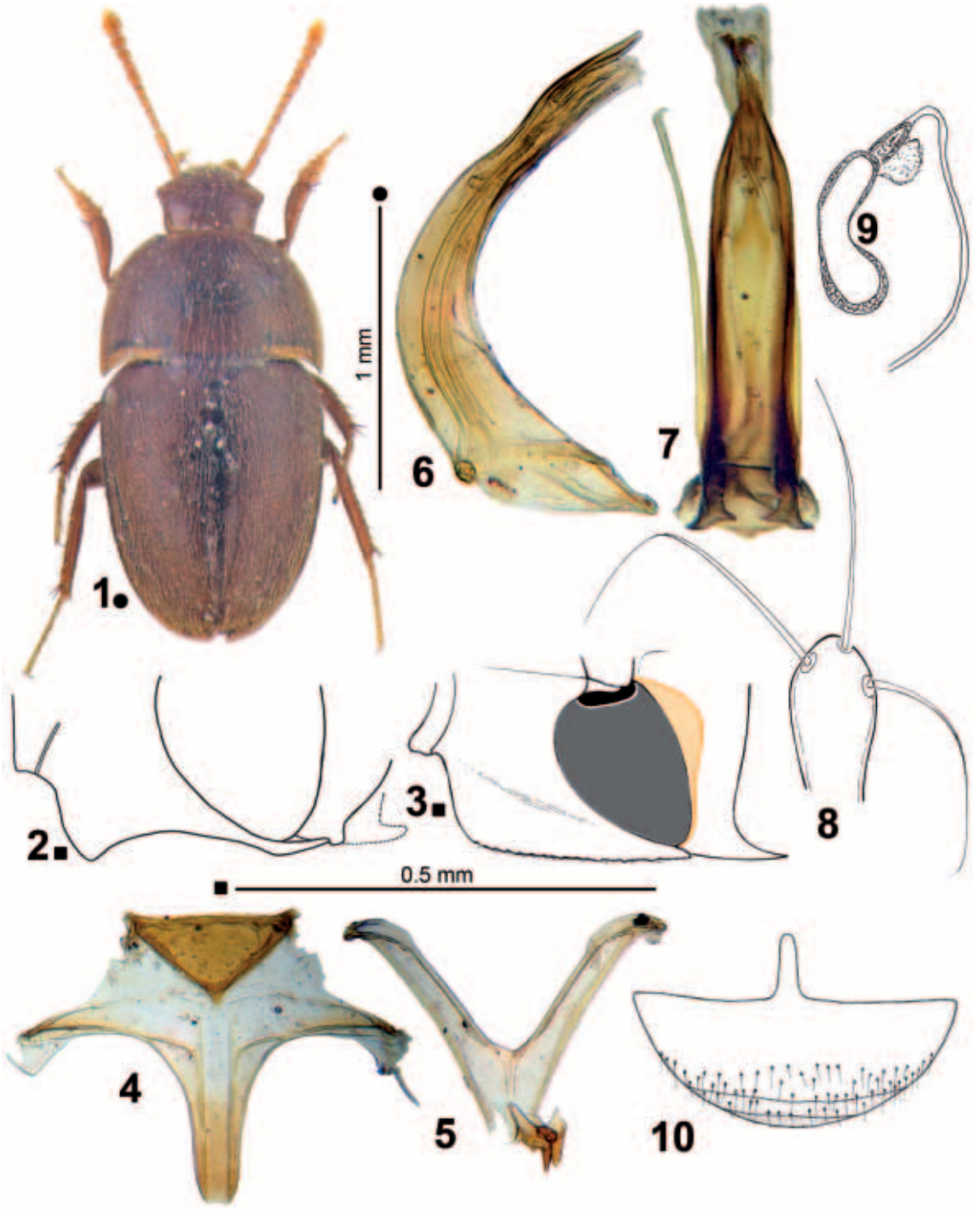
Endophallus (Fig. 211.7): «Y»-piece small and inconspicuous. Presence of a median phanera, vaguely «H»-shaped, and two pairs of rod-shaped phanerae (one basal and one apical).

Parameres (Fig. 211.8): Short and relatively robust, clearly shorter than the median lobe, with three short subequal setae distally, one apical and two internal, subapical. Tegmen not complete, not visible dorsally, ventral blade narrow.

Spermathecal complex: Spermatheca (Fig. 211.9) not very elongate, kidney-shaped, with a small hyaline connecting duct, without a differentiated basal lobe; ductus short, widened and sclerotized near insertion into spermatheca. Spermathecal gland present.

Female uroventrite VIII (Fig. 211.10): Apical margin broadly rounded, basal margin straight with well-developed spiculum.

DISCUSSION. When describing the taxon, Giachino & B.V. Guéorguiev (2006) already emphasised the apparent isolation of *Gueorguievella* from the other Leptodirini lineages present in Bulgaria and Greece. From a strictly morphological point of view, *Gueorguievella* could easily be related to the genus *Bathysciola*, in the old and inclusive sense of Jeannel (1911, 1924a). The same authors (Giachino & B.V. Guéorguiev 2006), in the light of the knowledge acquired on the systematics of the genus *Bathysciola* (Giachino 1992b, 1996b, 1998), stressed the risks of such a choice, which appears to be challenged by systematic and, above all, zoogeographic inconsistencies. Based on the results of molecular analysis, this warning now seems prophetic. These analysis have shown how the «*Bathysciola*



FIGURES 211.1–211.10: *Karadeniziella* series, *Gueorguievella* group. *Gueorguievella petrovi*: (**1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Pterothorax in lateral view with metaventrite suture of the specimen AN141, (**4**) Metatergal apparatus, ventral view of the metanotum and axillaria, (**5**) Metendosternite, (**6**) Aedeagus in dorsal view, (**7**) Aedeagus in lateral view, (**8**) Apex of the paramere, (**9**) Spermathecal complex, (**10**) Female uroventrite VIII. Figs **2**, **9**, **10** modified from Giachino & B.V. Guéorguiev (2006).

groups» (*sensu* Jeannel 1911, 1924a) corresponding to well-defined geographical areas are in fact distinct genera, often relevant to series that are phyletically so far apart (Fig. 2).

Analysis of the phylogram in Figure 1D, although incomplete, as we shall see below, due to the absence of molecular data for the vast majority of genera from Greece and Bulgaria, highlights the absence of a direct phyletic link between *Gueorguievella* and *Bathysciola* (in the new sense used here), as well as between *Gueorguievella* and the «old Italian *Bathysciola*» (which now belong to the genera *Salfia* stat. nov. and *Latellana* gen. nov.) and, again, between *Gueorguievella* and the «old Anatolian *Bathysciola*» (which now includes *Catopsinus*, *Cavazzutiella*, *Sbordoniola* and *Georgiana* gen. nov.). Similarly, the proximity of *Gueorguievella* to *Karadeniziella*, proposed by the phylograms in figures 1D and 2, with support of 82.2/30 in Tree-1 and 69.1/61 in Tree-2, should be viewed with caution given the great incompleteness that characterises the molecular data of the Leptodirini from the southern end of the Balkan peninsula.

Distribution. Bulgaria: Rhodopean massif.

Species

Gueorguievella petrovi Giachino & B.V. Guéorguiev, 2006
Gueorguievella petrovi Giachino & B.V. Guéorguiev, 2006: 58.

3.4.1.2 ***Karadeniziella*** group

Lakedemoniana gen. nov. is sister to *Karadeniziella omodeoi* with supports of 84.9/88 in Tree-1 (Fig. 1D) and supports of 86.4/76 in Tree-2 (Fig. 2); the clade formed by these two genera is sister to *Gueorguievella* with weak support (82.2/30 in Tree-1 and 69.1/61 in Tree-2) and the entire *Oryotus* series also with weak support (88.5/29 in Tree-1 and 85/48 in Tree-2). This logically reveals the biogeographical connection between Greece and Anatolia, although the disjunct distribution is obvious: between the Taygetos range in the Peloponnese for *Lakedemoniana* gen. nov. and the eastern end of Anatolia for the genus *Karadeniziella*.

Key to genera

1. Body elongate, noticeably longer than wide (Fig. 212.1); elytra marked by fine transverse striolae; apex of parameres with three setae.....*Karadeniziella*

- Body oval, rounded, very slightly longer than wide (Fig. 213.1); elytra marked by coarse, disordered punctation; apex of parameres with four setae .....
.....*Lakedemoniana* gen. nov.

Genus ***Karadeniziella*** Casale & Giachino, 1989
Karadeniziella Casale & Giachino, 1989: 170

Type species. *Karadeniziella omodeoi* Casale & Giachino, 1989 by original designation (habitus in Fig. 212.1).

Diagnosis. Medium sized species, 2.3-3.1 mm, with an elongated, moderately convex body; bathyscioid facies (Fig. 212.1).

Head: Retractable, with an incomplete occipital carina. Eyes very small but present, composed of rudiments of 4-5 ommatidia.

Antennae: Long, reaching the proximal third of the elytra in the male, barely reaching the base in the female.

Pronotum: Slightly transverse, convex, with the sides evenly arched forward, not sinuate posteriorly, with maximum width just before, or at the base itself.

Elytra: Elongated, parasutural stria present; elytral disc with roughly aligned transverse striolae.

Legs: Relatively long and slender. Males protarsi pentamerous, narrower than the apex of the tibia. Protibiae without comb, with two polydentate outer spurs. Meso- and metatibiae with incomplete apical basket.

Mesoventral keel (Fig. 212.2): Low, not angular and not extended on metaventrite.

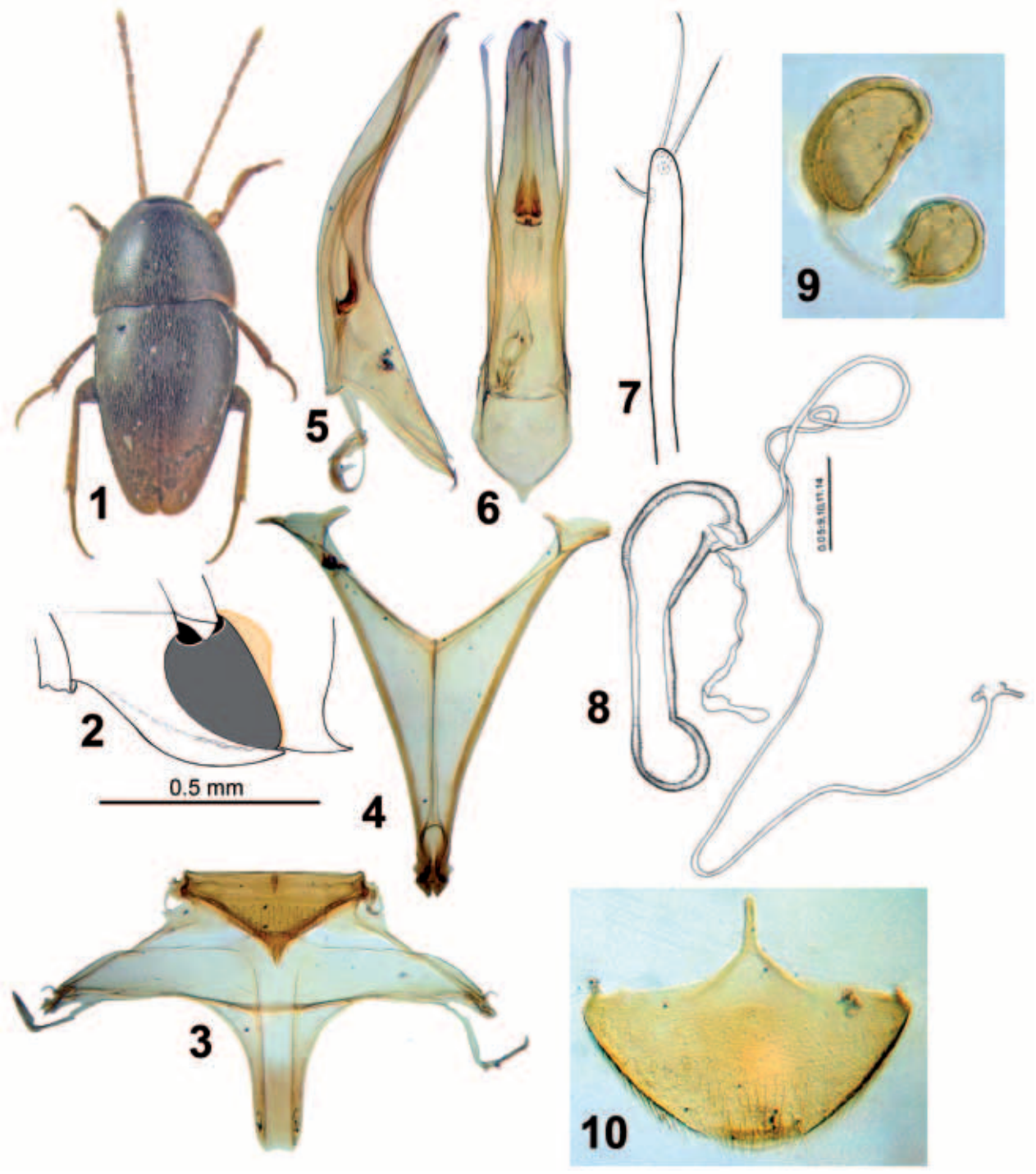
Suture of the metaventrite (Fig. 212.2): Sinuous, delimiting a small arcuate surface in the apical half and passing very close to the coxal cavity in the basal half.

Metatergal apparatus (Fig. 212.3): Well developed, with the wings of the metascutum short, quite broad, and the apophysis of the alacrista almost half as long as the elytra.

Metendosternite (Fig. 212.4): Large, robust, «Y»-shaped, with the posterior furcal plate subtriangular. Apophysis of arms wide and not hooked. Furcal trunk longer than area of greatest width; median furcal carina longer than the carina of the furcal arm.

Median lobe of aedeagus: Elongate, narrow and slightly arched. Slightly curved in lateral view (Fig. 212.5). Apex slightly and evenly rounded in dorsal view (Fig. 212.6).

Endophallus (Fig. 212.6): Basal «Y»-piece large, extending beyond the basal blade of the median lobe,



FIGURES 212.1–212.10: *Karadeniziella* series, *Karadeniziella* group. *Karadeniziella omodeoi*: *(***1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Metatergal apparatus, ventral view of the metanotum and axillaria, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of the paramere (modified from Giachino & Vailati 2003), (**8**) Spermathecal complex (modified from Casale & Giachino 1989), (**9**) Spermatheca, (**10**) Female uroventrite VIII.

with very long, twisted arms. A single, well sclerotized median phanera, in dorsal view vaguely shaped like an inverted «molar tooth». The median phanera extends into two equal, hyaline structures with a spiny surface. Apical part of endophallus with two hyaline rods.

Parameres (Fig. 212.7): Long and thin, not reaching apex of median lobe. Three setae, two apical of equal length and one very short preapical.

Spermathecal complex (Fig. 212.8): Spermatheca kidney-shaped, very elongate, with sclerotized and well-differentiated apical and basal lobes. Junction ductus long and thin, longer than each of the lobes; spermatic duct thin, about four times the length of the spermatheca, slightly sclerotized when inserted into the vagina. Spermathecal gland long, tubular and hyaline.

Female uroventrite VIII (Fig. 212.10): Spiculum long and thin,arising from a triangular extension of the base of the uroventrite.

Discussion. The genus *Karadeniziella* appears, from the phylogram analysis in figure 1D, as sister of *Lakedemoniana* gen. nov. with a support of 84.9/88; it is isolated and lacks close affinities with the Anatolian genera belonging to the *Catopsinus* series (*Besuchetiola*, *Catopsinus*, *Bithyniella* and *Coiffaitiola* groups). Even the apparent affinity, highlighted in the same phylogram, with two unpublished genera from the island of Euboea (Greece) must be considered with due care, as has already been pointed out in the Discussion section relating to the *Gueorguievella* series. The affinities of *Karadeniziella* are probably to be sought, as well as in the genera belonging to the *Drimeotus* group, in certain genera, as yet unknown, present in the Anatolian area, an area whose knowledge, as already emphasised by Giachino & Vailati (2000), is still somewhat incomplete for the Leptodirini.

Distribution. Turkey, Anatolia, Pontic Alps, prov. Ordu.

Species

Karadeniziella decortiorum Giachino & Vailati, 2003
Karadeniziella decortiorum Giachino & Vailati, 2003: 211.

Karadeniziella omodeoi Casale & Giachino, 1989
Karadeniziella omodeoi Casale & Giachino, 1989: 172

Genus ***Lakedemoniana*** nov.
https://zoobank.org/NomenclaturalActs/BE3D27A1-B00C-412B-A6FC-D8D6F7E1DE2C

Type species. *Lakedemoniana mizerakisi* sp. nov. by present designation (habitus in Fig. 213.1).

Description**.** Length 1.9 mm. Bathyscioid body (Fig. 213.1) very wide and short, regularly oval. Colour reddish yellow. Pubescence golden, thin and recumbent.

Head: Occipital carina absent. Thick and spaced punctation. Anophthalmous.

Antennae: As long as half the body (0.95 mm). First antennomere shorter than the 2nd; the 3rd to 6th of equal thickness, the first three of similar length, the 6th shorter; the 7th long and thick, the 8th sub-rounded, the 9th and 10th broad and conical in shape and the 11th the longest.

Pronotum: Broad, transverse and convex; sides evenly arched, decreasing strongly from base to apex. Base slightly bisinuate and basal angles acute. Punctation thick and spaced; without microreticulation between points.

Elytra: Very short, barely longer than pronotum. Convex, with maximum width at base; sides evenly curved and tapering from base to apex. Thick, spaced and disordered punctation over the entire surface. Parasutural stria absent.

Legs: Shorts. Male protarsi pentamerous, dilated. Protibiae slender, sub-rectilinear, with apical spurs and a few short spines on outer margin; mesotibiae curved, with stout spines on outer margin and apical spurs; metatibiae rectilinear, with a few spines on outer margin and apical spurs.

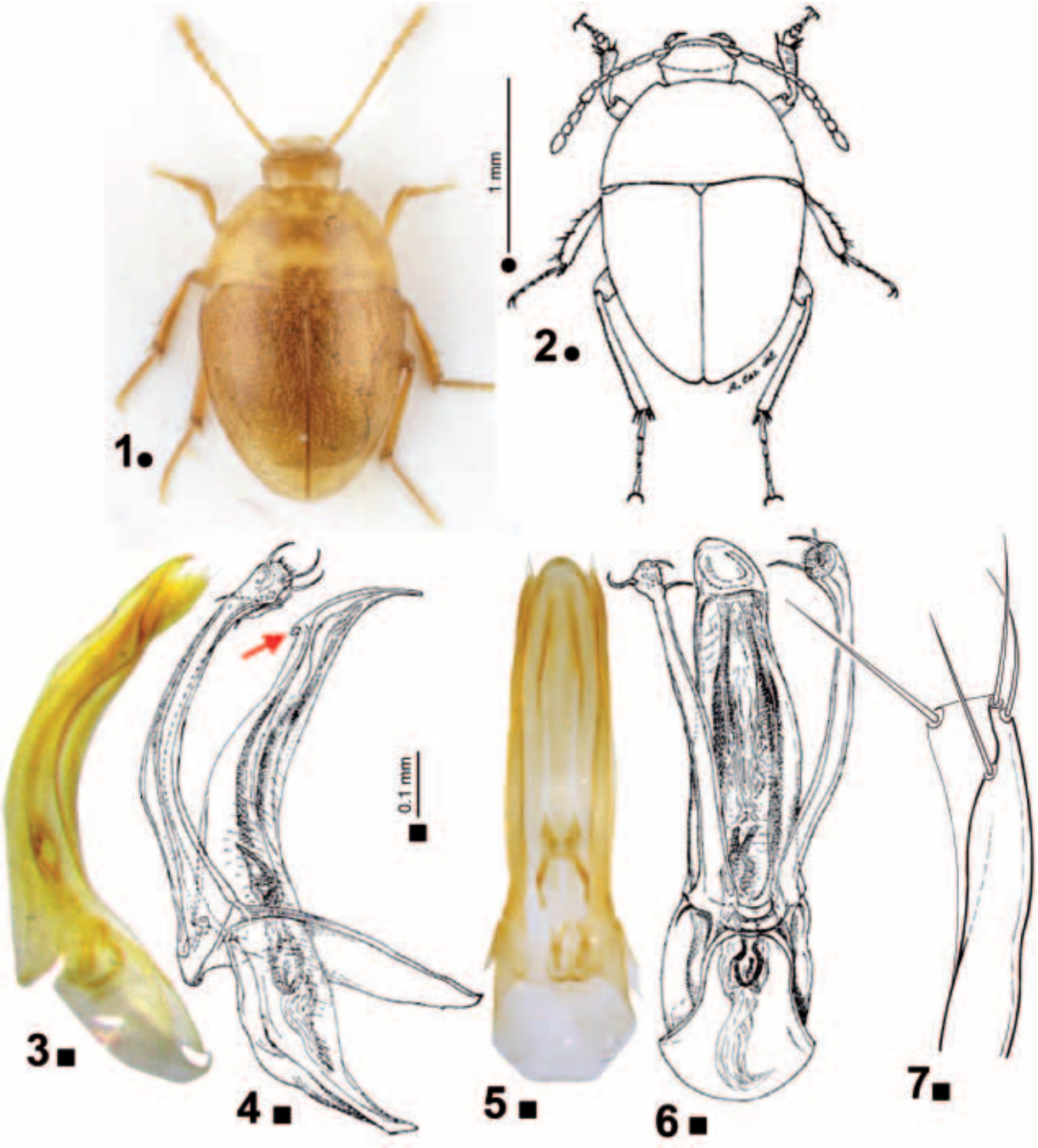
Mesoventral keel, *suture of the metaventrite*, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: In lateral view (Fig. 213.3) regularly curved, with a very slight dorsal depression in the apical quarter and the apex somewhat curved towards the ventral side. Dorsal view (Fig. 213.5) regular, with constant width up to the rounded apex.

Endophallus (Fig. 213.5): Three regions. Basal region with a «Y»-piece from which a stylet/flagellum and two phanerae emerge. Median region with four symmetrical phanerae in pairs: the upper ones broad and sub-triangular, the lower ones thin and curved; the whole forming an «H». Apical region with two reinforcing bands.

Parameres (Fig. 213.7): Thick and as long as the median lobe. Apex armed with four setae: two apical, one preapical and the fourth, also inserted apically, on a lateral membranous lamina.

Female: Unknown.



FIGURES 213.1–213.7: *Karadeniziella* series, *Karadeniziella* group. Habitus of: (**1**) *Lakedemoniana mizerakisi* **gen. nov. sp. nov.**, (**2**) *Muelleriella taygetana*. Aedeagus in lateral view of: (**3**) *L. mizerakisi* **gen. nov. sp. nov.**, (**4**) *M. taygetana*. Aedeagus in dorsal view of: (**5**) *L. mizerakisi* **gen. nov. sp. nov.**, (**6**) *M. taygetana*. Apex of the paramere of: (**7**) *L. mizerakisi* **gen. nov. sp. nov.** Red arrow pointing to the area emarginate dorsally, «harpoon»-like. Figs **2**, **4**, **6** modified from Casale (1983).

ETYMOLOGY. From Lakedemonia, «Λακεδαιμων», historical region of Greece located in the southeastern part of the Peloponnese peninsula, in reference to the range of the new species. Feminine name.

DISCUSSION. The holotype was collected by V. Mizerakis (State Museum of Natural History, Stuttgart, Germany) as part of his thesis work on the phylogeny of cave-dwelling Pselaphinae. *Lakedemoniana* gen. nov. is related to *Muelleriella taygetana;* which also lives on Mount Taygetos. It is not compared to *Muelleriella* because this genus is polyphyletic; *Muelleriella kerkyrana*, the nominotypic species, will remain the only representative of the genus as all other species so far assigned to this genus belong to different genera. The taxonomic revision of the genus *Muelleriella* is on the way, as part of the revision of the Greek Leptodirini (Giachino & Vailati *in prep*.) *Lakedemoniana* gen. nov. (Fig. 213.1) presents a similar appearance to *Muelleriella taygetana* (Fig. 213.2): broad, short and somewhat depressed body, very particular facies. The endophallus is also very similarly armed, with a sort of complex «Y»-piece and four symmetrical phanerae in pairs in the median region of the endophallus (Figs. 213.5, 213.6). However, the median lobe is very distinct, with a preapical denticle in lateral view in *Muelleriella taygetana* (Fig. 213.4), similar to that found in *Pangaeoniola* (Fig. 215.5), absent in *Lakedemoniana* gen. nov. (Fig. 213.3). The apex of the parameres is also very different: in *Muelleriella taygetana* parameres are strongly clubbed, the apex is flat and circular and numerous small setae and three large differentiated setae are inserted (Fig. 213.6); in *Lakedemoniana* gen. nov. they are broad but not clubbed, with four differentiated setae (Fig. 213.7).

DISTRIBUTION. Greece. Known only from the type locality, a cave on the western slope ot the Taygetos mountains, in the Peloponnese.

Species

Lakedemoniana mizerakisi sp. nov. (See Appendix New Species)

3.4.2 *Incertae sedis* in series ***Karadeniziella***

3.4.2.1 Genus ***Muelleriella*** Jeannel, 1924
Muelleriella Jeannel, 1924a: 39.

TYPE SPECIES. *Bathyscia kerkyrana* Reitter, 1884 by original designation (Habitus in Fig. 214.1).

DIAGNOSIS (Jeannel 1924a). Small size, 1.6-1.8 mm, bathyscioid body (Fig. 214.1).

Head: With an obvious occipital carina; anophthalmous.

Antennae: Short; first antennomere as long as the second; the 11th less than twice as long as the 10th.

Pronotum: Transverse, convex, larger than the base of the elytra; sides evenly arched forwards, not sinuous posteriorly.

Elytra: Oval, short, not elongated; without parasutural stria and without transverse striolae.

Legs: Male protarsi pentamerous and slightly dilated.

Mesoventral keel: High, with thick ventral margin, not prolonged on the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus (Fig. 214.3): Subrectilinear, slightly curved, with pointed, lanceolate apex (Fig. 214.4). Basal blade narrow and long, sub-triangular.

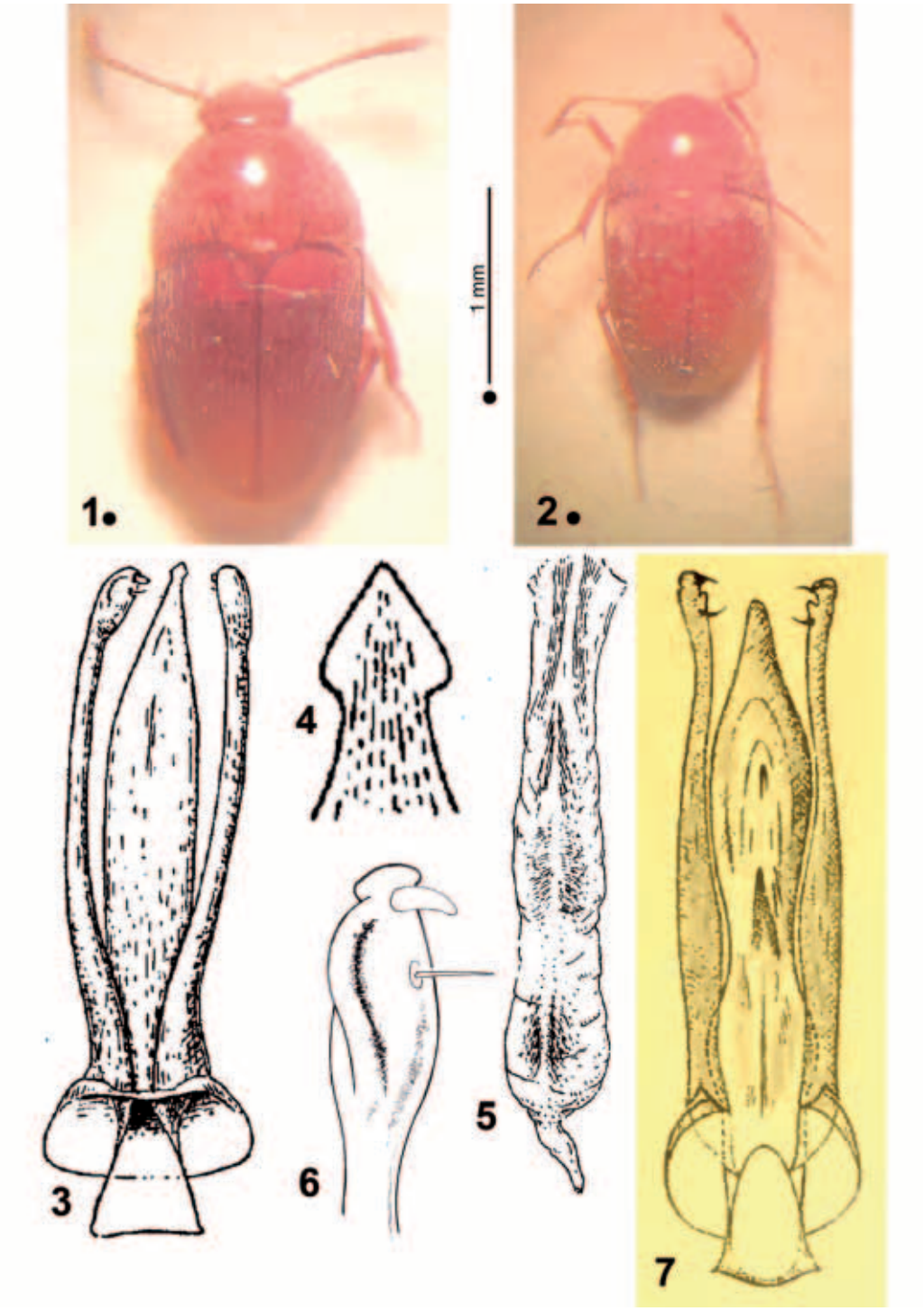
Endophallus (Fig. 214.5): Poorly differentiated, with flakes and small teeth more or less grouped in symmetrical bundles.

Parameres (Fig. 214.6): As long as median lobe, thick, club-shaped at apex. Bearing a short, thick tooth and a short seta on the inner side.

Spermathecal complex and *female uroventrite VIII*: Unknown.

DISCUSSION. No molecular data on *Muelleriella* are available. The taxonomic revision to which the genus *Muelleriella* is being subjected as part of the revision of the Leptodirini of Greece (Giachino & Vailati *in prep*.) has shown that at present only *M. kerkyrana* belongs to the genus *Muelleriella*. All the other species so far attributed to this genus belong to different genera. For these reasons, the description of the genus *Muelleriella* is based solely on the type species. All the other species: *M. cephalonica*, *M. cretica*, *M. moczarskii* and *M. taygetana* belong to different genera. In particular, *M. taygetana* is close to *Lakedemoniana* gen. nov. These two taxa have an aedeagus morphology and a series of external characters that seem to link them to the genus *Mixanigia* from southern Anatolia (Taurus range). On this hypothesis, see the Discussion section of *Mixanigia*.

DISTRIBUTION. Greece, Kérkyra island (*Muelleriella kerkyrana*).



FIGURES 214.1–214.7: *Incertae sedis* in *Karadeniziella* series. *Muelleriella kerkyrana*: (**1**) Habitus, (**3**) Aedeagus in dorsal view, (**4**) Magnification of the apical part of the aedeagus in dorsal view, (**5**) Endophallus, (**6**) Apex of paramere (redrawn from Jeannel 1924a). *Dalmatiola curzolensis*: (**2**) Habitus, (**7**) Aedeagus in dorsal view (modified from G. Müller 1917). Figs **3**–**5** modified from Jeannel (1924a).

Species

Muelleriella kerkyrana (Reitter, 1884)
Bathyscia kerkyrana Reitter, 1884a: 115.
Bathyscia (*Bathyscia*) *kerkyrana* Reitt.: Reitter, 1885a [1884]: 20.
Pholeuonella kerkyrana Reitter: Jeannel, 1910a: 29.
Bathysciola (*Pholeuonella*) *kerkyrana* Reitt.: Jeannel, 1914b: 15.
Mülleriella kerkyrana Reitter, 1884: Jeannel, 1924a: 41.

Muelleriella cephalonica Jeannel, 1929*
Muelleriella cephalonica Jeannel, 1929b: 79.

Muelleriella cretica Jeannel, 1929*
Muelleriella cretica Jeannel, 1929b: 79.

Muelleriella moczarskii Jeannel, 1924*
Muelleriella moczarskii Jeannel, 1924a: 41.

Muelleriella taygetana Casale, 1983*
Muelleriella taygetana Casale, 1983: 270.

* Species belonging to an undescribed genus.

3.4.2.2 Genus ***Dalmatiola*** Jeannel, 1924
Dalmatiola Jeannel, 1924a: 42.

Type species. *Bathyscia curzolensis* Ganglbauer, 1902 by original designation (Habitus in Fig. 214.2).

Diagnosis (Jeannel 1924a). Very small size, 1.5 mm. Bathyscioid facies (Fig. 214.2), with the body elliptical, elongated, fairly convex and slightly attenuated towards the rear. Pubescence short and recumbent. Depigmented.

Head: With entire occipital carina; eyes rudimentary without pigment or differentiated ommatidia.

Antennae: Thin and short, not extending beyond the base of the pronotum, with the club poorly differentiated; first antennomere thicker and as long as the second; the 11th less than twice as long as the 10th.

Pronotum: Transverse, with maximum width at the base, which is as wide as the base of the elytra; sides evenly arched and not sinuous in the basal area.

Elytra: Dotted without transverse striolation and with parasutural stria very close to the suture.

Legs: Short. Protarsi of males pentamerous, only slightly enlarged; tetramerous and gracile in females; tibiae sparsely spiny; protibiae with external spurs and without comb on apical and external margins; meso- and metatibiae with external spurs and without apical crown of spines, showing more spines on the external margin of the mesotibia.

Mesoventral keel: High, with the convex ventral margin, narrow, smooth and without ridges; posterior process reaching the middle of the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

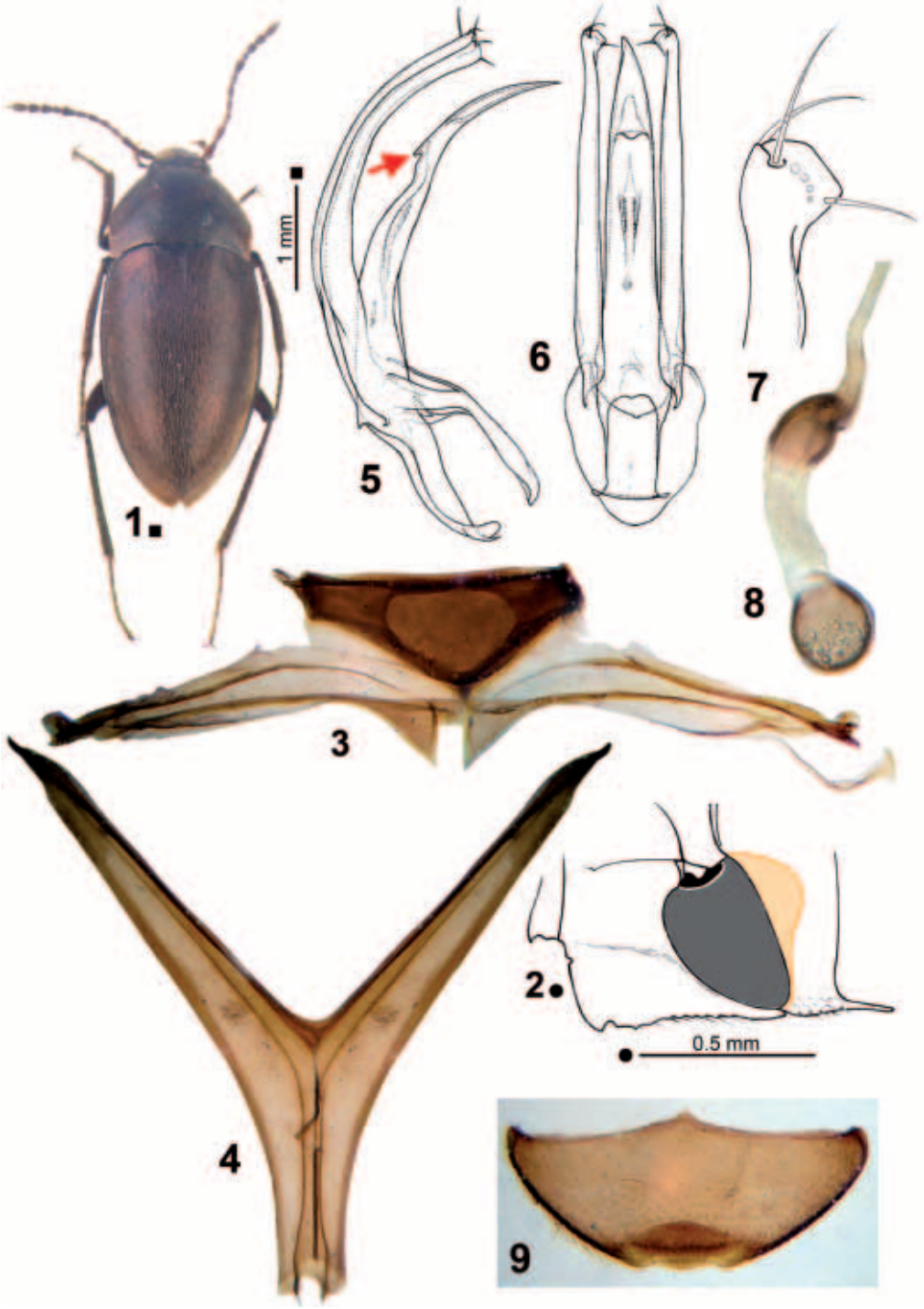
Median lobe of aedeagus: Long and narrow. In lateral view, slightly arched, with pointed tip, directed ventrally. In dorsal view (Fig. 214.7), lanceolate, with straight sides in basal and medial areas, gradually tapering to a long, sharp point. Basal lamina long, narrow with a subrectilinear apical margin.

Endophallus (Fig. 214.7): Without differentiated basal armour, only a few small teeth and scales clustered towards medio-dorsal area; apical area with two elongate, narrow reinforcement bands.

Parameres: Thick and somewhat arched, as long as the median lobe; apical area enlarged into a slightly elongated club, into which are inserted three very small setae. Tegmen plate short and wide.

Spermathecal complex and *female uroventrite VIII*: Unknown.

Discussion. Various pieces of evidence, both morphological and biogeographical, point to the inclusion of *Dalmatiola* near *Muelleriella kerkyrana*, although its position is certainly enigmatic. There is little information on this genus, and no molecular data have been obtained. Jeannel (1924a) placed it in the tribe Bathysciae, «Euryscapes» group, Division I and noted that its general shape resembles that of *Pholeuonella*. V.B. Guéorguiev (1976) included it in the subtribe Pholeuonina and Perreau (2000) followed the same criterion by placing it in the subtribe Pholeuina. Its relationship with *Pholeuonella* is geographically plausible but not morphologically. *Dalmatiola* coincides with *Pholeuonella* in bathyscioid shape, small size and pronotum shape , but the former genus has dotted elytra without transverse striolation, whereas *Pholeuonella* has transverse striolae; the endophallus of the two genera is very different: with few small teeth, flakes and scales grouped in *Dalmatiola* and armed with a single row of highly sclerotized teeth in *Pholeuonella*. Although this does not suggest an evolutionary relationship, Jeannel (1924a), in his description of the aedeagus of *Dalmatiola*, compared this new genus with *Muelleriella*, which he also described in the same work. The bathyscioid external appearance of *Dalmatiola* is also very close to that of *Muelleriella kerkyrana*, as are its small size, the shape of



FIGURES 215.1–215.9: *Incertae sedis* in *Karadeniziella* series. *Pangaeoniola casalei*: *(***1**) Habitus, (**2**) Pterothorax in lateral view, (**3**) Metatergal apparatus, ventral view of metanotum and axillaria, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of paramere (redrawn from Etonti & Etonti 1985), (**8**) Spermathecal complex, (**9**) Female uroventrite VIII. Red arrow pointing to the «harpoon»-like area emarginate dorsally. Figs **5**, **6** modified from Etonti & Etonti (1985).

the pronotum, the dotted elytra without transverse striolation, and, most importantly, the very similar appearance of the aedeagus, especially the endophallus, with only a few small teeth, flakes and more or less grouped scales. This relationship is also possible, and compatible with their respective ranges: on two islands a little further north (Korčula for *Dalmatiola*) in the Adriatic Sea, or a little further south (Kérkyra for *Muelleriella kerkyrana*) in the Ionian Sea. In conclusion, *Dalmatiola* is included in the *Karadeniziella* series as an «*incertae sedis*» genus, until molecular data become available to clarify this enigma.

Distribution. Croatia. It colonizes the musciculous environment of the island of Korčula in the southern Dalmatian region.

Species

Dalmatiola curzolensis (Ganglbauer, 1902)
Bathyscia curzolensis Ganglbauer, 1902: 47.
Pholeuonella curzolensis Ganglbauer, 1902: Jeannel, 1910a: 29.
Dalmatiola curzolensis Ganglbauer, 1902: Jeannel, 1924a: 42.

3.4.2.3 Genus ***Pangaeoniola*** G. Etonti & M. Etonti, 1985
Pangaeoniola G. Etonti & M. Etonti, 1985: 31.

Type species. *Pangaeoniola casalei* G. Etonti & M. Etonti, 1985 by original designation (habitus in Fig. 215.1).

Diagnosis. Medium-sized, 2.9-3.2 mm, with a subpholeuonoid facies and an elongated body (Fig. 215.1), more slender in the male.

Head: With a complete occipital carina; anophthalmous.

Antennae: Moderately elongated, reaching the base of the elytra; first antennomere shorter than the second.

Pronotum: Transverse, with maximum width at the third basal; sides slightly sinuated before the basal angles.

Elytra: Oval, elongated, with maximum width at 2/5 basal; parasutural stria absent; disc without transversal striolae.

Legs: Long but strong. Protarsi of males pentamerous and strongly dilated. Protibiae without comb. Meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 215.2): High, with the anterior margin slightly curved; ventral margin serrated especially in the anterior part and not extending into the metaventrite. Vertex with tooth and subrectilinear angle.

Suture of the metaventrite (Fig. 215.2): Suture delimiting an elongated arcuate part, wide in the upper three quarters and very close to the coxal cavity in the lower quarter.

Metatergal apparatus (Fig. 215.3): apophysis of the alacrista very reduced, apexes very acute; wings of metascutum very long and narrow.

Metendosternite (Fig. 215.4): «V»-shaped; Furcal arms distinctly longer than trunk, with narrow, tapering apical areas, tip slightly curved upwards; apical process or apophysis absent; posterior lamina of furca narrowing in apical area of arms and in basal area of trunk. Furcal trunk distinctly longer than the widest area, median furcal carina slightly bifurcated.

Median lobe of aedeagus: Large. In lateral view (Fig. 215.5), strongly and evenly arched along entire length; in apical quarter strongly emarginate dorsally, like a harpoon. In dorsal view (Fig. 215.6), narrow and elongate, with pointed and asymmetrical apex, curved to the right. Basal blade of median lobe developed, about ¼ of the length of the median lobe.

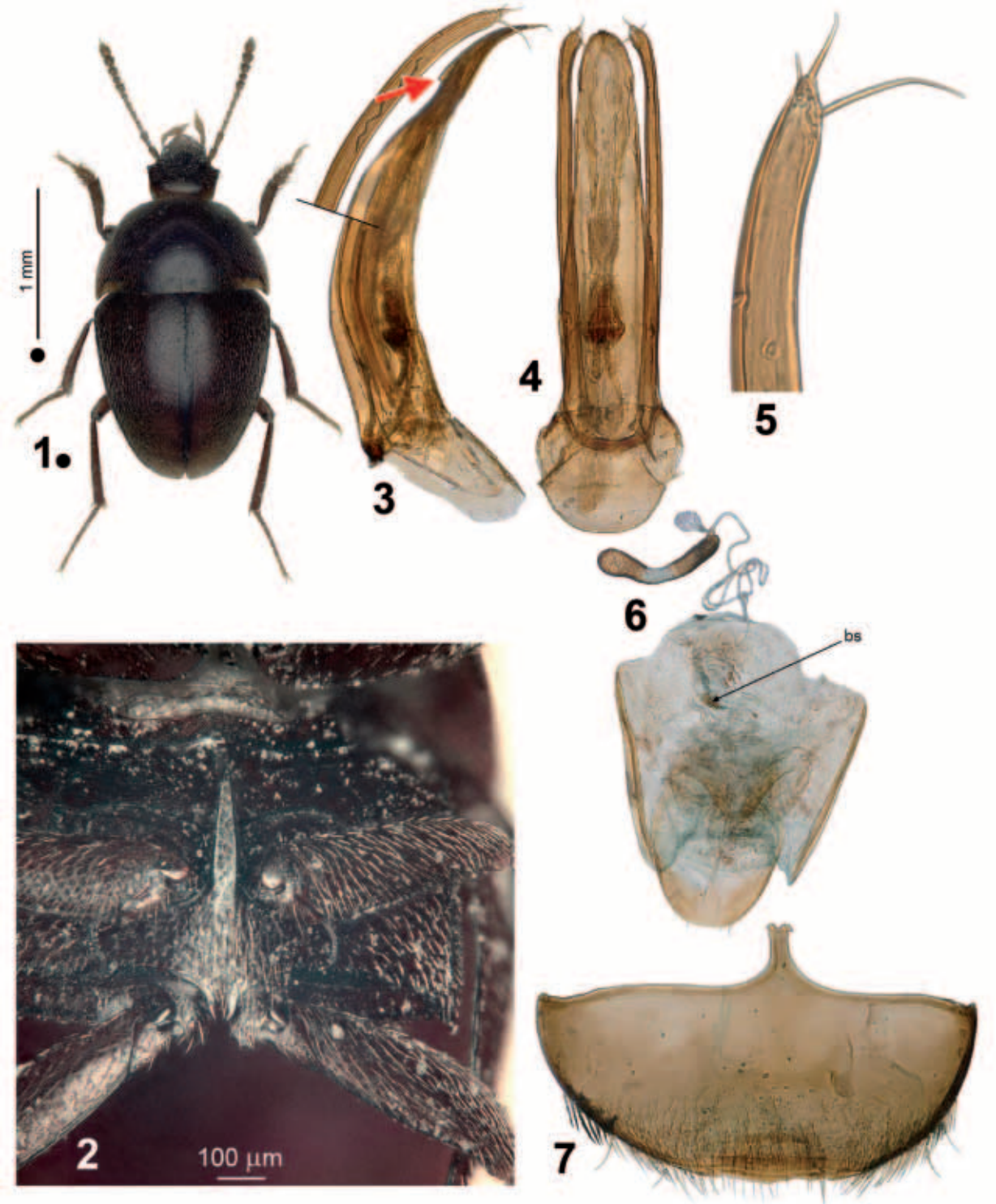
Endophallus (Fig. 215.6): Basal armature consisting of two small symmetrical phanerae which delimit the exit of the ejaculatory duct. Two short spiny bundles in the median region. Apical region without sclerotized elements.

Parameres (Fig. 215.7): Robust, about as long as the median lobe and, in lateral view, recurved like the latter. Apex, in dorsal view, widened inwards into a club. Three setae, two apical and one internal, preapical.

Spermathecal complex: Spermatheca (Fig. 215.8) small and elongated; apical lobe spherical and a little wider than the small basal lobe; hyaline junction duct as long as the sum of the two lobes; spermatic duct with area of attachment to the spermatheca a little enlarged; no spermathecal gland observed.

Female uroventrite VIII (Fig. 215.9): Posterior margin notched in the middle apical area, behind this area a broad darkened spot crossed by a groove and the entire posterior median surface with prominent dots; anterior margin with two arches that join to form a small protuberance; no distinct spiculum.

Discussion. G. Etonti & M. Etonti (1985) emphasised the similarities in the morphology of the aedeagus between *Pangaeoniola casalei* and *Muelleriella taygetana* from the Oros Taygetos. In the light of the current



FIGURES 216.1–216.7: *Incertae sedis* in *Karadeniziella* series. *Mixanigia faillei*: (**1**) Habitus, (**2**) Mesoventral keel in ventral view, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Spermathecal complex, (**7**) Female uroventrite VIII. Red arrow pointing to the «harpoon»-like area emarginate dorsally. Figs **1**–**7** modified from Perreau (2021).

knowledge of the Leptodirini of Greece (Giachino & Vailati *in prep*.), these similarities appear to be probably due to convergence phenomena. Among other things, it should be noted that, on the basis of current knowledge, the species *M. taygetana* belongs to an unpublished genus, different from *Muelleriella* (Giachino & Vailati *in prep*.) and probably related to *Mixanigia* from southern Turkey. *Pangaeoniola* shares with *Albaniola acutipennis* the apex of the median lobe of the aedeagus, which is slightly deviated from the axis of symmetry in dorsal view. Slight asymmetries have appeared independently in Cholevinae and this coincidence between *Pangaeoniola* and *Albaniola acutipennis* is probably homoplasy. However, *Pangaeoniola* inhabits the same mountain range as *Albaniola casalei*, which has an absolutely symmetrical median lobe of the aedeagus. *Albaniola casalei*, and others, must be separated from the genus *Albaniola* and incorporated into a new genus (Giachino & Vailati *in prep*.) In the absence of molecular data, *Pangaeoniola* must be considered as an apparently isolated genus with uncertain taxonomic affinities.

Distribution. Greece, Oros Pangeon.

Species

Pangaeoniola casalei G. Etonti & M. Etonti, 1985
Pangaeoniola casalei G. Etonti & M. Etonti, 1985: 32.

3.4.2.4 Genus ***Mixanigia*** Perreau, 2021
Mixanigia Perreau, 2021: 2.

Type species. *Mixanigia faillei* Perreau, 2021 by original designation (habitus in Fig. 216.1).

Diagnosis (Perreau 2021). Small to medium size, 2.1-2.4 mm, bathyscioid shape, ovoid and very convex body (Fig. 216.1). Shiny dark brown. Pubescence yellowish, formed of scattered short flat-lying hairs.

Head: Fairly thick, as broad as long, without occipital carina or microsculpture; anophthalmous.

Antennae: Short, extending beyond the base of the pronotum but not reaching the elytral third, with a differentiated club; second antennomere one and a half times longer than the first, being the longest of all the antennomeres; 11th antennomere one and a half times longer than the 10th; the 8th, 9th and 10th antennomeres slightly transverse.

Pronotum: Transverse, 1.8 times as wide as long; sides evenly rounded with the maximum width at the base being as wide as the base of the elytra; vertices pointing backwards and acute angles; surface shiny, dots rare, scattered, fine and very small associated with hairs; microreticulation undifferentiated.

Elytra: Ovoid, short, convex, shiny, with rare minute and superficial punctation associated with setae; convex and short, 1.1 times as long as wide; maximum width at the base; sides evenly arched to the apex, which is rounded, the apical area slightly narrowed; pubescence similar to that of the pronotum, shiny and stippled; no transverse striolation or microreticulation, a parasutural stria extending to the apical third of the elytra; its area slightly darker.

Legs: Short and robust. Protarsi of the male pentamerous and expanded, the first protarsomere as wide as the apical area of the protibia; tetramerous and not expanded in the female; meso- and metatarsi composed of five tarsomeres, not expanded in both sexes; all tarsi with a single robust empodial bristle; protibia without a lateral row of regular spines on the outer surface; meso- and metatibiae straight, without a crown of spines around the apical perimeter and straight; all tibiae with a trifid inner spur.

Mesoventral keel: High, short and stout, apophysis extending a little over anterior area of metaventrite and separating mesocoxae; vertex rounded and ventral margin broad and flattened in medio-posterior area (Fig. 216.2).

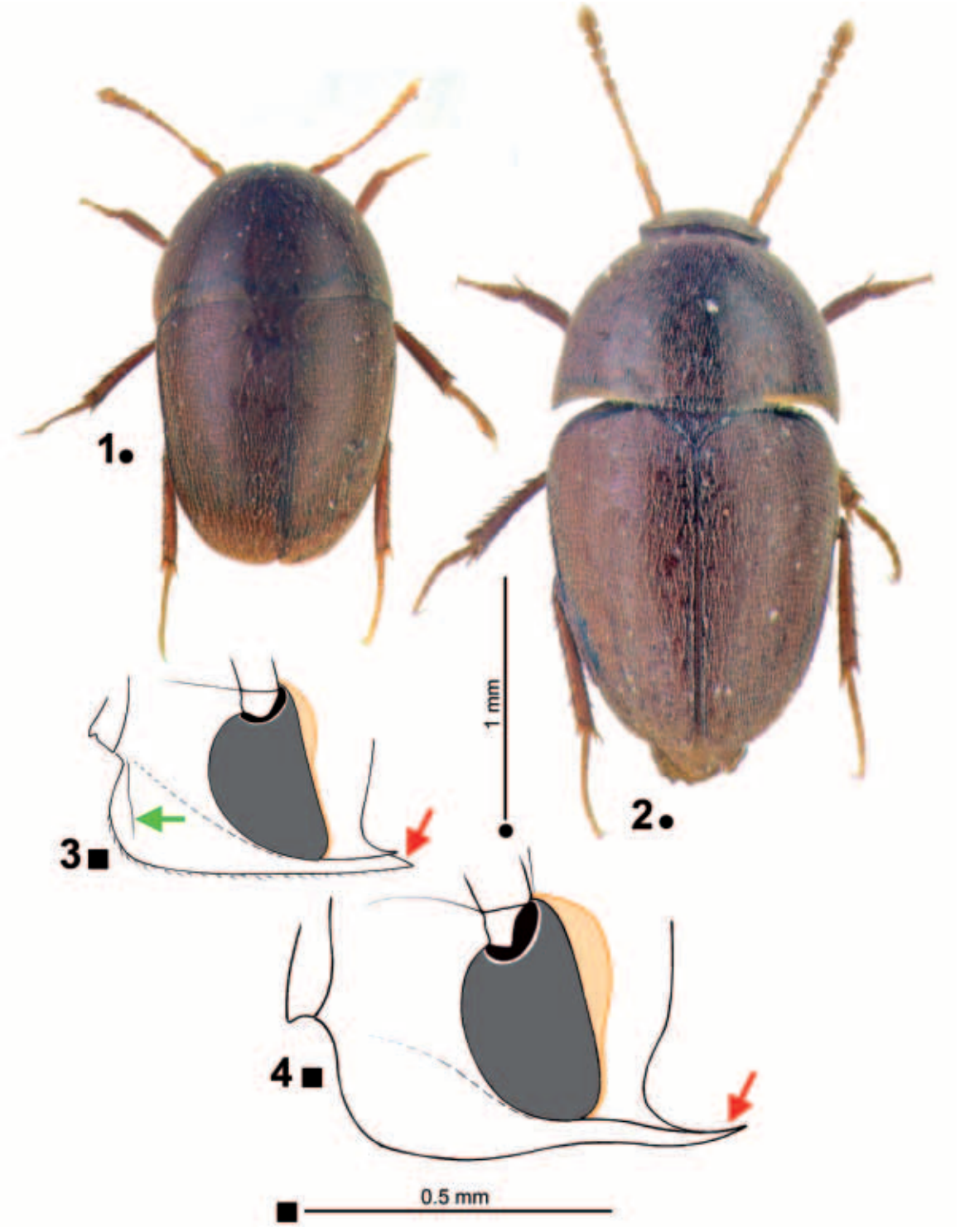
Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated. Arched in lateral view (Fig. 216.3), strongly emarginate dorsally, harpoon-shaped in the apical quarter, the apex very thin. In dorsal view (Fig. 216.4), sides subparallel, the middle basal area slightly wider, the apex broadly rounded with a small rectangular protuberance at the tip. Basal lamina short and posterior margin strongly arched, a little shorter and narrower than the ventral lamina of the tegmen.

Endophallus (Fig. 216.4): Basal region with a slightly chitinised loop surrounding the ejaculatory duct. The median region with two short arched laminae that meet above a structure with well-defined sclerotized pieces; the apical region with rather diffuse reinforcing bands.

Parameres (Fig. 216.5): In dorsal view, as long as the median lobe, quite stout, straight to the apical region, which curves inwards, and of uniform thickness to the apex, which is slightly dilated; apex with three setae, the insertion pores close together and equidistant, the latero-inferior seta somewhat longer.

Spermathecal complex (Fig. 216.6): Spermatheca



FIGURES 217.1–217.4: *Oryotus* series, *Pholeuonidius* group. Habitus of: (**1**) *Pholeuonidius halbherri*, (**2**) *Rhaetiella pinkeri*. Pterothorax in lateral view of: (**3**) *P. halbherri*, (**4**) *R. pinkeri*. Green arrow pointing to the suture of the anterior margin; red arrow pointing to the mesoventral keel extended over the metaventrite.

long and slender; apical lobe spherical, well sclerotized and a little wider than the rest of the spermatheca, following the axis of symmetry with the median region short and hyaline and the basal region elongated and sclerotized, with a small nodule into which the spermathecal gland empties and followed by a long, thin spermatic duct which ends in a small sclerotized piece, the basal sclerite.

Female uroventrite VIII (Fig. 216.7): Slightly more than twice as wide as long; spiculum short and narrow with slightly forked, bifid apex.

Discussion. As pointed out by Perreau (2021) in the original description, the systematic position of *Mixanigia* seems somewhat uncertain. The French author attempted to position *Mixanigia* in the Pholeuina subtribe on the basis of characters which, as we have amply illustrated in the introductory part of this contribution, are mostly due to convergence phenomena that mask the true phyletic affinities. Perreau (2021) placed particular emphasis on the presence of a single empodial seta in *Mixanigia*, a character that distinguishes it from all the genera known from the Near East, and pointed out that most genera of Leptodirini have two interongular empodial setae. Species with a single empodial seta belong to the genera *Platycholeus* (Newton 1998; Gnaspini *et al.* 2017a), and to a few Pyrenean genera such as *Speonomus* (Juberthie *et al*. 1981; Gers 1983, 1989; Gers & Dupuy 1988; Perreau 2000), *Trapezodirus* (Fresneda *et al*. 2011a), *Baronniesia* (Fig. 12.1), *Trocharanis* (Fig. 12.5), *Pholeuon* (Moldovan *et al*. 2007), *Drimeotus* (Fig. 12.2) or *Adelopsella* (Fig. 12.4), a Pholeuina genera whose ranges are very far from Turkey. It is possible that the extremely reduced second seta, universal in the Leptodirini, fused to the base of the other exists. It seems that the base of the two setae has fused and rotated, being arranged obliquely or vertically;this could be a synapomorphy of Leptodirini (Antunes-Carvalho *et al*. 2019).

We believe, with the necessary caution due to the lack of other definite synapomorphies, that the true affinities of *Mixanigia* could be found with *Muellerіella taygetana* (belonging to an unpublished genus) and, perhaps, also with *Pangaeoniola*; these three genera being characterised by a peculiar «harpoon» shape of the median lobe of the aedeagus (a feature also found surprisingly in *Ovobathysciola majori* and *O. sardoa* comb. nov.); the habitus also follows the particular pattern of *Muellerіella taygetana* and *Lakedemoniana* gen. nov. At least the presumed link with the Peloponnesian genera is zoogeographically congruent as a current relictual distribution of a «South Aegean» line originally present on the Hellenic Arc, extended from the Dinaric Alps (across Greece, the Peloponnese, Crete, the Carpathians and Rhodes) to Asia Minor during at least the Upper Miocene (Le Pichon & Angelier 1979; Higgins & Higgins 1996; Ten Veen & Postma 1999). It should be noted that the endophallus, with two short arched phanerae, is extremely similar to that of *Karadeniziella*, a genus inhabiting the same region. As there are no molecular data available, with only morphological evidence, *Mixanigia* must be considered as an isolated genus of the *Karadeniziella* series, close to *Muellerіella taygetana*, *Lakedemoniana* gen. nov. and *Pangaeoniola*. Its position within the *Karadeniziella* series is uncertain, and doubts are expressed as to whether it should be categorised as its own series closely related to the *Karadeniziella* series, or as a group within that series. The first option has been provisionally chosen.

Distribution. Turkey. Province of Alanya. Troglobitic genus known only from the four specimens from the type locality, Düden suyu Mağarasi, near Akseki, located in the mountainous karst of the Taurus region.

Species

Mixanigia faillei Perreau, 2021
Mixanigia faillei Perreau, 2021: 2.

3.4.3 Series ***Oryotus***

Diagnosis. Genera of small to medium-sized species, 1.2-4.4 mm, with abathyscioid or pholeuonoid body. Depigmented.

Head: Occipital carina complete, sometimes obtusely smooth; anophthalmous.

Antennae: Short or very long.

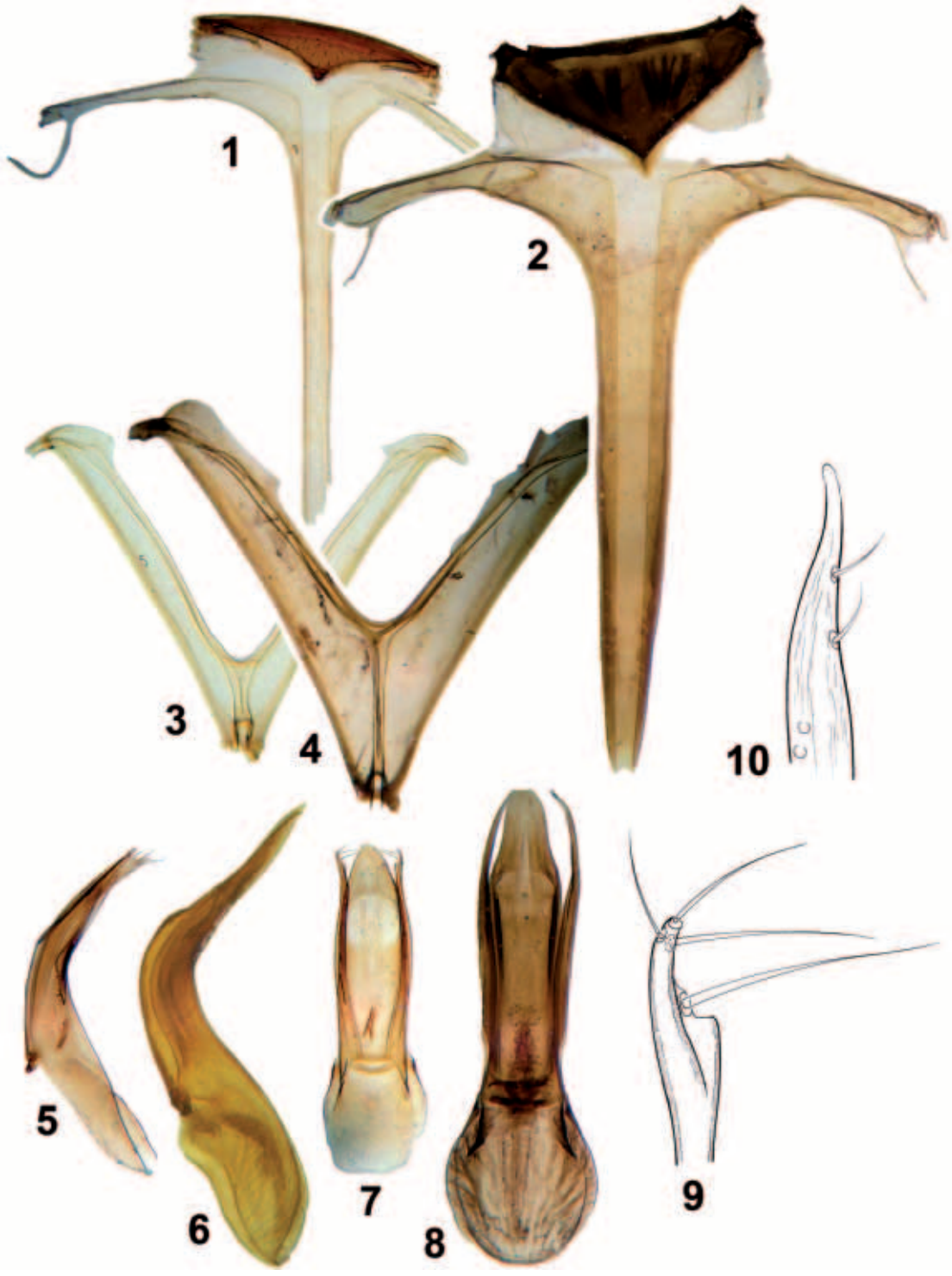
Pronotum: Transverse to cordate, disc regularly convex, the sides sinuate or not posteriorly.

Elytra: Ovoid or elliptical. Pubescence aligned or not in transversal striolae. Parasutural stria absent.

Legs: Male protarsi pentamerous or tetramerous, dilated or not. Protibiae with or without external comb.

Mesoventral keel (Figs. 217.3, 217.4, 221.1, 221.2, 225.4-225.6): Low and inconspicuous to high, lamellar, toothed or not; sometimes absent or detected only in area between coxal cavities. Not extension into the metaventrite.

Suture of metaventrite (Figs. 217.3, 217.4, 221.2, 225.5, 225.6): Sinuous, delimiting a small arcuate sur-



FIGURES 218.1–218.10: *Oryotus* series, *Pholeuonidius* group. Metatergal apparatus of: (**1**) *Pholeuonidius halbherri*, (**2**) *Rhaetiella pinkeri*. Metendosternite of: (**3**) *P. halbherri*, (**4**) *R. pinkeri*. Aedeagus in lateral view of: (**5**) *P. halbherri*, (**6**) *R. pinkeri*. Aedeagus in dorsal view of: (**7**) *P. halbherri*, (**8**) *R. pinkeri*. Apex of the paramere of: (**9**) *P. halbherri*, (**10**) *R. pinkeri*.

face in the apical half and passing very close to the coxal cavity in the basal half.

Metatergal apparatus: With apophysis of the alacrista very short (Figs. 221.3, 221.4) or long (Figs. 226.1, 226.2) in elongated genera or very long in bathyscioid genera (Figs. 218.1, 218.2).

Metendosternite (Figs. 218.3, 218.4, 221.5, 221.6, 226.3, 226.4): «V»-shaped, with or without apical process on arms.

Median lobe of aedeagus: Robust to elongate. Moderately curved to strongly flexed medially in lateral view (Figs. 218.5, 218.6, 222.1-222.3, 227.1-227.3); Apex curved downwards or upwards, sometimes bearing a large rounded median and ventral carina. In dorsal view (Figs. 218.7, 218.8, 223.1-223.4, 227.4-227.7) with subparallel sides and rounded or subtriangular or three-lobed apex, sometimes with a small apical tubercle.

Endophallus (Figs. 218.7, 218.8, 223.1-223.4, 227.4-227.7): «Y»-piece present, more or less obvious. Median and distal areas with or without phanerae.

Parameres (Figs. 218.9, 218.10, 223.5-223.4, 228.1-228.3): Strong or slender, longer or shorter than median lobe, with 2-4 apical setae.

Spermathecal complex (Figs. 219.1, 219.2, 224.1-224.3, 228.4-228.6): Spermatheca kidney-shaped or ampulla-shaped, with poorly or well developed proximal lobe and sclerotized or non-sclerotized duct at insertion.

Female uroventrite VIII (Figs. 219.3, 219.4, 224.4-224.7, 228.7, 228.8): Spiculum sometimes absent; when present, short and very stout, subtriangular or reduced to a small median tubercle.

Discussion. The phylogenetic tree (Fig. 1D), shows two clades in the *Oryotus* series with high support, 100/100, for the clade separating the *Oryotus* group from the *Aphaobius* group; support of 98.4/87 in Tree-1 (Fig. 1D) and 98/97 in Tree-2 (Fig. 2) for the clade separating these two groups from the *Pholeuonidius* group. This situation confirms, at least in part, the phyletic reconstructions used to date based on morphology (Perreau 2003). On the other hand, the proximity of *Pholeuonidius* group (characterised by genera with pentamerous male protarsi) to *Aphaobius* and *Oryotus* groups (with tetramerous male protarsi) was unexpected, at least from a classical phyletic point of view. However, the high support shown by the clade, 98.4/87, leaves no room for doubt; moreover, as discussed extensively in the general section on characters, tetramery in male protarsi appears to have arisen independently in different phyletic lineages.

From a morphological point of view, *Oryotus* has always been related to *Neobathyscia*; in one of the analysis carried out, this position was indeed obtained (Fig. 64: Tree-3) with good support, 97/81, although the rest of the topology of the tree obtained is rather incongruous. Given our current state of knowledge, we cannot rule out a future shift towards the *Oryotus* series in this clade, as molecular data are lacking for too many taxa in the *Neobathyscia* series. The same could be said of the *Karadeniziella* series. The phylogram in Figure 1D brings the *Karadeniziella* series closer to the *Oryotus* series with a support of 88.5/29, although this weak support could be modified, as could the position in the phylogenetic tree, if more species from the *Karadeniziella* series were added to the molecular analysis.

Key to groups

1. Males protarsi pentamerous. Mesoventral keel high and well developed, extended beyond metaventrite (Figs. 217.3, 217.4) .....*Pholeuonidius* group
- Males protarsi tetramerous. Mesoventral keel low and absent or reduced, not extended over the metaventrite (Figs. 221.1, 221.2, 225.4-225.6).....2

2. Eleventh antennomere about three times longer than the 8th antennomere. Elytra with punctation aligned in transverse striolae.....*Aphaobius* group
- Eleventh antennomere at most twice as long as the 8th antennomere. Elytra with punctation not aligned in transverse striolae.....*Oryotus* group

3.4.3.1 ***Pholeuonidius*** group

Diagnosis. Genera grouping species of small size, 1.2-2.6 mm, with abathyscioid body, ovoid in shape, pronotum wider than the elytra. Depigmented.

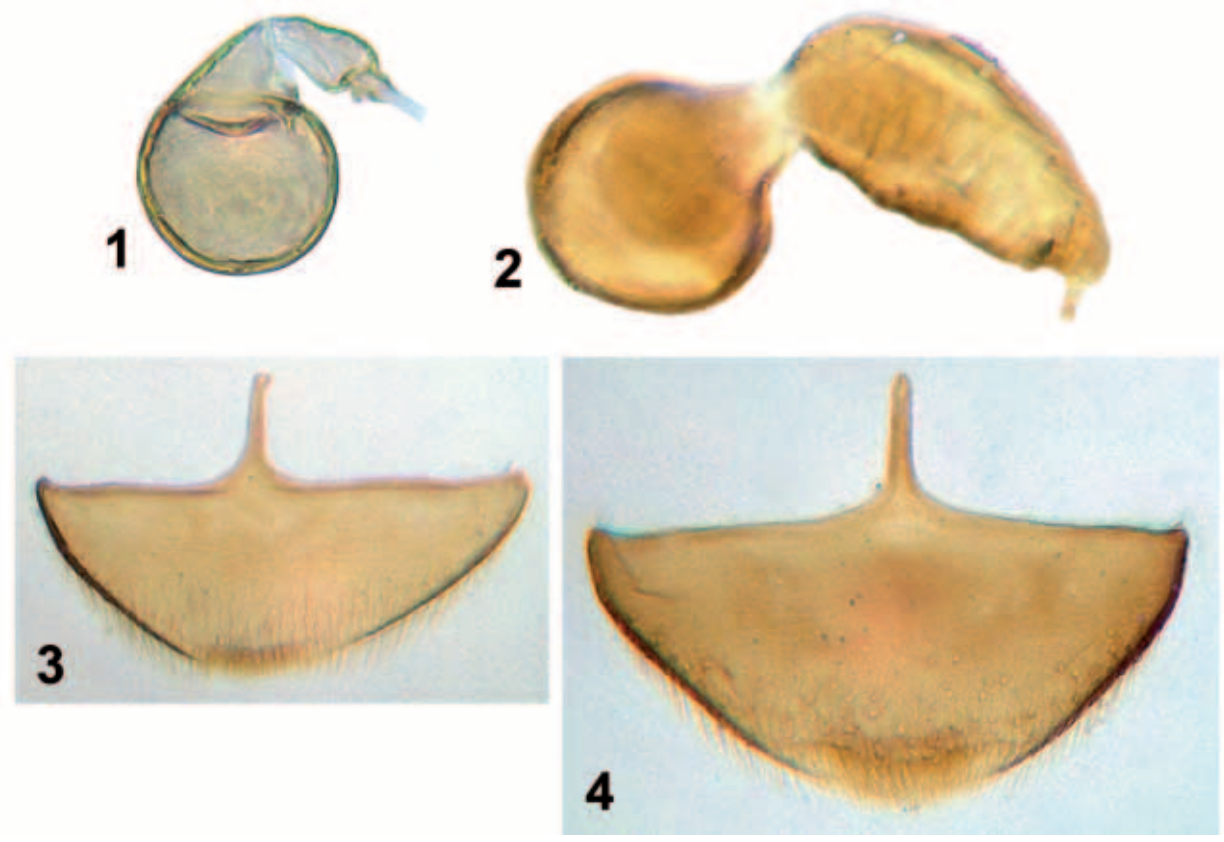
Head: Occipital carina complete; anophthalmous.

Antennae: Short, reaching, stretched backwards, to the base of the pronotum. First antennomere only slightly shorter than the second.

Pronotum: With evenly rounded sides, broad and globose, as wide as or just wider than the elytra. Maximum width approximately at the level of the basal angles, or just before; basal angles acute and turned backwards due to the accentuated sinuosity of the base.

Elytra: Oval, without parasutural stria and with fine but obvious transverse striolae.

Legs: Short and stout, with male protarsi pentamerous and well dilated. Protibiae with an external comb.



FIGURES 219.1–219.4: *Oryotus* series, *Pholeuonidius* group. Spermatheca of: (**1**) *Pholeuonidius halbherri*, (**2**) *Rhaetiella pinkeri*. Female uroventrite VIII of: (**3**) *P. halbherri*, (**4**) *R. pinkeri*.

Mesoventral keel (Figs. 217.3, 217.4): High, lamellar, with rounded, untoothed anterior margin; extended beyond metaventrite.

Suture of the metaventrite (Figs. 217.3, 217.4): In a more or less sinuous arc and passing at a short distance from the edge of the mesocoxal cavity, delimiting a small, elongated area, slightly wider in the anterior half and reduced in the posterior half.

Metatergal apparatus (Figs. 218.1, 218.2): With a very elongated apophysis of the alacrista, almost reaching the apex of the elytra.

Metendosternite (Figs. 218.3, 218.4): «V»-shaped. With arms of regular width along their entire length and a membranous expansion on the inner side of the apical end.

Median lobe of aedeagus: Small, regularly curved or strongly inflexed in its distal third, in lateral view (Figs. 218.5, 218.6). Regularly and gradually attenuated towards subtriangular apex in dorsal view (Figs. 218.7, 218.8).

Endophallus (Figs. 218.7, 218.8): Basal «Y»-piece present but completely unsclerotized. Without sclerotized parts or with sparsely sclerotized bands.

Parameres (Figs. 218.9, 218.10): Strong or thin, longer or shorter than median lobe, with 2-3 apical setae.

Spermathecal complex: Reniform (Figs. 219.1, 219.2) or bulbous spermatheca, with a poorly developed or well developed proximal lobe and a sclerotized or non- sclerotized duct at the insertion.

Female uroventrite VIII (Figs. 219.3, 219.4): With a long, slender spiculum.

Discussion. Molecular data are available only for the genus *Pholeuonidius*; in the phylogenetic tree (Fig. 1D), it is the basal genus of the clade of the *Oryotus* series and joins the *Oryotus* and *Aphaobius* groups with high suport, 98.4/87. Consequently, this group, which includes the genera *Pholeuonidius* and *Rhaetiella*, is defined, in part, on a morphological basis, in accordance with Giachino & Vailati (2005).

DISTRIBUTION. Italy. Provinces of Lecco, Brescia, Trento, Verona, Vicenza, Belluno, Treviso, Pordenone and Udine.

KEY TO GENERA

1. Median lobe of aedeagus, in lateral view, normally curved in the apical third (Fig. 218.5). Spermatheca with proximal lobe smaller than distal lobe (Fig. 219.1) .....*Pholeuonidius*
- Median lobe of aedeagus, in lateral view, abruptly curved in apical third (Fig. 218.6). Spermatheca with proximal lobe of similar size to distal one (Fig. 219.2) .....*Rhaetiella*

Genus ***Pholeuonidius*** Jeannel, 1911
Pholeuonidius Jeannel, 1911a: 267.

TYPE SPECIES. *Bathyscia halbherri* Reitter, 1887 by original designation (habitus in Fig. 217.1).

DIAGNOSIS. Small size, 1.2-2.0 mm, with bathyscioid body (Fig. 217.1), ovoid in shape, pronotum broader than elytra.

Head: Occipital carina complete.

Antennae: Short, reaching the base of the pronotum when stretched backwards. First antennomere only slightly shorter than the second.

Pronotum: With evenly rounded sides, broad and globose, wider than the elytra. Maximum width approximately at the basal angles, or just before; basal angles acute and turned backwards due to the accentuated sinuosity of the base.

Elytra: Oval, without parasutural stria and with fine but obvious transverse striolae.

Legs: Short and stout, with male protarsi pentamerous more or less dilated. Protibiae with an external comb.

Mesoventral keel (Fig. 217.3): High, lamellar, with rounded, untoothed anterior margin; ventral margin straight with setae; posterior process extended beyond metaventrite. A groove or suture close to the anterior surface; surface smooth and shiny from this line to the anterior margin, the rest of the keel reticulate.

Suture of the metaventrite (Fig. 217.3): In a sinuous arc, passing very close to the coxal cavity in the basal half, delimiting a reduced area in the upper half.

Metatergal apparatus (Fig. 218.1): With apophysis of the alacrista very elongate, almost reaching the elytral apex; wings of metascutum short and narrow.

Metendosternite (Fig. 218.3): «V»-shaped. Furcal arms long, a little more than three times the length of the trunk, with a well-developed apophysis and a posterior furcal plate of equal width along the entire length of the arm. Furcal trunk very short, slightly shorter than the widest part.

Median lobe of aedeagus: Small, regularly curved in lateral view (Fig. 218.5). Regularly and gradually attenuated towards apex in dorsal view (Fig. 218.7); apex subtriangular apex, sometimes with short tongue.

Endophallus (Fig. 218.7): «Y»-piece present but completely unsclerotized. With thin, slightly sclerotized basal and distal bands.

Parameres (Fig. 218.9): Relatively strong, longer or shorter than median lobe; apex rounded or laterally pointed; with 2-4 apical setae.

Spermathecal complex: Spermatheca (Fig. 219.1) very short, not reniform, bulbous, with a large apical lobe and a weak proximal lobe; no distinct union duct.

Female uroventrite VIII (Fig. 219.3): Spiculum long and narrow, with the apex very slightly dilated and truncated.

DISCUSSION. The phylogenetic tree (Fig. 1D) shows that *Pholeuonidius halbherri* is the sister group to the *Oryotus* group + *Aphaobius* group complex with high support, 98.4/87. This result contrasts with the classical phylogeny of the group, which has always linked *Pholeuonidius* to *Bathyscimorphus* (Jeannel 1924a; Perreau 2000), probably on the basis of simple convergence of characters. The fact that a genus with pentamerous male protarsi results as a sister group of two groups of tetramerous genera should not be surprising, since as discussed extensively in the introductory section, the tetramery of male protarsi appears to be an apomorphic character that appeared independently in different phyletic lineages.

DISTRIBUTION. Italy. Provinces of Trento, Verona, Vicenza, Belluno and Treviso.

Species

Pholeuonidius halbherri (Reitter, 1887)
Bathyscia Halbherri Reitter, 1877: 276.
Bathysciola Halbherri Reitter: Jeannel, 1910a: 28.
Pholeuonidius Halbherri Reitter: Jeannel, 1911a: 269.
Bathysciola (*Pholeuonidius*) *Halbherri* Reitter: Jeannel, 1914b: 15.
Bathysciola pumilio subsp. *valestrina* Jeannel: Faignez, 1927: 18.
Pholeuonidius halbherri Reitt.: Agazzi, 1957: 117.

Pholeuonidius pacei Paoletti, 1977
Pholeuonidius pacei Paoletti, 1977: 54.

Genus ***Rhaetiella*** Giachino & Vailati, 2005
Rhaetiella Giachino & Vailati, 2005a: 308.

Type species. *Pholeuonidius pinkeri* Jeannel, 1911 by original designation (habitus in Fig. 217.2).

Diagnosis. A genus of small size, 1.5-2.6 mm, with bathyscioid body (Fig. 217.2), ovoid in shape, the pronotum wider than the elytra.

Head: Occipital carina complete.

Antennae: Short, reaching to the base of the pronotum when, stretched backwards. First antennomere only slightly shorter than the second.

Pronotum: With evenly rounded sides, wide and globose, as wide as or just wider than the elytra; maximum width approximately at the basal angles, or just before, the angles acute and turned backwards due to the accentuated sinuosity of the base.

Elytra: Oval, without parasutural stria and with fine but obvious transverse striolae.

Legs: Short and stout, with the protarsi of the male pentamerous and well dilated. Protibiae with an external comb.

Mesoventral keel (Fig. 217.4): High, lamellar, with rounded, untoothed anterior margin; posterior process extended beyond metaventrite.

Suture of metaventrite (Fig. 217.4): In the upper two-thirds it delimits a well-developed arcuate area, reduced in the basal third.

Metatergal apparatus (Fig. 218.2): Wings of metascutum short and narrow, with the apophysis of the alacrista very elongate, almost reaching the elytral apex.

Metendosternite (Fig. 218.4): «V»-shaped. Furcal arms wide, almost twice the length of the trunk, with an elongated, conspicuous apophysis and a broad posterior furcal plate narrowing into the apical area of the arm; lateral furcal flange straight. Short furcal trunk very slightly shorter than the widest area.

Median lobe of aedeagus: Small. In lateral view (Fig. 218.6), stronglly flexed in the distal third. Regularly and progressively attenuated towards the subtruncate apex in dorsal view (Fig. 218.8).

Endophallus (Fig. 218.8): Basal «Y»-piece present but completely unsclerotized. No sclerotized parts.

Parameres (Fig. 218.10): Long and relatively slender, as long as or only slightly longer than median lobe; curved and tapering towards apical area, with two laterally inserted setae.

Spermathecal complex: Spermatheca (Fig. 219.2) kidney-shaped, with a well-developed proximal lobe, more elongated and as thick as the apical one, a very short union duct and an inserted sclerotized duct.

Female uroventrite VIII (Fig. 219.4): Spiculum long, narrow and with acute apex.

Discussion. As no molecular data are available on *Rhaetiella*, its position is defined on morphology alone, following the systematics proposed by Giachino & Vailati (2005).

Distribution. Italy. Provinces of Lecco, Brescia, Verona, Pordenone and Udine.

Species

Rhaetiella cansiliensis Giachino & Vailati, 2005
Rhaetiella cansiliensis Giachino & Vailati, 2005a: 316.

Rhaetiella ferroi **(**Paoletti, 1977)
Pholeuonidius ferroi Paoletti, 1977: 59.
Rhaetiella ferroi **(**Paoletti, 1977): Giachino & Vailati, 2005a: 314.

Rhaetiella pinkeri (Jeannel, 1911)
Pholeuonidius Pinkeri Jeannel, 1911a: 270.
Bathysciola (*Pholeuonidius*) *Pinkeri* Jeannel: Jeannel, 1914b:15.
Pholeuonidius Ferretti-Torricellii Ghidini, 1933: 49; Paoletti, 1977: 51.
Pholeuonidius pinkeri Jeannel: Paoletti, 1977: 51.
Rhaetiella pinkeri (Jeannel, 1911): Giachino & Vailati, 2005a: 310.

3.4.3.2 ***Aphaobius*** group Perreau, 2003 sensu novo

Diagnosis. Genera of medium-sized species, 2.0-3.9 mm, with an elongated bathyscioid, or subpholeuonoid body.

Head: Retractile with a complete occipital carina, sometimes obtusely smooth.

Antennae: Thin, short or elongated, but always shorter than the length of the body, with the 11th antennomere three to more than four times as long as the 8th.

Pronotum: Transverse to cordate, with the disc regularly convex.

Elytra: Ovoid or elliptical, broadly rounded at the apex. Pubescent, with aligned transverse striolae. Parasutural stria absent.

Legs: Male protarsi tetramerous, with first two

protarsomeres dilated or not. Protibiae without a comb on the outer surface. Meso- and metatibiae straight, without complete apical basket.

Mesoventral keel (Figs. 221.1, 221.2): Low and inconspicuous to high, lamellar, toothed or not. Not extended onto the metaventrite.

Suture of metaventrite (Fig. 221.2): Sinuous, delimiting a small arcuate surface in the apical half and passing very close to the coxal cavity in the basal half.

Metatergal apparatus (Figs. 221.3, 221.4): With a short apophysis of the alacrista.

Metendosternite (Figs. 221.5, 221.6): «V»-shaped, with very thin furcal trunk and arms.

Median lobe of aedeagus: Thick to elongated, with subparallel sides and rounded apex, sometimes with a small apical tubercle. Apex, in lateral view (Figs. 222.1-222.3), curved downwards, sometimes bearing a large rounded median and ventral carina. In dorsal view (Figs. 223.1-223.4) moderately curved to flexed in the middle.

Endophallus (Figs. 223.1-223.4): «Y»-piece evident. Median and distal areas with or without phanerae.

Parameres (Figs. 223.5-223.8): Thin or relatively weak, as long as median lobe or significantly longer, with simple or enlarged hyaline spoon-shaped apex; three or four apical setae.

Spermathecal complex: Spermatheca (Figs. 224.1-224.3) asymmetrical or slightly «C»-shaped, with the basal sclerotized lobe small and short, and distal lobe more dilated. Ductus very short (only known in genus *Aphaobiella*).

Female uroventrite VIII (Figs. 224.4-224.7): Spiculum sometimes absent; when present, short and very robust, subtriangular.

Discussion. Molecular data concerning this group are available for the genus *Aphaobius*, polytypic and morphologically well known (Bognolo & Vailati 2010), and for *Lotharia.* There is the earlier molecular data of Faille *et al*. (2016); the topology of the phylogenetic tree obtained by these authors for *Aphaobius* and *Lotharia* is identical to that provided in this study. The reciprocal positions of *Aphaobius* and *Lotharia* in the phylogenetic tree (Fig. 1D), are strictly connected with a high support of 99.9/100. There is also total support of 100/100 between the *Aphaobius* group and the *Oryotus* group. The *Aphaobius* group – or *Aphaobius* phyletic series *sensu* Perreau (2003), in part – based on both morphological and molecular data includes the following genera: *Aphaobius*, *Lotharia*, *Aphaobiella* and *Pretneria*.

Distribution. Italy, Friuli. Slovenia, Croatia (NW) and Austria (Karawanken).

Key to genera
(modified from Perreau, 2003)

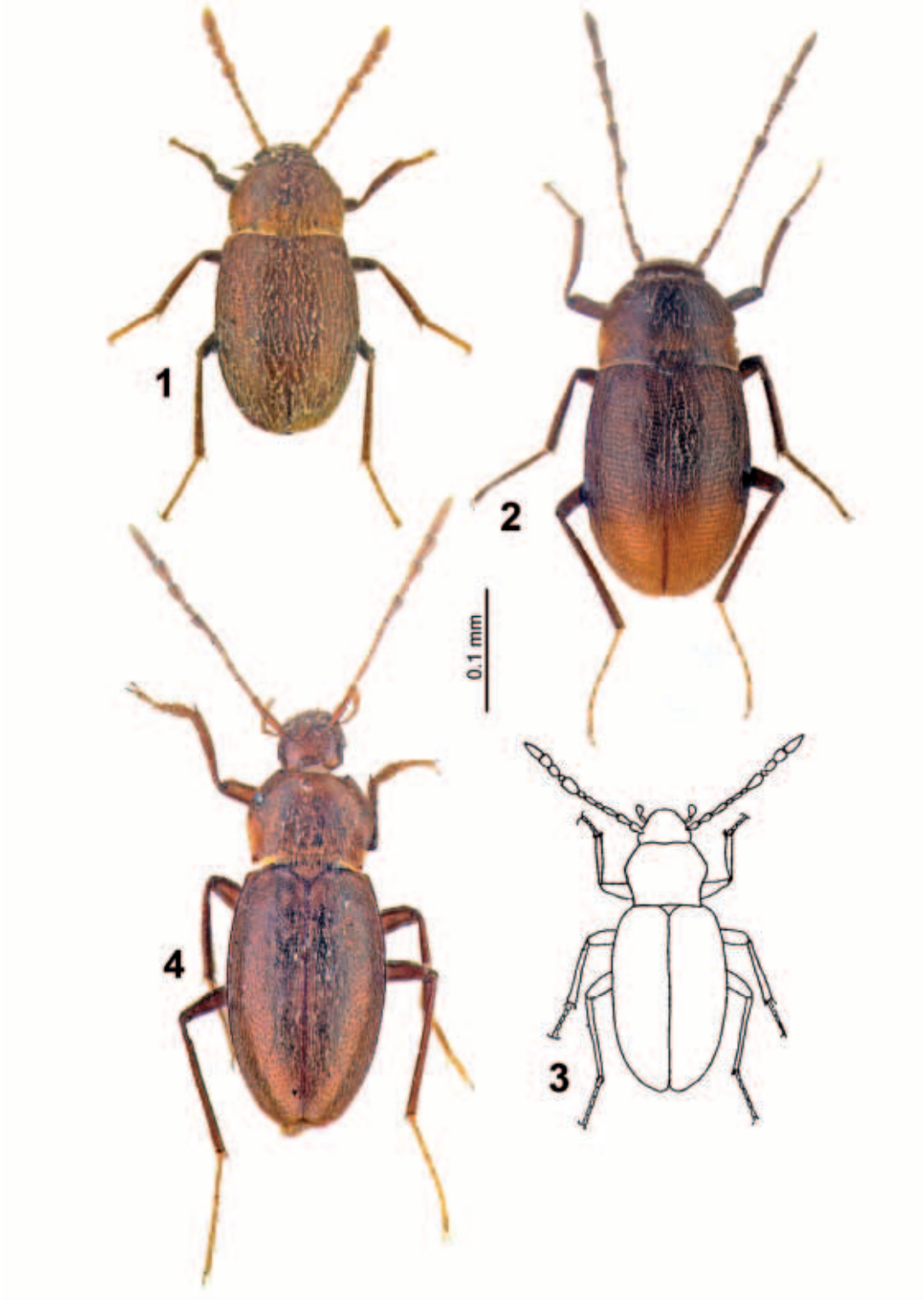
1. Elytra widely and separately rounded at the apex. Male protarsi dilated …... *Pretneria*
- Elytra briefly rounded at the apex and joined almost to the tip. Male protarsi undilated 2

2. Size greater than 3.0 mm (head folded). Pronotum not or only slightly narrowed at base, sides not sinuate or only slightly sinuate very close to base. Mesoventral keel prominent (Fig. 221.2). Antennae slender, 8th antennomere elongate, at least 1.5 times as long as wide, 7th about three times as long as wide, slender in basal half, widened only in apical half .....*Aphaobius*
- Size less than 2.5 mm (head folded). Pronotum clearly narrowed at base, sides strongly sinuate in posterior half. Mesoventral keel low (Fig. 221.1). Antennae with a more compact club, the 8th antennomere globose, not longer than wide, the 7th not more than twice as long as wide, widened from the base.....3

3. Body pholeuonoid (Fig. 220.3). Pronotum very strongly narrowed at the base, which is scarcely wider than the anterior margin. Apex of parameres dilated into a hyaline apical blade and provided with four apical setae (Fig. 223.7). Elytral punctation not accompanied by lifting of the associated scale and strictly aligned transversely, at least in the anterior half of the elytra.....*Lotharia*
- Body bathyscioid (Fig. 220.1). Pronotum less strongly narrowed at the base, which is about one and a half times wider than the anterior margin. Parameres without hyaline apical blade and with three apical setae (Fig. 223.5). Elytral punctation accompanied by lifting of the associated scale, transverse alignments of the dots fragmented and incomplete .....*Aphaobiella*

Genus ***Aphaobiella*** V.B. Guéorguiev, 1976
Aphaobius (*Aphaobiella*) Pretner, 1949: 143 (*Nomen nudum*).
Aphaobiella Pretner, 1949: V.B. Guéorguiev, 1976: 100.

Type species. *Aphaobius* (*Aphaobiella*) *budnar-lipoglavšeki* Pretner, 1949 by original designation (habitus in Fig. 220.1).



FIGURES 220.1–220.4: *Oryotus* series, *Aphaobius* group. Habitus of: (**1**) *Aphaobiella budnarlipoglavseki*, (**2**) *Aphaobius milleri*, (**3**) *Lotharia angulicollis* (modified from Mandl 1944), (**4**) *Pretneria latitarsis*.

DIAGNOSIS. Medium-sized, 2.2-2.4 mm, bathyscioid or slightly pholeuonoid (Fig. 220.1); elongate, with the base of the pronotum slightly narrowed. Yellow-orange, the integument (pronotum and elytra) uniformly covered with yellow pubescence, long and recumbent.

Head: Retractile, with a blunt occipital carina; pubescence long and semi-erect on frons, erect on the clypeus.

Antennae: Relatively short, slender, reaching the basal fifth of the elytra in both males and females. First antennomere shorter or as long as the second; the 11th antennomere almost three times as long as the 8th.

Pronotum: Transverse, wider at mid-length, disc flattened near the basal angles; lateral margins evenly curved anteriorly, not sinuate, sub-rectilinear posteriorly or sinuate just before the basal angles. Disc of pronotum slightly granular with obvious microsculpture.

Elytra: Elliptic, elongate, each elytron rounded and narrowed apically in both sexes. Elytral disc convex, slightly depressed along the suture in the central area; parasutural stria absent; disc with a shallow transverse striation.

Legs: Relatively robust with simple tarsal claws. Protarsi of males tetramerous and not dilated. Protibiae slightly arched externally, without external comb; meso- and metatibiae straight, with two external apical spurs and without complete apical basket.

Mesoventral keel (Fig. 221.1): Bluntly arched, with one small obvious, obtuse and rounded tooth. Not extended into the metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Large. In lateral view (Fig. 222.1), slightly and weakly curved, with slight dorsal double-sinuation in distal half; apex curved downwards sometimes bearing a large rounded median and ventral carina. In dorsal view (Fig. 223.1), robust, with subparallel lateral margins; subtruncate apex evidently emarginate, or pointed, in median area.

Endophallus (Fig. 223.1): With a «Y»-piece and two large parallel, striate, fusiform pieces distally.

Parameres (Fig. 223.5): Relatively weak with the club slightly dilated and slightly longer than the median lobe, slightly and gradually curved inwards. Chaetotaxy represented by three setae: the first in apical position, the second in subapical dorsal, and the third in inner position.

Spermathecal complex (Fig. 224.1): Spermatheca slightly «C»-shaped, well sclerotieed and transversely striated in proximal and distal parts; distal lobe more dilated; hyaline junction duct, shorter and narrower than lobes. Adnexal gland small and confluent with the insertion of the duct proximally. Ductus very short.

Female uroventrite VIII (Fig. 224.4): Spiculum short and very robust, subtriangular.

DISCUSSION. No molecular data are available on species of the genus *Aphaobiella*, so its inclusion in the *Aphaobius* group is only based on morphology: Jeannel (1924a), Perreau (2003) and Bognolo (2016).

DISTRIBUTION. Slovenia, Kamnik Alps.

Species

Aphaobiella budnarlipoglavseki (Pretner, 1949)
Aphaobiella budnarlipoglavseki budnarlipoglavseki (Pretner, 1949)
Aphaobius (*Aphaobiella*) *budnar-lipoglavšeki* Pretner, 1949: 143.
Aphaobiella budnarlipoglavseki budnarlipoglavseki (Pretner): Perreau, 2000: 173.
Aphaobiella budnarlipoglavseki mozirjensis (Pretner, 1949)
Aphaobius (*Aphaobiella*) *budnar-lipoglavšeki* subsp. *mozirjensis* Pretner, 1949: 146.
Aphaobiella budnarlipoglavseki mozirjensis (Pretner): Perreau, 2000: 173.

Aphaobiella kofleri Giachino, 2016
Aphaobiella kofleri Giachino, 2016: 19.

Aphaobiella mlejneki Moravec, 1996
Aphaobiella mlejneki Moravec, 1996: 67.

Aphaobiella tisnicensis (Pretner, 1949)
Aphaobius (*Aphaobiella*) *tisnicensis* Pretner, 1949: 147.
Aphaobiella tisnicensis (Pretner): Perreau, 2000: 174.

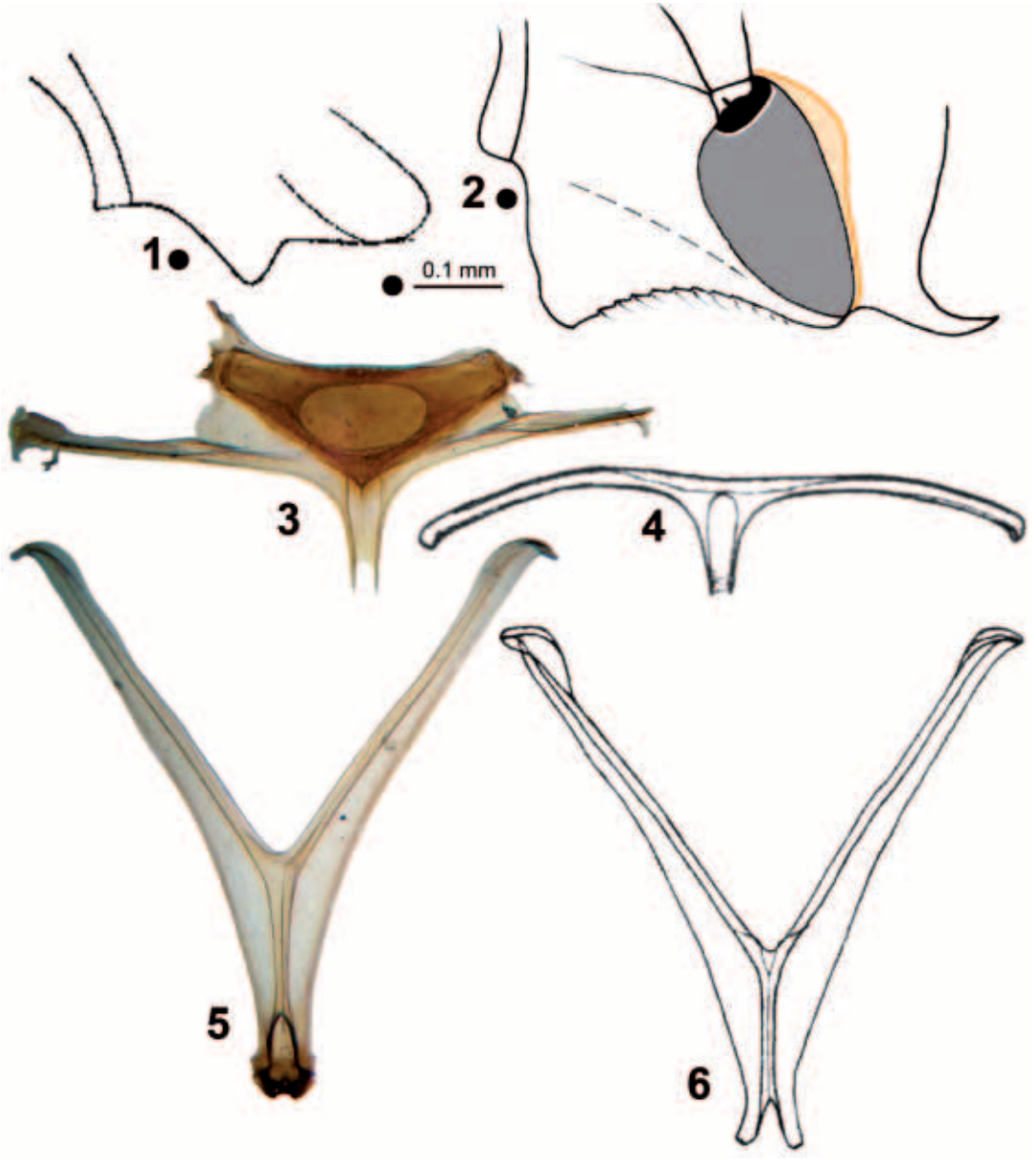
Genus ***Aphaobius*** Abeille de Perrin, 1878
Aphaobius Abeille de Perrin, 1878: 148.

TYPE SPECIES. *Adelops milleri* Schmidt, 1855 by monotypy (habitus in Fig. 220.2).

DIAGNOSIS. Medium-sized, 2.5-3.8 mm, with bathyscioid or slightly pholeuonoid facies and elongate body (Fig. 220.2). Pubescence moderately long and recumbent.

Head: Retractile, with a complete occipital carina.

Antennae: Thin, elongated, but always shorter than



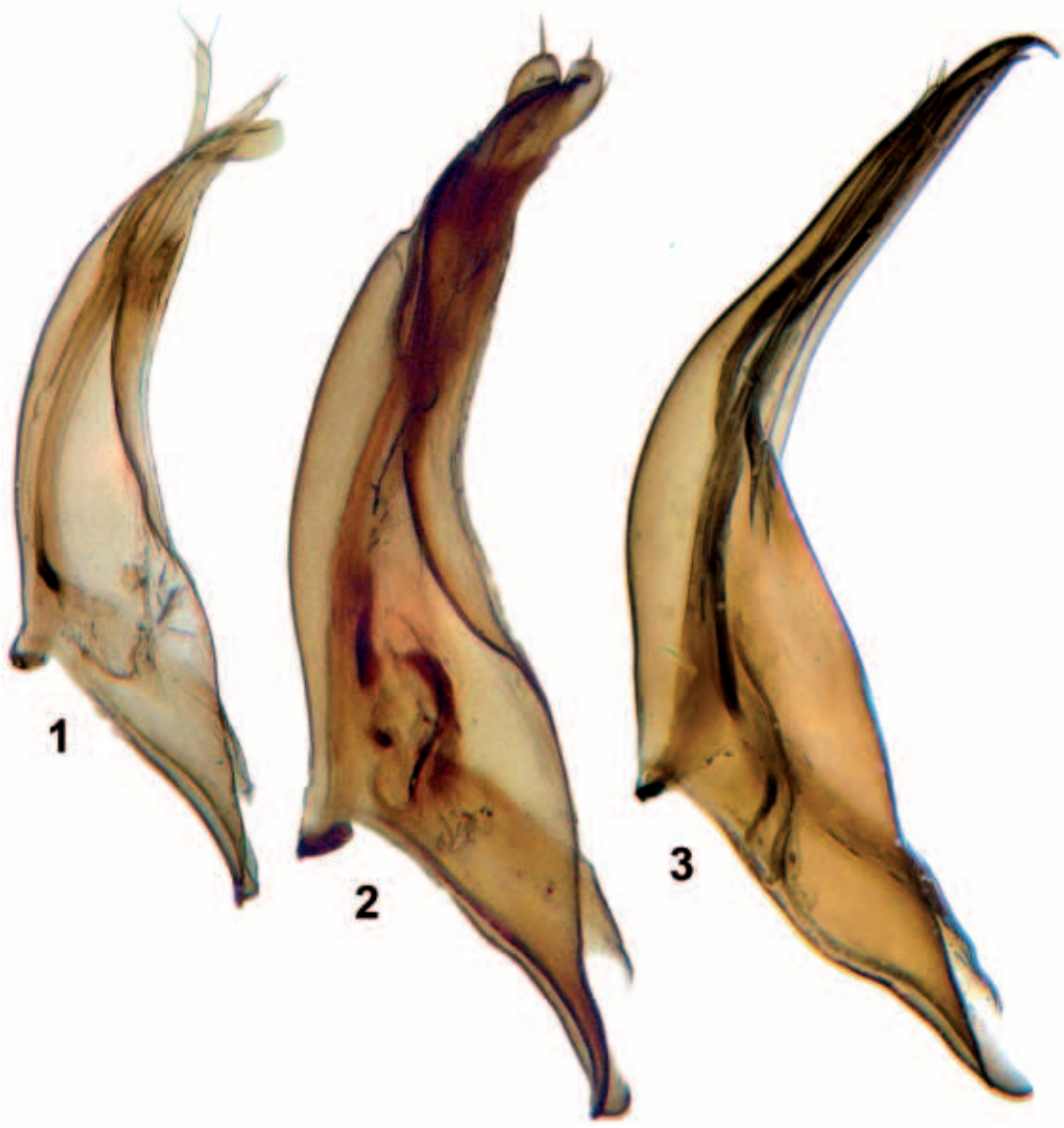
FIGURES 221.1–221.6: *Oryotus* series, *Aphaobius* group. Pterothorax in lateral view of: (**1**) *Aphaobiella kofleri* (modified from Giachino 2016), (**2**) *Aphaobius angusticollis*. Metatergal apparatus of: (**3**) *Aphaobius milleri*, (**4**) *Pretneria latitarsis*. Metendosternite of: (**5**) *A. milleri*, (**6**) *P. latitarsis*. Figs **4**, **6** modified from Bognolo (2000)

body length, with the 11th antennomere three to more than four times as long as the 8th.

Pronotum: Base narrower than the elytra, but always transverse, sides evenly rounded to slightly sinuate just before the base. Disc of pronotum regularly convex; punctation small.

Elytra: Ovoid, broadly rounded at the apex, with maximum width from the middle to the anterior third; pubescence long and recumbent; transverse striolae. Parasutural stria absent.

Legs: Male protarsi tetramerous, undilated. Protibiae not apically enlarged, without comb on outer sur-



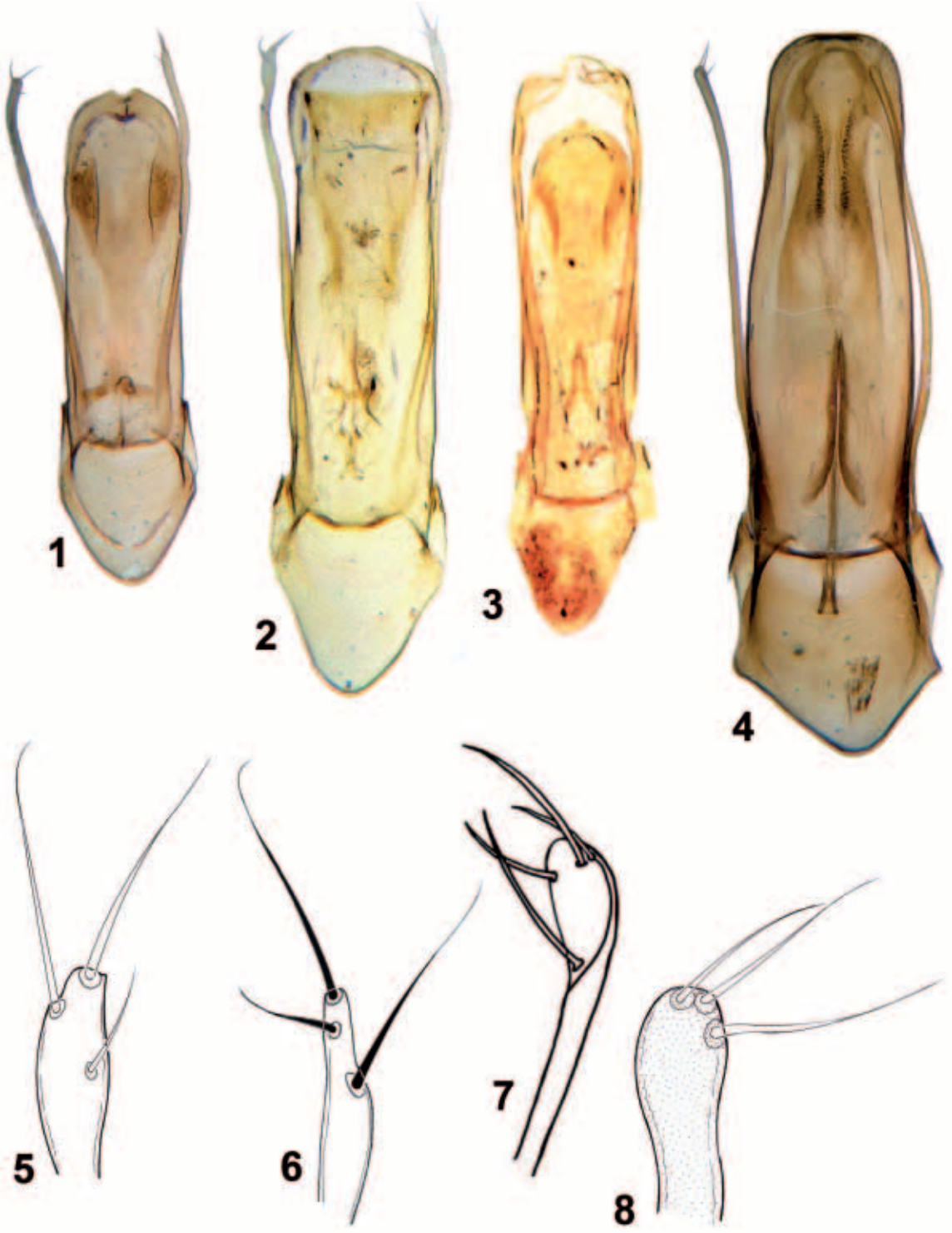
FIGURES 222.1–222.3: *Oryotus* series, *Aphaobius* group. Aedeagus in lateral view of: (**1**) *Aphaobiella budnarlipoglavseki*, (**2**) *Aphaobius haraldi* (modified from Faille *et al.* 2016), (**3**) *Pretneria latitarsis*.

face. Meso- and metatibiae straight, without apical basket.

Mesoventral keel (Fig. 221.2): High, lamellar, not extended on metaventrite. Anterior margin subrectilinear; ventral margin concave, crenulate, with short setae; the vertex slightly hooked, the angle slightly obtuse.

Suture of the metaventrite (Fig. 221.2): Delimiting an arcuate area, usually small, very narrow in the basal half as it is close to the coxal cavity.

Metatergal apparatus (Fig. 221.3): Wings of metascutum short and very narrow, the apophysis of alacrista short and with acute apices.



FIGURES 223.1–223.8: *Oryotus* series, *Aphaobius* group. Aedeagus in dorsal view of: (**1**) *Aphaobiella budnarlipoglavseki*, (**2**) *Aphaobius milleri*, (**3**) *Lotharia angulicollis*, (**4**) *Pretneria latitarsis*. Apex of the paramere of: (**5**) *A. budnarlipoglavseki*, (**6**) *Aphaobius brevicollis*, (**7**) *L. angulicollis*, (**8**) *P. latitarsis.* Figs **3**, **7** modified from Perreau (2003).

Metendosternite (Fig. 221.5): «V»-shaped. Furcal arms narrow and long, almost twice as long as the furcal trunk, with a hooked apical part without apophysis and a narrow, slightly arched posterior furcal plate; furcal trunk distinctly longer than the widest part.

Median lobe of aedeagus: Elongate, moderately curved in lateral view (Fig. 222.2). With subparallel sides and rounded apex in dorsal view (Fig. 223.2).

Endophallus (Fig. 223.2): «Y»-piece present. Median area with an inconspicuous but complex phanera, sometimes tetralobed.

Parameres (Fig. 223.6): Thin and as long as the median lobe or longer; each bearing three setae at the apex, two inserted in a narrower area, one apical, one subapical, the third distal being already inserted in the area where the paramere thickens.

Spermathecal complex: Spermatheca (Fig. 224.2) asymmetrical, with a small, short, sclerotized basal lobe, and a large, saccular, elongated distal lobe; union duct between the two lobes hyaline, short and narrow.

Female uroventrite VIII (Fig. 224.5): Simple, without spiculum, with a small, more or less membranous projection visible in the median area of the posterior margin.

Discussion. The inclusion of *Aphaobius* in this set of genera – *Aphaobius* group, or *Aphaobius* phyletic series *sensu* Perreau (2003), in part – is based on both morphological (Bognolo & Vailati 2010) and molecular (Faille *et al*. 2016) grounds. The position of *Aphaobius* in the phylogenetic tree (Fig. 1D) is strictly related to *Lotharia* (in basal position in the clade) with a support of 99.9/100.

Following the contribution of Bognolo & Vailati (2010) the species of this genus can be divided into four groups of species.

Distribution. Italy (Friuli), Slovenia, Croatia (NW). As pointed out by Bognolo & Vailati (2010) the global distribution of the genus *Aphaobius* shows a combination of species with large distribution areas and other species known from a single site or a very restricted geographical area.

Species

«***heydeni*** group» *sensu* Bognolo & Vailati, 2010
Aphaobius heydeni Reitter, 1884
Aphaobius Heydeni Reitter, 1885a [1884]: 17.

«***kraussi*** group» *sensu* Bognolo & Vailati, 2010

Aphaobius angusticollis Bognolo & Vailati, 2010
Aphaobius angusticollis Bognolo & Vailati, 2010: 15.

Aphaobius brevicornis Mandl, 1940
Aphaobius Milleri brevicornis Mandl, 1940: 31.
Aphaobius milleri brevicornis Mandl (1940): M.E. Schmidt, 1974: 159.
Aphaobius brevicornis Mandl, 1940: Bognolo & Vailati, 2010: 19.

Aphaobius gorenjskanus sp. nov. (See Appendix New Species)

Aphaobius haraldi Faille, Ribera & Fresneda, 2016
Aphaobius haraldi Faille, Ribera & Fresneda, 2016: 48.

Aphaobius knirschi G. Müller, 1913
Aphaobius Milleri Knirschi G. Müller, 1913a: 6.
Aphaobius milleri knirschi J. Müller, 1913: Mlejnek, 1992: 16.
Aphaobius knirschi Müller, 1913: Bognolo & Vailati, 2010: 16.

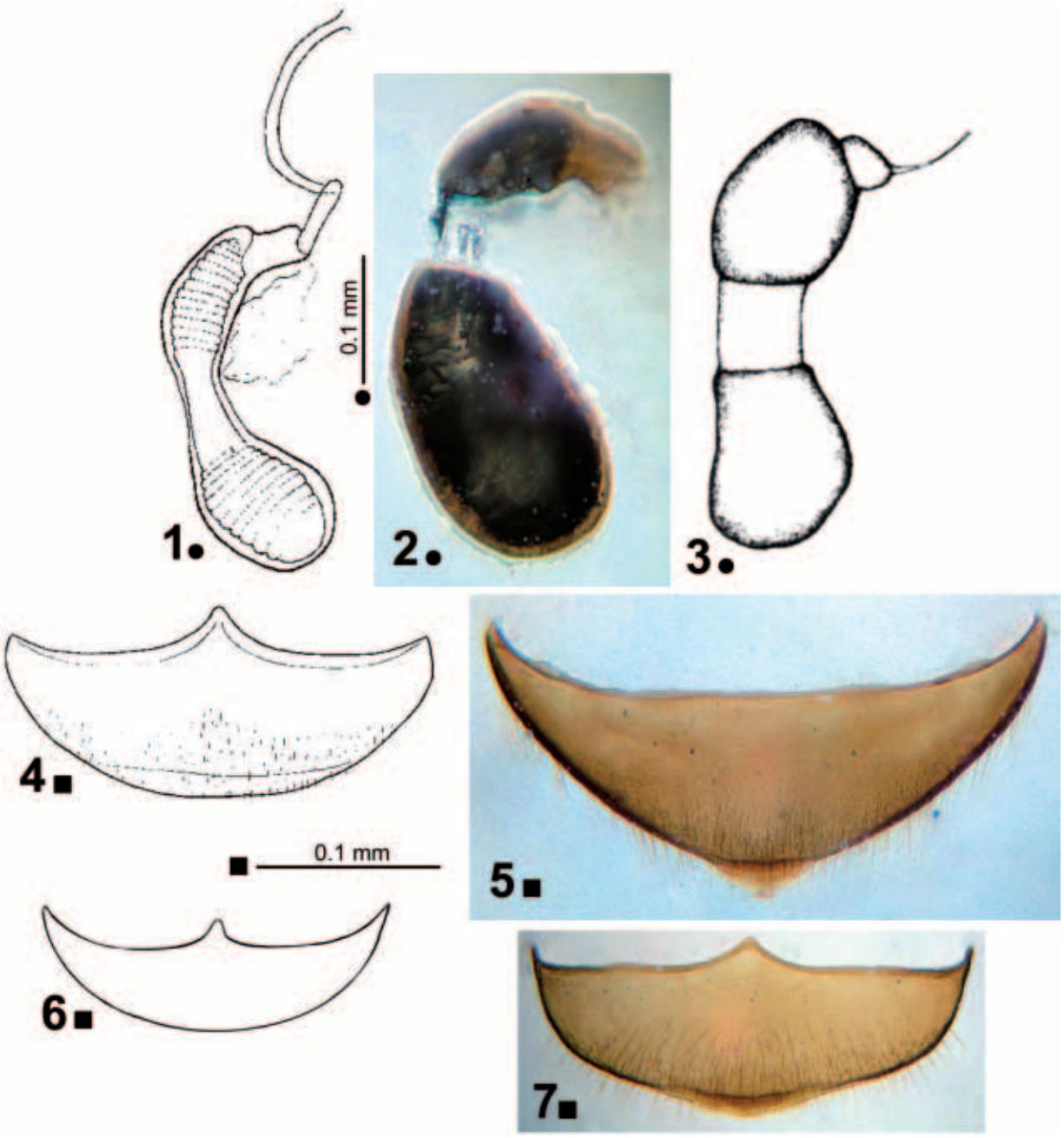
Aphaobius kraussi G. Müller, 1910
Aphaobius kraussi Penecke: G. Müller, 1910: 185.
Aphaobius milleri kraussi Müller, 1910: G. Müller, 1913a: 6.
Aphaobius milleri pretneri G. Müller, 1913a: 5.
Aphaobius milleri winkleri Mandl, 1944: 104.
Aphaobius milleri hölzeli Mandl, 1957: 5.
Aphaobius milleri alpinus Drovenik, Mlejnek & Moravec, 1995: 3.
Aphaobius kraussi Müller, 1910: Bognolo & Vailati, 2010: 21.

Aphaobius mixanigi Bognolo & Vailati, 2010
Aphaobius mixanigi Bognolo & Vailati, 2010: 13.

«***milleri*** group» *sensu* Bognolo & Vailati, 2010
Aphaobius adjae Giachino, 2023
Aphaobius adjae Giachino, 2023: 35.

Aphaobius alphonsi G. Müller, 1914
Aphaobius Milleri Alphonsi G. Müller, 1914: 1023.
Aphaobius milleri alphonsi Müller Perreau, 2000: 174.
Aphaobius alphonsi Müller, 1914: Bognolo & Vailati, 2010: 48.

Aphaobius forojuliensis G. Müller, 1931
Aphaobius Milleri forojuliensis G. Müller, 1931a: 198.



FIGURES 224.1–224.7: *Oryotus* series, *Aphaobius* group. Spermathecal complex of: (**1**) *Aphaobiella kofleri*, (**2**) *Aphaobius luckae* **sp. nov.**, (**3**) *Pretneria latitarsis* (modified from Bognolo 2000). Female uroventrite VIII of: (**4**) *A. kofleri*, (**5**) *A. luckae* **sp. nov.**, (**6**) *Lotharia angulicollis* (redrawn from Perreau 2003), (**7**) *P. latitarsis.* Figs **1**, **4** modified from Giachino (2016).

Aphaobius milleri forojulensis Müller, 1931: Pretner, 1969 [1968]: 10.
Aphaobius forojulensis Müller, 1931: Bognolo & Vailati, 2010: 24.

Aphaobius fortesculptus G. Müller, 1925
Aphaobius Milleri fortesculptus G. Müller, 1925: 46.
Aphaobius milleri fortesculptus Müller, 1925: Pretner, 1969 [1968]: 10.
Aphaobius fortesculptus Müller, 1925: Bognolo & Vailati, 2010: 34.

Aphaobius grottoloi Vailati, 2004
Aphaobius grottoloi Vailati, 2004: 91.

Aphaobius kahleni Bognolo & Vailati, 2010
Aphaobius kahleni Bognolo & Vailati, 2010: 37.

Aphaobius kaplai Bognolo & Vailati, 2010
Aphaobius kaplai Bognolo & Vailati, 2010: 32.

Aphaobius kofleri Bognolo & Vailati, 2010
Aphaobius kofleri Bognolo & Vailati, 2010: 46.

Aphaobius lebenbaueri Bognolo & Vailati, 2010
Aphaobius lebenbaueri Bognolo & Vailati, 2010: 28.

Aphaobius ljubnicensis G. Müller, 1914
Aphaobius Milleri ljubnicensis G. Müller, 1914: 1024.
Aphaobius milleri lubnicensis Müller, 1914: Pretner, 1969 [1968]: 11.
Aphaobius ljubnicensis Müller, 1914: Bognolo & Vailati, 2010: 44.

Aphaobius luckae sp. nov. (See Appendix New Species)

Aphaobius mateji Giachino, 2023
Aphaobius mateji Giachino, 2023: 34.

Aphaobius milleri (F. J. Schmidt, 1855)
Adelops Milleri F. J. Schmidt, 1855: 3.
Aphaobius Milleri Springeri G. Müller, 1910: 185.
Aphaobius Milleri Grabowskii G. Müller, 1917: 624.
Aphaobius Milleri longipennis G. Müller, 1931a: 198.
Aphaobius milleri (Schmidt, 1855): Pretner, 1969 [1968]: 11.
Aphaobius milleri springeri Müller, 1910: Pretner, 1969 [1968]: 11.
Aphaobius milleri grabowskii Müller, 1917: Pretner, 1969 [1968]: 11.
Aphaobius milleri longipennis Müller, 1931: Pretner, 1969 [1968]: 11.

Aphaobius miricae Bognolo & Vailati, 2010
Aphaobius miricae Bognolo & Vailati, 2010: 28.

Aphaobius robustus G. Müller, 1914
Aphaobius Milleri robustus G. Müller, 1914: 1025.
Aphaobius heydeni robustus Müller, 1914: Jeannel, 1924a: 232.
Aphaobius robustus Müller, 1914: Bognolo & Vailati, 2010: 35.

«***muellerianus*** group» *sensu* Bognolo & Vailati, 2010
Aphaobius muellerianus Pretner, 1963
Aphaobius müllerianus Pretner, 1963b: 60.

Aphaobius ninae Giachino, 2023
Aphaobius ninae Giachino, 2023: 34.

Genus ***Lotharia*** Mandl, 1944
Lotharia Mandl, 1944: 106.

Type species. *Lotharia angulicollis* Mandl, 1944 by monotypy (habitus in Fig. 220.3).

Diagnosis. Small-sized, 2.0 mm, pholeuonoid (Fig. 220.3), elongate, with the base of the pronotum narrow.

Head: Retractile, with a complete occipital carina.

Antennae: Thin, elongated, reaching just to the middle of the elytra when stretched backwards; the 11th antennomere more than three times as long as the 8th.

Pronotum: Cordiform, with the base narrower than the base of the elytra and the sides rounded, barely sinuate before the base. Disc regularly convex.

Elytra: Ovoid, broadly and separately rounded at the apex. Pubescence long and recumbent. With transverse striolae. Parasutural stria absent.

Legs: Relatively long and slender. Male protarsi tetramerous and undilated. Protibiae apically dilated; meso- and metatibiae straight, without apical basket; protibiae without comb of bristles on the outer surface.

Mesoventral keel (Perreau 2003): Low and not very evident.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Relatively thin. In dorsal view (Fig. 223.3), the sides subparallel and broadly rounded at apex, bearing a small apical tubercle.

Endophallus (Fig. 223.3): «Y»-piece present.

Preapical part with a set of hyaline spines bordering the entire area.

Parameres (Fig. 223.7): Significantly longer than the median lobe, with enlarged apex shaped like a hyaline spoon bearing four apical setae, one inserted at the base of spoon, the three others directly above.

Spermathecal complex: Unknown.

Female uroventrite VIII (Fig. 224.6): Spiculum very short and stout, apical margin in broad arc.

Discussion. Molecular data are available on the monotypic and morphologically poorly known genus *Lotharia*, so that its inclusion on the *Aphaobius* group is based on both morphological and molecular grounds. In the phylogenetic tree (Fig. 1D) it is the basal genus of the clade and the sister of the genus *Aphaobius* to which it is attached with a high support of 99.9/100.

Distribution. Austria. Karawanken.

Species

Lotharia angulicollis Mandl, 1944
Lotharia angulicollis Mandl, 1944: 106.

Genus ***Pretneria*** G. Müller, 1931
Aphaobius (*Pretneria*) G. Müller, 1931a: 198.
Pretneria Müller, 1931: Pretner, 1949: 151.

Type species. *Aphaobius* (*Pretneria*) *latitarsis* G. Müller, 1931 by monotypy (habitus in Fig. 220.4).

Diagnosis. Medium-sized, 2.9-3.9 mm, bathyscioid (Fig. 220.4), elongate, with the base of the pronotum slightly narrowed.

Head: Retractile, with a complete but obtusely smooth occipital carina. Mouth apparatus of «normal» shape, not specialised.

Antennae: Thin, elongated, not reaching the middle of the elytra when stretched backwards; the 11th antennomere more than three times longer than the 8th.

Pronotum: Transverse, with the base narrower than the base of the elytra; sides rounded, slightly sinuate before the base. Disc regularly convex.

Elytra: Ovoid, broadly and separately rounded at apex. Pubescence long and recumbent. Transverse striolae. Parasutural stria absent.

Legs: Relatively long and slender. Male protarsi tetramerous, with the first two protarsomeres dilated; the first very dilated and longer than the fourth. Protibiae apically dilated; meso- and metatibiae straight, without apical basket. Protibiae without comb of bristles on outer surface.

Mesoventral keel (Bognolo 2916): Low, lamellar, the anterior edge straight, not toothed and not extending beyond metaventrite. Lower margin bristly.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 221.4): Wings of metascutum long and very narrow, with apophysis of alacrista short, with acute apices.

Metendosternite (Fig. 221.6): «V»-shaped. Furcal arms narrow and long, twice as long as the furcal trunk, with well-defined apophysis; posterior furcal plate narrow and slightly arched. Furcal trunk longer than the widest area, with ends of mediofurcal keel very divergent .

Median lobe of aedeagus: Elongate. In lateral view (Fig. 222.3), curved and flexed in the middle, with the apex curved downwards. In dorsal view (Fig. 223.4) with subparallel sides, concave on the apical three quarters and a rounded apex.

Endophallus (Fig. 223.4): Basal «Y»-piece evident; median area with two short bristly bundles; apical area with two reinforcing bands reaching median area of median lobe.

Parameres (Fig. 223.8): Thin and elongate, shorter than median lobe, apical area rounded with three setae at apex.

Spermathecal complex: Spermatheca (Fig. 224.3) with distal and apical lobes similar in length and width, well sclerotized; union duct short, hyaline and a little narrower than the lobes; spermatic duct short, very thin, with a small nodule at its junction with the distal lobe of the spermatheca.

Female uroventrite VIII (Fig. 224.7): Spiculum very short or absent, median area of posterior margin with macule and slight protrusion of the arc.

Discussion. As no molecular data are available on species of the genus *Pretneria*, their inclusion in the *Aphaobius* group is based solely on morphology: Jeannel (1924a), Perreau (2003) and Bognolo (2016).

Distribution. Italy. Friuli, Monte San Simeone, Monte Canin, Monte Musi. Slovenia. Mt. Triglav, Mt. Pršivec, Mt. Prisojnik, Mt. Krn, Mt. Kanin, Trnovsky godz, Predgriže and Soriška Planina.

Species

Pretneria collai Bognolo, 2016
Pretneria collai Bognolo, 2016: 101.

Pretneria latitarsis (G. Müller, 1931)
Aphaobius (Pretneria) latitarsis G. Müller, 1931a: 198.
Pretneria latitarsis (Müller, 1931): Pretner, 1955: 49.

Pretneria melissae Bognolo, 2016
Pretneria melissae Bognolo, 2016: 97.

Pretneria metkae Bognolo, 2000
Pretneria metkae metkae Bognolo, 2000
Pretneria metkae Bognolo, 2000: 34.
Pretneria metkae metkae Bognolo, 2000: Perreau, 2003: 220.
Pretneria metkae mirae Bognolo & Kofler, 2001
Pretneria metkae mirae Bognolo & Kofler, 2001: 114.

Pretneria saulii (G. Müller, 1941)
Pretneria saulii saulii (G. Müller, 1941)
Aphaobius (Pretneria) saulii G. Müller, 1941: 214.
Pretneria saulii (Müller, 1941): Pretner, 1949: 152.
Pretneria saulii saulii (Müller, 1941): Bognolo, 2016: 103.
Pretneria saulii montismusii Bognolo, 2016
Pretneria saulii montismusii Bognolo, 2016: 107.

Pretneria soriscensis Perreau, 2003
Pretneria latitarsis soriscensis Perreau, 2003: 219.
Pretneria soriscensis Perreau, 2003: Bognolo, 2016: 113.

Pretneria ternovensis Bognolo, 2016
Pretneria ternovensis Bognolo, 2016:198.

3.4.3.3 ***Oryotus*** group

Diagnosis. Medium-sized genera, 2.4-4.4 mm, with a pholeuonoid body. Depigmented.

Head: Retractile, with a complete occipital carina, sometimes obtusely smooth; anophthalmous. Sometimes with a modified mouth apparatus for filter feeding.

Antennae: Thin, long, shorter or longer than the length of the body, with the second antennomere slightly longer or shorter than the first.

Pronotum: Cordiform, with the disc regularly convex and the sides sinuous or not posteriorly.

Elytra: Ovoid or elliptical, more or less rounded at apex. Punctation not aligned in transversal striolae. Parasutural stria absent.

Legs: Male protarsi tetramerous, with the first two protarsomeres more or less dilated; sometimes with the first protarsomeres enormously dilated; sometimes with the fourth mesotarsomere distally bearing a robust ventral spine, present in both male and female. Protibiae without a comb on the outer surface. Meso- and metatibiae without complete apical basket.

Mesoventral keel (Figs 225.4-225.6): Low with a tooth more or less right or obtuse and acute or blunt, or absent, or detected only in the area between the coxal cavities. When present, not extended into the metaventrite.

Suture of the metaventrite (Figs 225.5, 225.6): Sinuous, delimiting a small arcuate surface in the apical half and passing very close to the coxal cavity in the basal half.

Metatergal apparatus (Figs 226.1, 226.2): Reduced, or long and narrow.

Metendosternite (Figs 226.3, 226.4): «V»-shaped. Furcal arms longer than the trunk, with a developed apophysis; furcal plate narrowed towards the apical area of the arm with an arched flange. Furcal trunk wide and slightly longer than the widest part.

Median lobe of aedeagus: Long, more or less robust. In lateral view (Figs 227.1-227.3) the apex pointing downwards or sometimes upwards. In dorsal view (Figs 227.4-227.7) with ogive-shaped apex, more or less subtriangular or three-lobed.

Endophallus (Figs 227.4-227.7): «Y»-piece present, more or less evident. Median part with sclerotized phanerae in varying numbers and shapes. Distal part occupied by a formation of dense spinules or long chitinised bands.

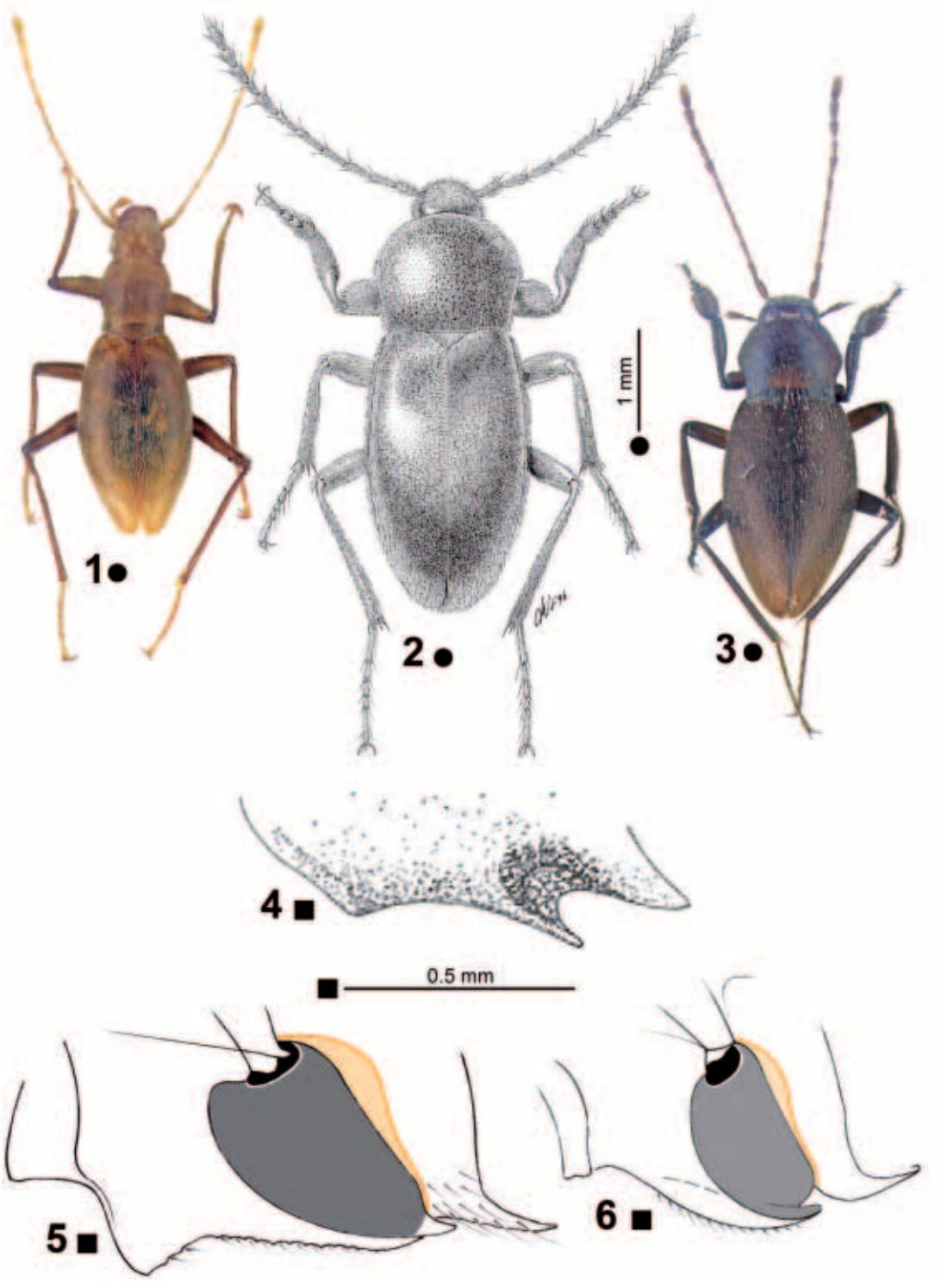
Parameres (Figs 228.1-228.3): Thin, shorter, or as long as the median lobe, with three apical setae.

Spermathecal complex (Figs 228.4-228.6): Spermatheca elongate and slightly curved in its distal and proximal parts, or less sclerotized, separated by an unsclerotized area. Ductus without dilatations.

Female uroventrite VIII (Figs 228.7, 228.8): Shows a ventral apophysis reduced to a small median tubercle.

Discussion. The *Oryotus* group appears, in the phylogenetic tree (Fig. 1D), as the sister group to the *Aphaobius* group, with the maximum possible support, 100/100. On the other hand, the entire clade of the *Oryotus* group shows very high support 99.4/100 and includes the genera *Oryotus*, *Cansiliella* and *Orostygia*.

Distribution. Italy. Provinces of Belluno, Treviso, Pordenone and Udine. Slovenia. Kamniske, Savinjske and Julijske Alps; Mt. Raduha.



FIGURES 225.1–225.6: *Oryotus* series, *Oryotus* group. Habitus of: (**1**) *Cansiliella servadeii*, (**2**) *Orostygia tibialis* (modified from Vailati 1998), (**3**) *Oryotus schmidti schmidti*. Pterothorax in lateral view of: (**4**) *C. tonielloi* (modified from Paoletti 1980), (**5**) *Orostygia marcelloi*, (**6**) *Oryotus ravasinii.*

KEY TO GENERA
(modified from Perreau 2003)

1. Mesoventral keel absent; mesocoxal cavities not closed. Mandibles ogival at apex in dorsal view ....*Cansiliella*
- Mesoventral keel complete, not extended on metaventrite; mesocoxal cavities closed. Mandibles thick and toothed at apex in dorsal view.....2

2. Sides of pronotum deeply sinuate towards middle, sides parallel or divergent at base. Elytral disc not convex, almost flat. Fourth mesotarsomere with a strongly sclerotized, inner apical spine, angular in the male, less thick and straight in the female. First protarsomere of the male at least twice as wide as the apex of the tibia. Apophysis of the alacrista no longer than a quarter of the length of the elytra (Fig. 226.2). Aedeagus flattened, ogival in lateral view along its entire length (Fig. 227.3). Spiculum of female uroventrite VIII reduced to a single tubercle (Fig. 228.8) .....*Oryotus*
- Sides of the pronotum not or only slightly sinuate towards the middle, converging towards the base in a straight line. Elytral disc convex. Fourth meso-tarsomere spineless in both sexes, with long apical setae similar to those of the other mesotarsomeres. Apophysis of the alacrista reaching almost half the length of the elytra (Fig. 226.1). Protarsi of the male at most as wide as the apex of the protibiae. Aedeagus subcylindrical, thick in lateral view and regularly tapering towards te apex (Fig. 227.2). Spiculum of he female uroventrite VIII in the form of a short spine (Fig. 228.7) .....*Orostygia*

Genus ***Cansiliella*** Paoletti, 1972
Cansiliella Paoletti, 1972: 119.

TYPE SPECIES. *Cansiliella tonielloi* Paoletti, 1972 by original designation (for habitus, see that of the similar species *Cansiliella servadeii* in Fig. 225.1).

DIAGNOSIS. Medium sized, 2.5-3.6 mm, with a pholeuonoid body (Fig. 225.1).

Head: Retractile with the occipital carina obtusely smooth. Mouth apparatus modified to filter food.

Antennae: Thin, very long, longer than the length of the body, with the second antennomere slightly shorter than the first.

Pronotum: Cordiform, the disc regularly convex.

Elytra: Elliptical, slightly convex, rounded at the apex. Punctation not aligned in transversal striolae. Parasutural stria absent.

Legs: Male protarsi tetramerous, with the first two protarsomeres slightly dilated. Fourth mesotarsomere without ventral spine. Protibiae without comb on outer surface. Meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 225.4): Absent. Partially confluent mesocoxal cavities.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Paoletti 1972): Reduced, with a slightly hinted apophysis of the alacrista, about ¾ the length of the scutellum.

Metendosternite: Unknown.

Median lobe of aedeagus: Long and thin. In lateral view (Fig. 227.1), regularly curved and slightly bisinuate apically. In dorsal view (Figs 227.4, 227.5), sides long and subparallel, the apex more or less subtriangular.

Endophallus (Figs 227.4, 227.5): Presence of a «Y»-piece. Basal region with two pairs of curved sclerites followed by another pair covering two rhomboid structures. Distal part occupied by a formation of dense spinules surmounted by two large banded sclerites.

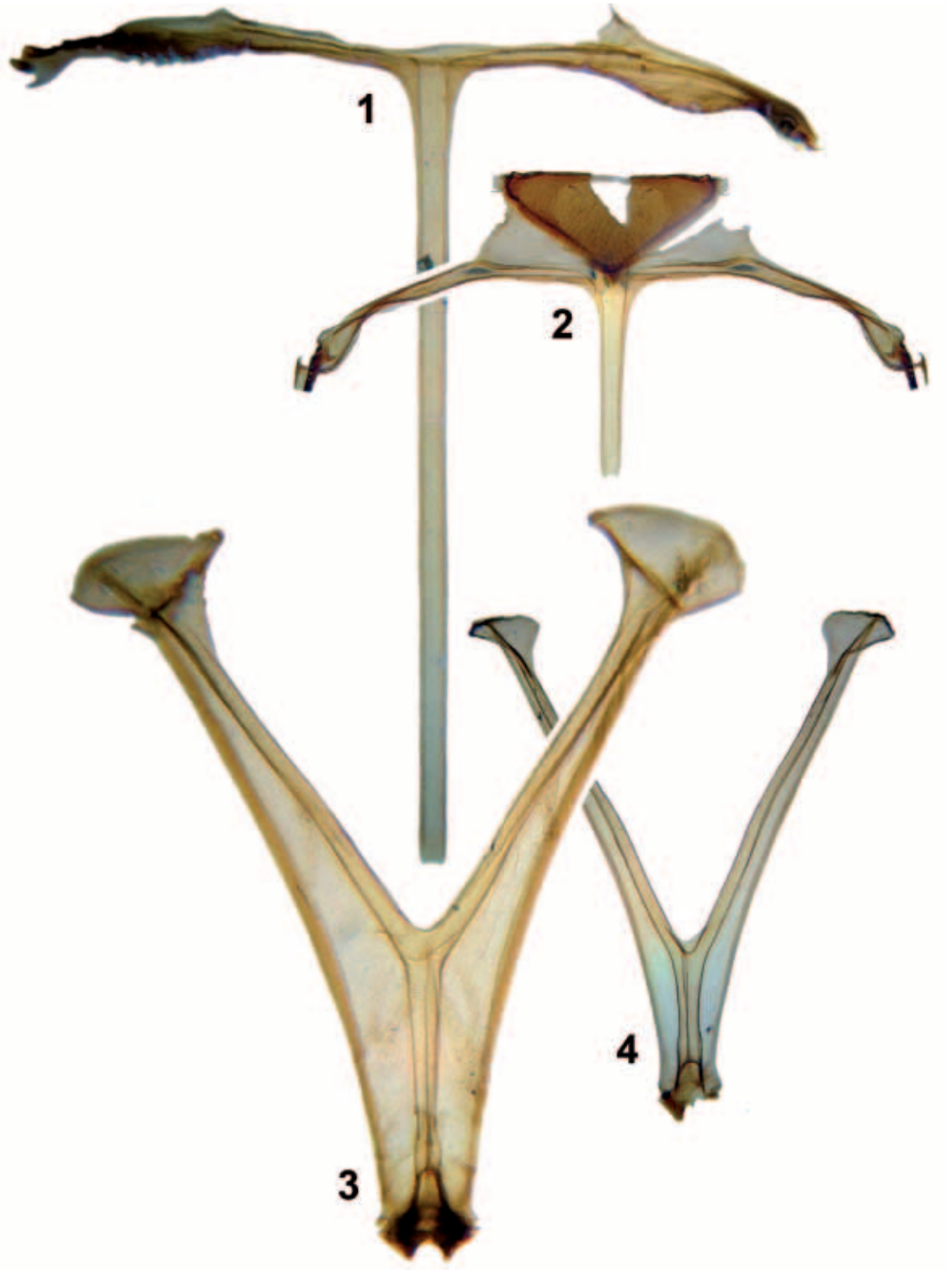
Parameres (Fig. 228.1): Moderately slender and only slightly shorter than the median lobe of the aedeagus, with three setae.

Spermathecal complex: Spermatheca (Fig. 228.4) with the proximal and distal parts well sclerotized, of equal thickness, the proximal lobe being a little longer; hyaline junction duct a little narrower than the lobes and as long as the proximal lobe; spermatic gland present.

Female uroventrite VIII: Unknown.

DISCUSSION. As indicated in the discussion of the genus *Oryotus*, the clade separating *Oryotus* from *Cansiliella* appears with very high support, 99.9/100 (Fig. 1D). For the most part, the molecular data confirm the hypotheses put forward, on a strictly morphological basis, by Paoletti (1972, 1980) and Piva (2000) that *Cansiliella* belongs to a phyletic lineage that also includes the genera *Oryotus* and *Orostygia*. The inclusion in the same lineage of the genus *Aphaobius*, which appears in the phylogenetic tree (Fig. 1D) as a sister clade to the *Oryotus* group, seems less correct.

DISTRIBUTION. Italy. Provinces of Belluno, Treviso and Pordenone.



FIGURES 226.1–226.4: *Oryotus* series, *Oryotus* group. Metatergal apparatus of: (**1**) *Orostygia marcelloi*, (**2**) *Oryotus ravasinii*. Metendosternite of: (**3**) *O. marcelloi*, (**4**) *O. ravasinii*.

Species

Cansiliella montisceseni Piva, 2000
Cansiliella montiscesini Piva, 2000: 127.

Cansiliella servadeii Paoletti, 1980
Cansiliella servadeii Paoletti, 1980: 68.

Cansiliella tonielloi Paoletti, 1972
Cansiliella tonielloi Paoletti, 1972: 120.

Genus ***Orostygia*** G. Müller, 1912
Orostygia G. Müller, 1912: 301.

Type species. *Orostygia moczarskii* G. Müller, 1912 by monotypy (for the habitus, see that of the similar species *Orostygia tibialis* in Fig. 225.2).

Diagnosis. Medium sized, 3.3-4.4 mm, with a pholeuonoid body (Fig. 225.2).

Head: Retractile, with complete occipital carina, sometimes obtusely smooth.

Antennae: Thin, long, but always shorter than the length of the body, with the second antennomere slightly longer or shorter than the first.

Pronotum: Cordiform, but with the sides not sinuate posteriorly and the disc regularly convex.

Elytra: Ovoid or elliptical, more or less rounded at the apex. Punctation not aligned in transversal striolae. Parasutural stria absent. Elytra welded along the entire elytral suture.

Legs: Male protarsi tetramerous, with first two protarsomeres more or less dilated. Fourth mesotarsomere without ventral spine. Protibiae without comb on outer surface. Meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 225.5): Low with the angle more or less straight or obtuse and a tooth acute or blunt. Not prolonged on the metaventrite.

Suture of the metaventrite: (Fig. 225.5): Delimiting an arcuate area, wider in the apical half and very narrow in the basal half.

Metatergal apparatus (Fig. 226.1): Wings of metascutum long and narrow, with the alacrista apophysis very long, longer than the length of the arms.

Metendosternite (Fig. 226.3): Robust, «V»-shaped. Furcal arms longer than the trunk, with a developed apophysis; furcal plate narrowing towards the apical area of the arm with an arched flange. Furcal trunk wide and slightly longer than the widest part; the median furcal keel subsequently bifurcating.

Median lobe of aedeagus: Long, robust. In lateral view (Fig. 227.2) moderately curved in the basal half, almost straight in the distal half with the apex pointing downwards or sometimes upwards. In dorsal view (Fig. 227.6), regularly attenuated from the base almost to the apex, narrowing until ending in a more or less three-lobed rounded tip.

Endophallus (Fig. 227.6): Well-developed «Y»-piece with parallel branches, followed by a pair of loosely cupped phanerae. Median area with a pair of curved phanerae. Apical area with two long chitinised bands.

Parameres (Fig. 228.2): Slightly shorter than the median lobe, distally ogival and curved inwards, with three setae.

Spermathecal complex (Fig. 228.5): Spermatheca elongate, with proximal and distal lobes strongly sclerotized. Spermatic duct without dilatations, very long and thin. Spermatic gland present.

Female uroventrite VIII (Fig. 228.7): Posterior margin in a wide, regular arc; median part of the anterior margin with a short, narrow spiculum.

Discussion. As indicated in the Discussion of the genus *Oryotus*, the clade separating *Oryotus* + *Cansiliella* from *Orostygia* appears with very high support, 99.4/100 (Fig. 1D). For the most part, the molecular data confirm the hypotheses put forward, on a strictly morphological basis, by Jeannel (1924a) and Piva (2005) that *Orostygia* belongs to a phyletic lineage that also includes the genera *Oryotus* and *Cansiliella*. The inclusion in the same lineage of the genus *Aphaobius* (and related genera *Pretneria*, *Lotharia* and *Aphaobiella*), which appears in the phylogenetic tree (Fig. 1D) as sister group to the *Oryotus* group with support of 100/100, seems less correct from a morphological point of view.

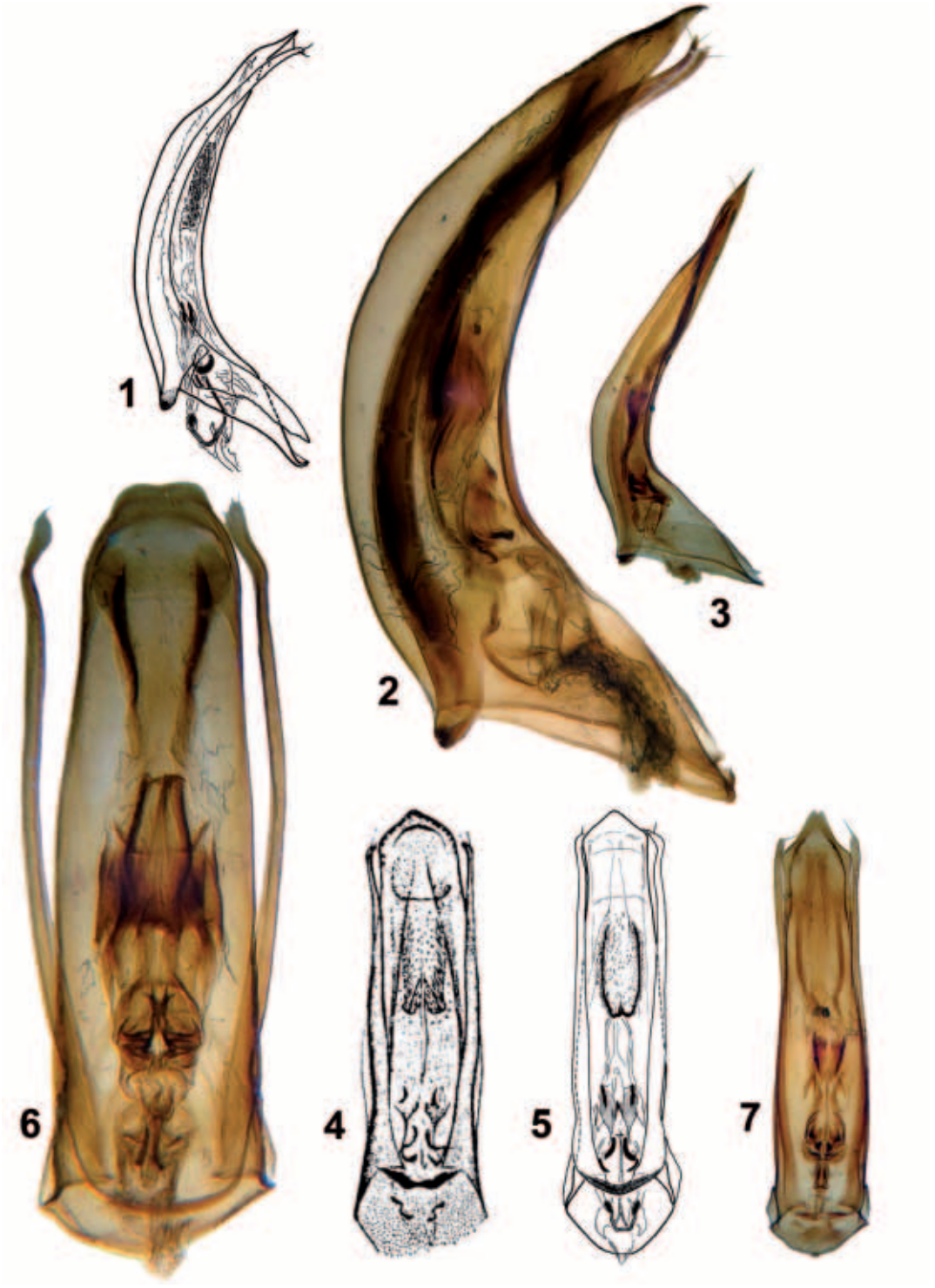
Distribution. Italy. Veneto, provinces of Belluno and Treviso; Friuli, provinces of Pordenone and Udine.

Species

Orostygia bassanii Daffner, 1988
Orostygia bassanii Daffner, 1988a: 20.

Orostygia bognoloi Piva, 2005
Orostygia bognoloi Piva, 2005: 13.

Orostygia doderoi G. Müller, 1919
Orostygia doderoi doderoi G. Müller, 1919
Orostygia Doderoi G. Müller, 1919b: 40.



FIGURES 227.1–227.7: *Oryotus* series, *Oryotus* group. Aedeagus in lateral view of: (**1**) *Cansiliella montisceseni*, (**2**) *Orostygia marcelloi*, (**3**) *Oryotus ravasinii*. Aedeagus in dorsal view of: (**4**) *C. tonielloi* (modified from Paoletti 1972), (**5**) *C. montisceseni*, (**6**) *O. marcelloi*, (**7**) *O. ravasinii*. Figs **1**, **5** modified from Piva (2000).

Orostygia doderoi doderoi G. Müller: Perreau, 2000: 177.
Orostygia doderoi bucciarellii Tamanini, 1955
Orostygia Doderoi Bucciarellii Tamanini, 1955a: 53.
Orostygia doderoi bucciarellii Tamanini: Perreau, 2000: 177.

Orostygia marcelloi Agazzi, 1957
Orostygia marcelloi Agazzi, 1957: 114.

Orostygia meggiolaroi Agazzi, 1968
Orostygia meggiolaroi Agazzi, 1968: 7.

Orostygia moczarskii G. Müller, 1912
Orostygia Moczarskii G. Müller, 1912: 302.
Orostygia moczarskii moczarskii Müller: Perreau, 2000: 177.

Orostygia mondini Piva, 2005
Orostygia mondini Piva, 2005: 10.

Orostygia pampaninii Paoletti, 1968
Orostygia pampaninii Paoletti, 1968: 156.

Orostygia pretneri G. Müller, 1931
Orostygia Pretneri G. Müller, 1931a: 204.

Orostygia rossii Porro & Quaia, 1969
Orostygia rossii Porro & Quaia, 1969: 23.
Orostygia bonomettoi M. Etonti, 1993: 45.
Orostygia amicorum M. Etonti & Bognolo, 1997: 5.

Orostygia tibialis Paoletti, 1979
Orostygia moczarskii tibialis Paoletti, 1979: 26.

Genus ***Oryotus*** L. Miller, 1856
Oryotus L. Miller, 1856a: 627.
Neotropospeonella Pace, 1983: 542 (Type species: *Neotropospeonella decui* Pace, 1983).

Type species. *Oryotus schmidtii* L. Miller, 1856 by monotypy (habitus in Fig. 225.3).

Diagnosis. Medium sized, 2.4-3.6 mm, with a pholeuonoid body (Fig. 225.3).

Head: Retractile, with a complete occipital carina, sometimes obtusely smooth.

Antennae: Thin, long, but always shorter than the length of the body, with the second antennomere slightly longer than the first.

Pronotum: Cordiform, with a regularly convex disc; posterior margins moderately or distinctly sinuate in the basal half.

Elytra: Ovoid or elliptical, more or less rounded at the apex. Punctation not aligned in transversal striolae. Parasutural stria absent.

Legs: Male protarsi tetramerous, with the first protarsomeres enormously dilated. Fourth mesotarsomere bearing a robust ventral spine distally, present in both males and females. Protibiae without a comb on the outer surface. Meso- and metatibiae without complete apical basket.

Mesoventral keel (Fig. 225.6): Low, not angulate, detected only in the area between the coxal cavities; ventral margin arched with a series of erect setae. No extension on metaventrite.

Suture of the metaventrite (Fig. 225.6): Delimiting a small arcuate area, very narrow in basal half because close to coxal cavity.

Metatergal apparatus (Fig. 226.2): Wings of the metascutum long and narrow, one wing of the metascutum being slightly longer than the apophysis of the alacrista which is long, the apices not sharp.

Metendosternite (Fig. 226.4): «V»-shaped, the furcal arms long and the trunk short; the arms narrow, about two and a half times as long as the trunk with a well-defined apophysis or terminal process; posterior furcal plate remaining narrow along the arm to the apex; trunk almost twice as long as the width of the basal area.

Median lobe of aedeagus: Long. In lateral view (Fig. 227.3), moderately curved in basal half and almost straight in distal half. In dorsal view (Fig. 227.7), sides parallel to almost the apex which is ogival, broadly rounded to slightly three-lobed and not or only slightly pointed.

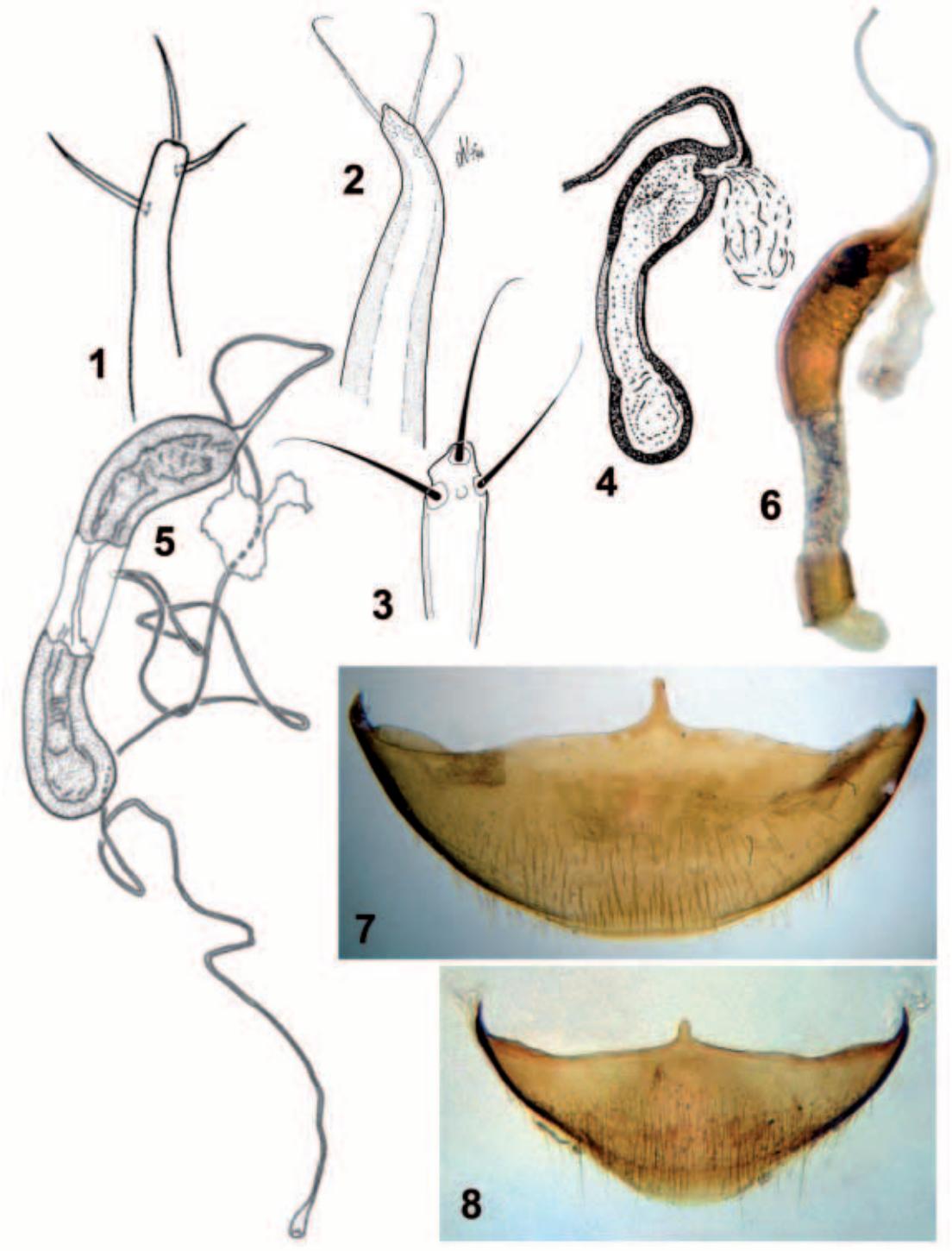
Endophallus (Fig. 227.7): Basal «Y»-piece present, small, immediately followed by two sclerotized phanerae on their distal-internal side. Median area with the two sclerotized phanerae in the form of rods or blades. Apical area with one or two pairs of reinforcing bands.

Parameres (Fig. 228.3): Very thin, shorter or as long as the median lobe, with three apical setae and a more or less developed membranous lobe

Spermathecal complex: Spermatheca (Fig. 228.6) elongated and slightly curved; distal and proximal lobes moderately sclerotized, separated by a long junction duct with an extensive non-sclerotized area. Ductus without dilatations. Spermathecal gland present.

Female uroventrite VIII (Fig. 228.8): Spiculum reduced to a small median tubercle.

Discussion.The *Oryotus* group appears in the phylogenetic tree (Fig. 1D) as the sister group to the



FIGURES 228.1–228.8: *Oryotus* series, *Oryotus* group. Apex of paramere of: (**1**) *Cansiliella montisceseni* (modified from Piva 2000), (**2**) *Orostygia tibialis* (modified from Vailati 1998), (**3**) *Oryotus ravasinii*. Spermathecal complex of: (**4**) *C. tonielloi* (modified from Paoletti 1972), (**5**) *Orostygia bognoloi* (modified from Piva 2005), (**6**) *O. ravasinii.* Female uroventrite VIII of: (**7**) *Orostygia marcelloi*, (**8**) *O. ravasinii.*

Aphaobius group, with the maximum possible support, 100/100. Internally, the clades separating *Oryotus* from *Cansiliella* with support of 99.9/100, and this group from *Orostygia* also appear well supported with 99.4/100. The values of support, 61.5/98 and 65.7/98, appear rather among the various species of the genus *Oryotus*. *Oryotus* has always been rightly considered to be monophyletic on a morphological basis (Perreau 2003). These values could be due to the small number of species analysed (3) compared with those actually known (10) as well as the considerable geographical distance between the species tested.

DISTRIBUTION. Italy. Provinces of Belluno, Pordenone and Udine. Slovenia. Kamniske, Savinjske and Julijske Alps; Mt. Raduha.

Species

Oryotus ausmeieri Perreau, 2003
Oryotus ausmeieri Perreau, 2003: 213.

Oryotus dreoni Piva & Zoia, 1989
Oryotus dreoni Piva & Zoia, 1989: 37.

Oryotus gasparoi Piva, 2005
Oryotus gasparoi Piva, 2005: 21.

Oryotus indentatus Pretner, 1955
Oryotus micklitzi indentatus Pretner, 1955: 45.
Oryotus indentatus Pretner, 1955: Piva, 2005: 17.

Oryotus micklitzi Reitter, 1884
Oriotus Micklitzi Reitter, 1885a [1884]: 14.
Oryotus carniolicus Meschnigg, 1946: 29.
Oriotus micklitzi micklitzi Reitter: Pretner, 1955: 44.
Pretneria droveniki M. Etonti, 2001: 22: Perreau, 2003: 214.
Oriotus micklitzi Reitter, 1884: Piva, 2005: 15.

Oryotus raduhensis Drovenik, Mlejnek & Moravec, 1995
Oryotus raduhensis Drovenik, Mlejnek & Moravec, 1995: 1.

Oryotus ravasinii G. Müller, 1922
Oryotus Ravasinii G. Müller, 1922b: 15.
Neotropospeonella decui Pace, 1983: 542: Perreau, 2003: 212.
Oryotus sebenelloi Daffner, 1988b: 11.
Oryotus ravasinii Müller: Pretner, 1955: 46.

Oryotus schmidti L. Miller, 1856
Oryotus schmidti schmidti L. Miller, 1856
Oryotus Schmidtii L. Miller, 1856a: 627.
Oryotus Schmidtii subsp. *Schmidtii* Miller: Jeannel, 1924a: 235.
Oryotus schmidtii schmidtii Miller: Pretner, 1955: 43.
Oryotus schmidti subdentatus G. Müller, 1904
Oryotus Schmidti subdentatus G. Müller, 1904a: 3.
Oryotus schmidti subdentatus Müller: Pretner, 1955: 44.

Oryotus tragoniae G. Müller, 1934
Oryotus tragoniae G. Müller, 1934: 180.

Oryotus trezzii Piva, 2005
Oryotus trezzii Piva, 2005: 19.

3.4.4 Series ***Hittitia***

DIAGNOSIS. Small to medium-sized genera, 1.2-3.5 mm, with bathyscioid and pholeuonoid facies, short, slightly convex and pubescent body.

Head: Retractable, with a complete occipital carina, full or blurred; eyes very small but present.

Antennae: Short, barely reaching or exceeding, stretched backwards, the base of the pronotum, with the first two antennomeres of almost equal length.

Pronotum: Wide, very transverse, with evenly and long-arched sides, not sinuate posteriorly, with maximum width at the base which is as wide as or narrower than the base of the elytra.

Elytra: Relatively stout, ovate, with or without transversely aligned striolae; parasutural stria blurred or absent.

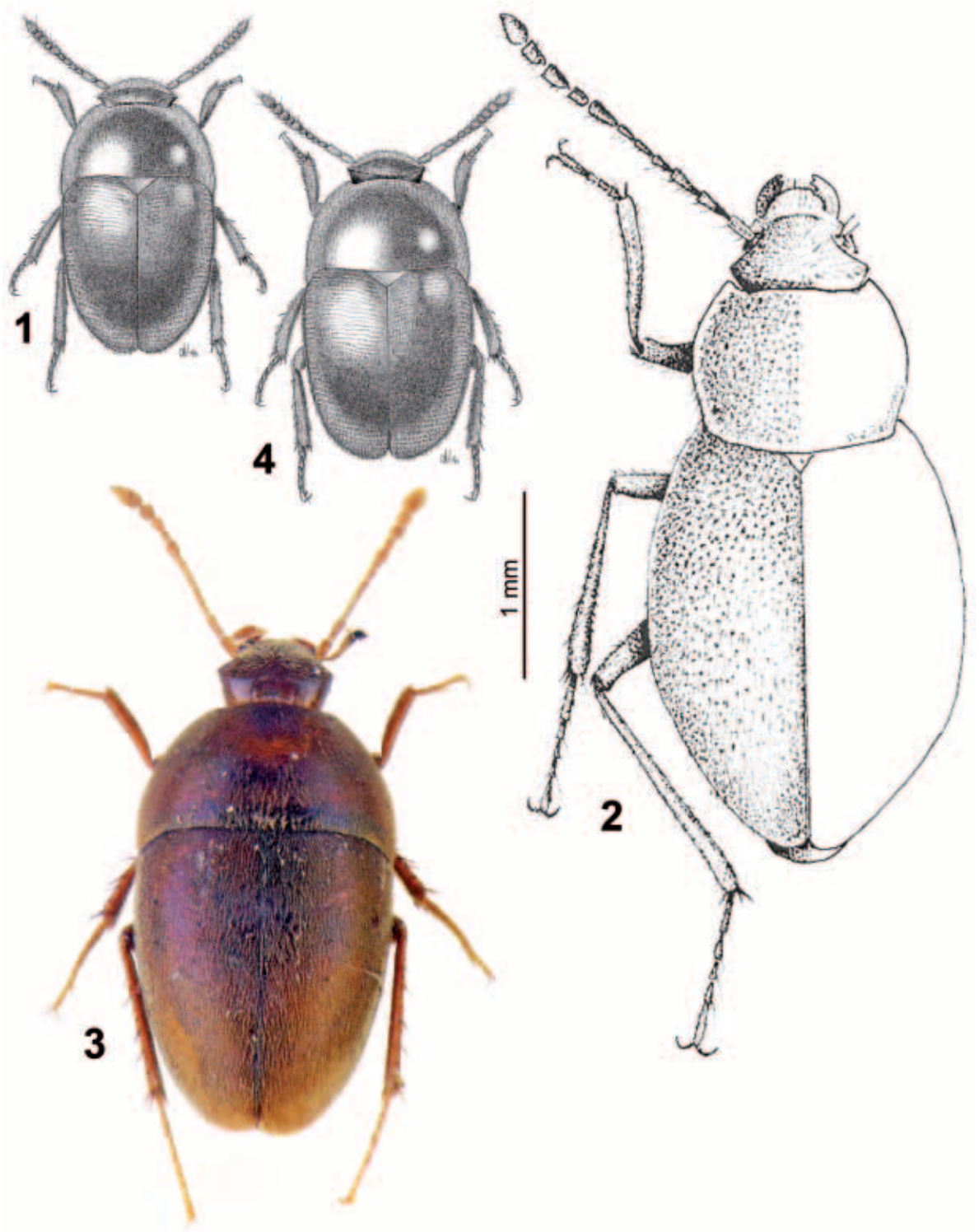
Legs: Short and strong. Male protarsi tetramerous and not dilated; protibiae slightly enlarged, with two stout spurs and no comb at apex; mesotibiae weakly arched and with spines on outer margin; metatibiae straight; meso- and metatibiae without apical basket. Metafemora sometimes toothed in male.

Mesoventral keel (Figs 230.1-230.4): High or low, broadly rounded anteriorly and not toothed, with a setose ventral margin extended or not on the metaventrite.

Suture of the metaventrite (Figs 230.3, 230.5): Sinuous, delimiting an arcuate surface in the apical half and passing very close to the coxal cavity in the basal half.

Metatergal apparatus (Figs 231.1, 231.2): Reduced, apophysis of the alacrista short. Longitudinal groove 4 to 6 times longer than wide.

Metendosternite (Figs 231.3, 231.4): «V»-shaped



FIGURES 229.1–229.4: *Hittitia* series. Habitus of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Huetheriella maximiliani* (modified from Casale & Giachino 1990), (**3**) *Pisidiella spatulifera*, (**4**) *Uludagites minuta* **comb. nov.** Figs **1, 4** modified from Casale *et al.* (1991).

in *Hittitia* and *Uludagites*, unknown in *Pisidiella* and *Huetheriella*.

Median lobe of aedeagus: Slightly curved in lateral view (Figs 232.1-232.3). In dorsal view (Figs 233.1-233.4) apex broadly rounded and not truncated, sometimes with two conspicuous lateral dilatations. Basal blade of the median lobe poorly developed.

Endophallus (Figs 233.1-233.4): «Y»-piece large, sometimes extending beyond the basal blade of the median lobe; a complex median phanera from which a flagellum extends.

Parameres (Figs 233.5-233.8): Long and slender, reaching or not reaching the apex of the median lobe, bearing three subequal setae, two apical and one subapical, internal.

Spermathecal complex (Figs 234.1-234.3): Spermatheca kidney-shaped, with a more developed proximal lobe. Ductus long, more or less dilated and sclerotized at insertion into the spermatheca, sometimes with a voluminous spherical dilatation before insertion; attached to the copulatory sac by a more or less developed or basal piece, sometimes missing. Spermathecal gland hyaline, shapeless.

Female uroventrite VIII (Figs 234.4-234.6): With well-developed, sometimes stocky and broadly triangular spiculum..

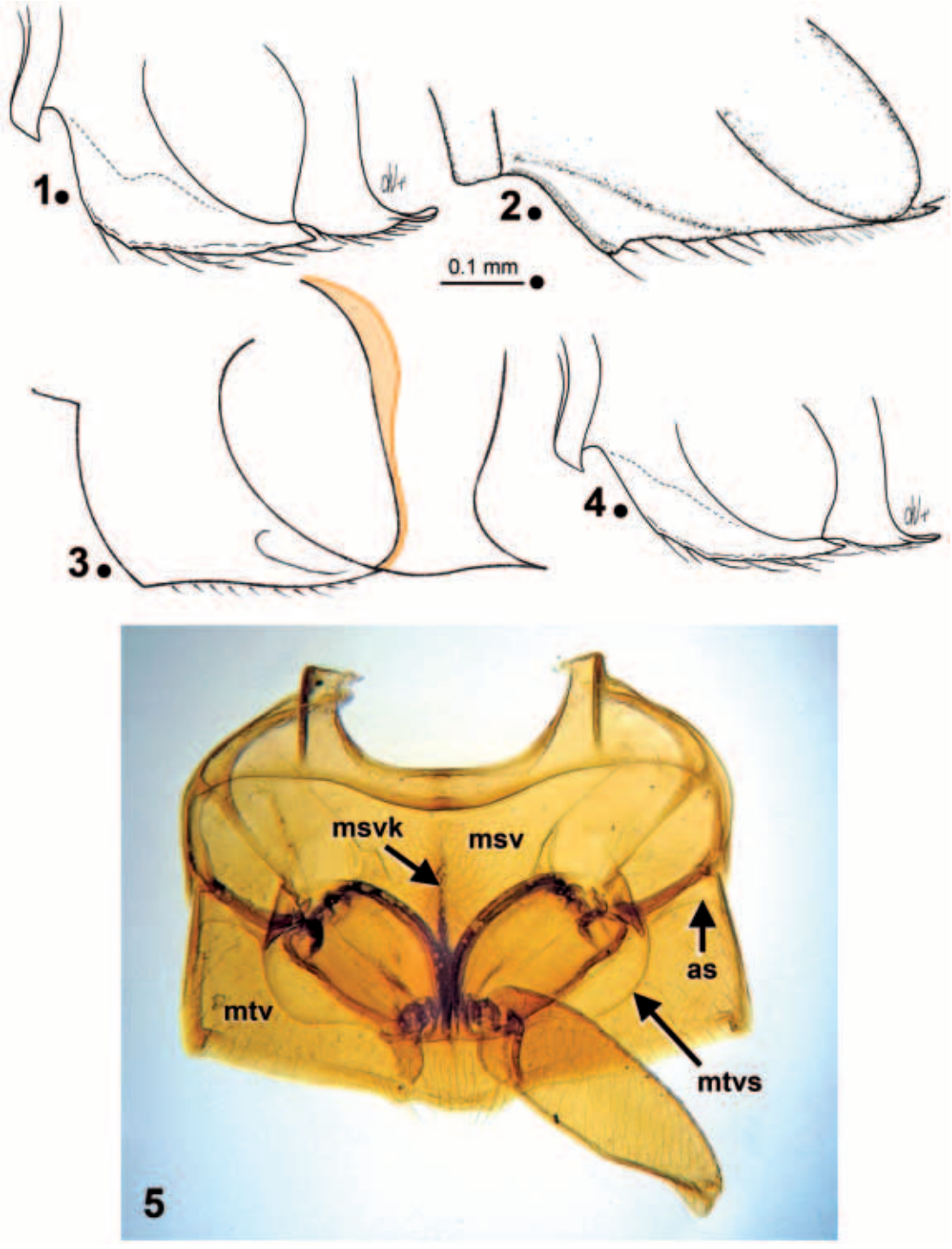
Discussion. As mentioned in the *Epiroella* series, the history and composition of this phyletic series is somewhat complicated. Originally considered, on a morphological basis, to consist solely of the genus *Phaneropella*, divided into four distinct subgenera: *Phaneropella*, *Epiroella*, *Hittitia* and *Uludagites*, a view that should instead be reconsidered, on both a morphological and molecular basis (Casale *et al*. 2013). In fact, these authors (Casale *et al*. 2013) discussed the need to upgrade all subgenera to genera, all grouped together in what appeared to be a coherent phyletic lineage, with an Anatolian-Balkan distribution, at the time of the description (Casale *et al*. 1991b). Casale *et al*. (2013) have limited themselves to elevating the taxon *Epiroella* to genus status, for which they described a new species, deferring the elevation to genus status of *Hittitia* and *Uludagites* to a later occasion. We now have molecular data on five generic taxa relevant to the phyletic lineage of *Phaneropella* (*sensu auctorum*): *Epiroella* (with the species *acharnanis*), *Hittitia* (with the species *schuelkei* and *kociani*), *Uludagites* (with the species *minuta*) and *Phaneropella* (with the species *lesinae*). The genera *Pisidiella* and *Huetheriella*, both belonging to the *Pisidiella* series (Perreau 2000), have been included in the *Hittitia* series because of certain morphological (including genitalia) affinities; however, to be sure of its position, it would be necessary to await the availability of molecular data. A *Hittitia* series, consisting of *Hittitia* and *Uludagites*, is evidenced by the molecular analysis (Fig. 1D) and well supported statistically (98.9/100) and by a distribution in the north-east and north-west of the Anatolian peninsula. This series represents the most basal cladogenesis of the *Catopsinus* and *Drimeotus* series, with weak support (36.6/39).

Key to genera

1. Pholeuonoid facies (Fig. 229.2). Medium size, between 3.0-3.5 mm. Pronotum distinctly narrower than elytra; base of pronotum distinctly narrower than base of elytra. Mesoventral keel low (Fig. 230.2). Female spermiduct with a large basal sclerite (Fig. 234.2) .....*Huetheriella*
- Bathyscioid facies (Figs 229.1, 229.3, 229.4). Size small between 1.2-1.8 mm. Pronotum as wide as or slightly narrower than elytra; base of pronotum as wide as or slightly narrower than base of elytra. Mesoventral keel high (Figs 230.1, 230.3, 230.4). Female spermiduct without or with a small basal sclerite (Figs 234.1, 234.3) 2

2. Without eyes. Elytra without transverse striolation. Mesoventral keel without posterior extension on metaventrite (Fig. 230.3). Parameres slightly longer than median lobe, with enlarged apical area forming a large elongate spoon (Fig. 233.7).....*Pisidiella*
- With eyes, although reduced to a few ommatidia. Elytra with transverse striolation. Mesoventral keel with posterior extension on the metaventrite (Figs 230.1, 230.4). Parameres not reaching apex of median lobe, not or only slightly dilated at apex (Figs 233.5, 233.8) 3

3. Male metafemora untoothed. Sides of the apical area of the median lobe of the aedeagus gradually narrow slightly (Fig. 233.1). Flagellum of endophallus short (Fig. 233.1). Parameres not dilated at apex (Fig. 233.5). Female uroventrite VIII with fine, straight well-developed spiculum (Fig. 234.4) .....*Hittitia*
- Male metafemora toothed. Sides of the apical area of the median lobe of the aedeagus very narrow (Fig. 233.4). Flagellum of endophallus long and robust (Fig. 233.4). Parameres slightly dilated at apex (Fig. 233.8). Female uroventrite VIII with stocky, broadly triangular ventral spiculum (Fig. 234.6) ...*Uludagites*



FIGURES 230.1–230.5: *Hittitia* series. Pterothorax in lateral view of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Huetheriella maximiliani* (modified from Casale & Giachino 1990), (**3**) *Pisidiella spatulifera*, (**4**) *Uludagites minuta* **comb. nov.**. Pterothorax in ventral view of: (**5**) *Hittitia schuelkei* **comb. nov.** Figs **1**, **4** modified from Casale *et al.* (1991). Abbreviations: **as**, anapleural suture; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture.

Genus ***Hittitia*** Casale, Giachino, Vailati & Rampini, 1991 stat. nov.
Phaneropella (*Hittitia*) Casale, Giachino, Vailati & Rampini, 1991: 207.

Type species. *Bathyscia* (*Bathyscia*) *turcica* Reitter, 1885 by original designation (habitus in Fig. 229.1).

Diagnosis. Small size, 1.2-1.5 mm, bathyscioid shape (Fig. 229.1), body short, slightly convex and pubescent.

Head: Retractable, with a complete occipital carina; eyes very small but present, formed by a small number of ommatidia.

Antennae: Short, just above the base of the pronotum when stretched backwards, with the first antennomere only slightly shorter than the second.

Pronotum: Broad, very transverse, with evenly and long-arched sides, not sinuate posteriorly, with maximum width at the base, which is as wide as the base of the elytra.

Elytra: Relatively stout, ovate, only slightly convex, almost flat in the central part of the disc; regularly attenuated in the posterior half, weakly dehiscent at the apex; with transversely aligned striolae; parasutural stria absent.

Legs: Short and strong. Male protarsi tetramerous and not dilated; protibiae slightly enlarged, with two stout spurs and no comb at apex; mesotibiae weakly arched and with spines on outer margin; metatibiae straight; meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 230.1): High, broadly and irregularly rounded anteriorly, with slightly convex, setose ventral margin; extended over part of metaventrite,

Suture of metaventrite (Fig. 230.5): In a regular arc, delimiting a well-developed area.

Metatergal apparatus (Fig. 231.1): Reduced, apophysis of the alacrista short, with concave sides and rounded apex. Longitudinal furrow 5 to 6 times longer than wide. Wings of metascutum subtriangular, a little more than twice as long as wide.

Metendosternite (Fig. 231.3): Furcal arms and trunk short, arms longest, with a well-developed membranous fin-like terminal apophysis; posterior lamina apically tapering and with straight lateral margin. Trunk a little wider than long, half of the keel with a long but not very wide posterior divergence.

Median lobe of aedeagus: Slightly curved in lateral view (Fig. 232.1). In dorsal view (Fig. 233.1) with broadly rounded, not truncate apex. Basal blade poorly developed.

Endophallus (Fig. 233.1): Large «Y»-piece with very developed lateral branches. Apical half of median lobe entirely occupied lengthwise by a voluminous flagellate phanera and two slightly sclerotized distal lateral rods.

Parameres (Fig. 233.5): Long and slender, not reaching the apex of the median lobe, with three subequal setae, two apical and one subapical, internal.

Spermathecal complex: Spermatheca (Fig. 234.1) peculiarly shaped, three-lobed, with voluminous spherical dilatation of ductus at insertion into spermatheca to form additional lobe; ductus dilated and sclerotized before insertion into additional lobe; a hyaline, shapeless gland attached.

Female uroventrite VIII (Fig. 234.4): Spiculum well developed; posterior margin tapered in apical area.

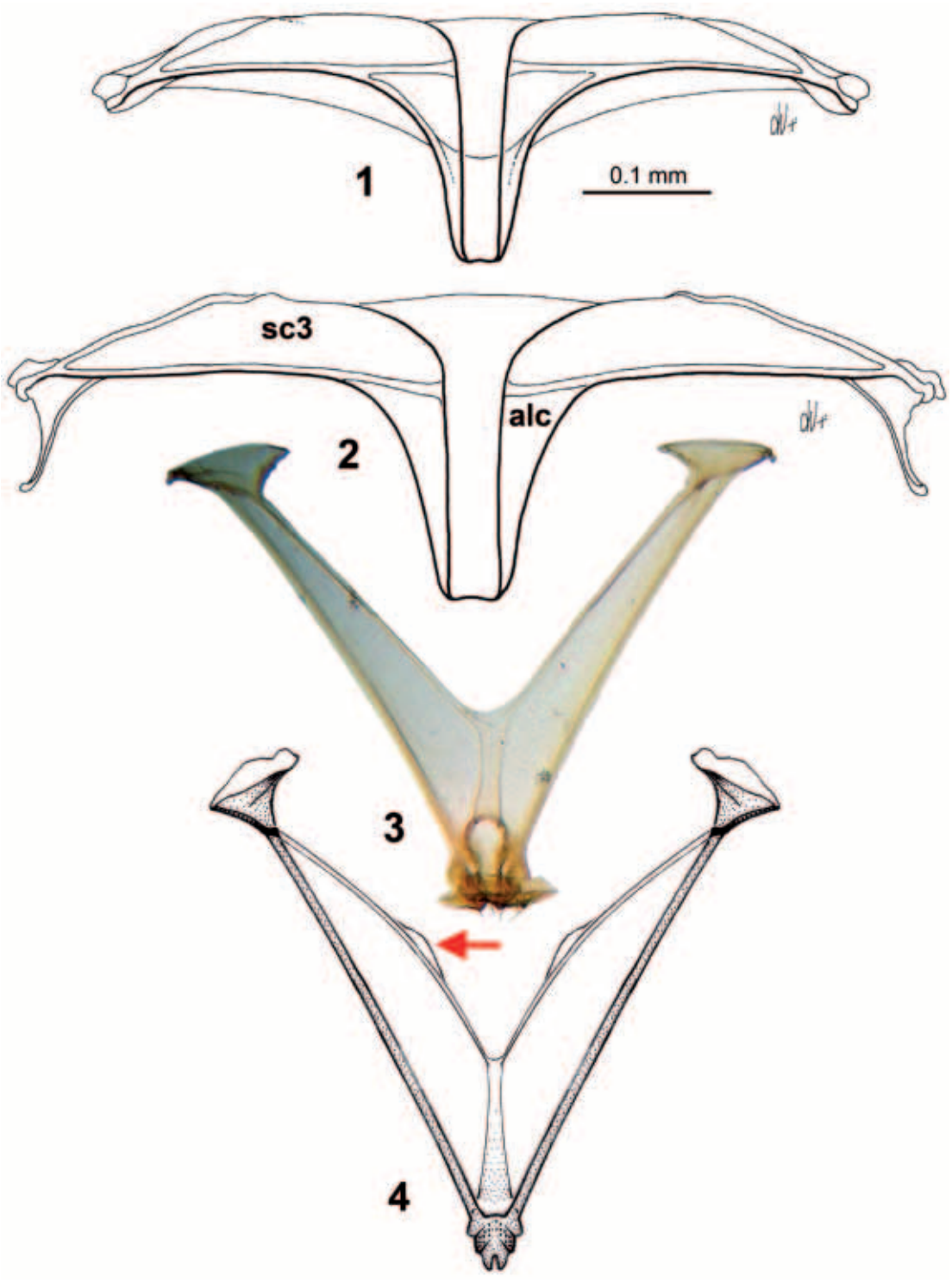
Discussion. *Hittitia* differs from *Uludagites* not only by the different shape of the apex of the median lobe, but also by the minor development of the median flagellum of the endophallus and by the peculiar shape of the distal part, close to the spermatheca, of the ductus which is sclerotized and hypertrophied. In the phylogenetic tree (Fig. 1D), the genera *Hittitia* and *Uludagites* are sisters, united by a very good support of 98.9/100. This phyletic series, with its North Anatolian distribution, also appears congruent from a zoogeographic point of view.

Distribution. NE Turkey.

Species

Hittitia schuelkei **(**Perreau, 2010) comb. nov.
Phaneropella (*Hittitia*) *schuelkei* Perreau, 2010: 47.

Hittitia turcica (Reitter, 1885) comb. nov.
Bathyscia (*Bathyscia*) *turcica* Reitter, 1885a [1884]: 20.
Bathyscia Uhagoni Subsp. *turcica* Reitter: Jeannel, 1907b: 422.
Phaneropella turcica Reitter: Jeannel, 1910a: 37.
Bathyscia (*Phaneropella) turcica* Reitter: Jeannel, 1914b: 17.
Phaneropella (*Hittitia) turcica* Reitter: Casale, Giachino, Vailati & Rampini, 1991: 209.



FIGURES 231.1–231.4: *Hittitia* series. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Uludagites minuta* **comb. nov.** Metendosternite of: (**3**) *H. schuelkei* **comb. nov.**, (**4**) *U. minuta* **comb. nov.** Figs **1**, **2** modified from Casale *et al.* (1991). Abbreviations: **alc**, alacrista; **sc3**, metascutum.

Genus ***Huetheriella*** Jeannel, 1934
Hütheriella Jeannel, 1934c: 21.
Huetheriella Jeannel, 1934: Casale & Giachino, 1990: 132.

Type species. *Hütheriella maximiliani* Jeannel, 1934 by subsequent designation (habitus in Fig. 229.2).

Diagnosis. Medium size, 3.1-3.5 mm, pholeuonoid facies with an ovoid-oblong, convex body (Fig. 229.2). Colour dark reddish or dark brown. Dense pubescence of more or less long and more or less raised hairs on the pronotum and elytra. Punctation strong and spaced on head and pronotum; dots largest, thickest, most rounded and deepest on elytra, especially in *H. notenboomi* (Perreau 2021: Figs. 17-19).

Head: Elongate, non retractable, occipital carina blurred; slightly narrower than anterior margin of pronotum; anophthalmous.

Antennae: Relatively long when reaching or slightly exceeding half the elytra. First antennomere as long or slightly shorter and more robust than the second; antennomeres of the club enlarged in the apical area, the 8th, 9th and 10th being slightly longer than wide and the 11th elliptical, pointed at the apex and slightly longer than the 10th.

Pronotum: Convex and slightly transverse, 1.2-1.3 times wider than long, with maximum width in the middle or slightly forward. Base as wide as or slightly wider than anterior margin, but narrower than base of elytra. Lateral margins arched in the median part, narrow towards the anterior margin; already curved or straight and towards the base weakly concave and sinuous or straight. Basal angles obtuse and vertices slightly acute.

Elytra: Very convex, ovate, 1.3 times as long as wide; distinctly wider than pronotum, with maximum width in middle or slightly forward. Apexes rounded and covering the pygidium. Shoulders more or less protruding. Punctation with dots arranged approximately in transverse rows in the basal half, but not in *H. pinargozu*. Parasutural stria absent.

Legs: Fairly long and slender; protibiae weakly arched with well-developed inner and outer spines, without lateral row of spines on outer surface; meso- and metatibiae without apical basket. Middle and hind tibiae straight. Protarsi tetramerous and undilated in both sexes; claws long, narrow and arched.

Mesoventral keel (Fig. 230.2): Low and small, shaped like a triangular lamina with convex anterior margin. Posterior edge weakly toothed and with setae, almost truncate in *H. maximiliani* and somewhat concave in *H. notenboomi*. Vertex in the form of a small obtuse angle.

Metatergal apparatus (Casale & Giachino 1990): Wings of the metascutum extremely reduced with the apophysis of the alacrista very elongated and narrow.

Suture of metaventrite and *metendosternite*: Unknown.

Median lobe of aedeagus: Large and robust. In lateral view, weak and evenly arched. In dorsal view (Fig. 233.2), width of sides arched in median area then gradually narrowing towards apex, not very acute and arcuate in *H. maximiliani* and more acute and subtruncate in *H. notenboomi.* Basal blade long and arcuately narrowed in the posterior median margin, longer and as wide as the ventral lamina of the tegmen.

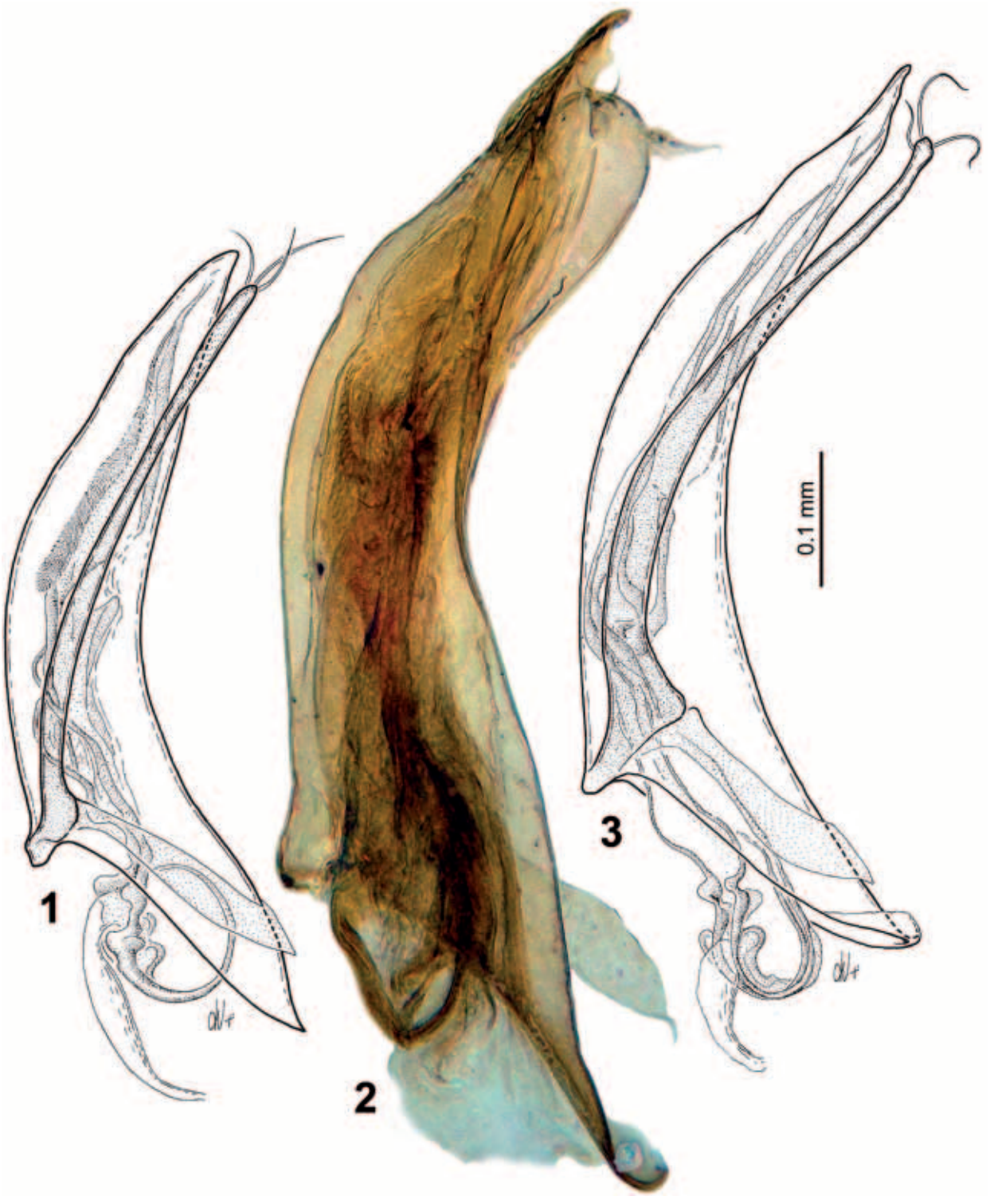
Endophallus (Fig. 233.2): Complex, with large basal lobe, irregular sclerotized pieces in basal and medial areas and reinforcement bands along medio-apical area, more or less robust.

Parameres (Fig. 233.6): Shorter than the median lobe. Apex club-shaped, strongly dilated, spoon-shaped with ventral margin partly membranous. Bearing three long setae of similar length and thickness, two outer subapical, one inner subapical.

Spermathecal complex (Fig. 234.2): Spermatheca elongate, with apical lobe oblong and thicker than basal lobe, both joined by a hyaline duct and as wide as basal lobe. Spermatic duct very long and thin, attached to the sac by a voluminous basal sclerite (Perreau 2021: Fig. 23) and forming in the anterior part a small nodule which joins the basal lobe; spermathecal gland present. Copulatory sac covered with spinulae in the anterior part.

Female uroventrite VIII (Fig. 234.5): Spiculum short and narrow, wider with a truncated apex in *H. maximiliani*; posterior middle margin in a more or less narrow arc.

Discussion. Laneyrie (1967) and V.B. Guéorguiev (1976) placed the genus *Huetheriella* among the «*incertae sedis*» genera, because the morphology of the anterior tarsi and genitalia was unknown. Previously, and for this reason, Jeannel (1934) did not place it in any series or subtribe, but stressed that it is morphologically close to *Leonhardia*. Casale & Giachino (1990), in publishing the morphology of the males and describing the characteristics of the protarsi (tetramerous) and the male and female genitalia, included this genus in the «Théléomorphes» of Division II of Jeannel (1924a). In the same article, they established that its position is close to *Pisidiella* and close to the phyletic lineage of *Phaneropella* due to various similar structures in the



FIGURES 232.1–232.4: *Hittitia* series. Aedeagus in lateral view of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Pisidiella spatulifera*, (**3**) *Uludagites minuta* **comb. nov.** Figs **1**, **3** modified from Casale *et al.* (1991).

aedeagus, particularly in the shape of parameres and endo-phallus. As already indicated by Perreau (2000), the genera *Huetheriella* and *Pisidiella* are included in the phyletic series *Pisidiella*. No molecular data are available to confirm this position.

Distribution. Turkey. Currently, all three species of this genus colonise the Küpe Dagi (Kybelon)-Gidengelmez Daglari karst massifs, which lie between the west of Lake Suğla, south of Seydişehir, and the west of Lake Beyşehir, on the northern slopes of Mount Dedegöl, on the Anatolian peninsula (Casale & Giachino 1990; Perreau 2021).

Species

Huetheriella maximiliani Jeannel, 1934
Hütheriella Maximiliani Jeannel, 1934c: 21.
Hutheriella Maximiliani Jeannel: Coiffait, 1959b: 31.
Huetheriella maximiliani Jeannel, 1934: Casale & Giachino, 1990: 133.

Huetheriella notenboomi Casale & Giachino, 1990
Huterilla clausoni Curti: Coiffait, 1989: 141 (*Nomen nudum*).
Huetheriella notenboomi Casale & Giachino, 1990: 133.

Huetheriella pinargozu Perreau, 2021
Huetheriella pinargozu Perreau, 2021: 293.

Genus ***Pisidiella*** Jeannel, 1930
Pisidiella Jeannel, 1930b: 226.

Type species. *Pisidiella spatulifera* Jeannel, 1930 by original designation (habitus in Fig. 229.3).

Diagnosis. Small size, between 1.8-2.8 mm. Bathyscioid facies (Fig. 229.3), ovoid body, wide, short and very convex. Colour reddish-brown, slightly shiny; integument with a fine pubescence, very short, lying down, yellowish and tight.

Head: Wider than long, as wide as the anterior part of the pronotum, with a complete occipital carina; punctation fine and scattered; anophthalmous.

Antennae: Thin, reaching almost halfway up the body; antennomeres of the club differentiated, a little flattened, widened in the apical area and detached. First antennomere equal to or slightly longer than the second; the 8th slightly transverse and subglobose; 9th and 10th antennomere slightly longer than wide, the 11th wider than the 10th and twice as long.

Pronotum: Transverse, 1.9 times wider than long, very convex, with maximum width just before the base. Base as wide as the anterior part of the elytra; lateral margins regularly arched. Basal vertices slightly acute, the basal angles acute.

Elytra: Convex, short, slightly longer than wide (1.2 times), with the maximum width in the basal area, the apex subtruncated. Elytral disk very finely punctate, with dense, non-aligned dots, without transverse striolation. Parasutural stria lacking.

Legs: Short. Protarsi of the males tetramerous and slender; protibiae without lateral comb on the outer surface. Meso- and metatibiae without apical baskets, but both armed with long spines.

Mesoventral keel (Fig. 230.3): Very high, with anterior margins a little convex, the ventral broad; vertex a little pointed, in soft tooth, and obtuse angle; without posterior extension on metaventrite.

Suture of metaventrite (Fig. 230.3): Undulated, delimiting a small area in the apical half and very close to the coxal cavity in the basal half.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Short and robust. In lateral view (Fig. 232.2), only slightly arched, with the dorsal face towards the apical fifth of gibbous appearance and the apex thick. In dorsal view (Fig. 233.3), sides subparallel ending in arch in the apical area; apex not very acute with a slight median incision. Basal blade elongate oval with posterior apex in narrowed arc.

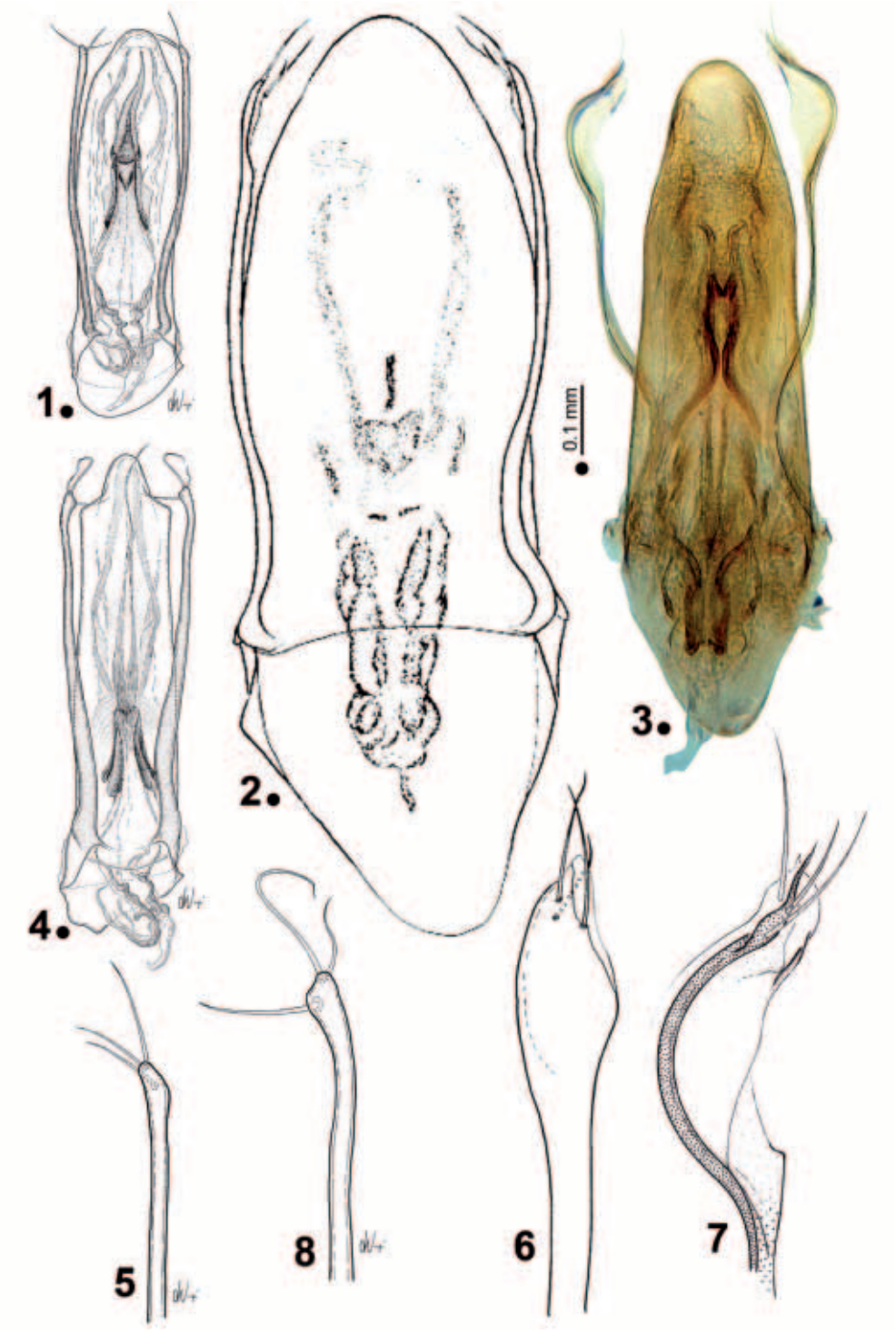
Endophallus (Fig. 233.3): Basal armour bearing a large «Y»-piece with well-developed arms. Median area with a group of small torns and diffuse scalosities.

Parameres (Fig. 233.7): Thin and curved in lateral view; a little longer than the median lobe, with an enlarged apical area forming a large elongate spoon. Apex bearing three small apical setae, two at the apex and one internal preapical. Ventral lamina of tegmen shorter, as wide as basal lamina.

Spermathecal complex: Spermatheca unknown. Spermiduct without or with a small basal sclerite at its junction with the copulatory sac (Perreau 2021).

Female uroventrite VIII: Unknown.

Discussion. *Pisidiella* shows similar characters in external morphology and, in particular, in the shape of the aedeagus with the genera *Hittitia* and *Uludagites* from Asia Minor (Jeannel 1930). It is also related to the genus *Huetheriella*, which has similarities in the shape of the aedeagus. Perreau (2000) included the genera *Pisidiella* and *Huetheriella* in the «*Pisidiella* phyletic series» of the Bathysciina subtribe. To be sure of its position, we will have to wait for molecular data.



FIGURES 233.1–233.8: *Hittitia* series. Aedeagus in dorsal view of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Huetheriella maximiliani*, (**3**) *Pisidiella spatulifera*, (**4**) *Uludagites minuta* **comb. nov.** Apex of paramere of: (**5**) *H. turcica* **comb. nov.**, (**6**) *H. maximiliani*, (**7**) *P. spatulifera*, (**8**) *U. minuta* **comb. nov.** Figs **1**, **4**, **5**, **8** modified from Casale *et al.* (1991); Figs **2**, **6** from Casale & Giachino (1990).

DISTRIBUTION. Turkey. All four species colonise caves in the western mountain karst of Taurus in Asia Minor.

Species

Pisidiella kosswigi Jeannel, 1947
Pisidiella kosswigi Jeannel, 1947e: 14.

Pisidiella minuscula Coiffait, 1974
Pisidiella minuscula Coiffait, 1974: 688.

Pisidiella ovoidea Jeannel, 1955
Pisidiella ovoidea Jeannel, 1955d: 8.

Pisidiella spatulifera Jeannel, 1930
Pisidiella spatulifera Jeannel, 1930b: 226.

Genus ***Uludagites*** Casale, Giachino, Vailati & Rampini, 1991 stat. nov.
Phaneropella (*Uludagites*) Casale, Giachino, Vailati & Rampini, 1991: 213.

TYPE SPECIES. *Phaneropella* (*Uludagites*) *minuta* Casale, Giachino, Vailati & Rampini, 1991 by original designation (habitus in Fig. 229.4).

DIAGNOSIS. Small size, 1.5 mm, bathyscioid (Fig. 229.4), body short, slightly convex and pubescent.

Head: Retractable, with a complete occipital carina, blunt in the middle; eyes very reduced but present.

Antennae: Short, barely reaching, stretched backwards, the base of the pronotum, with the first antennomere only slightly shorter than the second.

Pronotum: Broad, very transverse, with evenly and long-arched sides, not sinuate posteriorly, but slightly convergent, with maximum width at the base, which is slightly narrower than the base of the elytra.

Elytra: Stout, ovate, convex evenly attenuated in posterior half, normally dehiscent at apex, with transversely aligned striolae; parasutural stria absent.

Legs: Short and strong. Male protarsi tetramerous and not dilated; protibiae slightly enlarged, provided with two stout spurs and no comb at apex; mesotibiae weakly arched, with spines on outer margin; metatibiae straight; meso- and metatibiae without apical basket. Metafemora toothed in male.

Mesoventral keel (Fig. 230.4): High but broadly rounded, not toothed, with setose ventral margin; extending over part of metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 231.2): Reduced, with a short, broad apophysis of the alacrista, with relatively concave sides and a truncate, sub-square apex; wings of the metascutum subtriangular, a little more than twice as long as wide.

Metendosternite (Fig. 231.4): Furcal arms and trunk short, arms longest, with terminal apophysis with in the form of a well-developed, membranous internal fin; posterior lamina narrowed apically, with a straight lateral margin; a much reduced anterior furcal plate also seen towards the middle of the arm. Trunk almost as long as wide and half keel with a long but not very wide posterior divergence.

Median lobe of aedeagus: Long. In lateral view (Fig. 232.3), in broad, regular arc, the dorsal apical area slightly sinuate. Sides subparallel, in dorsal view (Fig. 233.4), with the apex rounded and provided with two clearly visible lateral subapical dilatations. Basal blade poorly developed.

Endophallus (Fig. 233.4): Clearly visible, sclerotized «Y»-piece , protruding beyond the basal blade of the median lobe. Presence of a complex submedian phaneroid from which a long flagellum extends briefly beyond the apex of the median lobe.

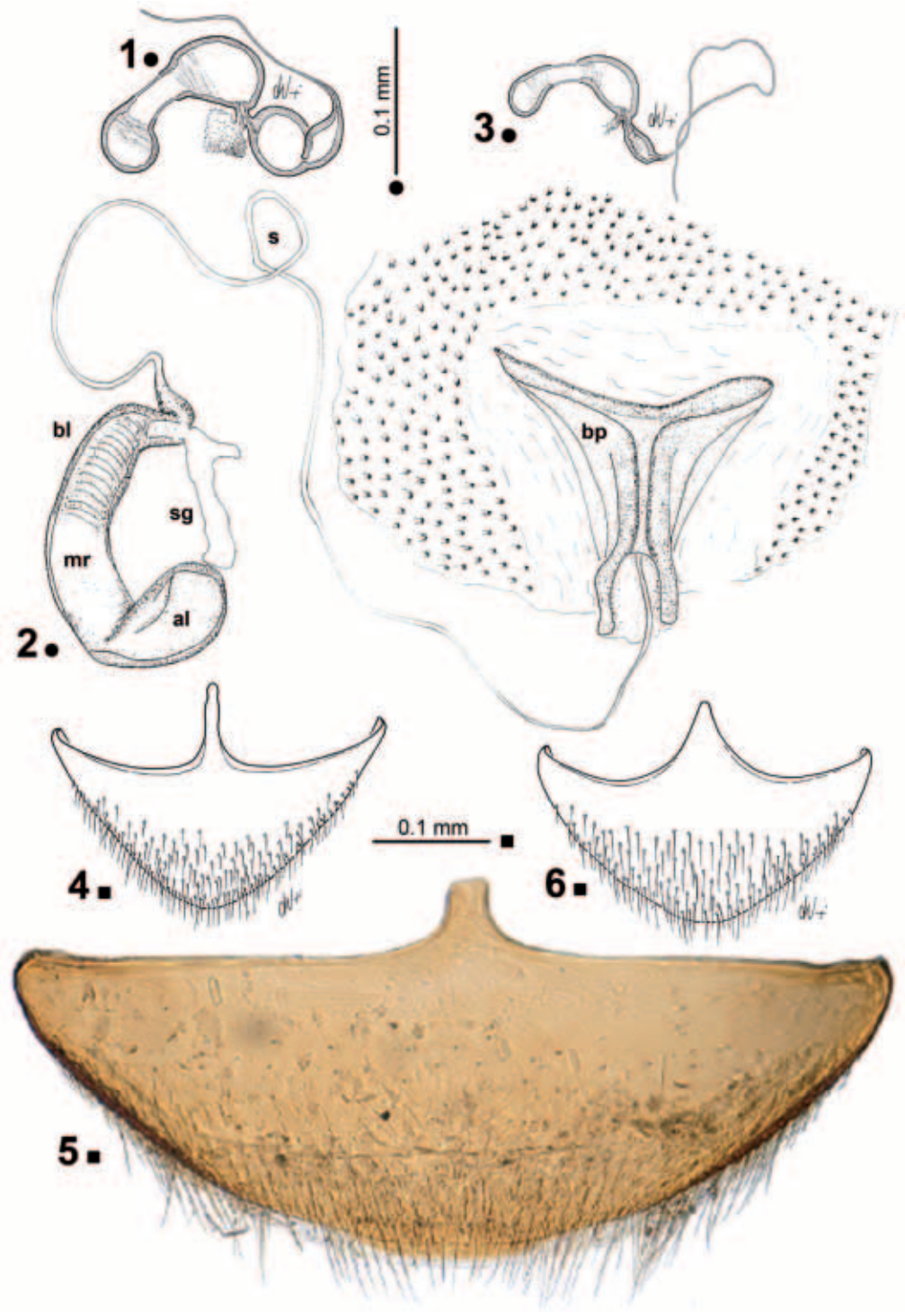
Parameres (Fig. 233.8): Thin, not reaching the apex of the median lobe, slightly dilated at the apex and bearing three setae, two apical and one internal subapical.

Spermathecal complex (Fig. 234.3): Spermatheca kidney-shaped, with a more developed proximal lobe. Ductus long and thin, obviously dilated and sclerotized at insertion into spermatheca; spermathecal gland hyaline, shapeless.

Female uroventrite VIII (Fig. 234.6): With a stubby, broadly triangular spiculum.

DISCUSSION. *Uludagites* differs from *Hittitia* not only by the different shape of the apex of the median lobe, but also by the extensive development of the median flagellum of the endophallus and by the absence of spherical dilatation of the distal, close to the spermatheca, part of the ductus. As indicated for the genus *Hittitia*, this phyletic series, with its North Anatolian distribution, also seems congruent from the zoogeographic point of view. *Uludagites* is the sister genus of *Hittitia* to which it is attached with a support of 98.9/100 (Fig. 1D).

DISTRIBUTION. Turkey. NW Anatolia, Bursa, Uludag.



FIGURES 234.1–234.6: *Hittitia* series. Spermathecal complex of: (**1**) *Hittitia turcica* **comb. nov.**, (**2**) *Huetheriella maximiliani* (modified from Casale & Giachino 1990), (**3**) *Uludagites minuta* **comb. nov.** Female uroventrite VIII of: (**4**) *H. turcica* **comb. nov.**, (**5**) *H. maximiliani* (modified from Perreau 2021), (**6**) *U. minuta* **comb. nov.** Figs **1**, **3**, **4**, **6** modified from Casale *et al.* (1991). Abbreviations: **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

Species

Uludagites minuta (Casale, Giachino, Vailati & Rampini, 1991) comb. nov.
Phaneropella (*Uludagites*) *minuta* Casale, Giachino, Vailati & Rampini, 1991: 216.

3.4.5 Series ***Drimeotus*** Jeannel, 1910

Diagnosis. Body with bathyscioid (*Sinobathyscia*) (Fig. 236.5), subpholeuonoid (*Drimeotus*) (Figs 235.1-235.4) and pholeuonoid (*Pholeuon*, *Protopholeuon*) facies (Figs 236.1-236.4). Depigmented and without metathoracic wings.

Head: Occipital carina complete, more or less blurred. Anophthalmous. Last segment of the maxillary palps short and conical.

Antennae: 11 antennomeres, inserted in the middle third of the head, with the first antennomere shorter or as long as the second.

Elytra: Without transverse striolae or parasutural stria.

Legs: Male protarsi pentamerous female protarsi tetramerous and always slender. Protibiae with two external spurs, without a comb on the apical and external margins; meso- and metatibiae without apical crowns of spines and with well-developed external spurs. Claws long and narrow.

Median lobe of aedeagus: In lateral view, notched (*Drimeotus* group) (Figs 240.1-240.5, 241.1-241.3) or with dorsal depression (*Sinobathyscia* group) (Fig. 241.4).

Endophallus (Figs 242.1-242.4, 243.1-243.3): With sclerotized structures in the median region; in the basal region, a bulb with a flagellum or a complex «U»-shaped structure.

Spermathecal complex (Figs 244.1-244.6): Spermatheca with both lobes sclerotized and a hyaline median region narrower than the terminal lobe.

Female uroventrite VIII (Figs 245.1-245.6): With a short spiculum.

Discussion. The clade is sister to the *Catopsinus* series with good support, 96.9/97. The phylogenetic tree (Fig. 1D) indicates that the series consists of two clades, the *Drimeotus* group and the *Sinobathyscia* group, as a sister group with high support in both analysis, Tree 1 = 97.9/100 and Tree 2 = 97.4/100 (Fig. 2).

Key to Group

1. Size between 2.8-6.5 mm. Antennae long with the first two antennomeres elongated. Pronotum with evenly arched or sinuous sides in the basal area. Elytra without transverse striation. Mesoventral keel not extending beyond the mesoventrite (Figs 237.1-237.5). Basal region of endophallus with a flagellum (Figs 242.1-242.4, 243.1-243.2). Parameres with three apical setae (Figs 243.4-243.11). Spermatic duct without nodule (Figs 244.1-244.5).....*Drimeotus* group
- Size between 1.3-1.5 mm. Antennae short, with the first two antennomeres strongly thickened. Lateral sides of the pronotum uniformly arched. Elytra with transverse striation. Mesoventral keel (Fig. 237.6) extending into part of metaventrite. Basal region of endophallus (Fig. 243.3) with a complex «U»-shaped structure. Parameres with two apical setae (Fig. 243.12). Spermatic duct with a nodule developed in the area of junction with the basal lobe (Fig. 244.6)...
.....*Sinobathyscia* group

3.4.5.1 ***Drimeotus*** group

Diagnosis. Habitus short and oval (sub-pholeuonoid) (Figs 235.1-235.4) or elongated and elliptical (pholeuonoid) (Figs 236.1-236.4). Orange colouration and tegument entirely covered by short-long and down-lying or upright pubescence.

Head: Epistomal suture slightly curved and more or less darkened.

Antennae: Long, all antennomeres longer than wide and the club poorly differentiated; first antennomere shorter and slightly thicker than the second one.

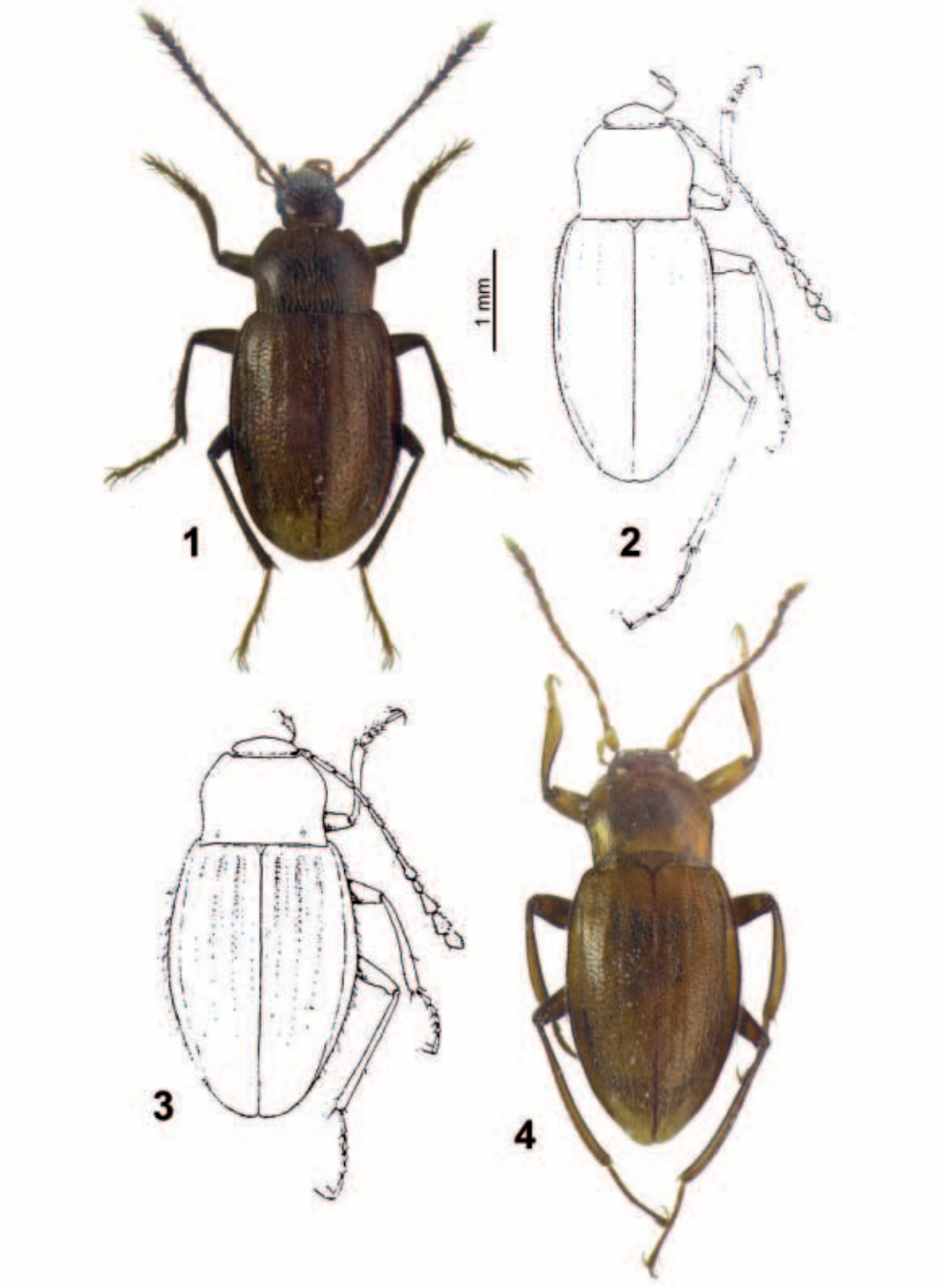
Elytra: Dotted, without transverse striation.

Legs: Male protarsi dilated, as wide or narrower than the apical end of the protibiae. Protibiae not tapered at the apex; meso- and metatibiae fitted with short and fine spines, which are straight and cylindrical, only curved and widened in the subgenus *Fericeus*.

Mesoventral keel (Figs 237.1-237.5): Atrophied or short, not exceeding the mesoventrite; if present it is tall or reduced to a more or less developed tooth.

Suture of the metaventrite (Figs 237.1-237.5): Close to the edge of the mesocoxal cavity, it describes a regular or very slightly waved arc and the area it delimits is elongated and narrow.

Median lobe of aedeagus (Figs 240.1-240.5, 241.1-241.3): Robust with a deep groove and a «*invagination en nid de pigeon*» (Jeannel, 1924a) pit,



FIGURES 235.1–235.4: *Drimeotus* series. Habitus of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *D.* (*Bihorites*) *laevimarginatus montistartari*, (**3**) *D.* (*Drimeotinus*) *attenuatus montiscetii*, (**4**) *D.* (*Fericeus*) *kraatzi*. Figs **2**, **3** modified from Jeannel (1930).

describes a structure that looks like an invagination of a pigeon nest located towards the apical quarter of the median lobe, except in the genus *Protopholeuon*.

Endophallus (Figs 242.1-242.4, 243.1, 243.2): Very uniform which in the basal region has a long and fine flagellum inserted at the dorsal side, towards the middle region two symmetrical clusters with a multitude of spines more or less developed and between them there is normally a small sclerotized piece in the shape of an «W».

Parameres (Figs 243.4-243.11): Thin, as long or almost as long as the median lobe, and 3-4 short setae are located at the apical area.

Spermathecal complex (Figs 244.1-244.5): Formed by a short spermatheca, with two sclerotized lobes, the apical one being globular and wider than the basal one; spermatic duct of uniform thickness or somewhat wider around the middle part near the spermathecal gland.

Female uroventrite VIII (Figs 245.1-245.5): With spiculum short and straight or curved in the apical area.

Discussion. In the phylogenetic tree (Fig. 1D) the group is supported by 100/100. The internal topology differs in the trees of the two independent analysis and neither of them overlaps with the findings in Bucur *et al*. (2003). However, this study ist usually not taken into account since the data which the analyse is based on are not provided. In Tree-1 two *Drimeotus* species seem to derive from two consecutive basal cladogenesis; in this *Drimeotus kraatzi* is sister to the entire remaining clade with 100/100 support; *Parapholeuon* in this tree is sister to the other *Pholeuon*, this includes *Protopholeuon*, which appear to have arisen by a nearly simultaneous cladogenesis, albeit the supports for this are all low (Fig. 1D). In Tree-2 (Fig. 2) *Drimeotus kraatzi* is also forming the basal taxon, however *Protopholeuon* is herein sister to *D. viehmanni* plus all *Pholeuon* species, here also with a low support. In the molecular study the representation of this group is rather scarce, species of various subgenera of both *Drimeotus* and *Pholeuon* are missing, and for *Pholeuon gracile* and *Pholeuon knisrchi proserpinae* the sequences of the coding genes are missing. Therefore proposed taxonomic changes are introduced with great caution to only establish taxonomic classification that is supported well by the analysis.

The *Drimeotus* series was established by Jeannel (1910a) and retained by Perreau (2000) for the genera *Drimeotus*, *Pholeuon*, and *Protopholeuon*. Until now, these three genera were attributed to the phyletic lineage of *Drimeotus*: *Pholeuon*, divided into three subgenera, *Pholeuon* (s. str.), *Parapholeuon,* and *Mesopholeuon*; *Drimeotus* which comprises five subgenera, *Drimeotus* (s. str.), *Bihorites*, *Drimeotinus*, *Fericeus* and *Trichopharis*, and lastly the genus *Protopholeuon*.

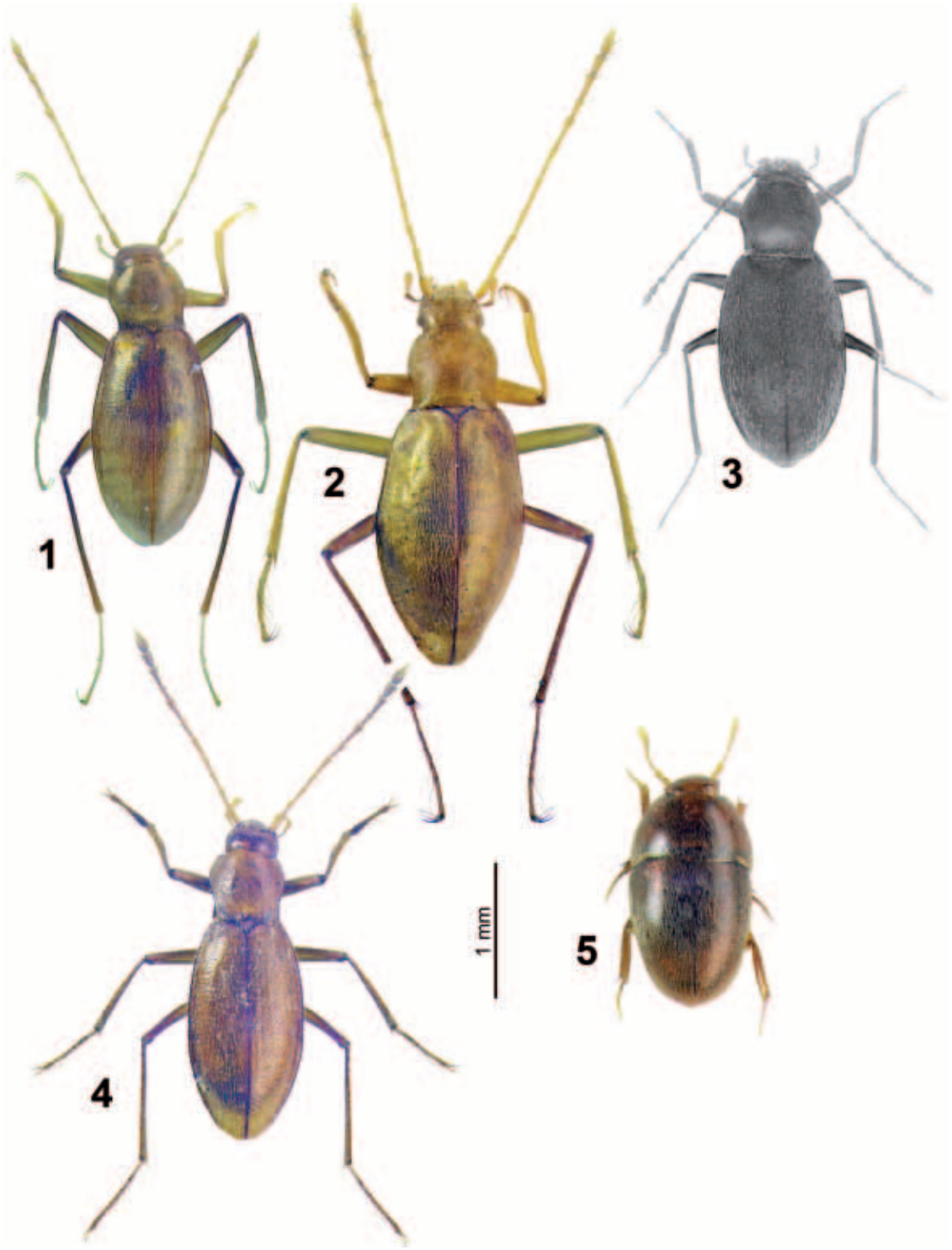
The studied morphological characters show a representation of the same model of the endophallus with similar characteristics in all of them – flagellum, two groups of spines, apical reinforcing bands and, in general, a small «W»-shaped piece –; the endophallus is identical to that of *Drimeotus* and *Pholeuon*. In addition there are more apparent characteristics of the aedeagus, a transverse groove forming a deep dorsal genital fossa, which was dubbed «*une invagination en nid de pigeon*» by Jeannel (1924a); only in *Protopholeuon* is reduced to a small depression. Jeannel (1924a: p. 313) observed that the aedeagi of *Drimeotus* and *Pholeuon* were identical, concluding that the resemblance is due to evolutionary convergence; which appears to date as a highly unlikely evolutionary scenario considering that these are sister genera that inhabit the same geographical region. *Pholeuon* and *Drimeotus* are most likely synonyms.

Distribution. Species of the *Drimeotus* group are endemic to the Western Carpathians north of the river Mures, which represents the area of the Apuseni mountains, Transylvania, Romania (Bucur *et al*. 2003).

Key to genera

1. Ovoid, wide and short body (Figs 235.1-235.4); transverse pronotum, clearly wider than long, with the base much wider than the anterior part; elytra with longitudinal ribs more or less marked; antennae with the eighth antennomere twice or nearly twice as long as wide; short mesoventral keel, but tall and well-developed (Figs 237.1, 237.2) 2
- Elliptical, narrow and elongated body (Figs 236.1-236.4); pronotum as long as or slightly longer than wide, with the base about as wide as the anterior part; elytra without ribs; antennae with the eighth article at least three times as long as wide; mesoventral keel atrophied or reduced to a more or less developed tooth (Figs 237.3-237.5).....6

2. Onychium of metatarsomeres very long, as long as the combined length of the other four tarsomeres; meso- and metatibiae of males curved and widened



FIGURES 236.1–236.5: *Drimeotus* series. Habitus of: (**1**) *Pholeuon* (*Parapholeuon*) *gracile gracile,* (**2**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**3**) *P.* (*Mesopholeuon*) *comani* (modified from Moldovan *et al.* 2007), (**4**) *Protopholeuon hungaricum,* (**5**) *Sinobathyscia tianma*.

into the shape of a sword – this character also on *Trichopharis* – pro- and mesotrochanters of males toothed .....*Drimeotus* (*Fericeus*)
- Onychium of metatarsomeres clearly shorter than first the four tarsomeres combined; straight meso- and metatibia – except *Trichopharis* – pro- and meso-trochanters of males non-toothed..... 3

3. Elytra with three blurred wavy ribs. Meso- and metatibiae curved, wide and flattened ....*Drimeotus* (*Trichopharis*)
- Elytra with four wavy ribs well marked or blurred. Meso- and metatibiae straight and neither wide nor flattened.....4

4. Elytra with four well defined wavy ribs, and between the intervals two regular longitudinal rows of thick spots. Parameres with apical part long, narrow and curved, with four small apical setae (Fig. 243.6) – *sensu* Jeannel (1924a) with five –..... .....*Drimeotus* (*Drimeotinus*)
- Elytra with four more or less blurred wavy ribs, without regular longitudinal rows of dots over the intervals. Parameres with apical part of different shape and with three apical setae (Figs 243.4, 243.5).....5

5. Very short and procumbent pubescence. Marginal rim of the elytra very narrow and uniform. Parameres bent at the apical region, short and pointed ....*Drimeotus* (*Bihorites*)
- Long and raised pubescence. Marginal rim very wide, asymmetrical, wider towards the middle. Parameres with the apical area long, slightly bent and dilated .....*Drimeotus* (*Drimeotus*)

6. Antennae with antennomeres IX-XI dilated; more elongated elytra; aedeagus with poorly marked dorsal depression, no pit (Fig. 241.3); slightly bent parameres in the apical area and the small lobe oblong and flattened (Fig. 243.10) .....*Protopholeuon*
- Antennae with antennomeres IX-XI not dilated; elytra shorter and wider in the middle; aedeagus with deep dorsal depression and cavern well-marked (Figs 240.5, 241.1, 241.2); parameres with apical part not elbowed and the lobe not oblong and flattened (Figs 243.7, 243.9) 7

7. Pubescence of the elytra long. Marginal groove or ridge wide and widening toward middle. Parameres with the apical area straight or slightly bent and the club somewhat widened or flattened in the shape of a small paddle (Fig. 243.7) ..*Pholeuon* (*Parapholeuon*)
- Pubescence of the elytra short. Marginal groove narrow and not widened towards the middle. Parameres with the apical area more curved or more bent, sometimes twisted (Fig. 243.9) 8

8. Size between 3.0-3.5 mm. Median lobe of aedeagus shorter, wider towards the apical third and the distance between the dorsal transverse invagination and the basal lamina shorter. Parameres thinner, with the apical area arched and not dilated..... .....*Pholeuon* (*Mesopholeuon*)
- Size between 4.5-6.6 mm. Median lobe of aedeagus longer, less widened towards the apical third and the distance between the dorsal transverse invagination and the basal lamina longer. Parameres thicker, with the apical area more bent, sometimes twisted, and generally more or less widened ....*Pholeuon* (*Pholeuon*)

Genus ***Drimeotus*** L. Miller, 1856
Drimeotus L. Miller, 1856b: 635.

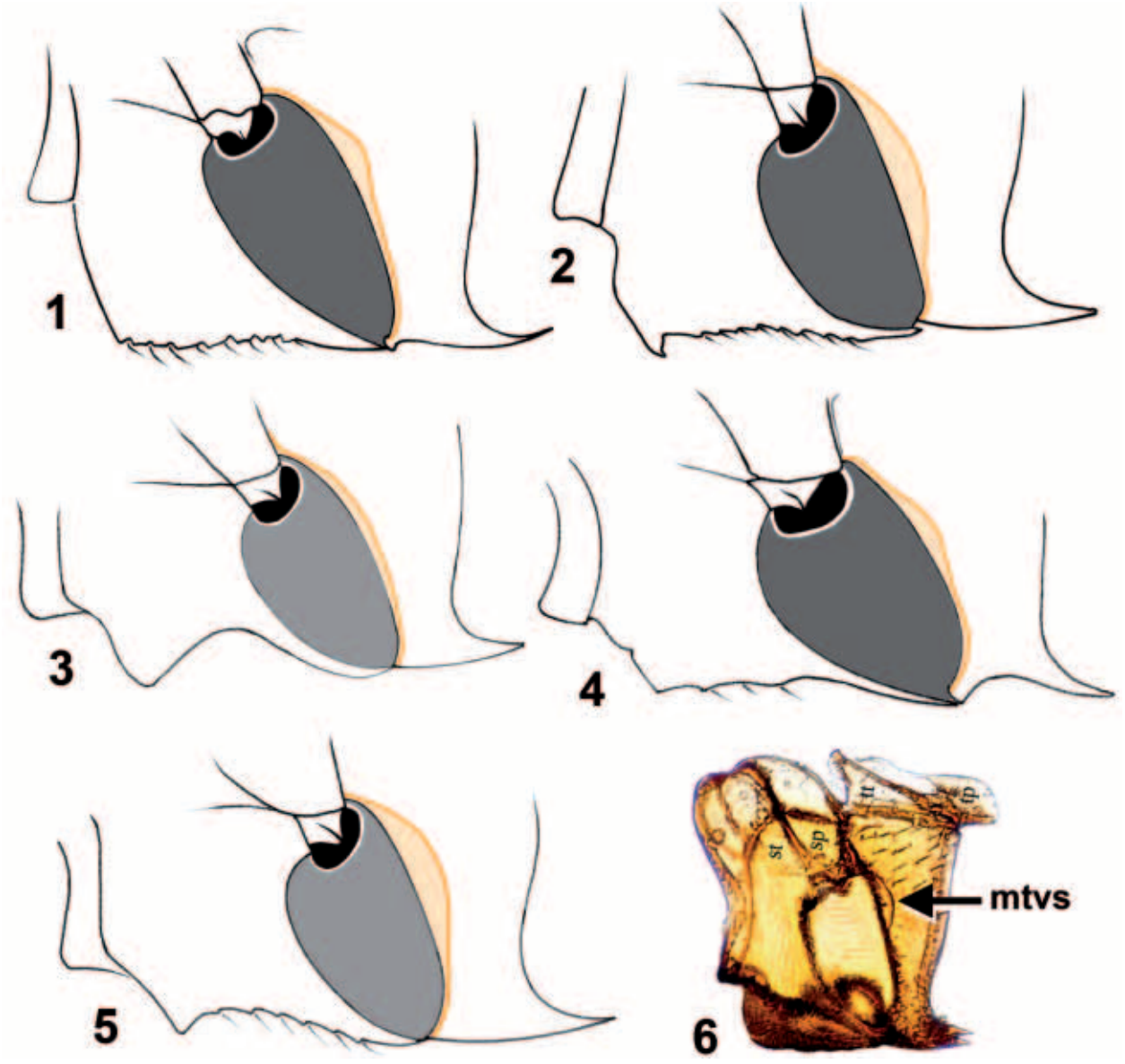
Type species. *Drimeotus kovacsii* L. Miller, 1856 by monotypy (for the habitus see that of the similar species *Drimeotus* (*Drimeotus*) *viehmanni* in Fig. 235.1).

Diagnosis. Length 2.8-4.6 mm. Body shape ovoid and slightly convex, anterior part slightly narrowed (Fig. 235.1); subpholeuonoid appearance. Body surface punctate with small dots on the head and the pronotum and the elytra are dotted with large and small dots; no transverse striation is observed, although in some cases a slightly marked or diffuse oblique striation. Variable pubescence, generally long and dense, formed around the margin of the elytra as a fringe of hairs which varies in the degree of development.

Antennae: Do not exceed half the length of the body, with the club antennomeres slightly dilated, not flattened and conical in shape; the 8th antennomere is almost twice as long as it is wide and the 2nd, 3rd, 7th and 11th antennomeres are similar in length.

Pronotum: With a hexagonal silhouette, wide and transverse, almost one and a half times wider than long, but always narrower than the elytra and with a basal area wider than the previous one; sides gently curved forwards, showing backwards a concave margin with a more or less pronounced sinuosity, pointed vertices and acute angles.

Elytra: Little convex, with more or less marked ripples, altogether about one and a half times longer



FIGURES 237.1–237.6: *Drimeotus* series. Pterothorax in lateral view of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *D.* (*Fericeus*) *kraatzi*, (**3**) *Pholeuon* (*Parapholeuon*) *mocsaryi*, (**4**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**5**) *Protopholeuon hungaricum,* (**6**) *Sinobathyscia tianma* (modified from Wang *et al*. 2017). Abbreviations: **mtvs**, metaventrite suture.

than wide; in general, the dotting is unordered, but sometimes the dots line up in six or seven longitudinal rows; marginal ridge or groove between wide and very wide, always the greatest width towards the middle.

Legs: Long and robust, generally spiny; male protarsi widened, generally narrower than apical area of the protibia, with the first protarsomere slightly longer than the second; straight or slightly curved mesotibiae and generally straight metatibiae, narrow and spiny, only curved and flattened in the subgenera *Fericeus* and *Trichopharis*.

Mesoventral keel (Figs 237.1, 237.2): High and not prolonged backwards; the anterior margin curved or sinuous and the ventral margin is narrow and

toothed, the apex has the shape of a tooth more or less developed and the angle a bit more than 90º; the intercoxal process of the metaventrite broad and somewhat concave.

Suture of the metaventrite (Figs 237.1, 237.2): With a slightly sinuous arc, encompasses a narrow area, somewhat wider in the apical third.

Metatergal apparatus (Fig. 238.1): With the two membranous wings of the metascutum short and triangular in appearance and the alacrista long, with narrow edges and pointed apices.

Metendosternite (Fig. 239.1): With long furcal arms, a little more than one and a half times the length of the trunk, with the apical area forming a sharp arc and the terminal apophysis reduced, but visible; narrow posterior lamina not reaching the apex, wider on trunk; furcal trunk slightly longer than wide and the posterior area of the median keel divergent.

Median lobe of aedeagus: Long, robust and curved, as long as a third of the length of the body. In lateral view (Figs 240.1-240.4), with a marked dorsal invagination towards the apical fifth; the apex ends in the shape of a forward inclined beak. In dorsal view (Figs 242.1, 242.2), the lateral margins are arched with the greatest width towards the apical third and the apical area is not very sharp. The basal pieces, ventral lamina of the tegmen and basal lamina of the median lobe, are generally short.

Endophallus (Figs 242.1, 242.2): With a singular armature. In the basal region there is a narrow and elongated slightly sclerotized lamina at which a long and fine filament or flagellum is anchored; in the middle region there are sclerotized structures formed by two large packages of more or less developed spines that are fixed at the base of the reinforcing bands and between them there is a small «W»-shaped piece.

Parameres (Figs 243.4-243.6): Long, thin and sharp, with the apical area curved or rod-shaped, slightly dilated, and equipped with three or four short setae.

Spermathecal complex (Fig. 244.1): Short spermatheca, with both lobes sclerotized; the apical one being globose and much more developed than the basal one, which is elongated, slightly curved and narrower; junction duct short and very hyaline; short spermatic duct, slightly sclerotized and a bit wider around the middle part; spermathecal gland is present.

Female uroventrite VIII (Fig. 245.1): Posterior margin curved, slightly concave in the middle; the spiculum is short and depending on the species, the apical area is straight or slightly curved.

Discussion. The most evident difference between *Drimeotus* and the other genera of the clade is the shape of the body, which shows a somewhat bathyscioid appearance, being clearly pholeuonoid in the other genera, in addition to the differences indicated in the genus key as described above.

Distribution. Romania, Transylvania, genus endemic to the Apuseni mountains.

Subgenus ***Bihorites*** Jeannel, 1923
Bihorites Jeannel, 1923b: 439.

Type species. *Drimeotus laevimarginatus* Moczarski, 1912 by original designation (habitus in Fig. 235.2).

Diagnosis. The basic characteristics for the identification of the subgenus are: size between 2.8-4.2 mm. Very short and procumbent pubescence.

Elytra: With four blurred ripples, without aligned dotted lines at intervals; very fine and rough dotting, the points aligned across, so that they almost form oblique striolae forwards and backwards; marginal rim of the elytra very narrow and uniform, hairs at the margin short.

Median lobe of aedeagus: In lateral view (Fig. 240.2) long, robust and curved, with a deep dorsal depression towards the apical fifth; after the depression the apical area is shaped like a long beak that curves towards the ventral side at the tip and is sharp; long basal lamina and in the middle of the posterior area a paddle-shaped prolongation.

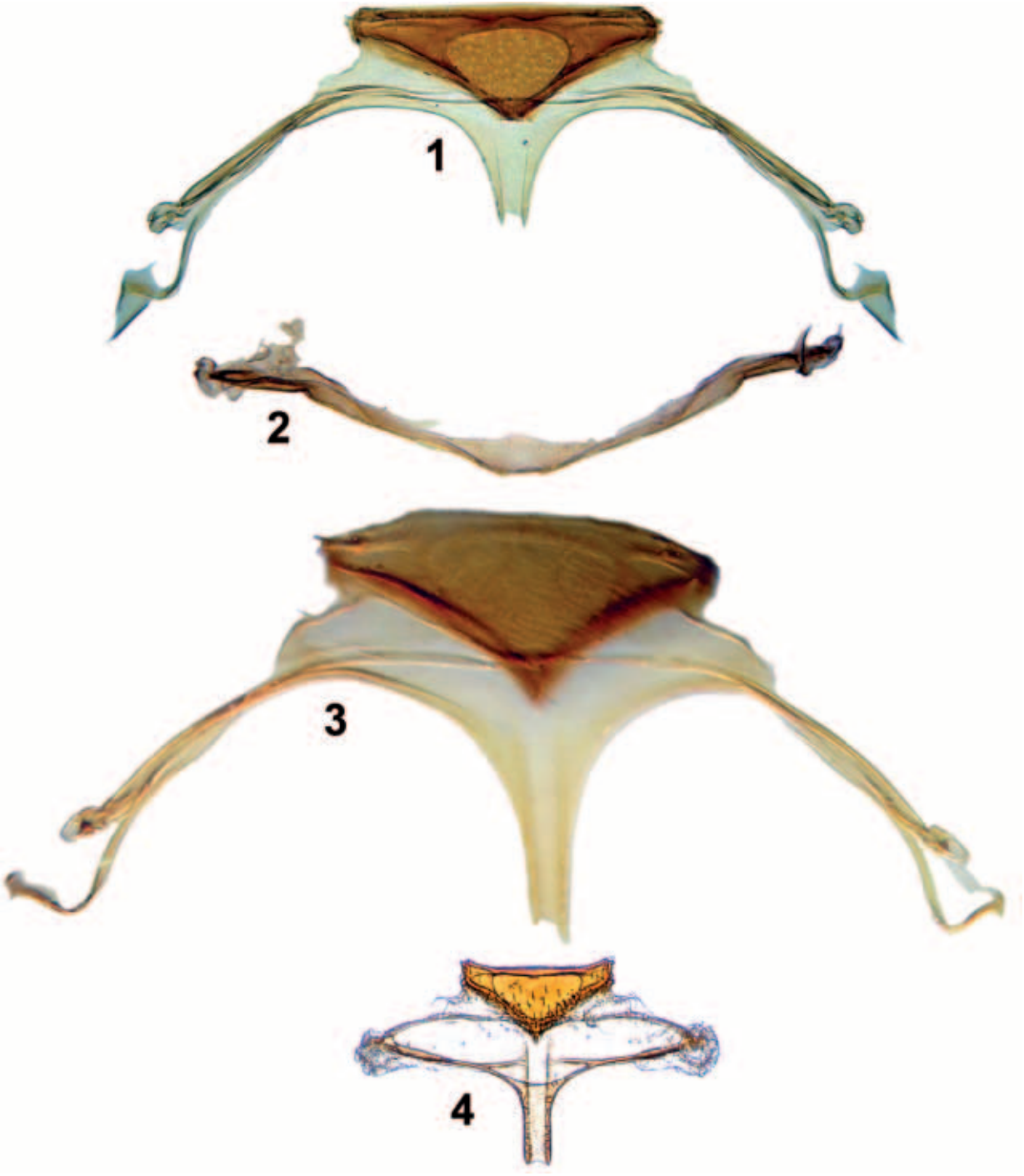
Parameres (Fig. 243.5): Bent at the apical region, short and sharp, this area armoured with three short setae, the basal one being slightly longer.

Distribution. Romania, Transylvania. It colonises underground cavities in the Bihor mountains, which are part of the Apuseni mountains in the Western Carpathians.

Species

Drimeotus (***Bihorites***) ***hickeri*** Knirsch, 1913
Drimeotus hickeri Knirsch, 1913d: 253.
Drimeotus (s. str.) *Hickeri* Knirsch: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *Hickeri* Knirsch: Jeannel, 1923b: 446.

Drimeotus (***Bihorites***) ***laevimarginatus*** Moczarski, 1912



FIGURES 238.1–238.4: *Drimeotus* series. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *Pholeuon* (*Parapholeuon*) *gracile gracile*, (**3**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**4**) *Sinobathyscia tianma* (modified from Wang *et al*. 2017).

Drimeotus* (*Bihorites*) *laevimarginatus acuticollis Jeannel, 1923
Drimeotus laevimarginatus acuticollis Jeannel, 1923b: 444.
Drimeotus (*Bihorites*) *laevimarginatus* Subsp. *acuticollis* Jeannel, 1923: Jeannel, 1924a: 307.
Drimeotus* (*Bihorites*) *laevimarginatus cryophilus Jeannel, 1923
Drimeotus laevimarginatus cryophilus Jeannel, 1923b: 444.
Drimeotus (*Bihorites*) *laevimarginatus* Subsp. *cryophilus* Jeannel, 1923: Jeannel, 1924a: 307.
Drimeotus* (*Bihorites*) *laevimarginatus csikii Mihók, 1912
Drimeotus csikii Mihók, 1912: 163.
Drimeotus (s. str.) *Csikii* Mihók: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *laevimarginatus* subsp. *Csikii* Mihok: Jeannel, 1923b: 442.
Drimeotus* (*Bihorites*) *laevimarginatus dieneri Bokor, 1913
Drimeotus dieneri Bokor, 1913a: 448.
Drimeotus (s. str.) *Dieneri* Bokor: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *laevimarginatus* subsp. *Dieneri* Bokor: Jeannel, 1923b: 442.
Drimeotus* (*Bihorites*) *laevimarginatus hungaricus Csiki, 1912
Drimeotus hungaricus Csiki, 1912a: 160.
Drimeotus latissimus Mihók, 1914: 145.
Drimeotus (s. str.) *hungaricus* Csiki: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *laevimarginatus* subsp. *hungaricus* Csiki: Jeannel, 1923b: 442.
Drimeotus* (*Bihorites*) *laevimarginatus laevimarginatus Moczarski, 1912
Drimeotus laevimarginatus Moczarski, 1912: 118.
Drimeotus (s. str.) *laevimarginatus* Moczarski: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *laevimarginatus* Moczarski: Jeannel, 1923b: 439.
Drimeotus* (*Bihorites*) *laevimarginatus montistartari Jeannel, 1930
Drimeotus montistartari Jeannel, 1930c: 53.
Drimeotus (*Bihorites*) *laevimarginatus montis-tartarii* Jeann: Laneyrie, 1967: 615.
Drimeotus (*Bihorites*) *laevimarginatus montistartari* Jeannel: Perreau, 2000: 272.
Drimeotus* (*Bihorites*) *laevimarginatus subterraneus Knirsch, 1913
Drimeotus subterraneus Knirsch, 1913c: 161.
Drimeotus diabolicus Bokor, 1913:a 443.
Drimeotus (s. str.) *subterraneus* Knirsch: Jeannel, 1914b: 44.
Drimeotus (*Bihorites*) *laevimarginatus* subsp. *subterraneus* Knirsch: Jeannel, 1923b: 442.
Drimeotus* (*Bihorites*) *laevimarginatus winkleri Jeannel, 1923
Drimeotus laevimarginatus winkleri Jeannel, 1923b: 444.
Drimeotus (*Bihorites*) *laevimarginatus* ssp. *Winkleri* Jeannel: Jeannel, 1924a: 307.

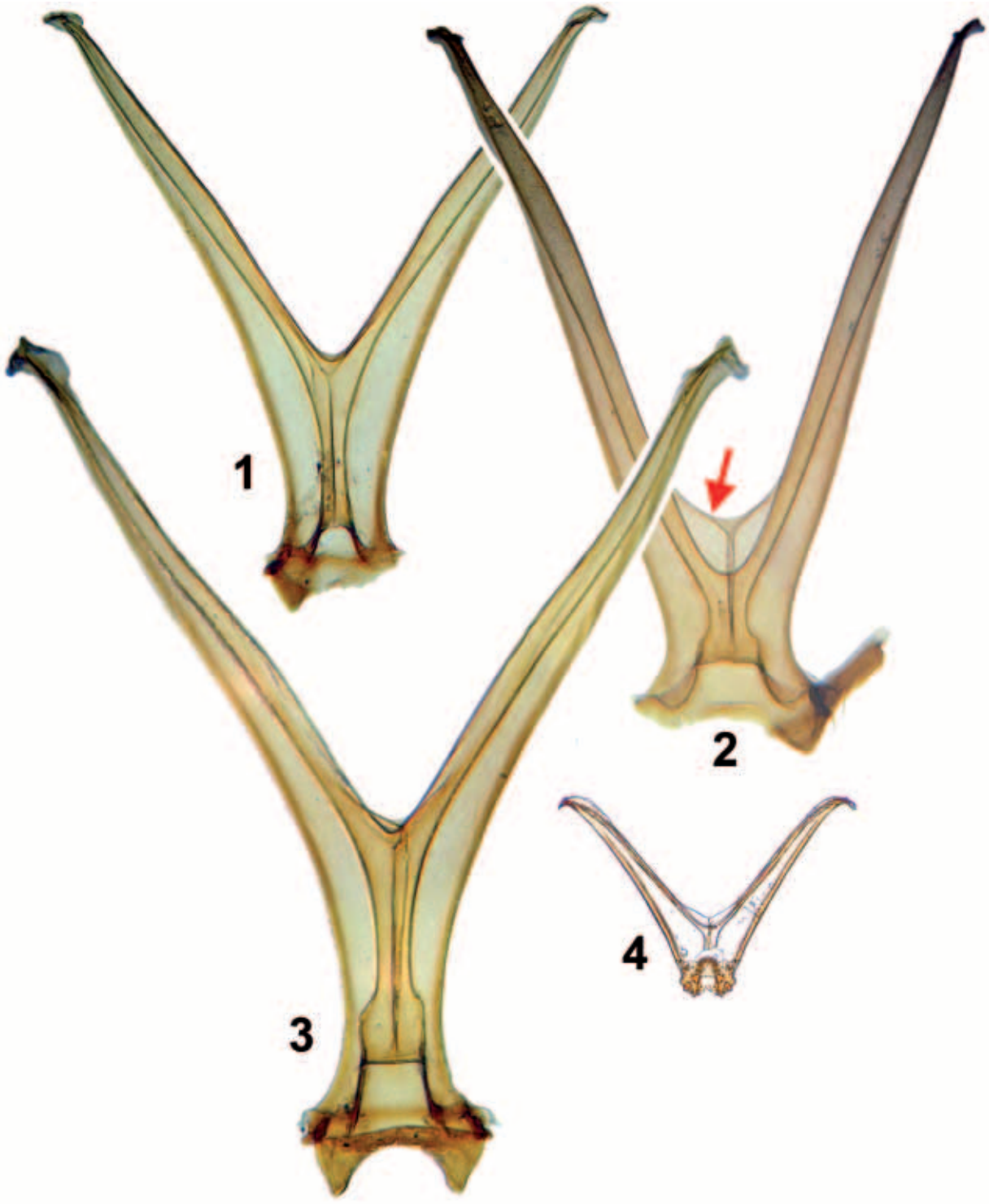
Drimeotus* (*Bihorites*) *mihoki Csiki, 1912
Drimeotus* (*Bihorites*) *mihoki condoricus Knirsch, 1913
Drimeotus condoricus Knirsch, 1913c: 162.
Drimeotus moczarskii Bokor, 1913a: 444.
Drimeotus (s. str.) *condoricus* Knirsch: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *Mihóki* subsp. *condoricus* Knirsch: Jeannel, 1923b: 446.
Drimeotus* (*Bihorites*) *mihoki corlatensis Jeannel, 1930
Drimeotus mihoki corlatensis Jeannel, 1930c: 55.
Drimeotus (*Bihorites*) *mihoki corlatensis* Jeannel: Perreau, 2000: 272.
Drimeotus* (*Bihorites*) *mihoki mihoki Csiki, 1912
Drimeotus mihoki Csiki, 1912a: 161.
Drimeotus laticollis Knirsch, 1913c: 163.
Drimeotus (s. str.) *Mihóki* Csiki: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *Mihoki* Csiki: Jeannel, 1923b: 446.
Drimeotus* (*Bihorites*) *mihoki rothi Jeannel, 1923
Drimeotus mihoki rothi Jeannel, 1923b: 447.
Drimeotus (*Bihorites*) *Mihóki* Subsp. *Rothi* Jeannel, 1923: Jeannel, 1924a: 308.
Drimeotus* (*Bihorites*) *mihoki similis Bokor, 1913
Drimeotus similis Bokor, 1913a: 446.
Drimeotus (s. str.) *similis* Bokor: Jeannel, 1914b: 43.
Drimeotus (*Bihorites*) *Mihoki* subsp. *similis* Bokor: Jeannel, 1923b: 446.

Subgenus ***Drimeotinus*** Jeannel, 1923
Drimeotinus Jeannel, 1923b: 439.

TYPE SPECIES. *Drimeotus ormayi* Reitter, 1889 by original designation (for the habitus see that of the similar species *Drimeotus* (*Drimeotinus*) *attenuatus montiscetii* in Fig. 235.3).

DIAGNOSIS. The most outstanding traits of differentiation of the subgenus are: size between 3.5-4.0 mm. Long and raised pubescence.

Elytra: With four well defined ripples, and between the intervals two regular longitudinal rows of



FIGURES 239.1–239.4: *Drimeotus* series. Metendosternite of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *Pholeuon* (*Parapholeuon*) *gracile gracile*, (**3**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**4**) *Sinobathyscia tianma* (modified from Wang *et al*. 2017). Red arrow pointing to the anterior furcal plate.

thick spots; wide marginal ridge of uniform width and the margin fringed with long hairs.

Median lobe of aedeagus: In lateral view (Fig. 240.3) similar to *Bihorites*, but the median lobe narrower and more elongated, and the apical area longer with a narrower, sharper and more curved tip towards the ventral side.

Parameres (Fig. 243.6): Apical part long, narrow and recurved, with four small apical setae, which was by Jeannel (1924a) described differently as exhibiting five setae.

Distribution. Romania, Transylvania. The troglobiomorphic species of this subgenus colonise cave systems in the Padurea Craiului mountains, in the North-Western part of the Apuseni mountains, Western Carpathians.

Species

Drimeotus* (*Drimeotinus*) *attenuatus Bokor, 1913
Drimeotus* (*Drimeotinus*) *attenuatus attenuatus Bokor, 1913
Drimeotus attenuatus Bokor, 1913a: 450.
Drimeotus (s. str.) *attenuatus* Bokor: Jeannel, 1914b: 42.
Drimeotus (*Drimeotinus*) *attenuatus* Bokor: Jeannel, 1923b: 442.
Drimeotus (*Drimeotinus*) *attenuatus attenuatus* Bokor: Perreau, 2000: 273.
Drimeotus* (*Drimeotinus*) *attenuatus montiscetii Jeannel, 1930
Drimeotus montiscetii Jeannel, 1930c: 50.
Drimeotus (*Drimeotinus*) *montis-cetii* Jeannel: Laneyrie, 1967: 615.
Drimeotus (*Drimeotinus*) *attenuatus montiscetii* Jeannel: Perreau, 2000: 273.

Drimeotus* (*Drimeotinus*) *ormayi Reitter, 1889
Drimeotus ormayi Reitter, 1889a: 301.
Drimeotus (s. str.) *Ormayi* Reitter: Jeannel, 1910a: 40.
Drimeotus (*Drimeotinus*) *Ormayi* Reitter: Jeannel, 1923b: 441.

Subgenus *Drimeotus*

Diagnosis. In addition to the general characteristics of the genus in the following there are also the most characteristic features suitable for clear determination: size ranging between 3.5-4.5 mm; long and raised pubescence, generally with regular distribution.

Elytra: Fairly strongly dotted, not rough, with large spots which are not well separated; there are four more or less blurred ridges, without regular longitudinal rows of dots over the intervals; marginal rim very wide, asymmetrical, wider towards the middle, and the edge with a fringe of hairs longer and more robust than those at the elytral surface.

Legs: Onychium of posterior tarsomeres clearly shorter than first the four tarsomeres combined. Spiny tibiae and non-serrated trochanters in males and females; straight meso- and metatibiae.

Mesoventral keel (Fig. 237.1): High, with the anterior border in a smooth regular arc and the apex in the form of a small spine.

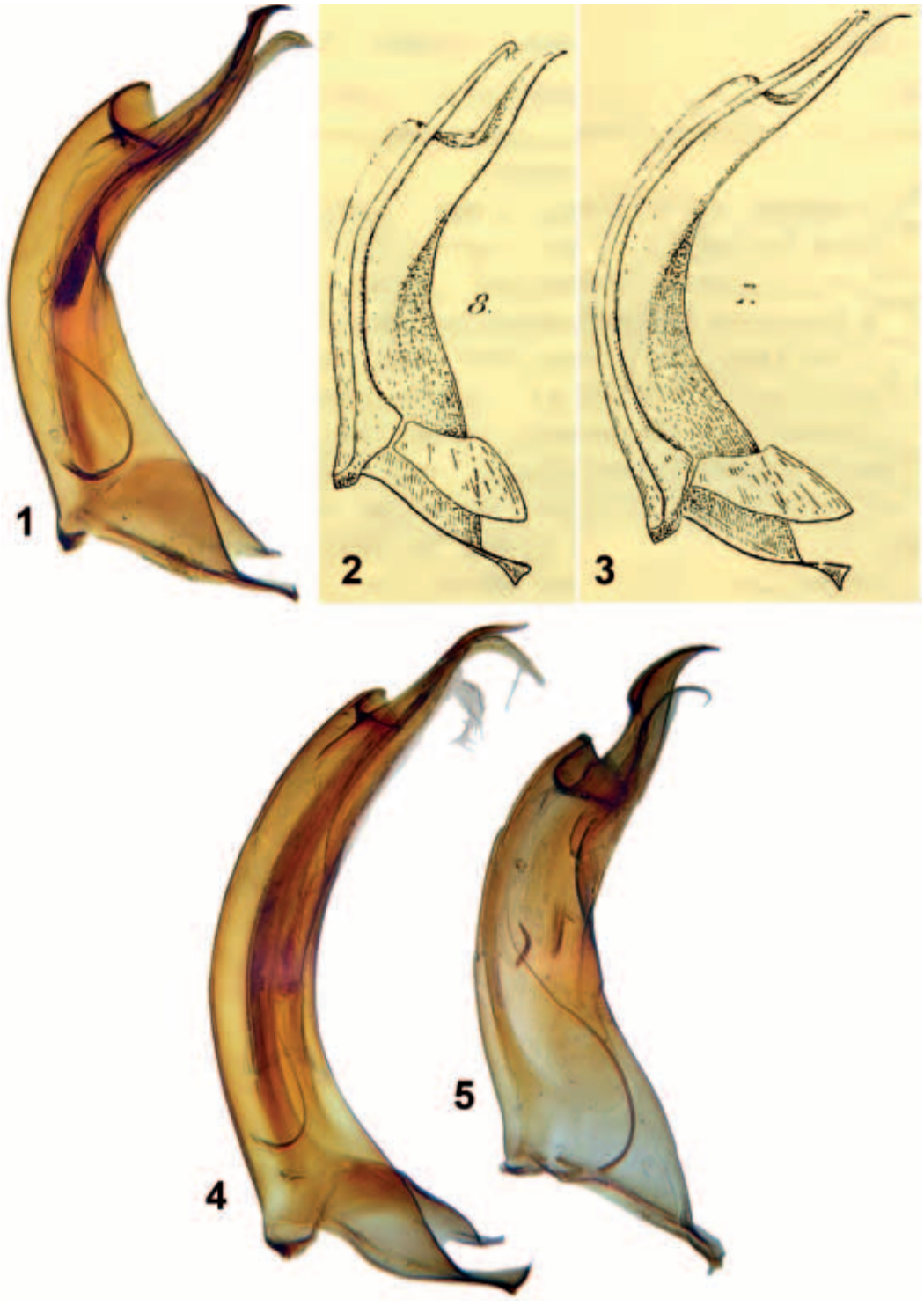
Median lobe of aedeagus: With very marked and deep dorsal invagination of the median lobe. In lateral view (Fig. 240.1) this ends in the form of a short beak, in some species slightly dilated or broken. Basal lamina of median lobe well-developed and the extension in the middle posterior area somewhat longer and the final area less wide. In dorsal view (Fig. 242.1), the most arched sides and the area where the invagination is widest.

Endophallus (Fig. 242.1): With the two groups of sclerotized spines, with species-specific degrees of development of those spines.

Parameres (Fig. 243.4): As long as or almost as long as the median lobe, with elbowed and slightly dilated apical area and with three small apical setae.

Discussion. Moldovan (2000b) established six groups for the species of this subgenus, the classification is based on certain external morphological characters; most importantly on the morphology of the aedeagus, mainly the dorsal invagination and apical and basal plates of the median lobe but also the groups of spines in the middle region of the endophallus. In addition to this, the geographical distribution is considered as an important information for taxonomic evaluation in cave species, even though there is no causal link between geographical distribution, molecular distance and morphological characters, it can be assumed that these are informative regarding the relationship amongst the species.

Distribution. Romania, Transylvania. The 12 species of this subgenus are endemic to the Padurea Craiului mountains found in the North-Western part of the Apuseni mountains, located between the Vad-Borod and Beiuş depressions.



FIGURES 240.1–240.5: *Drimeotus* series. Aedeagus in lateral view of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *D.* (*Bihorites*) *laevimarginatus laevimarginatus,* (**3**) *D.* (*Drimeotinus*) *ormayi*, (**4**) *D.* (*Fericeus*) *kraatzi*, (**5**) *Pholeuon* (*Parapholeuon*) *mocsaryi*. Figs **2**, **3** modified from Jeannel (1923).

Species

Drimeotus (***Drimeotus***) ***bokori*** Csiki, 1911
Drimeotus (***Drimeotus***) ***bokori bokori*** Csiki, 1911
Drimeotus bokori Csiki, 1911b: 138.
Drimeotus (s. str.) *Kováczi* subsp. *Bokori* Csiki: Jeannel, 1923b: 450.
Drimeotus Bokori subsp. *Bokori* Cs.: Jeannel, 1930c: 59.
Drimeotus (***Drimeotus***) ***bokori thoracicus*** Knirsch, 1913
Drimeotus thoracicus Knirsch, 1913a: 110.
Drimeotus (s. str.) *thoracicus* Knirsch: Jeannel, 1914b: 44.
Drimeotus (s. str.) *Kováczi* subsp. *thoracicus* Knirsch: Jeannel, 1923b: 449.
Drimeotus Bokori subsp. *thoracicus* Kn.: Jeannel, 1930c: 59.

Drimeotus (***Drimeotus***) ***breiti*** Jeannel, 1923
Drimeotus breiti Jeannel, 1923c: 604.
Drimeotus (s. str.) *Breiti* Jeannel, 1923: Jeannel, 1924a: 309.

Drimeotus (***Drimeotus***) ***chyzeri*** Biró, 1897
Drimeotus (***Drimeotus***) ***chyzeri chyzeri*** Biró, 1897
Drimeotus chyzeri Biró, 1897: 447.
Drimeotus (s. str.) *Chyzeri* Biro: Jeannel, 1910a: 41.
Drimeotus (***Drimeotus***) ***chyzeri vicinus*** Jeannel, 1930
Drimeotus chyzeri vicinus Jeannel, 1930c: 58.

Drimeotus (***Drimeotus***) ***entzi*** Biró, 1897
Drimeotus (***Drimeotus***) ***entzi chappuisi*** Winkler, 1933
Drimeotus entzi chappuisi Winkler, 1933: 77.
Drimeotus (*Drimeotus*) *entzi chappuisi* Winkler: Perreau, 2000: 274.
Drimeotus (***Drimeotus***) ***entzi entzi*** Biró, 1897
Drimeotus entzii Biró, 1897: 448.
Drimeotus (s. str.) *Entzi* Biro: Jeannel, 1910a: 41.
Drimeotus (s. str.) *entzii entzii* Biró: Perreau, 2000: 275.
Drimeotus (***Drimeotus***) ***entzi gracilis*** Jeannel, 1930
Drimeotus entzi gracilis Jeannel, 1930c: 57.
Drimeotus (*Drimeotus*) *entzi gracilis* Jeannel: Perreau, 2000: 275.

Drimeotus (***Drimeotus***) ***horvathi*** Biró, 1897
Drimeotus horváthi Biró, 1897: 448.
Drimeotus (s. str.) *Horvathi* Biro: Jeannel, 1910a: 41.

Drimeotus (***Drimeotus***) ***kovacsi*** L. Miller, 1856
Drimeotus kovacsii L. Miller, 1856b: 636.
Drimeotus Kovacsi Mill.: Reitter, 1885a [1884]: 14.
Drimeotus (s. str.) *Kovacsi* L. Miller: Jeannel, 1910a: 41.

Drimeotus (***Drimeotus***) ***octaviani*** Moldovan, 1997
Drimeotus octaviani Moldovan, 1997: 170.
Drimeotus (*Drimeotus*) *octaviani* Moldovan: Perreau, 2000: 275.

Drimeotus (***Drimeotus***) ***osoiensis*** Moldovan, 2000
Drimeotus osoiensis Moldovan, 2000b: 150.
Drimeotus (*Drimeotus*) *osoiensis* Moldovan, 2000: Perreau, 2004: 165.

Drimeotus (***Drimeotus***) ***plesai*** Moldovan, 2000
Drimeotus plesai Moldovan, 2000a: 90.
Drimeotus (*Drimeotus*) *plesai* Moldovan, 2000: Perreau, 2004: 165.

Drimeotus (***Drimeotus***) ***puscariui*** Jeannel, 1930
Drimeotus puscariui Jeannel, 1930c: 55.
Drimeotus (s. str.) *puscariui* Jeannel 1930: Racoviţă, 1985: 69.

Drimeotus (***Drimeotus***) ***racovitai*** Moldovan, 2000
Drimeotus racovitai Moldovan, 2000b: 150.
Drimeotus (*Drimeotus*) *rakovitai* Moldovan, 2000: Perreau, 2004: 165.

Drimeotus (***Drimeotus***) ***viehmanni*** Ienistea, 1955
Drimeotus kovacsi viehmanni Ienistea, 1955: 418, 425.
Drimeotus (s. str.) *viehmanni* Ienistea 1955: Racoviţă, 1985: 69.

Subgenus ***Fericeus*** Reitter, 1884
Fericeus Reitter, 1885a [1884]: 13.

Type species. *Drimeotus kraatzi* E. Frivaldszky & J. Frivaldszky, 1857 by monotypy (habitus in Fig. 235.4).

Diagnosis. The most prominent trait of the subgenus is its size, ranging between 3.8-4.0 mm. In general, it very much resembles *Drimeotus* s. str. with identical or very similar stated for important characters, with the pronotum slightly narrower and usually more convex, as well as a lateral-basal margin more sinuous than in *Drimeotus* s. str.; in addition a more oval elytra and the ripples more protruding.



FIGURES 241.1–241.4: *Drimeotus* series. Aedeagus in lateral view of: (**1**) *Pholeuon* (*Pholeuon*) *leptodirum leptodirum,* (**2**) *P.* (*Mesopholeuon*) *comani* (modified from Moldovan *et al*. 2007), (**3**) *Protopholeuon hungaricum,* (**4**) *Sinobathyscia tianma* (modified from Wang *et al*. 2017).

Legs: The onychium of metatarsomeres is very long, as long as the combined length of the other four tarsomeres; meso- and metatibiae of males are not reinforced, widened and curved into the shape of a sword, and with toothed pro- and mesotrochanters.

Mesoventral keel (Fig. 237.2): With the upper part of the anterior border concave and with the lower area straight; developed apex spine; toothed ventral edge.

Suture of the metaventrite (Fig. 237.2): Forms a regular arc, slightly sinuous at the base that delimits a narrow area which is slightly wider in the middle part.

Median lobe of aedeagus: Compared to *Drimeotus*

s. str., in lateral view (Fig. 240.4), with the dorsal transverse invagination less deep, with the apical area more pointed and narrower and the basal lamina more developed. In dorsal view (Fig. 242.2), slightly longer and narrower.

Endophallus (Fig. 242.2): With the two longest spine groups and the smallest spines; the reinforcing bands (bra) longer and narrower.

Parameres: With curved apical area, sharp and elongated, with three apical setae.

Discussion. The basic differences of this subgenus when compared to the closely related species are the well-marked ripples on the elytra and the unarmed meso- and metatibiae, which are widened and curved in males, in addition to the toothed pro- and mesotrochanters; also, in the median lobe of aedeagus (Fig. 240.4) where the dorsal transverse invagination is much less shallow.

Distribution. Romania, Transylvania. Monospecific subgenus found in the Ferice cave in the Crişul Pietros river basin, Apuseni mountains in the Western Carpathians.

Species

Drimeotus (***Fericeus***) ***kraatzi*** E. Frivaldszky & J. Frivaldszky, 1857
Drimeotus kraatzi E. Frivaldszky & J. Frivaldszky, 1857: 45.
Fericeus Kraatzi Friv.: Reitter, 1885a [1884]: 13.
Drimeotus (*Fericeus*) *Kraatzi* Frivaldszky: Jeannel, 1910a: 41.
Drimeotus (s. str.) *Kraatzi* E & J. Frivaldszky: Jeannel, 1914b: 44.

Subgenus ***Trichopharis*** Knirsch, 1925
Trichopharis Knirsch, 1925a: 43.

Type species. *Drimeotus blidarius* Knirsch, 1925 by monotypy.

Diagnosis (Knirsch 1925). The most apparent traits of the subgenus are: size 3.6 mm. Very short and raised pubescence.

No material has been available for study and no published image of the habitus could be found

Elytra: With three blurred ripples; fine, rough dotting, with the dots placed close together and arranged in diffuse transverse rows; marginal ridge of the elytra wide and regular, marginal hairs short.

Legs: With both, the meso- and the metatibiae curved, wide and flattened; mesotibiae with fine spines and metatibiae without spines. Meso- and metatrochanters without teeth. The onychium of metatarsals a touch shorter than the four anterior metatarsomeres.

Distribution. Romania, Transylvania. Troglobitic genus from the Apuseni mountains whose type series was captured in the Pîrăul Budului cave near Cociuba Mare, Western Carpathians.

Species

Drimeotus (***Trichopharis***) ***blidarius*** Knirsch, 1925
Drimeotus blidarius Knirsch, 1925a: 43.
Drimeotus (*Trichopharis*) *blidarius* Knirsch, 1925: Jeannel, 1925: 73.

Genus ***Pholeuon*** C. Hampe, 1856
Pholeuon C. Hampe, 1856: 463.
Apropeus Reitter, 1885a [1884]: 13 (Type species: *Pholeuon leptodirum* E. Frivaldszky & J. Frivaldszky, 1857).
Irenellum Csiki, 1911a: 106 (Type species: *Pholeuon* (*Irenellum*) *Mihóki* Csiki, 1911).

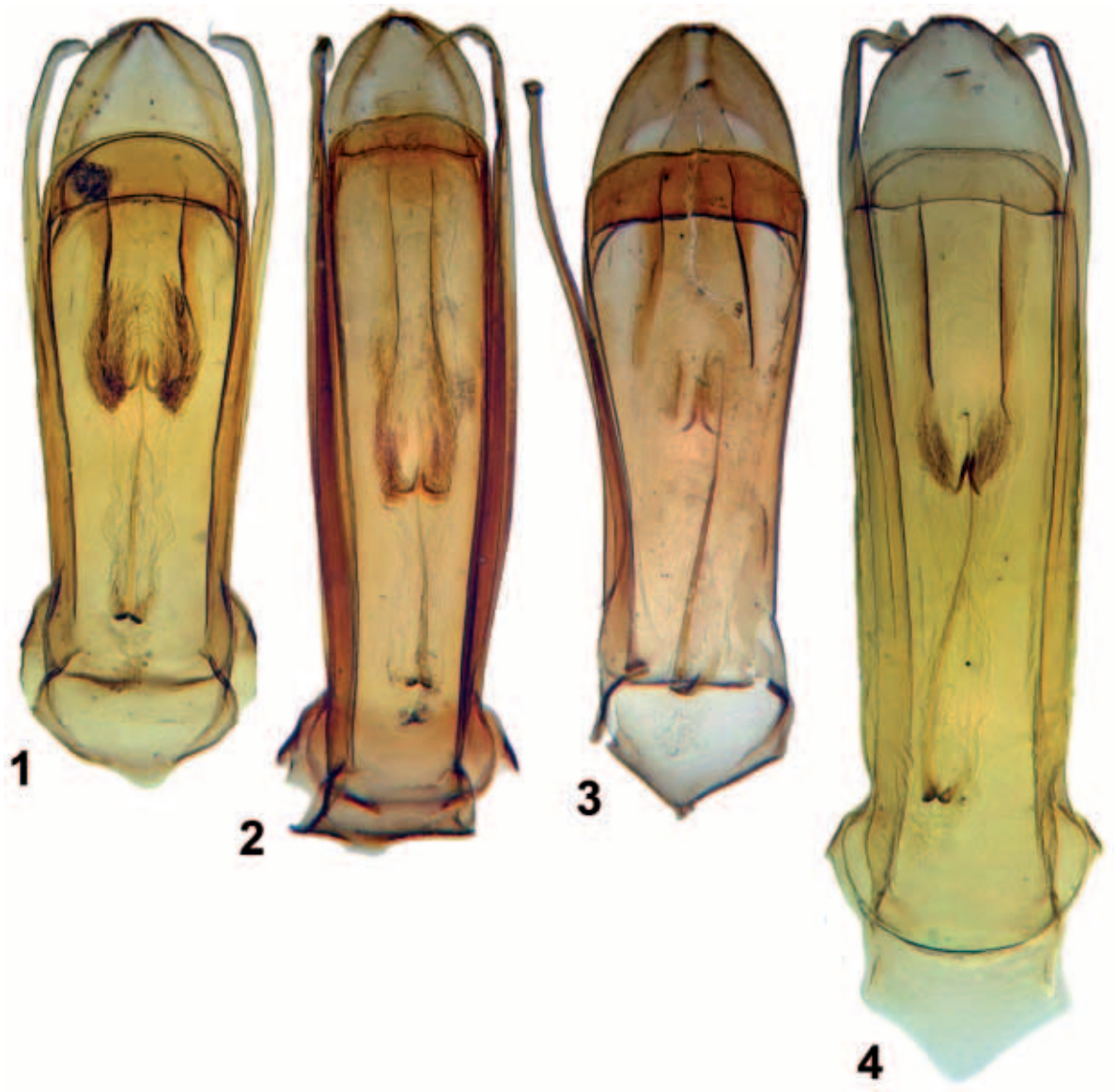
Type species. *Pholeuon angusticolle* Hampe, 1856 by monotypy (for the habitus see that of the similar species *Pholeuon* (*Pholeuon*) *leptodirum* in Fig. 236.2).

Diagnosis. Length, 4.5-6.5 mm. Body robust, elongated, convex and clearly narrowing towards the front (Fig. 236.2). Surface marked by fine punctation, without transverse striolae. Fine, short and lying pubescence.

Antennae: Generally longer than half a body length, with the club antennomeres not dilated, cylindrical and not flattened, the 8th antennomere usually more than twice as long as wide.

Pronotum: Subcordiform, narrow and elongated, ranging from as long as wide until slightly longer than wide (for *Pholeuon* s. str.) or slightly wider than long (for *Mesopholeuon*), lateral margins only ridged in the posterior half, curved anterior half and very narrow and sinuous on the posterior half; more or less pointed vertices and acute angles; base clearly narrower than the anterior part of the elytra.

Elytra: Rather convex, elongated, ranging one and a half to little more than twice as long as wide, with the maximum width around the middle and dilated posteriorly, which gives them a marked physogastria;



FIGURES 242.1–242.4: *Drimeotus* series. Aedeagus in dorsal view of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *D.* (*Fericeus*) *kraatzi*, (**3**) *Pholeuon* (*Parapholeuon*) *mocsaryi*, (**4**) *P.* (*Pholeuon*) *leptodirum leptodirum.*

short and regular pubescence; narrow marginal groove or ridge, not widening around the middle, in some cases blurred in the anterior part, and the hairs along the edge short; neither the ripples nor the aligned points are visible.

Legs: Very long and thin; male protarsi enlarged, being as wide or slightly narrower than most extended part of the tibiae; meso- and metatibiae cylindrical, straight, with small spines on the outer edge.

Mesoventral keel (Fig. 237.4): Atrophied or not well-developed, in this case reduced to a small tipped triangular tooth, with a narrow and weakly toothed ventral margin; intercoxal process of broad and convex metaventrite.

Suture of the metaventrite (Fig. 237.4): In a slightly sinuous arc that delimits a narrow area, slightly wider around the middle part.

Metatergal apparatus (Fig. 238.3): With long

metascutum wings, very narrow from the middle to the apex, and the apophysis of the alacrista long with narrow edges.

Metendosternite (Fig. 239.3): With long, narrow and slightly undulating furcal arms, almost twice the length of the trunk, with a sharp curved in the apical area and a reduced terminal apophysis; the posterior lamina, which is narrow, reaches the apical area of the arm and is wider in the area where it joins the trunk; in this area an curved lateral flange exists. Furcal trunk wider in the apical and basal areas, and almost two times longer than wide; posterior area of median keel of the furca widely divergent.

Median lobe of aedeagus: Long, rather narrow and curved, slightly more than four times longer than wide and as long as a third of the length of the body. In lateral view (Fig. 241.1), with a deep and wide dorsal depression towards the fifth apical, similar to that found in *Drimeotus;* the apical lamina of variable length and shape that ends in a beak-shaped apex inclining towards the front, usually slightly dilated. In dorsal view (Fig. 242.4), with slightly curved lateral margins, almost parallel, with a slightly tipped apical area; the basal pieces, ventral lamina of the tegmen and basal lamina, in general short, the latter somewhat tipped in the middle of the posterior margin.

Endophallus (Fig. 242.4): It presents a special armour; in the basal region a fine, long and curved filament whose wider base is fixed in the bottom of the sac; towards the middle region there are two packages of more or less developed sclerotized spines fixed at the base of the reinforcing bands that are fairly long, and between them there is a small piece in the shape of an «W».

Parameres (Fig. 243.9): Shorter than the median lobe, they show a bent apical area, and a short or long final prolongation, in this case curved in an «S»-shape with a sharp tip, armed with three short setae.

Spermathecal complex: Short spermatheca (Fig. 244.3), with well sclerotized lobes, the apical being spherical and slightly wider than the basal one, the latter elongated with slightly curved edges; hyaline junction duct as long as or slightly longer than the basal lobe; spermatic duct short, slightly sclerotized and swollen along the middle; a spermathecal gland is present.

Female uroventrite VIII (Fig. 245.4): With the middle area of the posterior margin gently concave; the spiculum is short, wide at the base and not very sharp at the apex.

Discussion. *Pholeuon* and *Protopholeuon* seem morphologically more specialized than *Drimeotus* and are assumed to be the first colonisers of the subterranean environment in the Apuseni mountains (Moldovan *et al.* 2007). In the phylogenetic tree (Fig. 1D) *Pholeuon* is sister to the genera *Protopholeuon* with very low to no support, 0/19. The external characters that best define this genus are the pubescence, the marginal ridge of the pronotum and, especially the shape of the mesoventral keel; in addition, in the aedeagus, the shape of the median lobe, of the parameres and the model of the endophallus are characters suitable to provide information for identification and differentiation of species.

Distribution. Romania, Transylvania. Endemic to the Apuseni mountains, Western Carpathians.

Subgenus ***Mesopholeuon*** Moldovan, Racoviţă & Dunay, 2007
Pholeuon (*Mesopholeuon*) Moldovan, Racoviţă & Dunay, 2007: 36.

Type species. *Pholeuon comani* Ienistea, 1955 by original designation (habitus in Fig. 236.3).

Diagnosis. Length 3.0-3.5 mm. Body elliptical, elongated and convex, slightly narrower towards the front (Fig. 236.3). Surface marked by small and scattered dots. Light brown colour. Short and dense pubescence.

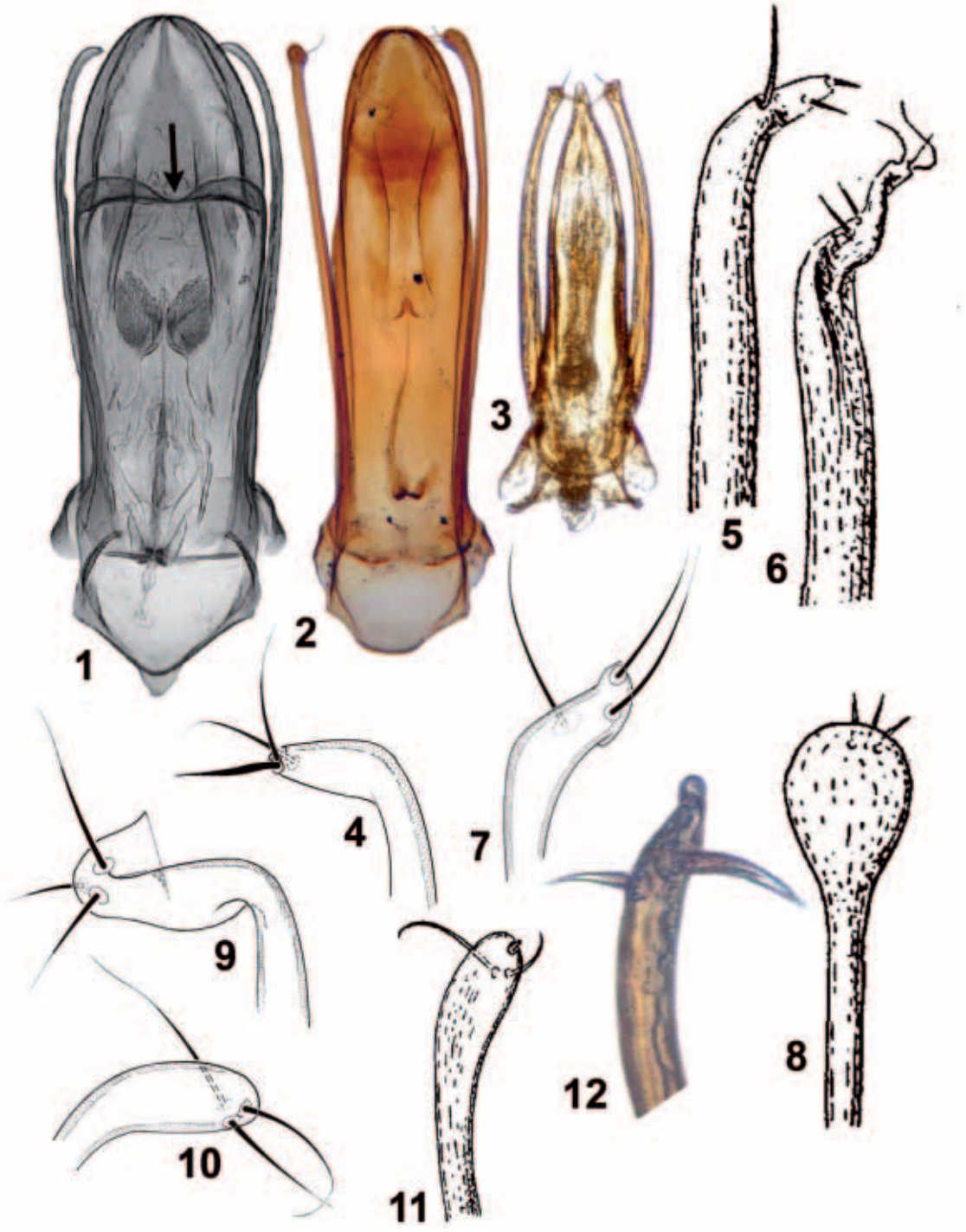
Antennae: Almost half the length of the body; 7th and 10th antennomeres one and a half times longer than wide, which are the shortest on the club.

Pronotum: Short and narrow, very slightly wider than long; very narrow in the anterior part, about half width of the basal area; rear borders nearly parallel, very slightly sinuous; basal area narrower than the anterior area of elytra.

Elytra: Elliptic and convex, slightly more than one and a half times longer than wide; widest in the anterior half, distinctly wider than the pronotum; dotting formed by scattered, unaligned small dots; short and dense pubescence.

Legs: Male protarsi slightly widened.

Median lobe of aedeagus: Short, thick and slightly curved, total length around a third of the body length. In lateral view (Fig. 241.2), the middle part of the lobe between the dorsal transverse invagination and the basal lamina shorter than in *Pholeuon* s. str. In dorsal view (Fig. 243.1), with regularly curved lateral edges, with the apical area in a wide arc and the invagination



FIGURES 243.1–243.12: *Drimeotus* series. Aedeagus in dorsal view of: (**1**) *Pholeuon* (*Mesopholeuon*) *comani* (modified from Moldovan *et al*. 2007), (**2**) *Protopholeuon hungaricum,* (**3**) *Sinobathyscia tianma*. Apex of paramere of: (**4**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**5**) *D.* (*Bihorites*) *mihoki*, (**6**) *D.* (*Drimeotinus*) *ormayi*, (**7**) *P.* (*Parapholeuon*) *mocsaryi*, (**8**) *P.* (*Parapholeuon*) *gracile gracile*, (**9**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**10**) *Protopholeuon hungaricum,* (**11**) idem, (**12**) *Sinobathyscia tianma*. Figs **5**, **6**, **8**, **11** modified from Jeannel (1924a); Figs **3**, **12** from Wang *et al*. (2017).

very reduced in the middle area. Basal lamina of the median lobe short, wide, and the middle posterior area pointed.

Endophallus (Fig. 243.1): With two groups of small sclerotized spines located at the base of the reinforcing bands, and in the basal region there is a fine and not very long filament or flagellum located.

Parameres (Moldovan *et al*. 2007): Slender, somewhat shorter than the median lobe, with the apical area not dilated and somewhat curved, with three small setae.

Spermathecal complex (Fig. 244.4): Similar to *Pholeuon,* although the spermatic duct (s) shows a somewhat wider middle part.

Discussion. *Mesopholeuon* represents an intermediate form being morphologically in between *Protopholeuon* and the subgenus *Pholeuon* s. str. The differentiating characters when compared to the subgenus *Pholeuon* s. str. are in the body shape and the form of the aedeagus. It represents the smallest *Pholeuon*, with a slightly more transverse pronotum and shorter antennae; the aedeagus exhibits taxonomically highly relevant differences; in it the middle part of the lobe is shorter in the part between the transverse invagination and the basal lamina; in addition, the dorsal invagination of the median lobe is more reduced in the middle part and the apical part of the parameres is thinner, slightly more curved.

Distribution. Romania, Transylvania. Southeastern area of the Apuseni mountains, in the Codru-Moma mountains area in Crişana (Moldovan *et al.* 2007).

Species

Pholeuon (***Mesopholeuon***) ***comani*** Ienistea, 1955
Pholeuon comani Ienistea, 1955: 417, 424.
Pholeuon (s. str.) *comani* Ienistea: Perreau, 2000: 280.
Pholeuon (*Mesopholeuon*) *comani* Ienistea: Moldovan, Racoviţă & Dunay, 2007: 36.

Subgenus ***Parapholeuon*** Ganglbauer, 1887
Pholeuon (*Parapholeuon*) Ganglbauer, 1887: 95.

Type species. *Pholeuon gracile* J. Frivaldszky, 1861 by original designation (habitus in Fig. 236.1).

Diagnosis. Length, 3.5-4.5 mm. Body shape elliptical, narrow, elongated and convex, clearly narrowed towards the front; pholeuonoid facies (Fig. 236.1). Sculpture formed by irregular and poorly defined dots, without transverse striation. Long, dense and raised pubescence.

Antennae: Reaching two thirds of the length of the body, the club antennomeres slightly dilated, not flattened and cylindrical, the 8th antennomere being a bit more than twice as long as it is wide.

Pronotum: Slightly convex, as wide as or slightly wider than long; lateral margins flanged throughout their length, rounded towards the front, straight and parallel in the posterior third; pointed vertices projecting outwards; rectilinear base, slightly wider than the anterior region.

Elytra: Convex and oval, almost twice as long as wide, with widest towards the middle; the marginal groove or ridge is wide, and widening toward middle, with long hairs at the edges; dots not aligned, larger than those on the head and pronotum.

Legs: Long and thin; male protarsi enlarged, being slightly narrower than the apical area of the protibiae; both meso- and metatibiae cylindrical, straight with small spines on the outer edge.

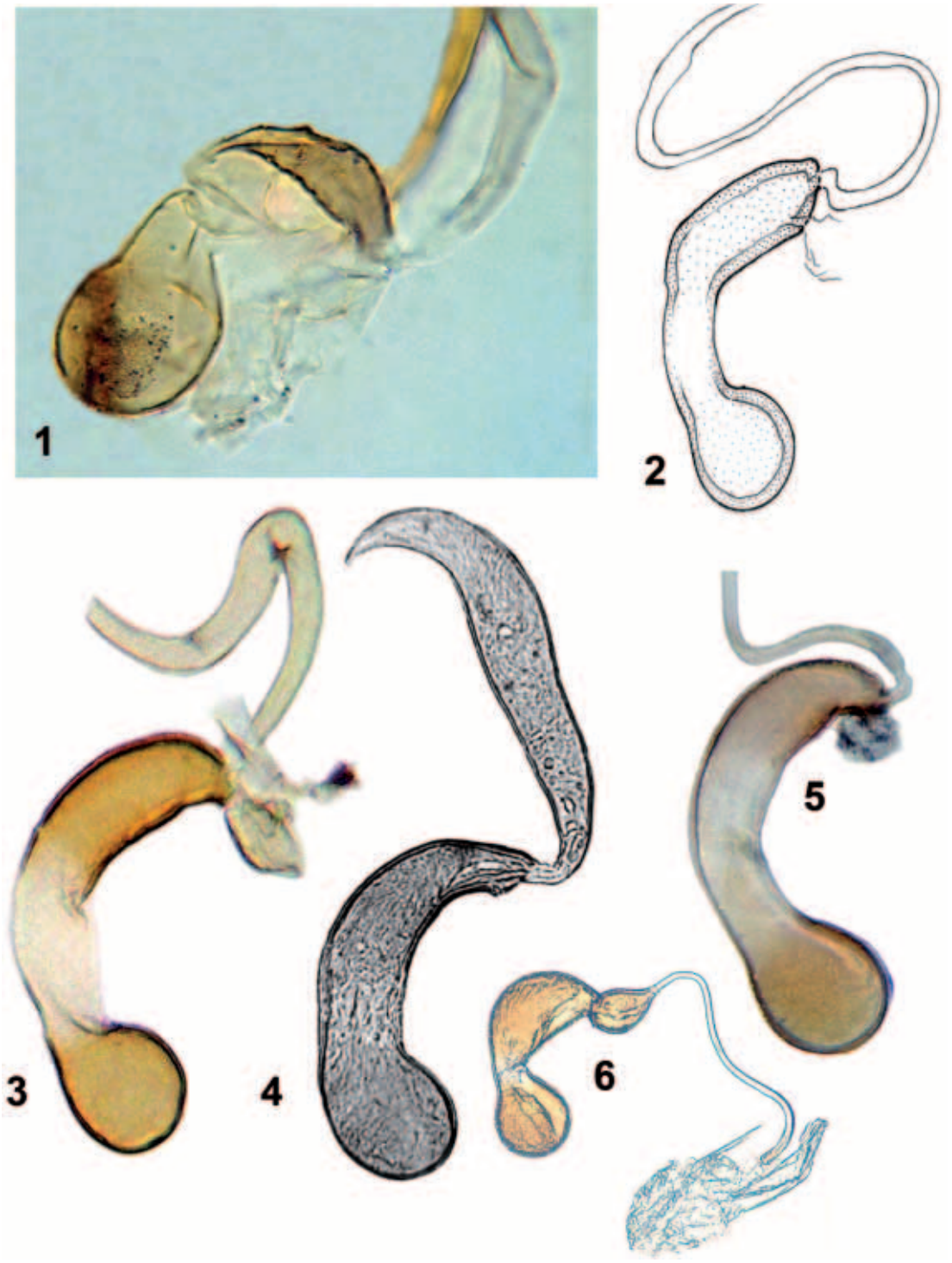
Mesoventral keel (Fig. 237.3): Well-developed, in the shape of a large, triangular tooth with a slightly sharp apex, the angle slightly wider than 90º; the anterior border slightly curved and the ventral one very concave and smooth.

Suture of the metaventrite (Fig. 237.3): In a regular arc, which encompasses a very narrow area.

Metatergal apparatus (Fig. 238.2): Metascutum wings long and very narrow, the apophysis of the alacrista hardly detectable.

Metendosternite (Fig. 239.2): Furcal arms long, stretched and slightly undulated, more than three times the length of the trunk, with an apical part forming a pointed arc and reduced terminal apophysis; a reduced furcal anterior lamina is present between internal edges of the anterior keel, while the posterior lamina is strongly reduced, almost non-existed in the apical part the posterior edge of the anterior keel and wider between the basal part of the arm and the trunk. Furcal trunk very short and wider than long, with the part of the middle part of the keel strongly divergent. The general form of the metendosternite is very much alike those in *Pholeuon*, although in this no anterior lamina is observed.

Median lobe of aedeagus: Short, thick and slightly curved, as long as one third of the total body length. In lateral view (Fig. 240.5), with a deep and wide dorsal invagination; apical lamina of the lobe pointed at the apex and curved towards the ventral side, this lamina is shorter and less dilated in *P. gracile* and longer and dilated in *P. angustiventre* and *P. mocsaryi*



FIGURES 244.1–244.6: *Drimeotus* series. Spermathecal complex of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *Pholeuon* (*Parapholeuon*) *mocsaryi*, (**3**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**4**) *P.* (*Mesopholeuon*) *comani* (modified from Moldovan *et al*. 2007), (**5**) *Protopholeuon hungaricum,* (**6**) *Sinobathyscia tianma* (modified from Wang *et al*. 2017).

(Racoviţă 1999: Fig. 8). In dorsal view (Fig. 242.3), the basal half is narrow and the lateral margins slightly concave; in the apical half wider and with more curved margins; short basal pieces.

Endophallus (Fig. 242.3): Exhibits a peculiar armour, in the basal region of the sac there is a narrow and elongated slightly sclerotized lamina in which a long and fine filament is fixed; in the middle region there are two packages of more or less developed spines, depending on the species, they are fixed at the base of the narrow reinforcing bands and, between them, there is a small sclerotized piece in the shape of an «W».

Parameres (Fig. 243.7): Thin and almost reaching the apex of the median lobe; they show the apical part slightly bent in *P. angustiventre* and *P. moczaryi*, in which three short setae are inserted and the club is inconspicuous; in *P. gracile* the apical area is not curved and forms a small flattened club with three small setae at the apex.

Spermathecal complex: Short spermatheca (Fig. 244.2), with both lobes sclerotized, the apical one being spherical and wider than the basal one, the latter elongated; between the two of them there is a short and hyaline junction duct; little sclerotized spermatic duct without basal nodule and with an almost regular width throughout its entire length; a spermathecal gland is present.

Female uroventrite VIII (Fig. 245.2): With the posterior margin forming a wide arc, the spiculum very short and curved, and sharp apex.

Discussion. Bucur *et al.* (2003) wrote about the geographical distribution of the phyletic lineage of *Drimeotus,* identifying five parts in the Apuseni mountains. In a first one there are three species of the genus *Parapholeuon* being found. Racoviţă (2011) highlighted that these three species of *Parapholeuon* inhabit an independent orographic area and that, in the dendrogram obtained by numerical analysis, these three species and the three subspecies of *P. gracile* form an independent clade. Lately, Bucur *et al.* (2022), showed in a comparative phylogeographical analysis, that there is an isolated area colonised by the three species of *Parapholeuon*, with no overlap with the species of *Pholeuon* s. str. (*P. angusticolle*, *P. knirschi,* and *P. leptodirum*). The morphological differences of *Parapholeuon,* compared to the other subgenera are very obvious, and including those concerning the length of the pubescence and the antennae, the shape of the mesoventral keel and the dotted elytra, as well as significant differences in the shape of the apex of the parameres and the shape of the apical area of the median lobe of aedeagus. Also, a clear isolation of its geographical area can be added (Moldovan *et al.* 2007).

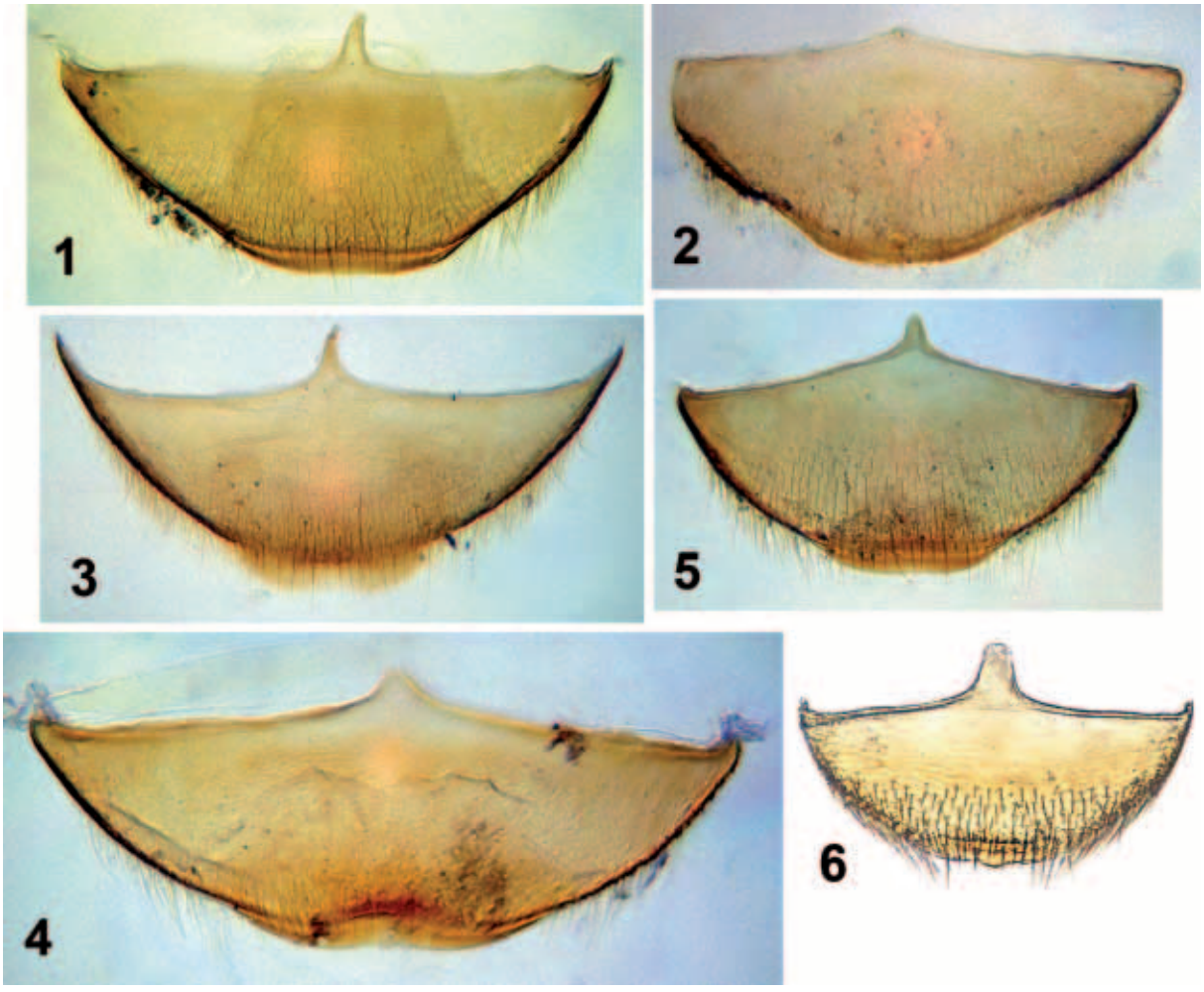
Distribution. Romania, Transylvania. Subgenus represented by three strictly troglobitic species that are distributed in the Pădurea Craiului karstic massif delimited by the three rivers with Vida to the west, Crişul Repede to the north and Brâtcuţa to the east, in the Western Carpathians (Racoviţă 1996, 1999). Moldovan *et al*. (2007) also pointed out for *Pholeuon*, *Protopholeuon* and the subgenus *Parapholeuon*, that their distribution in the Apuseni mountains, comprise of three isolated geographic areas, being the northernmost region colonised by *Parapholeuon* species.

Species

Pholeuon* (*Parapholeuon*) *augustiventre Racoviţă, 1996
Pholeuon (*Parapholeuon) augustiventre* Racoviţă, 1996: 102.

Pholeuon* (*Parapholeuon*) *gracile (J. Frivaldszky, 1861)
Pholeuon* (*Parapholeuon*) *gracile bokorianum (Csiki, 1911)
Pholeuon (*Irenellum*) *bokorianum* Csiki, 1911b: 137.
Pholeuon (*Parapholeuon*) *Bokorianum* Csiki: Jeannel, 1914b: 44.
Pholeuon (*Parapholeuon*) *gracile* ssp. *Bokorianum* Csiki: Jeannel, 1923b: 471.
Pholeuon* (*Parapholeuon*) *gracile chappuisi (Jeannel, 1930)
Pholeuon (*Parapholeuon) gracile chappuisi* Jeannel, 1930c: 61.
Pholeuon* (*Parapholeuon*) *gracile gracile (J. Frivaldszky, 1861)
Pholeuon gracile J. Frivaldszky, 1861: 387.
Pholeuon Gracile Friw.: Abeille de Perrin, 1876: 29.
Pholeuon (*Parapholeuon*) *gracile* Frivaldszky: Jeannel, 1910a: 41.
Pholeuon (*Parapholeuon*) *gracile* Subsp. *gracile* Frivaldszky: Jeannel, 1924a: 322.

Pholeuon* (*Parapholeuon*) *mocsaryi (Csiki, 1911)
Pholeuon (*Parapholeuon) Mocsáryi* Csiki, 1911a: 108.
Pholeuon (*Parapholeuon) moczaryi* Csiki: Racoviţă, 1971: 273.



FIGURES 245.1–245.6: *Drimeotus* series. Female uroventrite VIII of: (**1**) *Drimeotus* (*Drimeotus*) *viehmanni,* (**2**) *Pholeuon* (*Parapholeuon*) *gracile chappuuisi*, (**3**) *P.* (*Parapholeuon*) *mocsaryi*, (**4**) *P.* (*Pholeuon*) *leptodirum leptodirum,* (**5**) *Protopholeuon hungaricum,* (**6**) *Sinobathyscia kurbatovi* (modified from Wang *et al*. 2017).

Pholeuon (*Parapholeuon) bokori* Csiki, 1911a: 108.
Pholeuon (*Parapholeuon*) *Czáráni* Csiki, 1911a: 109.
Parapholeuon moczaryi Cs.: Mihut, 1997: 271.
Pholeuon gracile moczaryi Csiki: Bucur, Racoviţă & Seitz, 2001: 128.

Subgenus ***Pholeuon***

Diagnosis. The general characters that allow the identification of this genus were already described earlier. Here the differences to the subgenus *Mesopholeuon* will be highlighted, such as the unusually large size.

Pronotum: More robust, with the posterior vertices more pointed and more projecting outwards.

Elytra: More convex, more elongated, twice or almost two and a half times longer than wide, with the physogastry more pronounced.

Mesoventral keel (Fig. 237.4), *suture of the metaventrite* (Fig. 237.4), *metatergal apparatus* (Fig. 238.3) and *metendosternite* (Fig. 239.3): With the characters mentioned in the description above for these genus.

Median lobe of aedeagus: With longer and curved median lobe. In lateral view (Fig. 241.1), longer apical lamina which is also longer the middle part of the lobe

between the dorsal transverse invagination and the basal lamina. In dorsal view (Fig. 242.4), with an invagination wide and deeper.

Endophallus (Fig. 242.4): With the two groups of spines at the base of the reinforcing bands (bra), generally larger with more robust spines.

Parameres (Fig. 243.9): Slender, apical area more elongated and bent, generally curved.

Spermathecal complex (Fig. 244.3) and *female uroventrite VIII* (Fig. 245.4): Also with the characteristics mentioned in the description of the genus.

DISTRIBUTION. Romania, Transylvania. It colonises the central area that corresponds to the Bihor karstic massif in the Apuseni mountains of the Western Carpathians.

Species

Pholeuon (***Pholeuon***) ***angusticolle*** C. Hampe, 1856
Pholeuon (***Pholeuon***) ***angusticolle angusticolle*** C. Hampe, 1856
Pholeuon angusticolle C. Hampe, 1856: 463.
Pholeuon Angusticolle Hampe: Abeille de Perrin, 1876: 29.
Pholeuon (s. str.) *angusticolle* Hampe: Jeannel, 1910a: 41.
Pholeuon (s. str.) *angusticolle* Subsp. *angusticolle* Hampe, 1856: Jeannel, 1924a: 318.
Pholeuon (***Pholeuon***) ***angusticolle arpadi*** Csiki, 1912
Pholeuon arpadi Csiki, 1912a: 159.
Pholeuon csikii Mihók, 1912: 164.
Pholeuon (s. str.) *Arpádi* Csiki: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *angusticolle* subsp. *Arpadi* Csiki: Jeannel, 1923b: 460.
Pholeuon (***Pholeuon***) ***angusticolle bihariense*** Csiki, 1912
Pholeuon bihariense Csiki, 1912c: 539.
Pholeuon (s. str.) *bihariense* Csiki: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *angusticolle* subsp. *biharense* Csiki: Jeannel, 1923b: 459.
Pholeuon (s. str.) *angusticolle bihariense* Cs.: Moldovan, 1989: 41.
Pholeuon (***Pholeuon***) ***angusticolle mihoki*** Csiki, 1911
Pholeuon (*Irenellum*) *Mihóki* Csiki, 1911a: 107.
Pholeuon Mihóki Csiki: Jeannel, 1914b: 46.
Pholeuon (s. str.) *angusticolle* subsp. *Mihoki* Csiki: Jeannel, 1923.
Pholeuon (s. str.) *angusticolle mihoki* Csiki: Perreau, 2000: 278.
Pholeuon (***Pholeuon***) ***knirschi*** Breit, 1911
Pholeuon (***Pholeuon***) ***knirschi brachynotos*** Jeannel, 1923
Pholeuon proserpina brachynotos Jeannel, 1923b: 466.
Pholeuon (s. str.) *Proserpina* Subsp. *brachynotos* Jeannel, 1923: Jeannel, 1924a: 320.
Pholeuon (s. str.) *knirschi brachynotos* Jeannel, 1923: Racoviţă, 2005: 185.
Pholeuon (***Pholeuon***) ***knirschi brevicule*** Jeannel, 1923
Pholeuon knirschi brevicule Jeannel, 1923b: 463.
Pholeuon (s. str.) *Knirschi* Subsp. *brevicule* Jeannel, 1923: Jeannel, 1924a: 319.
Pholeuon (s. str.) *knirschi* Breit: Rusdea, 1989: 201.
Pholeuon (***Pholeuon***) ***knirschi cetatensis*** Jeannel, 1930
Pholeuon knirschi cetatensis Jeannel, 1930c: 60.
Pholeuon (***Pholeuon***) ***knirschi convexum*** Knirsch, 1913
Pholeuon convexum Knirsch, 1913b: 139.
Pholeuon kaleny aszense Bokor, 1913b: 589.
Pholeuon (s. str.) *convexum* Knirsch: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *Knirschi* subsp. *convexum* Knirsch: Jeannel, 1923b: 461.
Pholeuon kalenyászense Bokor, 1913b: 589.
Pholeuon (s. str.) *knirschi convexum* Knirsch: Perreau, 2000: 278.
Pholeuon (***Pholeuon***) ***knirschi dieneri*** Mihók, 1912
Pholeuon (*Irenellum*) *dieneri* Mihók, 1912: 165.
Pholeuon (*Irenellum*) *frivaldszkyi* Csiki, 1912c: 539.
Pholeuon (s. str.) *Dieneri* Mihok: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *Knirschi* subsp. *Dieneri* Mihók: Jeannel, 1923b: 462.
Pholeuon (*Pholeuon*) *Knirschi* subsp. *Frivaldszkyi* Csiki: Jeannel, 1923b: 462.
Pholeuon (***Pholeuon***) ***knirschi elemeri*** Csiki, 1912
Pholeuon (*Irenellum*) *elemeri* Csiki, 1912a: 158.
Pholeuon (*Parapholeuon*) *antrophilum* Knirsch, 1913c: 164.
Pholeuon (*Parapholeuon*) *antrophilum interceptum* Knirsch, 1913c: 165.
Pholeuon (s. str.) *Eleméri* Csiki: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *Knirschi* subsp. *Eleméri* Csiki: Jeannel, 1923b: 462.
Pholeuon (s. str.) *Elémeri* subsp. *interceptum* Knirsch: Jeannel, 1914b: 45.
Pholeuon (***Pholeuon***) ***knirschi glaciale*** Jeannel, 1923
Pholeuon proserpina glaciale Jeannel, 1923b: 466.
Pholeuon proserpina glaciale hebes Jeannel, 1923b: 467.

Pholeuon (s. str.) *Proserpina* Subsp. *glaciale* Jeannel, 1923: Jeannel, 1924a: 320.
Pholeuon (s. str.) *knirschi glaciale* Jeannel, 1923: Racoviţă, 2005: 185.
Pholeuon (s. str.) *proserpinae glaciale* Jeannel: Perreau, 2000: 281.
Pholeuon (***Pholeuon***) ***knirschi gyleki*** Moczarski, 1912
Pholeuon gyleki Moczarski, 1912: 117.
Pholeuon (*s. str.*) *Gyleki* Moczarski: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *Knirschi* subsp. *Gyleki* Moczarski: Jeannel, 1923b: 462.
Pholeuon (***Pholeuon***) ***knirschi intermittens*** Knirsch, 1913
Pholeuon (*Irenellum*) *proserpinae intermittens* Knirsch, 1913d: 254.
Pholeuon (*Pholeuon*) *Proserpina* ssp. *intermittens* Knirsch: Jeannel, 1923b: 465.
Pholeuon (s. str.) *knirschi intermittens* Knirsch, 1913: Racoviţă, 2005: 186.
Pholeuon (***Pholeuon***) ***knirschi knirschi*** Breit, 1911
Pholeuon knirschi Breit, 1911b: 172.
Pholeuon knirschi interruptum Csiki, 1912: 158.
Pholeuon (s. str.) *Knirschi* Breit: Csiki, 1911c: 141.
Pholeuon (*Irenellum*) *Knirschi* ab. *interruptum* Csiki, 1912a: 158.
Pholeuon (s. str.) *Knirschi* var. *interruptum* Csiki: Jeannel, 1914b: 46.
Pholeuon (s. str.) *knirschi knirschi* Breit: Perreau, 2000: 279.
Pholeuon (***Pholeuon***) ***knirschi proserpinae*** Knirsch, 1913
Pholeuon proserpinae Knirsch, 1913b: 140.
Pholeuon (s. str.) *Proserpinae* Knirsch: Jeannel, 1914b: 46.
Pholeuon (s. str.) *Proserpinae* Subsp. *Proserpinae* Knirsch, 1913: Jeannel, 1924a: 320.
Pholeuon (s. str.) *knirschi proserpinae* Knirsch, 1913: Racoviţă, 2005: 186.
Pholeuon (***Pholeuon***) ***knirschi serbani*** Ienistea, 1955
Pholeuon knirschi serbani Ienistea, 1955: 417, 425.
Pholeuon (s. str.) *knirschi serbani* Ienistea: Perreau, 2000: 279.

Pholeuon (***Pholeuon***) ***leptodirum*** E. Frivaldszky & J. Frivaldszky, 1857
Pholeuon (***Pholeuon***) ***leptodirum attila*** Csiki, 1912
Pholeuon attila Csiki, 1912a: 156.
Pholeuon (s. str.) *Attila* Csiki: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *leptoderum* subsp. *Attila* Csiki: Jeannel, 1923b: 468.
Pholeuon (***Pholeuon***) ***leptodirum biroi*** Csiki, 1912
Pholeuon biroi Csiki, 1912a: 157.
Pholeuon (s. str.) *Birói* Csiki: Jeannel, 1914b: 45.
Pholeuon (*Pholeuon*) *leptoderum* subsp. *Birói* Csiki: Jeannel, 1923b: 468.
Pholeuon (***Pholeuon***) ***leptodirum hazayi*** J. Frivaldszky, 1884
Pholeuon hazayi J. Frivaldszky, 1884: 280.
Pholeuon (s. str.) *Hazayi* J. Frivaldszky: Jeannel, 1914b: 46.
Pholeuon (*Pholeuon*) *leptoderum* subsp. *Hazayi* Frivaldszky: Jeannel, 1923b: 467.
Pholeuon (***Pholeuon***) ***leptodirum janitor*** Jeannel, 1923
Pholeuon leptoderum janitor Jeannel, 1923b: 469.
Pholeuon (s. str.) *leptoderum* Subsp. janitor Jeannel, 1923: Jeannel, 1924a: 321.
Pholeuon (s. str.) *leptodirum janitor* Jeannel: Perreau, 2000: 280.

Pholeuon (***Pholeuon***) ***leptodirum leptodirum*** E. Frivaldszky & J. Frivaldszky, 1857
Pholeuon leptodirum E. Frivaldszky & J. Frivaldszky, 1857: 44.
Pholeuon leptoderum Friv.: Motschulsky, 1869: 254.
Apropeus leptoderus Friv.: Reitter, 1885a [1884]: 13.
Pholeuon (s. str.) *leptoderum* Frivaldszky: Jeannel, 1910a: 41.
Pholeuon (s. str.) *leptoderum* Subsp. *leptoderum* Frivaldszky, 1857: Jeannel, 1924a: 321.
Pholeuon (s. str.) *leptodirum leptodirum* E. Frivaldszky & J. Frivaldszky: Perreau, 2000: 280.
Pholeuon (***Pholeuon***) ***leptodirum winkleri*** Jeannel, 1923
Pholeuon leptoderum winkleri Jeannel, 1923b: 469.
Pholeuon (s. str.) *leptoderum* Subsp. *Winkleri* Jeannel, 1923: Jeannel, 1924a: 322.
Pholeuon (s. str.) *leptodirum winkleri* Jeannel: Perreau, 2000: 280.

***Pholeuon* unavailable names**

Racoviţă (2005, 2007, 2009, 2010) propose different taxon names that does not comply with paragraf 16.4.1 and 16.4.2 of *the International Code of Zoological Nomenclature* (1999) regarding to the mandatory name-bearing type designation. Consequently, all the names of the taxa described are to be considered unavailable name.

Pholeuon angusticolle alunensis Racoviţă, 2009: 24 (Unavailable name).

Pholeuon angusticolle gujai Racoviţă, 2009: 24 (Unavailable name).
Pholeuon angusticolle longicornis Racoviţă, 2009: 24 (Unavailable name).
Pholeuon knirschi albacensis Racoviţă, 2005: 185 (Unavailable name).
Pholeuon knirschi christiani Racoviţă, 2005: 185 (Unavailable name).
Pholeuon knirschi onaci Racoviţă, 2007: 26 (Unavailable name).
Pholeuon knirschi vartopensis Racoviţă, 2005: 185 (Unavailable name).
Pholeuon leptodirum fagensis Racoviţă, 2010: 18 (Unavailable name).
Pholeuon leptodirum jeanneli Racoviţă, 2010: 18 (Unavailable name).
Pholeuon leptodirum moldovani Racoviţă, 2010: 18 (Unavailable name).
Pholeuon leptodirum nanus Racoviţă, 2010: 18 (Unavailable name).
Pholeuon leptodirum problematicus Racoviţă, 2010: 18 (Unavailable name).

Genus ***Protopholeuon*** Jeannel, 1923
Protopholeuon Jeannel, 1923b: 452.

Type species. *Pholeuon hungaricum* Csiki, 1904 by monotypy (habitus in Fig. 236.4).

Diagnosis. Length 3.8 mm. Elliptical shaped body, very elongated and narrowed in the anterior part (Fig. 236.4). Surface marked by irregular dots, fine on the head and the pronotum, thicker on the elytra. Long and raised pubescence.

Antennae: Fairly long, which exceed half the length of the body, with the club antennomeres slightly dilated and subcylindrical; the 8th antennomere slightly more than twice as long as it is wide and the 9th almost twice as long as the 10th and slightly longer than the 11th.

Pronotum: Elongated and slightly narrow, as wide as it is long and much narrower than the middle part of the elytra; lateral margins fully framed, curved in the anterior half, straight and narrowed in posterior half; pointed vertices projecting outwards; the base slightly wider than the anterior part and almost as wide as the anterior part of the elytra.

Elytra: Very elongated, elliptic, quite convex, almost twice as long as wide, reaching maximum width shortly behind the middle and convex posteriorly, which gives it a strong appearance of physogastry; dotted somewhat fine and aligned near the base, thicker, deeper and more spaced towards the middle, and very thick and spaced, but less deep in the apical area; marginal groove or ridge wide and regular.

Legs: Very long and very thin; males protarsi enlarged, but somewhat narrower than the apical area of the protibiae; meso- and metatibiae cylindrical, straight with small spines on the outer edge.

Mesoventral keel (Fig. 237.5): Low, formed by a small sharp tooth, ventral edge concave and serrated; intercoxal process of the metaventrite broad and convex.

Suture of the metaventrite (Fig. 237.5): In a regular arc very slightly concave towards the lower part, narrow delimiting area, a little wider towards the apical third.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Long and curved. In lateral view (Fig. 241.3), the dorsal depression is not strongly marked, for this reason there is no «*dove's nest*» pit, the peculiar structure named and described first by Jeannel (see above in text); lobe's apical blade elongated, narrowed, and the sharp apex curves to the ventral side. In dorsal view (Fig. 243.2), the lateral margins of the lobe curved and the apical area not pointed.

Endophallus (Fig. 243.2): Similar to *Pholeuon*, but the lamina on which the stylus is attached more developed.

Parameres (Fig. 243.10, 243.11): Slender, as long as the median lobe, with the apical area slightly curved and the club small, oblong and flattened, armed with three setae somewhat longer than in *Pholeuon*, of similar length between them and the nearby insertion pores.

Spermathecal complex: Short and curved spermatheca (Fig. 244.5), with both lobes sclerotized, the apical being globular and wider than the basal one, which is somewhat longer; hyaline junction duct present and as wide as the anterior part to the basal lobe but more elongated; spermatic duct, little sclerotized and more than twice the length of the spermatheca, of equal width throughout its length; there is a spermathecal gland.

Female uroventrite VIII (Fig. 245.5): With the middle part of the posterior margin forming a sub-rectilinear arc; sides of the anterior margin straight, with the spiculum very short, straight, narrow at the base and not very pointed at the apex.

Discussion. Monospecific genus. The external morphology is very similar to that of *Parapholeuon*

and *Pholeuon*; the pivotal character is here the shape of the median lobe of aedeagus: in *Protopholeuon,* the dorsal transverse sulcus is weak and therefore does not present the marked «*dove's nest*» pit.

Distribution. Romania. Known only from the cave Lucia Mare near Câmpeni in southern Bihor.

Species

Protopholeuon hungaricum (Csiki, 1904)
Pholeuon (*Parapholeuon*) *hungaricum* Csiki, 1904: 565.
Protopholeuon hungaricum Csiki: Jeannel, 1923b: 453.

3.4.5.2 ***Sinobathyscia*** group

Being the only genus in the group, the characteristics that define it correspont to those of the genus.

Genus ***Sinobathyscia*** Perreau, 1999
Sinobathyscia Perreau, 1999: 404.

Type species. *Sinobathyscia kurbatovi* Perreau, 1999 by original designation (for the habitus see that of the similar species *S. tianma* in Fig. 236.5).

Diagnosis. Very small size, between 1.3-1.5 mm. Bathyscioid facies; body shape (Fig. 236.5) chubby, oval and convex, not narrowed posteriorly.

Head: retractable, broader than long with a blurred occipital carina; fine and spaced stippling on a micro-reticulated background; anophthalmous.

Antennae: Very short not reaching the base of the pronotum; club differentiated with loose antennomeres, the 8th to 10th being very transverse, two times or almost two times as wide as long; the 11th thicker and slightly longer than the sum of the lengths of the 9th and 10th.

Pronotum: Very convex and transverse, 1.7-1.8 times wider than long; maximum width at the base; lateral margins gently curved, gradually stretching anteriorly and subparallel to the basal third; widest at the base which is as wide as the anterior part of the elytra; rear vertices rounded, slightly protruding to the back; acute angles. Very fine, small and spaced dots, with the dots distributed among a microreticulated background, but not striated.

Elytra: Short, oval, as long as their overall width, widest in the anterior quarter; slightly curved sides stretching gradually pointed ends that are show a weak transverse truncation; the dotting forms fine and spaced transverse striolae.

Legs: Short, fairly robust; protibiae with external spurs and small spines on outer margin, but without comb on apical and outer margins; male protarsi widened with the first tarsomere as wide as or slightly wider than the apical part of the protibia; meso- and metatibiae without an apical ring of spines, but with well-developed outer apical spurs.

Mesoventral keel (Fig. 237.6): Tall, robust and laminar, with a sharp vertex, the ventral edge slightly widened and the posterior extension reaching a part of the metaventrite.

Suture of the metaventrite (Fig. 237.6): It runs very close to the coxal cavity, only delimiting a very small area in the apical quarter.

Metatergal apparatus (Fig. 238.4): With the metascutum wings moderately elongated and rather wide, and the alacrista very long almost reaching the basal third of the elytra.

Metendosternite (Fig. 239.4): «V»-shaped. Furcal arms narrow, elongated and curved at the apex, without apophysis; posterior lamina reduced in width towards apex. Trunk very short, wider than long and about half the length of the arms; the middle keel short with diverting towards the posterior end.

Median lobe of aedeagus: Long and thin. In lateral view (Fig. 241.4), more strongly curved in the apical third, the dorsal side with a slight depression in the apical third; the pointed apex curves slightly towards the dorsal side. In dorsal view (Fig. 243.3) with subparallel sides in the basal half, then slightly curved and gradually tapering towards the apex, the latter lanceolate with a rounded tip. Basal lamina short and as long as the ventral lamina of the tegmen, the latter wider.

Endophallus (Fig. 243.3): Little complex armature. Two bands of spiny skin appendages along the middle region converging at the apical region; middle region with a pair of small sclerites and in the basal region a complex «U»-shaped structure.

Parameres (Fig. 243.12): Thick, especially in the basal area. In dorsal view, gently curved inwards, they reach – or slightly exceed – the apex of the median lobe; apical area slightly dilated, rectangular in shape, with projecting or sub-rounded apex with two strong apical setae inserted on the inner side. In lateral view, a rounded protuberance is observed at the apex.

Spermathecal complex (Fig. 244.6): Spermatheca large and well sclerotized; in it, the apical lobe is globose and the basal one slightly larger and subglobose; they are connected by a hyaline and very

short duct; short spermatic duct that widens at the base and at the junction with the spermatheca forming a highly developed nodule, which gives the spermatheca a three-lobed appearance; no spermathecal gland is seen.

Female uroventrite VIII (Fig. 245.6): With curved posterior edge slightly protruding in the middle; spiculum short, narrow, sides nearly parallel with the rounded apex.

Discussion. This genus is related to the more western genera whose species have colonised karstic areas of the western Carpathians (Romania) that belong to the *Drimeotus* group. Perreau (1999), describing the genus but ignoring the doubts caused by absence of male specimens about their taxonomic classification into the subtribes Bathysciina or Pholeuina. Later, once male specimens weren available, the character of pentameric male protarsi, the lack of a comb at the protibiae and an apical crown of thorns in the meso- and metatibiae allowed a more clearly a classification. Wang *et al*. (2017) suggests a placement of *Sinobathyscia* in Pholeuina, together with *Coreobathyscia* Szymczakowski and *Proleptodirina* Perkovsky, with the closest genus being *Coreobathyscia* (Wang *et al*. 2017). However, the proposed new order based on the phylogenetic tree obtained from a molecular study (Fig. 1D) was not confirmed by these data and the division of the subtribes of Leptodirini represent, apparently a polyphyly. *Sinobathyscia* is unambiguity found to be a sister group to the other clade of the *Drimeotus* series (genera *Drimeotus*, *Pholeuon* and *Protopholeuon*) that colonises the Apuseni mountains (Romania) with high support, 97.9/100. There are no molecular data on *Coreobathyscia* and *Proleptodirina,* but given their geographic location and position in the phylogeny, certain doubts are expressed about their inclusion in Leptodirini, in general as morphological convergence phenomena are frequent in the tribe. In addition, for the other far Eastern-Eurasian genera, Fresneda *et al.* (2011) showed that *Sciaphyes* is sister to the Anemadini and *Fusi* should be included in Catopini. *Sinobathyscia* has been included in the molecular study and it was found that this genus is a sister to *Drimeotus* with very good support, so its inclusion in the *Drimeotus* series is well supported. But this relationship between two groups which are geographically separated by about 8,000 km, at both ends of Eurasia, indicate that this may require further studies as it is a unusual pattern found here. Both *Sinobathyscia kurbatovi* and *S. tianma* were collected in urban parks, the first in Wuhan, «*litter in the park*» (Perreau 1999) without further data, and the second in tree debris in Tianmashan Park, Songjiang district in Shanghai (Wang *et al*. 2017). It was hypothesised on this that it might be the case that *Sinobathyscia* is a species discovered outside its distribution area, displaced for instance in the roots of trees transferred from its place of origin to the urban parks of those localities in Eastern China. A list of tree species introduced to Tianmashan has been obtained in order to investigate this; amongst all the tree species introduced in the urban park were some specimens of *Platanus orientalis* possibily from Iran which are the most likely candidate for the unintended introduction of some specimens or a small population of the beetles. The aedeagus of *Sinobathystia* is similar to those found in *Iranobathyscia jeanneli* from Mazanderan, in the extreme South of the Caspian Sea, where the tree species can be found. However, this is a speculative hypothesis and has to be taken with some reservation.

Distribution. A genus with two humicolous species distributed in Eastern China, Wuhan and Shanghai, on both banks of the Yangtze River.

Species

Sinobathyscia kurbatovi Perreau, 1999
Sinobathyscia kurbatovi Perreau, 1999: 404.

Sinobathyscia tianma Wang, Perreau, Růžička & Song, 2017
Sinobathyscia tianma Wang, Perreau, Růžička & Song, 2017: 353.

3.4.6 Series ***Catopsinus***

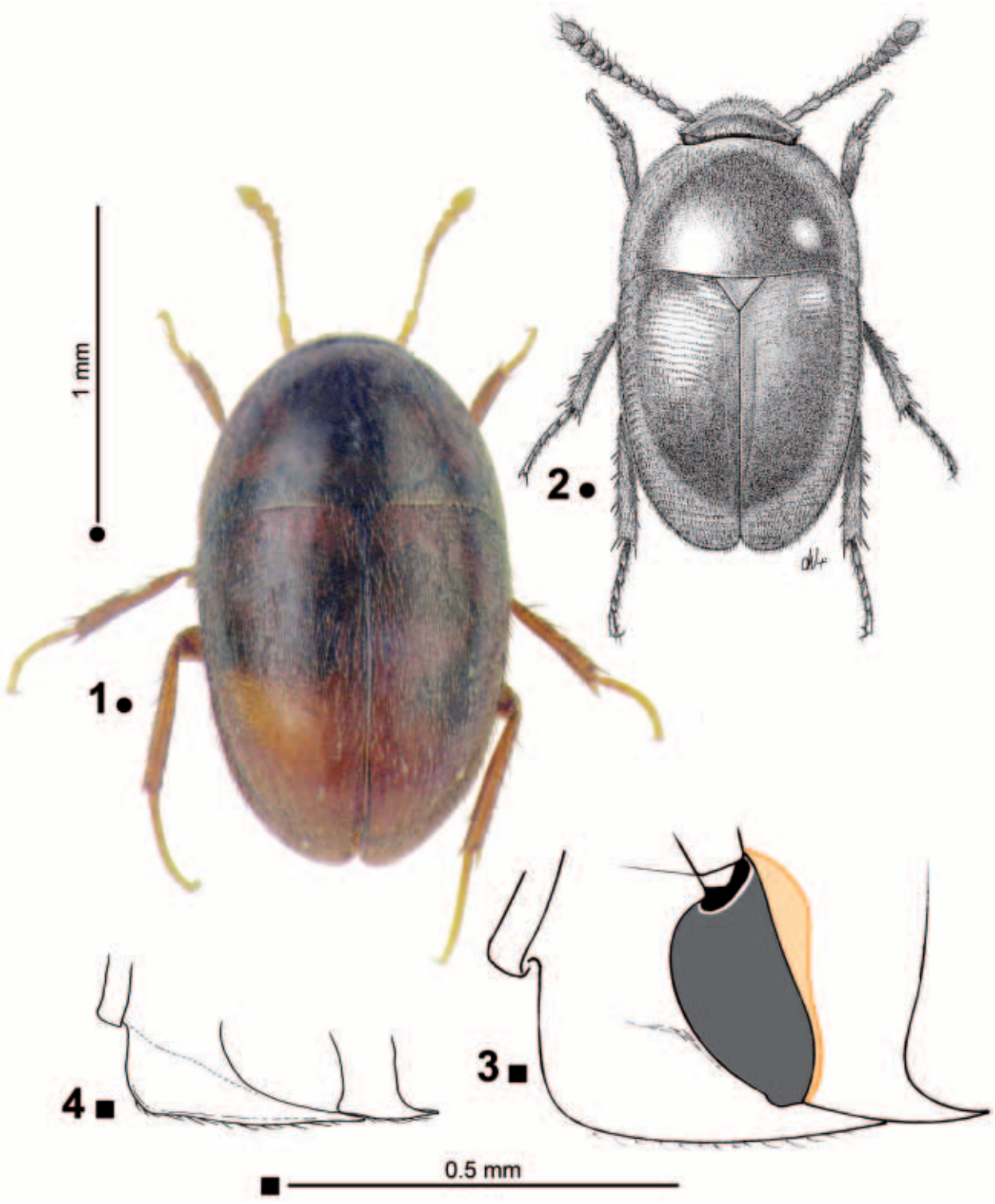
Diagnosis. Small to medium size, 1.1-3.7 mm, bathyscioid to pholeuonoid body.

Head: Retractile, with complete occipital carina; eyes normally absent, sometimes present but reduced.

Antennae: From short (not exceeding the basis of pronotum) to medium length (beyond half of the elytra); relative length of antennomeres variable.

Legs: Protarsi tetramerous or pentamerous. Apex of tibiae on the inner side with polydentate or pectinate (with two opposite rows of short numerous and subequal teeth) spurs. Apical baskets of meso- and metatibiae incomplete.

Mesoventral keel (Figs 246.3, 246.4, 250.1-250.5, 257.1-257.7, 258.1-258.5, 268.3): Variable in shape,



FIGURES 246.1–246.4: *Catopsinus* series, *Phaneropella* group. Habitus of: (**1**) *Besuchetiola priapus,* (**2**) *Phaneropella lesinae.* Pterothorax in lateral view of: (**3**) *B. priapus,* (**4**) *P. lesinae* (modified from Casale *et al*. 1989).

usually anterior profile not prominent, often elusive, with (or without) a more or less pronounced tooth at the anterior angle, or reduced and inconspicuous, sometimes prolonged posteriorly on the metaventrite.

Suture of the metaventrite (Figs 246.3, 250.2, 250.3, 250.5, 257.4, 258.5): Sinuous, it delimits a arcuate surface in the apical half and runs very close to the coxal cavity in the basal half.

Metatergal apparatus (Figs 247.1, 250.6, 250.7, 258.6-258.9): With apophysis of the alacrista from very short, barely outlined, to more longer than half the elytra.

Metendosternite (Figs 247.2, 247.3, 250.8, 250.9, 259.1-259.8): Normally not «V»-shaped, with triangular furcal arms which are wide at the base. Sometimes «V»-shaped, furcal arms non-triangular and narrow at the base

Median lobe of aedeagus: Very variable in shape and size but always with a «normal» sized (never hypertrophic) basal blade of the median lobe.

Endophallus: Of «Infraflagellate» type (*sensu* Jeannel 1924a) and very variable in structure. Usually there is a basal «Y»-piece (sometimes more or less atrophied) and a central phanera very variable in shape and extension, sometimes absent.

Parameres: There is a variable number of apical setae that also differ in their position; similarities in this region may be taxonomically informative.

Spermathecal complex: Spermatheca homogeneous in shape but with some variability within genera concerning the length of the spermathecal duct and the presence/absence of pre-spermathecal dilatations.

Female uroventrite VIII: Highly variable shape even within the different groups of genera, it does not seem as if these characters are valuable for taxonomic classification or even be used phyletically.

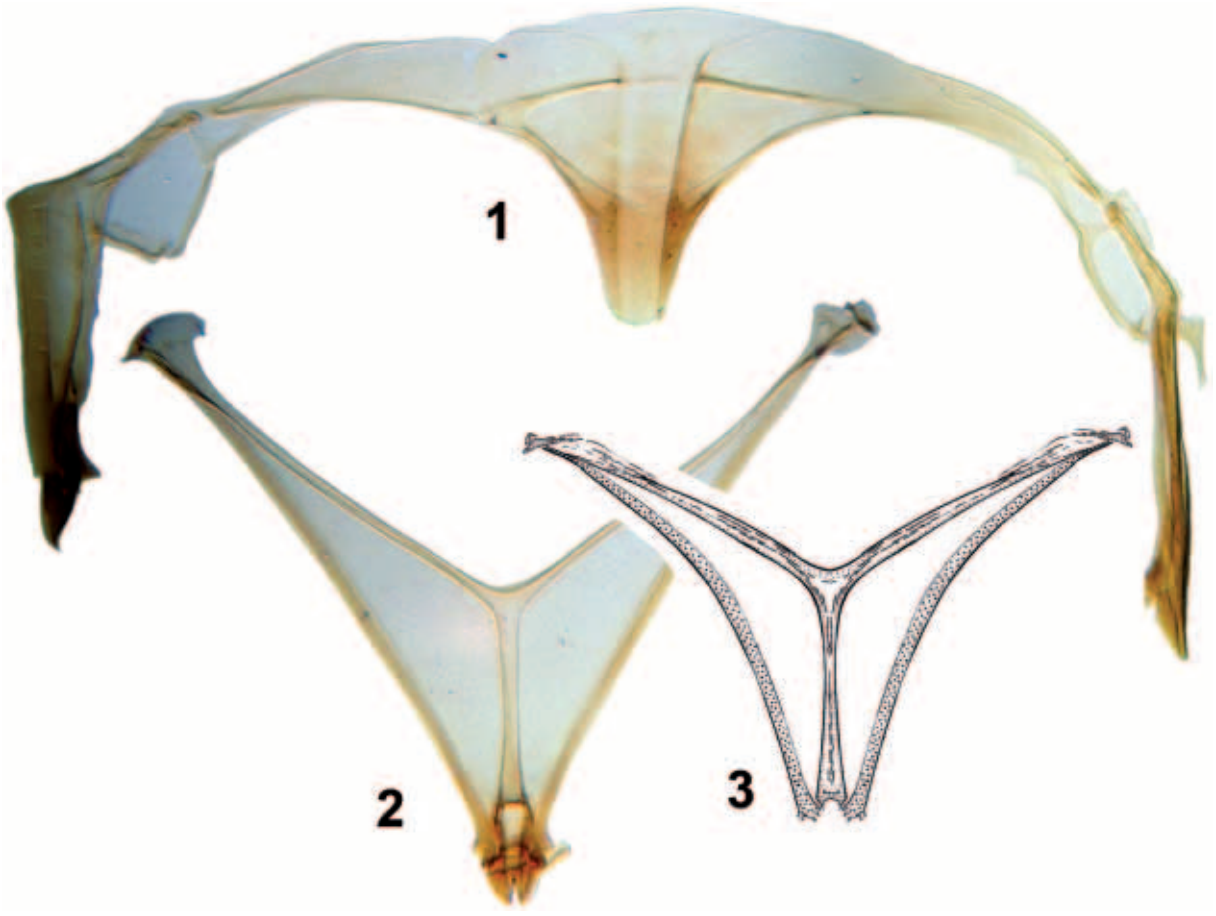
Discussion. As will be highlighted in detail in the discussion of individual groups, lacking of molecular data on a number of genera prevents currently a reliable and complete phyletic reconstruction of the relationships. Closely related clades identified in molecular analysis showed good support and provide a scaffold of the phylogenetic tree reflecting the evolutionary development. There will be further analysis, which are due to the use of morphological characters are far less reliable. Molecular phylogenetic studies were used to establish the *Catopsinus* series as being constituted of four groups: *Dellabeffaella, Catopsinus* and *Phaneropella* which are found to be related with high support of 100/100, however there were no molecular data available for the *Coiffaitiola* group which are considered to be close to the other groups and part of the series. In addition, *Catopsinus* series is linked to its sister series *Drimeotus* with a very high support of 96.9/97, and it was hypothesised on that this series are build by two groups, the *Drimeotus* and *Sinobathyscia* group, here also the support obtained is very high with 97.9/100 (Fig. 1D).

The clade formed by the *Catopsinus* and *Dellabeffaella* groups which was defined in a molecular analysis and that is sister to the *Phaneropella* group is found to be hightly supported with values of 88.1/97. This in runs mean that there is a division into the western (alpine) genera of the *Dellabeffaella* series (*Dellabeffaella* group) are, at the moment, zoogeographically hardly separated from the eastern (Iranian-Anatolian) groups of the same series (*Phaneropella* and *Catopsinus* groups). This disjunct distribution cannot be explained as a simple artefact due to the lack of data for important intermediate areas, first of all the Greek species, for which studies are currently underway. These studies led to the identification of at least 40 genera and more than 100 species new to science and currently being described in a separate monographic paper (Giachino & Vailati, *in prep*.). The continuously increasing knowledge on the species from the Greek territory can undoubtedly contribute to the clarification of this issue. The presence of the clades *Anthroherpon* and *Leptodirus* showing a Dinaric distribution, which are found in a geographical area between the alpine and Iranian-Anatolian groups of the *Catopsinus* series suggests the existence of two parallel distribution areas. In this case, there are no «obstacle» of *Anthroherpon* and *Leptodirus* and the disjoint distribution of the *Catopsinus* series can be explained:

– A distribution area reaching from the Trieste karst all the way to the Dinarides and to Albania-North Macedonia for the *Anthroherpon* and *Leptodirus* clades link roughly the distribution areas.

– The *Catopsinus* series occurs from the western Italian Alps through the Italian peninsula, Greece, Anatolia, Caucasus and Iran, also linking the distribution areas.

More molecular data are required to address the question for the phylogenetic relationship and the link between the northern and the southern species of the genus *Phaneropella.*These territories have been occupied in a distinct and independent colonisation event by species of the *Ovobathysciola* group (*Cytodromus* series). In geological terms the emerging lands from the Paratethys during the Miocene-Oligocene (Popov *et al*. 2004) must be seen as the fundamental event for the current distributions.



FIGURES 247.1–247.3: *Catopsinus* series, *Phaneropella* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Besuchetiola priapus*. Metendosternite of: (**2**) *B. priapus,* (**3**) *Phaneropella lesinae.*

KEY TO GROUPS

1. Male protarsi tetramerous or pentamerous. If pentamerous: elytra with parasutural stria and transverse striolae. Mesoventral keel with posterior apophysis prolonged over the metaventrite (Figs 246.3, 246.4). Metendosternite «V»- shaped (Figs 247.2, 247.3). Apex of the median lobe of aedeagus preceded by a small transverse crest and endophallus with a basal «Y»-piece with particularly elongated arms.....
.....*Phaneropella* group
- Male protarsi pentamerous without the characteristics set mentioned above.....2

2. Mesoventral keel high, prolonged over the metaventrite (Fig. 268.3) .....*Coiffaitiola* group
- Mesoventral keel low or high with posterior apophysis not prolonged over the metaventrite (Figs 250.1, 250.4, 257.1, 257.4-257.7, 258.3, 258.5); or reaches the anterior part of the metaventrite (Figs 250.2, 250.3, 250.5, 257.2, 257.3, 258.1, 258.2, 258.4) 3

3. Metatergal apparatus reduced, with short (Fig. 250.6, 250.7) or absent posterior apophysis of the alacrista; only in *Captosinus* moderately developed and long apophysis of the alacrista. Metendosternite (Figs 250.8, 250.9) «V»-shaped, with no triangular furcal arms.....*Catopsinus* group

- Metatergal apparatus large, with long posterior apophysis of the alacrista (Figs 258.6-258.8, 259.1, 259.2, 259.4, 259.5, 259.7, 259.9), except *Pseudoboldoria, Stoppaniola* and *Canavesiella* where it is moderately developed and with a short posterior apophysis of the alacrista (Figs 258.9, 259.3, 259.6). Metendosternite (Figs 260.1-260.7, 261.1-261.5) not «V»-shaped, with triangular furcal arms ....*Dellabeffaella* group

3.4.6.1 ***Phaneropella*** group

Diagnosis. Small size 1.2-2.0 mm. Bathyscioid shape.

Head: Retractile, with complete occipital carina and reduced eyes.

Antennae: Short, weak, not or only slightly exceeding the base of the pronotum; second antennomere as long as or longer than the first one.

Elytra: Stout, just longer than wide. Parasutural stria present, complete or reduced. Elytral disc strongly convex, striated transversally.

Legs: Male protarsi tetramerous or pentamerous but never dilated.

Median lobe of aedeagus: Very large so that it reaches the base of the pronotum or shorter, so that it extends along two or three ventrites.

Endophallus: Basal bulb that does not exceed the base of the median lobe in size, or very developed and strongly protruding from the base of the median lobe. Basal «Y»-piece rudimentary or with particularly elongated arms.

Spermathecal complex: Spermatheca sclerotized or hyaline, saccular or elongate and not sclerotized and devoid of the sclerotized spherical dilatation of the base of ductus. Spermathecal gland present.

Female uroventrite VIII: With spiculum long, not pointed.

Discussion. Regarding to the phylogenetic tree shown in figure 1D, *Phaneropella* appears as the sister genus of *Besuchetiola* with a support of 87/96, and forming the basal clade of the *Catopsinus* series; this is linked to the *Catopsinus* and *Dellabeffaella* groups with a support of 100/100. *Phaneropella*, has always been considered a «Théléomorphes» of Division II (Jeannel 1924a). The recent analysis presented here indicate the tetramerism has arisen several times in different lineages, that the finding that the tetrameous genus *Phaneropella* is close to the pentamer *Besuchetiola* is plausible also from the morphological perspective.

Key to genera

1. Largest species, 1.9-2.0 mm. Male protarsi pentamerous. Aedeagus very large, longer than the elytra (Figs 248.1, 248.3) .....*Besuchetiola*
- Smallest species, 1.2-1.5 mm. Male protarsi tetramerous. Aedeagus of «normal» length, shorter, extending along two or three ventrites (Figs 248.2, 248.4).....*Phaneropella*

Genus ***Besuchetiola*** Rampini & Zoia, 1991
Besuchetiola Rampini & Zoia, 1991: 795.

Type species. *Besuchetiola priapus* Rampini & Zoia, 1991 by original designation (habitus in Fig. 246.1).

Diagnosis. Small size, 1.9-2.0 mm, bathyscioid body ovoid, elongated and very convex (Fig. 246.1). Integuments with golden, thick and lying pubescence.

Head: Retractile, with complete occipital carina; eyes present but reduced.

Antennae: Short, not exceeding the base of the pronotum, lying backwards. First antennomere shorter than the second one; 8th slightly transverse; 11th 1.5 times longer and just wider than the 10th. Antennal club flattened, slightly enlarged.

Pronotum: Wide and transverse, very convex, with the maximum width at the base, which is as wide as the base of the elytra. Lateral sides regularly rounded, with a bisinuated base and in an acute angle.

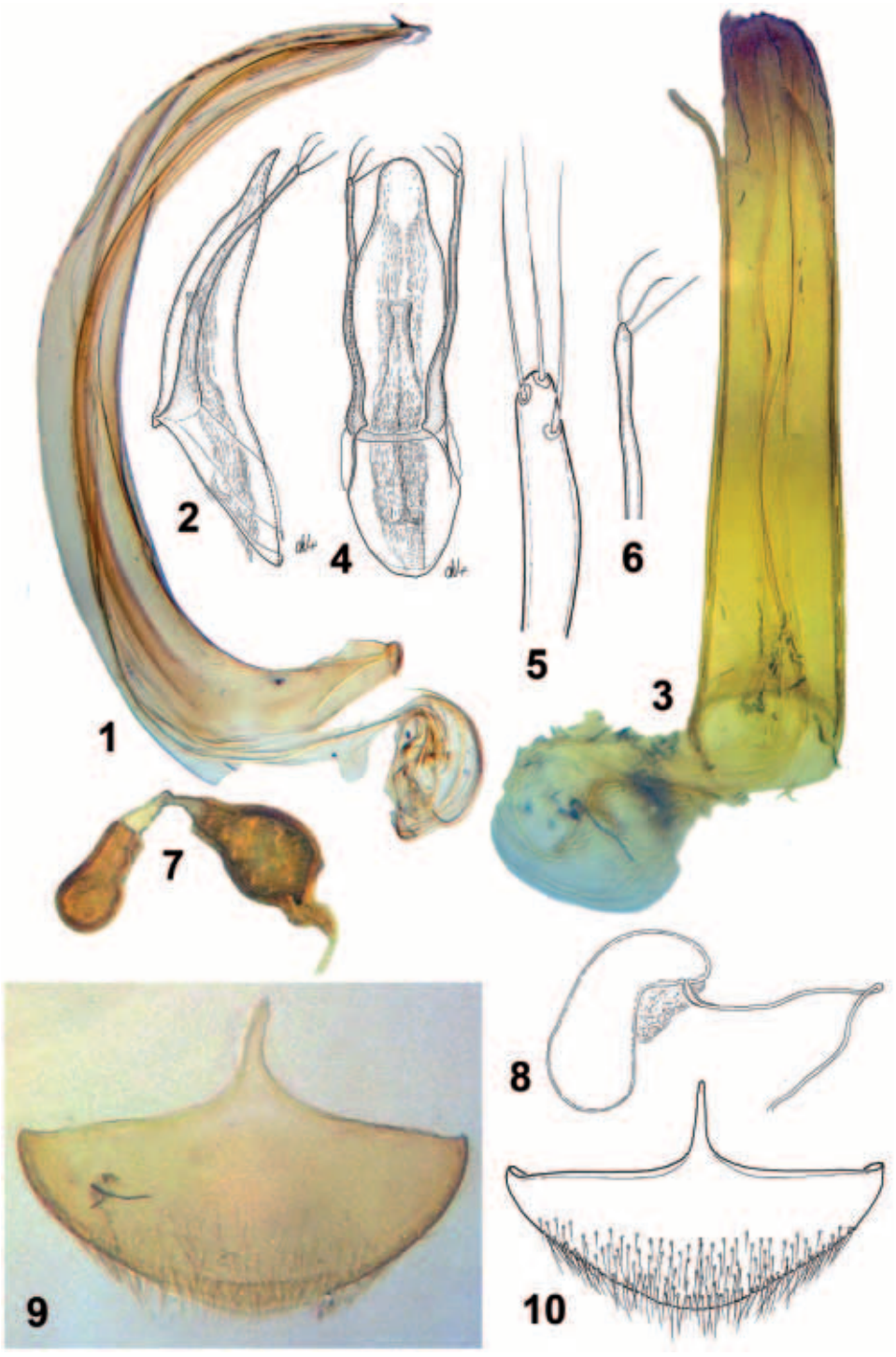
Elytra: Stout, just longer than wide, with maximum width at the base. Sides regularly rounded, more sharply attenuated at apex. Parasutural stria faded, present, but very superficial, only towards the apex. Elytral disc with microsculpture aligned in fine transversal striolae.

Legs: Metafemora with unarmed posterior margin. Apex of the tibiae with polydentate internal spurs. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentameres, never dilated, even less wide than apex of the protibiae.

Mesoventral keel (Fig. 246.3): High, forming an obtuse angle and rounded vertex, toothless. Anterior edge straight, ventral one thin, flattened and prolonged on the metaventrite.

Suture of the metaventrite (Fig. 246.3): Sinuous, it delimits a small arcuate surface in the apical half that continue very close to the coxal cavity in the basal half.

Metatergal apparatus (Fig. 247.1): Wings of the metascutum long and narrow, apophysis of the alacrista of medium length and non-sharpened apices.



FIGURES 248.1–248.10: *Catopsinus* series, *Phaneropella* group. Aedeagus in lateral view of: (**1**) *Besuchetiola priapus,* (**2**) *Phaneropella lesinae*. Aedeagus in dorsal view of: (**3**) *B. priapus,* (**4**) *P. lesinae*. Apex of paramere of (**5**) *B. priapus,* (**6**) *P. lesinae*. Spermathecal complex of: (**7**) *B. priapus,* (**8**) *P. lesinae*. Female uroventrite VIII of: (**9**) *B. priapus,* (**10**) *P. lesinae*. Figs **2**–**6**, **8**, **10** modified from Casale *et al*. (1989).

Metendosternite (Fig. 247.2): In «V»-shape, one arm and half of the furcal trunk delimit a triangular surface. Furcal arms longer than the trunk, very narrow in the apical area with a small well-differentiated apophysis; short furcal trunk, very wide in the apical part and mid-keel with marked posterior divergence.

Median lobe of aedeagus (Figs 248.1, 248.3): Vast, longer than the entire abdomen. In the resting position, it is in an inclined position with respect to the axis of the body and also occupies part of the posterior half of the prothorax. Narrow, sub-cylindrical and strongly arched at both ends, has the apex equipped with a small transverse crest, facing backwards. Basal blade of the median lobe very short and slightly sclerotized, about 1/7 of the total length of the median lobe.

Endophallus (Fig. 248.3): Basal bulb very developed and strongly protruding from the base of the median lobe. Basal «Y»-piece with particularly elongated arms. Ampulla and associated ejaculatory duct, clearly distinguishable. There are two pairs of thin ribbon-like sclerotized structures that occupy the entire length of the median lobe.

Parameres (Fig. 248.5): Long and thin, not exceeding the apex of the median lobe, arched and provided with three short and thin setae: two apical and one subapical. Basal blade of the tegmen very short, with base of the parameres not joint dorsally.

Spermathecal complex: Spermatheca (Fig. 248.7) of elongated shape, dilated in the proximal third and strongly restricted in the middle portion, which is very little sclerotized; well sclerotized lobes, the apical one spherical and the proximal one globose and larger. The annex gland opens near the dilated and sclerotized proximal tract of the ductus.

Female uroventrite VIII (Fig. 248.9): Spiculum relatively long, stout, subtriangular, arched and slightly ogival at the top.

Discussion. Rampini & Zoia (1991) highlighted that *Besuchetiola* shows a phylogenetic affinity with some of the «*Bathysciola*» (*sensu auctorum*) of the Iranian-Anatolian area. According to these authors (Zoia & Rampini 1994), *B. suramensis* was identified to belong to a distinct phyletic series (*Bithyniella* series) which would include, in addition to *Bithyniella*, *Sengletiola*, *Iranobathyscia*, *Capraiola* and *Sbordoniola*. The species was later transferred to the genus *Sbordoniola* in the work published by Perreau (2020), however, given our results it is a genus in its right and named *Georgiana* gen. nov. This in turn leads subsequently to the inclusion of *Besuchetiola* in the *Bithyniella* series (*sensu* Zoia & Rampini 1994), this findings are based on morphology only. Numerous morphological characters indicated that *Besuchetiola* is phylogenetically close to the *Catopsinus* group, as it would also be expected as the analysis led to a tree that is showing that the group is derived from the same basal branch. The overlap in morphology is particularly apparent in the following characters: presence of reduced eyes, male protarsi pentameres, tibiae with polydentate inner spurs, presence of elytral parasutural stria (present although rudimentary in *Besuchetiola*), presence of transverse striolae on elytra, metendosternite not «V»-shaped, with triangular furcal arms, endophallus with obvious basal «Y»-piece and parameres equipped with three setae. Distinctive characters *Besuchetiola* and *Catopsinus* differ in are the prolonged mesoventral keel on the metaventrite, the big size of aedeagus, the parameres of non-tuning fork-shape are armed with three subequal apical setae. *Besuchetiola* is excluded from the *Catopsinus* group since it derived in a basal cladogenesis of the entire series, constituting its sister group with a support of 100/100 (Fig. 1D) together with *Phaneropella*.

Distribution. Turkey, Pontic chain, from Giresun (West) to Hopa-Artvin (East).

Species

Besuchetiola priapus Rampini & Zoia, 1991
Besuchetiola priapus Rampini & Zoia, 1991: 797.

Genus ***Phaneropella*** Jeannel, 1910
Phaneropella Jeannel, 1910a: 15.

Type species. *Adelops lesinae* Reitter, 1881 by original designation (habitus in Fig. 246.2).

Diagnosis. Small size, 1.2-1.5 mm, bathyscioid facies (Fig. 246.2).

Head: Retractile, with a complete occipital carina, and eyes very reduced but functional.

Antennae: Short, weak, scarcely exceeding the base of pronotum; second antennomere as long as the first one.

Pronotum: Transverse, convex, covered with a short and decumbent pubescence. Maximal width at the base, as breadth as the base of the elytra. Lateral side not sinuate, long and regularly curved up to the anterior angles and less curved down to the posterior angles. Posterior angles acute, posteriorly prominent.

Elytra: Oval, stout, short, with maximal width at the anterior third, distally separately and regularly

rounded. Elytral disc strongly convex, striate transversally. Parasutural stria present, complete.

Legs: Short and thick; anterior tarsi tetramerous and not dilated in males. Protibiae without a comb, provided with two apical external spurs. Meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 246.4): High, with slightly curved front edge, not toothed; ventral edge straight, without groove, and the posterior apophysis prolonged over part of the metaventrite.

Suture of the metaventrite and *metatergal apparatus*: Unknown.

Metendosternite (Fig. 247.3): «V»-shaped. Furcal arms somewhat longer than trunk, both narrow progressively towards the apex, which is sharp, curves in an arc and lacking a clear terminal apophysis; width of posterior lamina decreases sharply towards apex with concave edge in middle part. Trunk as long as it is wide; with the middle keel on the trunk diverging posteriorly.

Median lobe of aedeagus: Small, stocky and subretilinear. In lateral view (Fig. 248.2), slightly arched and slightly sunk-in dorsally at the side near the apical part. In dorsal view (Fig. 248.4), widened in the middle part and preapically narrowed, with deeply sinuous sides; apex strongly rounded. Basal blade wide and broadly rounded posteriorly.

Endophallus (Fig. 248.4): Basal «Y»-piece rudimentary; median area without any signs of a flagellum, but equipped with a slightly sclerotized phanera, in shape of an inverted «U».

Parameres (Fig. 248.6): Thin, slightly shorter than the median lobe, bearing three long and subequal apical setae.

Spermathecal complex (Fig. 248.8): Spermatheca saccular and hyaline, not sclerotized and without sclerotized spherical dilation of the base of ductus. Very thin spermatic duct, not dilated in the area of union to the spermatheca. There is spermathecal gland.

Female uroventrite VIII (Fig. 248.10): Short and broad, with spiculum long, narrows towards the apex which is sharp.

Discussion. With regard to the phylogenetic tree shown in Figure 1D, *Phaneropella* appears to be a sister genus of *Besuchetiola* with a fairly high support, 87/96. Considering that there is an enormous gap between the currently known geographic areas in which the genera were found, it seems from the zoogeographical point of view in the first place inappropriate to plead for the described relationship, however, if taken into account that there is a high number of species still to be described from the areas in and around Greece it seems likely that the distribution areas are indeed not all that isolated. The assumption that the findings of species belonging to either of the genera in dispute it seems a likely scenario which is supported by the information from Giachino and Vailati, which are currently working on this group and stated in a personal communication that there are a few taxa to be described from this region. Hence, such a comprehensive work may completely close the geographical gap and show that there is no disjoint distribution.

Distribution. *Phaneropella lesinae* is characterised by a trans-Adriatic distribution; present on the Dalmatian coast (Croatia), in Bosnia-Herzegovina and in Italy (Gargano promontory).

Species

Phaneropella lesinae (Reitter, 1881)
Adelops Lesinae Reitter, 1881a: 216.
Bathyscia Karamani Reitter, 1885a [1884]: 255.
Bathyscia (*Bathyscia*) *lesinae* Reitt.: Reitter, 1885a [1884]: 21.
Bathyscia Lesinae Reitt.: G. Müller, 1904c: 316.
Phaneropella Lesinae Reitter: Jeannel, 1910a: 37.
Bathyscia (*Adelopsella*) *Lesinae* Reitt.: J. Sahlberg, 1913: 48.
Bathyscia (*Phaneropella*) *Lesinae* Reitt.: Jeannel, 1914b: 17.
Phaneropella Lesinae Reitter, 1881: Jeannel, 1924a: 219.
Phaneropella (s. str.) *lesinae* (Reitter, 1981): Casale, Giachino, Vailati & Rampini, 1991: 209.

3.4.6.2 ***Catopsinus*** group

This group is characterised by exhibiting morphological characters such as pentamerous protarsi in males and a reduced metatergal apparatus, with the distal edge rectilinear or equipped with an extremely reduced posterior apophysis; sutural edges of the elytra closely joined (permanent or temporary coaptation); up to the apical angles which are rounded in a very small area and adjacent; metendosternite «V»-shaped, with no triangular furcal arms; present or absent parasutural stria; polydentate apical spurs of tibiae; endophallus with basal «Y»-piece.

Discussion. The molecular analysis based also on the available data for one species of *Catopsinus*, further

two of *Georgiana* gen. nov. and one of a species from the *Zoiana* gen. nov. show that this group is sister to the representatives of the series distributed throughout the western Alps with acceptably high support of 88.1/97 (Fig. 1D). The integrity of the *Catopsinus* group as identified in the phylogenetic tree based on molecular data is highly supported by values of 98/98. However, morphological criteria from *Bithyniella*, *Sengletiola* and *Iranobathyscia* should also be included, and add to the support. The character state concerning the regression of the optic system appears to proceed differently in the genera of this phyletic line. While *Bithyniella* includes also completely blind species, such as *Sengletiola* and some species of *Sbordoniola* and *Catopsinus*. In *Iranobathyscia* and some other species of *Sbordoniola*, *Sengletiola* and *Catopsinus* eye spots are still present, or even very reduced eyes as found in *Zoiana* gen. nov. and *Georgiana* gen. nov..

From a zoogeographical point of view, this group of genera appears strongly separated by whole regions in which neither of them occur. *Bithyniella* distributed in the far West along the Pontic chain and the others genera occuring in the East, occupying the Caucasus (*Catopsinus*, *Georgiana* gen. nov. or *Zoiana* gen. nov.) and Northern Iran (*Sbordoniola*, *Iranobathyscia* or *Sengletiola*). These finding are possibly an artefact based on incomplete sampling in areas which are difficult or impossible to go to due to political circumstances or neglect of some regions by the researchers as widely discussed by Giachino & Vailati (2000) for the Cholevinae and particularly for Leptodirini from Anatolia.

Key to genera

1. Parasutural stria clearly present.....*Catopsinus*
- Parasutural stria absent.....2

2. Elytral disc without transversal striolae.....
.....*Bithyniella*
- Elytral disc with transversal striolae 3

3. Median lobe of aedeagus with a small transverse ridge near the apex (Figs 251.7, 251.8) ....*Sengletiola*
- Median lobe of aedeagus without a transverse ridge (Figs 251.3-251.6, 251.9) 4

4. First metatarsomere clearly longer than the second .....*Iranobathyscia*
- First metatarsomere not or only slightly longer than the second 5

5. Antennae with the first antennomere as long as or slightly longer than the second one. Mesoventral keel with ventral edge wide, with a groove along the middle part .....*Zoiana* gen. nov.
- Antennae with the first antennomere shorter than the second one. Mesoventral keel with ventral edge wide or thin, without groove 6

6. Thin parameres along their entire length (Figs 251.3, 251.4, 252.3) .....*Georgiana* gen. nov.
- Thick parameres (Fig. 252.6); in lateral view with a thickening in its medial part (Fig. 251.6) *Sbordoniola*

Genus ***Bithyniella*** Jeannel, 1955
Bathysciola (*Bithyniella*) Jeannel, 1955b: 117.
Bithyniella Jeannel, 1955: Rampini & Zoia, 1991: 800.
Parabithyniella Rampini & Zoia, 1991: 792 (Type species: *Parabithyniella viti* Rampini & Zoia, 1991).

Type species. *Bathysciola* (*Bithyniella*) *strinatii* Jeannel, 1955 by monotypy (habitus in Fig. 249.1).

Diagnosis. Small size, 1.4-1.7 mm; bathyscioid body (Fig. 249.1), convex, relatively wide. Covered with golden, fine and lying pubescence.

Head: With complete occipital carina; anophthalmous.

Antennae: Short and delicate, not reaching the base of the pronotum. First antennomere shorter than the second. Sub-equal 3rd, 4th, 5th and 6th antennomeres, about twice as long as wide; the 8th transverse, 9th and 10th slightly wider than long; the 11th just wider and about twice as long as the previous one.

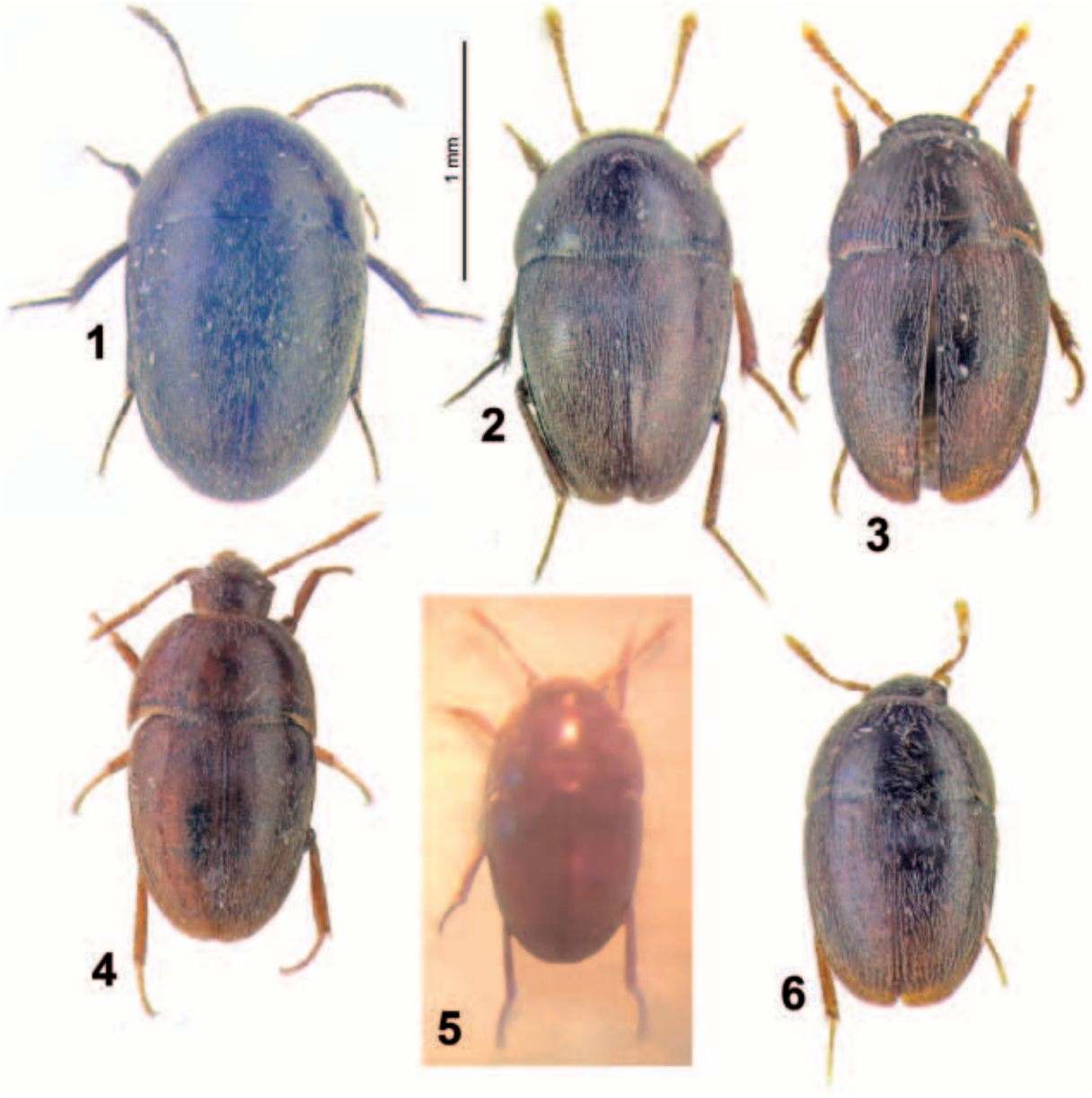
Pronotum: Broad, transverse, convex, as wide as elytra. Lateral sides more curved in the basal third, narrowed at the base, which is just bisinuated, with the basal angles acute.

Elytra: With sutural edges, but without parasutural stria. Maximum width at the base, gradually narrowing towards the apex. Elytral disc without transversal striolae.

Legs: Relatively short and delicate. Internal tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentameres and dilated. Distal edge of metafemora without tooth.

Metaventrite: Not carinated. Intercoxal apophysis slightly separated by a small space from each other.

Mesoventral keel (Fig. 250.1): High, forming an obtuse angle and toothed vertex. Anterior edge slightly arched or sub-rectilinear, the ventral one flattened, not prolonged on the metaventrite.



FIGURES 249.1–249.5: *Catopsinus* series, *Catopsinus* group. Habitus of: (**1**) *Bithyniella strinatii,* (**2**) *Catopsinus rudoyi* **sp. nov.**, (**3**) *Georgiana suramensis* **comb. nov**., (**4**) *Sbordoniola persica persica*, (**5**) *Sengletiola motschulskyi*, (**6**) *Zoiana kociani* **comb. nov**.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Rampini & Zoia 1991): Extremely reduced, with posterior edge of the metatergite rectilinear and absent posterior apophysis of the alacrista.

Metendosternite (Rampini & Zoia 1991): «V»-shaped, with no triangular furcal arms.

Median lobe of aedeagus: Elongated, arcuated. In lateral view (Fig. 251.1), regularly arcuated and sieve-structure at the apex, which is not bent downwards. In dorsal view (Fig. 252.1), slightly sinuated in the basal half and gradually narrowed in the apical one. Apex just rounded. Basal blade wide, prolonged in a short and well-sclerotized apophysis.

Endophallus (Fig. 252.1): Basal «Y»-piece present, with two evident, thin and longitudinal sclerotized phanerae. Median area with two short longitudinal phanerae and one, or two, central sclerites. Distal area with two sets of lateral teeth with serration, very little sclerotized.

Parameres (Fig. 253.1): As long as the median lobe, sinuate in the basal third, in dorsal view, exhibiting a tuning fork shape. Curved in dorso-ventral direction along their entire length. Apex not enlarged, exhibit a very large, spiniform, apical seta and two more very long setae in a preapical position.

Spermathecal complex (Fig. 253.8): Spermatheca elongated, with the distal part globular and proximal one elongated, both sclerotized. Intermediate part hyaline. Ductus very long and thin, not enlarged or sclerotized at insertion side at the spermatheca. A spermathecal gland is present.

Female uroventrite VIII (Rampini & Zoia 1991): Spiculum long and stout, enlarged at apex. Anterior edges subrectilinear and slightly convergent.

Discussion. *Bithyniella* presents all the characteristics defining the group. It is nevertheless clearly separated from all other genera of the lineage by the absence of the transversal striolae at the elytra. So far it was not possible to analyse the particular morphological character states of *Bithyniella* in the other genera of the lineage (with the exception of *Sbordoniola*), which consists of the presents a «V»-shaped metendosternite, with no triangular furcal arms and is in this quite different to that of *Besuchetiola* (*Phaneropella* group). *Bithyniella* differs from *Besuchetiola* also in the total absence of eyes, the absence of parasutural stria and transversal striolae to the elytra and the shorter aedeagus.

Distribution. Turkey, NW Anatolie.

Species

Bithyniella strinatii (Jeannel, 1955)
Bathysciola (*Bithyniella*) *Strinatii* Jeannel, 1955b: 117.
Bithyniella strinatii Jeannel: Rampini & Zoia, 1991: 800.

Bithyniella viti (Rampini & Zoia, 1991)
Parabithyniella viti Rampini & Zoia, 1991: 792.
Bithyniella viti (Rampini & Zoia, 1991): Rampini & Zoia, 1993: 163.

Genus ***Catopsinus*** Motschulsky, 1868
Catopsinus Motschulsky, 1868: 58.

Type species. *Catops pusillus* Motschulsky, 1840 by monotypy (for the habitus see that of the similar species *Catopsinus rudoyi* sp. nov. in Fig. 249.2).

Diagnosis. Small size, 1.4-2.0 mm, bathyscioid body (Fig. 249.2), convex, elongated, slightly narrower posteriorly than anteriorly. Covered with golden, fine and lying pubescence.

Head: With complete occipital carina, anophthalmous or with reduced generally pigmented eyes formed by less than ten ommatidia.

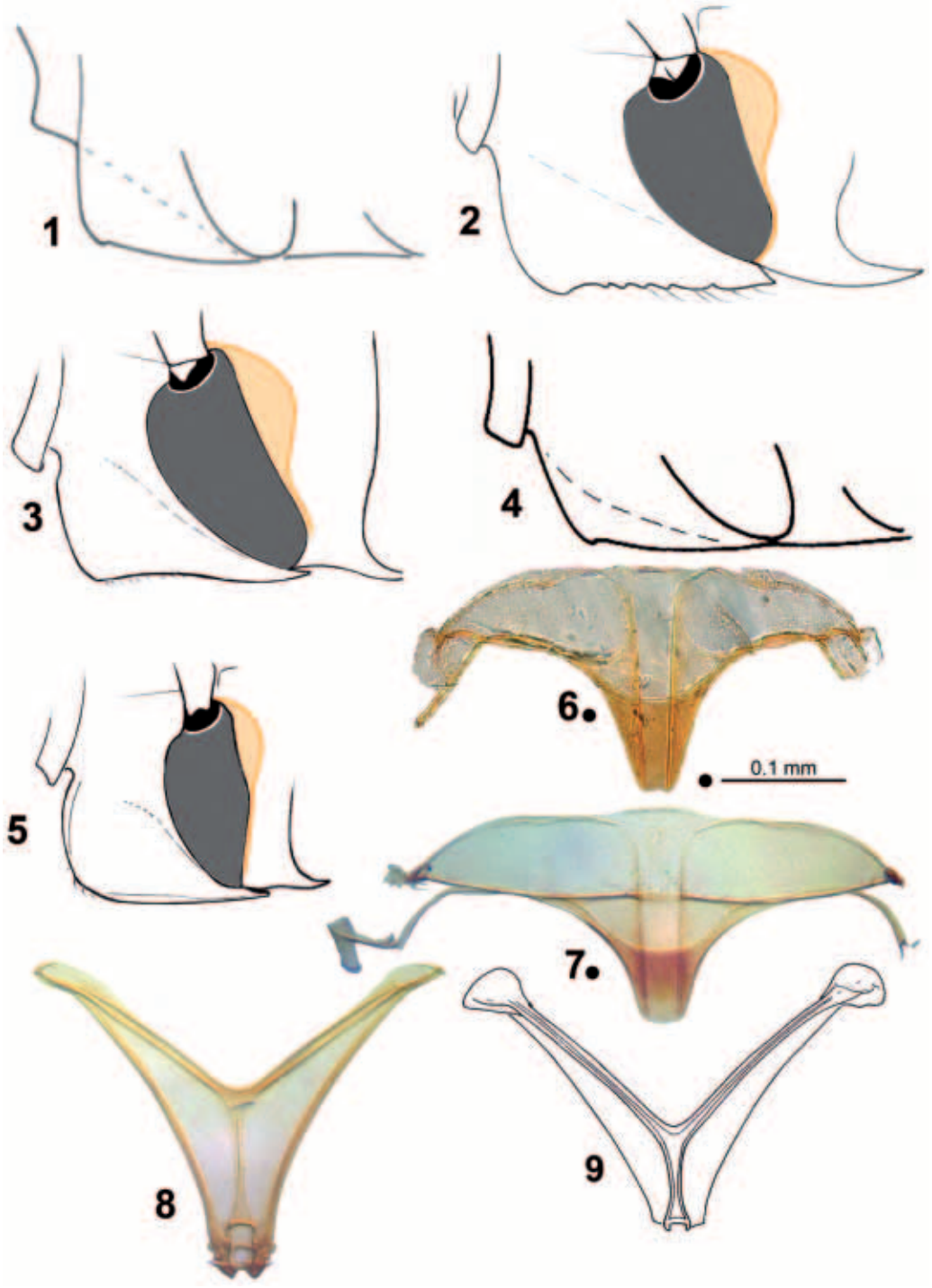
Antennae: Short and delicate, reaching the basal third of the pronotum. First antennomere shorter than the second and approximately of the same width. Subequal 3rd, 4th and 5th antennomeres, about twice as long as wide; the 8th transverse, 9th and 10th slightly wider than long; the 11th just wider than and about twice as long as the previous one.

Pronotum: Broad, convex, transverse, as wide as and sometimes slightly wider than the elytra. Lateral sides regularly curved, narrowed at the base, which is just bisinuated, with the basal angles slightly acute.

Elytra: With occasional coaptation in the sutural edges, slightly flattened on the disc and gradually tapered posteriorly. Rounded sutural angles. Parasutural stria present. Elytral disc with microsculpture aligned in fine transversal striolae.

Legs: Relatively short and delicate. Internal tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentameres, not dilated or dilated. Distal edge of metafemora without tooth.

Mesoventral keel (Fig. 250.2): High, forming an obtuse angle, rounded, toothless or slightly toothed vertex. Anterior edge slightly arched or sub-rectilinear, the ventral one thin, not prolonged on the metaventrite.



FIGURES 250.1–250.8: *Catopsinus* series, *Catopsinus* group. Pterothorax in lateral view of: (**1**) *Bithyniella strinatii* (modified from Rampini & Zoia 1993), (**2**) *Catopsinus rudoyi* **sp. nov.**, (**3**) *Georgiana brignolii* **comb. nov**., (**4**) *Sengletiola motschulskyi*, (**5**) *Zoiana kociani* **comb. nov**. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**6**) *C. hlavaci* (modified from Perreau 2021), (**7**) *G. brignolii* **comb. nov**. Metendosternite of: (**8**) *G. brignolii* **comb. nov**., (**9**) *Sbordoniola mazanderanica mazanderanica*. Figs **4**, **8** modified from Zoia & Rampini (1994).

Metaventrite: Not carinated. Intercoxal apophysis very short, the coxal cavities just separated from each other.

Suture of the metaventrite (Fig. 250.2): It describes an arc clearly separated from the edge of the meso-coxal cavity in the first half of its course, then runs contiguous and parallel to the edge, without delimiting an area.

Metatergal apparatus (Fig. 250.6): Short with the wings of the metascutum somewhat longer than wide; long apophysis of the alacrista, reaching slightly beyond the basal third of elytra.

Metendosternite: Unknown.

Median lobe of aedeagus: Large, stout, in dorsal view with the maximum width, at the insertion of the parameres when the base is excluded. In lateral view (Fig. 251.2), more sharply restricted in the distal half and more decided in its curvature in the median area; there is a kind of irregular part on the dorsal side before the apex, which is slightly and regularly curved downwards. Sides, in dorsal view (Fig. 252.2), from subparallel, to regularly converging towards the apex, which is wide and more or less widely rounded.

Endophallus (Fig. 252.2): Presents three regions; in the basal region there is a «Y»-piece well-developed with reduced apical nodules; in the middle region, there are hyaline dorsal phanerae, two possibly curved finer ones with the inverted curves apparently joined at their upper end, and an axial piece formed by two elongated pieces very close to each other; in the apical region there are reinforcing bands that rest on membranous ligules and between the two further two exist, but finer and hyaline.

Parameres (Fig. 328.7, 328.8): In dorsal view, in the shape of a tuning fork. Not reaching to reaching beyond the apex of the median lobe, delicate, significantly enlarged towards the apex. Apex without a membranous lobe and armed with three setae of different length. Tegmen large, relatively short, closed dorsally by a sclerotized band.

Spermathecal complex (Fig. 253.9): Spermatheca «C»-shaped, very sclerotized, normally rather elongated and thin; with the apical lobe shorter and somewhat narrower than basal lobe. Ductus short, very thin, enlarged and sclerotized to form a chamber or nodule near the spermatheca. Ductus insertion into vagina is highly unusual as it seems a more or less developed calyx swelling of the ductus, sclerotized or not, but with the walls having a strongly irregular, notched, surface. With well-defined spermathecal gland.

Female uroventrite VIII (Fig. 254.1): With spiculum well-developed, long and thin.

Discussion. The resurrection by Perreau (2021) of *Catopsinus* as a genus was the logical consequence of a whole series of works on the polyphily or paraphily described of the genus *Bathysciola.* These taxonomic publications from different authors in the last 30 years have looked at this group in detail referring to them the «oriental *Bathysciola*» (Giachino 1996, 1998; Rampini & Zoia 1991; Zoia & Rampini 1994, 1996). The availability of molecular data allowed to confirm, the relationship amongst the groups *Catopsinus*, *Dellabeffaella* and *Phaneropella*, with a highest support of 100/100 (see Fig. 1D). At the level of morphological character analysis this is represented by the following character states: absence, or presence of eyes, male protarsi pentameres or tetrameres, tibiae with polydentate inner spurs, presence of elytral parasutural stria (present although faded almost away in *Besuchetiola*, *Phaneropella* group), absence or presence of transverse striolae on elytra, metendosternite not «V»-shaped, with triangular furcal arms, endophallus with apparent basal «Y»-piece and parameres equipped with three setae. In molecular phylogeny tree (Fig. 1D) *Catopsinus* (with *C. rudoyi* sp. nov.) joins *Zoiana* gen. nov. and *Georgiana* sp. nov. with a high support of 98/98.

Distribution. Armenia, Azerbaijan, Georgia, Turkey (Eastern Anatolia: Tunceli, Lice), Lebanon, Israel.

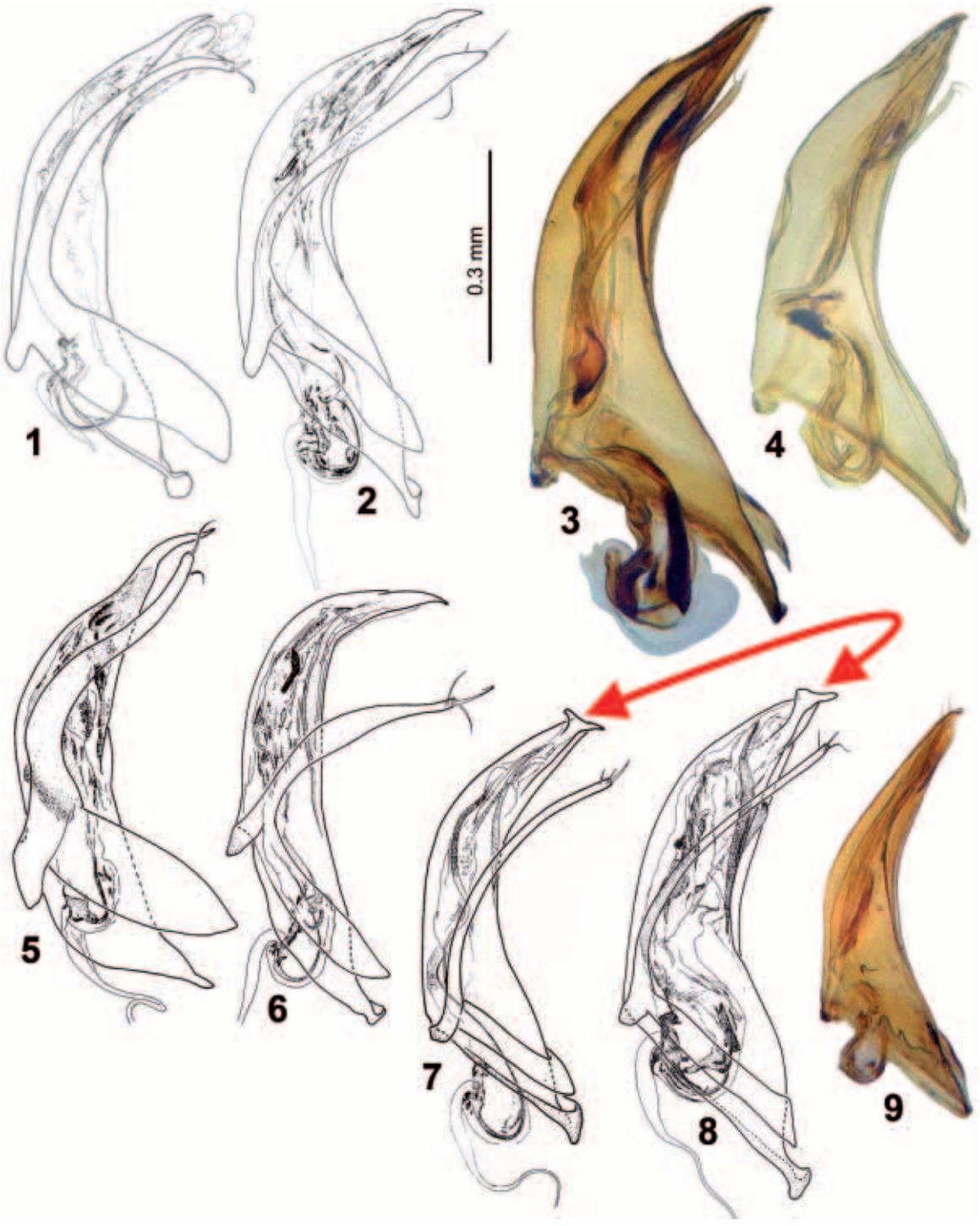
Species

We have molecular data available only for *Catopsinus rudoyi* sp. nov. (with endophallus similar to that of *C. pusillus*, type species of the genus), but morphologically the following species have also to be placed in this genus (ex «*Bathysciola pusilla* group» *sensu* Giachino 1998).

Catopsinus cavazzutii (Giachino, 1996)
Bathysciola cavazzutii Giachino, 1996: 51.
Bathysciola (s. str.) *cavazzutii* Giachino: Perreau: 2000: 232.
Catopsinus cavazzutii (Giachino, 1996): Perreau, 2021: 7.

Catopsinus hlavaci Perreau, 2021
Catopsinus hlavaci Perreau, 2021: 11.

Catopsinus lindbergi (Jeannel, 1957)
Bathysciola Lindbergi Jeannel, 1957: 23.
Bathysciola lindbergi Jeannel: Coiffait, 1959b: 30.



FIGURES 251.1–251.9: *Catopsinus* series, *Catopsinus* group. Aedeagus in lateral view of: (**1**) *Bithyniella strinatii* (modified from Rampini & Zoia 1993), (**2**) *Catopsinus pusillus*, (**3**) *Georgiana suramensis* **comb. nov**., (**4**) *G. brignolii* **comb. nov**., (**5**) *Iranobathyscia jeanneli,* (**6**) *Sbordoniola persica persica*, (**7**) *Sengletiola motschulskyi*, (**8**) *S. orientalis* **comb. nov.**, (**9**) *Zoiana kociani* **comb. nov.** Figs **2**, **5**–**8** modified from Zoia & Rampini (1994). Red arrow pointing to equivalent structures.

Bathysciola (s. str.) *lindbergi* Jeannel: Perreau: 2000: 233.
Catopsinus lindbergi (Jeannel, 1957): Perreau, 2021: 14.

Catopsinus loebli Perreau, 2021
Catopsinus loebli Perreau, 2021: 15.

Catopsinus meybohmi Perreau, 2021
Catopsinus meybohmi Perreau, 2021: 15.

Catopsinus peyronis (Abeille de Perrin, 1875)
Adelops Peyronis Abeille de Perrin, 1875c: 216.
Bathyscia syriaca Reitter, 1885 [1884]: 255.
Bathyscia (*Bathyscia*) *Peyronis* Abeille: Reitter, 1885 [1884]: 21.
Bathyscia Peyroni Abeille, 1975: Jeannel, 1907c: 64.
Bathysciola Peyroni Abeille: Jeannel, 1910a: 26.
Bathysciola (s. str.) *Peyroni* Abeille de Perrin: Jeannel, 1914b: 11.
Bathysciola (s. str.) *peyronis* (Abeille de Perrin): Perreau: 2000: 233.
Catopsinus peyronis (Abeille de Perrin, 1875): Perreau, 2021: 16.

Catopsinus pusillus (Motschulsky, 1840)
Catops pusillus Motschulsky, 1840: 175.
Adelops pusilla (Motschulsky): Weise *in* Schneider & Leder 1878: 142.
Bathyscia (*Bathyscia*) *pusilla* (Motschulsky): Reitter 1885 [1884]: 21.
Catops (*Catops*) *pusillus*, Motsch.: Murray, 1856: 393.
Catopsinus pusillus Motschoulsky: Motschulsky, 1868: 58.
Bathysciola pusilla Motschoulsky: Jeannel, 1910a: 26.
Bathysciola (s. str.) *pusilla* Motsch.: Jeannel, 1914b: 11.

Catopsinus rudoyi sp. nov. (See Appendix New Species)

Genus ***Georgiana*** nov.
https://zoobank.org/NomenclaturalActs/BC326FD1-2176-4C9F-A353-A607352B436B

Type species. *Bathysciola suramensis* Jeannel, 1930 by present designation (habitus in Fig. 249.3).

Description**.** Length 1.5-1.7 mm. Bathyscioid body (Fig. 249.3), strongly convex, regular oval shape. Reddish brown colour. Golden, fine and recumbent pubescence.

Head: Occipital carina complete. Extremely fine, dense and superficial punctation. Third segment of the maxillary palps conical in shape, very thin and somewhat shorter than the previous one. With small unpigmented eyes.

Antennae: Short and thin, slightly longer in the male in which they slightly exceed the basal third of the pronotum. First antennomere shorter than the second and approximately of the same width; 3rd, 4th and 5th antennomeres subequal, about 1.5 times longer than wide; the 6th clearly shorter than the previous one; the 7th somewhat longer than wide; the 8th very transverse; the 9th and 10th markedly wider than long; the 11th ovoid, slightly wider and almost twice as long as the previous one.

Pronotum: Broad, transverse and strongly convex; sides regularly arched, subparallel near the base of the pronotum and, from this point gradually widening towards the base. Base slightly bisinuate and basal angles acute. Extremely fine, superficial and sparse punctation; with a very fine micro-reticulation between the points.

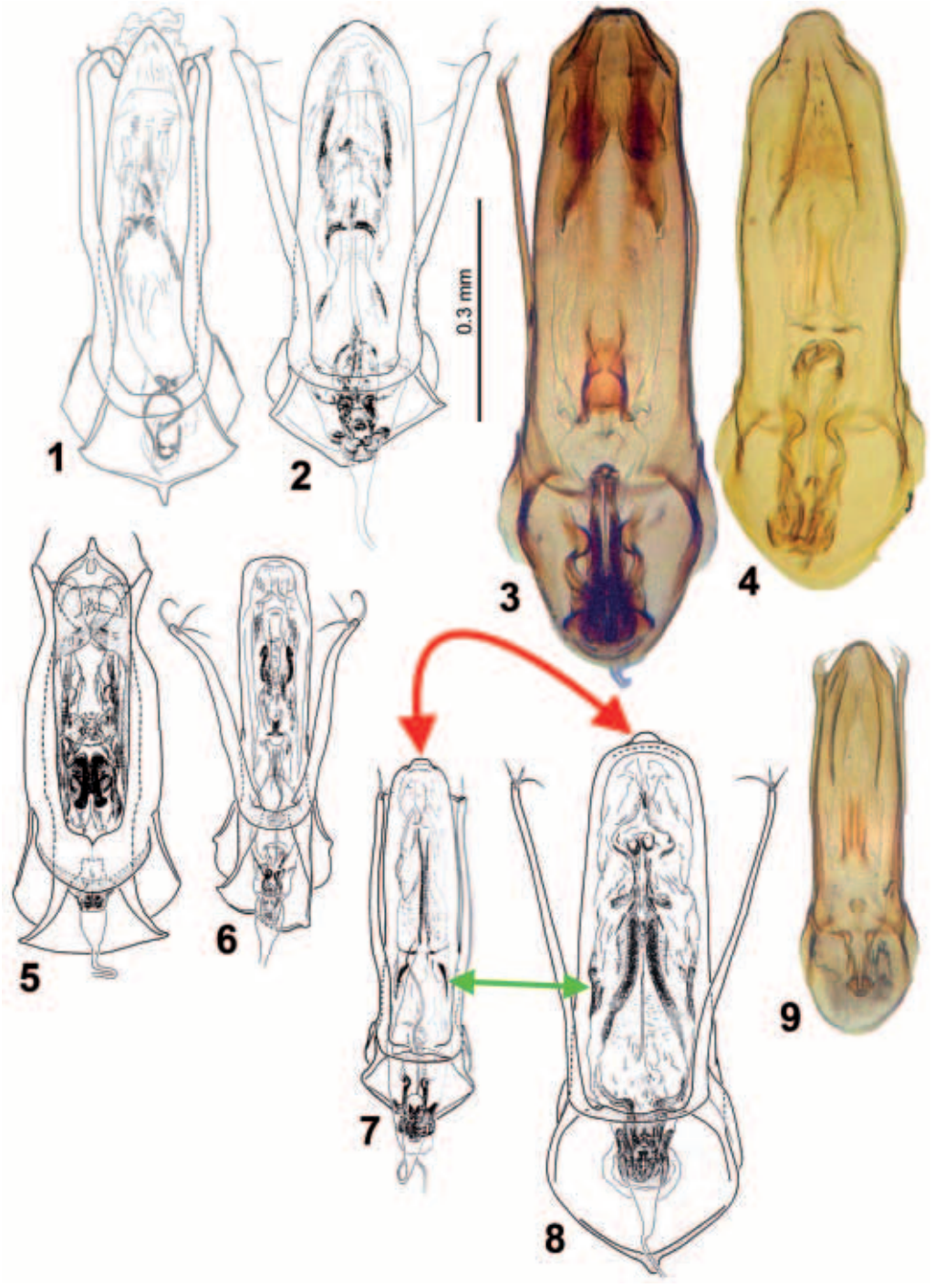
Elytra: Transiently coapted, convex and with maximum width at base; sides subrectilinear near the base in the male and more regularly curved in the female. Parasutural stria absent, only very blurred in the proximal third of the elytra and a narrow, darker band is clearly distinguishable along the entire length of the elytra. Fine punctation, arranged in an aligned manner so that it forms transverse striolae that tend to disintegrate in the apical part of the elytra.

Legs: Short but slender. Male protarsi pentameres slightly dilated. Protibiae thin, sub-rectilinear, apical spurs present and some short spines on the outer edge; mesotibiae significantly curved, equipped with robust spines on the external edge and apical spurs. Metafemora simple, without spines on the posterior edge; metatibiae rectilinear, provided with spines on the external edge and apical spurs.

Mesoventral keel (Fig. 250.3): Elevated, with the apex forming an almost right angle, without tooth; the anterior edge arched and the ventral slightly concave, the ventral ridge without groove, not prolonged over the metaventrite or it is just reached.

Suture of the metaventrite (Fig. 250.3): Sinuous, in the two apical thirds it delimits a well-defined arched area and runs very close to the coxal cavity in the basal third.

Metatergal apparatus (Fig. 250.7): Wings of metascutum broad and quite long, with well-developed apophysis of the alacrista that slightly exceed the basal third of the length of the elytra.



FIGURES 252.1–252.9: *Catopsinus* series, *Catopsinus* group. Aedeagus in dorsal view of: (**1**) *Bithyniella strinatii* (modified from Rampini & Zoia 1993), (**2**) *Catopsinus pusillus*, (**3**) *Georgiana suramensis* **comb. nov**., (**4**) *G. brignolii* **comb. nov**., (**5**) *Iranobathyscia jeanneli*, (**6**) *Sbordoniola persica persica*, (**7**) *Sengletiola motschulskyi*, (**8**) *S. orientalis* **comb. nov.**, (**9**) *Zoiana kociani* **comb. nov.** Figs **2**, **3**, **6–8** modified from Zoia & Rampini (1994). Red and green arrows pointing to equivalent structures.

Metendosternite (Fig. 250.8): «V»-shaped, with triangular furcal arms; arms somewhat longer than the trunk, with poorly defined apical apophysis, posterior furcal plate narrowing towards apical area of the arm and posteriorly an arched flange. Furcal trunk long, the length being as long as the area of greatest width.

Median lobe of aedeagus: In lateral view (Fig. 251.3), it gradually narrows and bents regularly along its entire length except at the distal end, which is sinuous on the dorsal side. In dorsal view (Fig. 252.3), the maximum width is at the point of insertion of the parameres; with slightly sinuous sides tapering gradually towards the apex, this narrows abruptly and ends in a short extension with a truncated distal edge.

Endophallus (Fig. 252.3): There is «Y»-piece and a basal ventral complex, the latter very developed; both pieces strongly sclerotized. In the middle region there is only one large complex piece, with the sides recurved on themselves and prolonged at both ends. The apical region shows reinforcing complex bands formed by various overlapping pieces.

Parameres (Fig. 253.2): Fine, shorter than the median lobe, without apical club and armed with three relatively long fine setae. Tegmen wide and short.

Spermathecal complex: Spermatheca (Fig. 253.10) elongated, with the apical and basal lobes of the same width and well sclerotized, the basal being somewhat more elongated and the apical more spherical; tubular and hyaline junction duct. The spermatic duct is very thin and it widens in a short section between the mouth of the small spermathecal gland and the junction to the basal lobe.

Female uroventrite VIII (Fig. 254.2): Twice as broad as long with a series of well-defined, distant dots throughout the apical half; spiculum long with not too sharp at the tip.

Etymology. In reference to its distribution area in Georgia. Feminine name.

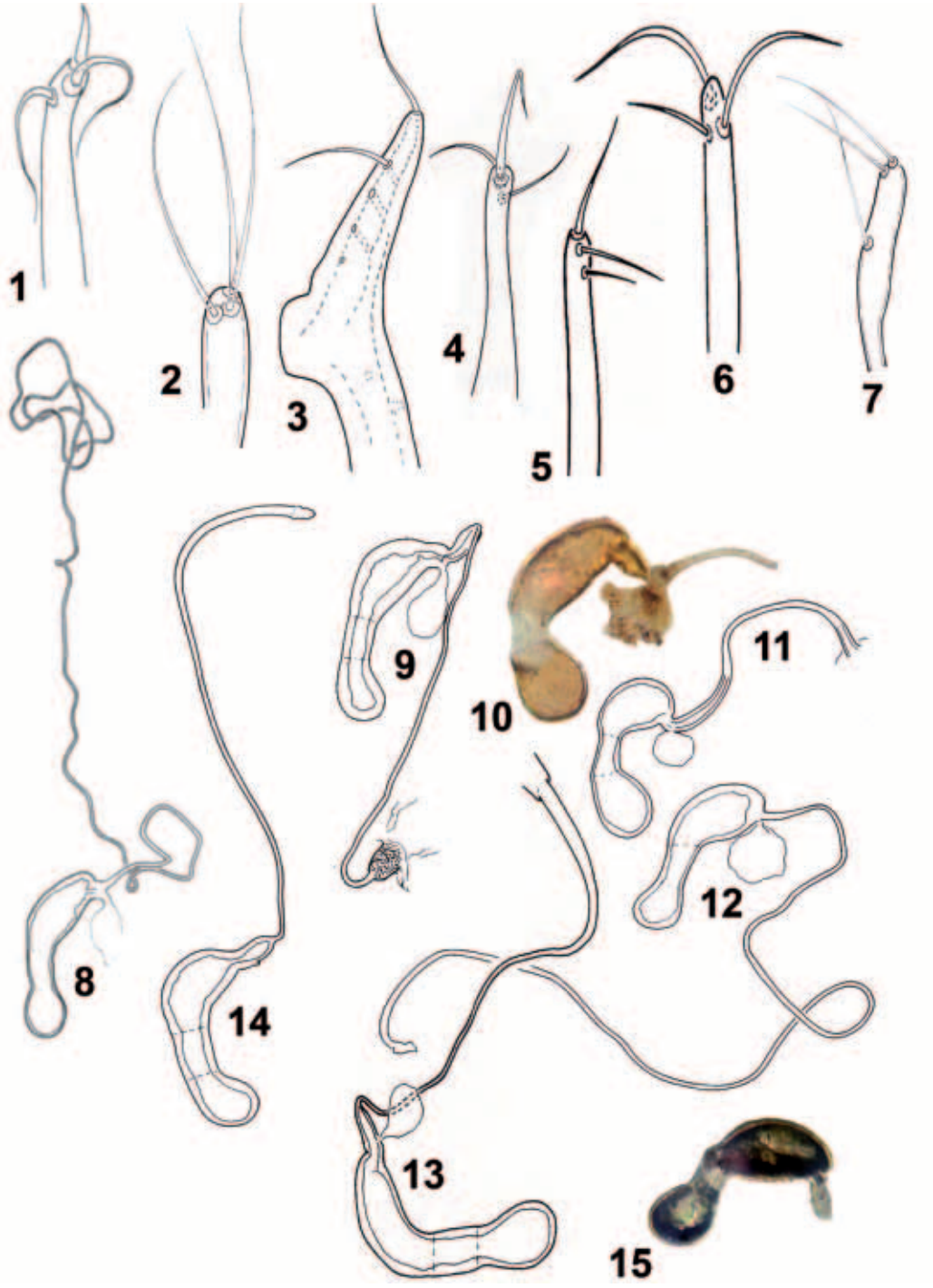
Discussion. Jeannel (1930) in the description of the species related *Bathysciola suramensis* to *Bathysciola persica* (currently the type species of *Sbordoniola*). However, Perreau (2021) suggested that it might be more related to *Bathysciola brignolii* due to the similarity of the median lobe of aedeagus. In fact, this is a very strong hint indeed, supporting that it is closer to *Sbordoniola* than to *Bathysciola patrizii* (*Bathysciola* of *patrizii* species group of Perreau (2021) now transferred to the genus *Cavazzutiella*) or to *Catopsinus* (a genus composed of species also traditionally included in *Bathysciola*). Further Perreau (2021) concluded that the set of species consiting of *B. brignolii* + *B. suramensis* may be a genus in its own right and grouped them into what was called «*suramensis* species group». The molecular study (Fig. 1D) shows that *Georgiana suramensis* comb. nov. (specimen M503) is sister to *Zoiana kociani* comb. nov. (specimen M502) with a support of 54.8/100 and long genetic distance, and these two are sister to *Bathysciola brignolii* (specimen RA496) with a support 100/100, albeit also exhibiting a long genetic distance in the molecular analysis. However, the point of view of Perreau (2021) introducing it into the «*suramensis* species group», was adopted by us and therefore *Bathysciola brignolii* included in the genus *Georgiana* nov. However there are several finding being in conflict with the topology of the phylogenetic tree (Fig. 1D), they are listed in the following:

– The mitochondrial DNA sequences of *Georgiana suramensis* comb. nov. have not been obtained, only the 18s + 28s nuclear genes. An analysis has been done, applying the same evolutionary model as in Tree-1, of the *Catopsinus* clade with only nuclear genes. The result (not shown) point towards a scenario in which *Zoiana kociani* comb. nov. is sister to *Georgiana suramensis* comb. nov. + *Bathysciola brignolii*, an arrangement that is in agreement with the morphological data. Consequently it is believed that the topology of Tree-1/Tree-2 with *Bathysciola brignolii* sister of *Zoiana kociani* comb. nov. + *Georgiana suramensis* comb. nov. might be simply due to the absence of mitochondrial data: bar (barcode), cob (Cytochrome b) and COI (Cytochrome c oxidase 1) genes.

– The aedeagus of *Bathysciola brignolii* (Fig. 251.4, 252.4) follows exactly the same pattern as that of *Georgiana suramensis* comb. nov. (Figs 251.3, 252.3). With the topology of Tree-1 or Tree-2 (Fig. 2) it cannot be included in this genus and another new genus would have to be described for this species alone. But the aedeagus of *Georgiana suramensis* comb. nov. and *Bathysciola brignolii* are so similar and the support of *Georgiana suramensis* comb. nov. + *Zoiana kociani* comb. nov. so low (Fig. 1D: UFBoot = 54.8), that describing this other new genus with these data seems not appropriate.

For the above reasons, *Bathysciola brignolii* will provisionally be included in the genus *Georgiana* nov.

Georgiana gen. nov. presents a set of characters clearly defining it as a genus: reduced eyes not pigmented; antennae not reaching the base of the pronotum; elytra without parasutural stria, with transverse striolae; mesoventral keel not prolonged on the metaventrite and without groove; endophallus with



FIGURES 253.1–253.15: *Catopsinus* series, *Catopsinus* group. Apex of paramere of: (**1**) *Bithyniella strinatii*, (**2**) *Georgiana suramensis* **comb. nov**., (**3**) *Iranobathyscia jeanneli*, (**4**) *Sbordoniola persica persica*, (**5**) *Sengletiola motschulskyi*, (**6**) *S. orientalis* **comb. nov.**, (**7**) *Zoiana kociani* **comb. nov.** Spermathecal complex of: (**8**) *B. strinatii*, (**9**) *Catopsinus pusillus*, (**10**) *G. brignolii* **comb. nov**., (**11**) *I. jeanneli*, (**12**) *S. persica persica*, (**13**) *S. motschulskyi*, (**14**) *S. orientalis* **comb. nov.**, (**15**) *Z. kociani* **comb. nov.** Figs **1**, **8** modified from Rampini & Zoia (1993); Figs **3**–**6**, **9**, **11**–**14** modified from Zoia & Rampini (1994).

well-differentiated «Y»-piece and ventral complex, with a single complex phanera in the median region; spermatheca with the basal part of the spermatic duct non-dilated. *Georgiana* gen. nov. is easily differentiated from *Zoiana* gen. nov. due to its somewhat larger size, 1.6-1.7 mm, in *Zoiana* gen. nov. 1.1-1.5 mm; also by the much longer, robust and curved aedeagus in *Georgiana* gen. nov. The endophallus is very different, although they share the existence of «Y»-piece and a ventral complex, this latter much more developed in *Georgiana* gen. nov.; in the middle region there are dorsal and ventral phanerae in *Zoiana* gen. nov., while in *Georgiana* gen. nov. a single large and complex piece is present; the apical region shows simple reinforcing bands in *Zoiana* gen. nov., being complex and formed by various overlapping pieces in *Georgiana* gen. nov. It is differentiated from *Sbordoniola* by the shape of the median lobe of aedeagus in both lateral (Figs 251.3, 251.6) and dorsal view (Figs 252.3, 252.6); by the different sclerotized parts of the endophallus (Figs 252.3, 252.6) and their distribution. See Discussion section of *Zoiana* gen. nov.

Distribution. Georgia and Turkey. It is distributed throughout the *Yalnızçam* or Arsiani mountains range (*Yalnızçam Dağları* in the far east of the Pontic Alps, the *Doğu Karadeniz Dağları*), Eastern Anatolia Region, northeast Turkey and southwest Georgia. It is present in numerous localities of Meskheti range and Svaneti (Perreau 2021).

Species

Georgiana brignolii (Zoia & Rampini, 1996) comb. nov.
Bathysciola brignolii Zoia & Rampini, 1996: 201.
Bathysciola caucasica Giachino, 1998: 106.

Georgiana suramensis (Jeannel, 1930) comb. nov.
Bathysciola suramensis Jeannel, 1930b: 223.

Genus ***Iranobathyscia*** Zoia & Rampini, 1994
Iranobathyscia Zoia & Rampini, 1994: 786.

Type species. *Iranobathyscia jeanneli* Zoia & Rampini, 1994 by original designation (habitus in Fig. 249.4).

Diagnosis. Small size, 1.4-1.5 mm, bathyscioid body, convex (Fig. 249.4). Covered with golden, fine and lying pubescence.

Head: With complete occipital carina and eye spots.

Antennae: Short and delicate, reaching the base of the pronotum. First antennomere just shorter than the second one. Sub-equal 3rd, 4th, and 5th antennomeres, about three times as long as wide; the 6th shorter than the 5th; the 8th stretched, almost 1.5 times longer than wide, 9th slightly longer than wide; 10th sub-squares, wider than the previous one; the 11th over 1.5 times longer than wide.

Pronotum: Broad, transverse, strongly convex, as wide as the elytra. Lateral sides more curved in the apical third, with maximum width just before the base, which is bisinuated; the basal angles acute.

Elytra: With permanent coaptation of the sutural edges, without parasutural stria. Maximum width at the base, gradually curved towards the apex. Elytral disc with regular and dense transversal striolae.

Legs: Relatively short. Internal tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentameres, strongly dilated. Distal edge of metafemora without tooth, but provided by two strong spines at the proximal end.

Mesoventral keel (Zoia & Rampini 1994): High, forming an obtuse, not toothed angle. Anterior edge slightly arched, the ventral one very thin, not prolonged on the metaventrite.

Metaventrite: Not carinated. Intercoxal apophysis very short and adjacent each other.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Zoia & Rampini 1994): Extremely reduced, with posterior edge of metatergite rectilinear and absent apophysis of the alacrista.

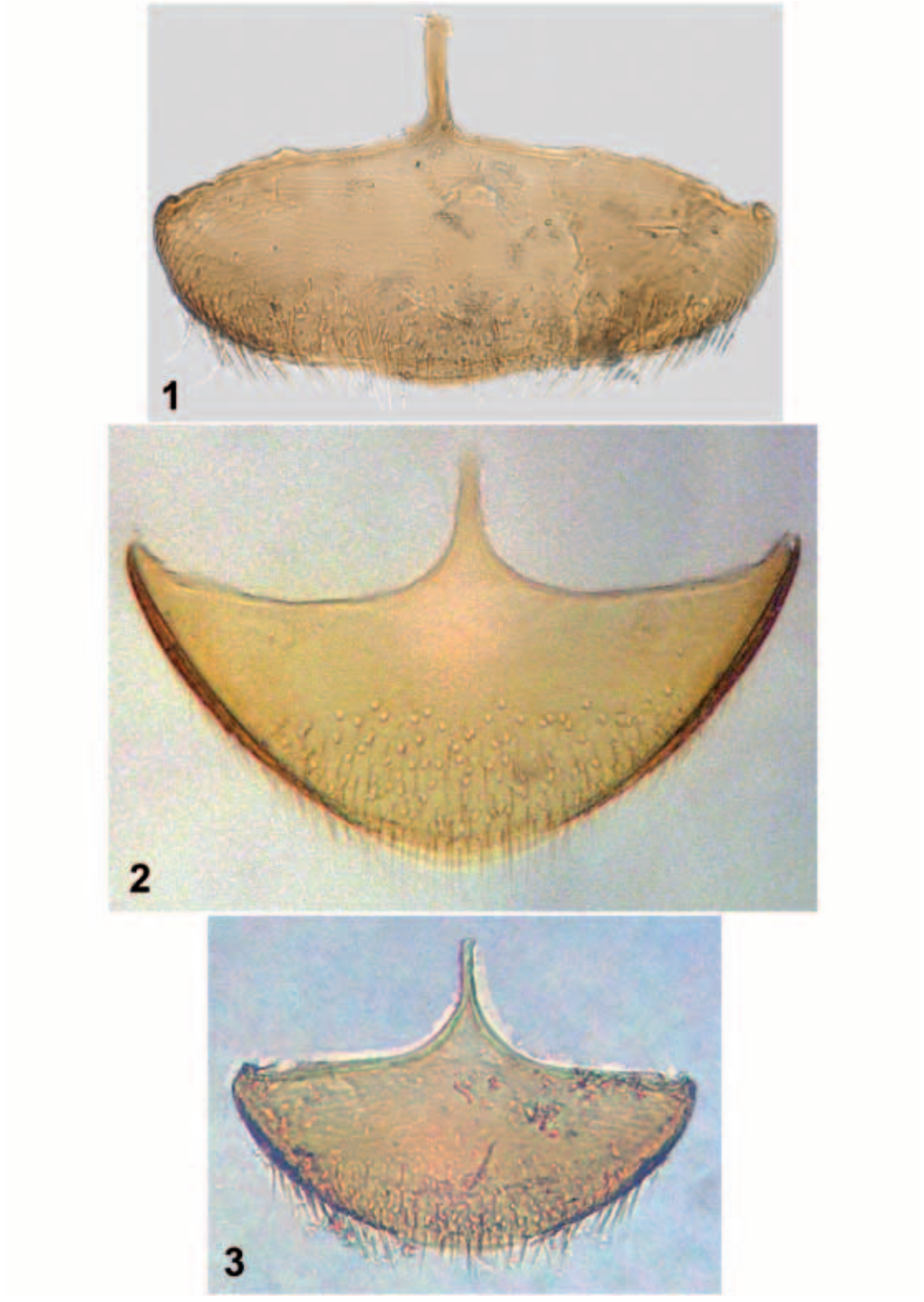
Metendosternite: Unknown.

Median lobe of aedeagus: Relatively large, stout, poorly and not regularly arcuated. In lateral view (Fig. 251.5), bisinuated in preapical part and then abruptly bent downwards. In dorsal view (Fig. 252.5), with maximum width, when excluding the base, towards the middle; then it abruptly narrowing towards the apex to form a short, thin pointed tip. Basal blade wide, without sclerotized apophysis.

Endophallus (Fig. 252.5): Basal «Y»-piece present, but small and poorly sclerotized. Median area with two central, long, longitudinal and brackets-shape phanerae. Distal area without evident phanerae.

Parameres (Fig. 253.3): Stout, shorter than the median lobe. Bisinuated in dorso-ventral direction. Apex enlarged, in dorsal view, shoe-shaped, provided with two, subequal, setae: one apical and another, inner one, preapical. Tegmen wide, dorsally closed by a strongly sclerotized band.

Spermathecal complex (Fig. 253.11): Small-sized,



FIGURES 254.1–254.2: *Catopsinus* series, *Catopsinus* group. Female uroventrite VIII of: (**1**) *Catopsinus hlavaci* (modified from Perreau 2021), (**2**) *Georgiana brignolii* **comb. nov**., (**3**) *Zoiana kociani* **comb. nov.**

kidney-shaped, short and poorly sclerotized spermatheca, with the two similar lobes. Spermatic duct short, with a small and short, sclerotized, dilatation when inserting into the spermatheca. There is a spermathecal gland.

Female uroventrite VIII: Unknown.

DISCUSSION. *Iranobathyscia* presents all the character states defining the group, it is clearly separated from *Bithyniella* by the presence of transversal striolae to the elytra, while it is separated from all other genera of this group by the diverse, pointed shape of the apex of median lobe of aedeagus and as well as the very peculiar shape of parameres. From *Capraiola* and *Sengletiola* it also differs by the strongly dilated protarsi in the males (not, or only slightly dilated in the *Sengletiola*).

DISTRIBUTION. Nord Iran, Mazanderan province.

Species

Iranobathyscia jeanneli Zoia & Rampini, 1994
Iranobathyscia jeanneli Zoia & Rampini, 1994: 786.

Genus ***Sbordoniola*** Zoia & Rampini, 1994
Sbordoniola Zoia & Rampini, 1994: 801.

TYPE SPECIES. *Bathyscia persica* Abeille de Perrin, 1881 by original designation (habitus in Fig 249.5).

DIAGNOSIS. Small size, 1.2-1.7 mm, bathyscioid body (Fig. 249.5), convex. Covered with golden, fine and lying pubescence.

Head: With complete occipital carina and anophthalmous or with eye spots.

Antennae: Very short and delicate, not reaching, or just reaching, the base of the pronotum. First antennomere shorter than the second one; Sub-equal 3rd, 4th, and 5th antennomeres; the 6th shorter than the 5th; 8th from slightly transverse to sub-square; 9th and 10th subsquares, wider than the previous one; the 11th more than two times longer than wide.

Pronotum: Broad, transverse, strongly convex, as wide as the elytra. Lateral sides regularly curved, with maximum width just before, or at the base, which is bisinuated; the basal angles acute.

Elytra: With permanent or temporary coaptation of the sutural edges, without parasutural stria. Maximum width at, or just after, the base, gradually curved towards the apex. Elytral disc with regular and dense transversal striolae.

Legs: Relatively short and stout. Internal tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparsely distributed spines. Male protarsi pentameres, normally dilated. Distal edge of metafemora with or without tooth.

Mesoventral keel (Zoia & Rampini 1994): High, forming an obtuse, toothed or not toothed, angle. Anterior edge slightly arched, the ventral one straight, thin, not prolonged on the metaventrite.

Metaventrite: Not carinated. Intercoxal apophysis very short and adjacent each other.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Zoia & Rampini 1994): Extremely reduced, with posterior edge of the metatergite rectilinear and absent, or just sketched, apophysis of the alacrista.

Metendosternite (Fig. 250.9): «V»-shaped, with no triangular furcal arms; arms rather long, twice as long as the trunk, with well-developed apophysis apical; posterior furcal plate with posterior arched flange. Furcal trunk short, somewhat wider than long.

Median lobe of aedeagus: Elongated, with medium-sized basal blade. In lateral view (Fig. 251.6) curved, more or less gradually narrowing and pointed at apex, which is more or less folded downwards. In dorsal view (Fig. 252.6), with apex from largely rounded to ogival, sometimes trapezoidal.

Endophallus (Fig. 252.6). «Y»-shape basal piece present, normally well sclerotized. Median area with a phanerae of different shape. Distal area with two phanerae more or less developed, parallel or convergent.

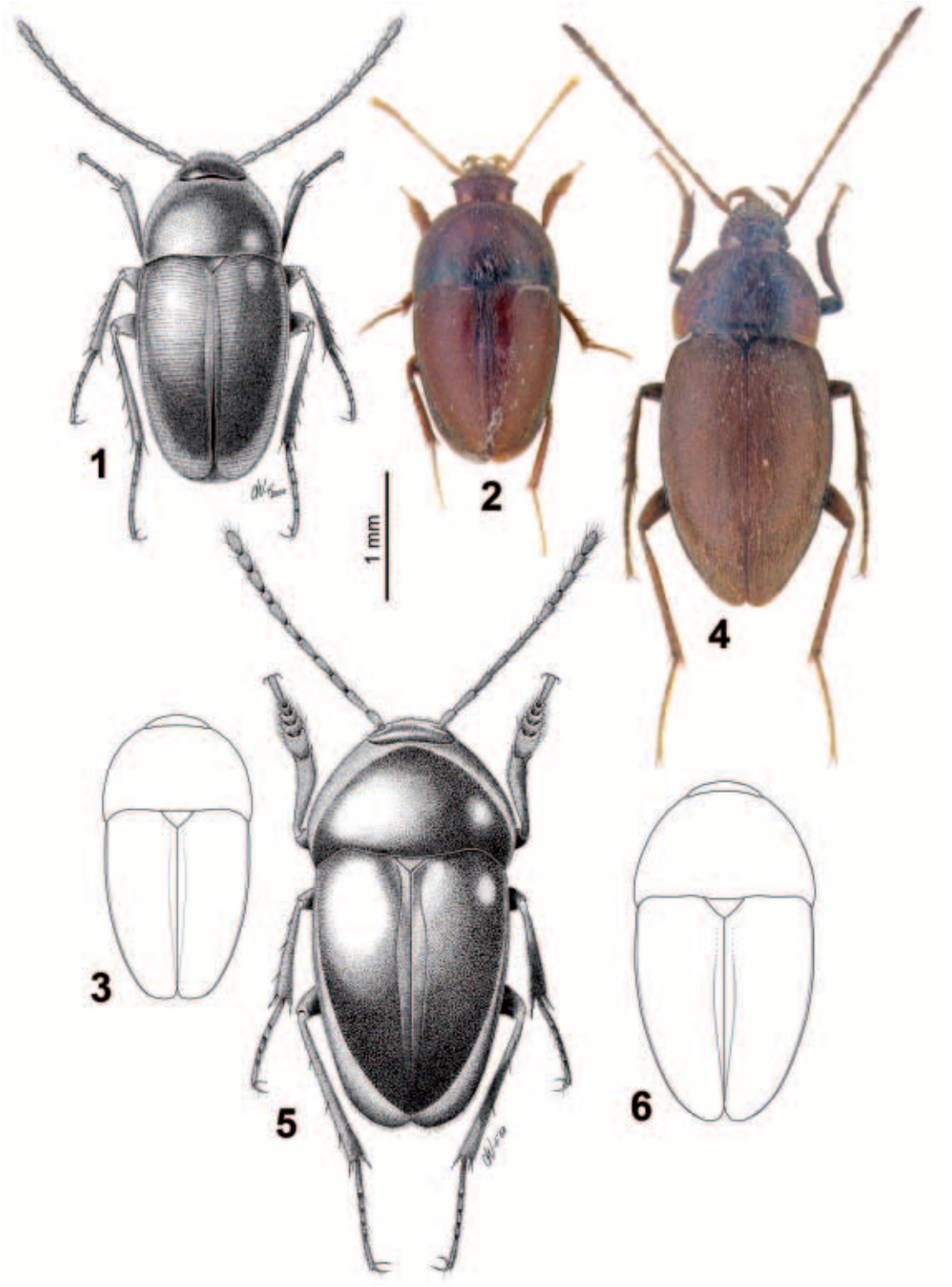
Parameres (Fig. 253.4): More or less robust but always thin at the apex and provided with two to four setae of different strength and length. Tegmen closed dorsally with a more or less sclerotized band.

Spermathecal complex (Fig. 253.12): Medium or medium-small sized spermatheca, kidney-shaped, slightly sclerotized, with the apical lobe spherical and shorter than the oblong basal lobe. Medium length ductus, sometimes significantly enlarged to form a subspherical chamber before the spermatheca; sometimes with a short sclerotized sleeve when inserted into vagina. There is spermathecal gland.

Female uroventrite VIII: Unknown.

DISCUSSION. *Sbordoniola* presents the characters defining the group. It is clearly separated from *Bithyniella* by the presence of transversal striolae to the elytra.

DISTRIBUTION. Nord Iran, Mazanderan province.



FIGURES 255.1–255.6: *Catopsinus* series, *Dellabeffaella* group. Habitus of: (**1**) *Archeoboldoria pascuttoi*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai*, (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini.* Figs **1**, **4**, **5**, **6** by D. Vailati.

Species

Sbordoniola ciliata Zoia & Rampini, 1994
Sbordoniola ciliata Zoia & Rampini, 1994: 801.

Sbordoniola elburzensis Zoia & Rampini, 1994
Sbordoniola elburzensis Zoia & Rampini, 1994: 811.

Sbordoniola fausti (Reitter, 1883)
Bathyscia Fausti Reitter, 1883: 72.
Bathyscia (*Bathyscia*) *Fausti* Reitter: Reitter, 1885 [1884]: 21.
Bathysciola (s. str.) *Fausti* Reitt.: Jeannel, 1914b: 8.
Bathysciola fausti (Reitter): Perreau, 2000: 232.
Sbordoniola fausti (Reitter, 1883): Perreau, 2021: 18.

Sbordoniola gianassoi Giachino, 2003
Sbordoniola gianassoi Giachino, 2003: 249.

Sbordoniola ircanica Zoia & Rampini, 1994
Sbordoniola ircanica Zoia & Rampini, 1994: 819.

Sbordoniola mazanderanica Zoia & Rampini, 1994
Sbordoniola mazanderanica dentata Zoia & Rampini, 1994
Sbordoniola mazanderanica dentata Zoia & Rampini, 1994: 808.
Sbordoniola mazanderanica mazanderanica Zoia & Rampini, 1994
Sbordoniola mazanderanica mazanderanica Zoia & Rampini, 1994: 804.

Sbordoniola persica (Abeille de Perrin, 1881)
Sbordoniola persica abeillei Zoia & Rampini, 1994
Sbordoniola persica abeillei Zoia & Rampini, 1994: 798.
Sbordoniola persica persica (Abeille de Perrin, 1881)

Bathyscia (*Adelops*) *persica* Abeille de Perrin, 1881: ix.
Bathyscia (*Bathyscia*) *persica* Abeille: Reitter, 1885 [1884]: 20.
Bathyscia caspia Abeille: Jeannel, 1907c: 64.
Bathyscia persica Abeille: Jeannel, 1907: 64.
Bathyscia Uhagoni Subsp. *persica* Abeille: Jeannel, 1907b: 422.
Bathysciola persica Abeille: Jeannel, 1910a: 26.
Bathyscia (s. str.) *persica* Abeille de Perrin: Jeannel, 1914b: 10.
Sbordoniola persica persica (Abeille, 1881): Zoia & Rampini, 1994: 795.

Sbordoniola sudcaspica Zoia & Rampini, 1994
Sbordoniola sudcaspica Zoia & Rampini, 1994: 815.

Genus ***Sengletiola*** Zoia & Rampini, 1994
Sengletiola Zoia & Rampini, 1994: 782.
Capraiola Zoia & Rampini, 1994: 790 syn. nov. (Type species: *Capraiola orientalis* Zoia & Rampini, 1994).

Type species. *Sengletiola motschulskyi* Zoia & Rampini, 1994 by original designation (habitus in Fig. 249.6).

Diagnosis. Small size, 1.1-1.4 mm, bathyscioid body (Fig. 249.6), convex. Covered with golden, fine and lying pubescence.

Head: With complete occipital carina; anophthalmous (*Sengletiola motschulskyi*) or with eye spots (*Sengletiola orientalis* comb. nov.)

Antennae: Very short and delicate, reaching or not reaching the base of pronotum. First antennomere shorter or as long as the second one. Sub-equal 3rd, 4th, and 5th antennomeres; the 6th shorter than the 5th one; the 8th, 9th and 10th slightly transverse; the 11th over 1.5 times longer than wide, just wider and about twice as long as the previous one.

Pronotum: Broad, transverse, strongly convex, as wide or just narrower as the elytra. Lateral sides regularly curved, with maximum width at the base, which is bisinuated; the basal angles slightly acute.

Elytra: With temporary coaptation of the sutural edges, without parasutural stria. Maximum width at the base, gradually narrowed towards the apex. Elytral disc with regular and dense transversal striolae.

Legs: Relatively short. Internal tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentameres, dilated or not. Distal edge of metafemora without tooth.

Mesoventral keel (Fig. 250.4): High, forming an obtuse angle and slightly toothed vertex. Anterior edge slightly arched, the ventral one flattened, without groove, not prolonged on the metaventrite.

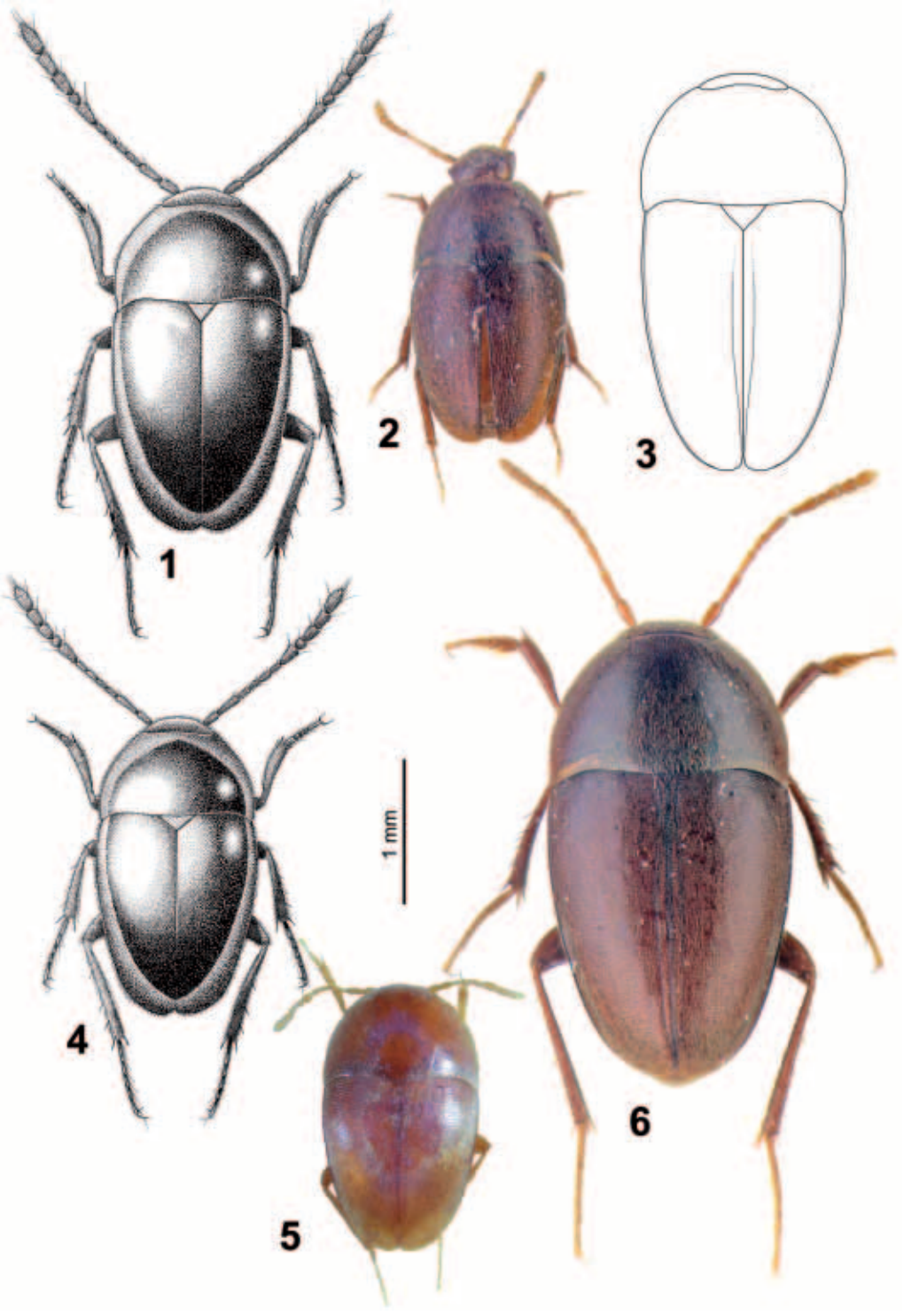
Metaventrite: Not carinated. Intercoxal apophysis of the metaventrite short and adjacent each other.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Zoia & Rampini 1994): Extremely reduced, with posterior edge of metatergite rectilinear and absent or just sketched the apophysis of the alacrista.

Metendosternite: Unknown.

Median lobe of aedeagus: Relatively large, elongate and regularly arcuated. In lateral view (Fig.



FIGURES 256.1–256.6: *Catopsinus* series, *Dellabeffaella* group. Habitus of: (**1**) *Pseudoboldoria bergamasca bergamasca*. (**2**) *Reitteriola pumilio*, (**3**) *Rondolinia adelinae*, (**4**) *Stoppaniola robiati*, (**5**) *Tamaniniella vallarsae*, (**6**) *Valdesiella olmii* **comb. nov.** Figs **1**, **3**, **4** by D. Vailati.

251.7, 251.8), with apex shoe-shaped, bent downwards. In dorsal view (Fig. 252.7, 252.8), with maximum width at the basal third, gradually narrowing towards the rounded apex, that consisting of a robust transverse band chitinized and raised, prolonged forward with a rounded tip. Basal blade wide, with edges well-sclerotized and prolonged in a very short apophysis.

Endophallus (Fig. 252.7, 252.8): Basal «Y»-piece present, well sclerotized. Median area with a couple of long, longitudinal and poorly sclerotized phanerae or with two long dorsal phanerae; in both cases with two short lateral sclerites.

Parameres (Fig. 253.5, 253.6): Slight, in dorsal view, just sinuated in the basal third. Apex provided with three setae: one apical and two subapical. Tegmen wide, closed dorsally.

Spermathecal complex (Fig. 253.13, 253.14): Spermatheca quite long and kidney-shaped; subspherical apical lobe slightly wider and much shorter than the basal one; spermatic duct relatively short and slightly sclerotized, it forms a dilated chamber before the junction to the spermatheca and into which a small spermathecal gland ends; this duct also widens in the area of junction to the copulatory bag.

Female uroventrite VIII: Unknown.

Discussion. *Sengletiola* presents characters defining the group. It is clearly separated from *Bithyniella* by the presence of transversal striolae to the elytra. While it is separated from all the other genera of this group by the very diverse shape of the apex of the median lobe of aedeagus, partially similar to that of *Besucheti-ola* (*Phaneropella* group). *Sengletiola* and *Capraiola* share the same structure of the median lobe of the aedeagus: in lateral view both have an apical denticle (Figs 251.7, 251.8) and in dorsal view a peduncule at the apex (Figs 252.7, 252.8). The endophallus is different in structure although it apperantly follows the similar pattern: in *Sengletiola* (Fig. 252.7) the two large ventral phanerae are missing albeit the two short and lateral sclerites are in the same position as the one in *Capraiola* (Fig. 252.8). However, this piece is here apparently attached to the apex of the median lobe of aedeagus represents a unique structure as nothing similar is found in any other Leptodirini. Since *Sengletiola* and *Capraiola* inhabit exactly the same mountainous area in the area of the southern Caspian Sea, it appears likely that such a piece being found as a result of an evolutionary convergence must be ruled out. Accordingly, the synonymy is established: *Sengletiola* Zoia & Rampini, 1994 = *Capraiola* Zoia & Rampini, 1994 syn. nov. Both names are proposed in the same paper (Zoia & Rampini 1994) but *Sengletiola* is the first to be described so it has priority.

Distribution. Nord Iran, Mazanderan province.

Species

Sengletiola motschulskyi Zoia & Rampini, 1994
Sengletiola motschulskyi Zoia & Rampini, 1994: 783.

Sengletiola orientalis (Zoia & Rampini, 1994) comb. nov.
Capraiola orientalis Zoia & Rampini, 1994: 790.

Genus ***Zoiana*** nov.
https://zoobank.org/NomenclaturalActs/639004D6-0AF4-423F-B8F5-A77430FCAF11

Type species. *Phaneropella* (*Hittitia*) *kociani* Švec, 2016 by present designation (habitus in Fig. 249.7).

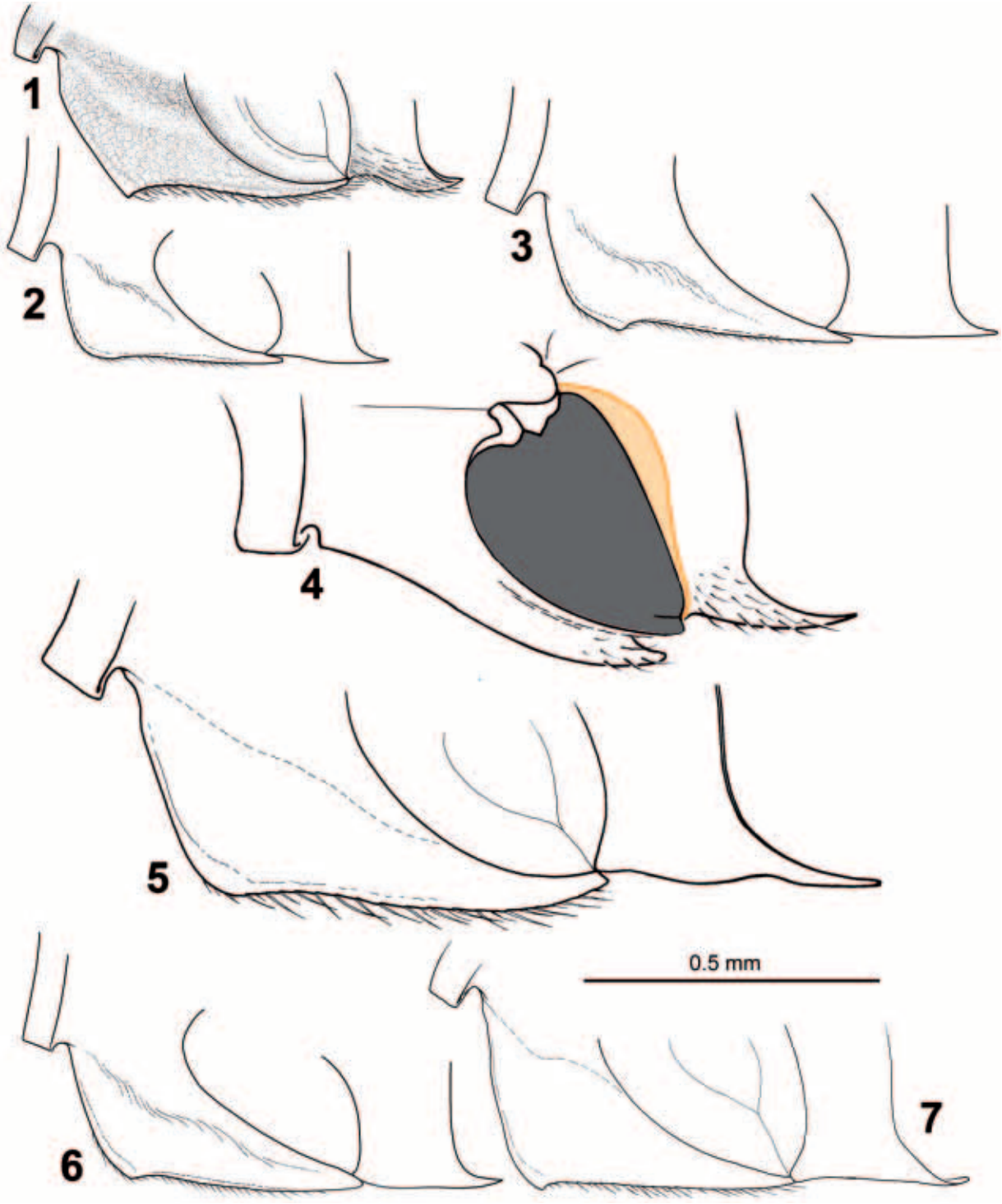
Description. Small size, 1.1-1.5 mm, body oblong oval and strongly convex (Fig. 249.7); bathyscioid facies. Colouration reddish-brown; pubescence yellowish, predominantly recumbent setae.

Head: Retractile, without occipital carina; well-marked punctation and clearly separated and distant dots; eyes very reduced, pigmented.

Antennae: Short, weak, do not exceeding the base of the pronotum; second antennomere as long as the first one and considerably thick, thickness comparable in the 7th; the 8th antennomere is markedly transverse, much wider than it is long; the 9th and 10th are also transverse.

Pronotum: Transverse, convex, covered with a short and decumbed pubescence. Smooth microsculpture and inconspicuous punctation, very small and fine dots but scarcer and finer than on the head. Maximum width at the base, as broad as the base of the elytra. Lateral side long and regularly curved up to the anterior angles and less curved down to the posterior angles. Posterior angles acute, pointed vertices and directed backwards on the base of the elytra in dorsal view.

Elytra: Oval and very convex, wider in the basal third and as wide as long or the width slightly less, with rounded apices. Dorsal surface clearly microreticulate; punctures stronger than in the head and pronotum, slightly rasp-like shaped. The punctures, especially at posterior half of the elytra tend to align into transversal lines clearly stronger towards the apex



FIGURES 257.1–257.7: *Catopsinus* series, *Dellabeffaella* group. Pterothorax in lateral view of: (**1**) *Archeoboldoria lanai*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai*, (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini*, (**7**) *Pseudoboldoria bergamasca bergamasca*. Figs **1**–**3**, **5**–**7** by D. Vailati.

of the elytra. Therefore, at least part of the surface of the elytra appears to present transverse striolae. Pubescence similar to that of the pronotum. Without parasutural stria. Scutellum very small and triangular.

Legs: Short and thick; male protarsi tetramerous and not dilated. Protibiae slightly bent without a comb, provided with two apical external spurs. Mesotibiae with slightly sinuated inner apical half and a polydentate internal apical spur; external margin with robust spines and two simple apical spurs. Meso- and metatibiae without apical basket.

Mesoventral keel (Fig. 250.5): High, with slightly curved front edge, sub-rectilineous angle and rounded vertex; ventral edge slightly curved, wide, with a groove along the middle part and the posterior prolongation over a small part of the anterior area of the metaventrite.

Suture of the metaventrite (Fig. 250.5): It delimits a small and arched area in the apical half and it then continues parallel and very close to the coxal cavity.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Small and stout. In lateral view (Fig. 251.9), slightly arched; dorsal side slightly sunken in the basal third and subrectilinear in the apical half; apex thickened and somewhat bent towards the ventral side. In dorsal view (Fig. 252.9), sides slightly sinuous, with the maximum width in the middle part; in the apical part the rectilinear or slightly concave sides progressively narrow into a amply rounded apex. Basal blade wide and broadly rounded posteriorly.

Endophallus (Fig. 252.9): Basal region with «Y»-piece well differentiated with long and recurved arms, equipped with a tubule and apical fibres of the «Y»-piece strongly curved on both sides of the bag; at its base there is basal lamina; existence of a basal ventral complex with apical armor, through which a flagellum runs. In the middle region there are overlapping dorsal and ventral phanerae. Apical region with reinforcing bands long, which are extended by a hyaline tissue on the external side of the phanerae of the middle region.

Parameres (Fig. 253.7): Thin, slightly sinuous in dorsal view and sub-rectilinear in lateral view; shorter than the median lobe; apical part dilated in tea-spoon shaped where three long apical setae originate, subequal and oriented inwards: two at the apex and the third with preapical insertion.

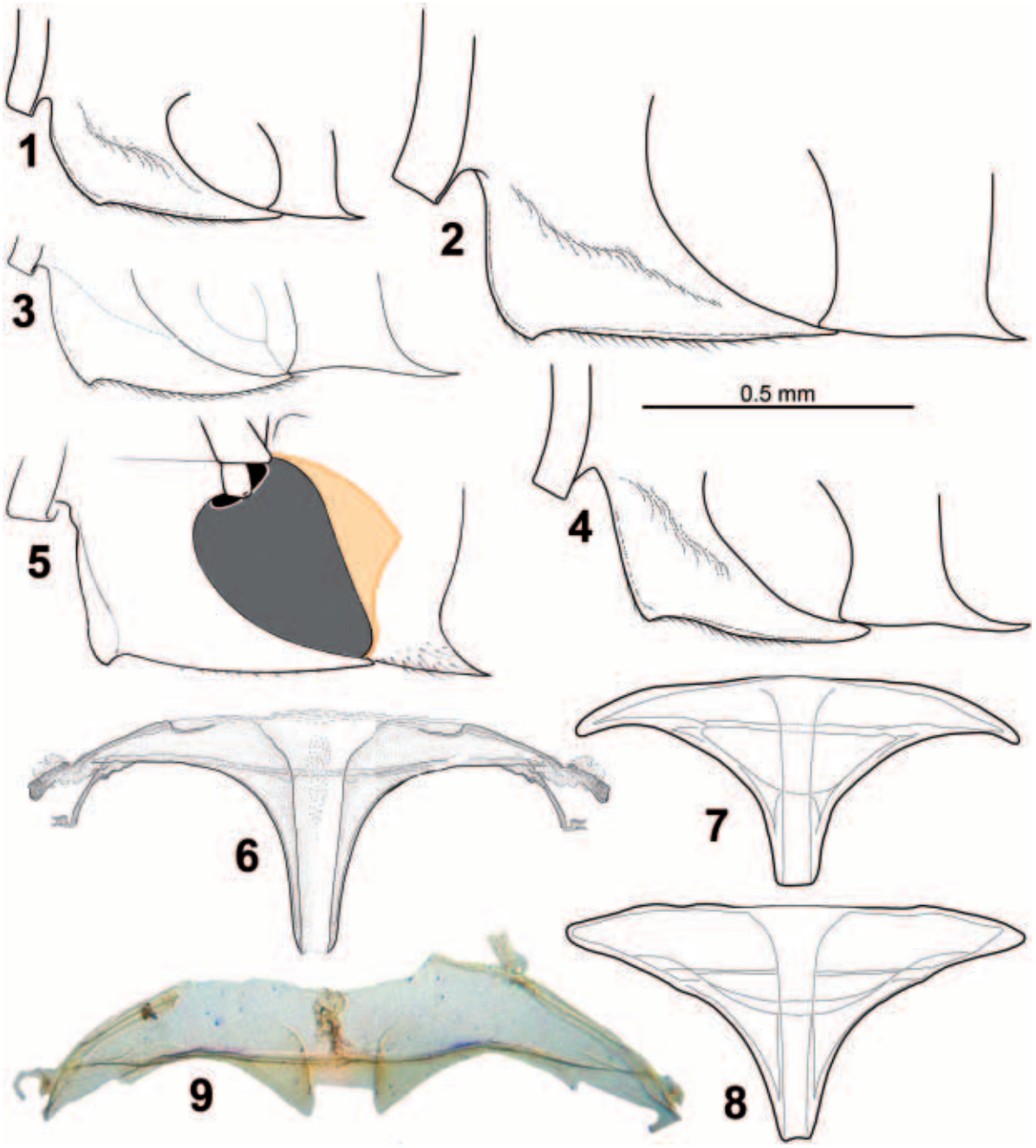
Spermathecal complex: Spermatheca (Fig. 253.15) small with the apical and basal lobes well sclerotized and developed, the basal one being more thick, elongated oval, the apical subspherical; narrower, short and hyaline median union duct; thin spermatic duct, not dilated in the area where it joins the basal lobe, spermathecal gland not visible.

Female uroventrite VIII (Fig. 254.3): Short and wide, with the apical margin in a wide arc; spiculum long and narrow.

ETYMOLOGY. Genus dedicated to the entomologist S. Zoia (Milan, Italy) who has worked on the Leptodirini from the eastern parts of its distribution area. Feminine name.

DISCUSSION. *Zoiana* gen. nov. presents a set of characters that clearly define it: reduced eyes; antennae not reaching the base of the pronotum and transverse 1st, 2nd, 7th to 10th antennomere; elytra without parasutural stria but with transverse striolae; mesoventral keel with broad ventral edge and a groove, a little prolonged on the metaventrite; endophallus with well-differentiated «Y»-piece in the basal region, with dorsal and ventral phanerae in the median region; spermatheca with the basal part of the spermatic duct non-dilated. *Zoiana* gen. nov. is sister to *Georgiana suramensis* comb. nov. (specimen M503) with a support of 54.8/100 and both are sister to the genus *Sbordoniola* with a very high support, 100/100 (Fig. 1D). *Zoiana* gen. nov is easily differentiated from *Georgiana* gen. nov. by to the size, which is somewhat smaller 1.1-1.5 mm in *Zoiana* gen. nov., than in *Georgiana suramensis* comb. nov. with 1.6-1.7 mm, this small difference becomes apparent when specimens of both genera are directly compared; the same pattern appears when the aedeagi are compared, which is much longer, more robust and curved in *Georgiana* gen. nov. The endophallus of both genera is very different although they share the existence of a «Y»-piece and a ventral complex, while the latter is much more developed in *Georgiana* gen. nov.; in the middle region there are dorsal and ventral phanerae in *Zoiana* gen. nov. whereas in *Georgiana* gen. nov. there is only one large complex piece, with the sides recurved on themselves and extended at both ends; the apical region show simple reinforcing bands in *Zoiana* gen. nov., which are complex and formed by several overlapping pieces in *Georgiana* gen. nov.

Zoiana gen. nov. is easily differentiated from *Sbordoniola* by the mesoventral keel with a wide and grooved lower edge, while in *Sbordoniola* the lower edge is sharp and without a groove; also by the shape of the middle lobe of the aedeagus, both in lateral (Figs 251.6, 251.9) and dorsal view (Figs 252.6, 252.9); by the different sclerotized pieces and their distribution in the endophallus (Figs 252.6, 252.9); by



FIGURES 258.1–258.9: *Catopsinus* series, *Dellabeffaella* group. Pterothorax in lateral view of: (**1**) *Reitteriola pumilio*, (**2**) *Rondolinia adelinae*, (**3**) *Stoppaniola robiati*, (**4**) *Tamaniniella pivai* **sp. nov**., (**5**) *Valdesiella olmii* **comb. nov.** Metatergal apparatus, ventral view of the metanotum and axillaria of: (**6**) *Archeoboldoria lanai*, (**7**) *Baudiola tarsalis*, (**8**) *Canapiciella angeli*, (**9**) *Canavesiella lanai*. Figs **1**–**4**, **6**–**8** by D. Vailati.

the different shape of the club, the thickness and the insertion of the three setae of the parameres (Figs 253.4, 253.7).

Specimens of *Phaneropella medea* have not been studied, but the description (Perkovsky 1990) indicate that the basic characters are sufficiently similar to clearly identify it as belonging to *Zoiana* gen. nov. This species therefore is included in the new genus as *Zoiana medea* comb. nov. at least until molecular data are available and confirm or reject this classification. The reasons based on morphological the following characters support its inclusion: body shape and size, tetramerous male protarsus, no parasutural striae on the elytra and the parameres with three apical setae, inclined to the paramere axis, backwards and inwards (Perreau 1999), all characters also observed in *Zoiana kociani* comb. nov. In addition in *Zoiana medea* comb. nov. the parameres do not seem to have an apical club, the insertion of the three setae is contiguous and the endophallus has a basal «Y»-piece and two symmetrical elongate median sclerites (Perreau 1999); and although the spermatheca is similar, in *Zoiana medea* comb. nov. there is a spermiduct lobe (Perreau 1999: Fig. 13) that connects with the basal lobe of the spermatheca which does not exist in *Zoiana kociani* comb. nov. and the spermiduct connects directly with the basal lobe of the spermatheca. Of all the characteristics, the most relevant is the mesoventral keel with a wide lower edge and a groove, in *Zoiana medea* comb. nov. (Perkovsky 1990), a characteristic that has only been observed in *Zoiana kociani* comb. nov., in the genera *Espanoliella* and *Amphogeus* stat. nov., of the *Espanoliella* group of the *Quaestus* series and in the genera *Atticiella* and *Maroniella* (*Sophrochaeta* series), and *Speophyes* (*Cytodromus* series). Finally, also in these two species of *Zoiana* gen. nov. the mesoventral keel extends over the anterior edge of the metaventrite.

Distribution. *Zoiana* gen. nov. was localised at two points about 120 km apart, both in Georgia. *Zoiana kociani* comb. nov. is present in two areas in Svaneti, one at an altitude of 1,480 m, near Mestia; the second in the river Khuberi valley at 720 m. *Zoiana medea* comb. nov. is only known from Kashtak and Gumistrinsky res. Zumur (Perreau 1999) in Abkhazia (Georgia).

Species

Zoiana kociani (Švec, 2016) comb. nov.
Phaneropella (*Hittitia*) *kociani* Švec, 2016: 490

Zoiana medea (Perkovsky, 1990) comb. nov.
Phaneropella medea Perkovsky, 1990: 76.

3.4.6.3 ***Dellabeffaella*** group

Diagnosis. Group characterised by metendosternite not «V»-shaped, with triangular furcal arms, protibiae with incomplete apical baskets and pectinate or polydentate tibial spurs and mesoventral keel not prolonged on the metaventrite.

Discussion. In our phylogenetic tree (Fig. 1D) this group appears divided in two main clades, the first including the genera of the *Dellabeffaella* subgroup, with a low support of 26.5/70 and the second one including the *Archeoboldoria* subgroup, with a support of 87.5/71. This entire clade however is found to be highly supported (97.6/100).

Key to subgroups

1. Parasutural stria present.....2
- Parasutural stria lacking .....
.....*Dellabeffaella* subgroup-pars (*Pseudoboldoria*, *Stoppaniola*, *Baudiola*, *Canavesiella*)

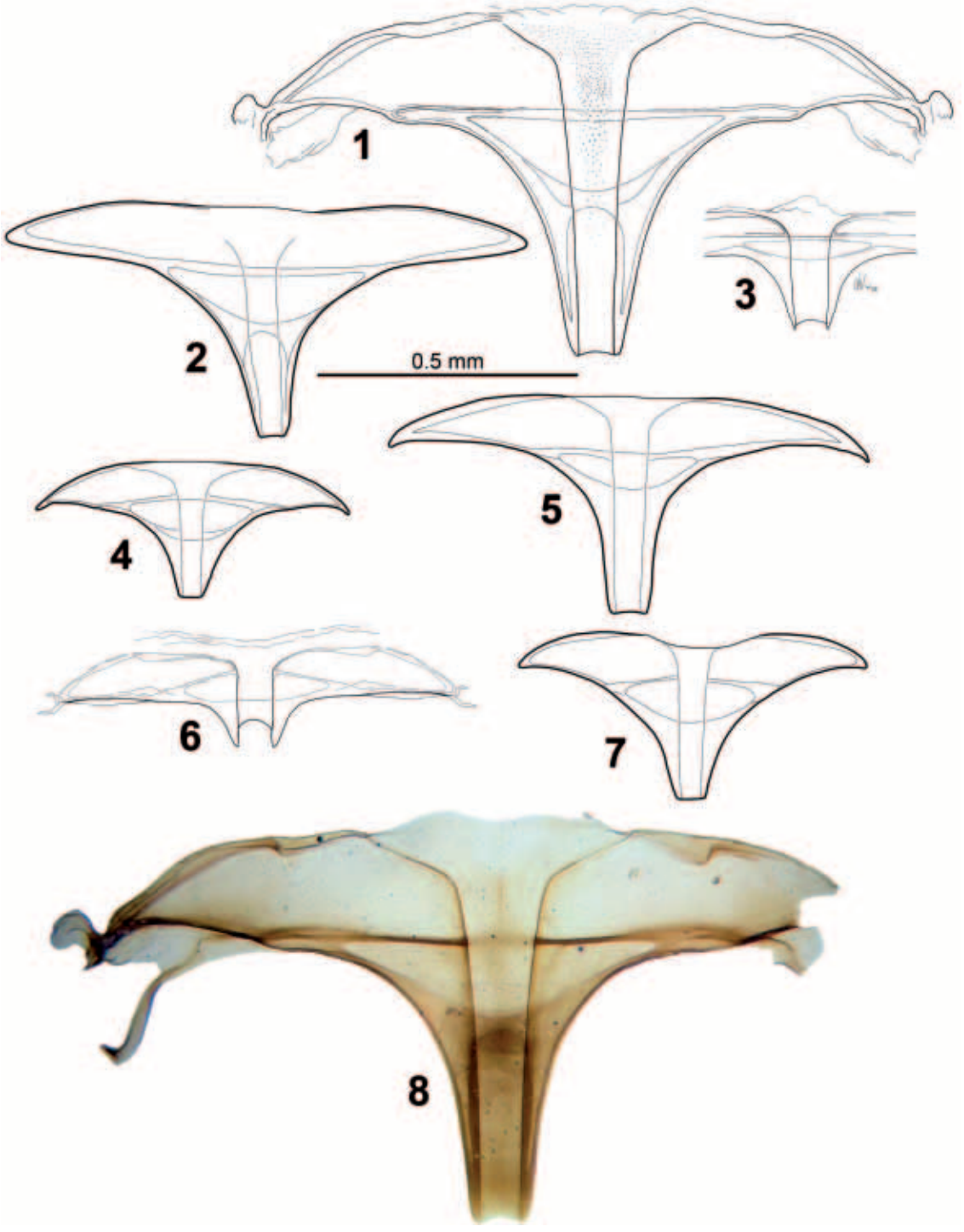
2. Male protarsi not dilated.....3
- Male protarsi dilated.....4

3. Elytra trasversally striate *Archeoboldoria* subgroup pars (*Reitteriola*, *Archeoboldoria*)
- Elytra not trasversally striate .....
.....*Dellabeffaella* subgroup-pars (*Doderiola*, *Tamaniniella*)

4. Elytra trasversally striate.....*Dellabeffaella* subgroup-pars (*Dellabeffaella*, *Valdesiella* gen. nov., *Canapiciella*)
- Elytra not trasversally striated .....
.....*Archeoboldoria* subgroup-pars (*Rondolinia*)

Dellabeffaella subgroup

This is a subgroup three clades are identified but is only weakly supported 26.5/70, one of these consisting of the genera *Dellabeffaella*, *Valdesiella* gen. nov., *Canavesiella* and *Canapiciella* with very high support



FIGURES 259.1–259.8: *Catopsinus* series, *Dellabeffaella* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Dellabeffaella roccae,* (**2**) *Doderiola agostini*, (**3**) *Pseudoboldoria bergamasca bergamasca*, (**4**) *Reitteriola pumilio*, (**5**) *Rondolinia adelinae*, (**6**) *Stoppaniola robiatii*, (**7**) *Tamaniniella vallarsae*, (**8**) *Valdesiella olmii* **comb. nov.** Figs **1**–**7** by D. Vailati.

99.8/100, another with the genus *Baudiola* that relates to the previous genera also with a high support 93.3/100 and, finally, the clade with the genera *Pseudoboldoria* and *Tamaniniella* related to full support 100/100 (Fig. 1D). In this sense the sub-group in itself shows good support but the position as a group is not strongly supported.

As already pointed out, the detailed analysis of the geographical distribution of the three clades of *Dellabeffaella* subgroup reveals a complex zoogeographic situation, not based on simple vicariance phenomena (Vailati 2017; Giachino & Vailati 2019) but that there are effects not dividing but joined distribution area which widely overlap. This situation is probably to be related to past palaeogeographic and palaeoclimatic phenomena, similar, at least in part, to those suggested by Vailati (1988, 2017, 2017b) for the «*Boldoria* phyletic series» (*sensu* Vailati 1988). These phenomena are attributable to multiple expansions and contractions of the original distribution areas under the impulse of the geological-tectonic and climatic changes of the past.

Key to genera

1. Pectinate inner tibial spurs (with symmetrical indent).....2
- Polydentate inner tibial spurs (with asymmetrical indent).....6

2. Parasutural stria present, complete 3
- Parasutural stria lacking 4

3. Male antennae moderately elongated, reaching at most, lying backwards, the half of the elytra. 8th antennomere almost twice as long as wide. Pronotum wider than the elytra, with the maximum width well in front of the posterior angles.....*Dellabeffaella*
- Male antennae less elongated, reaching at most, lying backwards, the anterior third of the elytra. 8th antennomere as long as wide. Pronotum narrower than the elytra, with the maximum width at the apex of the basal third.....*Valdesiella* gen. nov.

4. Male protarsi dilated.....*Canavesiella*
- Male protarsi not dilated 5

5. Posterior margin of the metafemora, with small tooth, more or less pronounced, widely obtuse, sometimes almost faded away, but always present. Median lobe of aedeagus not abruptly narrowed at the apex, more rounded, without salient preapical lateral expansions (Fig. 265.2). In lateral view, more or less curved (Fig. 263.2). Parameres with three long subequal setae originating apically (Fig. 265.14).....*Stoppaniola*
- Posterior margin of the metafemora smooth, unarmed. Median lobe of aedeagus more or less narrowed at apex, rounded to pointed, preceded (except in *Pseudoboldoria barii*) by lateral preapical expansions sometimes very pronounced, angular, flattened and salient (Fig. 264.7). Parameres generally bearing two properly apical and unequal setae and a longer preapical seta (Fig. 265.11).....*Pseudoboldoria*

6. Elytra without parasutural stria; spermatheca very large (Fig. 266.2).....*Baudiola*
- Elytra with parasutural stria; spermatheca shorter (Figs 266.3, 266.5, 266.10).....7

7. Male protarsi moderately dilated .....*Canapiciella*
- Male protarsi non-dilated 8

8. Parameres with two apical setae and one moved far back about halfway of paramere (Fig. 265.15).....
.....*Tamaniniella*
- Parameres with three apical setae (Fig. 265.10).....
.....*Doderiola*

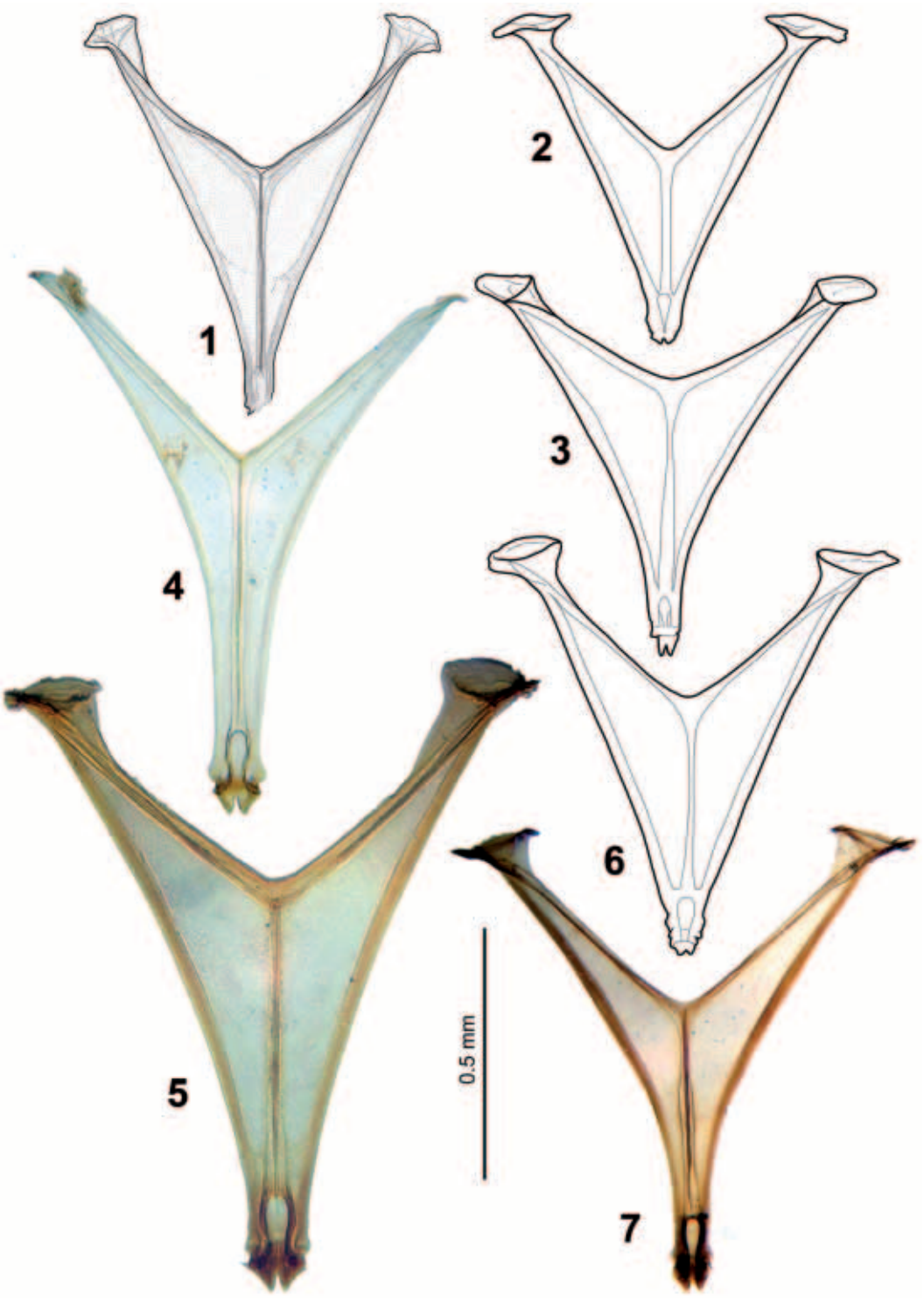
Clade ***Pseudoboldoria***

The *Dellabeffaella* subgroup is in the tree as shown in Fig.1D found in a basal position (Fig. 1D). The lineage of the genera *Pseudoboldoria* + *Tamaniniella* are separated from each other by a clade with high support (100/100) and the genus *Stoppaniola* for which no molecular data are available. This morphologically homogeneous group of genera, is supported by molecular data for *Pseudoboldoria* and *Tamaniniella* and to which most likely also *Stoppaniola* belongs to but where supported is limited to the morphological evidence (Vailati 2017). It is a group characterised by: non-dilated male protarsi, non «V»-shaped metendosternite with triangular furcal arms and endophallus with well-developed basal «Y»-piece.

Genus ***Pseudoboldoria*** Ghidini, 1937
Boldoria (*Pseudoboldoria*) Ghidini, 1937: 63.
Pseudoboldoria Ghidini, 1937: Vailati, 1988: 48.

Type species. *Bathyscia* (*Bathysciola*) *Krugeri* G. Müller, 1914 by original designation (habitus in Fig. 256.1).

Diagnosis. Medium size, 1.9-2.8 mm, bathyscioid body, generally elliptical in shape (Fig. 256.1).



FIGURES 260.1–260.7: *Catopsinus* series, *Dellabeffaella* group. Metendosternite of: (**1**) *Archeoboldoria lanai*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai*, (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini*, (**7**) *Pseudoboldoria krugeri*. Figs **1–3**, **6** by D. Vailati.

Antennae: Male antennae moderately elongated, reaching, when lying backwards, about half of the elytra. First antennomere of equal length or shorter than the second one. The 8th generally transverse or just longer than wide. The 11th stout, wide, flattened, rounded at apex, as long as the previous one plus a third of the 9th one.

Pronotum: Wide at the base, with the sides always regularly rounded.

Elytra: Without parasutural stria, but sometimes with a very faint trace at the basal quarter in the scutellar region, which is depressed. Provided with transversal striolae, from fine to coarse, from light to well marked.

Legs: Metafemora with unarmed posterior margin. Apex of the tibiae with pectinate internal spurs. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and never dilated, even less wide than half of apex of protibiae.

Mesoventral keel (Fig. 257.7): High, but not protruding forward. The anterior profile from obliquely elusive to straight, more or less slightly curved; ventral profile straight. Always showing, below the front angle, a small, but well-pronounced tooth. Posteriorly without apophysis prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.3): Moderately developed, stout, with short apophysis of the alacrista and with longitudinal furrow two to three times longer than wide.

Metendosternite (Fig. 260.7): «Y»-shaped, with triangular furcal arms. Arms somewhat shorter than the trunk, the posterior lamina narrows progressively until the apical part where a well-developed apophysis is observed. Long furcal trunk, clearly longer than the widest part.

Median lobe of aedeagus: As long as a third of the body length, more stout than in *Stoppaniola*. In lateral view (Fig. 262.7) moderately curved, with a straight and thick apex. In dorsal view (Fig. 263.7) with subparallel sides for almost the entire length; in the preapical region, wide, flattened, with more or less pronounced dorsolateral expansions, flattened and always salient.

Endophallus (Fig. 263.7): Basal «Y»-piece well-developed and sclerotized. There are a complex phanera in median basal position and two apical, subparallel and moderately sclerotized lists.

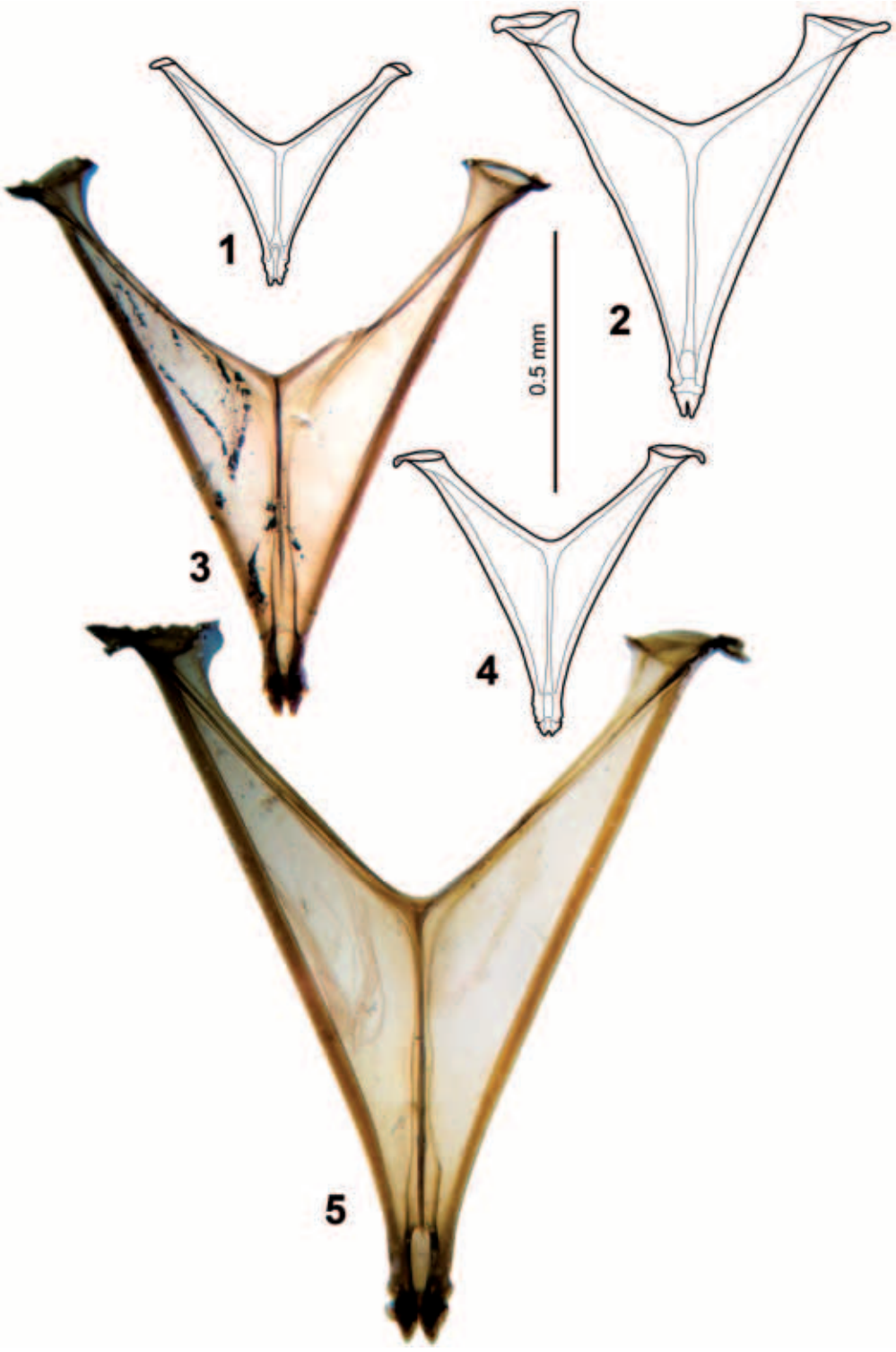
Parameres (Fig. 265.11): Long but not slender, slightly shorter than the median lobe. At apex two unequal setae and a preapical third originate, ventral, longer and more robust; except *P. belluccii* with 2-3 short additional setae.

Spermathecal complex (Fig. 266.6): Short spermatheca tends to be symmetrical, with the proximal lobe sub-spherical and distal lobe oval elongated and somewhat narrower. Median part generally short, length less than twice the width. Spermatic duct somewhat widened and sclerotized in the area near the insertion in the proximal lobe.

Female uroventrite VIII (Fig. 267.7): Spiculum present, but very small, pointed or barely hinted at by a sunken protuberance.

Discussion. *Pseudoboldoria*, like *Tamaniniella*, shows a non-toothed metafemora (with a tooth at the posterior edge in *Stoppaniola*). It is overall similar to *Stoppaniola* in the absence of parasutural stria of the elytra (present in *Tamaniniella*) and the pectinate internal tibial spurs (polydentate in *Tamaniniella*). However, there is also a similarity to *Reitteriola* by the profile of the median lobe of aedeagus in lateral view and for the shape of the spermatheca. But to the same time exhibiting an identical structure of the endophallus as found in *Stoppaniola*: at least those of *Pseudoboldoria bergamasca bergamasca* (Fig. 264.7) and *Stoppaniola robiatii* (Fig. 265.2) are identical, indicating that there is a close affinity between these two. It is quite possible that *Pseudoboldoria* and *Stoppaniola* are sister genera, and this clade originated from *Tamaniniella*, which is with respect to the structure of the endophallus is very disctinct (Fig. 265.3). The long genetic distance that separates *Pseudoboldoria* from *Tamaniniella* supports this hypothesis, but at the moment there are no molecular data from *Stoppaniola* to confirm or deny this. Hence the molecular analysis with the limited data available (Fig. 1D) indicates that *Pseudoboldoria* is more closely related to *Tamaniniella* (support 100/100) than to *Archeoboldoria*, which would be more consistent with the information derived from the zoogeographic perspective. Vailati (1988, 2017) established three groups for *Pseudoboldoria* species.

Distribution. Italy. Orobie Alps and Bergamasque Prealps: Grigne Mt, Resegone Mt, Imagna valley, Brembana and Seriana valleys, Cavallina valley, Sebino (Bergamo area) and up to the middle Camonica valley. Brescian Prealps: Guglielmo Mt and right side of the Trompia valley.



FIGURES 261.1–261.5: *Catopsinus* series, *Dellabeffaella* group. Metendosternite of: (**1**) *Reitteriola pumilio*, (**2**) *Rondolinia adelinae*, (**3**) *Stoppaniola schatzmayri*, (**4**) *Tamaniniella vallarsae*, (**5**) *Valdesiella olmii* **comb. nov.** Figs **1**, **2**, **4** by D. Vailati.

Species

«***bari*** group» *sensu* Vailati, 1988
Pseudoboldoria barii (Focarile, 1950)
Boldoria (*Pseudoboldoria*) *Barii* Focarile, 1950: 22.
Boldoria (*Pseudoboldoria*) *barii* Focarile: Regalin, 1983: 145.
Pseudoboldoria barii (Focarile, 1950): Vailati, 1988: 83.

«***bergamasca*** group» *sensu* Vailati, 1988
Pseudoboldoria bergamasca (Jeannel, 1914)
Pseudoboldoria bergamasca bergamasca (Jeannel, 1914)
Speonesiotes bergamascus Jeannel, 1914c: 202.
Bathysciola bergamasca Jeann.: G. Müller, 1919b: 37.
Bathysciola (*Boldoria*) *bergamasca* Jeannel, 1914: Jeannel, 1924a: 117.
Boldoria (*Pseudoboldoria*) *bergamasca* Jeannel: Ghidini, 1937: 67.
Pseudoboldoria bergamasca bergamasca (Jeannel, 1914): Vailati, 1988: 88.
Pseudoboldoria bergamasca binaghii (Jeannel, 1931)
Bathysciola (*Boldoria*) *bergamasca* subsp. *Binaghii* Jeannel, 1931c: 54.
Boldoria (*Pseudoboldoria*) *bergamasca* ssp. *Binaghii* Jeannel, 1931: Ghidini, 1937: 67.
Pseudoboldoria bergamasca binaghii (Jeannel, 1931): Vailati, 1988: 94.

Pseudoboldoria kruegeri (G. Müller, 1914)
Pseudoboldoria kruegeri kruegeri (G. Müller, 1914)
Bathyscia (*Bathysciola*) *Krügeri* G. Müller, 1914: 1013.
Bathysciola (*Boldoria*) *evasa* Ghidini, 1937: 58.
Bathysciola (*Boldoria*) *Krügeri* J. Müller, 1914: Jeannel, 1924a: 117.
Boldoria (*Pseudoboldoria*) *Krügeri* Müller, 1914: Ghidini, 1937: 65.
Pseudoboldoria kruegeri kruegeri (Müller, 1914): Vailati, 1988: 98.
Boldoria (*Pseudoboldoria*) *evasa* Ghidini, 1937: 64.
Pseudoboldoria kruegeri orobica Vailati, 1988
Boldoria (*Pseudoboldoria*) *orobica* Focarile, 1965 (*in litt*.): Focarile, 1965: 43.
Pseudoboldoria kruegeri orobica Vailati, 1988: 104.

Pseudoboldoria intermedia Vailati, 1988
Boldoria (*Pseudoboldoria*) *intermedia* Focarile, 1965 (*in litt*.): Focarile, 1965: 43.
Pseudoboldoria intermedia Vailati, 1988: 108.

Pseudoboldoria longobarda Vailati, 1988
Pseudoboldoria longobarda Vailati, 1988: 113.

«***gratiae*** group» *sensu* Vailati, 1988
Pseudoboldoria belluccii (Regalin, 1985)
Boldoria (*Pseudoboldoria*) *belluccii* Regalin, 1985: 65.
Pseudoboldoria belluccii (Regalin, 1985): Vailati, 1988: 124.

Pseudoboldoria gratiae (Monguzzi, 1984)
Boldoria (*Pseudoboldoria*) *gratiae* Monguzzi, 1984: 7.
Pseudoboldoria gratiae (Monguzzi, 1984): Vailati, 1988: 117.

Genus ***Stoppaniola*** Vailati, 2017
Stoppaniola Vailati, 2017: 17.

Type species. *Bathyscia Robiati* Reitter, 1889 by original designation (habitus in Fig. 256.4).

Diagnosis. Medium size, 2.0-2.9 mm, bathyscioid body (Fig. 256.4), generally elliptical in shape, sometimes slightly narrowed posteriorly.

Antennae: Male antennae moderately elongated, reaching, when lying backwards, about the half of the elytra. Length ratio of the first two segments variable: the first antennomere can be shorter, equal or longer than the second one. The 8th from transverse to just longer than wide; the 11th from lanceolate to rhomboidal, as long as the previous one plus almost half of the 9th one.

Pronotum: Wide at the base, with the sides always regularly rounded.

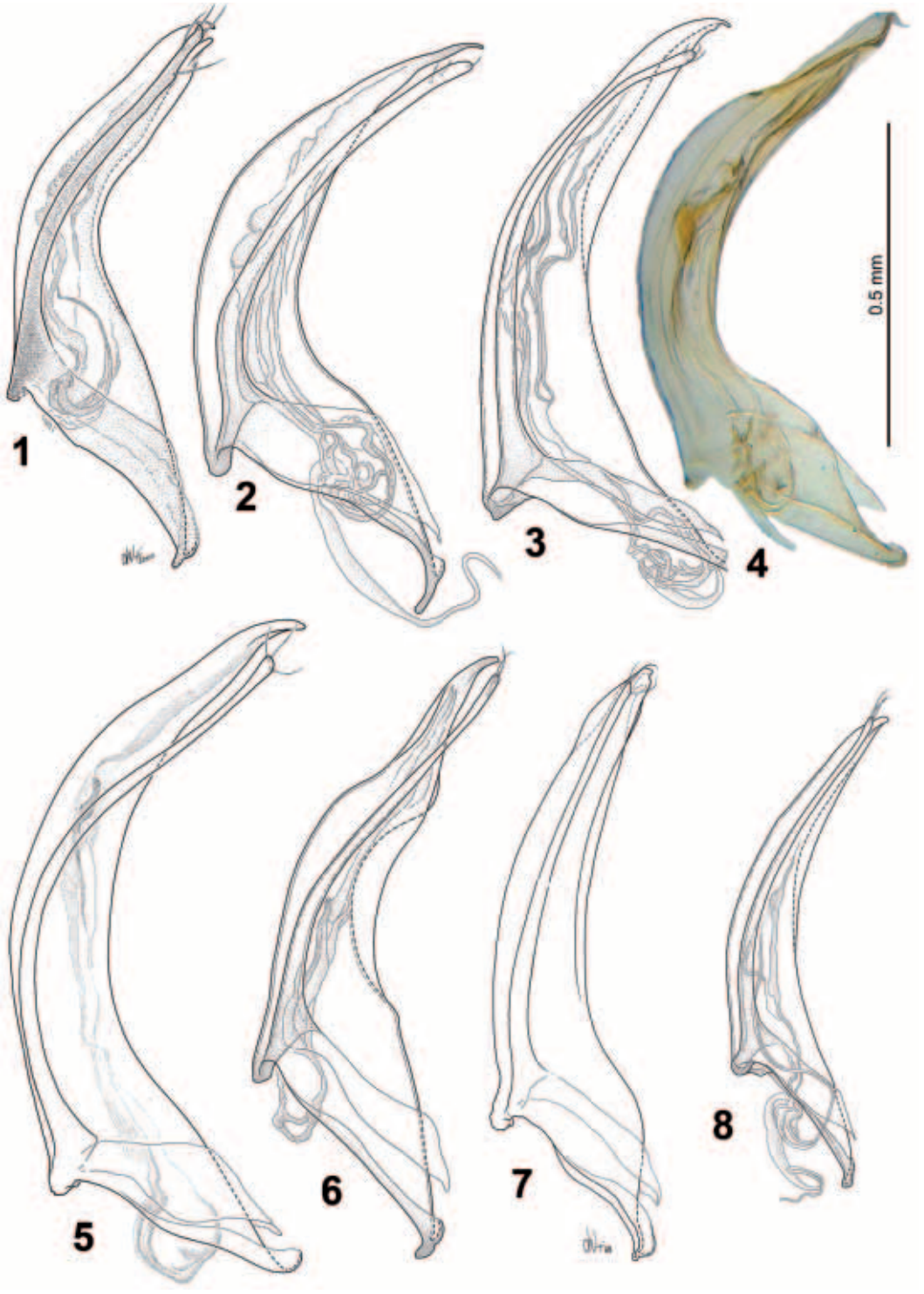
Elytra: Without parasutural stria and provided with transverse striolae, from fine to coarse, but always well marked.

Legs: Metafemora with a small tooth in the centre of the posterior edge, more or less apparent, sometimes faded, but always present. Apex of the tibiae with pectinate internal spurs. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and never dilated, as wide as half of protibiae apex.

Mesoventral keel (Fig. 258.3): High, but not protruding forward, front profile obliquely elusive, more or less slightly curved. Ventral profile from straight to slightly sinuous. Always equipped, below the front angle, with a small and strongly pronounced tooth. Posterior apophysis not prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.6): Moderate to large, but stout, with short apophysis of the alacrista. Longitudinal furrow two to three times longer than



FIGURES 262.1–262.8: *Catopsinus* series, *Dellabeffaella* group. Aedeagus in lateral view of: (**1**) *Archeoboldoria pascuttoi*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai*, (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini,* (**7**) *Pseudoboldoria bergamasca bergamasca*, (**8**) *Reitteriola pumilio*. Figs **1**–**3**, **5**–**8** by D. Vailati.

wide. Wings of the metascutum long and broad at the base.

Metendosternite (Fig. 261.3): «Y»-shaped. Furcal arms shorter than trunk length; posterior lamina of furcal arm and half trunk triangular; apophysis or apical process of arm well-developed in the form of a circle. Furcal trunk wide at base, somewhat longer than wide.

Median lobe of aedeagus: Particularly elongated; from slightly less to more than half of the body length. In lateral view (Fig. 263.2), regularly curved, slender, with a straight and somewhat enlarged apex. In dorsal view (Fig. 265.2), with sides subparallel for almost the entire length, therefore a little narrowed towards the apex, which is rounded, spatula-shaped.

Endophallus (Fig. 265.2): Basal «Y»-piece well-developed and sclerotized. Median phanera in protruding position in the distal half, formed by a ribbed plate and by two symmetrical «compass» arms, facing proximally, and which extend just to the arms of «Y»-piece. There are two subparallel apical lists, moderately sclerotized.

Parameres (Fig. 265.14): Long and extremely slender, slightly shorter or as long as the median lobe, with undifferentiated club equipped with three setae at the apex.

Spermathecal complex: Spermatheca (Fig. 266.9) with the proximal part slightly elongated and larger than the distal part, which is spherical and less voluminous. Median part generally elongated, at least twice the width. Very thin spermatic duct joins without dilated area to the proximal lobe. No spermathecal gland is observed.

Female uroventrite VIII (Fig. 267.10): Some species without spiculum. In other species with the front edge at most only slightly marked by a largely obtuse angle or with barely pronounced, short, stout and triangular spiculum.

Discussion. Genus for which no molecular data are available and therefore placed into this clade according to morphology. Following Vailati (2017), the morphology of this genus indicate an inclusion into the *Dellabeffaella* series, closly related to the genus *Pseudoboldoria*. *Stoppaniola* differs from *Pseudoboldoria* and *Tamaniniella* by a toothed metafemora (without a tooth at the posterior edge in the last mentioned genera). The absence of parasutural stria of the elytra is a structure that is found in a very similar form also in *Pseudoboldoria* present in *Tamaniniella* the same applies to the pectinate internal tibial spurs (polydentate in *Tamaniniella*). According to the current state of knowledge, Vailati (1988, 2017) established in this genus two groups of species. See Discussion section of the genus *Pseudoboldoria*.

Distribution. Italy. Comasque Prealps: Mt Generoso massif and Lariano Triangle, as well as a site south of the moraine amphitheater of Lake Como (Lecco branch), already almost in the Po valley, located in the basset edges of the «Ceppo d'Adda». Bergamasque Prealps: Resegone Mountain group, Valle Imagna, upper Valsassina, mountains between the Brembana and Seriana valleys and foothills between the lower Brembana valley and the Cavallina valley.

Species

«***robiati*** group» *sensu* Vailati, 1988
Stoppaniola focarilei (Vailati, 1988)
Pseudoboldoria focarilei Vailati, 1988: 58.
Boldoria (*Pseudoboldoria*) *barii* Focarile: Inzaghi & Regalin, 1982: 33.
Stoppaniola focarilei (Vailati, 1988): Vailati, 2017: 18.

Stoppaniola malanchinii (Pavan & Ronchetti, 1949)
Boldoria (*Pseudoboldoria*) *Malanchinii* Pavan & Ronchetti, 1949: 28
Boldoria (*Pseudoboldoria*) *alticola* Focarile, 1950: 23.
B. malanchinii Pavan & Ronchetti: Rossi, 1976: 253.
Pseudoboldoria malanchinii Pavan e Ronchetti, 1949: Vailati, 1988: 65.
Stoppaniola malanchinii (Pavan e Ronchetti, 1949): Vailati, 2017: 18.

Stoppaniola personata (Vailati, 1988)
Pseudoboldoria personata Vailati, 1988: 56.
Stoppaniola personata (Vailati, 1988): Vailati, 2017: 18.

Stoppaniola robiati (Reitter, 1889)
Bathyscia Robiati Reitter, 1889c: 293.
Bathysciola Robiati Reitter: Jeannel, 1910a: 28.
Bathysciola (s. str.) *Robiati* Reitt.: Jeannel, 1914b: 11.
Bathyscia (*Boldoria*) *Robiati* Reitter, 1889: Jeannel, 1924a: 117.
Boldoria (*Pseudoboldoria*) *Robiattii* Reitter: Focarile, 1962: 71.
Boldoria robiati: Bernasconi, 1964: 563.
Boldoria (*Pseudoboldoria*) sp.: Focarile, 1965: 43.
Boldoria (*Pseudoboldoria*) *robiatii* (Reitter, 1889): Inzaghi & Regalin, 1981: 36.
Pseudoboldoria robiatii (Reitter, 1889): Vailati, 1988: 49.



FIGURES 263.1–263.4: *Catopsinus* series, *Dellabeffaella* group. Aedeagus in lateral view of: (**1**) *Rondolinia adelinae*, (**2**) *Stoppaniola robiatii*, (**3**) *Tamaniniella pivai* **sp. nov.**, (**4**) *Valdesiella olmii* **comb. nov.** Figs **1**–**3** by D. Vailati.

Pseudoboldoria robiatii (Reitter, 1889): Vailati, 1991: 223.
Stoppaniola robiati (Reitter, 1889): Vailati, 2017: 18.

«***schatzmayri*** group» *sensu* Vailati, 1988
Stoppaniola bucciarellii (Rossi, 1963)
Boldoria (*Pseudoboldoria*) bucciarellii Rossi, 1963: 138.
Pseudoboldoria bucciarellii (Rossi, 1963): Vailati, 1988: 68.
Stoppaniola bucciarellii (Rossi, 1963): Vailati, 2017: 18.

Stoppaniola comottiana (Vailati, 1988)
Pseudoboldoria comottiana Vailati, 1988: 80.
Stoppaniola comottiana (Vailati, 1988): Vailati, 2017: 18.

Stoppaniola schatzmayri (Focarile, 1952)
Boldoria (*Pseudoboldoria*) *Schatzmayri* Focarile, 1952: 102.
Pseudoboldoria schatzmayri (Focarile, 1952): Vailati, 1988: 74.
Stoppaniola schatzmayri (Focarile, 1952): Vailati, 2017: 18.

Genus ***Tamaniniella*** Giachino & Vailati, 2019
Tamaniniella Giachino & Vailati, 2019: 92.

Type species. *Bathyscia vallarsae* Halbherr, 1898 by original designation (habitus in Fig. 256.5).

Diagnosis. Medium-small size, 1.5-1.9 mm, bathyscioid body (Fig. 256.5), oval in shape, with large pronotum, wider than elytra.

Head: Anophthalmous.

Antennae: Male antennae short, just passing, when stretched backwards, the base of the pronotum. First antennomere much shorter than the second one; the 8th wider than long; the 11th ogival and about twice as long as the previous one.

Pronotum: With regularly rounded sides, broad and globular. Wider than the elytra, with the maximum width just before of the basal angles, which are acute and facing backwards due to the accentuated sinuosity of the pronotum base, which is also slightly narrow.

Elytra: With an almost complete and well marked parasutural stria (anteriorly evanescent), fine and not very dense transverse striolae.

Legs: Metafemora with unarmed posterior margin. Apex of the tibiae with polydentate internal spurs. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and never dilated, less wide than apex of the protibiae.

Mesoventral keel (Fig. 258.4): High, but not protruding forward. The anterior profile, obliquely and rectilinearly elusive, and the ventral one, slightly sinuous, form an obtuse angle, equipped inferiorly with a pronounced tooth. Posterior apophysis does not reach or slightly exceeds the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.7): Large, with apophysis of the alacrista approximately one third of the elytra length; wings of the metascutum somewhat longer than wide.

Metendosternite (Fig. 261.4): «Y»-shaped, with triangular furcal arms, wide at the base; arms somewhat shorter than the trunk with well differentiated terminal apophysis; furcal trunk slightly longer than the widest area.

Median lobe of aedeagus: Proportionally large, elongated. In lateral view (Fig. 263.3), little and regularly curved, slender, with the apex slightly facing downwards. In dorsal view (Fig. 265.3) with the sides subparallel in the basal 2/3, therefore slightly converging towards the apex which is ogive and largely rounded.

Endophallus (Fig. 265.3): Basal «Y»-piece large and well-sclerotized. Median phanera small but complex; there are two long parallel and moderately sclerotized apical lists.

Parameres (Fig. 265.15): Long and very slender, clearly shorter than the median lobe, with apex, in dorsal view, simple. Three setae: one long, apical; one short, subapical and internal; and another one long, internal and set back.

Spermathecal complex (Fig. 266.10): Spermatheca small, with smaller spherical distal lobe and the proximal one globular; hyaline union duct narrows at the junction to the distal lobe and is somewhat longer and much narrower than the lobes. Duct distally not enlarged or sclerotized at the insertion on spermatheca. There is a spermathecal gland.

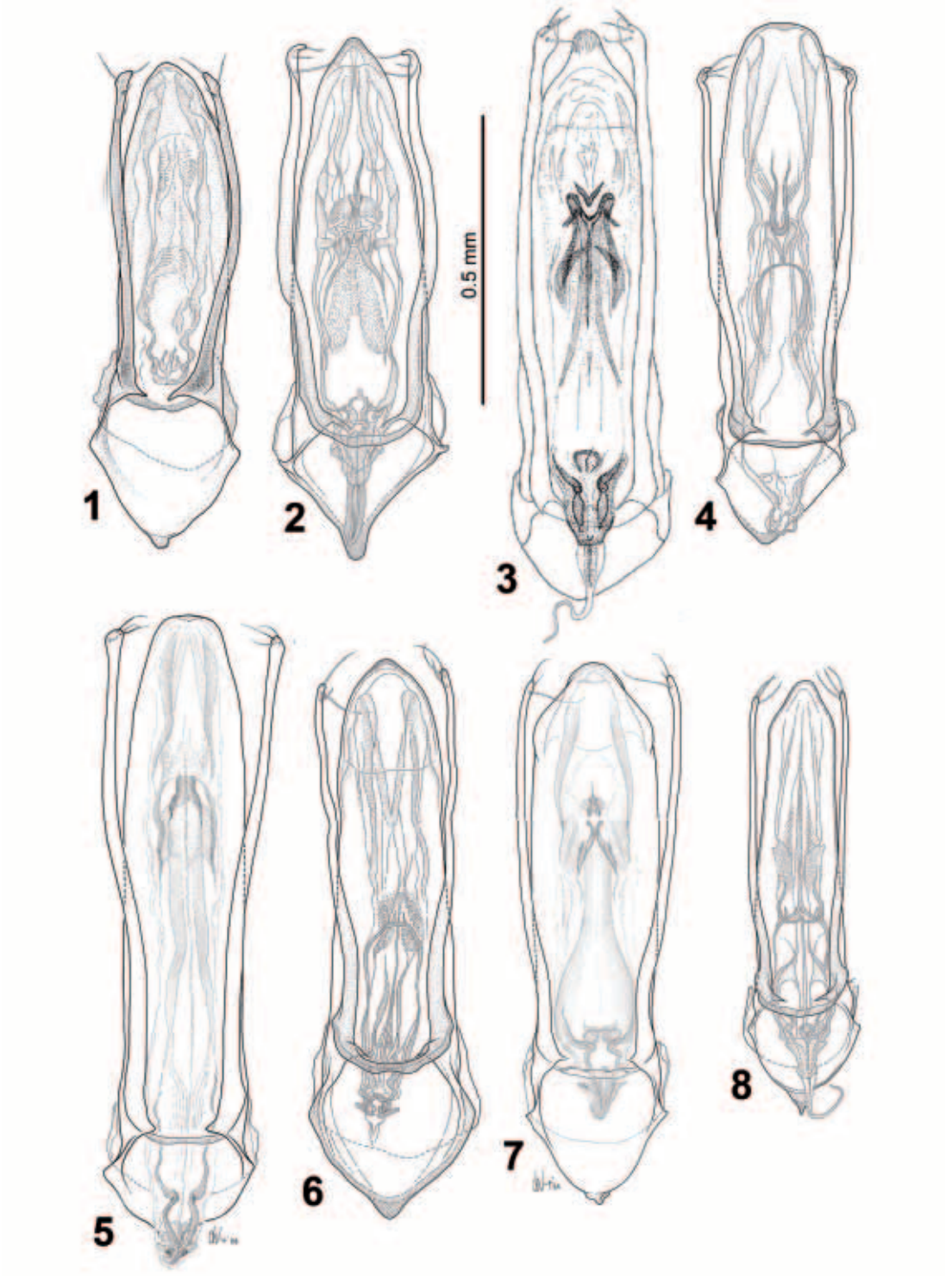
Female uroventrite VIII (Fig. 267.11): Spiculum little developed in length, stout, triangular. Frontal edge of uroventrite with clearly convergent and straight sides.

Discussion. *Tamaniniella*, like *Pseudoboldoria*, shows a non-toothed metafemora, with a tooth at the posterior edge in *Stoppaniola*. However, it is also similar to *Reitteriola* by the presence of parasutural stria of the elytra (absent in *Pseudoboldoria* and *Stoppaniola*) and the polydentate internal tibial spurs (pectinate in *Pseudoboldoria* and *Stoppaniola*). On the other hand it exhibits a character also found in *Pseudoboldoria* as the profile of the median lobe of aedeagus in lateral view.

Molecular analysis (Fig. 1D) indicate *Tamaniniella* to be more closely related to *Pseudoboldoria* (100/100) rather than to the genera of the *Boldoria* series (as it would be more logical to expect in a zoogeographic perspective). The confirmation or rejection of this finding can only be asserted by more analysis including data of some taxa of the genus *Stoppaniola* and more genera of the *Boldoria* series.

Note. Giachino & Vailati (2019), when describing the genus *Tamaniniella*, mistakenly believed that the genus included only one species, illustrated as *T. vallarsae* using a specimen from the surroundings of San Giorgio, in the Veronese Lessini (VR), Italy. Subsequently, as suggested by molecular analysis carried out for specimens from the type locality of *T. vallarsae* and from the Veronese Lessini – Roverè 1000 Cave, near Roverè (VR) –, that the specimens of these two localities belong to different species. The second species of *Tamaniniella* is therefore described in this contribution (See Appendix New Species).

Distribution. Italy. Veneto and Trentino: Lessini mountains, Val Lagarina and Folgaria.



FIGURES 264.1–264.8: *Catopsinus* series, *Dellabeffaella* group. Aedeagus in dorsal view of: (**1**) *Archeoboldoria pascuttoi*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai* (modified from Giachino 1993), (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini,* (**7**) *Pseudoboldoria bergamasca bergamasca*, (**8**) *Reitteriola pumilio.* Figs **1**–**3**, **5**–**8** by D. Vailati.

Species

Tamaniniella vallarsae (Halbherr, 1898)
Bathyscia Vallarsae Halbherr, 1898: 180.
Bathysciola (s. str.) *Vallarsae* Halbherr: Jeannel, 1914b: 13.
Bathysciola (s. str.) *vallarsae* (Halbherr): Perreau, 2000: 241.
Tamaniniella vallarsae (Halbherr, 1898): Giachino & Vailati, 2019: 92.

Tamaniniella pivai sp. nov. (see Appendix New Species)

Clade ***Baudiola***

The clade *Baudiola* is characterised by the following character set: metendosternite not «V»-shaped, with furcal arms triangular, wide at the base; meso- and metatibiae with incomplete apical baskets; male protarsi largely, or moderately, dilated; median lobe of aedeagus slender, ogival in shape in the distal half; endophallus with well sclerotized basal «Y»-piece, and complex, well sclerotized, median phanera; parameres apically sometimes spoon-shaped; spermatheca asymmetrical, elongated and sometimes very large; spermathecal duct distally partly sclerotized in a small region.

This is a clade with a high support (93.3/100) for the genus *Baudiola* – the genus *Doderiola* also belongs to this, but no molecular data are available – in a basal position with respect to phyletic lineage including the genera *Dellabeffaella*, *Valdesiella* gen. nov., *Canavesiella* and *Canapiciella* (Fig. 1D).

Genus ***Baudiola*** Giachino & Vailati, 2019
Baudiola Giachino & Vailati, 2019: 90.

Type species. *Adelops tarsalis* Kiesenwetter, 1861 by original designation (habitus in Fig. 255.2).

Diagnosis. Medium size, 2.0-2.2 mm, bathyscioid body (Fig. 255.2), elliptical in shape, with pronotum not wider than the elytra.

Head: With eyes, provided with 6-8 apparently functional ommatidia.

Antennae: Male antennae short, exceed when stretched backwards, the base of the pronotum. First antennomere slightly shorter than the second; the 8th as long as wide; the 11th ogival and twice the previous one.

Pronotum: With regularly rounded sides, not wider than the elytra; with the maximum width at the posterior angles; basal angles acute and facing backwards due to the accentuated sinuosity of the base.

Elytra: Without parasutural stria, with fine and not very thick transversal striolae.

Legs: Metafemora without median tooth at the posterior edge. Tibial internal spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and highly dilated, as wide as, or slightly wider, than the protibiae apex.

Mesoventral keel (Fig. 257.2): High, but not protruding forward. The almost vertical anterior profile, and the ventral one, slightly sinuate, form an almost right angle, rounded, inferiorly without a tooth. Posterior apophysis not prolonged on the metaventrite or slightly exceeding it.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 258.7): Large, with apophysis of the alacrista about a quarter of the elytra.

Metendosternite (Fig. 260.2): «Y»-shaped, with triangular furcal arms, wide at the base; arms slightly shorter than the trunk, with well-developed apophysis; furcal trunk slightly longer than the widest area.

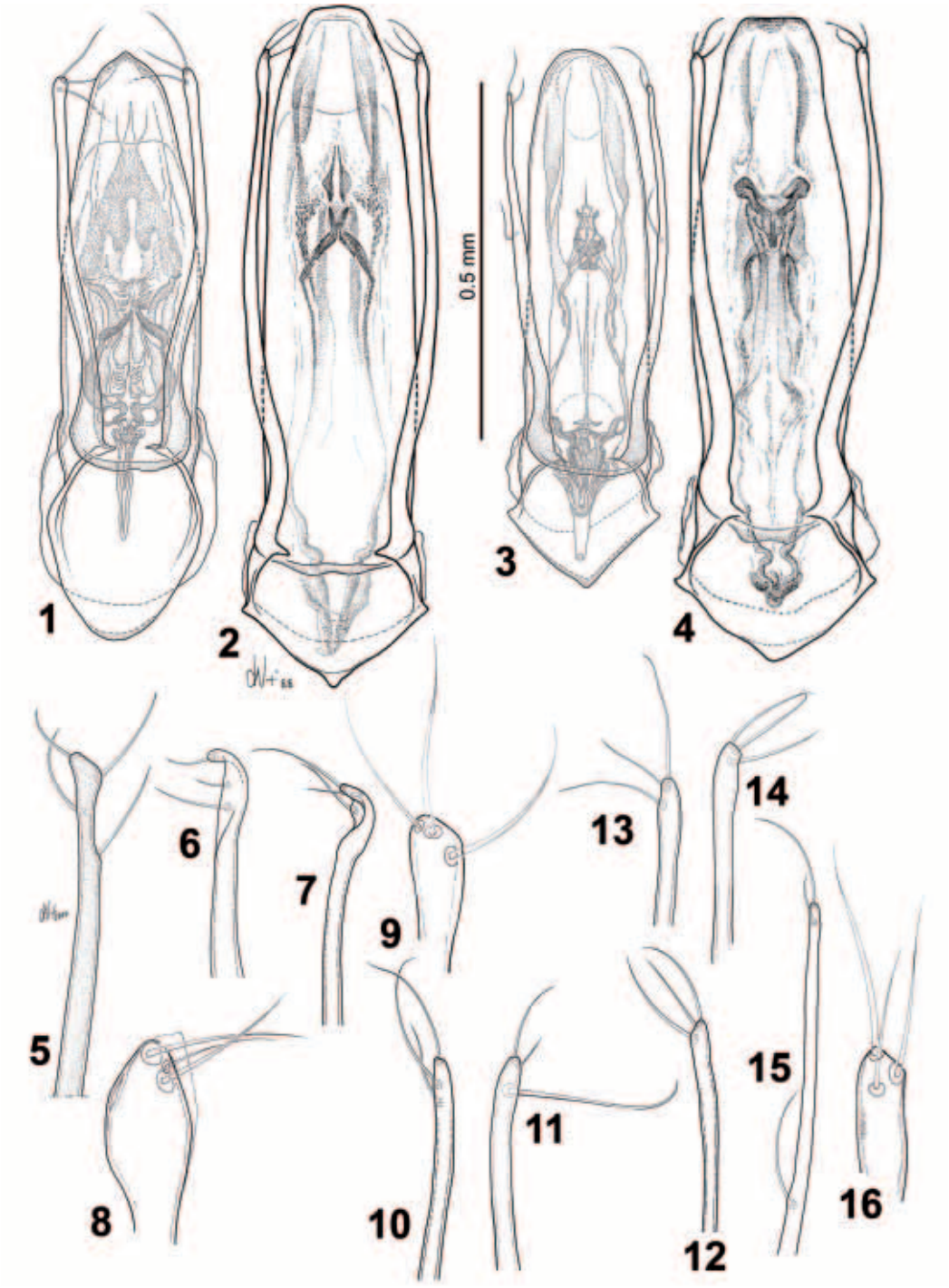
Median lobe of aedeagus: Long, but relatively stout in shape. In lateral view (Fig. 262.2), it is widely and regularly curved, slender, with the apex slightly facing downwards. In a dorsal view (Fig. 264.2), with the sides subsinuated and converging from the base to the apex, which is subtriangular and slightly truncated.

Endophallus (Fig. 264.2): Basal «Y»-piece large and well-sclerotized. Median phanera large with arms joining the «Y»-piece arms and very complex. There are two narrow apical lists, converging and moderately sclerotized.

Parameres (Fig. 265.6): Long and slender. In dorsal view, vaguely of a tuning fork-shaped, just shorter than the median lobe. Apex, in dorsal view, spoon-shaped. Provided with three internal setae with equidistant insertion: one apical, medium long, and two subapical, the first one short, the second one long.

Spermathecal complex: Spermatheca (Fig. 266.2) very large, hypertrophic, with the proximal part ovally elongated, slightly longer but slightly narrower than the distal lobe slightly globular; long hyaline union duct somewhat narrower than lobes. Duct distally very enlarged and sclerotized at the insertion into the spermatheca. There is a spermathecal gland.

Female uroventrite VIII (Fig. 267.2): Spiculum very long, particularly thin. Front edge of uroventrite with distinctly concave sides.



FIGURES 265.1–264.16: *Catopsinus* series, *Dellabeffaella* group. Aedeagus in dorsal view of: (**1**) *Rondolinia adelinae*, (**2**) *Stoppaniola robiati*, (**3**) *Tamaniniella pivai* **sp. nov**., (**4**) *Valdesiella olmii* **comb. nov.** Apex of paramere of: (**5**) *Archeoboldoria pascuttoi*, (**6**) *Baudiola tarsalis*, (**7**) *Canapiciella angeli,* (**8**) *Canavesiella lanai*, (**9**) *Dellabeffaella roccae,* (**10**) *Doderiola agostini,* (**11**) *Pseudoboldoria bergamasca bergamasca*, (**12**) *Reitteriola pumilio*, (**13**) *R. adelinae*, (**14**) *S. robiati*, (**15**) *T. pivai* sp. nov., (**16**) *Valdesiella olmii* **comb. nov.** Figs **1**–**7**, **10**–**16** by D. Vailati.

Discussion. *Baudiola* is similar to *Canapiciella* and *Doderiola* due to the strucutre of the polydentate internal spurs of the tibiae (pectinate in *Dellabeffaella, Valdesiella* gen. nov. and *Canavesiella*), in addition *Canavesiella* lack the parasutural stria (present in *Dellabeffaella*, *Valdesiella* gen. nov., *Canapiciella* and *Doderiola*). From all the other genera of the *Dellabeffaella* clade, *Baudiola* differs also by the presence of reduced eyes and large spermatheca. Finally, from *Canavesiella* it differs by the presence of apparent transversal striolae to the elytra. *Baudiola* is linked with *Dellabeffaella* clade with a support of 93.3/100 (Fig. 1D). Specific for the clade *Dellabeffaella*, *Baudiola* and *Doderiola* is the eastern vicariant distribution of *Canavesiella* and *Canapiciella*. *Baudiola* shows a widely sympatric distribution range with *Doderiola* as well as with *Archeoboldoria* and *Rondolinia* from the *Archeoboldoria* subgroup.

Distribution. Italy, Northern Piedmont (from Oropa valley to orographic right of Lake Maggiore). Switzerland (Canton Ticino).

Species

Baudiola tarsalis (Kiesenwetter, 1861)
Adelops tarsalis Kiesenwetter, 1861: 377.
Bathyscia kerimii Fairmaire, 1872: 54.
Bathysciola tarsalis Kiesenwetter, 1861 Jeannel, 1910a: 27.
Quaestus tarsalis Kiesenw.: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *tarsalis* Kiesw.: Reitter, 1885 [1884]: 22.
Bathysciola (s. str.) *tarsalis* Kiesw.: Jeannel, 1914b: 12.
Bathysciola (*Bathysciola*) *tarsalis* Kiesenwetter, 1861: Perreau, 2004: 162.
Baudiola tarsalis (Kiesenwetter, 1861): Giachino & Vailati, 2019: 90.

Genus ***Doderiola*** Giachino & Vailati, 2019
Doderiola Giachino & Vailati, 2019: 88.

Type species. *Bathysciola agostini* Jeannel, 1924 by original designation (habitus in Fig. 255.6).

Diagnosis. Medium size, 2.7-2.8 mm, bathyscioid body (Fig. 255.6), ovoid in shape, with a large pronotum, slightly wider than the elytra.

Head: Anophthalmous.

Antennae: Male antennae relatively long, exceeding, when streched backwards, the base of the pronotum. First antennomere much shorter than the second one; the 8th longer than wide; the 11th ogival and about twice as long as the previous one.

Pronotum: With sides regularly rounded and decidedly converging forward. Large and globular, slightly wider than the elytra, with the maximum width just before of the posterior angles. Basal angles acute and facing backwards due to the accentuated sinuosity of the base, which is also slightly narrow.

Elytra: With almost complete and well marked parasutural stria, fading anteriorly; transversal striolae fine, superficial and not very thick.

Legs: Metafemora without median tooth at the posterior edge. Tibial internal spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and not dilated, narrower than the protibiae apex.

Mesoventral keel (Fig. 257.6): High, but not protruding forward. The anterior profile, transversly elusive, and the ventral one, slightly sinuated, forms an obtuse angle equipped inferiorly with a blunt tooth. Posteriorly without apophysis prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.2): Large, with apophysis of the alacrista about a quarter of the elytra.

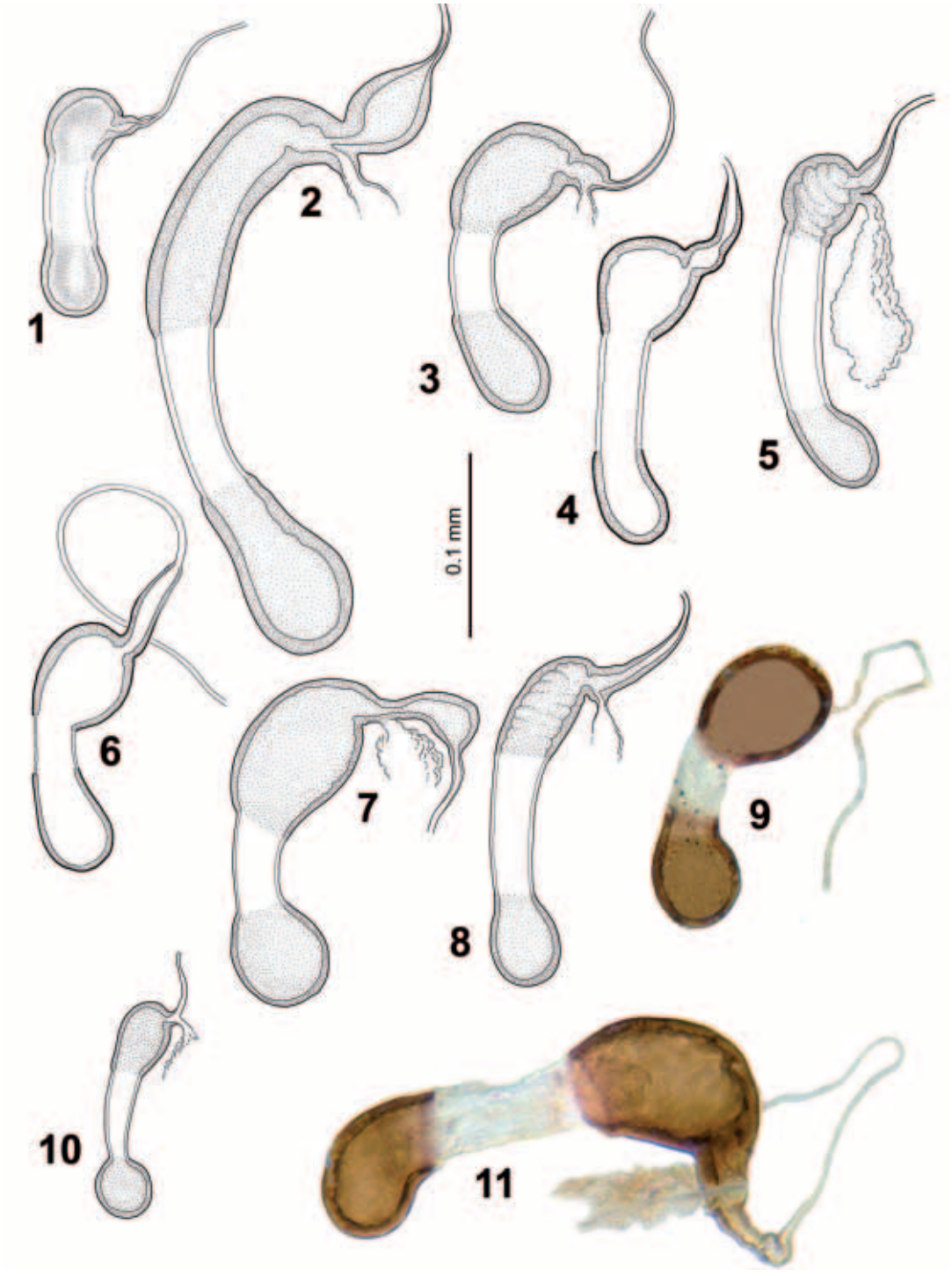
Metendosternite (Fig. 260.6): «Y»-shaped, with triangular furcal arms, wide at the base; arms as long as or slightly shorter than the trunk, with well-developed apophysis; lateral furcal ridge straight; furcal trunk slightly longer than the widest area.

Median lobe of aedeagus: Elongated shape. In lateral view (Fig. 262.6), widely sinuated in the apical third, slender, with the apex pointing slightly downwards. In dorsal view (Fig. 264.6), with the sides subparallel in basal 2/3, therefore slightly sinuated, and then converging towards the apex, which is ogive-shaped, largely rounded, but only a slightly indicated.

Endophallus (Fig. 264.6): Basal «Y»-piece large and well-sclerotized. Median phanera large and complex. There are two parallel apical lists, subtriangular, converging at the base and are moderately sclerotized.

Parameres (Fig. 265.10): Long and very slender, shorter than the median lobe, with apex, in dorsal view, simple. Provided with three setae: one apical, long, and two internal, subapicals, the second one shorter.

Spermathecal complex: Spermatheca (Fig. 266.5) large, with the proximal part globular and the distal one only slightly smaller and elongated; hyaline union duct, very long and somewhat narrower than the lobes. Duct distally slightly enlarged and sclerotized at the



FIGURES 266.1–266.11: *Catopsinus* series, *Dellabeffaella* group. Spermathecal complex of: (**1**) *Archeoboldoria pascuttoi*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Dellabeffaella roccae,* (**5**) *Doderiola agostini,* (**6**) *Pseudoboldoria bergamasca bergamasca*, (**7**) *Reitteriola pumilio*, (**8**) *Rondolinia adelinae*, (**9**) *Stoppaniola schatzmayri*, (**10**) *Tamaniniella pivai* **sp. nov**., (**11**) *Valdesiella olmii* **comb. nov.** Figs **1**–**8**, **10** by D. Vailati.

insertion into the spermatheca. There is a spermathecal gland present.

Female uroventrite VIII (Fig. 267.6): Spiculum long, slender, triangular. Front edge of uroventrite, on the sides, completely straight.

Discussion. Due to the lack of molecular data for the *Doderiola*, it was on purely morphological basis assigned to the *Dellabeffaella* group, in the clade *Baudiola*. *Doderiola* is similar to *Canapiciella* and *Baudiola* with respect to the character of the polydentate internal spurs of the tibiae (pectinate in *Dellabeffaella, Valdesiella* gen. nov. and *Canavesiella*), however it is similar to the *Dellabeffaella, Valdesiella* gen. nov. and *Canapiciella* by exhibiting parasutural stria (absent in *Canavesiella* and *Baudiola*). From *Baudiola* it differ also by the absence of eyes and the «normal»-sized spermatheca and from *Canavesiella* by the presence of apparent transversal striolae to the elytra.

Doderiola has a the western vicarian distribution with *Rondolinia* and it is widely sympatric with *Archeoboldoria* both from the clade *Archeoboldoria*.

Distribution. Italy, Piedmont, Alpine chain north of Biella, Oropa and Sessera valleys.

Species

Doderiola agostini (Jeannel, 1924)
Bathysciola (s. str.) *Agostini* Jeannel, 1924a: 86.
Bathysciola (s. str.) *agostini* Jeannel: Casale, 1974: 80.
Doderiola agostini (Jeannel, 1924) Giachino & Vailati, 2019: 89.

Clade ***Dellabeffaella***

The clade *Dellabeffaella* (+ clade *Baudiola*) is characterised by the following characters set: metendosternite not «V»-shaped, with triangular furcal arms, wide at the base; meso- and metatibiae with incomplete apical baskets; males protarsi largely, or moderately, dilated; median lobe of aedeagus slender, ogival in shape in the distal half; endophallus with well sclerotized basal «Y»-piece, and complex, well sclerotized, median phanera; parameres apically sometimes spoon-shaped; spermatheca asymmetrical, elongated and sometimes very large; spermathecal duct distally partly sclerotized in a small region.

This clade with a high support, 99.8/100, includes the genera *Canapiciella*, *Canavesiella*, *Dellabeffaella* and *Valdesiella* gen. nov. (Fig. 1D).

Genus ***Canapiciella*** Giachino & Vailati, 2019
Canapiciella Giachino & Vailati, 2019: 87.

Type species. *Bathysciola angeli* Jeannel, 1924 by original designation (habitus in Fig. 255.3).

Diagnosis. Medium size, 2.2-2.3 mm, bathyscioid body (Fig. 255.3), ovoid in shape, with a large pronotum, wider than the elytra.

Head: Anophthalmous.

Antennae: Male antennae short, just exceeding, when stretched backwards, the base of the pronotum. First antennomere much shorter than the second one; the 8th as long as wide; the 11th ogival and twice the previous one.

Pronotum: With regularly rounded sides, broad and globular, wider than the elytra. Maximum width just before the basal angles, which are acute and facing backwards due to the accentuated sinuosity of the base, which is also slightly narrow.

Elytra: With almost complete and well marked parasutural stria, anteriorly fading; fine and not very thick transverse striolae.

Legs: Metafemora without median tooth at the posterior edge. Tibial internal spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparsely distributed spines. Male protarsi pentamerous and slightly dilated, narrower than the protibiae apex.

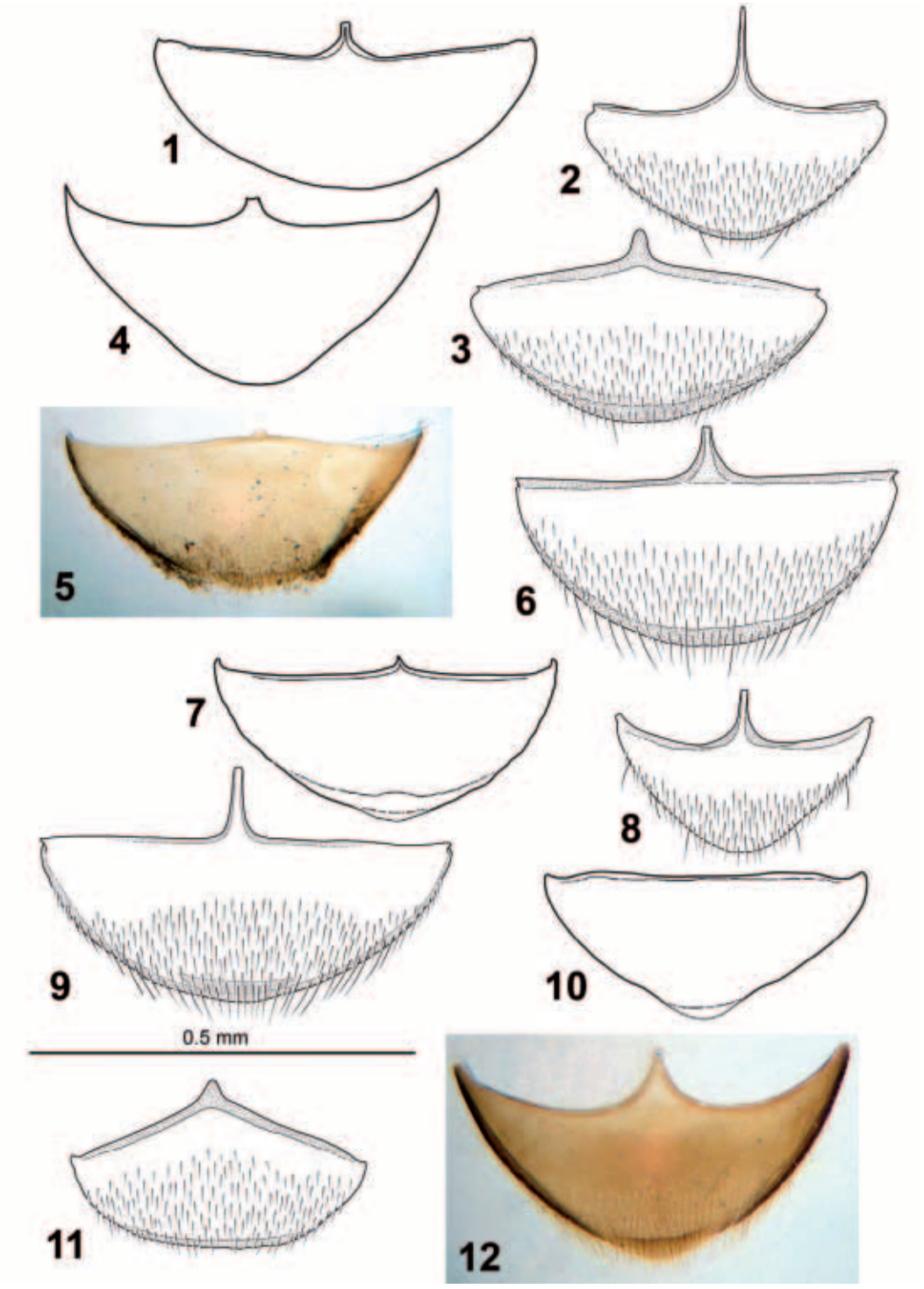
Mesoventral keel (Fig. 257.3): High, but not protruding forward. The anterior profile, transversely elusive, and the ventral one, rectilinear, forming an obtuse angle equipped inferiorly with a pronounced tooth. Posteriorly the apophysis does not reach or slightly surpasses the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 258.8): Large, with apophysis of the alacrista about a quarter of the elytra; metascutum wings short, somewhat longer than broad with blunt apices.

Metendosternite (Fig. 260.3): «Y»-shaped, with triangular furcal arms, wide at the base; arms shorter than the furcal trunk with well-developed apical apophysis; lateral furcal flange with a very slight concavity in the lower area of the trunk; furcal trunk longer than the widest area.

Median lobe of aedeagus: Elongated in shape. In lateral view (Fig. 262.3), it is widely and regularly curved, slender, with the apex markedly pointing downwards. In dorsal view (Fig. 264.3), with subparallel sides in 2/3 basal, therefore slightly converging towards the apex, which is ogive and largely rounded.



FIGURES 267.1–267.12: *Catopsinus* series, *Dellabeffaella* group. Female uroventrite VIII of: (**1**) *Archeoboldoria doderona*, (**2**) *Baudiola tarsalis*, (**3**) *Canapiciella angeli,* (**4**) *Canavesiella lanai* (modified from Giachino 1993), (**5**) *Dellabeffaella roccae,* (**6**) *Doderiola agostini,* (**7**) *Pseudoboldoria bergamasca bergamasca*, (**8**) *Reitteriola pumilio*, (**9**) *Rondolinia adelinae*, (**10**) *Stoppaniola malanchinii*, (**11**) *Tamaniniella pivai* **sp. nov**., (**12**) *Valdesiella olmii* **comb. nov.** Figs **1**–**3**, **6**–**11** by D. Vailati.

Endophallus (Fig. 264.3): Large and well-sclerotized basal «Y»-piece. Median phanera large and complex, with arc-shaped «M»-shaped and elongated «U»-shaped structures. There are two parallel apical lists, subtriangular, inverted and moderately sclerotized.

Parameres (Fig. 265.7): Long and slender, clearly shorter than the median lobe. Apex, in dorsal view, spoon-shaped, provided with three internal setae: one apical, longer, and two subapical.

Spermathecal complex: Spermatheca (Fig. 266.3) large, with proximal part globular and distal one smaller and elongated; hyaline union duct somewhat longer than wide and a little narrower than the lobes. Duct distally enlarged and sclerotized at the insertion into the spermatheca. There is a spermathecal gland present.

Female uroventrite VIII (Fig. 267.3): Short and stout, triangular spiculum. Front edge of uroventrite with slightly convergent and rectilinear sides.

Discussion. *Canapiciella* is similar to *Doderiola* and *Baudiola* in exhibiting polydentate internal spurs of the tibiae (pectinate in *Dellabeffaella, Valdesiella* gen. nov. and *Canavesiella*), while the character shared with *Doderiola, Dellabeffaella* and *Valdesiella* gen. nov. the presence of parasutural stria is (absent in *Canavesiella* and *Baudiola*). From *Baudiola* it differs by anophthalmous head and a «normal-sized» spermatheca, which is not hypertrophic. Finally, from *Canavesiella*, it differs by the presence of apparent transversal striolae to the elytra.

As already stressed in the discussion of the clade *Dellabeffaella*, the comparison of the phylogenetic tree obtained by processing molecular data (Fig. 1D) with that previously classification using morphological characters is believed to be phyletically important (Vailati 1988; Giachino 1993) to identify significant differences. Characters such as: presence/absence of the parasutural stria of the elytra, toothed/unarmed mesoventral keel, internal tibial spurs pectinate/polydentate, non-dilated/dilated male protarsomeres, shape of the median lobe of aedeagus, of the endophallus and of the parameres (including position of setae) (Vailati 2017; Giachino & Vailati 2019).

The results obtained from the comparative approach using molecular and morphological data indicate that the weak values of the morphological characters looked at are often masking phenomena of convergence or adaptation to the environment. However these morphological charaters might not be helpful for a high-level taxonomic approach but can be used for a definition of single genera.

Canapiciella was found to be linked to *Dellabeffaella* with a support of 82.4/57.

Biogeographical finding show that *Canapiciella* is the northern vicariant of *Dellabeffaella* and the western one of *Doderiola* and *Baudiola*. It is partially sympatric with *Canavesiella* and, just in restrict area on the left side of the Aosta valley also with *Archeoboldoria*. *Canapiciella* is widely sympatric with *Reitteriola* of the clade *Reitteriola*.

Distribution. Italy, Piedmont, High Canavese (Turin province), Orco and Soana valleys. A probable new species, known on a single female specimen, is present on the left side, at the mouth of the Aosta valley.

Species

Canapiciella angeli (Jeannel, 1924)
Bathysciola Angeli Jeannel, 1924a: 52.
Bathysciola (s. str.) *Angeli* Jeannel, 1924: Jeannel, 1924a: 104.
Bathysciola (*Bathysciola*) *angeli* Jeannel, 1924: Perreau, 2004: 160.
Canapiciella angeli (Jeannel, 1924): Giachino & Vailati, 2019: 87.

Genus ***Canavesiella*** Giachino, 1993
Canavesiella Giachino, 1993b: 349.

Type species. *Canavesiella lanai* Giachino, 1993 by original designation (habitus in Fig. 255.4).

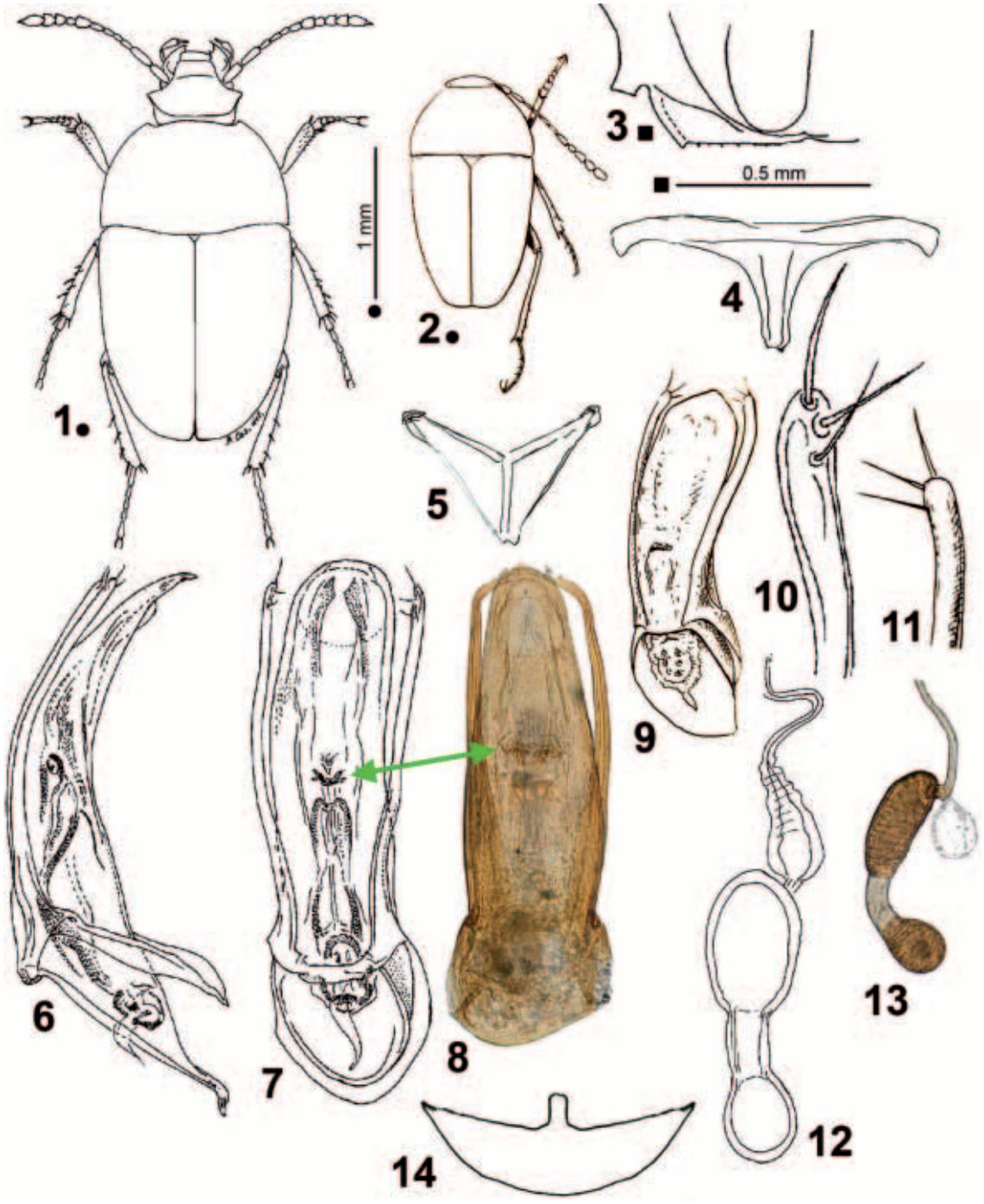
Diagnosis. Medium-large size, 3.0-3.6 mm, bathyscioid body, with a particularly elongated elliptical shape (Fig. 255.4). An accentuated narrowing at the base of pronotum divides the body into two distinct parts.

Head: Anophthalmous.

Antennae: Male antennae elongated, exceeding, when extended backwards, the distal third of the elytra. First antennomere slightly longer than the second one; the 8th elongated, more than twice as long as wide; the 11th lanceolate and long like the previous one, plus half of the 9th one.

Pronotum: With regularly rounded sides and maximum width just before the middle. Particularly narrow at the base, which is subrectilinear, only slightly arched at the basal angles, which are almost straight but rounded.

Elytra: Without parasutural stria and with coarse, irregular and fading, transverse striolae, giving them a raspy appearance.



FIGURES 268.1–268.14: *Catopsinus* series, *Coiffaitiola* group. Habitus of: (**1**) *Cavazzutiella taurica*, (**2**) *Coiffaitiola rudis*. Pterothorax in lateral view of: (**3**) *C. taurica.* Metatergal apparatus, ventral view of the metanotum and axillaria of: (**4**) *C. rudis*. Metendosternite: (**5**) *C. rudis*. Aedeagus in lateral view of: (**6**) *C. taurica*. Aedeagus in dorsal view of: (**7**) *C. taurica*, (**8**) *Cavazzutiella patrizii*, (**9**) *C. rudis*. Apex of the paramere of: (**10**) *C. taurica*, (**11**) *C. rudis*. Spermathecal complex of: (**12**) *C. taurica*, (**13**) *C. patrizii*. Female uroventrite VIII: (**14**) *C. rudis*. Green arrow pointing to equivalent structures. Figs **1**, **3**, **6**, **7**, **10**, **12** modified from Casale & Giachino (1985); Figs **2**, **9**, **11** from Jeannel (1955); Figs **8**, **13** from Perreau (2021).

Legs: Metafemora without median tooth at the posterior edge. Tibial internal spurs pectinate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Male protarsi pentamerous and slightly dilated, narrower than the protibiae apex.

Mesoventral keel (Fig. 257.4): Low, extremely small, just indicated, the mesocoxal cavities in contact.

Suture of the metaventrite (Fig. 257.4): Slightly sinuous arc, in the lower third very close to the coxal cavity and in the upper two thirds it delimits a narrow elongated arched area.

Metatergal apparatus (Fig. 258.9): Small, with very short apophysis of the alacrista. Longitudinal furrow slightly longer than wide.

Metendosternite (Fig. 260.4): «Y»-shaped, with furcal arms triangular, wide at the base. Arms shorter than trunk, without distinct apophysis and hooked apical area; posterior furcal lamina progressively narrowing to apex and posterior arched flange. Furcal trunk long and narrow, twice as long as the widest part.

Median lobe of aedeagus: With an elongated shape, about a third of the body length. In lateral view (Fig. 262.4), it is widely and regularly curved, slender, with apex flattened and abruptly turned upwards. In dorsal view (Fig. 264.4) with the subparallel sides up to the preapical area, then converging towards the apex, which has a prominent, rounded, not pointed, apical tongue.

Endophallus (Fig. 264.4): Basal «Y»-piece large and well-sclerotized. Median region with phanera large and complex, saddle shaped. Phanerae absent in the apical region.

Parameres (Fig. 265.8): Long and slender, as long as the median lobe. With the club enlarged in paddle-shape, provided with three sub-equal setae with very close insertion.

Spermathecal complex (Giachino 1993): Spermatheca large, elongated, with the proximal lobe globular and the distal one smaller and elongated. Duct distally partly sclerotized in a small region around the insertion into the spermatheca.

Female uroventrite VIII (Fig. 267.4): Spiculum very short, stout, reduced to a little developed tongue in length and with truncated, sub squared apex.

Discussion. *Canavesiella* is sharing the character of pectinate internal spurs of the tibiae with *Dellabeffaella* and *Valdesiella* gen. nov. (polydentate in *Canapiciella, Baudiola* and *Doderiola*), on the hand it shares with *Baudiola* character of the absence of parasutural stria (present in *Valdesiella* gen. nov., *Dellabeffaella*, *Canapiciella* and *Doderiola*). The difference to *Baudiola* lies in the anophthalmous head and normal-sized – not hypertrophic – spermatheca. The median phanera of the endophallus is in its structure very similar to that of *Valdesiella* gen. nov. Finally, from all other genera of the clade *Dellabeffaella* it differs by the absence of apparent transversal striolae on the elytra. *Canavesiella* in a phylogenetic analysis it was found to be related to *Valdesiella* gen. nov. with a support of 60.9/55 (Fig. 1D). *Canavesiella* is the northern vicariant of *Dellabeffaella* and the western one of *Doderiola* and *Baudiola*. It is partially sympatric with *Canapiciella* but widely sympatric with *Reitteriola* of the *Reitteriola* clade.

Distribution. Italy, Piedmont, north-eastern Graian Alps, Ribordone and Chiusella valleys.

Species

Canavesiella casalei Giachino, 1993
Canavesiella casalei Giachino, 1993b: 355.

Canavesiella lanai Giachino, 1993
Canavesiella lanai Giachino, 1993b: 352.

Genus ***Dellabeffaella*** Capra, 1924
Royerella (*Della-Beffaella*) Capra, 1924: 155.
Dellabeffaella Capra, 1924: Sbordoni *et al*., 1982: 295.

Type species. *Royerella* (*Della-Beffaella*) *Roccae* Capra, 1924 by monotypy (habitus in Fig. 255.5).

Diagnosis. Large size, 2.6-3.5 mm, bathyscioid body (Fig. 255.5), ovoid in shape, with very large front part.

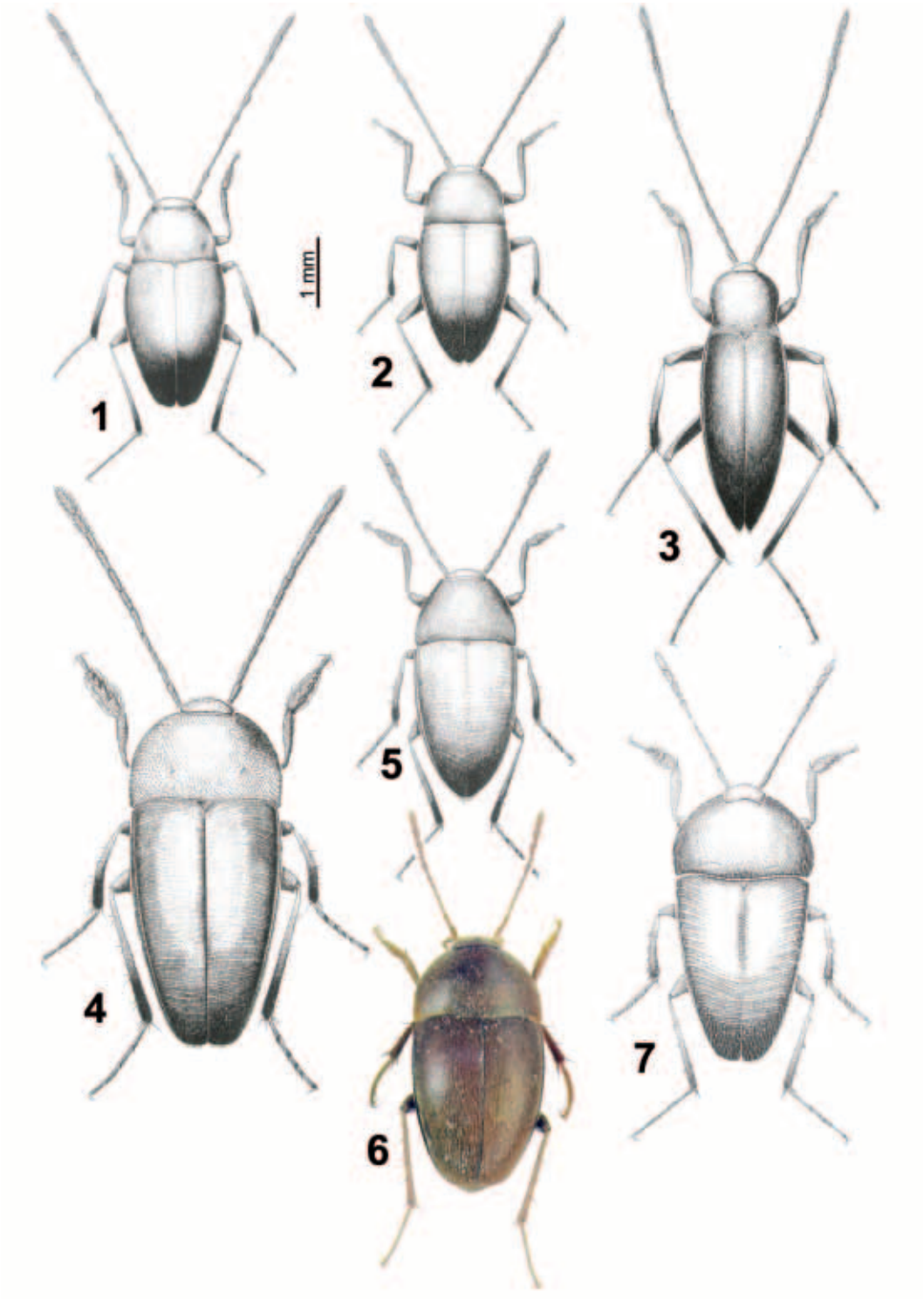
Head: Anophthalmous.

Antennae: Male antennae moderately elongated, reaching at most, when lying backwards, half of the elytra. First antennomere much shorter than the second one; the 8th almost twice as long as wide; the 11th lanceolate and as long as the previous one, plus almost half of the 9th one.

Pronotum: With regularly rounded sides, particularly broad and globular. Wider than the elytra, with the maximum width far in front of the posterior angles. Basal angles acute and facing backwards due to the accentuated sinuosity of the base, which is also considerably narrow.

Elytra: With well marked and complete, parasutural stria; with fine and thick transverse striolae.

Legs: Metafemora without median tooth at the



FIGURES 269.1–269.7: *Speonomus* series, *Euryspeonomus* group. Habitus of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *Dupreia beruetei* **comb. nov.,** (**7**) *Josettekia mendizabali.* Figs **1**–**5**, **7** modified from Salgado *et al*. (2008).

posterior edge. Tibial internal spurs pectinate. Meso- and metatibiae with incomplete apical baskets of short and sparsely distributed spines. Male protarsi pentamerous and highly dilated wider than the protibiae apex.

Mesoventral keel (Fig. 257.5): High, but not protruding forward. The anterior profile, transversely elusive, and the ventral one, slightly sinuous, forms an obtuse angle with the vertex equipped with a more or less pronounced tooth, sometimes rounded and faded. Posteriorly with apophysis covering the anterior border of the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.1): Large, with apophysis of the very long alcrista at least a quarter of the elytra; metascutum wings long with wide base.

Metendosternite (Fig. 260.5): «Y»-shaped, with triangular furcal arms, wide at the base; arms distinctly shorter than the trunk, with well-developed apophysis and lateral furcal flange gently arched; furcal trunk long, one and a half times longer than widest area.

Median lobe of aedeagus: Elongated, about a third of the body long. In lateral view (Fig. 262.5), widely and regularly curved, slender, with the apex slightly pointing downwards. In dorsal view (Fig. 264.5), with the subparallel sides in the basal half, then converging towards the apex, which is ogive and pointed.

Endophallus (Fig. 264.5): Basal «Y»-piece large and well-sclerotized. Median phanera large and little complex. There are two apical lists, parallel and moderately sclerotized.

Parameres (Fig. 265.9): Long and slender, slightly shorter than the median lobe. Provided with an elongated and slightly dilated club with three sub-equal setae at the apex.

Spermathecal complex (Fig. 266.4): Spermatheca large, with the proximal lobe globular, the distal one smaller and elongated and the hyaline union duct of uniform width and longer than the distal part. Duct distally and partly sclerotized, short enlarged area at the insertion into the spermatheca.

Female uroventrite VIII (Fig. 267.5): Spiculum very short, triangular, slightly enlarged at the top or in the form of a very small protrusion.

Discussion. *Dellabeffaella* shares with *Canavesiella* the character of a pectinate internal spurs of the tibiae (polydentate in *Canapiciella, Baudiola* and *Doderiola*), and with *Canapiciella* and *Doderiola* the presence of parasutural stria (absent in *Canavesiella* and *Baudiola*). Unlike *Baudiola* it has an anophthalmous head and normal-sized – not hypertrophic – spermatheca. From *Canavesiella* it differs by the presence of evident transversal striolae to the elytra and the median phanera of the endophallus large and less complex. *Dellabeffaella* is in the phylogenetic analysis found to be related to *Canapiciella* with a support of 82.4/57 (Fig. 1D). *Dellabeffaella* is the southern vicariant of *Canapiciella*. A partial, but wide, sympatric distribution is found for *Reitteriola* of the clade *Reitteriola*.

Distribution. Italy, Piedmont, South-Eastern Graian Alps, Lanzo valley.

Species

Dellabeffaella roccae (Capra, 1924)
Royerella (*Della-Beffaella*) *Roccae* Capra, 1924: 155.
Royerella (*Dellabeffaella*) *Roccai* Capra, 1924: Jeannel, 1924a: 199.
Dellabeffaella roccai (Capra): Casale, 1980: 319.
Dellabeffaella roccae (Capra): Perreau, 2000: 265.

Genus ***Valdesiella*** nov.
https://zoobank.org/NomenclaturalActs/BB9C0380-82D6-43C9-87CA-2E785B31888F

Type species. *Dellabeffaella olmii* Casale, 1980 by present designation (habitus in Fig. 256.6).

Description**.** Large size, 2.7-3.3 mm, bathyscioid body (Fig. 256.6), elliptical in shape.

Head: Anophthalmous.

Antennae: Male antennae reaching at most, when lying backwards, the anterior third of the elytra. First antennomere much shorter than the second one; the 8th as long as wide; the 11th lanceolate and as long as the previous one, plus almost half of the 9th one.

Pronotum: With regularly rounded sides, broad and globular. Narrower than the elytra, with the maximum width at the apex of the basal third. Basal angles acute and facing backwards due to the moderate sinuosity of the base, which is also moderately narrow.

Elytra: With well marked, complete, parasutural stria, with fine and thick transverse striolae.

Legs: Little elongate. Metafemora without median tooth at the posterior edge. Tibial internal spurs pectinate. Meso- and metatibiae with incomplete apical baskets of short and sparsely distributed spines. Males protarsi pentameres dilated, as wide as the protibiae apex.

Mesoventral keel (Fig. 258.5): High, but not protruding forward. The anterior profile, transversely elu-

sive and straight, and the ventral one, slightly sinuous, forms an obtuse angle, provided with a more or less pronounced tooth, sometimes rounded and faded. Posteriorly without apophysis prolonged on border of the metaventrite.

Suture of the metaventrite (Fig. 258.5): Formed by the upper half in a slightly convex arch and the lower half in a concave arch bordering the coxal cavity with a well manifested subtriangular area.

Metatergal apparatus (Fig. 259.8): Large, with apophysis of the alacrista at least a quarter of the elytra; metascutum wings wide, although clearly longer than wide.

Metendosternite (Fig. 261.5): Large, «Y» shaped, with furcal arms triangular, wide at the base; arms somewhat shorter than the trunk with well-developed apical process or apophysis. Furcal trunk clearly longer than wide.

Median lobe of aedeagus: Elongated, about a third of the body length. In lateral view (Fig. 263.4), widely and regularly curved, slender, with the apex strongly pointing downwards. In dorsal view (Fig. 265.4), with the subparallel sides in the basal half, then converging towards the apex, which is ogive and pointed.

Endophallus (Fig. 265.4): Basal «Y»-piece large and well-sclerotized. Median phanera large and complex, in saddle shape. There are two apical lists, parallel and moderately sclerotized.

Parameres (Fig. 265.16): Long and slender, slightly shorter than the median lobe. Provided with three sub-equal setae at the apex.

Spermathecal complex: Spermatheca (Fig. 266.11) large, with the proximal part globular and the distal one smaller and elongated, slightly curved. Hyaline union duct longer than wide and narrower than the lobes. Ductus distally sclerotized and thickened for a short part at the insertion into the spermatheca.

Female uroventrite VIII (Fig. 267.12): Spiculum short, stout, triangular, slightly enlarged at the top; sides of the anterior margin very concave.

Etymology. From the population of the Waldensians, followers of Waldo of Lyon settled in the Pellice, Germanasca and Chisone valleys. In the sixteenth century subject to religious persecution used the Gheisa d'la Tana (locus typicus of *Valdesiella olmii* comb. nov.) as a refuge and rock church. The name of the genus is feminine.

Discussion. At the time of the description (Casale 1980) assigned the species *D. olmii* to the genus *Dellabeffaella*, the only specialised Leptodirini, which is together with *Parabathyscia oodes* geographically relatively close to *Valdesiella* gen. nov. within a radius of 50 km in linear distance. The classification was confirmed later by the works of Vailati (1988, 2017). One results of the molecular analysis is shown in the Figure 1D, therein the species *D. roccae* and *D. olmii* are both sister to *Canapiciella* and *Canavesiella*. This finding has caused us to review the congeneric state of these two species of *Dellabeffaella* with revised morphological criteria. The new analyse on a morphological basis and the position of these species in the molecular phylogenetic tree, as shown in Fig.1D, strongly suggested that they are separate genera rather than species of the same, therefore two distinct genera were installed.

Valdesiella gen. nov. is similar to *Canavesiella* and also exhibits pectinate internal spurs of the tibiae (polydentate in *Canapiciella, Baudiola* and *Doderiola*), the characters shares with *Canapiciella* and *Doderiola* ist the presence of parasutural stria (absent in *Canavesiella* and *Baudiola*). The differences in characters states found when comparing it with *Baudiola* was the anophthalmous head and the normal-sized – not hypertrophic – spermatheca. *Canavesiella* instead differs in the apparent transversal striolae to the elytra which are present. Morphological differences are also found when compared with *Valdesiella* gen. nov., which exhibits the following characters states described in how they differ to *Dellabeffaella*: the body with front part less wide male antennae less elongated than in *Dellabeffaella*; the 8th as long as wide, twice as long as wide; basal angles of the pronotum acute and facing backwards but less than in *Dellabeffaella*; legs less elongate; the anterior profile of the mesoventral keel transversely elusive and straight, less curved; the ventral one posteriorly without apophysis prolonged around the edge of the metaventrite, prolonged beyond the edge; median phanera of the endophallus large and complex, saddle-shaped, less complex; apex of the parameres less dilated. Considering the outcome of the molecular analysis *Valdesiella* ge. nov. is found to be related to *Canavesiella* with a support of 60.9/55 (Fig. 1D). *Valdesiella* gen. nov. is the southern vicariant of *Dellabeffaella*. Opposed to this it is partially, but over a wide area, sympatric with *Reitteriola* of the clade *Reitteriola*.

Distribution. Italy, Piedmont, central and southern Cottian Alps, Pellice, Germanasca and Chisone valleys.

Species

Valdesiella olmii (Casale, 1980) comb. nov.
Dellabeffaella olmii Casale, 1980: 315.

Archeoboldoria subgroup

This is considered a subgroup which could be established only with medium support (87.5/71) but separates two clades, one consisting of the genera *Archeoboldoria* and *Rondolinia* which is highly supported by 91.7/100 and another formed by the genus *Reitteriola* that is found in basal position in this clade (Fig. 1D).

KEY TO GENERA

1. Body smaller, 1.6-1.7 mm, bathyscioid facies (Fig. 256.2). Eyes reduced but present. Male protarsomeres not dilated.....*Reitteriola*
- Body larger, 2.4-3.5 mm, elongated (Fig. 256.3) or elliptical (Fig. 255.1). Eyes absent. Male protarsomeres not or only slightly dilated.....2

2. Body elliptical (Fig. 256.3), antennae shorter and male protarsi slightly dilated. Elytra without transverse striolae. Polydentate inner tibial spurs with asymmetrical indent. Metafemora with an apparent tooth at the posterior edge. Parameres with the ventral (posterior) seta subapical (Fig. 265.13). Female uroventrite VIII with spiculum very developed in length, slender (Fig. 267.9).....*Rondolinia*
- Body elongated (Fig. 255.1), antennae longer and male protarsi never dilated. Elytra with strong transverse striolae. Pectinate inner tibial spurs with symmetrical notch. Metafemora without tooth at the posterior edge. Parameres with the ventral (posterior) seta shifted backwards (Fig. 265.5). Female uroventrite VIII with spiculum poorly developed and narrow (Fig. 267.1) .....*Archeoboldoria*

Clade ***Reitteriola***

Found to be basal to the *Archeoboldoria* subgroup, with *Reitteriola* as sister to the genera *Rondolinia* + *Archeoboldoria* with a support of 87.5/71. A fairly long genetic distance (Fig. 1D) identified between them supports a clear separation from the sister genera.

Genus ***Reitteriola*** Giachino & Vailati, 2019
Reitteriola Giachino & Vailati, 2019: 91.

TYPE SPECIES. *Bathyscia pumilio* Reitter, 1885 by original designation (habitus in Fig. 256.2).

DIAGNOSIS. Small size, 1.6-1.7 mm, bathyscioid body (Fig. 256.2), ovoid in shape, with pronotum not wider than the elytra.

Head: Oculated, exhibiting two white and rhombic areas.

Antennae: Male antennae short, not reaching, when stretched backwards, the base of the pronotum. First antennomere just shorter than the second one; the 8th wider than long; the 11th ogival and about twice as long as the previous one.

Pronotum: With regularly rounded sides, broad and globular, not wider than the elytra. Maximum width approximately at the basal angles, which are acute and facing backwards due to the base accentuated sinuosity.

Elytra: With parasutural stria almost complete and well marked, anteriorly faded; with apparent and dense transverse striolae.

Legs: Metafemora with unarmed posterior margin. Apex of the tibiae with polydentate internal spurs. Meso- and metatibiae with incomplete apical baskets of short and sparsly distributed spines. Male protarsi pentamerous and never dilated, less wide than the apex of protibiae.

Mesoventral keel (Fig. 258.1): High, but not protruding forward. The anterior profile widely curved and the ventral one slightly curved forming an obtuse angle equipped with a inferior, only slightly apparent tooth. Posteriorly without prolonged apophysis on the metaventrite.

Suture of the metaventrite: Unknown.

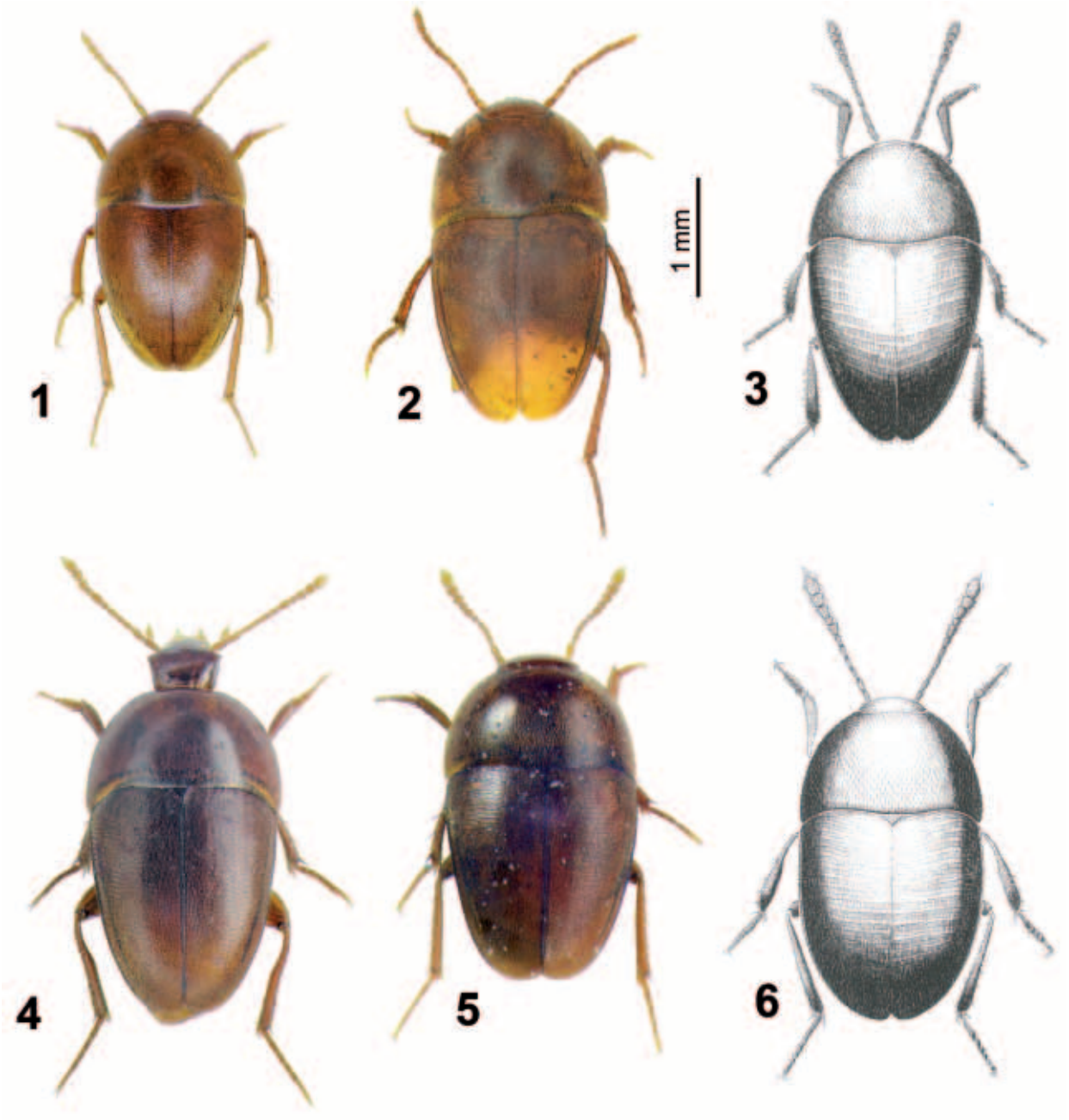
Metatergal apparatus (Fig. 259.4): Large, with apophysis of the alacrista long approximately one third of the elytra; short arcuate metascutum wings somewhat longer than wide and sharp apices.

Metendosternite (Fig. 261.1): «Y» shaped, with furcal arms triangular, wide at the base; narrow arms as long as or slightly shorter than the trunk, with poorly defined apical apophysis. Furcal trunk slightly longer than the widest area.

Median lobe of aedeagus: Elongate. In lateral view (Fig. 262.8), little and regularly curved, slender, with the apex not facing down. In dorsal view (Fig. 264.8), with sides approximately parallel in the basal 5/6th, therefore decidedly converging towards the apex, which is subtriangular, but not acute, rounded.

Endophallus (Fig. 264.8): Basal «Y»-piece large and well-sclerotized. Median phanera large and complex; there are two thin parallel and very little sclerotized apical lists.

Parameres (Fig. 265.12): Long and slender, slightly shorter than the median lobe, with apex, in



FIGURES 270.1–270.6: *Speonomus* series, *Euryspeonomus* group. Habitus of: (**1**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**2**) *Casalella meridionalis* **comb. nov.** (modified from Fresneda *et al*. 2010), (**3**) *Zariquieyella mystica* **comb. nov.**, (**4**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* **comb. nov.**, (**5**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**6**) *Vallespirana grenieri* **comb. nov.** Figs **3**, **6** modified from Salgado *et al*. (2008).

dorsal view, simple; provided with three apical and sub-equal setae.

Spermathecal complex: Spermatheca (Fig. 266.7) large, with the proximal lobe ovoid and the distal one smaller, globular; short hyaline union duct as long as wide and much narrower than the lobes. Ductus distally enlarged and sclerotized with a nodule in close proximity to the insertion into the spermatheca.

Female uroventrite VIII (Fig. 267.8): Spiculum developed in length, thin; front edge of the uroventrite with decidedly concave sides.

Discussion. *Reitteriola* belongs to a morphologically homogeneous group of genera. Based on molecular data *Archeoboldoria* and *Rondolinia* are belonging to this group. It is a group that is morphologically characterised by: male with none, or slightly dilated protarsi, metendosternite not «V»-shaped with triangular furcal arms and endophallus with well-developed basal «Y»-piece. *Reitteriola*, like *Archeoboldoria*, shows a non-toothed metafemora, with a tooth at the posterior edge in *Rondolinia*. Nevertheless, it is similar to *Rondolinia* and *Archeoboldoria* in the presence of parasutural stria of elytra and to *Rondolinia* in the polydentate internal tibial spurs. In the phylogenetic analysis *Reitteriola* is found to be related to the *Archeoboldoria* clade with a support of 87.5/71 (Fig. 1D).

Distribution. Italy. Western Alps, from Graie to Marittime Alps and Northern Apennines, SE to the Tuscan-Emilian Apennines.

Species

Reitteriola pumilio (Reitter, 1885)
Bathyscia (*Bathyscia*) *pumilio* Reitter, 1885 [1884]: 25.
Bathyscia lesinae Reitt., 1881 (pars): Jeannel, 1907c: 64.
Bathyscia Murialdii Balbi, 1888: 154.
Bathysciola pumilio subsp. *Biglianii* Jeannel, 1924c: 49.
Bathysciola pumilio Reitter: Jeannel, 1910a: 27.
Bathysciola (s. str.) *pumilio* Subsp. *Biglianii* Jeannel, 1924: Jeannel, 1924a: 102.
Bathysciola (s. str.) *pumilio* (Reitter): Perreau, 2000: 240.
Reitteriola pumilio (Reitter, 1885): Giachino & Vailati, 2019: 91.

Clade ***Archeoboldoria***

Rondolinia and *Archeoboldoria* belong to a clade characterised by the following set of morphological characters: metendosternite not «V»-shaped, triangular, wide at the base, furcal arms; mesoventral keel with pronounced tooth; meso- and metatibiae with incomplete apical baskets; males protarsi not or only slightly dilated; elytra with complete parasutural stria; median lobe of aedeagus stout, ogival in shape in the distal half; endophallus with basal «Y»-piece well sclerotized; parameres long, slightly shorter than the median lobe; spermatheca almost symmetrical, slightly dilated; spermathecal duct distally partly sclerotized over a small area.

This clade is highly supported, 91.7/100, and unifies the sister genera *Archeoboldoria* and *Rondolinia* (Fig. 1D).

Genus ***Archeoboldoria*** Ghidini, 1937
Boldoria (*Archeoboldoria*) Ghidini, 1937: 69.
Archeoboldoria Ghidini: Vailati, 1988: 39.

Type species. *Bathysciola* (*Boldoria) Doderona* Jeannel, 1924 by original designation (for the habitus see that of the similar species *Archeoboldoria pascuttoi* in Fig. 255.1).

Diagnosis. Medium size, 2.4-2.8 mm, bathyscioid body (Fig. 255.1), elongated, slightly narrowed at the base of the pronotum.

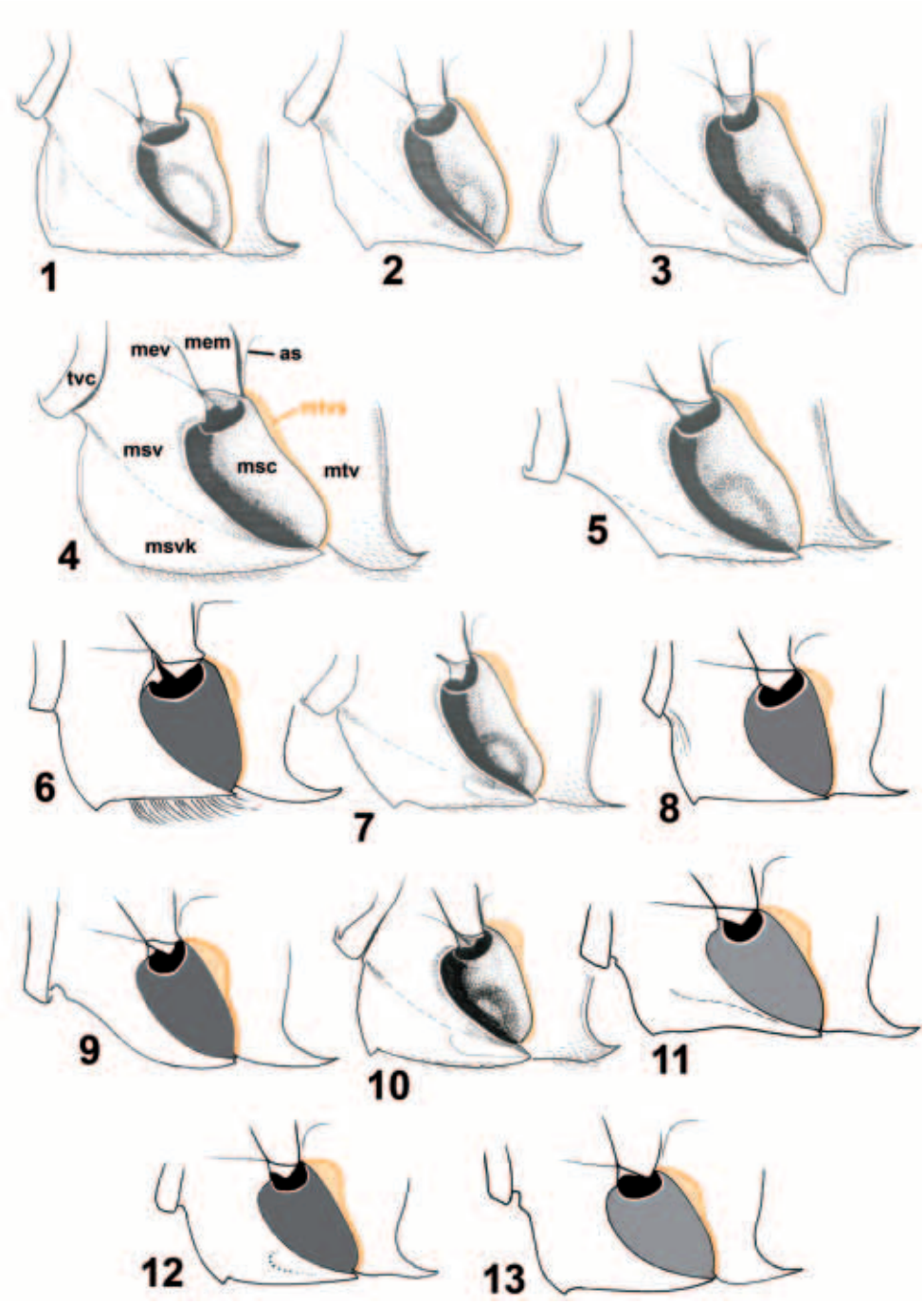
Antennae: Male antennae moderately elongated, overcoming, when extended backwards, at least half but can also reach the distal third of the elytra. First antennomere slightly shorter than the second; the 8th from one and a half to more than twice the length than the width; the 11th lanceolate and slightly longer than the previous one.

Pronotum: With sides from regularly rounded to rectilinear, markedly converging in the anterior half, with basal angles from acute to almost right and base narrow.

Elytra: With parasutural stria complete, well marked and with strong transverse striolae clearly apparent on the disc.

Legs: Metafemora without tooth at the posterior edge. Tibial internal spurs pectinate. Meso- and metatibiae with incomplete apical baskets of short and sparsely distributed spines. Male protarsi pentamerous and never dilated, as wide as half of protibial apex.

Mesoventral keel (Fig. 257.1): Obtuse, with anterior profile transversly elusive, slightly arcuated



FIGURES 271.1–271.13: *Speonomus* series, *Euryspeonomus* group. Pterothorax in lateral view of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *Dupreia beruetei* **comb. nov.**, (**7**) *Josettekia mendizabali,* (**8**) *Nafarroa sorogainensis,* (**9**) *Casalella meridionalis* **comb. nov.**, (**10**) *Zariquieyella mystica* **comb. nov.**, (**11**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* **comb. nov.**, (**12**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**13**) *Vallespirana grenieri* **comb. nov.** Figs **1**–**5,** **7**, **10** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

below. Provided with a very pronounced, but not pointed, tooth, due to the anterior concavity of the ventral profile. Without posterior apophysis prolonged on the metaventrite.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 258.6): Large, with apophysis of the alacrista elongated and narrow, at least as long as one fifth of the elytra. Longitudinal furrow six to seven times longer than wide; long and narrow metascutum wings.

Metendosternite (Fig. 260.1): «Y» shaped, with furcal arms triangular, wide at the base and the apical part dilated, funnel-shaped apophysis. Furcal arms shorter than the furcal trunk, this length, one and a half times longer than the basal width.

Median lobe of aedeagus: Stout, slightly elongated, about a third of the body length. In lateral view (Fig. 262.1), moderately curved, with the apex slightly facing downwards. In dorsal view (Fig. 264.1), with subparallel sides at the base and arched before the narrowing the distal half; apex in ogival shape but not pointed.

Endophallus (Fig. 264.1): Basal «Y»-piece well sclerotized. Median phanera poorly defined, surrounded by silk «Y»-spinulose bundles that extend distally with two, partially sclerotized, lists.

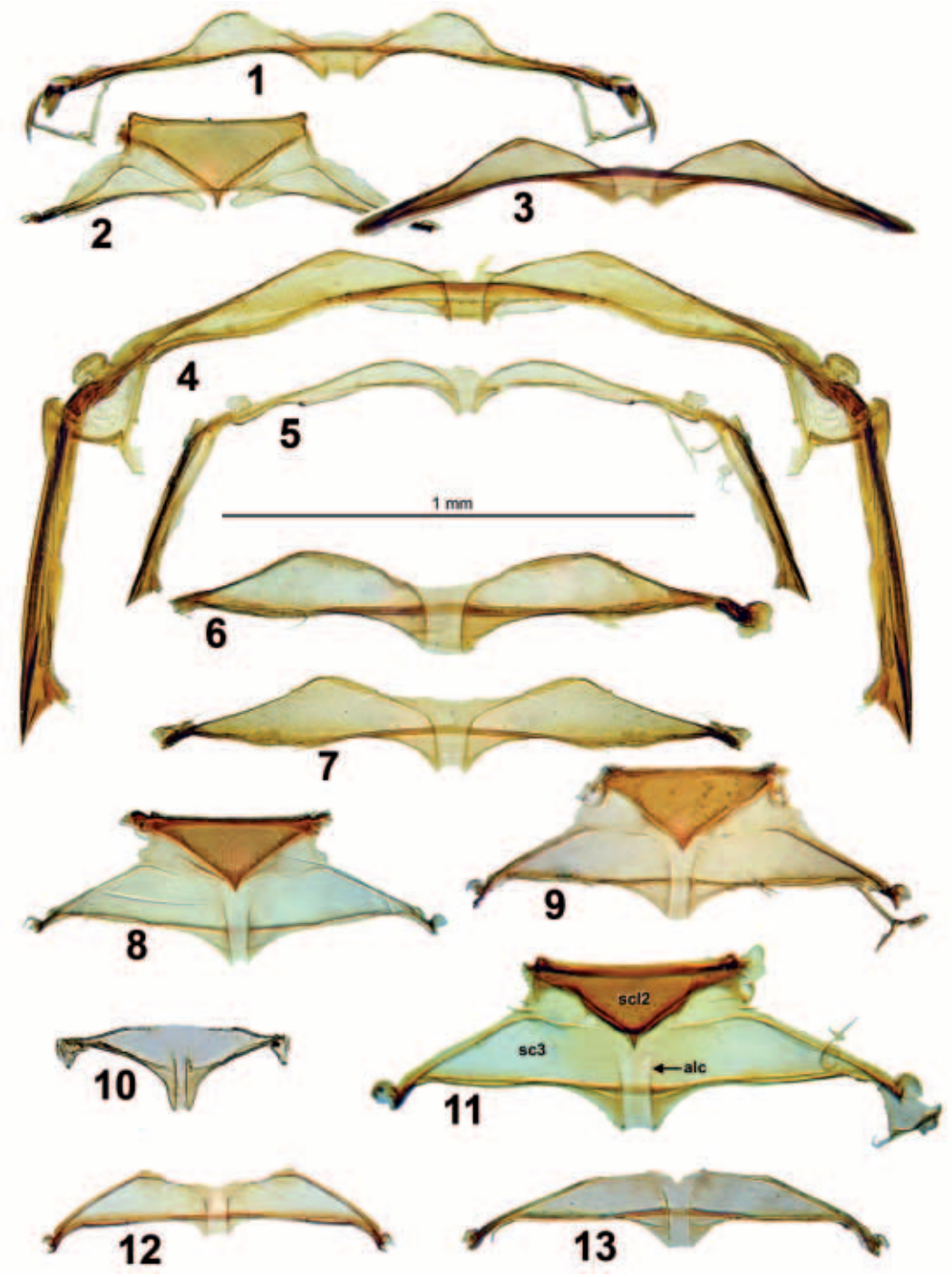
Parameres (Fig. 265.5): Long, slightly shorter than the median lobe, dilated at apex in triangular spatula-shape. Equipped with four setae, an apical seta, one (or two in *A. pascuttoi*) preapical and one, ventral, strongly shifted proximally, from the distal third to almost half the paramere (with the exception of *A. pascuttoi*, in which it is placed much more in the front part, at around the distal sixth of the paramere). The ventral seta is placed in a point where there is a significant change in the thickness of the paramere itself.

Spermathecal complex: Spermatheca (Fig. 266.1) almost symmetrical, with the proximal and distal lobes sclerotized and slightly dilated, small and equally elongated. Hyaline union duct somewhat narrower than the lobes but longer. Duct distally sclerotized in a small area and somewhat dilated in the area where it joins the spermatheca. In *Archeoboldoria martinottii* sp. nov. the lobes are very similar and the union duct shorter and equal in width to the lobes.

Female uroventrite VIII (Fig. 267.1): Spiculum very poorly developed and narrow.

Discussion. See Discussion section of *Rondolinia* for characters differing when compared to *Archeoboldoria*. The comparison of the phylogenetic tree obtained by processing molecular data (Fig. 1D) with the previous hypothesis generated by using morphological characters which were believed to be phylogenetically meaningful (Vailati 1988) generated significant different results. Characters such as: presence/absence of the parasutural stria of the elytra, toothed/unarmed mesoventral keel, internal tibial spurs pectinate/polydentate, non-dilated/dilated protarsomeres in the male, toothed/unarmed metafemora, relative length of the first and second antennomeres, shape of the median lobe of aedeagus, of the endophallus and of the parameres (including position of setae) (Vailati 2017; Giachino & Vailati 2019), appear scattered around on the tree of shown in figure 1D, producing a pattern that has no apparent phyletic plausibility. Considering that the signals obtained in the molecular data are phylogenetically relevant, those generated by the morphological characters used exhibit to be only very low capacities for generating information reflecting the evolutionary relationship among the taxa. Nevertheless, it becomes clear that at they highly suitable to define single genera. On the other hand, the problem linked to the use of classical, «jeannelian» (character states used by R. Jeannel), morphological characters in the Leptodirini, are also extremely useful to identify important phenomena of adaptation to the subterranean environment, this has already been profoundly discussed (Casale *et al*. 1991; Giachino *et al*. 1998; Fresneda *et al*. 2007). However, the well known problem of convergence due to environmental contraints in subterranean animals and its influence on taxonomic classification is severely hampering studies and are advocating for molecular studies. The molecular phylogeny as shown in figure 1D indicates that *Archeoboldoria* is related to *Rondolinia* with a support of 91.7/100 (Fig. 1D). From a zoogeographic point of view, *Archeoboldoria* appears, at the moment, strictly vicariant to *Rondolinia*. On the other hand, the zoogeographic relationships with some genera of the clades *Baudiola* and *Dellabeffaella* of *Dellabeffaella* subgroup appear more complex, with some of which (*Canapiciella*, *Doderiola* and *Baudiola*), *Archeoboldoria* shows overlapping distribution patterns. In the westernmost end of its range *Archeoboldoria* partially overlaps in its geographic distribution area with *Reitteriola*, this is where it reaches its limits in the northeast.

Distribution. Italy. Northeast Graian Alps on the right side, at the mouth of the Aosta valley. Biellesi and Cusiane Alps between Dora Baltea river and Orta lake.



FIGURES 272.1–272.13: *Speonomus* series, *Euryspeonomus* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *ciaurrizi,* (**6**) *Dupreia beruetei* **comb. nov.**, (**7**) *Josettekia angelinae,* (**8**) *Nafarroa sorogainensis,* (**9**) *Casalella finismillennii* **comb. nov.**, (**10**) *Zariquieyella mystica* **comb. nov.**, (**11**) *Pyrenaeola* (*Pyrenaeola*) *aranensis* **comb. nov.**, (**12**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**13**) *Vallespirana grenieri* **comb. nov.** Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Species

Archeoboldoria doderona (Jeannel, 1924)
Bathysciola (*Boldoria*) *Doderona* Jeannel, 1924a: 117.
Boldoria (*Archeobold*.) *Barajoni* Focarile, 1952: 103.
Boldoria barajoni Focarile, 1952: 103: Vailati, 1988: 42.
Boldoria (*Archeoboldoria*) *doderona* Jeannel, 1924: Ghidini, 1937: 69.
Archeoboldoria doderoana (Jeannel, 1924): Vailati, 1988: 42.
Archeoboldoria doderona (Jeannel): Perreau, 2000: 264.

Archeoboldoria lanai Giachino & Vailati, 1998
Archeoboldoria lanai Giachino & Vailati, 1998a [1997]: 163.

Archeoboldoria martinottii sp. nov. (See Appendix New Species)

Archeoboldoria pascuttoi Giachino, Lana & Vailati, 2001
Archeoboldoria pascuttoi Giachino, Lana & Vailati, 2001: 240.

Archeoboldoria sturanii Casale & Giachino, 2010
Archeoboldoria sturanii Casale & Giachino, 2010: 227.

Genus ***Rondolinia*** Giachino & Vailati, 2019
Rondolinia Giachino & Vailati, 2019: 89.

Type species. *Bathysciola adelinae* Jeannel, 1934 by original designation (habitus in Fig. 256.3).

Diagnosis. Medium size, 2.6-3.5 mm, bathyscioid body (Fig. 256.3), elliptical in shape, with wide pronotum, slightly wider than the elytra.

Head: Anophthalmous.

Antennae: Male antennae relatively long, extended backwards, exceeding the base of the pronotum. First antennomere slightly shorter than the second one; the 8th as long as wide; the 11th ogival, slightly less than twice the length of the previous one.

Pronotum: With regularly rounded sides, broad and globular, slightly wider than the elytra. Maximum width just before the posterior angles. Basal angles acute, facing backwards due to the accentuated sinuosity of the base, which is also slightly narrow.

Elytra: With parasutural stria almost complete and well marked, anteriorly transverse; without transverse striolae.

Legs: Metafemora with an evident median tooth at the posterior edge. Tibial internal spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short and sparse spines. Males protarsi pentameres slightly dilated, narrower than the protibiae apex.

Mesoventral keel (Fig. 258.2): Large and high, protruding forward, front profile rounded, not elusive. Ventral profile, posteriorly slightly sinuated. Together they form an obtuse angle, equipped with a pronounced tooth; posteriorly the apophysis does not exceed the metaventrite or slightly exceeds it.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 259.5): Large, with narrower, more elongated metascutum wings and sharp, curved apices; with apophysis of the alacrista long about a quarter of the elytra.

Metendosternite (Fig. 261.2): «Y» shaped, with furcal arms triangular, wide at the base; arms slightly shorter than the furcal trunk and the apical apophysis poorly defined. Furcal trunk a little longer than the widest area.

Median lobe of aedeagus: Elongated in shape. In lateral view (Fig. 263.1), widely, but not regularly, curved, slender, with the apex not facing downwards. In dorsal view (Fig. 265.1), with subparallel sides in the basal half, therefore decidedly and rectilinearly converging towards the apex which is ogive and tapered.

Endophallus (Fig. 265.1): Basal «Y»-piece small, well sclerotized. There is a large and particularly complex median phanera. Apically there is an arrowhead-shaped scaly structure.

Parameres (Fig. 265.13): Long and slender, slightly shorter than the median lobe, with apex, in dorsal view, simple. Equipped with three setae: one apical long, and two subapical internal, the first one shorter.

Spermathecal complex (Fig. 266.8): Spermatheca large and long, with the proximal lobe not dilated and the distal one globular, slightly larger and shorter; hyaline union duct, very long, about three times longer than wide and somewhat narrower than the lobes. Duct distally slightly enlarged and sclerotized at the insertion side into the spermatheca. Spermathecal gland present.

Female uroventrite VIII (Fig. 267.9): Spiculum very developed in length, slender. Front edge of the uroventrite with completely horizontal sides.

Discussion. *Rondolinia* differs from *Archeoboldoria* by the following character states: elytra without transverse striolae (strong in *Archeoboldoria*), polydentate internal

tibial spurs (pectinate in *Archeoboldoria*), metafemora with an apparent tooth at the posterior edge (without tooth in *Archeoboldoria*), the parameres with the ventral (posterior) seta subapical (dislocated towards the back in *Archeoboldoria*) and a longer apophysis of the female uroventrite VIII. As shown in the phylogenetic tree based on molecular data in figure 1D, *Rondolinia* is found to be related to *Archeoboldoria* with a support of 91.7/100 (Fig. 1D). From a zoogeographic point of view, *Rondolinia* appears, at the moment, strictly vicariant to *Archeo-boldoria*. On the other hand, the zoogeographic relationships of *Rondolinia* with the genera of the clade *Baudiola* of the *Dellabeffaella* subgroup appear more complex, with *Baudiola* it shares a large distribution area. As mentioned by Vailati (1988, 2017) this situation is probably linked to significant and repeated phenomena of areal contraction and expansion, with consequent speciation phenomena.

Distribution. Italy, Piedmont, lower Val Sesia.

Species

Rondolinia adelinae (Jeannel, 1934)
Bathysciola (s. str.) *Adelinae* Jeannel, 1934a: 95.
Bathysciola adelinae Jeannel, 1934: Casale & Rondolini, 1983: 74.
Rondolinia adelinae (Jeannel, 1934): Giachino & Vailati, 2019: 89.

3.4.7 *Incertae sedis* in series ***Catopsinus***

3.4.7.1 ***Coiffaitiola*** group

Group of genera characterised by bathyscioid habitus, small body size and pentamerous male protarsi; elytra transversely striated or not; parasutural stria weakly evident or absent. Mesoventral keel high, prolonged over the entire metaventrite. Endophallus with a developed basal «Y»-piece.

Discussion. No molecular data available. The position of this group, identified following the contributions of Jeannel (1955d), Cerruti (1959) and Casale & Giachino (1985), is doubtfully assigned to the series *Catopsinus* on a morphological basis.

Key to genera

1. Antennae longer; elongate and transversely striolated elytra; median area of endophallus without evident phanera (Fig. 268.6); dorsally open tegmen ....*Coiffaitiola*

- Antennae shorter; elytra less elongate and not striolated; median area of endophallus with a complex phanera (Fig. 268.5); tegmen closed dorsally..... .....*Cavazzutiella*

Genus ***Cavazzutiella*** Casale & Giachino, 1985
Cavazzutiella Casale & Giachino, 1985: 221.

Type species. *Cavazzutiella taurica* Casale & Giachino, 1985 by original designation (habitus in Fig. 268.1).

Diagnosis. Size small, 1.8-2.2 mm, body bathyscioid (Fig. 268.1), convex. Covered with golden, fine, lying pubescence.

Head: With complete occipital carina; anophthalmous.

Antennae: Short and delicate, just reaching the base of the pronotum. First antennomere slightly shorter than the second. Antennomeres 3rd to 7th longer than wide. The 8th small, not transverse, ovoid. The 9th and 10th about as long as wide or slightly longer. The 11th about twice as long as the 10th.

Pronotum: Broad, transverse, strongly convex, as wide as or just larger than the elytra. Lateral sides less curved in anterior half, with maximum width just anterior or at base, which is bisinuate; basal angles square or acute.

Elytra: With coaptation of sutural margins, with parasutural stria inconspicuous or absent. Maximum width just before the base, gradually narrowed and rounded towards the apex. Elytral disc with transversal striolae.

Legs: Relatively slender. Inner tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short, sparse spines. Male protarsi pentamerous, dilated, narrower than apex of protibia.

Mesoventral keel (Fig. 268.3): High, forming an obtuse angle and a toothed vertex. Anterior margin almost straight, ventral margin straight, extended along entire metaventrite.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus: Small, stout and only slightly arched. In lateral view (Fig. 268.6), apex not or only slightly curved downwards. In dorsal view (Fig. 268.7), maximum width at half and broadly rounded, sometimes with pointed apex. Basal blade broad, with unsclerotized margins.

Endophallus (Fig. 268.7): «Y»-piece present, well sclerotized. Median area with complex phanera: basal part vaguely horseshoe-shaped, apical part «M»- or «U»-shaped.

Parameres (Fig. 268.10): Relatively slender, as long as or shorter than median lobe of aedeagus. Apex sometimes enlarged on inner side, with three setae: two apical and one subapical, dorsal; sometimes apical setae spiniform. Tegmen wide, closed dorsally by an obvious band.

Spermathecal complex: Spermatheca (Fig. 268.12) small, kidney-shaped, with proximal part more developed. Ductus very long and thin, provided with a sclerotized nodule sometimes dilated before insertion into the spermatheca.

Female uroventrite VIII: Unknown.

Discussion. *Cavazzutiella* differs from *Coiffaitiola* in having much shorter antennae, the absence of elytral striolation and a stockier, less elongated body shape. The species *patrizii*, originally described as *Bathysciola*,has also been tentatively and dubiously assigned to the genus *Cavazzutiella*. The attribution to the genus *Cavazzutiella* is made on the basis of similarities in external morphological characters such as the general shape of the body, the structure of the antennae (relative length of the antennomeres), the shape of the mesoventral keel, the absence of parasutural stria on the elytra (completely absent in *C. taurica*, rudimentary and visible with extreme difficulty in *C. patrizii*) and the presence of transverse striolae on the elytra. There are also similarities, particularly in the morphology of the endophallus (Fig. 268.8: green arrow pointing the similar sclerotized piece to the median region) and in the shape of the spermatheca (Fig. 268.13). However, significant differences remain between these two species, particularly in the apical armature of the parameres, which is substantially different in the two species, to the point of raising doubts that can only be resolved with the future availability of more abundant material from the two species, or with the availability of fresh material for molecular analysis. Recently, *C. patrizii*, which we have inserted, albeit dubiously, into the genus *Cavazzutiella*, was still treated as a distinct group from *Bathysciola sensu auctorum* by Perreau (2021).

Distribution. Turkey, provinces of Antalya and Burdur.

Species

Cavazzutiella patrizii (Cerruti, 1959) comb. nov.
Bathysciola (s. str.) *Patrizii* Cerruti, 1959: 125.
Bathysciola (s. str.) *patrizii* Cerruti: Perreau, 2000: 234.

Cavazzutiella taurica Casale & Giachino, 1985
Cavazzutiella taurica Casale & Giachino, 1985: 224.

Genus ***Coiffaitiola*** Jeannel, 1955
Coiffaitiola Jeannel, 1955d: 3.

Type species. *Coiffaitiola rudis* Jeannel, 1955 by original designation (habitus in Fig. 268.2).

Diagnosis. Small size, 1.5-1.6 mm, body bathyscioid (Fig. 268.2), convex. Covered with a fine, recumbent and golden pubescence.

Head: With a complete occipital carina; anophthalmous.

Antennae: Short and delicate, extending beyond the base of the pronotum. First antennomere slightly shorter than the second. The 4th, 5th and 6th subequal; the 3rd longer than the 4th; the 8th, 9th and 10th about square; the 11th more than one and a half times as long as it is wide.

Pronotum: Broad, transverse, strongly convex, as wide as the elytra. Lateral sides less curved in the anterior half, with maximum width just before the base, which is bisinuate; the basal angles straight.

Elytra: With temporary coaptation of the sutural margins and an inconspicuous parasutural stria. Maximum width at the base, gradually narrowed towards the apex; elytral disc without transverse striolae.

Legs: Relatively slender. Inner tibial spurs polydentate. Meso- and metatibiae with incomplete apical baskets of short, sparse spines. Male protarsi pentamerous, dilated, narrower than the apex of the protibia. Distal edge of metafemora without tooth.

Mesoventral keel (Jeannel 1955): High, forming an obtuse, toothed angle. Anterior almost straight, ventral straight, strongly extended on metaventrite.

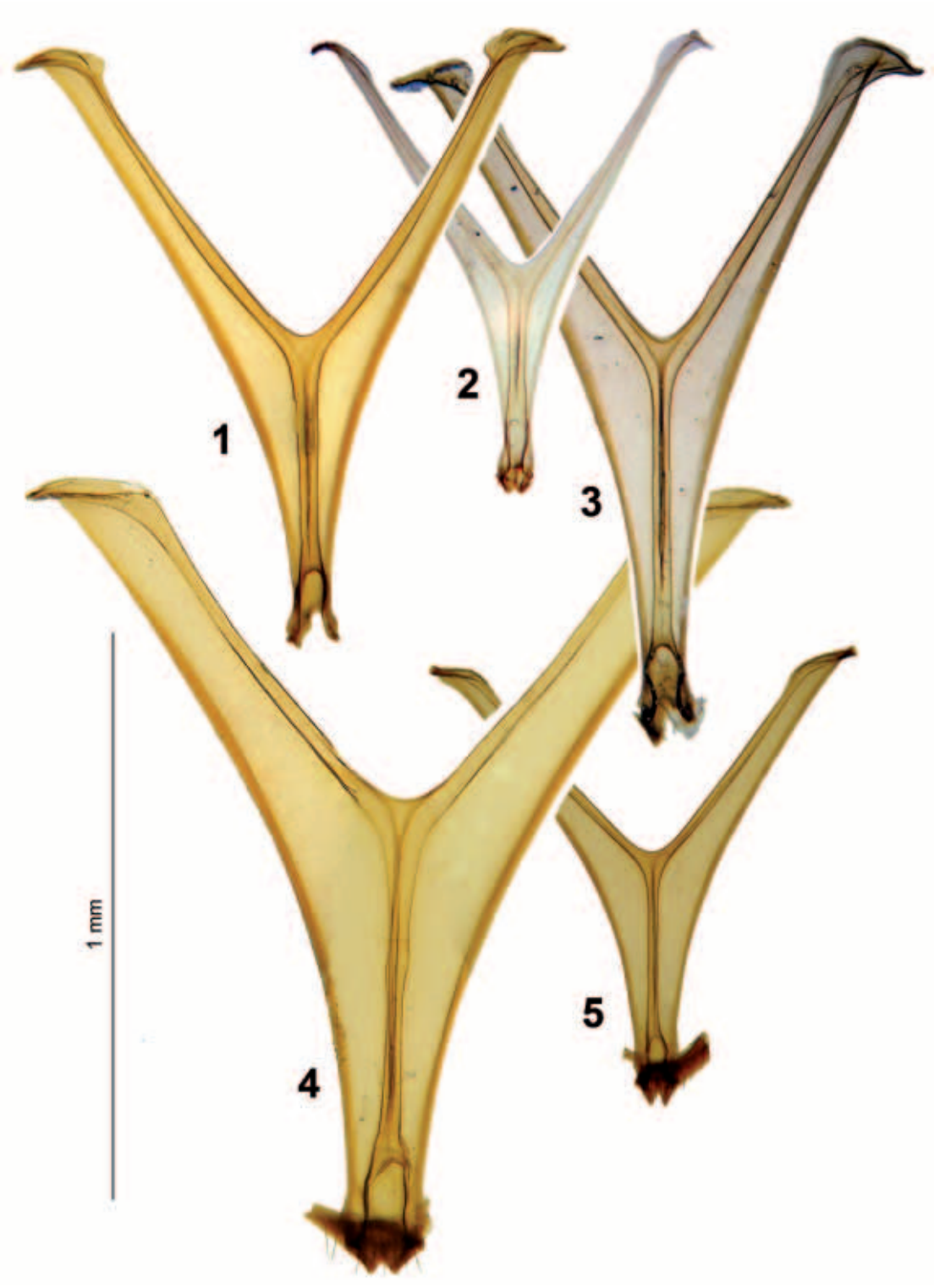
Metaventrite: Not keeled. Intercoxal apophysis adjacent.

Suture of the metaventrite: Unknown.

Metatergal apparatus (Fig. 268.4): Moderately developed, stocky, with short apophysis of the alacrista, one-third length of elytra.

Metendosternite (Fig. 268.5): «V»-shaped; short arms as long as trunk; posterior furcal lamina forms isosceles triangle between arm and trunk with basal side straight; no distinct apophysis. Short furcal trunk clearly wider than long.

Median lobe of aedeagus: Small, stout and slightly arched. In lateral view, apex curved downwards. In dorsal view (Fig. 268.9), maximum width at half and apex broadly rounded. Basal blade broad, with non-sclerotized margins.



FIGURES 273.1–273.5: *Speonomus* series, *Euryspeonomus* group. Metendosternite of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *ciaurrizi.*

Endophallus (Jeannel 1955): Basal «Y»-piece present, well sclerotized. Median and apical areas without obvious phanerae.

Parameres (Fig. 268.11): Relatively robust, as long as median lobe of aedeagus. Apex with three setae: one apical and two subapical, internal. Tegmen wide, open dorsally.

Spermathecal complex: Unknown.

Female uroventrite VIII (Fig. 268.14): Spiculum present, moderately long, stout, with blunt apex.

Discussion. *Coiffaitiola* differs from *Cavazzutiella* in having distinctly longer antennae, the presence of elytral striolation and a less stocky body shape, with more elongate elytra. See Discussion section for the genus *Cavazzutiella*.

Distribution. Turkey, Burdur province.

Species

Coiffaitiola rudis Jeannel, 1955
Coiffaitiola rudis Jeannel, 1955d: 5.

3.4.8 Series ***Speonomus***

Diagnosis. Elytra with more or less marked transverse striolae, in some cases replaced by isolated or disordered points; parasutural stria present or absent depending on the group. Anophthalmous and depigmented species.

Mesoventral keel: Short, not extending beyond the metaventrite, high or reduced, sometimes absent.

Suture of the metaventrite: Delimiting an arched area, generally small, narrow and more or less elongated.

Median lobe of aedeagus: Arched and thick at the base.

Endophallus: With three regions and always a «Y»-piece at the base, except in *Pseudospeonomus,* which has a ring-shaped sclerotized part.

Spermatheca: Elongated, generally five times or more longer than it is wide.

Discussion. The series has high support in all analysis, 100/100, in both Tree-1 (Fig. 1C) and Tree-2 (Fig. 2); it is sister to the clade formed by the series *Catopsinus* + *Drimeotus* + *Hittitia* with low support, 81.3/41 in Tree-1 and 74.7/56 in Tree-2.

Two characters of taxonomic importance are present or absent in the different groups of this series: the presence or absence of a penicillum and/or membranous lamina at the apex of the parameres. Given the topology of the tree, the following could be considered:

– The absence of penicillum is a secondary loss of structure that occurred three times independently.

– Or, given that the absence of penicillum is normal in most Leptodirini and especially that it occurs in the clades with the most basal divergence, even in outgroups, then it is the ancestral state and the development of penicillum occurred five times independently in the clades: *Parvospeonomus, Vanderberghia* gen. nov., *Bathysciella-Machaeroscelis-Bellesia, Ceretophyes-Perriniella-Troglophyes* and the large clade of the *Speonomus* group.

Given that the sister clade of the entire Pyrenean series – the *Euryspeonomus* group from the «Basque-Pyrenean» part (parameres with four setae) – and the sister of the two, the «*Catopsinus* series» (parameres with three setae) have neither penicillum nor membranous lamina, the second hypothesis should be considered more plausible, although it implies more independent occurrences of the same character.

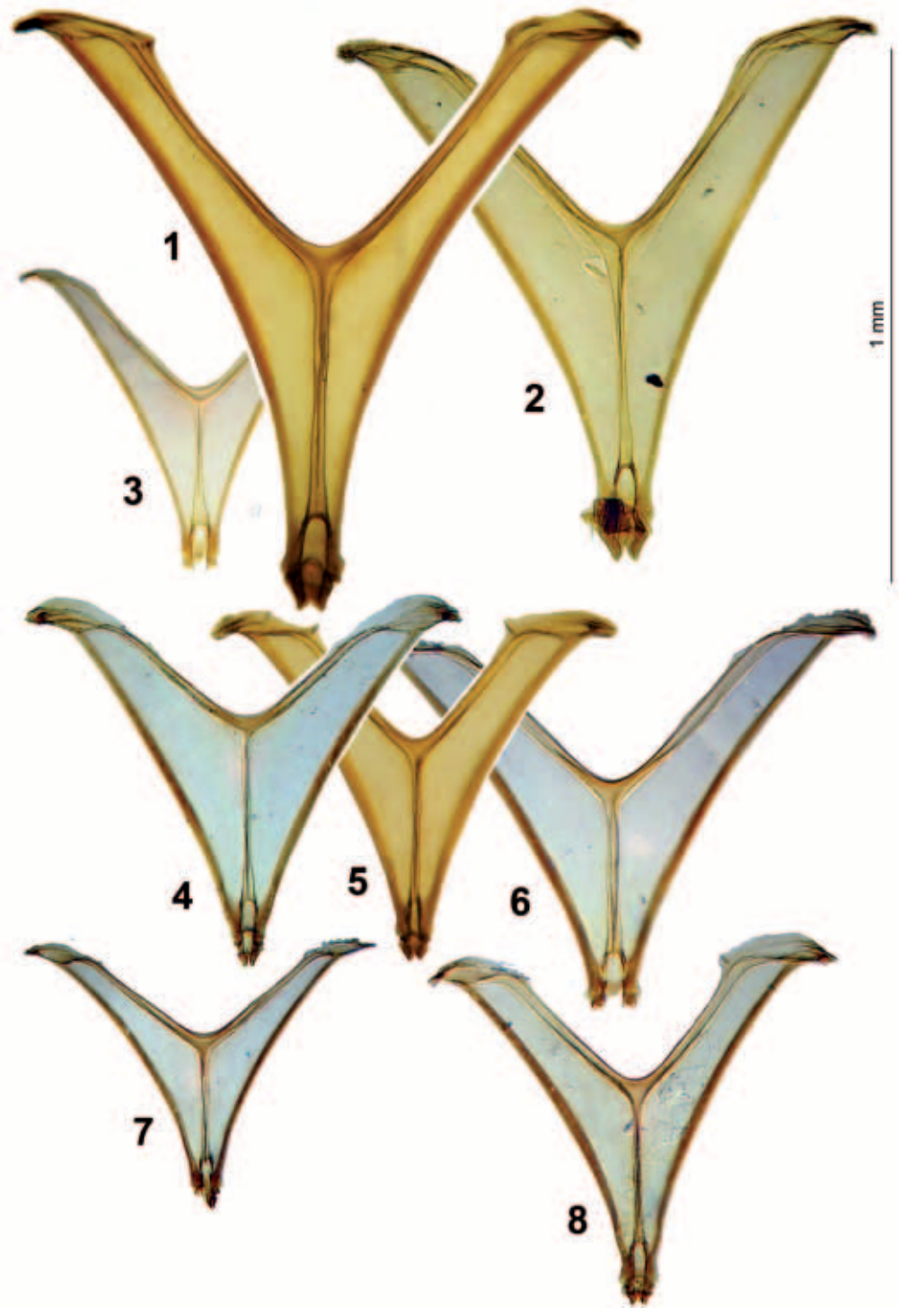
Among the clades with penicillum two models can be identified:

– There are two or three short, fine setae, and the dense penicillum is inserted into a cavity or depression: *Parvospeonomus, Vanderberghia* gen. nov. clade (ex *Speonomus speluncarum* species group), *Bathysciella* clade, *Machaeroscelis-Bellesia* clade, *Ceretophyes-Perriniella-Troglophyes* clade.

– There are three setae, varying in thickness, length and curvature, a membranous lamina of variable size and a penicillum which may be denser or rarer: genera *Speonomites*, *Troglocharinus*, *Speonomus*, and *Trapezodirus-Salgadoia-Naspunius-Stygiophyes-Lagariella*. In *Troglocharinus orcinus*, there is no penicillum, only a few rare setae, although in this case the structure corresponds to the characteristic pattern of parameres with two large setae and one fine one, with a membranous lamina and where the penicillum has been lost. In this case it is clear that it is a secondary loss of the penicillum. *Ariejasia* gen. nov. is also a special case as it has three long setae of varying length and thickness and the penicillum is in fact formed by long pedunculus or strips originating from the margin of the membranous lamina.

Key to groups

1. Parameres without penicillum (Figs 277.11-277.25, 283.6, 290.1, 299.7-299.9) 2



FIGURES 274.1–274.8: *Speonomus* series, *Euryspeonomus* group. Metendosternite of: (**1**) *Dupreia beruetei* **comb. nov.**, (**2**) *Josettekia angelinae,* (**3**) *Nafarroa sorogainensis,* (**4**) *Casalella finismillennii* **comb. nov.**, (**5**) *Zariquieyella diegoi* **comb. nov.**, (**6**) *Pyrenaeola* (*Pyrenaeola*) *aranensis* **comb. nov.**, (**7**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**8**) *Vallespirana grenieri* **comb. nov.**

- Parameres with penicillum, formed by setae or strips (Figs 283.5, 290.2-290.6, 295.7-295.9, 312.1-312.11) (except *Troglocharinus orcinus*, with pholeuonoid facies, three setae and a membranous lamina in the apical part of the parameres) 5

2. Parameres with four setae or spines in the apical area (Figs 277.12-277.20, 277.22-277.25), one case with nine (Fig. 277.21) and another with about 30 setae (Fig. 277.11) .....*Euryspeonomus* group
- Parameres with three setae in the apical part (Figs 283.6, 290.1, 299.7-299.9) 3

3. Pholeuonoid facies (Figs 297.1-297.3).....
.....*Antrocharis* group
- Bathyscioid facies (Figs 282.1, 282.2, 284.1).....4

4. Elytra without transverse striolae. High mesoventral keel (Fig. 282.4). Metendosternite with furcal arms almost three times as long as the trunk and with a terminal apophysis (Fig. 282.8). Apex of parameres very acute (Fig. 283.6); basal region of endophallus with a sclerotized ring and teeth on the inner margin (Fig. 283.4).....
...*Pseudospeonomus* (*Parvospeonomus* group (pars))
- Elytra with transverse striolae visible in basal area. Metendosternite with furcal arms shorter than the trunk and without terminal apophysis (Fig. 287.1). Low mesoventral keel (Fig. 285.1). Apical area of parameres rounded (Fig. 290.1); basal area of endophallus with a «Y»-piece (Fig. 289.1) .....
.....*Baronniesia* (*Bathysciella* group (pars))

5. Parameres with a more or less developed membranous lamina (Figs 312.1-312.11).....
.....*Speonomus* group
- Parameres without membranous lamina (Figs 283.5, 290.2-290.6, 295.7-295.9).....6

6. Elytra without parasutural stria, sometimes with a depression without dots 7
- Elytra with parasutural stria 8

7. Parameres with a cavity and a dense penicillum with long setae (Figs 290.2-290.6).....
.....*Bathysciella* group (pars)
- Parameres without cavity, sparse penicillum and short setae (Fig. 295.7-295.9) .....
.....*Troglophyes* (*Troglophyes* group (pars))

8. Body short and oval (Fig. 282.1). Protarsi of males thin, not dilated. Metendosternite with posterior lamina of furca very narrow in arms (Fig. 282.7). Flagellum of the «Y»-piece very long and filiform (Fig. 283.3) .....*Parvospeonomus* group (pars)
- Body elongate and elliptical (Figs 293.1-293.3). Male protarsi dilated, at least as wide as apical end of protibiae. Metendosternite with posterior lamina of furca well developed in arms (Figs 294.4-294.6). «Y»-piece flagellum shorter and more robust (Figs 295.4-295.6) .....*Troglophyes* group (pars)

3.4.8.1 ***Euryspeonomus*** group

Diagnosis. Bathyscioid or pholeuonoid body shape. Reddish-yellowish colouration , the integument entirely covered with a fine, short, recumbent, yellowish pubescence. Depigmented. Integument of the pronotum marked by irregular punctation and that of the elytra by irregular punctation or transverse striolae. Last article of maxillary palps short and conical.

Head: Small, without occipital carina. Epistomal suture clearly visible. Anophthalmous.

Antennae: Eleventh segments highly variable in length and shape; the club sometimes well differentiated.

Pronotum: Transverse, with arched or bell-shaped lateral margins.

Elytra: Short and broad or elongated and narrow, without parasutural stria.

Mesoventral keel: Mesocoxal cavities separated by a keel, situated on the median line of the mesoventrite, forming a triangular lamina.

Metaventrite: Forming a protruding bifid process or apophysis that separates the posterior coxae.

Legs: Protarsi pentamerous in males and tetramerous in females; dilated in males, with highly variable dilation.

Male genital segment: Very small, open and with two long pedunculus.

Mesoventral keel (Figs 271.1-271.13): High or low and without extension on the metaventrite.

Suture of the metaventrite (Figs 271.1-271.13): Arched in its anterior part which delimits a small area between the suture and the edge of the cavity, then very close. Similar in all species of the clade, except for small differences.

Metatergal apparatus (Figs 272.1-272.13): With the apophysis of the alacrista absent, much reduced or prolonged, the metascutum of varying surface depending on the genus.

Metendosternite (Figs 273.1-273.5, 274.1-274.8): Small with furcal arms shorter than trunk or large, with furcal arms longer than furcal trunk; in either case furcal arms may be robust or slender and usually has a thick terminal apophysis.



FIGURES 275.1–275.17: *Speonomus* series, *Euryspeonomus* group. Aedeagus in lateral view of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *E.* (*U.*) *ciaurrizi,* (**7**) *Dupreia beruetei* **comb. nov.**, (**8**) *Josettekia angelinae,* (**9**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**10**) *Casalella meridionalis* **comb. nov.**, (**11**) *Zariquieyella schiodtei* **comb. nov.**, (**12**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* **comb. nov.**, (**13**) *P.* (*P.*) *arcuatipes* **comb. nov.**, (**14**) *P.* (*P.*) *rectipes* **comb. nov.**, (**15**) *P.* (*P.*) *simplex* **comb. nov.**, (**16**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**17**) *Vallespirana grenieri* **comb. nov.** Figs **1**–**8** modified from Salgado *et al*. (2008); Figs **16**, **17** from Fresneda & Salgado (2006).

Median lobe of aedeagus: No characteristic pattern of the clade has been found. It will be detailed for each genus.

Endophallus (Figs 276.1-276.8, 276.10, 277.1): With three differentiated regions, the apical with two reinforcing bands, the medial with several strongly sclerotized phanerae and the basal with a «Y»-piece and a flagellum. This structure is characteristic of each genus.

Parameres (Figs 277.12-277.20, 277.22-277.25): They have four setae or spines which may be of different length, thickness and point of insertion; there are two exceptions in the number of setae (> 4 setae) in the apical area (Figs 277.11, 277.21).

Spermathecal complex (Figs 278.1-278.17): Spermatheca of «type 1» *sensu* Perreau (1989), with two sclerotized lobes connected by a hyaline tube. It also has a long spermatic duct which may be thickened at its insertion into the basal lobe, with a sclerotized basal process at its insertion with the copulatory bursa. Spermathecal gland present.

Female uroventrite VIII (Figs 279.1-279.16): Spiculum either formed by a small projection, or long and slender, or moderately broad.

Discussion. In the phylogenetic tree (Fig. 1C), the *Euryspeomomus* group as a whole has a degree of union of 100/100 and represents the sister clade, with support of 100/100, of the Catalan-Pyrenean clade – *Parvospeonomus* gr., *Bathysciella* gr., *Troglophyes* gr., *Antrocharis* gr. and *Speonomus* gr. – where the endogean elements at the origin of all the hypogean radiation of the Pyrenean mountains are found. It presents an apomorphy: the parameres have four setae or spines which can be of different lengths, insertions and thicknesses. However, there are two species in two of the subclades that have numerous setae: *Aranzadiella leizaolai*, with about thirty long setae, and *Casalella finismillennii* comb. nov. with nine setae. Given the topology of the phylogenetic tree, this increase in the number of setae must be considered a derived character, as the phenomenon occurred twice independently. Four setae are also found in *Speocharinus llosesi* or *Quaestus incognitus*, which belong to the *Quaestus* series.

Possible states related to the insertion of the setae:

– The setae have distant insertions that can be distributed along the apical fourth of the paramere: hypogean elements with a strictly Basque distribution in the genera *Aranzadiella*, *Dupreia* gen. nov., *Euryspeonomus* and *Speocharidius*. In *Josettekia* and *Nafarroa*, the insertions are further towards the apex, although they are spaced apart.

– The setae are contiguous and inserted at the apical end of the paramere: endogean elements with a Basque-Pyrenean distribution of the genera *Casalella* gen. nov., *Zariquieyella*, *Pyrenaeola* gen. nov. (+ *Garunnia* subgen. nov.) and *Vallespirana* gen. nov.

The geographical range of the Leptodirini of the Basque-Pyrenean clade extends westwards to the reliefs on both banks of the River Deba in Guipúzcoa, where they overlap with the distribution of the Leptodirini of the Cantabrian clade (Salgado *et al*. 2008; Ortuño *et al*. 2011). To the east, they extend as far as the Costabona massif, the first major peak over 2,000 m high located on the edge of the Pyrenean massif, not far from the Mediterranean sea. This does not rule out considering the Basque reliefs as a centre of diversification with a certain entity of their own, since there is a certain particular faunal homogeneity: the Basque Leptodirini originate in endogean elements of the central Pyrenees (Cieslak *et al*. 2014a: Fig. 2), after dispersing westwards where, at the western end of its range, they entered the subterranean environment at the level of the Basque reliefs , evolving towards distinctly troglobiomorphic hypogean forms. In any case, the group is phylogenetically closely related to the Pyrenean Leptodirini, constituting the basal cladogenesis of these species: it is its sister clade.

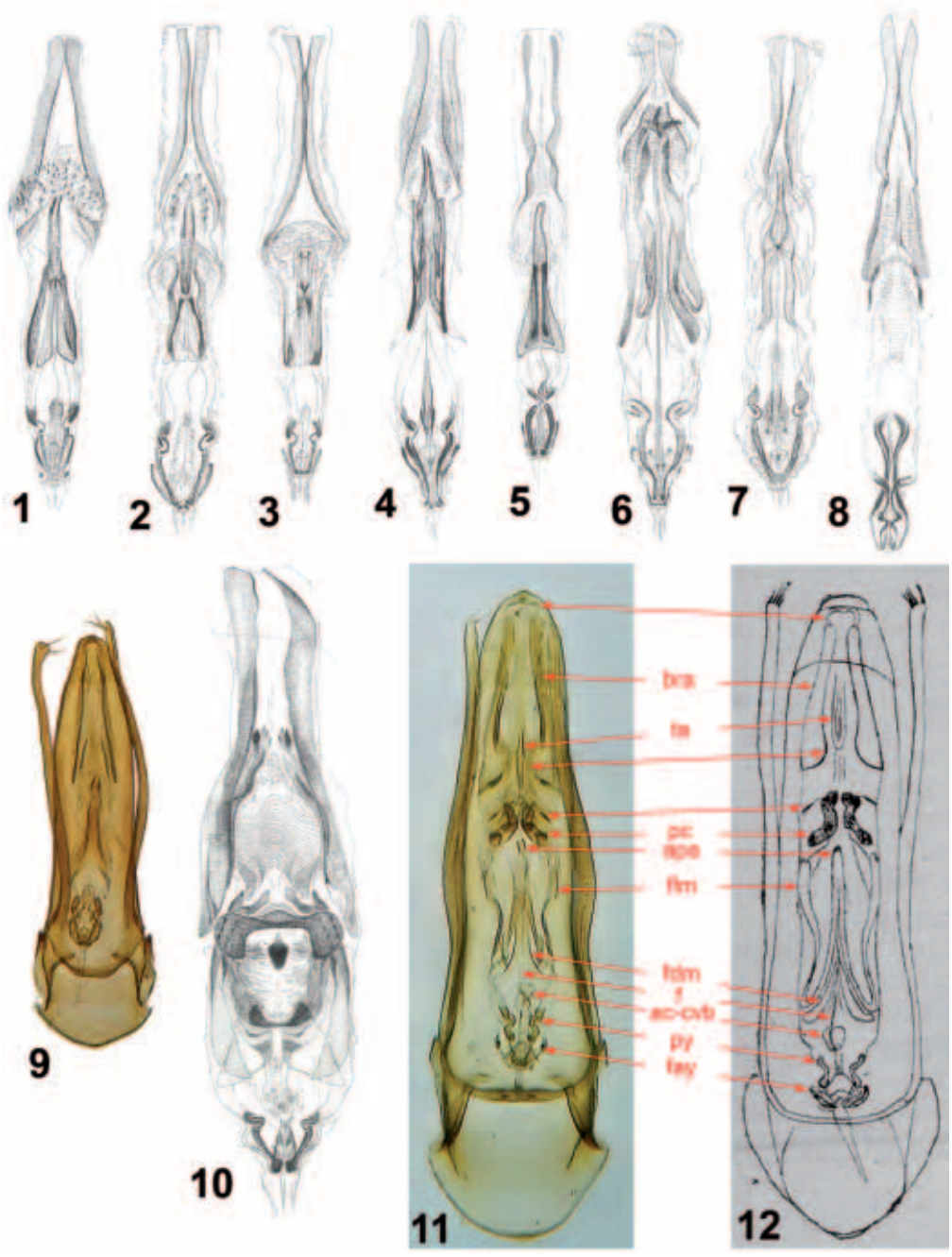
The *Trechus* Clairville, 1806 – Coleoptera, Carabidae, Trechinae – of the «*brucki*» group have exactly the same range, although their origin must be in the Basque reliefs (Faille *et al*. 2012) and the dispersion has occurred in the opposite direction, to the east; in the Basque reliefs, they coincide with the Leptodirini in that they have evolved into hypogean troglobiomorphic forms whereas in the Pyrenees they are forest or orophilic forms unmodified for the subterranean environment.

There are two possible states of elytral sculpture:

– Sculpture consisting of irregular punctation: genera *Aranzadiella*, *Speocharidius* and *Nafarroa*.

– Sculpture made up of transverse striolae: *Dupreia* gen. nov., *Euryspeonomus*, *Casalella* gen. nov., *Josettekia*, *Zariquieyella*, *Vallespirana* gen. nov. and *Pyrenaeola* gen. nov. (with transverse striolae formed by thick, granular, spaced dots, and microreticulation).

All Basque-Pyrenean Leptodirini have transversely arranged striolae except *Aranzadiella*, *Speocharidius* and *Nafarroa*. In the genus *Casalella* gen. nov. all species have vaguely transversely aligned rough dots on the basal half and irregular punctation on the apical half. Similarly, in the genus *Pyrenaeola* gen. nov. there are five taxa with vaguely transversely



FIGURES 276.1–276.12: *Speonomus* series, *Euryspeonomus* group. Endophallus of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *E.* (*U.*) *ciaurrizi,* (**7**) *Dupreia beruetei* **comb. nov.**, (**8**) *Josettekia mendizabali,* (**10**) *Casalella meridionalis* **comb. nov**. Aedeagus in dorsal view of: (**9**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**11**) *Bathyscia schiodtei* Kiesenwetter, 1850 (*Zariquieyella schiodtei* **comb. nov.**) from France, Arthez d'Asson, Grotte de Nabails, (**12**) holotype of *Hoffmannia biokovensis* Knirsch, 1928 (modified from Knirsch 1928: Fig. Penis). Figs **1**–**8** modified from Salgado *et al*. (2008); Fig. **10** from Fresneda & Salgado (2006). Abbreviations: **ac-cvb**, apical crown of the ventral- basal complex; **apa**, armature of the axial piece; **bra**, apical reinforcing bands; **fay**, phanerae attached to the «Y»- piece; **fdm**, dorsal phanerae of the median region; **flm**, lateral phanerae of the median region; **fy**, flagellum of the «Y»-piece; **pc**, phanerae complex; **py**, «Y»-piece; **ta**: apical tube.

ordered deep dots and two with rows of transverse striolae – it is not clear in which of these groups *Pyrenaeola secqi* comb. nov. should be included – *Speocharidius* and *Aranzadiella* are sisters with 100/100 support and *Nafarroa*, with irregular punctation, is in the sister clade with *Euryspeonomus*, *Dupreia* gen. nov., and *Josettekia*, all three genera with transverse striolae. The cladogenesis node for the sister clades of *Speocharidius*, *Aranzadiella* and *Euryspeonomus, Nafarroa, Josettekia* and *Dupreia* gen. nov. is well supported (96.3/99) and all these clades join the *Zariquieyella* clade with a support of 91.2/75.

Within the clade of the *Anthroherpon* series, the genera *Anthroherpon*, *Graciliella*, *Hadesia*, *Nauticiella* and *Leptomeson* show irregular punctation, while at the base of the clade, *Speonesiotes* shows transversely arranged striolae. Either state is distributed in the phylogenetic tree of the Leptodirini. *Platycholeus*, sister of the Leptodirini clade, has irregular punctation but longitudinal striae. In the sister clade of Leptodirini + *Platycholeus*, both states co-occur: Cholevini and Catopini with irregular punctation and longitudinal striae, with the exception of *Fusi*, which has transverse striolae, and Anemadini, Sciaphyini and Ptomaphagini also with transverse striolae. Transverse striolae are found in Leiodinae, *Leiodes tudiensis* Sáez, Blanco & Fresneda, 2012 or *Colenis bonnairii* Jacquelin du Val, 1859. It is not clear which of these two states is the ancestral one. Since the appearance of the second state, whichever it is, the two character states have coexisted throughout the radiation of the Leptodirini (throughout the phylogenetic tree).

Key to genera

1. Parameres with four setae arranged along the apical are, the insertion pores between the apical and the most basal being far apart (Figs 277.11-277.19); if the setal pores are relatively close or if there are more than 25 setae or if the parameres clearly extend beyond the apex of the median lobe of the aedeagus.....2
- Parameres with four setae inserted at the apex with the insertion pores close together (Figs 277.20-277.25); only one species has nine setae and in this case the parameres do not reach the apex of the median lobe of the aedeagus 9

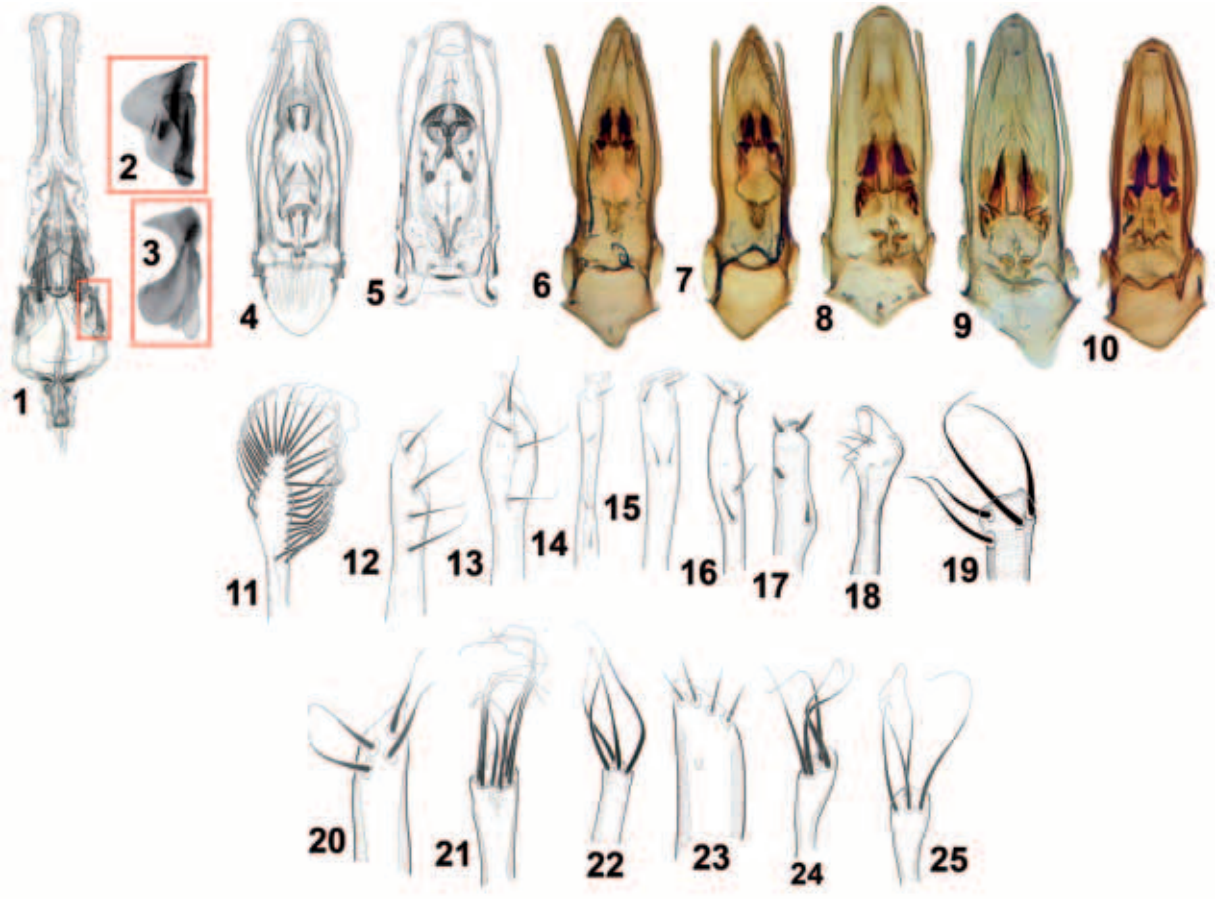
2. Elytra with transverse striolae 3
- Elytra without transverse striolae.....6

3. Apical area of parameres with four setae, three of them close to the apex with pores close by and the fourth further away (Fig. 277.18). Endophallus without dorsal phanera in median region, ventral phanerae forming an inverted horseshoe; reinforcing bands in apical region resting on strongly sclerotized rough trapezoidal pieces with pilosity below (Fig. 276.8). Basal process of spermatic complex long and with dentitions (Fig. 278.8) .....*Josettekia*
- Apical area of parameres with insertion pores of the four distal setae, either singly or in pairs (Figs 277.14-277.17). Endophallus with dorsal phanerae in median region, the ventral phanerae not forming an inverted horseshoe; reinforcing bands in apical region resting on unsclerotized membranous ligules, without pilosity below (Figs 276.4-276.7). Basal process of spermatic complex in a ring and without dentition (Figs 278.4-278.7) 4

4. Mesoventral keel high, the apex with a small denticle (Fig. 271.6). Metatergal apparatus with a broad metascutum (Fig. 272.6). Parameres with a small sclerotized hook at apex and four stout, spiny setae, two apical with insertion pores close together and the other two on inner margin with insertion pores far apart (Fig. 277.17) .....*Dupreia* gen. nov.
- Mesoventral keel low or high, if high the apex is rounded (Figs 271.4, 271.5). Metatergal apparatus with a very narrow metascutum (Figs 272.4, 272.5). Parameres with a small membranous area at the apex and the four fine setae inserted one by one with distant pores or two by two, both pairs with distant pores (Figs 277.14-277.16).....5

5. Size greater than 4.5 mm. Antennae without differentiated club. Mesoventral keel high, the apex rounded (Fig. 271.4). Furcal arms of metendosternite as long as furcal trunk (Fig. 273.4). Setae of the apical part of the parameres arranged one by one with the insertion pores distant from each other (Fig. 277.14). Endophallus with long, thick reinforcing bands (Fig. 276.4).....*Euryspeonomus* (*Euryspeonomus*)
- Size less than 3.5 mm. Antennae with differentiated club. Mesoventral keel low, with a small tooth at the apex (Fig. 271.5). Furcal arms of metendosternite slightly longer than furcal trunk (Fig. 273.5). Setae in apical area of parameres arranged in pairs and pores of two pairs far apart (Figs 277.15, 277.16). Endophallus with short or long, thin reinforcing bands (Figs 276.5, 276.6) .....*Euryspeonomus* (*Urbasolus*)

6. Body oval, broad (Fig. 270.1). Pronotum with regularly arched sides. Metendosternite with apical area very narrow, arched, the terminal apophysis very re-



FIGURES 277.1–277.25: *Speonomus* series, *Euryspeonomus* group. Endophallus of: (**1-2**) *Pyrenaeola* (*Pyrenaeola*) *arcuatipes* **comb. nov.** and magnification of the floating piece, (**3**) magnification of the floating piece of *P.* (*P.*) *rectipes* **comb. nov.** Aedeagus in dorsal view of: (**4**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**5**) *Vallespirana grenieri* **comb. nov.**, (**6**) *Adelops lapidicola* (lectotype), (**7**) *P.* (*P.*) *lapidicola* **comb. nov.** from Grotte de Terreblanque, (**8**) *P.* (*P.*) *arcuatipes* **comb. nov.** from Grotte d'Aubert, (**9**) *P.* (*P.*) *simplex* **comb. nov.** from Gouffre de Djerbao, (**10**) *P.* (*P.*) *rectipes* **comb. nov.** from Grotte de Gouillou. Apex of the paramere of: (**11**) *Aranzadiella leizaolai,* (**12**) *Speocharidius* (*Kobiella*) *galani,* (**13**) *S.* (*Speocharidius*) *breuili,* (**14**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**15**) *E.* (*Urbasolus*) *eloseguii,* (**16**) *E.* (*U.*) *ciaurrizi,* (**17**) *Dupreia beruetei* **comb. nov.**, (**18**) *Josettekia angelinae,* (**19**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**20**) *Casalella meridionalis* **comb. nov.**, (**21**) *C. finismillennii* **comb. nov.**, (**22**) *Zariquieyella mystica* **comb. nov.**, (**23**) *P.* (*P.*) *arcuatipes* **comb. nov.**, (**24**) *P.* (*Garunnia*) *convena* **comb. nov.**, (**25**) *Vallespirana grenieri* **comb. nov.** Figs **1**, **4**, **5**, **20**–**25** modified from Fresneda & Salgado (2006); Figs **11**–**18** from Salgado *et al*. (2008).

duced; furcal trunk almost as wide as long (Fig. 274.3). Endophallus without sac covered with spines or spinules between bases of reinforcing bands (Fig. 276.9). Apical area of parameres with four setae and close insertion pores (Fig. 277.19). Basal process of spermatic duct in the form of a dilated and sclerotized tube (Fig. 278.9) .....*Nafarroa*

- Body elliptical, elongate (Figs 269.1-269.3). Pronotum bell-shaped. Metendosternite with dilated apical area and well-developed terminal apophysis; furcal trunk distinctly longer than wide (Figs 273.1-273.3). Endophallus with a sac covered with spines or spinules between the bases of the reinforcing bands (Figs 276.1-276.3). Apical area of parameres with four setae and distant insertion pores or with about 30 setae (Figs 277.11-277.13). Basal process of the spermatic duct funnel-shaped and sclerotized (Figs 278.1-278.3) ...7

7. Parameres much longer than the median lobe, with the apical area enlarged into a spoon shape and the

margins with about 30 long, thick setae (Fig. 277.11). Median region of endophallus with phanerae that do not meet to form a «W»-shaped structure (Fig. 276.1) .....*Aranzadiella*
- Parameres as long as median lobe, with apical area not enlarged and four setae much shorter and finer (Figs 277.12, 277.13). Median region of endophallus with phanerae forming a «W»-shaped structure (Figs 276.2, 276.3) 8

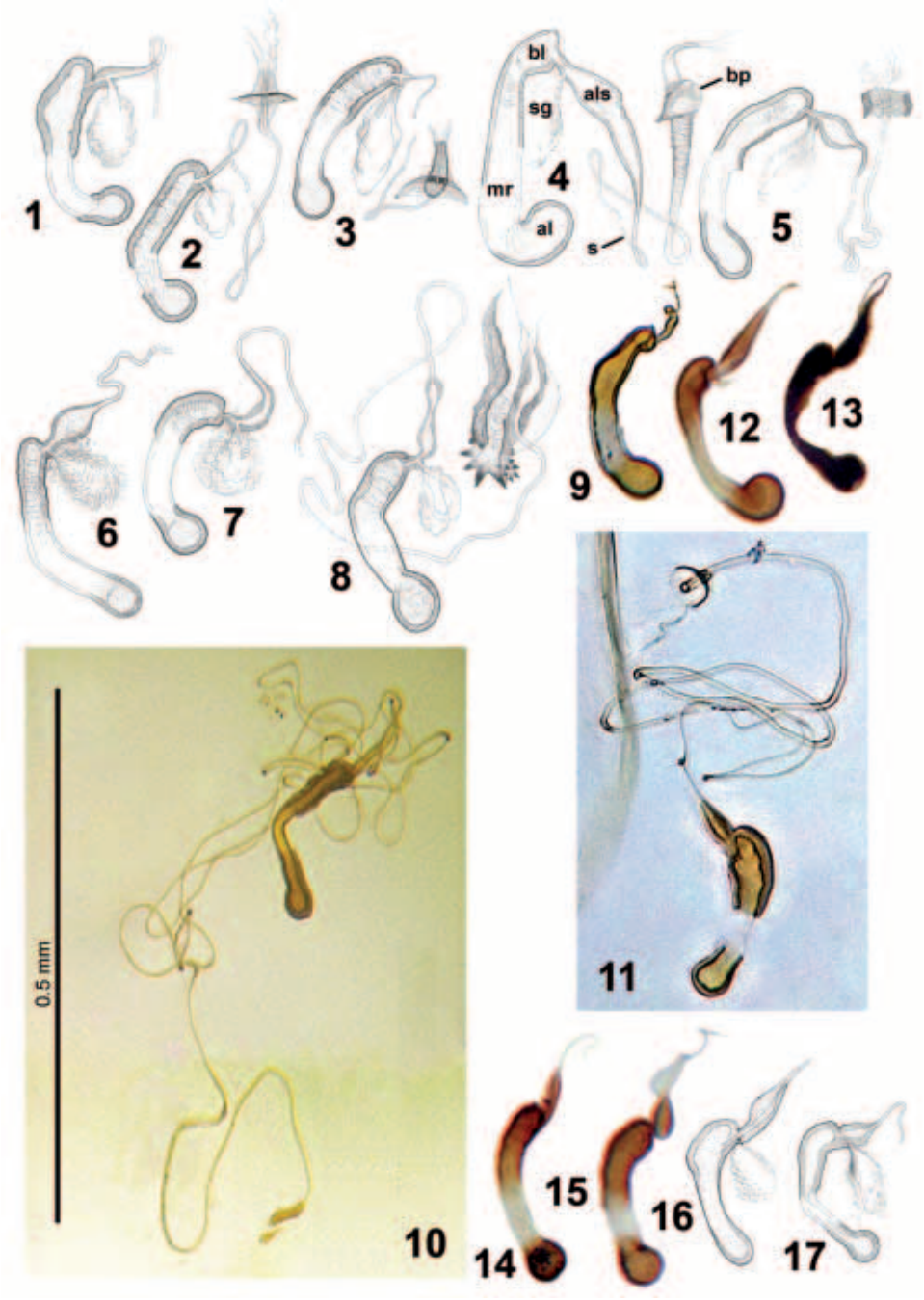
8. Size greater than 3 mm. Mesoventral keel without hooked tooth at apex; male metaventrite with strong prominence (Fig. 271.3). Metendosternite with furcal arms as long as trunk, the posterior lamina clearly visible towards apical area, the terminal apophysis large (Fig. 273.3). Aedeagus in lateral view, slender and elongate, with a smooth and regular dorsal curve from base to apex (Fig. 275.3). Apex of parameres with a small, pointed membranous lamina (Fig. 277.13)..... .....*Speocharidius* (*Speocharidius*)
- Size not exceeding 3 mm. Mesoventral keel with a hooked tooth at the apex; male metaventrite without prominence (Fig. 271.2). Metendosternite with furcal arms longer than trunk, posterior lamina much reduced towards apical area and terminal apophysis small (Fig. 273.2). Aedeagus in lateral view, short and gibbous, very curved in median region and strongly depressed in apical region (Fig. 275.2). Apex of parameres without membranous lamina (Fig. 277.12) .....*Speocharidius* (*Kobiella*)

9. Endophallus with phanerae attached to the «Y»-piece; upper median region with three nodules on each side, well sclerotized and articulated to each other, which become the «phaneroid complex»; reinforcing bands in the apical region with a broad, heavily sclerotized basal end (Figs 276.11, 276.12) ....*Zariquieyella*
- Endophallus without phanerae attached to the «Y»-piece; upper median region without «phaneroid complex», the reinforcing bands of the apical region with the basal end of another shape, usually with membranous sacs or ligules (Figs 276.10, 277.1, 277.4, 277.5) 10

10. Elytral sculpture formed by a microreticulum in the form of scales imbricated between the transverse striolae over the entire elytra. Suture of the metaventrite delimiting a fairly well-developed part (Figs 271.11, 271.12). Median region of endophallus with two complexes of triangular or small sclerotized phanerae and in the centre there is no floating nodule, although sometimes in the lower part of the median region there is a transverse lamina; reinforcing bands of the apical region rest on ligules of unstriate tegument, which may or may not have spines (Figs 277.1, 277.4) 11
- Elytral sculpture without microreticulum of overlapping scales and with or without transverse striation. Suture of the metaventrite delimiting a small area (Fig. 271.13). Median region of endophallus with a series of robust sclerotized phanerae with a floating, well-sclerotized nodule of variable shape in the centre; reinforcing bands of the apical region (bra) rest on ligules with striated integument, sometimes surmounted by spines (Figs 276.10, 277.5) 12

11. Transverse striolae on elytra very well marked, formed by thick, granular, spaced dots. Metendosternite with posterior lamina of furca broad, the terminal apophysis well developed (Fig. 274.6). Median region of endophallus with two complex, large, heavily sclerotized, triangular and elongated phanerae on either sides of axis of symmetry; reinforcing bands in apical region resting on membranous ligules without spinous integument (Fig. 277.1) .....*Pyrenaeola* gen. nov.
- Transverse striolae on elytra fine, denser and formed of small dots close together. Metendosternite with the posterior lamina of the furca narrow and the terminal apophysis reduced (Fig. 274.7). Median region of endophallus with two small phanerae, hairy or joined to form a bridge; reinforcing bands of the apical region rest on membranous ligules with the surface of the integument spiny (Fig. 277.4) ....*Pyrenaeola* (*Garunnia* subgen. nov.)

12. Males with a tuft of thick, long setae in a more or less visible prominence in the frontal area. Elytra without transverse striolae, although rough spots loosely aligned transversely in the basal half and disordered in the apical area are seen in the basal half. Mesoventral keel low and regularly curved (Fig. 271.9). Median lobe of aedeagus, in lateral view, with sharp, curved apical area (Fig. 275.10). Centre of median region of endophallus with elongated or rounded nodule (Fig. 276.10) .....*Casalella* gen. nov.
- Males without a tuft of thick, long setae in the frontal region. Thin, regular transverse striolae throughout the elytra. High mesoventral keel with a small denticle at the apex (Fig. 271.13). Median lobe of aedeagus, in lateral view, with the apical part forming a thick, curved beak (Fig. 275.17). Centre of median region of endophallus with very robust «T»-shaped nodule (Fig. 277.5).....*Vallespirana* gen. nov.



FIGURES 278.1–278.17: *Speonomus* series, *Euryspeonomus* group. Spermathecal complex of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *E.* (*U.*) *ciaurrizi,* (**7**) *Dupreia beruetei* **comb. nov.**, (**8**) *Josettekia mendizabali,* (**9**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**10**) *Casalella liqueana* **comb. nov.**, (**11**) *Zariquieyella schiodtei* **comb. nov.**, (**12**) *Pyrenaeola* (*Pyrenaeola*) *lapidicola* **comb. nov.**, (**13**) *P.* (*P.*) *rectipes* **comb. nov.**, (**14**) *P.* (*P.*) *simplex* **comb. nov.**, (**15**) *P.* (*P.*) *aranensis* **comb. nov.**, (**16**) *P.* (*Garunnia*) *convena* **comb. nov.**, (**17**) *Vallespirana grenieri* **comb. nov.** Figs **1**–**8** modified from Salgado *et al*. (2008); Figs **16**, **17** from Fresneda & Salgado (2006). Abbreviations: **al**, apical lobe; **als**, lobe of the apical spermiduct; **bl**, basal lobe; **bp**, basal piece; **mr**, medial region; **s**, spermaduct; **sg**, spermathecal gland.

Hypogean clade of *Aranzadiella-Speocharidius*

This clade is characterised by irregular punctation throughout the body, by the presence of a membranous sac covered with thick spines or scales, located between the bases of the reinforcing bands towards the apical area of the endophallus and by the absence of a nodule in the area of insertion of the spermatic duct into the spermatheca. Within the *Euryspeonomus* clade, the sister genera *Aranzadiella* and *Speocharidius* (with a support of 100/100) appear to be sisters of the clade formed by the genera *Dupreia* gen. nov., *Euryspeonomus*, *Josettekia* and *Nafarroa* with a support of 96.3/99 (Fig. 1C).

Genus ***Aranzadiella*** Español, 1972
Aranzadiella Español, 1972b: 60.

Type species. *Aranzadiella leizaolai* Español, 1972 by original designation (habitus in Fig. 269.1).

Diagnosis. Monospecific genus about 3.0 mm long, with an elliptical, elongated body (Fig. 269.1) and a sculpture formed by irregular punctation all over the body.

Antennae: Filiform with no obvious club and remarkably elongated, all segments longer than wide.

Pronotum: Bell-shaped, with maximum width at the base; posterior angles acute with sharp, divergent vertices.

Elytra: Elongated and cuneiform, its maximum width located in the first third of its length.

Legs: Long, slender, the male protarsi thickened, the first tarsomere wider than the apex of the tibia.

Mesoventral keel (Fig. 271.1): High, somewhat hooked and slightly convex, with ridged anterior margin; posterior margin weakly denticulate and with setae.

Suture of the metaventrite (Fig. 271.1): Following the model described for the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.1): With a much reduced metascutum, the tips of the apophysis of the alacrista blunt.

Metendosternite (Fig. 273.1): Furcal arms longer than the furcal trunk; posterior lamina tapering slightly towards the apical area, the posterior margin is straight along the arm, then slightly arched, with a well-defined terminal apophysis. Furcal trunk longer than the area of greatest basal width, the median keel with reduced posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 275.1), strongly folded in middle; in preapical region, somewhat humped and thickened.

Endophallus (Fig. 276.1): Phanerae attached to «Y»-piece, including dorsal and ventral phanerae, a sac covered with thick spines situated between reinforcing bands; these are implanted on membranous ligules.

Parameres (Fig. 277.11): Much longer than the median lobe and enlarged in the shape of a spoon at its apical end; margins of this part with about thirty thick and long setae.

Spermathecal complex: Spermatheca (Fig. 278.1) gently curved, with a spherical, sclerotized apical lobe; median region narrowed and hyaline, the basal lobe long, thick and sclerotized; spermatic duct about 12 times as long as spermatheca, inserted ventrally, thick but not forming a nodule; basal process sparsely sclerotized inserted into copulatory bursa and funnel-shaped; presence of a spermathecal gland.

Female uroventrite VIII (Fig. 279.1): Spiculum reduced to a small denticle.

Discussion. Español (1972b) related this taxon to *Bathysciella*. While it is true that the appearance of *Aranzadiella* is reminiscent of *Bathysciella*, the characteristics of the aedeagus do not allow a relationship to be established between these two taxa. *Bathysciella* has three differentiated setae, a cavity and a penicillum at the apex of the parameres, a character it shares with the other genera of its clade – *Bellesia*, *Speonomus* of the *speluncarum* (Jeannel 1947) and *ehlersi* (Perreau 2000) groups, *Machaeroscelis* stat. nov., *Phacomorphus*, including the subgenus *Phacomorphoides* syn. nov. and *Bathysciella* – and with the Eastern Pyrenees clade – *Ceretophyes*, *Parvospeonomus*, *Perriniella* and *Troglophyes* –. The genus *Aranzadiella* is sister of *Speocharidius* with a support of 100/100 (Fig. 1C) and is its geographical neighbour; it shares with it the existence of a membranous sac covered with thick spines which is situated at the upper end of the median region of the endophallus, between the base of the apical reinforcement bands. It is the only representative of the hypogean clade of Basque Leptodirini to have numerous setae at the apex of the parameres, which distinguishes it from the other genus in its clade, *Speocharidius*, which has four setae.

Distribution. Iberian endemism only known from two localities on both banks of the Deba river: the Cueva del Viento de Mendaro on the east bank of the river and the Kobeta pit, in Olatz, on the west bank (Fresneda & Salgado 2017).

Species

Aranzadiella leizaolai Español, 1972
Aranzadiella leizaolai Español, 1972b: 61.

Genus ***Speocharidius*** Jeannel, 1919
Speocharidius Jeannel, 1919: 130.

Type species. *Speocharidius breuili* Jeannel, 1919 by original designation (habitus in Fig. 269.3).

Diagnosis. Size between 2.6-4.8 mm. Body elliptical (Fig. 269.3), very long and narrow in the posterior region; very fine sculpture formed of non-aligned dots, without transverse striolae.

Antennae: Long and filiform, reaching at least two-thirds of the length of the body.

Pronotum: Transverse, slightly narrower than the maximum width of the elytra, with acute, divergent vertices.

Elytra: Long, about two and a half times as long as wide, and somewhat dehiscent at the apex; no parasutural stria.

Legs: Long, middle and hind tibiae with a few small spines on the outer surface; male protarsi as wide as or slightly wider than the apical area of the tibia.

Median lobe of aedeagus (Figs 275.2, 275.3): Viewed from the side, elongated or short and the dorsal surface variable, depending on the subgenus.

Endophallus (Figs 276.2, 276.3): In the basal region, a «Y»-piece and phanerae attached to it; in the medial region, a «W»-shaped structure formed of phanerae can be distinguished, and in the apical region, in the middle of the base of the two reinforcing bands, a sac-like structure covered with spines of varying thickness.

Parameres (Figs 277.12, 277.13): Slender and as long as the median lobe, without a distinct club, with four medium-length setae, and a small membranous lamina visible or not at the apex.

Spermathecal complex (Figs 278.2, 278.3): Formed by an elongate spermatheca with well-sclerotized apical and basal lobes, and a hyaline median region; spermatic duct very long and thin at its junction with the spermatheca; a nodule is not differentiated and is attached to the *bursa copulatrix* by a sclerotized funnel-shaped basal process; spermathecal gland present.

Subgenus ***Kobiella*** Español & Bellés, 1980
Kobiella Español & Bellés, 1980a: 33.

Type species. *Speocharidius galani* Español, 1970 by original designation (habitus in Fig. 269.2).

Diagnosis. Size between 2.6-3.0 mm. Body elliptical, broad and moderately elongated (Fig. 269.2).

Antennae: Very long and filiform, exceeding two thirds of the length of the body.

Pronotum: Transverse bell-shaped, broader at the base, sides slightly rounded anteriorly and somewhat sinuous towards the basal two-thirds; posterior angles acute with acute and somewhat divergent vertices.

Elytra: Maximum width in the anterior third, gradually narrowing towards the rear and rounded apically.

Legs: Thin and moderately elongated, male protarsi dilated, with the first protarsomere as wide as the maximum width of the tibia.

Mesoventral keel (Fig. 271.2): High and short, with slightly broken anterior margin and more or less hooked toothed apex.

Suture of metaventrite (Fig. 271.2): In agreement with the description of the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.2): Metascutum reduced and without apophysis of the alacrista, with blunt apices.

Metendosternite (Fig. 273.2): Furcal arms very narrow, longer than furcal trunk; posterior lamina almost disappearing in apical area and entire margin very slightly arched a terminal apophysis although apex very slightly dilated. Trunk longer than area of greatest basal width and median keel with narrow posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 275.2), short and very curved, gibbous in middle dorsal region and abruptly depressed in apical part, which is very sharp.

Endophallus (Fig. 276.2): Dorsal and ventral phanerae in the median region; in the latter and in the lower end are inserted others which extend towards the upper end of the region and together draw a discrete «W»; at the upper end of the middle region there is a membranous sac in the integument of which are inserted thick spines; in the apical area the two reinforcement bands are visible.

Parameres (Fig. 277.12): Slender, as long as the median lobe and not forming a club, with the median part slightly curved towards the ventral face; four long equidistant setae are inserted on the inner face of the apical part and no membranous lamina, but a small pit. Tegmen displaced anteriorly, revealing the entire posterior part of the median lobe.

Spermathecal complex (Fig. 278.2): Spermatheca with a very elongated basal lobe with almost parallel sides, slightly narrower and about three times longer than the apical lobe, which is rounded; median region very short and hyaline; spermatic duct very long, widening slightly in the anterior region and then narrowing until joining the basal process of the copulatory bursa, which is a small sclerotized piece with an infundibuliform structure; spermathecal gland attached to the spermatheca at the junction of the spermatic duct.

Female uroventrite VIII (Fig. 279.2): With very short spiculum.

Discussion. *Kobiella* differs from the other genera of its clade in many respects. From the nominotypic subgenus *Speocharidius* because its size is generally less than 3.0 mm, due to its low sexual dimorphism, the males having a hooked tooth at the apex of the mesoventral keel and the metaventrite without prominence; the aedeagus, seen in profile, is short, gibbous, strongly curved in the median region and strongly depressed in the apical region (Fig. 275.2); the apex of the parameres has no membranous lamina (Fig. 277.12). In *Speocharidius,* on the other hand, its size is greater than 3.0 mm; sexual dimorphism is very evident in the male, the apex of the mesoventral keel lacks a hooked tooth and the metaventrite has a sharp, hooked keel (Fig. 271.3); the aedeagus, seen in profile, is slender and elongate, with a smooth, regular dorsal curve from base to apex (Fig. 275.3); the apex of the parameres bears a small, pointed membranous lamina (Fig. 277.13). It differs from *Aranzadiella* in that it is the only representative of the hypogean clade of Basque Leptodirini to have numerous setae at the apex of the parameres, and the parameres clearly extend beyond the apex of the median lobe and the apical part is enlarged.

Distribution. Iberian hypogean endemism. The only cave where it lives is in Usúrbil – Gipuzkoa –, on the left bank of the River Orio (Fresneda & Salgado 2017).

Species

Speocharidius* (*Kobiella*) *galani Español, 1970
Speocharidius galani Español, 1970: 59.
Kobiella galani Español: Español & Bellès, 1980a: 33.
Speocharidius (*Kobiella*) *galani* Español: Fresneda & Salgado, 2000: 49.

Subgenus ***Speocharidius***

Diagnosis. Size always greater than 3.0 mm. Pholeuonoid facies (Fig. 269.3). Sexual dimorphism very marked in the male due to the more slender shape of the body, the greater length of the antennae, the more campanulate pronotum, the metaventral keel and the dilated protarsi.

Mesoventral and metaventral keels (Fig. 271.3): Mesoventral keel tall and short, with a very obtuse angle, the apex forming a small tooth; anterior margin rounded and posterior margin concave in the anterior half and convex in the posterior half, not reaching the metaventrite. Anterior area of the metaventrite of males with a stout, hooked projection extending ventrally to the tip of these sternites, while not forming a spine in females, the apophysis not extending over the metaventrite.

Suture of the metaventrite (Fig. 271.3): In accordance with the description of the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.3): With long metascutum and reduced apophysis of the alacrista, with not very acute apices.

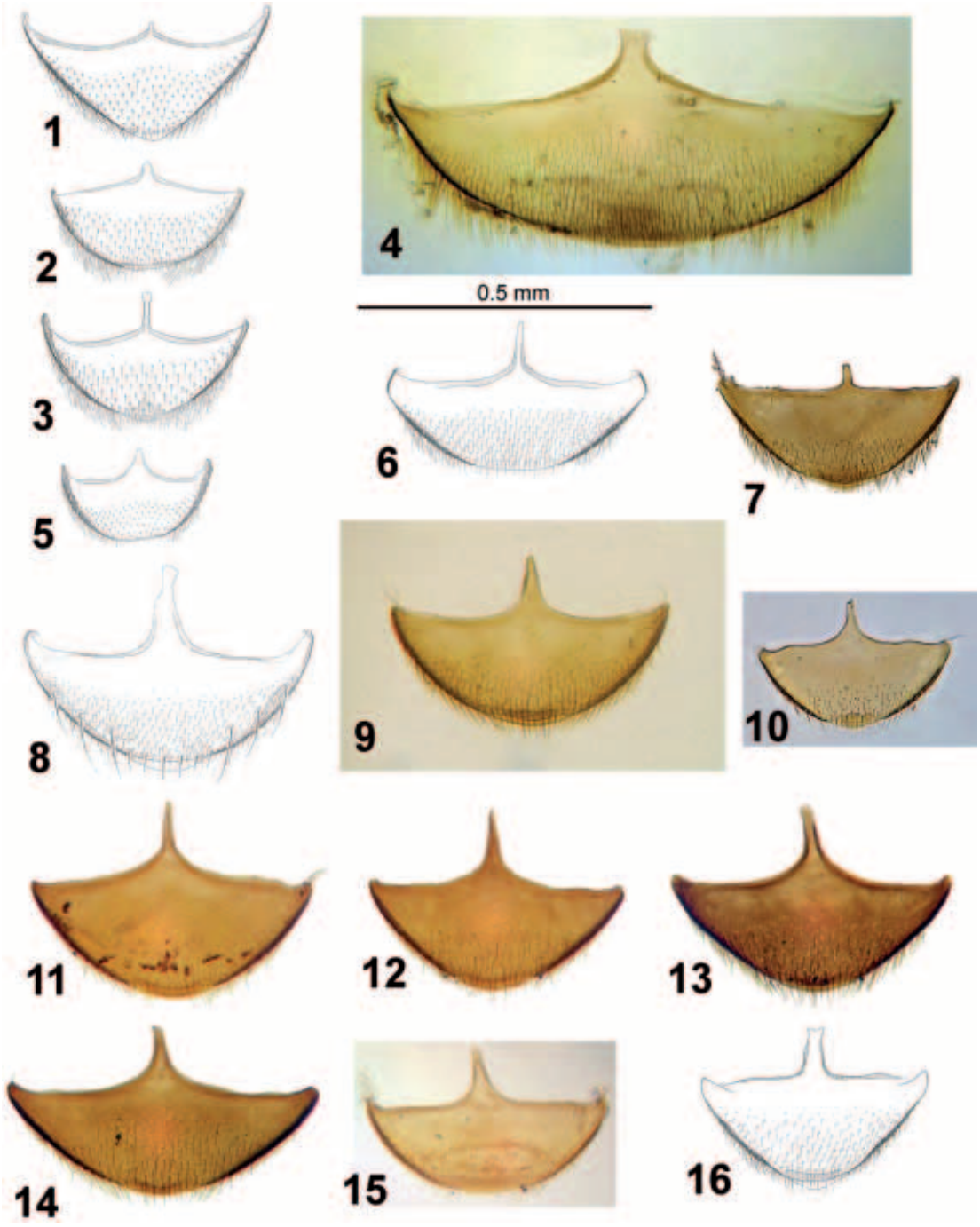
Metendosternite (Fig. 273.3): Furcal arms narrow, as long as furcal trunk; posterior lamina narrowing towards apical area, the margin very slightly arched, with large terminal apophysis. Trunk long, almost twice as long as the area of greatest basal width and the median keel, with obvious posterior divergence.

Median lobe of aedeagus (Fig. 275.3): Slender, elongate and slightly but evenly curved from base to apex, ending in a sharp point.

Endophallus (Fig. 276.3): In the median region, and in addition to the phanerae, ventral structures in the lower end of which are inserted other phanerae which extend towards the upper end of the median region, together forming a very evident «W»; at the upper end of the median region, presence of a membranous sac whose integument is warty, the surface spiny.

Parameres (Fig. 277.13): Attached to the sides of the median lobe, thin and as long as the lobe, with four short setae on the inner side of the apical area and a small membranous lamina at the apex.

Spermathecal complex (Fig. 278.3): Spermatheca with well-sclerotized apical and basal lobes and a hyaline median region; the spermathecal gland is attached in the area where the spermatic duct joins the spermatheca, this duct very long and thin, its union with the copulatory bursa made by a funnel-shaped sclerotized basal process.



FIGURES 279.1–279.16: *Speonomus* series, *Euryspeonomus* group. Female uroventrite VIII of: (**1**) *Aranzadiella leizaolai,* (**2**) *Speocharidius* (*Kobiella*) *galani,* (**3**) *S.* (*Speocharidius*) *breuili,* (**4**) *Euryspeonomus* (*Euryspeonomus*) *breuili,* (**5**) *E.* (*Urbasolus*) *eloseguii,* (**6**) *Dupreia beruetei* **comb. nov.**, (**7**) *Nafarroa sorogainensis* (modified from Fresneda & Dupré 2010), (**8**) *Josettekia mendizabali,* (**9**) *Casalella meridionalis* **comb. nov.**, (**10**) *Zariquieyella schiodtei* **comb. nov.**, (**11**) *Pyrenaeola* (*Pyrenaeola*) *simplex* **comb. nov.**, (**12**) *P.* (*P.*) *lapidicola* **comb. nov.**, (**13**) *P.* (*P.*) *rectipes* **comb. nov.**, (**14**) *P.* (*P.*) *aranensis* **comb. nov.**, (**15**) *P.* (*Garunnia*) *larcennei* **comb. nov.**, (**16**) *Vallespirana grenieri* **comb. nov.** Figs **1**–**3**, **5**, **6**, **8** modified from Salgado *et al*. (2008); Fig. **16** from Fresneda & Salgado (2006).

Female uroventrite VIII (Fig. 279.3): Spiculum very narrow and not very long.

Discussion. Distinctive characters have been provided in the Discussion section on *Kobiella*.

Distribution. Iberian hypogean endemism. It is known from several cavities embedded in the Cretaceous limestones belonging to the Ernio, Gazume, Pagoeta massifs and in the Cretaceous Itzarraitz massif, in its eastern block, near the left bank of the Urola river (Fresneda & Salgado 2017).

Species

Speocharidius (***Speocharidius***) ***bolivari*** Jeannel, 1919
Speocharidius Bolivari Jeannel, 1919: 133.

Speocharidius (***Speocharidius***) ***breuili*** Jeannel, 1919
Speocharidius Breuili Jeannel, 1919: 131.
Speocharidius filicornis Jeannel, 1919: 134.

Speocharidius (***Speocharidius***) ***vivesi*** Español & Bellés, 1980
Speocharidius vivesi Español & Bellés, 1980a: 33.

Hypogean clade of *Euryspeonomus*

This clade comprises one genus, two subgenera, three species, and one subspecies. Its morphology is so diverse that it is not easy to find morphological features that characterise it. The median region of the endophallus has two additional phanerae superimposed on the pair of ventral phanerae. The differentiated setae at the apex of the parameres are arranged one by one along the apical quarter or arranged in pairs and inserted in the terminal part, and not grouped at the apex. Within the clade of the *Euryspeonomus* group, the genus *Euryspeonomus* appears as a sister of the genera *Dupreia* gen. nov., *Josettekia* and *Nafarroa* with a support of 89/94 (Fig. 1C).

Genus ***Euryspeonomus*** Jeannel, 1919
Speonomus (*Euryspeonomus*) Jeannel, 1919: 134.
Euryspeonomus Jeannel: Bellés, Comas, Escolà & Español, 1978: 64.

Type species. *Speonomus breuili* Jeannel, 1919 by original designation (habitus in Fig. 269.4).

Diagnosis. Size between 2.3-5.1 mm. Bathyscioid morphology (Figs 269.4, 269.5), with sculpture on the pronotum formed by irregular punctation and on the elytra by transverse striolae of different development.

Pronotum: Transverse, with lateral margins regularly curved, the greatest width in the posterior third or at the base.

Elytra: Wide, without parasutural stria.

Legs: Long, males with dilated protarsi; metatibiae straight, mesotibiae arched in males, straight in females; both with a series of thick spines on the outer surface.

Mesoventral keel (Figs 271.4, 271.5): High or low with rounded vertex or tiny denticle.

Median lobe of aedeagus (Figs 275.4-275.6): In lateral view, regularly curved with pointed apex.

Endophallus (Figs 276.4-276.6): The apical reinforcing bands do not rest on sclerotized nodules; a few phanera attached to the «Y»-piece in the basal region; additional dorsal sclerotized pieces, the supradorsal phanera, with a very long apical crown, which almost touches the lower extension of the ventral phanera, are present in the medial region.

Parameres (Figs 277.14-277.16): Without club; apical area with four short, differently inserted setae and at the tip a small membranous lobe.

Spermathecal complex (Figs 278.4-278.6): Spermatheca long with slightly sclerotized lobes and a hyaline median region; spermatic duct as long as spermatheca which inserts basally through a more or less long well-differentiated nodule, and joins the copulatory bursa through a ring-shaped sclerotized basal process which surrounds the duct. Well differentiated spermathecal gland.

Female uroventrite VIII (Figs 279.4, 279.5): Shape depends on subgenus.

Subgenus ***Euryspeonomus***

Diagnosis. Size between 4.9-5.1 mm. Body oblong with a regularly oval outline, but with an obvious pronotum-elytral angle (Fig. 269.4).

Head: Integument with very fine punctation, little impression, dense and a little scratchy.

Antennae: Proportionally short, segments six and seven longer and slightly larger than the others; antennomeres 9th, 10th and 11th not thickened.

Pronotum: Widest in the posterior third, the posterior angles a little acute; the vertices a little prolonged on the elytra; integument densely covered with slightly granular and irregular dots. Scutellum wide.

Elytra: Maximum width situated in the middle of the length; lateral margins subparallel, of equal width until near the apex, where they narrow sharply; a

broad dorsally curved marginal ridge extends from the base to the immediate vicinity of the apex; integument entirely covered with transverse striae, although reduced in the apical region where they seem to be limited to a series of dots separated from each other.

Legs: Long and robust; protibiae straight with the first three protarsal segments dilated in the male, the first wider than the apex of the tibia and adopting a subquadrangular shape; mesotibiae arched in the male, metatibiae straight in both sexes; meso- and metatibiae with a series of thick spines on their outer edge.

Mesoventral keel (Fig. 271.4): High, with arched anterior margin and very rounded apex.

Suture of metaventrite (Fig. 271.4): Conforms to description of *Euryspeonomus* clade group.

Metatergal apparatus (fig. 272.4): Metascutum narrow and elongate, alacrista process reduced, apices acute.

Metendosternite (Fig. 273.4): Robust, with furcal arms as long as furcal trunk; posterior lamina broad and retaining same width along arm, margin very slightly arched; terminal apophysis sparsly developed. Trunk longer than area of greatest basal width, median keel with posterior divergence clearly evident.

Median lobe of aedeagus (Fig. 275.4): Regularly arched to the apex, which ends in a posteriorly curved point with a marked dorsal preapical thickening.

Endophallus (Fig. 276.4): Characterised by the development of the symmetrical branches of the divergent «Y»-piece and the apical extensions of the lateral pieces of the ventral complex; apex of the supernumerary phanerae of the median region strongly angular, the reinforcing bands of the apical region proportionally short and thick.

Parameres (Fig. 277.14): Exceeding apex of median lobe; they are robust to the tip where a membranous lamina is present; four fine, short setae arranged along the terminal part, the last inserted at the apex.

Spermathecal complex (Fig. 278.4): Spermatheca long and slightly curved; apical lobe spherical, possibly forming an obtuse angle with the median region; median region hyaline and distinctly inferior in section to that of the lobes; basal lobe very thick, forming a right angle with the median region; both lobes sparsely sclerotized. Spermatic duct, inserted by a thick, long nodule at the base, then thickening and sclerotizing near its insertion with the copulatory bursa, where there is a ring-shaped basal process.

Female uroventrite VIII (Fig. 279.4): Spiculum very short, triangular, with truncate apex.

Discussion. The endophallus has thick reinforcing bands (Fig. 276.4); the setae of the apex of the parameres are arranged one by one along the apical quarter (Fig. 277.14); the mesoventral keel is high and rounded (Fig. 271.4). In contrast, *Urbasolus* is significantly smaller, the antennae have a differentiated club, the mesoventral keel is low and the spiny apex is directed posteriorly, the spines of the meso- and metatibiae are thinner, the reinforcing bands of the apical region of the endophallus are very thin, and the apex of the parameres has four setae arranged in pairs. In the *Euryspeonomus* clade (Fig. 1C), the two subgenera are united with a support of 100/100.

Distribution. Iberian hypogean endemism. The only species of the subgenus has been collected from numerous localities throughout the Sierra de Aralar, Navarra and Gipuzkoa (Fresneda & Salgado 2017).

Species

Euryspeonomus (***Euryspeonomus***) ***breuili*** (Jeannel, 1919)
Speonomus (*Euryspeonomus*) *Breuili* Jeannel, 1919: 135.
Speonomus (*Euryspeonomus*) *breuili kilixketai* Español, 1945: 269.
Speonomus (*Euryspeonomus*) *breuili* Jeannel: Bolívar, 1921: 527.
Euryspeonomus (*Euryspeonomus*) *breuili* (Jeannel): Bellés, Comas, Escolà & Español, 1978: 64.

Subgenus ***Urbasolus*** Español, 1948
Urbasolus Español, 1948: 238.

Type species. *Speonomus* (*Urbasolus*) *eloseguii* Español, 1948 by original designation (habitus in Fig. 269.5).

Diagnosis. Size between 2.3 and 3.1 mm. Body oval and convex or elliptical, narrow and elongated, without pronotum-elytral angle (Fig. 269.5).

Head: Integument marked by fine, dense and rough punctation.

Antennae: Reaching or exceeding half the length of the body and thickened from the 7th segment.

Pronotum: Widest at base; posterior angles acute, with blunt vertices; integument marked by fine, rough and irregular punctation.

Elytra: Widest in the proximal third or at the base, the lateral margins regularly curved and striated; without parasutural stria; integument marked by vague

transverse striolae, sparsely impressed and rough, arranged very close together.

Legs: Moderately elongate; protibiae very thin; male protarsi thickened, first article as wide as distal end of protibia or very wide, almost twice the distal end of protibia.

Mesoventral keel (Fig. 271.5): Low and directed posteriorly, forming an obtuse angle with a small denticle at the apex.

Suture of the metaventrite (Fig. 271.5): In agreement with the description of the clade of the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.5): Metascutum very narrow and rather elongated, the apophysis of the alacrista reduced with sharp points.

Metendosternite (Fig. 273.5): Furcal arms slightly longer than furcal trunk; posterior lamina narrow and almost the same width as apical area, with slightly arched margin; terminal apophysis very reduced, almost non-existent. Trunk distinctly longer than area of greatest basal width, the median keel with little apparent posterior divergence.

Median lobe of aedeagus: Short, thick and slightly curved; tapering from apical third, apex extended into a hook curved ventrally (Fig. 275.6); sometimes evenly curved and gradually acuminate from apical quarter, with small dorsal depression in this area and apex extended into a sharp, straight point (Fig. 275.5).

Endophallus: The apical reinforcement bands either very short and divergent towards the apex, the «Y»-piece appearing to terminate at the union nodule (Fig. 276.6); or longer, subparallel and very thin (Fig. 276.5).

Parameres: Very thin, slightly shorter than the median lobe, with the apical sixth enlarged, where the four short setae and a reduced and sharp membranous lamina are inserted in pairs (Fig. 277.16), or as long as the median lobe, regularly arched and a little thickened at the apex where a well-developed membranous lamina can be seen; four setae on the inner side, two at the base of the lamina and two a little lower (Fig. 277.15).

Spermathecal complex: Spermatheca slightly curved, the lobes poorly differentiated (Fig. 278.5) or irregularly curved, the lobes slightly thicker than the median region (Fig. 278.6); spermatic duct inserted into the copulatory bursa via a basal process formed by a highly sclerotized ring which surrounds the tubule and is preceded by a clearly visible dilated area.

Female uroventrite VIII (Fig. 279.5): Spiculum short and triangular.

Discussion. Distinctive characters have been provided in the discussion of the subgenus *Euryspeonomus*. Although there is not a great genetic distance between the two species of the subgenus (Fig. 1C), the morphological differences are considerable; the support between the two species is 100/100.

Distribution. Iberian hypogean endemism. It is known from various underground cavities in the northern region of the Sierra de Aralar, Urbasa and the western end of the Andía – Navarra – and in the Sierras de Entzia – Álava – (Fresneda & Salgado 2017).

Species

Euryspeonomus (***Urbasolus***) ***ciaurrizi*** (Bolívar, 1921)
Euryspeonomus **(*Urbasolus*)** ***ciaurrizi ciaurrizi*** (Bolívar, 1921)
Speonomus ciaurrizi Bolívar, 1921: 530.
Speonomus (*Speonomidius*) *Ciaurrizi* C. Bolivar, 1921: Jeannel, 1924a: 164.
Euryspeonomus (*Urbasolus*) *ciaurrizi ciaurrizi* (Bolívar): Perreau, 2000: 304.
Euryspeonomus (***Urbasolus***) ***ciaurrizi igaratzai*** (Español, 1945)
Speonomus ciaurrizi igaratzai Español, 1945: 270.
Euryspeonomus (*Urbasolus*) *ciaurrizi igaratzai* (Español): Perreau, 2000: 304.

Euryspeonomus (***Urbasolus***) ***eloseguii*** (Español, 1948)
Speonomus eloseguii Español, 1948: 240.
Speonomus (*Urbasolus*) *elosegui* Español: Español, 1950: 114.
Euryspeonomus (*Urbasolus*) *elosegui* Español: Santamaría, 1993: 791.

Hypogean clade of *Dupreia* gen. nov., *Josettekia* and *Nafarroa*

Within the clade of the *Euryspeonomus* group, the genera *Dupreia* gen. nov., *Josettekia* and *Nafarroa* appear as sister of the genus *Euryspeonomus* with a support of 89/94 (Fig. 1C).

Genus ***Dupreia*** nov.
https://zoobank.org/NomenclaturalActs/FAFE1C1E-D10A-4B70-BDB8-B245F14A0C27

Type species. *Euryspeonomus beruetei* Dupré, 1991 by present designation (habitus in Fig. 269.6).

Description**.** Size between 3.2 and 3.3 mm. Body oblong, with a marked pronotum-elytral angle (Fig. 269.6).

Antennae: Reaching half the length of the body and thickened from the 7th article.

Pronotum: Transverse, the lateral margins evenly curved along the whole length; greatest width in the posterior third; posterior angles acute and vertices not very prolonged on the elytra; integument marked by fine punctation and sparsely impressed on the disc, except near the margins, especially basal, where the punctation is rough.

Elytra: Broad, widest along proximal half but slightly narrower at base; integument entirely covered by thick, rough, distant transverse striolae; no parasutural stria.

Legs: First three segments of male protarsi with adhesive setae, the first slightly narrower than the apical end of the protibia; tibiae straight, except male mesotibiae, which are arched.

Mesoventral keel (Fig. 271.6): High, with convex anterior margin and at apex a minute denticle; ventral margin straight with numerous long setae.

Suture of metaventrite (Fig. 271.6): As described for the clade of the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.6): Metascutum short and broad; reduced alacrista apophysis, the apices pointed.

Metendosternite (Fig. 274.1): Furcal arms as long as the furcal trunk; posterior lamina broad, retaining same width along arm, with slightly arched margin; terminal apophysis thick. Furcal trunk longer than area of greatest basal width and median keel with marked posterior divergence.

Median lobe of aedeagus (Fig. 275.7): Curved at obtuse angle, basal part stout; distal end extending into a curved point ventrally.

Endophallus (Fig. 276.7): Branches of «Y»-piece slightly divergent in basal region, lateral pieces of ventral complex with poorly developed apical extensions; supranumeric phanera evenly arched in median region, the apex not curved; reinforcing bands in apical region long and fairly thick.

Parameres (Fig. 277.17): Robust to the tip and reaching to the apex of the median lobe; on the ventral side, apex with a thickening provided with a small apical hook strongly recurved posteriorly, without an apical membranous lamina; four very short, thick spines on the terminal paddle, two inserted at the apex with the insertion pores close, and the other two distant.

Spermathecal complex (Fig. 278.7): Spermatheca slightly curved, with a spherical apical lobe in the same plane as the median region, which is hyaline and much smaller in cross-section than the lobes; basal lobe thick and progressively curved in relation to the median region until reaching 90°; basally, spermatic duct inserted through a thick, long nodule; this duct with a basal process formed by a ring that surrounds the tubule at the point of insertion with the copulatory bursa; spermathecal gland present.

Female uroventrite VIII (Fig. 279.6): Spiculum long and thin.

Etymology. This genus was created to honour the late entomologist and friend E. Dupré (Tarnos, France), discoverer of the species in this new genus. Feminine.

Discussion. Sister genus to *Josettekia*, characterised by the presence of four short, thick spiny setae in the terminal region of the parameres, two inserted at the apex with insertion pores close together and the other two distant. In *Josettekia*, the setae are fine and the insertion pores are close together; moreover, the endophallus of this genus has no phanera in the median region. It also differs from *Euryspeonomus*, the genus in which it was included in its description, in the spines of the parameres: in *Euryspeonomus* the setae are fine, and in this genus there is a more or less developed membranous lamina at the apex of the parameres, whereas in *Josettekia* there is a small hook-shaped sclerotized thickening. Its general appearance has led it to be considered close to *Euryspeonomus* (*Euryspeonomus*) *breuili*, although much smaller in size. The endophallus is similar to that of this species, but with the following differences: in *Dupreia* gen. nov. the branches of the «Y»-piece are less divergent in the basal region, the lateral pieces of the ventral complex have less developed apical extensions, and the apical crown is more inwardly curved; in the median region, the supernumerary phanerae are more regularly arched and the apex does not have a pronounced angle; in the apical region, the reinforcing bands are proportionally longer. *Dupreia* gen. nov. is sister to the genus *Josettekia* with high support, 93.7/94 (Fig. 1C).

Distribution. Iberian endemism. The single species of the genus is known only from the type locality: at an altitude of 300 m, the cavity opens in the reliefs on the left bank of the Bidasoa river, in the Baztán Valley, Navarra (Fresneda & Salgado 2017).

Species

Dupreia beruetei (Dupré, 1991) comb. nov.
Euryspeonomus beruetei Dupré, 1991: 269.

Genus ***Josettekia*** Bellés & Déliot, 1983
Josettekia Bellés & Déliot, 1983: 237.

Type species. *Josettekia angelinae* Bellés & Déliot, 1983 by original designation (habitus in Fig. 269.7).

Diagnosis. Size between 3.5 and 3.7 mm. Habitus as in figure 269.7.

Head: With extremely fine, superficial and scattered punctation.

Antennae: Short and stout with the 9th to 11th segments somewhat thickened or enlarged into a spoon shape; 8th as long as wide, subspherical and very small.

Pronotum: Transverse, with lateral margins evenly curved throughout; maximum width at base; posterior angles straight with apex rounded and not resting on elytra; base with a double and slight sinuosity and integument finely roughened, the existence of dots not appreciated.

Elytra: Broader at the base; taken as a whole, distinctly triangular and convex as the suture is not sunken; lateral margins evenly curved along their length or very acuminate in the apical third and the marginal ridge curved dorsally; apex of both elytra rounded so that the suture is at the bottom of a triangular notch; integument entirely covered with fine, slightly impressed transverse striolae, although in the apical region they are not so obvious and appear to be disintegrated into separated points; no parasutural stria.

Legs: Long and stout; protibiae straight, and first three segments of male protarsus dilated; first protarsomere wider than apex of tibia and subquadrangular in shape; mesotibiae arched and metatibiae straight; both with series of thick spicules on outer margin.

Mesoventral keel (Fig. 271.7): Not very high, with slightly arched anterior margin and toothed apex.

Suture of the metaventrite (Fig. 271.7): As described for the clade of the *Euryspeonomus* group.

Metatergal apparatus (Fig. 272.7): Metascutum short and broad, the alacrista apophysis reduced.

Metendosternite (Fig. 274.2): Furcal arms as long as furcal trunk, with terminal apophysis; posterior lamina very broad, retaining same width along arm, with margin very slightly arched. Trunk slightly longer than area of greatest basal width, median keel with obvious posterior divergence.

Median lobe of aedeagus (Fig. 275.8): Base thickened, median region subcylindrical and apical region progressively narrowed to apex; ventrally thickened and dorsally depressed, or more regular and distinctly angled.

Endophallus (Fig. 276.8): Very simple and divided into three regions. Apical region with two symmetrical reinforcing bands, long or very short, resting on two rough trapezoidal pieces situated in the upper part of the median region; in the lower part of these pieces is a fine, densely arranged pilosity; ventral phanerae with the shape of an inverted horseshoe whose hyaline-looking arms extend to the base of the sac; a «Y»-piece of peculiar shape present in the basal region: of this structure, only the beginning of the two branches can be seen which, in other genera, form the «Y»-piece and which converge towards the point of union of the spermatic duct to form a short stylet not exceeding the length of the ventral complex.

Parameres (Fig. 277.18): Robust, thickened from the first third and somewhat sinuate; extending beyond the apex of the median lobe, sometimes with a thick bowl or minute membranous plate at the tip; four very fine, short setae, three with insertion pores very close together, the other with the pore a little further apart.

Spermathecal complex (Fig. 278.8): Spermatheca robust and shorter than in the preceding genera; both lobes thickened and sclerotized, especially the basal one; median region short; spermiduct long, three to six times the length of the spermatheca and inserted into it by a long nodule which in one of the species appears to be double; union with the copulatory bursa by a basal process strongly sclerotized and provided with thick teeth. Spermathecal gland present.

Female uroventrite VIII (Fig. 279.8): Spiculum long, slender and truncate.

Discussion. In the original description (Bellés & Déliot 1983) this genus was included in the «section *Speonomus* Jeannel » (*sensu* Bellés *et al*. 1978); according to its describers, it was related to *Speonomidius* or to *Euryspeonomus*-*Speocharidius* depending on the characters considered. The endophallus of *Josettekia*, with a stylet and ventral and dorsal basal complexes (Dupré 1991: Fig. 5) is very different from that described for *Euryspeonomus* or *Speocharidius* (Dupré 1990: (Figs. 12-13, 21; Dupré 1991: Fig. 3; Dupré 1992: (Figs. 21-22). It should be noted that the dorsal phanerae identified by Dupré (1991), look more like a stylet; this structure suggests that this genus is closer to *Speonomidius* (as suggested by Dupré 1991):

the inverted «Y»-piece in the basal region of the endophallus of *Speonomidius* is in fact a true stylet very similar to that of species in the *Quaestus* clade. Fresneda (1999) also did not conclude on the affinities of the genus when *Euryspeonomus mendizabali* was transferred to the genus *Josettekia*. In *Josettekia*, the endophallus does not correspond to the universal model of the Leptodirini of the Basque-Pyrenean reliefs, with three regions, a «Y»-piece and phanerae in the median region. The sudden appearance of new structures unrelated to those of their ancestors is unusual, as there is only one similar case among the Leptodirini of these reliefs, *Bellesia espanyoli*: the peculiarities of its endophallus led Fresneda & Hernando (1994b) to suggest that it should be related to *Speonomidius* and *Josettekia*. Molecular techniques have cleared up all these enigmas, *Josettekia* being sister to the *Dupreia* gen. nov. clade and both being directly related to *Nafarroa* with a support of 72.5/88 (Fig. 1C).

Distribution. *Josettekia* colonises the northern foothills of the Sierra de Aralar in Navarra and the Ernio and Pagoeta massifs in Gipuzkoa (Fresneda & Salgado 2017).

Species

Josettekia angelinae Bellés & Déliot, 1983
Josettekia angelinae Bellés & Déliot, 1983: 238.

Josettekia mendizabali (Bolívar, 1921)
Speonomus mendizabali Bolívar, 1921: 528.
Speonomus (*Euryspeonomus*) *Mendizabali* C. Bolivar, 1921: Jeannel, 1924a: 164.
Josettekia mendizabali (Bolivar, 1921): Fresneda, 1999: 7.

Genus ***Nafarroa*** Fresneda & Dupré, 2010
Nafarroa Fresneda & Dupré, 2010: 2.

Type species. *Nafarroa sorogainensis* Fresneda & Dupré, 2010 by original designation (habitus in Fig. 270.1).

Diagnosis. Length 1.8 mm. Oval and robust, the pronotum as wide as the elytra (Fig. 270.1). Dense punctation all over.

Antennae: Short with a differentiated club.

Pronotum: Strongly transverse with strongly arched sides, widest at base; punctation fine and faint.

Elytra: Slightly longer than wide, depressed, the apex of both together forming a regular curve with a tiny notch where the two meet; lateral margins regularly curved to the apex; punctation sparse, strongly marked and somewhat rough, without transverse striolae or parasutural stria.

Legs: Proportionately short. In the male, mesotibiae arched and spiny, and metatibiae straight; protarsi pentamerous with the first three segments only slightly expanded, the first narrower than the apex of the protibia; onychium as long as the first three.

Mesoventral keel (Fig. 271.8): High, forming an obtuse angle with the pointed apex and not extending onto the metaventrite.

Suture of the metaventrite (Fig. 271.8): Anterior half of the suture clearly separated from the edge of the mesocoxa, delimiting a small area.

Metatergal apparatus (Fig. 272.8): Metascutum short and very wide; apophysis of the alacrista reduced, the apices sharp.

Metendosternite (Fig. 274.3): Furcal arms slightly longer than furcal trunk; posterior lamina gradually narrowing along arm to apex, which is arched, very narrow and pointed, with subrectilinear margin in middle; terminal apophysis, if present, greatly reduced. Trunk almost as wide as long, measured in the area of greatest basal width and mid-keel with reduced posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 275.9), curved at an obtuse angle in the middle, the basal part proportionally reduced and the apex sharp and strongly curved towards the ventral side. In dorsal view (Fig. 276.9), strongly ogival from base to tip, the apex rounded; lateral margins sinuous.

Endophallus (Fig. 276.9): three characteristic regions. In the apical region, long, narrow reinforcing bands resting on membranous ligulae. Median region with a thin flagellum arising from the «Y»-piece, a short axial piece with armour at its upper end and dorsal and ventral phanerae. Basal region with the arms of the «Y»-piece straight, and on either side small phanerae joined together.

Parameres (Fig. 277.19): Longer than median lobe, robust throughout and rounded at apex. Four fairly long and stout apical setae with the insertion pores close together, inserted two by two on the sides of the apex.

Spermathecal complex (Fig. 278.9): Spermatheca thin and elongated, slightly curved and with two differentiated lobes, the apical spherical and larger than the basal; the basal not very developed, its calibre identical or even smaller in the posterior part than that of the median region; spermathecal gland inserted in the same place as the spermatic duct, which is 10 to 12

times longer than the spermatheca and slightly thicker in the area of the insertion site; at the point of contact with the copulatory bursa, the basal process simply indicated by a thickening of the duct, which is slightly more sclerotized than the rest.

Female uroventrite VIII (Fig. 279.7): Short spiculum showing truncated apex.

Discussion. *Nafarroa* has a fairly simple endophallus (Fig. 276.9), with dorsal and ventral phanerae similar to those of the Basque and Pyrenean Leptodirini or of *Dupreia* gen. nov., which belongs to the same clade. In the endophallus of *Dupreia* gen. nov. the annex phanera of the «Y»-piece are rounded and greatly reduced, and the apex of the parameres is adorned with four short, thick spines arranged in pairs; *Dupreia* gen. nov. also has transverse striolae on the elytra. It differs from *Josettekia*, the other genus in its clade, whose endophallus has no dorsal phanerae and the ventral phanerae form a curious «horseshoe» – Dupré 1990; Fresneda 1999 – and which also has a sclerotized nodule at the base of the apical reinforcement bands. In addition, the *Nafarroa* spermathecal complex has no true basal process at the junction of the spermatic duct with the copulatory bursa and no distinct nodule in the duct prior to its junction with the spermatheca; both of these structures are present in *Dupreia* gen. nov. and *Josettekia*. In the tree in Figure 1C, *Nafarroa* appears as a sister to *Josettekia* and *Dupreia* gen. nov. with a support of 72.5/88. This clade joins the genus *Eurys-peonomus* with a support of 89/94.

Distribution. A single cave located in the Quinto Real massif, western Pyrenees, Navarra, Spain (Fresneda & Dupré 2010).

Species

Nafarroa sorogainensis Fresneda & Dupré, 2010
Nafarroa sorogainensis Fresneda & Dupré, 2010: 10.

Clade of the endogean genera: *Casalella* gen. nov., *Pyrenaeola* gen. nov., *Pyrenaeola* (*Garunnia* subgen. nov.), *Vallespirana* gen. nov. and *Zariquieyella*

The species of the genera described were previously included in the large genus *Bathysciola*. This genus was established by R. Jeannel in 1910, who designated *Bathyscia aubei* as the type species. However, the species described under the name *Catops pusillus*, the type species of *Catopsinus*, a genus currently considered to be synonymous with *Bathysciola,* is now considered to belong to the same genus. *Catopsinus* thus takes precedence over *Bathysciola*. The issue has been partially resolved by M. Perreau, who recently rehabilitated *Catopsinus* (Perreau 2021). Jeannel (1924a) divided the genus *Bathysciola* into eight sections. The classification proposed by this author is based on external morphological characters and groups together species with different models of male genitalia, different models of spermathecal complex, oculate species and anophthalmous species. This genus, which currently contains numerous species distributed from the western Pyrenees to the Caucasus, could be compared to a bag in which taxa have been added with criteria of dubious phylogenetic value. Basically, species were incorporated when they were found in an endogean, humicolous or muscicolous environment and their form was bathyscioid. In the phylogenetic tree (Fig. 2), *Bathysciola* species appear distributed in very diverse clades, always as basal cladogenesis of clades typical of a specific region. Consequently, the Leptodirini seem to have dispersed by these elements – depigmented, usually anophthalmous and with a semi-contracted cycle – endogean, humicolous or muscicolous in a forest environment, and in each specific region, some of them colonised the subterranean environment, diversifying and being at the origin of a more or less extensive radiation that evolved towards marked troglobiomorphic forms. It seems speculative to assert that in hypogean clades without basal «*Bathysciola*», these have become extinct or have all colonized the subterranean domain: at the surface, they are much more exposed to variations in precipitation or temperature. In order to bring the taxonomy of the group into line with the molecular data, it appears necessary to fragment the genus. The need for a revision of the complex has already been mentioned by Vailati (1988) who indicated, with reference to the «*Bathysciola* complex» that: «*... ancora resta in attesa di migliore definizione*.»; Giachino (1998) also indicated that the systematic situation of the genus is uncertain and that it needs to be completely restructured. Fresneda & Salgado (2000), in a study in which the genus *Bathysciola* appears in several dichotomies of the proposed identification key for the Iberian Leptodirini, made the same point: it is an extremely heterogeneous group for which it is said that «*... it will probably have to be fragmented into various genera*.» The need to revise the genus has been expressed by Jeannel (1910a), Vailati (1988), Giachino (1998), Newton (1998), Perreau (2000) and Fresneda & Salgado (2000, 2006). Fresneda *et al*. (2007), providing a cladistic analysis, already recog-

nised the polyphyletic assemblage in *Bathysciola* that previous authors had suspected, and Ribera *et al*. (2010) confirmed the polyphyletic assemblage with a molecular phylogeny. The species of *Bathysciola* with the absence of transverse striolae on the elytra and the presence of a parasutural stria not parallel to the suture were grouped together by Jeannel (1924a) in what he called section IV. This section therefore encompasses the true *Bathysciola* since it includes the type species. The extension of the genus is limited to *Bathysciola* of the *aubei* group (Giachino & Vailati 2019). This group of genera has a small metendosternite, reduced in length, with the furcal trunk equal to or shorter than the furcal arms, and the three branches very wide.

In the Basque reliefs, all the elements of the endogean clade have penetrated the subterranean environment. If we consider climatic factors as the driving force behind subterranean colonisation, such as a drop in precipitation leading to a change in biome, it seems likely that the endogean elements died out on the surface in this region but were preserved in the Pyrenees in a hypothetical forest refuge with less climatic variations. It would be curious, to say the least, if part of the population remained on the surface whereas another part entered the subterranean environment, preserving the descendants of both forms of colonisation until the present day, although it would be a good example of hypothetical sympatric speciation. On the other hand, the three endogean clades ((*Zariquieyella* (*Casalella* gen. nov.-*Vallespirana* gen. nov. + *Pyrenaeola* gen. nov.-*Garunnia* subgen. nov.)) separated almost simultaneously and now coexist in one area of the central Pyrenees: between the Salat and Garonne rivers. For animals that apparently exploit the same resources in the same environment, it seems inappropriate to favour a sympatric speciation model. Some elements must have arrived there later: it is likely that *Casalella* gen. nov. comes from the eastern Pyrenees and *Zariquieyella* from the western Pyrenees, from the Garonne to the west, where most species are found: only *Zariquieyella mystica* comb. nov. crosses this border. *Pyrenaeola* gen. nov. (*s. str*.) has a very restricted distribution, just in the area where the three genera coexist: this is thought to be its cradle. The presence of *Casalella* gen. nov. and *Pyrenaeola* gen. nov. along the Garonne basin would be explained by passive colonisation carried by the waters of the river: these animals were found in flood debris on the banks. In the clade of the *Euryspeonomus* group, the basal clade is formed by the genera *Casalella* gen. nov. and *Vallespirana* gen. nov. which join the other clades of the group with a high support of 100/100 (Fig. 1C).

Genus ***Casalella*** nov.
https://zoobank.org/NomenclaturalActs/E0808B6B-39BD-43CB-8895-9DEE322FE73F

Type species. *Adelops meridionalis* Jacquelin du Val, 1854 by present designation (habitus in Fig. 270.2).

Diagnosis. Size between 2.0 and 2.4 mm. Oblong-oval shape with a regular outline (Fig. 270.2). Body surface covered with fine, yellowish, flat-lying hairs.

Head: Very fine punctation and pilosity somewhat more robust and erect than on the rest of the body; male with a tuft of thick, long setae on the forehead which may be located on a frontal prominence; no tuft of setae or prominence in the female.

Antennae: Slightly shorter than half the length of the body.

Pronotum: Transverse with regularly curved lateral margins, as wide as the elytra and very convex; greatest width between the centre and the base, and acute posterior angles with rounded vertex; integument marked by very fine, dense and irregular punctation; a fine micro-network giving it a matt appearance; pronotum-elytral angle null or very obtuse.

Elytra: The greatest width at the base and the lateral margins strongly and regularly curved up to the apex, which is rounded; sculpture formed by rough dots vaguely aligned transversely in the basal half, disordered in the apical half. No parasutural stria.

*Leg*s: Proportionally short, with the first article of the male protarsus triangular or quadrangular and a little narrower than the distal end of the protibia, if heart-shaped then wider than the distal end of the protibia; metatibiae straight, mesotibiae arched and metafemorae without femoral spine.

Mesoventral keel (Fig. 271.9): Low, condensed into a ridge and evenly curved; not extended on metaventrite.

Suture of metaventrite (Fig. 271.9): A little more than the anterior half of the suture clearly separated from the edge of the mesocoxa, delimiting a small area along the entire edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 272.9): Reduced, metascutum moderately broad and without sutures; alacrista without apical nodule and basal processes short.

Metendosternite (Fig. 274.4): Furcal arms as long as furcal trunk; posterior lamina very broad and retaining almost the same width to apical area, margin very slightly arched; large terminal apophysis. Trunk very wide, especially in the basal area, whose width is equal to the length of the trunk; median keel

whose posterior divergence is slightly evident.

Median lobe of aedeagus (Fig. 275.10): Basal region robust and strongly folded in the middle; apical half strongly narrowing, very thin, the apex prolonged, pointed or surmounted by a small nodule.

Endophallus: In lateral view, phanerae in the median region forming a sort of parenthesis. In dorsal view (Fig. 276.10), complicated phanerae superimposed and strongly sclerotized in the median region; the whole forms a sort of ring which may leave a central space free where is an apparently floating nodule of various shapes, more rounded or more elongated; at the upper end of these phanerae, and between the reinforcing bands of the apical region, there may be one or more sacs, the integument of which is strongly striated.

Parameres: Sinuate, as long as or slightly shorter than median lobe, withthickened club-shaped apex containing nine stout setae (Fig. 277.21), or with thin apex with four setae of variable length and thickness (Fig. 277.20).

Spermathecal complex (Fig. 278.10): Spermatheca elongate and curved from one end to the other, the two lobes well differentiated, their cross-section greater than that of the median region; spermatic duct very long, about 20 times as long as the spermatheca, inserting into the basal lobe by a nodule; basal process at the junction with the copulatory bursa in the form of a sclerotized, thickened and striated cylinder; spermathecal gland present.

Female uroventrite VIII (Fig. 279.9): Different in all three species. Spiculum robust and apex truncated, or spiculum short and thin, or spiculum very thin and apex pointed.

ETYMOLOGY. This genus is established in honour of the entomologist and friend Achille Casale (Torino, Italy). Feminine.

DISCUSSION. The *Bathysciola* species in the «*meridionalis*» group , proposed by Fresneda & Salgado (2006) are included in this genus. Fresneda & Salgado (2006) and Fresneda & Fery (2009) indicate the validity of three taxa: *Bathysciola grenieri*, *B. finismillennii* and *B. meridionalis* (= *B. nitidula*); subsequently, *B. liqueana* was described. The molecular study indicates that *B. grenieri* should be excluded from the group and highlights the inconsistency of the character put forward for its inclusion. The external morphology of the assemblage formed by *Casalella finismillenni* comb. nov., *C. liqueana* comb. nov. and *C. meridionalis* comb. nov. is very homogeneous: very similar appearance, same elytral punctation, same low and rounded mesoventral keel, same type of particular sexual dimorphism, tuft of thick and long setae on the male forehead. The apex of the parameres has four setae, as in all representatives of the Basque district clade, with the exception of *Aranzadiella*, which has about thirty, and *Casalella finismillennii* comb. nov. in which the parameres are armed with nine long, robust setae; males of *C. finismillennii* comb. nov. also have the tuft of frontal hairs but it is inserted into an angular prominence on the forehead, which is absent in *C. liqueana* comb. nov. and *C. meridionalis* comb. nov. The sister genus to *Casalella* gen. nov. is *Vallespirana* gen. nov. both related with 100/100 support and representing the basal clade of the *Euryspeonomus* group (Fig. 1C).

DISTRIBUTION. *Casalella finismillennii* comb. nov. is typical of the Salat valley, near Seix – Ariège, France –; *C. liqueana* comb. nov. inhabits the Lez valley, a tributary of the Salat, and *C. meridionalis* comb. nov. is found from near Foix, in the Plantaurel massif, to the mouth of the Garonne at Bordeaux. The latter is the species of the genus with the widest range and seems to have moved along the basins of the Ariège and Garonne rivers: this is probably a case of passive colonisation from the Pyrenees downstream by these rivers.

Species

Casalella finismillennii (Fresneda & Salgado, 2006) comb. nov.
Bathysciola finismillennii Fresneda & Salgado, 2006: 47.

Casalella liqueana (Fresneda, Bourdeau & Faille, 2010) comb. nov.
Bathysciola liqueana Fresneda, Bourdeau & Faille, 2010a: 132.

Casalella meridionalis (Jacquelin du Val, 1854) comb. nov.
Adelops meridionalis Jacquelin du Val, 1854: xxxvi.
Bathyscia nitidula Normand, 1907b: 272.
Bathyscia (*Bathyscia*) *meridionalis* Duv.: Reitter, 1885 [1884]: 33.
Bathyscia meridionalis Duv.: Delherm de Larcenne, 1890: 36.
Bathysciola meridionalis Duval: Jeannel, 1910a: 29.

Genus ***Pyrenaeola*** nov.
https://zoobank.org/NomenclaturalActs/BF9FC4ED-538C-433D-B8B1-15DB160EA5E4

Type species. *Adelops lapidicola* Saulcy, 1872 by present designation (habitus in Fig. 270.4).

Description**.** Size between 1.8-2.5 mm. Genus with bathyscioid facies, depigmented species. Elongated oval shape (Fig. 270.4), convex, with a regularly arched outline, slightly narrowed towards the rear. Colour reddish or dark reddish. Pubescence yellowish, very short, recumbent and sparse.

Head: Occipital carina absent or blurred; anophthalmous.

Antennae: Slightly thick and short, slightly exceeding the base of the pronotum; 3rd antennomere slightly longer than each of the 4th, 5th and 6th antennomeres which are very similar; 8th antennomere subglobose, those of the club just transverse.

Pronotum: Transverse, between 1.7-1.8 times wider than long; lateral margins regularly arched; greatest width along basal third as wide as greatest width of elytra; base sinuate; posterior angles acute and vertex blunt to slightly pointed; integument with well-printed microreticulation, punctation with small, shallow dots, more visible towards posterior angles.

Elytra: Short and broad, between 1.1 times as the length and width of the whole; sculpture characterised by well-marked transverse striolae formed by thick, granular, widely spaced dots; no parasutural stria.

Legs: Proportionally short and fairly robust; male protarsi more or less dilated, but always narrower than the apical area of the protibiae; mesotibiae more or less arched and metatibiae straight or arched; concavity visible in the inner margin of the fifth basal.

Mesoventral keel (Fig. 271.11): Slightly raised, vertex with slight denticle and obtuse angle; anterior margin between rounded and subrectilinear; ventral margin arched or slightly sinuate.

Suture of metaventrite (Fig. 271.11): Anterior half of the suture separated from the edge of the mesocoxa delimiting an arcuate area, then close and parallel to the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 272.11): Reduced, metascutum moderately broad and without suture; alacrista without apical nodule, the basal apophysis short with acute apices.

Metendosternite (Fig. 274.6): Furcal arms a little longer than furcal trunk; posterior lamina wide and slightly arcuate, narrowing a little in apical area which is arcuate and pointed; terminal apophysis well developed. Furcal trunk of the basal part very wide, the width of this part being equal to the length of the trunk; median keel with little apparent posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 275.12), bent at obtuse angle from middle; sometimes with ventral thickening at upper end of basal region; apical area in arc of circle directed ventrally, apex pointed. In dorsal view (Fig. 277.7), sides almost parallel, slightly convergent or narrowing towards the apex, which may be more or less rounded or even pointed.

Endophallus (Fig. 277.1): Characterised by the absence of phanerae attached to the «Y»-piece and showing in the median region two elongated, triangular-shaped, heavily sclerotized phaneroid complexes arranged on either side of the axis of symmetry of the sac; apical reinforcing bands resting on membranous ligulae without a spiny integument.

*Parameres (*Fig. 277.23): Slightly shorter than the median lobe, the basal part strongly thinned, a thickening in the median part, and at the apex four setae which may be minute and transversely aligned.

Spermathecal complex: Spermatheca long, curved and robust (Fig. 278.12), with two differentiated lobes, the apical spherical and the basal tubular, both of similar width, connected by a cylindrical median region slightly narrower than the lobes; spermatic duct relatively short, although longer than the spermatheca; at the point of insertion at the spermatheca is a generally elongated nodule and the spermathecal gland. The spermatic duct connected to the bursa copulatrix by a sclerotized structure.

Female uroventrite VIII (Fig. 279.12): Transverse, the spiculum very long and thin.

Etymology. The name refers to its range in the Pyrenees. Feminine.

Discussion. The *Bathysciola* species of the «*lapidicola*» group , proposed by Fresneda & Salgado (2006), are incorporated into this genus. The species making up this group are related to *Casalella* gen. nov., the former *Bathysciola* of the «*meridionalis*» group (Fresneda *et al*. 2010a) due to certain similarities in the endophallus: it seems that the basal pieces of the two longitudinal complexes of phanerae typical of the group of *Pyrenaeola* gen. nov. are fused by their internal margin in *Casalella* gen. nov., so that in the latter they almost form a «U» or a kind of ring composed of many pieces. No resemblance is observed with other models of endophallus. In any case, the differences between the endophallus of the *Pyrenaeola*

gen. nov. and *Casalella* gen. nov. species are significant and affect the number, shape and location of the sclerotized parts, i.e. the structure of the endophallus. The molecular study indicates that *Pyrenaeola* gen. nov. is located in the same clade as *Zariquieyella* and *Casalella* gen. nov., the first cladogenesis of the large Leptodirini clade of the Basque biospeleological district. It is the sister genus of the clade formed by these two genera, with moderate support 51.7/83 (Fig. 1C).

Jeannel (1924a) indicated that the type series of *Adelops lapidicola* Saulcy, 1872 comes from the Grotte de Lestelas; in the original description (Saulcy 1872) it is indicated that the species was collected in two localities, Lestelas and Aubert: in the identification labels of the specimens of the type series, «pierres» is specified, so it seems obvious that they were collected under stones in Aubert as well as in Lestelas, as indicated in the description of the species. Jeannel (1924a) chose Lestelas and not Aubert as the type locality, but this choice is not valid since the type locality is that from which the holotype – article 76.1 of the ICZN (1999) – comes, in the case of *P. lapidicola* comb. nov. the lectotype – article 76.2 of the ICZN (1999) –, which is designated in this article. It is curious that, just as the description of *P. arcuatipes* comb. nov. dates from 1924, the type series – according to R. Jeannel's handwritten labels – was surprisingly collected two years later, in 1926; it is also verified that, just as in the specimens incorporated by R. Jeannel into the general collection of the MNHNP, the specimens' original collection is always recorded – «MUSÉUM PARIS / Coll F. P. de Saulcy / Coll A. ARGOD. 1931» for *P. lapidicola* comb. nov. – in the case of *P. arcuatipes* comb. nov. the label is «MUSÉUM PARIS / Coll. R. Jeannel 1931», whereas the original description reads «coll. A. Dodero» (Jeannel 1924a). For all these reasons, certain reservations are expressed as to the type series of *P. arcuatipes* comb. nov.: perhaps R. Jeannel added other specimens later or replaced the original specimen or originals in Dodero's collection, or made a labeling error. In any case, one of the specimens bears a red «TYPE» label and, in addition, all the specimens have handwritten labels from the descriptor: these specimens must be considered as the type series.

The lectotype of *Adelops lapidicola* is designated for the simple reason of stability of zoological nomenclature: the existence of other closely related species requires its unequivocal characterization, and in addition two species are mixed up in the type series: *Pyrenaeola lapidicola* comb. nov. (Lestelas) and *P. arcuatipes* comb. nov. (Aubert).

Type series. Male lectotype of *Adelops lapidicola* Saulcy, 1872 (present designation) (Fig. 281): «Estellas pierres / Abeille» [white rectangular label (hw Abeille de Perrin)], «Collect / de Saulcy» [white rectangular label (pr)], «MUSÉUM PARIS / Coll F. C. de SAULCY / Coll A. ARGOD. 1931» [white rectangular label (pr)], «TYPE» [red rectangular label (pr)], «*lapidicola* / type» [white rectangular label (hw)], acetate paper label with aedeagus mounted in Canada balsam identified by the number one; red handwritten label added «1. LECTOTYPUS / *Adelops lapidicola* / Saulcy, 1872 / Fresneda, *et al*., 2024» (MNHNP); two male specimens, the lectotype and a paralectotype, are glued to the label; a number one for the former and a number two for the latter have been noted on the same label, a numbering that is also indicated on the lectotype and paralectotype labels; hence the red handwritten label «2. PARALECTOTYPUS / *Adelops lapidicola* / Saulcy, 1872 / Fresneda, *et al*., 2024» (MNHNP). Paralectotypes of *Adelops lapidicola* Saulcy, 1872: a female labelled «Estellas pierres / Abeille» [white rectangular label (hw Abeille de Perrin)], «Collect / de Saulcy» [white rectangular label (pr)], «MUSÉUM PARIS / Coll F. C. de SAULCY / Coll A. ARGOD. 1931» [white rectangular label (pr)], «COTYPE» [white rectangular label with red letters (i)], «*lapidicola* / type» [white rectangular label (hw)]; addition of a red handwritten label «PARALECTOTYPUS / *Adelops lapidicola* / Saulcy, 1872 / Fresneda, *et al*., 2024» (MNHNP). A male labelled «Aubert pierres / Abeille» [white rectangular label (hw Abeille de Perrin)], «Collect / de Saulcy» [rectangular white label (pr)], «MUSÉUM PARIS / Coll F. P. De Saulcy / Coll A. ARGOD. 1931» [rectangular white label (pr)], «COTYPE» [white rectangular label with red letters (pr)], «*lapidicola*» [white rectangular label (hw Abeille de Perrin)]; addition of a red handwritten label «PARALECTOTYPUS / *Adelops lapidicola* / Saulcy, 1872 / Fresneda, *et al*., 2024» and determination label «*Pyrenaeola arcuatipes* Jeannel / Fresneda *et al*., det. 2024)» (MNHNP).

Once the identity of the taxa had been clarified, the taxonomic status of two other taxa was changed from subspecies to *bona species* (*Pyrenaeola rectipes* comb. nov. and *P. simplex* comb. nov., previously subspecies of *P. lapidicola* comb. nov.). The reasons are as follows:

– *Pyrenaeola lapidicola* comb. nov. is well characterised by the pointed median lobe of the aedeagus (Fig. 277.7) and the shape of the pro- and metatibiae (Fig. 280.3, 280.7), although its endophallus (Fig. 277.7) corresponds exactly to those of *P. arcuatipes*



FIGURES 280.1–280.8: *Speonomus* series, *Euryspeonomus* group. Protibia and metatibia of: (**1-5**) *Pyrenaeola* (*Pyrenaeola*) *arcuatipes* **comb. nov.** from Grotte d'Aubert, *P.* (*P.*) *simplex* **comb. nov.** from (**2**) Grotte de la Bouhadère and (**6**) Gouffre de Djerbao, *P.* (*P.*) *lapidicola* **comb. nov.** from (**3**) Grotte de Gourgue and (**7**) Grotte de Terreblanque, (**4-8**) *P.* (*P.*) *rectipes* **comb. nov.** from Grotte de Gouillou.

comb. nov. (Figs 277.1, 277.2) and *P. simplex* comb. nov. (Fig. 277.9).

– *Pyrenaeola rectipes* comb. nov. is also well distinguished by the peculiarities of its endophallus (Figs 277.3, 277.10), although the median lobe of its aedeagus (Fig. 277.10) is very similar to that of *P. simplex* comb. nov. (Fig. 277.9) (both less rounded than in *P. arcuatipes* comb. nov.); its pro- and metatibiae (Figs 280.4, 280.8), on the other hand, are close to the model of *P. lapidicola* comb. nov. (Figs 280.3, 280.7).

– *Pyrenaeola arcuatipes* comb. nov. and *P. simplex* comb. nov. could be considered as two forms (subspecies) of the same species. But the median lobe of the aedeagus of *P. simplex* comb. nov. (Fig. 277.9) is of the type of *P. rectipes* comb. nov. (Fig. 277.10) (which for other reasons, to which we must added the shape of its median lobe, has been considered a valid species), although its endophallus meets the pattern of *P. arcuatipes* comb. nov. (Figs 277.1, 277.2) and *P. lapidicola* comb. nov. (Fig. 277.7), and their pro- and metatibiae (Figs 280.3, 280.7) are close to those of *P. arcuatipes* comb. nov. (Figs 280.1, 280.5).

P. secqi comb. nov. (Secq 2013) has also been incorporated into this group, originally included in the «*larcennei* group» of *Bathysciola* of Fresneda & Salgado (2006). From the description of this species, its endophallus unequivocally matches the pattern described for *Pyrenaeola* gen. nov., but the presence of four long setae and a membranous extension of the paramere apex reveals a relationship with *P.* (*Garunnia*) *larcennei* comb. nov.: they are sister clades (Fig. 1C).

The text by Coiffait (1959a) indicates that *Bathysciola aranensis* is related to *Casalella meridionalis* comb. nov. According to the review by Fresneda & Salgado (2006), *Casalella meridionalis* comb. nov. gives its name to a group of species that have a very characteristic genital pattern. This group was recently studied by Fresneda *et al*. (2010a). Fresneda & Fery (2009) made some observations

based on the study of the holotype of *Pyrenaeola aranensis* comb. nov, which are detailed below: the elytral surface is made up of thick, granular and separated dots, as in species of *Pyrenaeola* gen. nov. which in the latter form well-differentiated transverse striolae, which is not the case in *Casalella* gen. nov. In contrast, in «*larcennei*» (*sensu* Fresneda & Salgado 2006), *Zariquieyella* and *Vallespirana grenieri* comb. nov., the elytral striolae are fine, densely arranged and formed of very small, closely spaced dots. *Pyrenaeola aranensis* comb. nov. has the only synapomorphy observable in females that is characteristic of other taxa of *Pyrenaeola* gen. nov.: in the integument visible between the elytral striolae, there is a microreticulation in the form of overlapping scales. There is no doubt that it belongs to the genus *Pyrenaeola* gen. nov.; moreover, it is considered here as a good species, judging by the differences observed in the female uroventrite VIII – strongly transverse, with a short spiculum, clearly triangular in shape – and the spermatheca – short, thick, slightly curved, with the median region very reduced –.

The very robust appearance of the aedeagus is characteristic of *Pyrenaeola arcuatipes* comb. nov. and *P. simplex* comb. nov., whereas its slender or very slender appearance is characteristic of *P. rectipes* comb. nov., *P. secqi* comb. nov. and *P. lapidicola* comb. nov. The aedeagus of *P. simplex* comb. nov. (Fig. 275.15) follows the pattern described for *P. arcuatipes* comb. nov. (Fig. 275.13), although in dorsal view the tip is not so broadly rounded (Fig. 277.9); the spermatheca appears slightly more robust in *P. simplex* comb. nov. (Fig. 278.14) than in *P. arcuatipes* comb. nov. although the difference is small; female uroventrite VIII is identical in both species (Fig. 279.11). The most striking differences are to be found in the secondary sexual characters: in the shape of the protibiae, small, thin from one end to the other, very slightly thickened towards the apex (Figs 280.2) in *P. simplex* comb. nov. or very broad, clearly triangular, with the inner part thickened (Figs 280.1) in *P. arcuatipes* comb. nov.; or in the shape of the metatibiae, triangular and curved along their entire length, a little more clearly in the basal third (Fig. 280.6) in *P. simplex* comb. nov., or rectilinear and of regular section in their basal third, where they bend at an obtuse angle, and from which they thicken regularly to the apex (Fig. 280.5) in *P. arcuatipes* comb. nov. In *P. secqi* comb. nov. the metatibiae are simple. The shape of the aedeagus in lateral view of *P. rectipes* comb. nov. (Fig. 275.14) is intermediate between the robustness of *P. arcuatipes* comb. nov. (Fig. 275.13) or *P. simplex* comb. nov. (Fig. 275.15) and the slenderness of *P. lapidicola* comb. nov. (Fig. 275.12); in dorsal view, *P. rectipes* comb. nov. (Fig. 277.10) has a slender appearance and a certain resemblance to *P. lapidicola* comb. nov. (Fig. 277.7); in any case the pointed aedeagus of *P. lapidicola* comb. nov. distinguishes it not only from that of *P. rectipes* comb. nov. which is narrowly rounded one with a tiny lobe at the tip, but also from the other taxa in the group. The metatibiae of *P. rectipes* comb. nov. (Fig. 280.8) are somewhat reminiscent of those described for *P. lapidicola* comb. nov. (Fig. 280.7), since the slight thickening is found in the inner part; however, they are straight, very different from those of *P. lapidicola* comb. nov., which are very curved in the basal third: at this point they thicken strongly on their inner face and are then subparallel at the apex with the outer margin somewhat concave. *Pyrenaeola rectipes* comb. nov. is also characterised by floating parts (Fresneda 1998) formed from a simple lamina folded into the endophallus, whereas the other four species of which the male is known have them formed from a complex lamina in which there are two strongly sclerotized pedunculus. The structures of the females do not provide much information: with the exception of *P. aranensis* comb. nov. the other species have almost identical spermathecae (Figs 278.12-278.15) and VIII female uroventrite (Figs 279.11-279.14); in *P. secqi* comb. nov. these structures are unknown. In the clade (Fig. 1C) of the genus *Pyrenaeola* gen. nov. the subgenera *Pyrenaeola* and *Garunnia* subgen. nov. are related by high support (98.7/100).

Distribution. This group of species has a very restricted distribution in the low-lying mountainous areas of the French departments of Haute-Garonne and Ariège, and from Vall d'Aran in Lleida, Spain. All localities are on the northern slope of the Pyrenees. The range extends from the Lez basin in the east to the Garonne basin in the west, and from the mountainous boundary with the great Garonne depression to the north to the proximity of the Pyrenees watershed in the south. Muscicolous, endogeous or hypogeous.

Species

Pyrenaeola* (*Pyrenaeola*) *aranensis (Coiffait, 1959) comb. nov.
Bathysciola aranensis Coiffait, 1959a: 162.

Pyrenaeola* (*Pyrenaeola*) *arcuatipes (Jeannel, 1924) comb. nov.

Bathysciola (*Bathysciola*) *arcuatipes* Jeannel, 1924a: 112.
Bathysciola arcuatipes Jeannel: Fagniez, 1927: 20.

Pyrenaeola* (*Pyrenaeola*) *lapidicola (Saulcy, 1872) comb. nov.
Adelops lapidicola Saulcy, 1872: 22.
Bathyscia (*Bathyscia*) *lapidicola* Saulcy: Reitter, 1885 [1884]: 33.
Bathysciola lapidicola Saulcy: Jeannel, 1910a: 29.

Pyrenaeola* (*Pyrenaeola*) *rectipes (Coiffait, 1959) stat. nov. comb. nov.
Bathysciola lapidicola rectipes Coiffait, 1959a: 162.

Pyrenaeola* (*Pyrenaeola*) *secqi (Secq, 2013) comb. nov.
Bathysciola secqi Secq, 2013: 423.
Pyrenaeola* (*Pyrenaeola*) *simplex (Coiffait, 1959) stat. nov. comb. nov.
Bathysciola lapidicola simplex Coiffait, 1959a: 161.

Subgenus ***Garunnia*** nov.
https://zoobank.org/NomenclaturalActs/5F23E8B9-66A0-4FD1-8FB5-CA044B075F61

Type species. *Bathyscia larcennei* Abeille de Perrin, 1883 by present designation (habitus in Fig. 270.5).

Description. Size about 2.0 mm. Oval shape (Fig. 270.5). Reddish colouration and faint yellowish pubescence , fine, dense, tight and flattened. Sculpture formed by fine, superficial and scattered dots on the pronotum, and transverse striolae on the elytra.

Antennae: Proportionally short, with the 8th article subglobose and the club segments somewhat transverse.

Pronotum: Transverse, as wide as the elytra as a whole, with the lateral margins regularly arched; greatest width in the basal third, the base sinuous; posterior angles acute, the vertex blunt; integument marked by a microreticulum with scattered superficial points.

Elytra: Proportionally short and wide; sculpture formed by a very distinctive microreticulation in the form of scales superimposed between the transverse striolae, which are thin and formed of dots close together and quite small. No parasutural stria.

Legs: Proportionally short; male protarsi slightly thickened, slightly narrower than distal end of protibia.

Mesoventral keel (Fig. 271.12): High, anterior margin convex, forming obtuse angle with hooked apex; posterior margin slightly arched.

Suture of the metaventrite (Fig. 271.12): Just over the anterior half of the suture well separated from edge of mesocoxa which delimits wider area, as in *Casalella* gen. nov.

Metatergal apparatus (Fig. 272.12): Metascutum broad and short; apophysis of the alacrista much reduced with pointed apices.

Metendosternite (Fig. 274.7): Furcal arms as long as furcal trunk; posterior lamina narrow, gradually narrowing towards apical area which is small and very pointed; terminal apophysis visible but reduced. Furcal trunk similar to the preceding subgenus but narrower, the width of base equal to the length of the trunk; median keel with very reduced posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 275.16), the basal region strongly thickened ventrally and bent into a regular curve shortly before half its length; distal half gradually diminishing, sometimes with slightly dorsal side slightly depressed; apex pointed and slightly curved ventrally.

Endophallus (Fig. 277.4): In the upper part of the median region, two small phanerae joined by a small sclerotized bridge or two small strongly sclerotized ciliated phanerae; in the lower part and at a distance from those described, a transverse plate where two thin and long phanerae overlap with an oblique arrangement; in the basal part of these phanerae, two visibles nodules emit a peduncle extending to near the «Y»-piece.

Parameres (Fig. 277.24): Slightly shorter than median lobe and provided at apex with four long subequal setae; apex sometimes showing membranous extension.

Spermathecal complex (Fig. 278.16): Spermatheca small, somewhat arcuate, with a basal lobe of greater calibre than the apical.

Female uroventrite VIII (Fig. 279.15): Transverse, the spiculum long and slender, with slightly curved apical area, the apex not very acute.

Etymology. In reference to the Garunni, an Aquitanian people who inhabited the region in pre-Roman times, named by Gaius Julius Caesar in the work «*De Bello Gallico*». Feminine.

Discussion. Like the species of *Pyrenaeola* gen. nov. (*s. str.*), *Garunnia* subgen. nov. has an elytral sculpture formed by a microreticulation in the form of superimposed scales arranged between the transverse striolae

of the elytra. It differs from the nominotypical subgenus in that it is composed of smaller, less robust species, with well-marked, fine, densely arranged elytral transverse striolae formed by small, closely spaced dots, whereas they are formed by thick, granular, widely spaced dots in subgenus *Pyrenaeola* gen. nov. (*s. str*.). The endophallus of the two subgenera is considerably different. *Garunnia* subgen. nov. has in the upper part of the median region two small and strongly sclerotized phanerae; in the lower part of the same region there is a transverse plate where two thin and long phanerae with an oblique arrangement overlap and in the lower part of these phanerae two separate nodules can be seen from which a peduncle emerges which extends to the vicinity of the «Y»-piece. *Pyrenaeola* gen. nov. (*s. str*.) is characterised by the presence in the median region of two complexes of elongated triangular phanerae, arranged on either side of the axis of symmetry of the sac. The differences between the genital structures of these two subgenera are so great that it was initially thought that they should be grouped in different genera. The intermediate morphology of *P. secqi* comb. nov. was decisive in including *P. convena* comb. nov. and *P. larcennei* comb. nov. in *Garunnia* subgen. nov. *Pyrenaeola secqi* comb. nov. has an endophallus conforming to that of *Pyrenaeola* gen. nov. (*s. str*.) while the parameres have four long setae and a membranous lamina at the apex as in *P*. (*Garunnia*) *larcennei* comb. nov., not the four minute setae characteristic of *Pyrenaeola* gen. nov. (*s. str*.).

Pyrenaeola (*Garunnia*) *convena* comb. nov. was described (Jeannel 1924a) as a subspecies of *P*. (*Garunnia*) *larcennei* comb. nov. The differences observed between their respective genital structures justify the specific independence of the two taxa (Fresneda & Salgado 2006). The median lobe of aedeagus in lateral view has a similar appearance in both species, but on closer examination the differences can be seen without difficulty: in *P*. (*Garunnia*) *convena* comb. nov. the basal region is thick but without any particular localised thickening and the distal half gradually tapers with the dorsal surface somewhat depressed; in contrast, in *P*. (*Garunnia*) *larcennei* comb. nov., a prominent rounded bulge is visible ventrally. The parameres of *P*. (*Garunnia*) *convena* comb. nov. do not have a membranous extension at the apex, unlike in *P*. (*Garunnia*) *larcennei* comb. nov. Although the endophallus follows the same pattern in both species, its constituent parts are different: in *P*. (*Garunnia*) *convena* comb. nov. in the upper part of the median region there are two small, strongly sclerotized and hairy phanerae, whereas in *P*. (*Garunnia*) *larcennei* comb. nov. there are two smooth phanerae formed by several sheets which are connected by a small sclerotized bridge; there are numerous differences in all the parts of the sclerotized armour.

Distribution. Northern slopes of the central Pyrenees, in the departments of Ariège, Haute-Garonne and Hautes-Pyrénées, as far as Gers – France –.

Species

Pyrenaeola* (*Garunnia*) *convena (Jeannel, 1924) comb. nov.
Bathysciola (s. str.) *Larcennei* Subsp. *convena* Jeannel, 1924a: 109.
Bathysciola (*Bathysciola*) *convena* Jeannel, 1924: Fresneda & Salgado, 2006: 52.

Pyrenaeola* (*Garunnia*) *larcennei (Abeille de Perrin, 1883) comb. nov.
Bathyscia Larcennei Abeille de Perrin, 1883: 1.
Bathyscia Lucantei, Ab.: Delherm de Larcenne, 1883 [1877-1885]: 9.
Bathyscia (*Bathyscia*) *Larcennei* Ab.: Reitter, 1885 [1884]: 33.
Bathyscia Schioedtei subsp. *Larcennei* Abeille: Jeannel, 1907b: 423.
Bathysciola Schiödtei subsp. *Larcennei* Abeille: Jeannel, 1910a: 29.
Bathysciola (s. str.) *Larcennei* Abeille, 1883: Jeannel, 1924a: 109.

Genus ***Vallespirana*** nov.
https://zoobank.org/NomenclaturalActs/0AB788B0-1286-45C6-9ED2-B2F1C64BC225

Type species. *Adelops grenieri* Saulcy, 1872 by present designation (habitus in Fig. 270.6).

Diagnosis. Size between 2.0 and 2.1 mm. Body (Fig. 270.6) of regular oval shape, slightly acuminate towards the rear and very convex no pronotum-elytral angle. Very fine and sparse punctation on the head, making the integument very shiny.

Antennae: Short, not reaching the posterior angles of the pronotum, with the first two antennomeres long and thick, the 3rd to 6th subequal, cylindrical and elongated, the 7th similar to these but a little longer, the 8th small and globose, the last three somewhat thickened.

Pronotum: Transverse, as wide as the elytra and very convex; lateral margins curved, the greatest width at the base which is sinuous; posterior angles



FIGURE 281: *Speonomus* series, *Euryspeonomus* group. Lectotype and paralectotype of *Adelops lapidicola* Saulcy, 1872.

acute with the vertices a little elongated; punctation granular.

Elytra: Widest at the base, the lateral margins regularly curved up to the apex which is very rounded; there is a narrow marginal ridge and no parasutural stria; integument marked by fine transverse striolae, numerous and close together.

Legs: Short; male protarsi enlarged, with first article slightly narrower than distal end of protibia; metatibiae straight, strongly triangular, and metafemora without femoral spine.

Mesoventral keel (Fig. 271.13): High; anterior and posterior edges slightly convex, forming a right angle with a small tooth at apex.

Suture of the metaventrite (Fig. 271.13): Anterior half of suture separated from edge of mesocoxa delimiting a small area.

Metatergal apparatus (Fig. 272.13): Metascutum moderately broad and long; apophysis of alacrista reduced.

Metendosternite (Fig. 274.8): Furcal arms a little longer than furcal trunk, with a large terminal apophysis; posterior lamina well developed and remaining the same width along arm, with margin very slightly arched. Furcal trunk slightly longer than area of greatest basal width and median keel with reduced posterior divergence.

Median lobe of aedeagus: In lateral view (Figs 275.17), the basal two-thirds very robust, the apical end forming a robust thickening; in dorsal view, apical end broad, almost straight, with a slight concavity in the middle.

Endophallus: In lateral view, presence of phanerae in the median region forming a sort of recumbent parenthesis. In dorsal view (Fig. 277.5), median region with complicated phanerae superimposed with strong sclerotization; among these, some apparently fused by their internal margin, and the whole in the shape of a «T».

Parameres (Fig. 277.25): Sinuate, slightly shorter than median lobe, with thickened club-shaped apex, bearing four long, stout, sinuous setae.

Spermathecal complex: Spermatheca (Fig. 278.17) long, curved and robust, with two hemispherically differentiated lobes which are connected by a hyaline cylindrical median region, narrower than the lobes; spermatic duct relatively short, although longer than the spermatheca; at the insertion point there is a thick nodule where the spermathecal gland is inserted.

Female uroventrite VIII (Fig. 279.16): Spiculum short, wide, with truncated apex.

ETYMOLOGY. In reference to the current name of the region, already referred to as «Viscounty of Vallespir» in the year 990, 10th century. It is located in Rosselló, Pyrénées-Orientales, France, where the type locality of the species is found. Feminine.

DISCUSSION. *Vallespirana grenieri* comb. nov., is the sister group of *Casalella* gen. nov., linked, with a support of 91.6/66, to the former *Bathysciola meridionalis* group in which it was included (Fig. 1C): it has a high, angular mesoventral keel, fine transverse striolae over the entire elytral surface, and males lack a tuft of hairs on the forehead; in *Casalella* gen. nov. the mesoventral keel is reduced to a lash-like rim, the elytra are marked by scattered dots and males have a tuft of hairs inserted into a prominence on the forehead. The genital structures and distribution of this species have been studied by Fresneda & Fery (2009): seven paralectotypes of *Bathyscia schiodtei* Kiesenwetter, 1850 are specimens of *Vallespirana grenieri* comb. nov. from La Preste (Pyrénées-Orientales, France) (Fresneda & Fery 2009).

DISTRIBUTION. *Vallespirana grenieri* comb. nov. is found in the eastern Pyrenees, between the Canigou-Costabonne massifs and the Ariège river basin – France – Andorra and Girona in Spain.

Species

Vallespirana grenieri (Saulcy, 1872) comb. nov.
Adelops Grenieri Saulcy, 1872: 22.
Bathyscia (*Bathyscia*) *Grenieri* Saulcy: Reitter, 1885 [1884]: 33.
Bathyscia Schiodtei subsp. *Grenieri* Saulcy: Jeannel, 1907b: 423.
Bathysciola Schiödtei subsp. *Grenieri* Saulcy: Jeannel, 1910a: 29.
Bathysciola (s. str.) *Grenieri* Saulcy, 1872: Jeannel, 1924a: 110.
Bathysciola grenieri (Saulcy): B. Secq & M. Secq, 1996: 10.

Genus ***Zariquieyella*** Jeannel, 1929
Hoffmannia Knirsch, 1928 [1927]: 101 (*Nom. praeocc*., homonymy with *Hoffmannia* Gemellaro, 1888 – Mollusca, Ceratitida –; *Hoffmannia* Pagentstecher, 1900 – Lepidoptera –.
Zariquieyella Jeannel, 1929a [1928]: 297 (Substitution name).

Type species. *Hoffmannia biokovensis* Knirsch, 1928 syn. nov. (= *Bathyscia schiodtei* Kiesenwetter, 1850) by monotypy (habitus in Fig. 270.3).

Diagnosis. Size between 1.5-2.5 mm. Elongated-oval shape (Fig. 270.3). Reddish colouration and yellowish pubescence, fine, dense, tight and flattened. Sculpture formed by fine, superficial and scattered dots on the pronotum, and transverse striolae on the elytra.

Antennae: Proportionally short, with the 8th article subglobose and the club segments barely transverse.

Pronotum: Transverse, as wide as the elytra as a whole, with regularly arched lateral margins; greatest width in the basal third and the base sinuous; posterior angles acute, the vertex blunt; integument marked by superficial rugosities or by punctation which can be dense and rough, although superficial.

Elytra: Proportionally short and broad; no parasutural stria.

Legs: Proportionally short, male protarsi thickened; a metafemoral spine in some species.

Mesoventral keel (Fig. 271.10): High, with convex anterior margin and toothed or rounded apex.

Metaventrite: A median crest on its anterior half, which appears to be an extension of the mesoventral keel.

Suture of the metaventrite (Fig. 271.10): Upper half of suture clearly separated from edge of mesocoxa, delimiting a small area.

Metatergal apparatus (Fig. 272.10): Metascutum broad and short; apophysis of the alacrista prolonged and apices not very pointed.

Metendosternite (Fig. 274.5): Furcal arms a little longer than furcal trunk; posterior lamina broad, same width as apical area and with slightly arched margin; large terminal apophysis. Trunk a little longer than the area of greatest basal width; median keel with very little obvious posterior divergence.

Median lobe of aedeagus: In lateral view (Figs 275.11), slightly curved at an obtuse angle towards the middle; dorsal surface with slight sinuosity along its course. In dorsal view (Fig. 276.11, 276.12), long and evenly tapering from base to apex.

Endophallus (Fig. 276.11, 276.12): Characterised by the presence of three regions; in the basal region, a «Y»-piece consisting of two very thin symmetrical rods with a thick bean-shaped nodule at the end which articulates by means of a tubule with another nodule of the same shape;phanerae attached to the «Y»-piece; in the median region, ventral, dorsal and two very long lateral phanerae; at the upper end of the median region, the «phanerae complex» (Fresneda & Salgado, 2006) formed by three interconnected nodules; in the apical region, reinforcing bands with a thick, heavily sclerotized basal end.

Parameres (Fig. 277.22): not reaching the apex of the median lobe, the apex provided with four long sinuous setae whose insertion pores close together.

Spermathecal complex (Fig. 278.11): Spermatheca elongated, slightly curved, with two differentiated lobes separated by a marked hyaline median part; apical lobe spherical and as wide as the basal one, the latter much longer; spermatic duct 7-9 times longer than the spermatheca, decreasing in calibre from the base to the other end, where it connects to the spermatheca and the spermathecal gland empties; basal process of the spermatic duct consisting of a sclerotized disc with a diameter considerably greater than that of the duct which passes through its centre.

Female uroventrite VIII (Fig. 279.10): Spiculum short with slightly acute apex and broad base, triangular in overall shape.

Discussion. *Hoffmannia biokovensis* Knirsch, 1928 is a more recent synonym of *Bathyscia schiodtei* Kiesenwetter, 1850. The structure of the endophallus is very characteristic and corresponds exactly to that of the species in the *Bathysciola schiodtei* group (Fresneda & Salgado 2006): the endophallus of the different species in the group are presented by Fresneda & Fery (2009). The correspondence of the structures is illustrated in Figures 276.11 and 276.12: the endophallus are identical, piece by piece. Of all the structures, the phaneroid complex of the apex of the median region stands out as a synapomorphy of the *Bathysciola schiodtei* group (Fresneda & Salgado 2006), which is also present in *Hoffmannia biokovensis*. Among the species of the *Bathysciola schiodtei* group, it is with this species that *Hoffmannia biokovensis* coincides through a totally identical aedeagus; above all, it coincides with the endophallus shown by specimens from the vicinity of Lourdes in France, central Pyrenees, and which corresponds unambiguously to *Bathysciola schiodtei.* Consequently, the synonymy *Bathyscia schiodtei* Kiesenwetter, 1850 = *Hoffmannia biokovensis* Knirsch, 1928 syn. nov. is established. Thus, the genus name must be applied to all species in the *Bathysciola schiodtei* group; as *Hoffmannia* Knirsch is a homonym of *Hoffmannia* Gemellaro, 1888 – Mollusca, Ceratitida – and *Hoffmannia* Pagentstecher, 1900 – Lepidoptera –, the substitution name proposed by Jeannel (1929) *Zariquieyella* must be used.

The vicissitudes followed by the samples of Knirsch (1928) are reported by Jeannel (1929), who is

also very critical of this author. L. Weirather sent the samples to R. Zariquiey in Barcelona for him to study them and describe the novelties. Once R. Zariquiey had studied the material and written a version of the work, he sent the text and the samples to R. Jeannel for his critical opinion. R. Zariquiey later published his work in 1928. It is not known where E. Knirsch bought this material, but it was already labelled in R. Zariquiey's handwriting, as Knirsch (1928) indicated and as Jeannel (1929) confirmed. One possible hypothesis is that R. Zariquiey sent L. Weirather some of the properly labelled material and that it was this material that E. Knirsch consulted; it is not unreasonable to imagine that R. Zariquiey included Pyrenean species in the batch of specimens that he had to send to L. Weirather, or that he added specimens by mistake. This would explain the presence of *Bathyscia schiodtei* among the samples that led to the error made by E. Knirsch. Locality errors may exist and some have already been documented among the Leptodirini: *Eskualdunella* (= *Cytodromus*) from the Pyrenees has as its type species *Cytodromus dapsoides* from the Vercors region of the French Alps (Faille *et al*. 2009) or, again, the citation of the genus *Ceuthmonocharis* for the central Italian Alps (Giachino & Vailati 2005). In Knirsch's article (1928), the author states that the samples he purchased came from «Western Serbia» and were collected by the Austrian biospeleologist L. Weirather of Innsbruck. Seventeen taxa are described in this article, including two genera. With regard to *Hoffmannia biokovensis* it can be said that:

– the male holotype appears to be the only specimen.

– The type locality is generic. Biokovo is part of the Dinaric Alps; it is a large massif of 196 km^2, the second highest mountain range in Croatia, situated along the Dalmatian coast between the rivers Cetina and Neretva. The other type localities of Knirsch (1928) are concrete places.

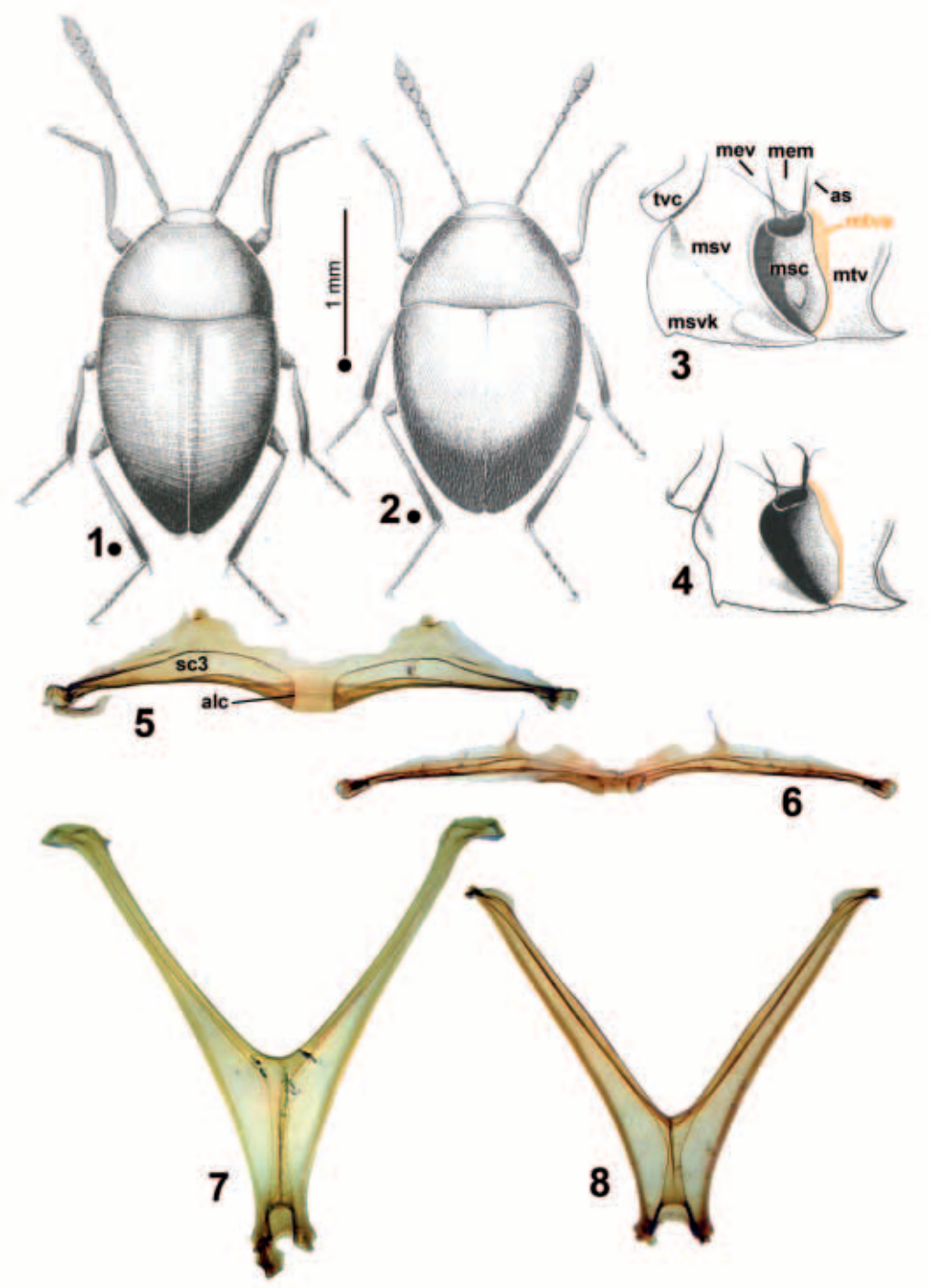
– No further captures were reported after the species was described; which is striking given that the subterranean fauna of Biokovo appears to be well known, with many Leptodirini genera inhabiting the massif. Very little information is available in the entomological literature. V.B. Guéorguiev (1976) included *Zariquieyella* in the Pholeuonina subtribe and Perreau (2000) followed the same criterion and placed it in the Pholeuina subtribe and the «*Spelaeochlamys*» phyletic series.

Zariquieyella it is the sister clade to all the hypogean elements: *Aranzadiella*, *Dupreia* gen. nov., *Euryspeonomus*, *Josettekia*, *Nafarroa*, and *Speocharidius* to which it is related with a support of 91.2/75 (Fig. 1C). Part of the «Groupe *schiodtei*» of Perreau (2000), which was redefined by Fresneda & Salgado (2006), has been incorporated into this genus. Fifteen taxa have been described, eleven of which are currently recognised as valid and have been incorporated into the genus *Zariquieyella*. Only the presence of four setae inserted at the apical tip of the parameres makes it possible to attach this genus to the Basque clade, no other common morphological element has been found, not even with the other two genera of its subclade. The structures of the endophallus are exclusive, although they correspond to the general model of the vast majority of Basque-Pyrenean Leptodirini: three regions, «Y»-piece and phanerae in the median region. It is also the only genus in the Basque clade in which the males of certain species have a metafemoral spine. The existence of certain structures complex («phanerae complex» by Fresneda & Salgado 2006) formed by three articulated nodules at the upper end of the median region is a synapomorphy of the genus.

Doubts remain as to the identity of some of the sequenced specimens. As there are no determining characters in the external morphology, confusion in the determination of the species has been the norm; consequently, their distributions are very incompletely or even erroneously known, and it is also a group with a wide distribution in the Pyrenean massif that even extends far into its western confines. The authors have collected a large quantity of material from which several possible new species have been identified; but in addition, molecular study has revealed the existence of other species which, from a morphological point of view, had gone unnoticed.. For all these reasons, *Zariquieyella* – the «*Bathysciola schiodtei*» group – is awaiting a thorough revision in the near future.

Note on some specimens used for the molecular study of the genus *Zariquieyella*:

– *Zariquieyella fadriquei* comb. nov. AF195 (Villanúa, Esjamundo cave). Specimens from this source had previously been attributed to *Zariquieyella obermaieri* comb. nov. but molecular study revealed that those from Cueva del Camino (AN239), also in Villanúa and a short distance from the former but on the opposite bank of the River Aragón, belong to a different species. After examining the specimens from Cueva de Esjamundo, it can be seen that the endophallus of its aedeagus corresponds to that described for *Z. fadriquei* comb. nov. from Aragüés del Puerto. Thus, provisionally, we consider that those from Cueva del Camino are representatives of *Z. obermaieri* comb. nov. whose typical locality is nearby, although on the other bank, the eastern bank of the Gállego river.



FIGURES 282.1–282.8: *Speonomus* series, *Parvospeonomus* group. Habitus and pterothorax in lateral view of: (**1**–**3**) *Parvospeonomus urgellesi*, (**2**–**4**) *Pseudospeonomus raholai*. Metatergal apparatus, ventral view of metanotum and axillaria of: (**5**) *P. urgellesi*, (**6**) *Ps. raholai*. Metendosternite of: (**7**) *P. guimjuani*, (**8**) *Ps. raholai*. Figs **1**–**4** modified from Salgado *et al*. (2008). Abbreviations: Metatergal apparatus: **alc**, alacrista; **sc3**, metascutum. Pterothorax: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **mtv**, metaventrite; **mtvs**, metaventral suture; **msv**, mesoventrite; **tvc**, transverse collar.

– *Zariquieyella parallela* comb. nov. AF73 (Saint Cricq du Gave, Grotte des Fées). This specimen is close to *Z. parallela* comb. nov. (Rébénacq, Grotte d'Arréglade) with a very similar aedeagus but larger in size. It seems clear that this population derives from individuals passively transported by the Gave de Pau as has been postulated for *Aphaenops* (*Geotrechidius*) *soussieuxi* (Perreau & Quéinnec 1987) – Coleoptera, Carabidae, Trechinae – with an identical distribution. Although it appears to be a new species, it will not be described for the time being: the genus needs to be reviewed and a complete study of the various populations carried out.

– *Zariquieyella* sp. AN235 (Arette, Gouffre Achama Lecia). Two species coexist in this locality, *Z. schiodtei* comb. nov./*Z. diegoi* comb. nov. and another presumably new species which has only been identified as such by morphological criteria. The morphological study of this new species suggests a relationship with *Z. grandis* comb. nov. The molecular study shows that the one that has been sequenced is the sister of *Z. diegoi* comb. nov. IRC14 and of *Z. grandis* comb. nov. AC144. These doubts can only be resolved by a global examination of the group.

Distribution. Species of this genus inhabit the Pyrenees, colonising mainly the western half on both slopes, where they have diversified into numerous taxa. There is one enigmatic species that is considerably isolated in Calvados, in the north of France: this is most likely a locality error. They extend from the Salat basin – Ariège, France – in the east, to the Oria Ibaia basin in Gipuzkoa – Spain –. On the southern slopes of the Pyrenees, they colonise the western half of the Pyrenees, from the Tena Valley – Huesca – in the west, where they appear to be the only Leptodirini – with the exception of *Vanderberghia ere* comb. nov., from Peña Forca-Alanos, in the Echo valley –.

Species

Zariquieyella bigerrica (Jeannel, 1930) comb. nov.
Bathysciola parallela bigerrica Jeannel, 1930b: 224.
Bathysciola schiodtei convexa Coiffait, 1959a: 16.
Bathysciola (*Bathysciola*) *bigerrica* Jeannel: Fresneda & Salgado, 2006: 55.

Zariquieyella breuili (Bolívar, 1921) comb. nov.
Bathysciola (*Bathysciola*) *breuili* Bolívar, 1921: 525.
Bathysciola (*Bathysciola*) *azuai* Bolívar, 1921: 524.
Bathysciola (s. str.) *Schiödtei* Subsp. *Breuili* C. Bolivar, 1921: Jeannel, 1924a: 110.
Bathysciola (s. str.) *Schiödtei* Subsp. *Azuai* C. Bolivar, 1921: Jeannel, 1924a: 110.

Zariquieyella diegoi (Salgado & Fresneda, 2001) comb. nov.
Bathysciola diegoi Salgado & Fresneda, 2001: 184.

Zariquieyella fadriquei (Fresneda & Comas, 2007) comb. nov.
Bathysciola fadriquei Fresneda & Comas, 2007: 326.

Zariquieyella fauveli (Jeannel, 1924) comb. nov.
Bathysciola Fauveli Jeannel, 1924a: 11.

Zariquieyella grandis (Fairmaire, 1856) comb. nov.
Adelops grandis Fairmaire, 1856: 525.
Adelops depressus Saulcy, 1863: 17.
Bathysciola Larcennei navarica Coiffait, 1959a: 160.
Bathyscia grandis Fairmaire: Jeannel, 1907b: 424.
Bathysciola Schiödtei subsp. *grandis* Fairmaire: Jeannel, 1910a: 29.
Bathyscia (*Bathyscia*) *Schioedtei* Kiesw.: Reitter, 1885 [1884]: 32.

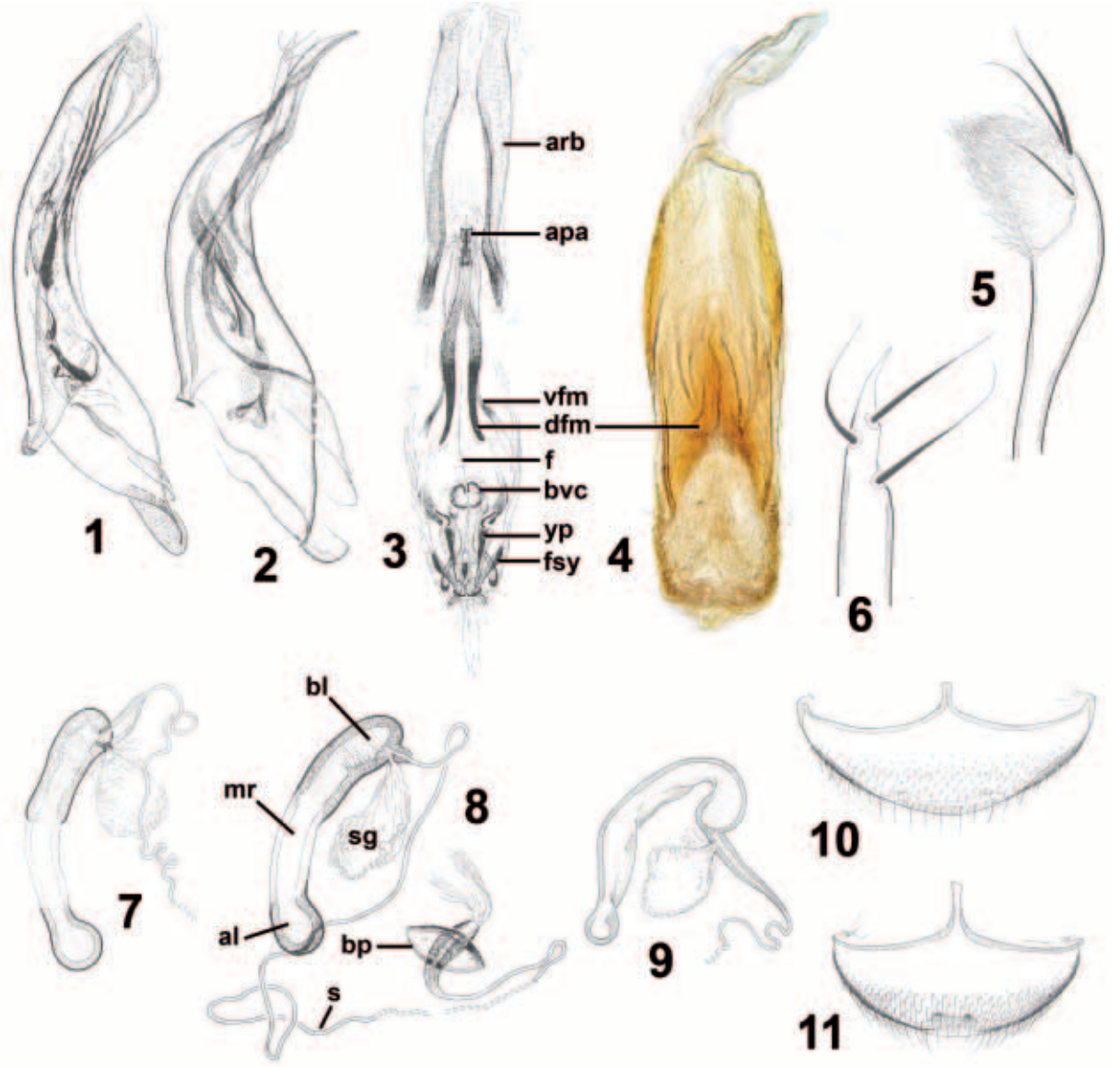
Zariquieyella mystica (Fresneda & Fery, 2009) comb. nov.
Bathysciola mystica Fresneda & Fery, 2009: 4.

Zariquieyella obermaieri (Bolívar, 1918) comb. nov.
Bathysciola (*Bathysciola*) *Obermaieri* Bolívar, 1918: 447.
Bathysciola (s. str.) *rugosa* Subsp. *obermaieri* C. Bolivar: Jeannel, 1924a: 112.
Bathysciola schiodtei obermaieri Bolivar: Escolà, 1980: 35.

Zariquieyella parallela (Jeannel, 1907) comb. nov.
Bathyscia parallela Jeannel, 1907b: 422.
Bathysciola parallela Jeannel: Jeannel, 1910a: 29.

Zariquieyella rugosa (Sharp, 1872) comb. nov.
Adelops rugosus Sharp, 1872: 270.
Bathyscia (*Bathyscia*) *rugosa* Sharp: Reitter, 1885 [1884]: 38.
Bathyscia Schiödtei subsp. *rugosa* Sharp: Jeannel, 1907b: 424.
Bathysciola rugosa Sharp: Jeannel, 1910a: 29.
Bathysciola (*Bathysciola*) *rugosa* Sharp: Jeannel, 1914b: 11.

Zariquieyella schiodtei (Kiesenwetter, 1850) comb. nov.



FIGURES 283.1–283.11: *Speonomus* series, *Parvospeonomus* group. Aedeagus in lateral view of: (**1**) *Parvospeonomus urgellesi*, (**2**) *Pseudospeonomus raholai*. Endophallus of: (**3**) *P. urgellesi*, (**4**) *Ps. raholai*. Apex of the paramere of: (**5**) *P. urgellesi*, (**6**) *Ps. raholai*. Spermathecal complex of: (**7**) *P. urgellesi*, (**8**) *P. delarouzeei*, (**9**) *Ps. raho*lai. Female uroventrite VIII of: (**10**) *P. urgellesi*, (**11**) *Ps. raholai*. Figs **1–3, 5–11** modified from Salgado *et al*. (2008). Abbreviations: Endophallus: **apa**, armature of the axial piece; **arb**, apical reinforcement band; **bvc**, basal ventral complex; **f**, flagellum; **fsy**, phanerae next to the «Y»-shaped piece; **dfm**, dorsal phanerae of the median region; **vfm**, ventral phanerae of the median region; **yp**, «Y»-shaped piece. Spermathecal complex: **s**, spermiduct; **sg**, spermathecal gland; **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, median region.

Bathyscia Schiödtei Kiesenwetter, 1850: 223.
Adelops Schiödtei Kiesenwetter: L. Miller, 1855: 508.
Bathyscia (*Bathyscia*) *Schiödtei* Kiesw.: Reitter, 1885 [1884]: 38.
Bathysciola Schiödtei Kiesenwetter: Jeannel, 1910a: 28.
Hoffmannia biokovensis Knirsch, 1928 [1927]: 101 syn. nov.
Zariquieyella biokovensis Knirsch: Jeannel, 1929a [1928]: 297.

3.4.8.2 ***Parvospeonomus*** group

Diagnosis. Bathyscioid shape, with the body short and oval; orange colouration and integument entirely covered by fine, short, laying and yellowish pubescence; depigmented.

Head: with the occipital carina complete; epistomal suture slightly curved and darkened; last article of the maxillary palps short and conical; anophthalmous.

Antennae: Of 11 segments and the club differentiated.

Legs: Protarsi pentamerous in males and tetramerous in females; male protarsomeres not dilated; tibiae with two internal pectinate or bifid spurs, two simple external ones and a series of unequal spines between them; there are spaced spines along the outer face. Protibiae not attenuated at the apex; mesotibiae slightly curved and metatibiae straight.

Suture of the metaventrite: Close to the edge of the mesocoxal cavity and the area it delimits elongated, but small.

Male genital segment: Very reduced, open, with two long pedunculus.

Discussion. In the molecular tree (Fig. 1C), the *Parvospeonomus* group is supported by 99.6/100 and was found to be sister of the *Bathysciella* + *Troglophyes* + *Antrocharis* + *Speonomus* groups with very high support, 99.8/100. There are no common morphological characters in the genital structures of the two genera of the clade. The clade is morphologically diverse although one of the two genera – *Parvospeonomus* – is similar in their structure of the apex of the parameres to the character state found in the *Bathysciella* clade group and surprisingly also in the genus *Batinoscelis* stat. nov. from Sardinia. However, further analysis are need to investigate if this is a case of evolutionary convergence. The other genus, *Pseudospeonomus*, it appears to be an independent and isolated evolutionary process strictly limited to the species of this genus.

Key to genera

1. Elytra with transverse striolae and parasutural stria (Fig. 282.1). Metendosternite furca with arms longer than the trunk, posterior lamina almost non-existent in the middle part and trunk longer than wide (Fig. 282.7). Parameres with three setae, cavity and dense penicillum in the apical part. Basal region of the endophallus with «Y»-piece (Fig. 283.3).....
.....*Parvospeonomus*

- Elytra without transverse striolae and without parasutural stria (Fig. 282.2). Metendosternite furca with the arms almost three times as long as the trunk, the posterior lamina narrow but well visible in the middle area and the trunk as wide as it is long (Fig. 282.8). Parameres with three setae, but without cavity or penicillum in the apical part and in the latter a sharp prolongation. Basal region of the endophallus with a sclerotized ring covered with teeth on its internal margin, but without a «Y»-piece (Fig. 283.4) .....
.....*Pseudospeonomus*

Genus ***Parvospeonomus*** Bellés & Escolà, 1977
Speonomus (*Parvospeonomus*) Bellés & Escolà, 1977: 33.
Parvospeonomus Bellés & Escolà: Fresneda, 1998: 73.

Type species. *Speonomus urgellesi* Español, 1965 by original designation (habitus in Fig. 282.1).

Diagnosis. Size ranging between 1.7-3.2 mm. Regular body outline or with a pronotum-elytral angle being clearly visible; all species markedly convex (Fig. 282.1). Irregular body punctation on the head and pronotum, which forms transverse striolae on the elytra.

Antennae: Relatively short for the group, just reaching or very little exceed half the body length; all the antennomeres longer than wide, except the 8th which is subglobose, thickening from the 7th antennomere on towards the end. Females with the antennae slightly shorter in proportion to the overall size difference.

Pronotum: Transverse and its widest point at the base or a slightly before; the base may be slightly wider, narrower, or equal to that of the elytra, lateral margins strongly and regularly narrowing towards the anterior margin.

Elytra: Slightly longer than wide, widest point around the anterior half or basal third; in the posterior region they taper in a regular curve towards the apex; there is a parasutural stria.

Legs: Short, and male protarsus not dilated, except in *P. canyellesi* here a slight dilatation is observed; tibiae with internal pectinate spurs.

Mesoventral keel (Fig. 282.3): High, with the anterior border convex and flanged, it forms a right angle with a hooked vertex; slightly convex lower border and rounded ridge; posterior process does not extend over metaventrite.

Suture of the metaventrite (Fig. 282.3): Slightly separated from the edge of the mesocoxal cavity, it delimits a narrow and elongated area.

Metatergal apparatus (Fig. 282.5): With the metascutum very narrow and long; the apophyses of the alacrista reduced with pointed apices.

Metendosternite (Fig. 282.7): Furcal arms much longer than the furcal trunk, slightly sinuous and the terminal apophysis well-developed; posterior lamina very narrow in the middle part, so that the posterior rim is almost in contact with the anterior rim. Furcal trunk longer than the area of greatest basal width and the median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 283.1), curved from the base to the apex, but in the centre the curvature is little accentuated; in the dorsal region the structure is curving at the two tips, basal and apical areas; apex prolonged ending in a blunt tip.

Endophallus (Fig. 283.3): Divided into three regions. In the basal region there is a «Y»- piece whose symmetrical arms are connect to the muscular bundles of the basal region but do not come into contact with the phanerae of the middle region; on both sides of the «Y»-piece are adjoining phanerae that extend along the sides of the sac to the dorsal phanerae in the middle region; in this same region there are two ventral and two dorsal phanerae; two muscular bundles originating in the armor of the axial piece which is descending towards the basal region along the sides of the sac; there are no dorsal bags, yet their appendages do seem to exist; in the apical region, the reinforcing bands are visible, with their inner margin thickened and noticeably more sclerotized than the rest of the structure.

Parameres (Fig. 283.5): As long as median lobe; apical end widening so that an elongated cavity is formed, in its interior a penicillum with long and numerous hairs is present; three robust setae, of equal length and thickness, are inserted in the margin of the cavity.

Spermathecal complex (Fig. 283.7, 283.8): Spermatheca regularly curved from base to apex, with hyaline median region; basal lobe slightly larger than the middle region and apical lobe spherical and also somewhat thickened, both lobes well sclerotized; near the base in a ventral position equipped with a tiny nodule through which the spermatic duct empties into the basal lobe; in that same place there is the spermathecal gland; spermatic duct thin and about 18-20 times longer than the spermatheca; at the point of insertion with the copulatrix bursa thickened and surrounded by a basal process in the form of a wide ring.

Female uroventrite VIII (Fig. 283.10): Spiculum fine and elongated or equally fine but short.

Discussion. In the phylogenetic tree (Fig. 1C) *Parvospeonomus* is sister of *Pseudospeonomus* with a high support, 99.6/100. The genus is characterised by morphological characters such as the apex of the parameres are equipped with three quite robust and long setae, and the dense penicillum that is inserted inside a cavity or depression. The endophallus was studied in detail by Bellés (1984) who established the nomenclature of numerous pieces that form the sac. The endophallus model is strongly resembling that of *Vanderberghia* gen. nov. – *Speonomus* of the «*speluncarum*» group – among the Iberian genera; the phanerae attached to the «Y»-piece of the dorsal complex form a structure that is only found in this endophallus model, in the genus *Naspunius* and in the genera from the Basque-Navarrese foothills, including *Zariquieyella* (ex. *Bathysciola* of the «*schiodtei*» group) that extend into the Central Pyrenees along both slopes. It is certain that among of all of these, the most similar is that of *Vanderberghia* gen. nov. However, in the apical region of *Parvospeonomus* there is a wrinkled membranous bag, located between the reinforcing bands, while in the other genus there are two bags, densely covered with spicules; also, the apex of the parameres is very similar since they are similar by exhibiting a cavity, a dense penicillum inside it and three differentiated setae.

The taxonomic classification of this genus has undergone numerous profound changes since Fairmaire (1860) described *Adelops delarouzeei*. Until 1974, a total of nine taxa had been described, but their differentiation using morphological criteria was highly problematic, given the great intraspecies variability, especially in the *P. delarouzeei* complex. Bellés (1974) reviewed the group of species – at that time included in the genus *Speonomus*, section I of Jeannel (1924a) – and only considered four of them valid species, regarding the rest as synonyms for *P. delarouzeei*. Bellés & Escolà (1977) described the subgenus *Parvospeonomus* for this group, maintaining the naming of the endophallus structure as described by Bellés (1974). Subsequently, Delay *et al*. (1980) studied the enzymatic systems of the *P. delarouzeei* complex to establish the genetic differences between different populations and, in conclusion, rehabilitated the species *P. brucki*, a criterion reaffirmed by Juberthie *et al*. (1984) based on ecological, ethological, morphometric and biogeographical data. Also the ethological studies of Juberthie-Jupeau & Cazals (1984a, 1984b, 1984c, 1985a, 1985b, 1988, 1989a, 1989b, 1991b), as well as Juberthie and co-workers study (1984) on enzyme polymorphism, seem to lead

to an interpretation opposing that of Bellés (1974). In any case, the studies of the researchers of the *Laboratoire Souterraine* of the C.N.R.S. in Moulis (Saint-Girons, France) were continuiously working on specimens clearly beloning to new species but without describing them formally. Nevertheless these new species were named and referred to in a series of studies by different names: *Speonomus charlottae*, *S. emiliae* and *S. galdarensis* (*Nomen nudum sensu* Perreau 2000). Perreau (2000) in his catalogue, adopted the unfinished taxonomic arrangement of the Moulis researchers, although emphasising the fact that the formal taxonomic act of description had not taken place. In the list of species, the distribution of Perreau (2004) has been followed, although the molecular data show that it is necessary to change the taxonomic classification of some taxa. But no molecular data are available for *P. d. brucki*, *P. d. delarouzeei*, *P. d. faurai* and *P. d. faurai esponellai* so consequently, no taxonomic classification has yet been proposed.

Distribution. France and Spain. This genus has eight species that are distributed from the Tech and Têt valleys in the eastern Pyrenees on the northern slope of the Pyrenees, to the pre-coastal – Montseny – and Catalan coastal – Montnegre – mountain ranges to the south, and from the Llobregat river to the west to areas close to the Mediterranean coast to the east (Escolà & Bellés 1984; Fresneda & Salgado 2017).

Species

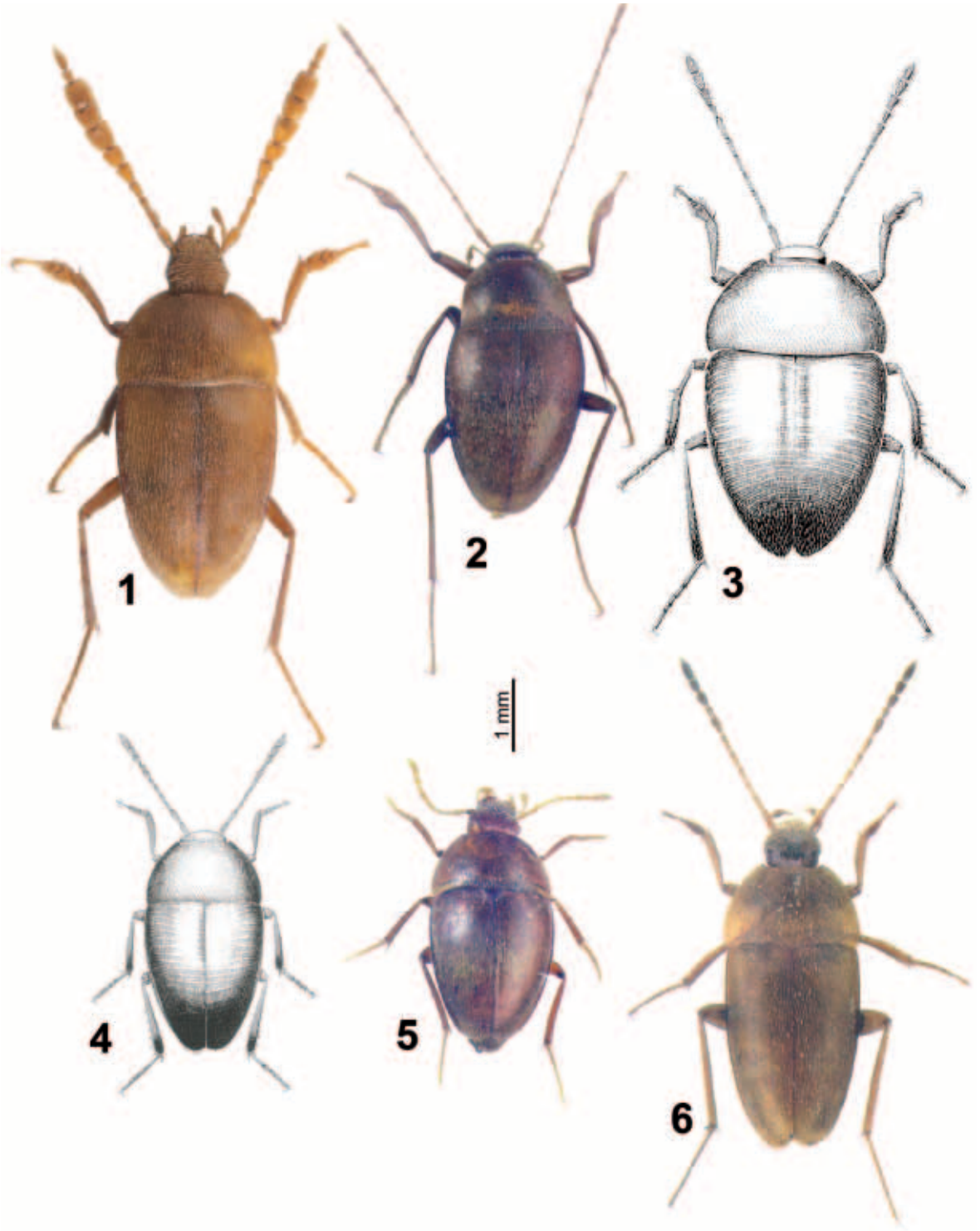
Parvospeonomus canyellesi (Lagar, 1974)
Speonomus canyellesi Lagar, 1974b: 28.
Parvospeonomus canyellesi (Lagar, 1974): Fresneda, 1998: 72.

Parvospeonomus cruillensis Comas, 2021
Parvospeonomus cruillensis Comas, 2021: 30.

Parvospeonomus delarouzeei (Fairmaire, 1860)
Parvospeonomus delarouzeei brucki (Fairmaire, 1863)
Adelops Bruckii Fairmaire, 1863: 8.
Bathyscia (*Bathyscia*) *Delarouzeei* Fairmaire: Reitter, 1885 [1884]: 32.
Speonomus brucki (Fairmaire): Delay, Sbordoni, Cobolli-Sbordoni & Matthaeis, 1980: 235.
Parvospeonomus delarouzeei brucki (Fairmaire): Perreau, 2000: 307.
Parvospeonomus delarouzeei catalonicus (Jeannel, 1910)
Speonomus Delarouzeei catalonicus Jeannel, 1910b: 154.
Adelops martorelli: Zariquiey, 1922a: 123 (*Nomen nudum*).
Speonomus catalonicus (Jeannel): Juberthie-Jupeau & Cazals, 1984a: 171.
Speonomus delarouzeei (Fairmaire): Bellés & Pallarès, 1985: 7.
Parvospeonomus delarouzeei catalonicus (Jeannel): Perreau, 2000: 307.
Parvospeonomus delarouzeei delarouzeei (Fairmaire, 1860)
Adelops Delarouzeei Fairmaire, 1860: 631.
Speonomus charlottae: Juberthie-Jupeau & Cazals, 1987: 63 (*Nomen nudum*).
Speonomus emiliae: Juberthie-Jupeau & Cazals, 1987: 63 (*Nomen nudum*).
Speonomus galdarensis: Moldovan, 1998: 85 (*Nomen nudum*).
Bathyscia Delarouzeei (Fairmaire): Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *Delarouzeei* Fairm.: Reitter, 1885 [1884]: 32.
Speonomus (s. str.) *Delarouzeei* (Fairmaire): Jeannel, 1910a: 32.
Speonomus (s. str.) *delarouzeei* (Fairmaire): Español, 1956: 111
Speonomus (*Parvospeonomus*) *delarouzeei* s. l.: Bellès, 1984: 7.
Parvospeonomus delarouzeei (Fairmaire, 1860): Fresneda, 1998: 74.
Parvospeonomus delarouzeei delarouzeei (Fairmaire): Perreau, 2000: 307.
Parvospeonomus delarouzeei faurai (Jeannel, 1910)
Speonomus (s. str.) *Faurai* Jeannel, 1910b: 153.
Parvospeonomus delarouzei (Fairmaire, 1860): Fresneda, 1998: 74.
Parvospeonomus delarouzei faurai (Jeannel): Perreau, 2000: 307.
Parvospeonomus delarouzeei guimjuani (Zariquiey, 1919)
Speonomus guimjuani Zariquiey, 1919: 46.
Speonomus faurai esponellai Zariquiey, 1940: 533.
Speonomus (s. str.) *Delarouzeei* Subsp. *Guimjuani* Zariquiey, 1919: Jeannel, 1924a: 150.
Parvospeonomus faurai esponellai (Zariquiey): Perreau, 2000: 308.

Parvospeonomus garrigai Comas, 2021
Parvospeonomus garrigai Comas, 2021: 32.

Parvospeonomus urgellesi (Español, 1965)
Speonomus (s. str.) *urgellesi* Español, 1965b [1964]: 55.
Speonomus urgellesi Español: Bellés, 1973b: 63.



FIGURES 284.1–284.6: *Speonomus* series, *Bathysciella* group. Habitus of: (**1**) *Baronniesia delioti* (modified from Fresneda *et al*., 2009), (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**6**) *Vanderberghia speluncarum speluncarum* **comb. nov.** Figs **3**, **4**, **6** modified from Salgado *et al.* (2008).

Parvospeonomus urgellesi (Español, 1965): Fresneda, 1998: 74.

Parvospeonomus vilarrubiasi (Zariquiey, 1940)
Speonomus vilarrubiasi Zariquiey, 1940: 532.
Speonomus (*Speonomus*) *vilarrubiasi* Zariquiey: Lagar, 1954: 251.
Speonomus (*Parvospeonomus*) *vilarrubiasi* Zariquiey: Bellès, 1984: 7.
Parvospeonomus vilarrubiasi (Zariquiey): Fresneda, 1998: 75.

Genus ***Pseudospeonomus*** Comas, Fresneda & Salgado, 2007
Pseudochlamys Comas, 1977c: 136 (*Nom. praeocc*. Homonymy with *Pseudochlamys* Lacordaire, 1848 – Coleoptera –.
Pseudospeonomus Comas, Fresneda & Salgado, 2007: 123 (Substitution name).

Type species. *Anillochlamys raholai* Zariquiey, 1922 by original designation (habitus in Fig. 282.2).

Diagnosis. Size ranging between 1.9-2.1 mm. Body contour regularly curved and not very convex (Fig. 282.2). Integument surface with fairly deep impressed dots on the head and very small dots on the pronotum, somewhat rough and irregularly arranged on the elytra, without transverse striolae.

Antennae: Of 11 antennomeres slightly exceeding the middle of the body, with segments 9-11 strongly enlarged and the 8th subglobose.

Pronotum: With regularly arched lateral margins and widest point before base; posterior angles right.

Elytra: Elliptical, continuing the curvature of the sides of the pronotum and widest at the base; no parasutural stria.

Legs: Tibiae with bifid internal spurs.

Mesoventral carina (Fig. 282.4): High and forms an obtuse angle with the vertex hooked; anterior border notched and lined from end to end, and inferior border convex, with a sharp arista; it does not extend over the metaventrite.

Suture of the metaventrite (Fig. 282.4): Contiguous from end to end to the edge of the mesocoxal cavity; it delimits a very narrow and elongated area.

Metatergal apparatus (Fig. 282.6): With the metascutum very narrow and very long; the apophysis of the alacrista almost non-existent and the apices blunt.

Metendosternite (Fig. 282.8): Furcal arms very long almost three times as long as the furcal trunk, slightly sinuous and the terminal apophysis small; posterior furcal plate narrow, progressively narrowing towards the apex. Furcal trunk short, as wide as long and the keel median posteriorly strongly widened divergence.

Median lobe of aedeagus: In lateral view (Fig. 283.2) regularly curved, with a marked depression and sinuous towards the apical quarter. In dorsal view very robust, with the median region very widened, with sub-parallel sides, and the apex in the form of an arc;.

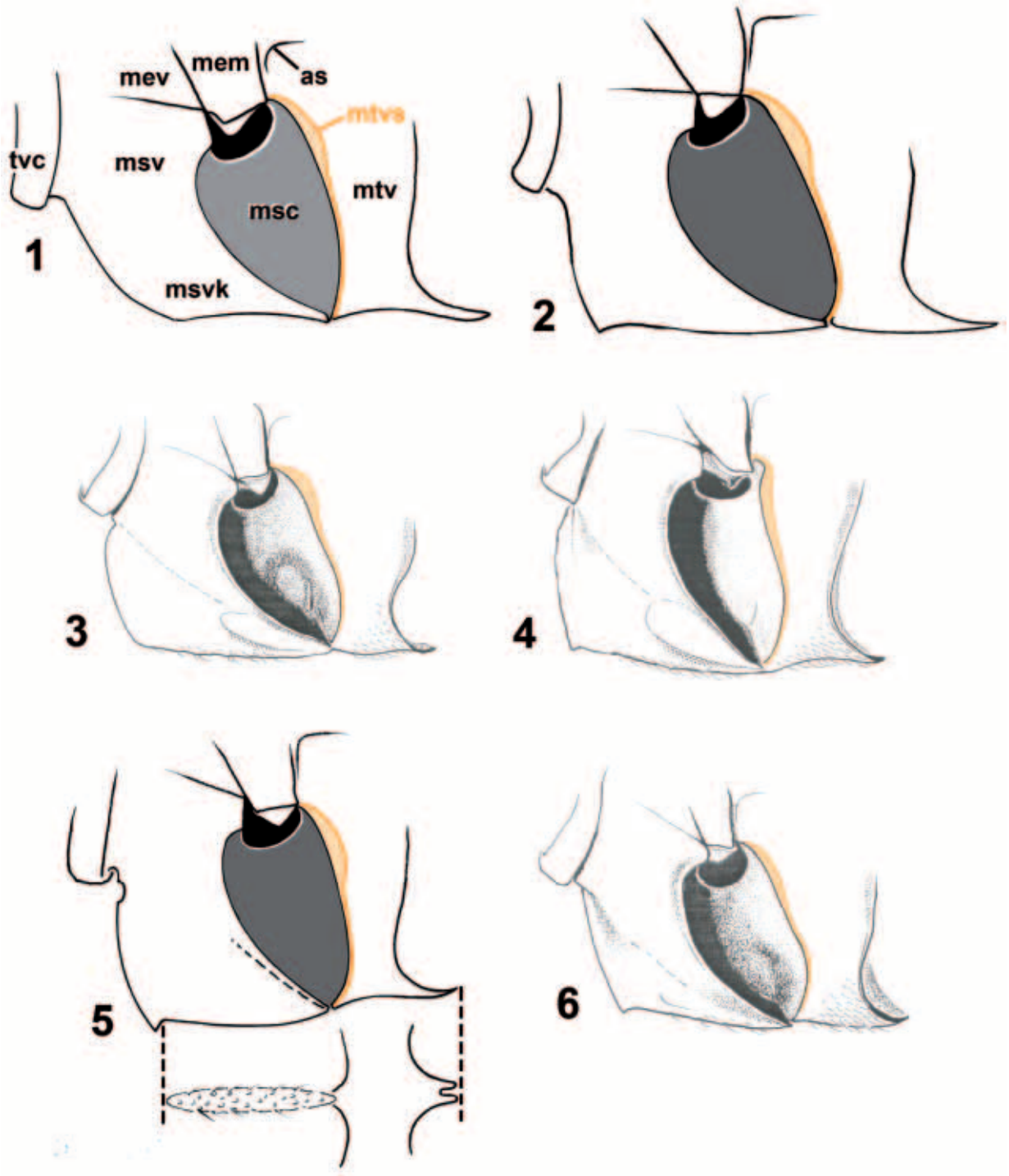
Endophallus (Fig. 283.4): In the basal region a sclerotized ring covered with teeth on its inner margin, but not a defined «Y»-piece; there are two reinforcing bands with the surface of the basal half covered with spicules and two long, very fine phanerae in the outermost position; in an axial situation, can be observed two hyaline triangular pieces symmetrical in relation to the axis of symmetry of the endophallus.

Parameres (Fig. 283.6): Shorter than the median lobe, slender and arched, with a sharp apical prolongation and three long, slightly curved, thin setae.

Spermathecal complex (Fig. 283.9): Spermatheca long, narrow and uniformly hyaline; apical lobe minute and spherical, and the basal elbowed, longer and wider in the posterior part; junction duct long, rough on ventral side and slightly narrower than basal lobe; spermatic duct short, inserts into the copulatory bag lacking any sclerotized connecting piece, this duct widens and is progressively sclerotising near the point of insertion with the spermatheca; there is a well-developed spermathecal gland.

VIII female uroventrite (Fig. 283.11): Spiculum slightly elongated and fine, with the apex truncated.

Discussion. In the phylogenetic tree (FIG. 1C) *Pseudospeonomus* is sister of *Parvospeonomus* with a high support, 99.6/100 (Fig. 1C). This taxon was described as a subgenus of *Anillochlamys* (Comas 1977b) and later the classification was changed into a genus (Bellés *et al*. 1978). The peculiarities of the endophallus, with a basal denticulate ring, without «Y»-piece, and two axial phanerae, which are not found in any of the genera of the *Spelaeochlamys* series, nor in *Parvospeonomus* (its sister group), are very clearly distinct morphological features justifying to assign it to the taxonomic group based on morphological characteristics alone. The median lobe of aedeagus, strongly sinuous in the apical third or fourth, is common in *Anillochlamys*, *Paranillochlamys* and *Spelaeochlamys*, might be just a misleading coincidence caused by evolutionary convergence. There is no character that relates it to *Parvospeonomus* and only molecular study



FIGURES 285.1–285.6: *Speonomus* series, *Bathysciella* group. Pterothorax lateral view of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.,** (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.,** (**6**) *Vanderberghia lopezsellesi* **comb. nov.** Figs **3**, **4**, **6** modified from Salgado *et al.* (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

may hinted to its «real» relationship based showing to which group it belongs to; hence it appears not to be a coincidence that its geographic distribution area is adjacent to that of *Parvospeonomus*.

Distribution. Spain. It colonises the mountainous foothills of Cap de Creus that form the northern coast of the province of Girona. Cova Tassana is the typical locality, in Cadaqués (Zariquiey 1922a, 1922b). It is also known from the Cau del Lliri, Malaterra and Guineu caves, all in Roses.

Species

Pseudospeonomus raholai (Zariquiey, 1922)
Anillochlamys raholai Zariquiey, 1922: 159.
Anillochlamys raholai luis-bofilli Zariquiey, 1940: 529.
Anillochlamys (*Pseudochlamys*) *raholai* Zar.: Comas, 1977c: 136.
Pseudochlamys raholai (Zariquiey): Bellés, Comás, Escolà & Español, 1978: 62.
Pseudochlamys raholai luisbofilli (Zariquiey): Bellés, Comás, Escolà & Español, 1978: 62.
Pseudospeonomus raholai (Zariquiey): Comas, Fresneda & Salgado, 2007: 124.

3.4.8.3 ***Bathysciella*** group

Diagnosis. Bathyscioid facies (Figs 284.1-284.6). Reddish colouration and integument entirely covered by fine, short, lying-down and yellowish pubescence. Depigmented.

Head: With the occipital carina complete, although poorly marked. Epistomal suture slightly curved, almost straight and almost always dark. Last article of maxillary palps short and conical. Anophthalmous.

Antennae: With eleven segments somewhat thickened from the 7th antennomere (the 8th reduced), except in one case in which the male has them strongly dilated and flattened from the 5th to the 9th antennomere; variable length depending on the genera and on being slightly longer than half the length of the elytral suture or longer than all of it.

Pronotum: Normally transverse with sides regularly arched from anterior to posterior angles, although in one case it is bell-shaped (*Bathysciella jeanneli*), with acute posterior angles and protruding vertices.

Elytra: Without parasutural stria, in some cases it may be indicated by a longitudinal depression; transverse striolation more or less defined.

Legs: Protarsi pentamerous in males and tetramerous in females.

Mesoventral keel (Figs 285.1-285.6): Elevated or low and does not extend over the metaventrite.

Suture of the metaventrite (Figs 285.1-285.6): close to the edge of the mesocoxal cavity, the area that it delimits narrow and elongated.

Metatergal apparatus (Figs 286.1-286.5): With broad metascutum wings and very reduced alacrista apophyses.

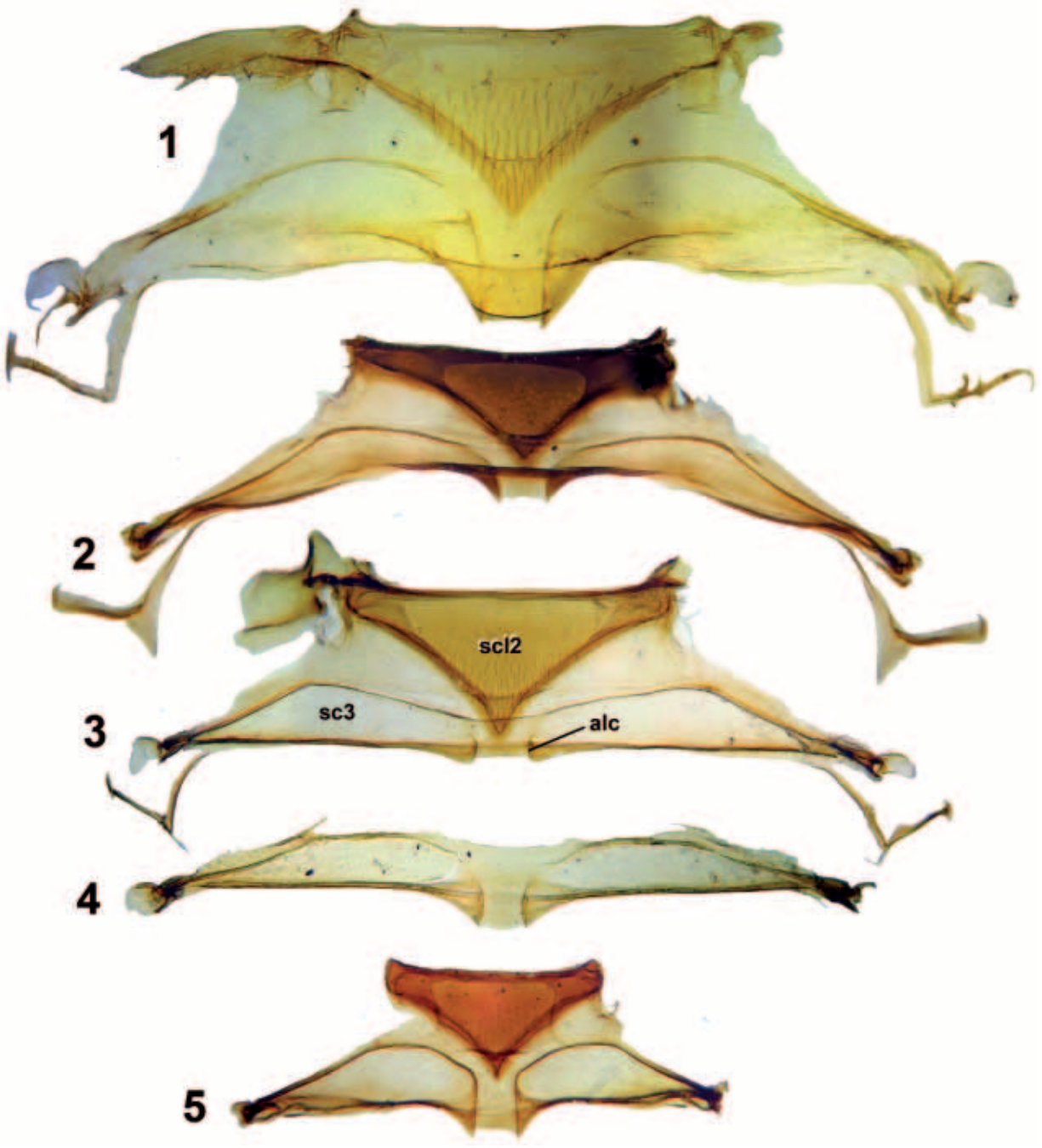
Metendosternite (Figs 287.1-287.6): In «Y», with the median furcal keel shorter than the anterior furcal suture, except in the genera of the clade *Baronniesia*.

Male genital segment: Very reduced, open and with two long pedunculus.

Endophallus: With three regions. Two models that will be described in detail for each genus separately in their description.

Spermathecal complex (Figs 291.1-291.6): Spermatheca of «type 1» *sensu* Perreau (1989) thin and elongated, slightly curved from one extremity to the other and with two well-differentiated lobes.

Discussion. In the phylogenetic tree (Fig. 1C), the entire *Bathysciella* clade is linked with a support of 98/100, moreover the *Bathysciella* group clade appears as a sister to the *Speonomus*, *Antrocharis* and *Troglophyes* groups with high support of 99.4/100. This is concerning the morphological structure of the genitalia a polymorphous group. Except in *Baronniesia*, all other genera have the parameres with two or three not very long setae masked by a dense penicillum found within a cavity. This character is shared with *Parvospeonomus*, *Ceretophyes-Perriniella-Troglophyes* or *Batinoscelis*; which are scattered throughout other branches of the phylogenetic tree, indicating that there are either further revisions needed after more complete sampling and availability of more molecular data or that this a is not a taxonomically valuable character. In *Bathysciella* sensu novo the apical reinforcing bands of the endophallus are inserted into thick, strongly sclerotized nodules, and they are fixed on membranous ligules in its sister group *Vanderberghia* gen. nov. and in *Machaeroscelis* stat. nov.; in *Bellesia* there are four densely pubescent apical reinforcement bands and in *Baronniesia* the endophallus has two inverted «M»-phanerae. Dupré (1989) indicates that *Speonomus rudauxi* must belong to the subgenus *Phacomorphoides*; however, Perreau (2000, 2004) includes the species in the *Speonomus* group «*zophosinus*». Geographically, the hypothesis of Dupré (1989) is more plausible, although for this same reason it would also be possible that it could be incorporated into the genus *Vanderberghia* gen. nov. – *Spe-*



FIGURES 286.1–286.5: *Speonomus* series, *Bathysciella* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *Bellesia espanyoli,* (**4**) *Machaeroscelis infernus infernus* **comb. nov.**, (**5**) *Vanderberghia bourgoini* **comb. nov.** Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

onomus of the «*speluncarum*» group of Jeannel (1947e) – that is described in this work. Until more data is available, it will be included in the section dedicated to the *Incertae sedis* of the clade. Given its position in the clade, it is not easy to explain why *Baronniesia* does not have a penicillum or a cavity at the apex of the parameres, a conformation that it shares with *Antrocharis*, *Gesciella* and *Paratroglophyes*. Furthermore, *Baronniesia* also concurs with these in having two additional strongly sclerotized phanerae forming an inverted «M» in the endophallus. This could be the archaic state of some structures that have been transmitted to the branches of the tree and resurface within clades that already have the penicillum derived state. *Perriniella-Troglophyes-Ceretophyes*, a sister group of the *Antrocharis* clade, exhibit these derived structures, as do all representatives of the *Speonomus* group (except *Troglocharinus orcinus* and subspecies).

Key to genera

1. Median lobe of aedeagus with a marked dorsal depression and no bulge on the anterior margin (Figs 288.6, 288.7). Parameres with an elongated and triangular cavity in the apical part in which are inserted the setae and a dense penicillum (Fig. 290.6). Middle region of the endophallus with well-sclerotized and developed phanerae, two divergent dorsal ones and two ventral ones that, when joined by the apical parts, form a horseshoe structure; also in the middle apical part of this region there are two bags of integument covered with spinules, generally robust, between the bases of the reinforcing bands (Fig. 289.9) .... *Vanderberghia* gen. nov.
- Median lobe of aedeagus without dorsal depression, if it exists there is a bulge on the anterior margin (Figs 288.1-288.5). Parameres with or without penicillum, if it is present the cavity is oval or rounded (Figs 290.1-290.5). Middle region of the endophallus with different arrangement of the dorsal and ventral phanerae, these do not form a horseshoe structure and in the middle apical area between the bases of the reinforcing bands no bags covered with spinules are observed (Figs 289.1-289.4, 289.7-289.9) 2

2. Male antennae with the 5th to 9th antennomeres strongly enlarged, and the 10th and 11th antennomeres reduced. Transverse striolae poorly defined, only in the basal area of the elytra. Mesoventral keel low, with rounded edges (Fig. 285.1). Metendosternite with the furcal arms shorter than the furcal trunk (Fig. 287.1). Parameres with three apical setae, without cavity or penicillum (Fig. 290.1). Endophallus with two sclerotized pieces that form an inverted «M» in the apical area of the median region and reinforcing bands in the apical region with rounded and sclerotized bases that are inserted into atrial-shaped structures (Fig. 289.7) .....*Baronniesia*
- Antennae of the males with the segments of normal structure, generally filiform and the antennomeres of the club being somewhat more dilated. Transverse striolae well defined throughout the elytra. Mesoventral keel high, with the apex hooked or sharp, rarely rounded (Figs 285.2-285.5). Metendosternite with the furcal arms as long as or longer than the furcal trunk (Fig. 287.2-287.5). Parameres with three setae in the apical area, existing cavity and penicillum (Figs 290.2-290.5). Endophallus with different sclerotized pieces in the apical part of the middle region and reinforcing bands of the apical region inserted in a membranous or sclerotized tegument (Figs 289.2-289.4, 289.8).....3

3. Metafemora of males with a femoral spine on the posterior border, except *B. jeanneli*. Median lobe of aedeagus, in lateral view, with a dorsal depression and a more or less pointed protuberance on the anterior margin; the sharp apex curved towards the dorsal or ventral side (Fig. 288.2). Apical region of the endophallus with a pair of short reinforcing bands implanted on irregular sclerotized nodules and, between them, in the centre of the apical part of the middle region, there is an «X»-piece or some sclerotized strips (Fig. 289.2) .....*Bathysciella* sensu novo
- Metafemora of males without femoral spine. Median lobe of aedeagus, in lateral view, without depression or dorsal protuberance and the apex more or less sharp that curves towards the ventral side (Figs 288.4, 288.5). Apical region of the endophallus with a pair of long reinforcing bands or four covered with spinules, in both cases they are not implanted on sclerotized nodules and between them no «X»-piece or sclerotized strips (Figs 289.4, 289.8) 4

4. Parasutural stria of the elytra with a depression along the medial and anterior areas. Male protarsomeres not dilated. Apical part of the furcal arms of the metendosternite with terminal apophysis, although poorly developed (Fig. 287.5). Apical region of the endophallus with a pair of long reinforcing bands that rest on membranous ligules and between them, in the centre of the apical part of the middle region, there is an axial piece flanked by two phanerae with a triangu-



FIGURES 287.1–287.6: *Speonomus* series, *Bathysciella* group. Metendosternite of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**6**) *Vanderberghia gaudini arivensis* **comb. nov.**

lar base, and the whole is covered by a striated and scaly tissue (Fig. 289.4) .....*Machaeroscelis* stat. nov.
- Parasutural stria of the elytra without depression. Males protarsomeres dilated. Apical part of the furcal arms of the metendosternite without terminal apophysis (Fig. 287.4). Apical region of the endophallus with four thick reinforcing bands that rest on large membranous bags covered with spinules and, between them, in the centre of the apical area without other structures (Fig. 289.8).....*Bellesia*

Genus ***Baronniesia*** Fresneda, Bourdeau & Faille, 2009
Baronniesia Fresneda, Bourdeau & Faille, 2009b: 2.

TYPE SPECIES. *Baronniesia delioti* Fresneda, Bourdeau & Faille, 2009 by original designation (habitus in Fig. 284.1).

DIAGNOSIS. Size ranging between 4.0 and 5.0 mm. Bathyscioid facies (Fig. 284.1). Integument of the pronotum marked by irregular punctation; elytra strongly punctuated; punctures wide and rough, forming poorly defined transverse grooves, especially in the front area.

Antennae: A little shorter than the elytral suture, with the male's antennomeres strongly thickened: first globulous, second to the 4th progressively wider and 5th to the 9th strongly widened forming a palette, 10th and 11th very small. Female antennae filiform.

Pronotum: Transverse, very slightly wider than long, with the sides regularly curved and the greatest width in the basal third; base very sinuous and posterior angles with a very rounded apex.

Elytra: Acuminate, with strongly tapering margins towards the apex and slightly convex; with elytral-pronotum angle very obtuse; elytra elongated and wide, depressed, without parasutural stria.

Legs: Male protarsomeres strongly dilated, the first wider than the distal end of the protibia. Hairy tibiae with two pectinate internal spurs, two simple external ones, a series of unequal spines between both and distant spines on the external face; protibiae tapered, mesotibiae curved, and metatibiae straight.

Mesoventral keel (Fig. 285.1): Low, with rounded edges and vertex and a narrow edge ridge, it does not extend over the metaventrite.

Suture of the metaventrite (Fig. 285.1): Defines a very narrow area along the edge of the mesocoxal cavity.

Metatergal apparatus (Fig. 286.1): With the wings of the metascutum rather short and wide, the alacrista poorly developed and the apices very pointed.

Metendosternite (Fig. 287.1): Furcal arms straight and shorter than the furcal trunk, the apex arched and the tip pointed, without terminal apophysis; posterior lamina somewhat narrower in the apical area, with a wide and smooth arched edge. Furcal trunk clearly longer than the part of greatest basal width and the median keel with the posterior divergence widened and elongated.

Median lobe of aedeagus: Curved in obtuse angle in lateral view (Fig. 288.1), but without any depression or sinuosity; decreases regularly from the base to the apex, which is strongly curved in the central part; terminal tip strongly curved in the ventral part; basal part proportionally large. Width decreasing from the base to the apex in dorsal view (Fig. 289.1); apex round with the central part truncated; lateral margins sinuated.

Endophallus (Fig. 289.7): Reinforcement bands only in apical section, very long and reaching the base, which is round and more sclerotized, inserted on two additional large ear-like setae located at the external apical part of the dorsals phanerae – «dorsal sac of the apex of the middle area» of Fresneda (1998) –. Middle area with dorsal and ventral phanerae and two additional slightly curved sclerotized pieces forming an inverted «M» located above the dorsal and ventral phanerae. Apical part of the «Y»-piece in the basal area, above the connection nodule very thin and elongated; setae associated with the «Y»-piece with a very sclerotized and large basal nodule; ventral basal complex very robust and sclerotized.

Parameres (Fig. 290.1): Shorter than the median lobe, very thin in all their length and carrying three long setae at the apex (one shorter), without any penicillum, cavity or membranous lamina.

Spermathecal complex (Fig. 291.1): Apical lobe of the spermatheca spherical and smaller than the basal lobe, with a spermathecal gland inserted at the same place as the spermiduct. Spermiduct 10-12 times longer than the spermatheca which gets larger close to the insertion with spermatheca and crosses a sclerotized disc at the contact with the bursa copulatrix. Main part of the spermiduct strongly curved in the surroundings of spermatheca.

Female uroventrite VIII (Fig. 292.1): With a spiculum wide and long, and a rounded apex.

DISCUSSION. In the phylogenetic tree (Fig. 1C), *Baronniesia* appears as a sister of *Bathysciella* sensu novo, *Machaeroscelis* stat. nov. and *Bellesia* genera with a support of 100/100. This genus is characterised by its large size, being one of the largest species of Lep-



FIGURES 288.1–288.7: *Speonomus* series, *Bathysciella* group. Aedeagus in lateral view of: (**1**) *Baronniesia delioti* (modified from Fresneda *et al*., 2009), (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**6**) *Vanderberghia lopezsellesi* **comb. nov.**, (**7**) *V. ehlersi* **comb. nov.** Figs **3**, **4**, **6** modified from Salgado *et al.* (2008).

todirini known from the Pyrenean chain. Sexual dimorphism is very accentuated: male with dilated pentamere protarsi, antennomeres 5th to 9th exceptionally wide, forming a sort of blade, filiform in females. Elytra strongly punctuated; punctures wide and rough, forming poorly defined transverse grooves.

DISTRIBUTION. France. Only known from the type locality, the subterranean river of Artigaléou-Arodets in Esparrós, Massif of Baronnies, Hautes-Pyrénées.

Species

Baronniesia delioti Fresneda, Bourdeau & Faille, 2009
Baronniesia delioti Fresneda, Bourdeau & Faille, 2009b: 8.

Genus ***Bathysciella*** Jeannel, 1906 sensu novo
Bathysciella Jeannel, 1906a: 23.
Phacomorphus Jeannel, 1908a: 60 syn. nov. (Type species: *Bathyscia Mascarauxi* Sainte Claire Deville, 1905).
Phacomorphus (*Phacomorphoides*) Dupré, 1996: 13 syn. nov. (Type species: *Bathyscia Alexinae* Jeannel, 1906).

TYPE SPECIES. *Bathyscia jeanneli* Abeille de Perrin, 1904 by monotypy (habitus in Fig. 284.2).

DIAGNOSIS. Size ranging between 2.6-4.7 mm. Body elongated (Fig. 284.2) or openly ovoid (Fig. 284.3). Integument of the pronotum marked by irregular punctation and of the elytra by thin and close transverse striolae.

Antennae: Longer or slightly shorter than the elytral suture, filiform and without a thickened club in both sexes.

Pronotum: Bell-shaped (*Bathysciella jeanneli*), with acute posterior angles, projecting vertices and rectilinear base; or strongly transverse (ex *Phacomorphus* s. str., in this work considered a synonym of *Bathysciella* sensu novo) with the sides strongly converging towards the apical edge, the posterior angles straight with the apex rounded and the base sinuous; or nearly as long as it is wide (ex *Phacomorphoides*, in this work considered a synonym of *Bathysciella* sensu novo) and regularly curved sides, straight back angles with rounded apex and sinuous base.

Elytra: Convex, long and wide or proportionally short and very wide, even strongly acuminate; no elytral-pronotum angle evident; parasutural stria marked by a longitudinal depression, not by points.

Legs: Male protarsomeres dilated; the first protarsomere being narrower or wider than the distal end of the protibia, depending on the species; male metafemora simple (*Bathysciella jeanneli*) or with femoral spine on their posterior edge; tibiae hairy, with two internal pectinate spurs, two simple external ones and a series of unequal spines between them; spines may be spaced apart on the external face (absent in *Bathysciella jeanneli*); straight protibiae, curved mesotibiae, and straight metatibiae.

Mesoventral keel (Figs 285.2, 285.3): High, with a well-marked or arched dentiform vertex, anterior border convex and rim, and posterior border slightly convex, with a rounded edge ridge; it does not extend over the metaventrite.

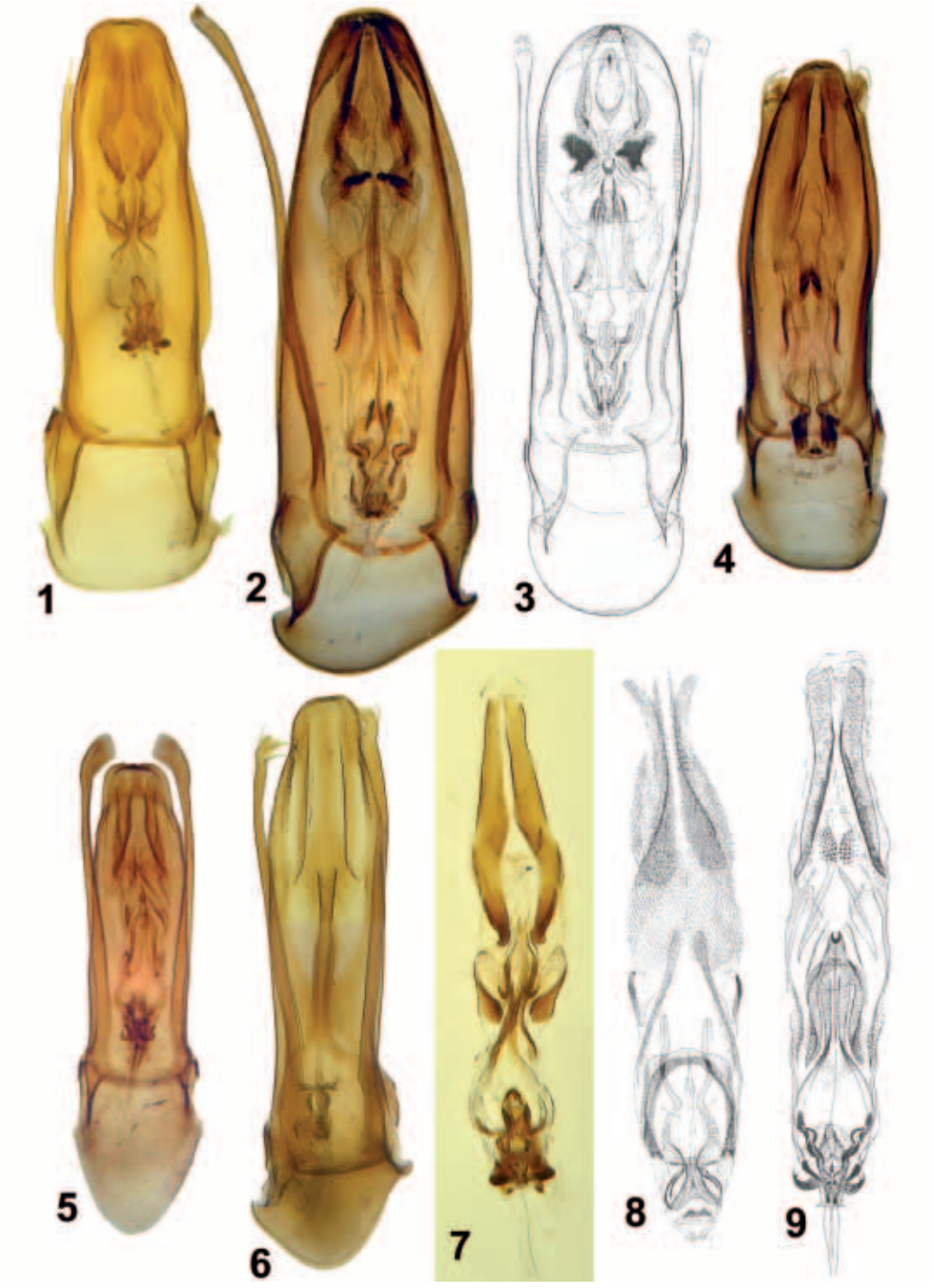
Suture of the metaventrite (Figs 285.2, 285.3): It runs a short distance from the edge of the mesocoxal cavity so that it delimits a narrow and elongated area, somewhat wider in the upper half.

Metatergal apparatus (Fig. 286.2): With the metascutum long and not very narrow; the alacrista poorly developed and the apices sharp.

Metendosternite (Figs 287.2, 287.3): Two models, one with the furcal arms longer than the furcal trunk, the other with the arms as long as the furcal trunk, in both cases the apex arched and the tip pointed, with the terminal apophysis well defined. Also, two forms in the posterior lamina of the furca, one with the same width along the arm, with a straight edge along the arm, and subrectilinear in the middle and in the trunk; another with the posterior lamina of the furca narrowed in the middle and the edge arched. Furcal trunk in one comparatively longer and in both the trunk is longer than the area of greatest basal width and the median keel with widened posterior divergence.

Median lobe of aedeagus: Little arched, with a very robust basal portion (Figs 288.2, 288.3). There is a marked dorsal notch that precedes a tooth in preapical position and the apex is sharp and curved towards the ventral side. Not in *Bathysciella jeanneli*, which lacks a tooth, without a marked notch, and the apex is sharp and curved towards the dorsal side. In dorsal view (Figs 289.2, 289.3) with sides regularly tapering from the base to the apex, which is broadly rounded.

Endophallus (Figs 289.2, 289.3): Characterised by having a slightly sclerotized «X»-shaped piece in the apical region and located between the apical reinforcement bands at its base, or in its absence, then there are some sclerotized pieces; also, because the apical rein-



FIGURES 289.1–289.9: *Speonomus* series, *Bathysciella* group. Aedeagus in dorsal view of: (**1**) *Baronniesia delioti* (modified from Fresneda *et al*., 2009), (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Machaeroscelis infernus infernus* **comb. nov.**, (**5**) *Vanderberghia orgibetensis* **comb. nov.** (**6**) *V. ehlersi* **comb. nov.** Endophallus of: (**7**) *Baronniesia delioti*, (**8**) *Bellesia espanyoli*, (**9**) *Vanderberghia lopezsellesi* **comb. nov.** Figs **3**, **8**, **9** modified from Salgado *et al.* (2008).

forcing bands are implanted on strongly sclerotized nodules with a very irregular shape.

Parameres (Figs 290.2, 290.3): With a cavity where a dense penicillum and three long and thick setae are inserted, one of apical insertion and two in the lateral-basal part below the cavity.

Spermathecal complex (Figs 291.2, 291.3): Tubuliform spermatheca, irregularly or regularly curved with spherical or elongated apical lobes, the basal one being longer; the hyaline junction duct narrower or as wide as the lobes. Spermiduct with annular or funnel-shaped basal process sclerotized at the point of insertion with the copulatory bag. There is a spermathecal gland that empties into the base of the proximal lobe.

Female uroventrite VIII (Figs 292.2, 292.3): With the spiculum short and reduced to a simple denticle.

Discussion. In the phylogenetic tree (Fig. 1C) and within the clade *Bathysciella* sensu novo group, the genus *Bathysciella* sensu novo is sister to the genera *Machaeroscelis* stat. nov. and *Bellesia* with a support of 84.3/100. This is an extremely polymorphic genus in terms of general body shape but uniform in terms of male genitalia, especially the endophallus. Dupré (1989) studied these structures in detail and in that article he stated «*A notre grande surprise, l'examen du sac interne révèle une armature identique, toutes proportions gardées, à celle de S. elgueae*»; *Speonomus elgueae* is the species used as a model for the description of the endophallus by Dupré (1989). He then described the details of shape and arrangement of the pieces that differentiate the genera and species that, in any case, share the established endophallus model. The topology of the clade in the phylogenetic tree and the uniformity of pattern of the endophallus lead to the synonymy of *Phacomorphus* and *Phacomorphoides* with *Bathysciella* sensu novo, the oldest name: *Bathysciella* Jeannel, 1906 = *Phacomorphus* Jeannel, 1908 syn. nov. = *Phacomorphoides* Dupré, 1996 syn. nov. The topology of the clade is *Bathysciella sioberi* comb. nov. (*B. ittana* comb. nov. (*B. alexinae* comb. nov. + *B. jeanneli*) together with (*B. mascarauxi* comb. nov. (*B. duprei* comb. nov. (*B. bordei* comb. nov. + *B. fratyi* comb. nov.))), where it can be observed that after a succession of cladogenesis *B. alexinae* comb. nov. is the sister species of *B. jeanneli* with very little genetic distance and good support, and the species that constituted *Phacomorphus* form a derived clade. Dupré (1989) raised the subspecies *arbaillensis* and *ittanus* to the rank of *bona species*.

Distribution. France. Pyrénées-Atlantiques, massifs of Arbailles, Igounze, Mendibeltza, Arradoy, Orhy, Vert de Barlanès river basin and upper La Nive river basin. Spain. Southern foothills of the Berrendi mountain range, on the left bank of the Irati river, Aezkoa valley, Navarra (Dupré 1987, 1989, 1996).

Species

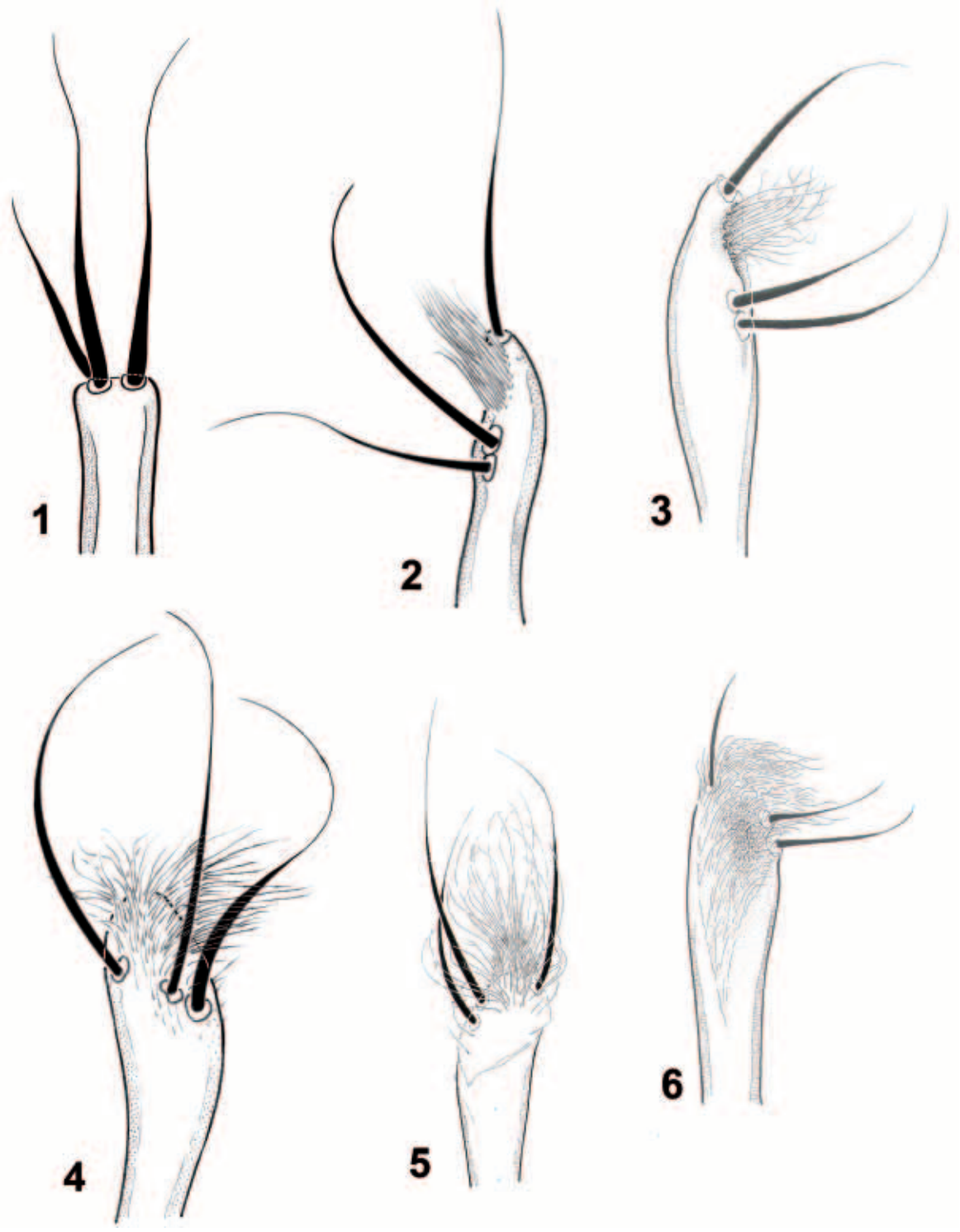
Bathysciella alexinae (Jeannel, 1906) comb. nov.
Bathyscia Alexinae Jeannel, 1906a: 23.
Speonomus Alexinae Jeannel: Jeannel, 1908a: 301.
Speonomus (*Phacomorphoides*) *alexinae* Jeannel: Dupré, 1989: 87.
Phacomorphus (*Phacomorphoides*) *alexinae alexinae* (Jeannel): Perreau, 2000: 309.

Bathysciella arbaillensis (Jeannel, 1952) comb. nov.
Speonomus (s. str.) *Sioberi* subsp. *arbaillensis* Jeannel, 1952a: 51.
Speonomus (*Phacomorphoides*) *sioberi arbaillensis* Jeannel: Dupré, 1989: 87.
Phacomorphus (*Phacomorphoides*) *sioberi arbaillensis* Jeannel: Perreau, 2004: 169.

Bathysciella bordei (Peyerimhoff, 1908) comb. nov.
Speonomus (*Phacomorphus*) *Bordei* Peyerimhoff, 1908: 302.
Phacomorphus Bordei Peyerimhoff: Fagniez, 1927: 21.
Speonomus (*Phacomorphus*) *bordei* Peyerimhoff: Laneyrie, 1988: 74.
Phacomorphus (s. str.) *bordei* (Peyerimhoff): Perreau, 2000: 310.

Bathysciella duprei (Laneyrie, 1988) comb. nov.
Speonomus (*Phacomorphus*) *duprei* Laneyrie, 1988: 77.
Phacomorphus (s. str) *duprei* (Laneyrie): Perreau, 2000: 310.

Bathysciella elgueae (Abeille de Perrin, 1904) comb. nov.
Bathyscia Elgueae Abeille de Perrin, 1904: 243.
Speonomus Elgueae Abeille: Jeannel, 1908b: 301.
Speonomus elgueae Abeille: Laneyrie, 1988: 71.
Speonomus (*Phacomorphus*) *elgueae* Abeille: Dupré, 1989: 86.
Phacomorphus (s. str.) *elgueae* (Abeille): Perreau, 2000: 310.



FIGURES 290.1–290.6: *Speonomus* series, *Bathysciella* group. Apex of the paramere of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**6**) *Vanderberghia lopezsellesi* **comb. nov.** Figs **3**, **5**, **6** modified from Salgado *et al.* (2008).

Bathysciella etchecoparti (Bellés & Déliot, 1983) comb. nov.
Speonomus etchecoparti Bellés & Déliot, 1983: 240.
Phacomorphus (s. str.) *etchecoparti* (Bellés & Déliot): Perreau, 2000: 310.

Bathysciella fratyi (Dupré, 1995) comb. nov.
Speonomus (*Phacomorphus*) *fratyi* Dupré, 1995: 4.
Phacomorphus (s. str.) *fratyi* (Dupré): Perreau, 2000: 310.

Bathysciella intermedia (Coiffait, 1947) comb. nov.
Speonomus intermedius Coiffait, 1947b: 76.
Speonomus (*Phacomorphus*) *intermedius* Coiff.: Coiffait, 1959a: 178.
Phacomorphus (s. str.) *intermedius* (Coiffait): Perreau, 2000: 311.

Bathysciella ittana (Jeannel, 1906) comb. nov.
Bathyscia Alexinae subsp. ittana Jeannel, 1906a: 24.
Speonomus Alexinae-ittanus Jeannel, 1906: Jeannel, 1908a: 304.
Speonomus (*Phacomorphoides*) *alexinae ittanus* Jeannel: Dupré, 1989: 87.
Phacomorphus (*Phacomorphoides*) *alexinae ittanus* (Jeannel): Perreau, 2000: 309.

Bathysciella jeanneli (Abeille de Perrin, 1904)
Bathyscia Jeanneli Abeille de Perrin, 1904: 242.
Bathysciella Jeanneli (Abeille): Jeannel, 1906a: 23.
Bathysciella jeanneli (Abeille): Deleurance, 1957: 2318.

Bathysciella mascarauxi (Sainte Claire Deville, 1905) comb. nov.
Bathyscia Mascarauxi Sainte Claire Deville, 1905a: 160.
Speonomus Mascarauxi Deville: Jeannel, 1908a: 301.
Speonomus (*Phacomorphus*) *Mascarauxi*: Jeannel, 1908b: 60.
Phacomorphus Mascarauxi Sainte Claire Deville: Fagniez, 1927: 21.
Phacomorphus (s. str.) *mascarauxi* (Sainte Claire Deville): Perreau, 2000: 311.

Bathysciella sioberi (Coiffait, 1947) comb. nov.
Speonomus Sioberi Coiffait, 1947a: 68.
Speonomus (*Phacomorphoides*) *sioberi* Coiffait: Dupré, 1989: 87.
Phacomorphus (*Phacomorphoides*) *sioberi sioberi* (Coiffait): Perreau, 2000: 310.

Bathysciella subsulcata (Coiffait, 1950) comb. nov.
Speonomus subsulcatus Coiffait, 1950b: 67.
Speonomus (*Phacomorphus*) *subsulcatus* Coiffait: Dupré, 1989: 86.
Phacomorphus (s. str.) *subsulcatus* (Coiffait): Perreau, 2000: 311.

Genus ***Bellesia*** Fresneda & Hernando, 1994
Bellesia Fresneda & Hernando, 1994b: 57.

Type species. *Speonomus espanyoli* Auroux & Bellés, 1974 by original designation (habitus in Fig. 284.4).

Diagnosis. Size ranging between 2.5-3.2 mm. Body ovoid, convex and regularly curved contour (Fig. 284.4). Sculpture of the tegument formed by irregular superficial punctation on the head and pronotum, and numerous fine transverse striolae on the elytra.

Antennae: Slightly longer than half the length of the elytral suture and the club slightly thickened.

Pronotum: With regularly arched lateral margins, widest at the base, and straight posterior angles.

Elytra: Elliptical continuing the curvature of the sides of the pronotum, with the greatest width in the basal quarter and without parasutural stria.

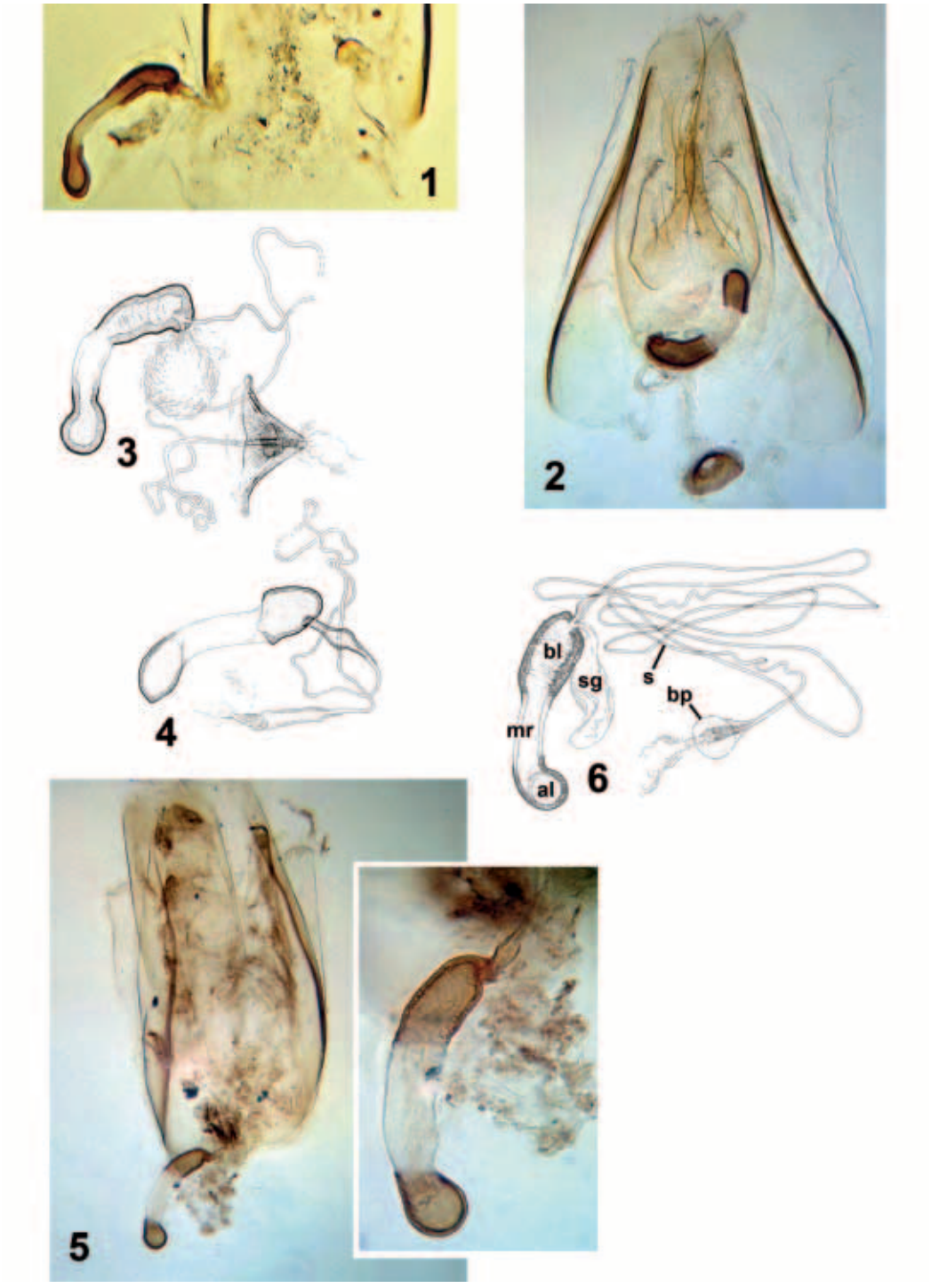
Legs: Proportionally short, with the protarsi not or slightly dilated in the male. Tibiae hairy, with two internal pectinate spurs, two simple external ones, a series of unequal spines between both and distant spines on the external face that are highly developed in the mesotibiae; straight protibiae, curved mesotibiae, and straight metatibiae.

Mesoventral keel (Fig. 285.4): High; anterior and inferior borders form an obtuse angle and hooked apex; the anterior border being slightly curved and framed and the inferior border very slightly curved and the ridge rounded.

Suture of the metaventrite (Fig. 285.4): Very close along the edge of the mesocoxal cavity, practically contiguous.

Metatergal apparatus (Fig. 286.3): With the metascutum very narrow and elongated, and the alacrista reduced, with only slightly pointed apices, almost blunt.

Metendosternite (Fig. 287.4): Furcal arms straight, long and slender, longer than the furcal trunk, the apex arched and the tip pointed, without terminal apophysis; posterior lamina narrow in the middle and slightly widened in the apical area, with a wide arched edge; edge of anterior furcal suture slightly concave. Furcal trunk much longer than area of greatest basal width and median keel with posterior divergence evident.



FIGURES 291.1–291.6: *Speonomus* series, *Bathysciella* group. Spermathecal complex of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**6**) *Vanderberghia ere* **comb. nov.** Abbreviations: **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland. Figs **3**, **4**, **6** modified from Salgado *et al.* (2008).

Median lobe of aedeagus: In lateral vision (Fig. 288.4) slightly curved; thick at the base and diminishes visibly towards the apex, which is prolonged into a narrow lamina.

Endophallus (Fig. 289.8): It presents in the apical region four thick reinforcing bands similar to bags densely covered with spicules; in the middle region there are two pairs of phanerae, and in the basal one there are a sclerotized ring and a short stylet.

Parameres (Fig. 290.5): As long as the median lobe, the apical part thick, funnel-shaped, with three setae and a highly developed penicillum implanted at the upper end of a cavity.

Spermathecal complex (Fig. 291.4): Characteristic spermatheca because it incorporates a lateral nodule in which the spermatic duct is inserted; this is about twice as long as the spermatheca and at the point of insertion with the copulatory bursa it is slightly thickened and somewhat sclerotized.

Female uroventrite VIII (Fig. 292.4): With a short and fine spiculum, and the apex somewhat thickened and spatula-shaped.

Discussion. In the phylogenetic tree (Fig. 1C) *Bellesia* is sister to *Machaeroscelis* stat. nov., both are linked with a high support 99.4/100. The very peculiar structure of the apical reinforcing bands of the endophallus is a synapomorphy of the genus. The basal axial structure of the endophallus of *Bellesia* constitutes a stylet similar to those so frequent in the genera of the *Quaestus* series; that is divided into two arms at the base, so that it resembles an inverted «Y»; this characteristic is what has been called «inverted «Y»-piece» that has served to characterize the genus *Speonomidius* (Bellés *et al*. 1978) and the genus *Josettekia* (Dupré 1991). Morphologically, it seems to be more closely related to *Josettekia* from Basque-Navarre foothills (due to the morphology of the basal region of the endophallus) than to those of its clade. With *Josettekia* it shares the character that the basal piece of the endophallus does not have the typical «Y»-piece. The true «Y»-piece – homologous to that of the *Speonomus* series models – in *Josettekia* (as observed in Dupré 1991) is slightly sclerotized and it actually forms a wide «U» whose arms go up the sides of the sac towards the middle region. The affinities of this taxon have been a real enigma since its model of endophallus is a derived state within the clade to which it belongs: it seems to have nothing in common with *Machaeroscelis* stat. nov., its sister genus. The existence of a membranous lamina at the apex of the parameres was an observational error by Fresneda & Hernando (1994) since the penicillum is actually found in a cavity: an apomorphy of the entire *Bathysciella* group to which it belongs.

Distribution. Spain. Iberian hypogeous endemism known from a single cave located in the Añisclo valley, Huesca, southern slope of the central Pyrenees.

Species

Bellesia espanyoli (Auroux & Bellés, 1974)
Speonomus espanyoli Auroux & Bellés, 1974: 86.
Bellesia espanyoli (Auroux & Bellés, 1974): Fresneda & Hernando, 1994b: 58.

Genus ***Machaeroscelis*** Jeannel, 1924 stat. nov.
Machaeroscelis Jeannel, 1924a: 131.

Type species. *Adelops infernus* Dieck, 1869 by original designation (habitus in Fig. 284.5).

Diagnosis. Size 2.5 mm. Body oval and very convex (Fig. 284.5); Integument of the pronotum marked by irregular punctation and on the elytra by regular and particularly fine transverse striolae.

Antennae: Considerably shorter than the elytral suture, though longer than half their length; antennomeres of the club thickened.

Pronotum: Transverse, wider than long, with regularly curved sides and wide apical border as befits a large head; straight posterior angles with the apex broadly rounded and the base somewhat sinuous.

Elytra: With margins regularly curved from end to end; no elytral-pronotum angle apparent; elytra short, broad, convex, with broadly rounded and dehiscent apices, and the parasutural stria indicated by a longitudinal depression, no dots are visible.

Legs: Short. Male protarsomeres not dilated; tibiae hairy, with two bifid internal spurs, two simple external ones, a series of unequal spines between them and spines on the external face; protibiae straight; mesotibiae and metatibiae strongly compressed, not cylindrical and bristling with spines as thick as the spurs, both straight.

Mesoventral keel (Fig. 285.5): High, at right angles to the hooked apex; anterior border sinuous, with the apical part strongly curved and ridged; ventral border convex with a wide, flat, pubescent and ridged.

Suture of the metaventrite (Fig. 285.5): Somewhat distant from the edge of the mesocoxal cavity and outlines an obvious elongated area.

Metatergal apparatus (Fig. 286.4): With the

metascutum very narrow and elongated, and the alacrista absolutely reduced with apices pointed.

Metendosternite (Fig. 287.5): Furcal arms straight, somewhat longer than the furcal trunk, the apex arched with poorly developed terminal apophysis; posterior lamina remains nearly the same width along the arm, with a smooth arcuate edge. Furcal trunk long, almost twice the area of greatest basal width and median keel with manifest posterior divergence.

Median lobe of aedeagus: Regularly curved from one to the other end and the basal portion ventrally thickened (Fig. 288.5); in dorsal view (Fig. 289.4) regularly tapered from base to apex which is broadly rounded; it is structurally simple.

Endophallus (Fig. 289.4): In the basal region there is a «Y»-piece with parallel arms connected by junction nodule to the apical fibres of the «Y»-piece, which extend towards the middle region; there are two large and strongly sclerotized phanerae or basal lamina on both sides of the «Y»-piece and in an axial position a basal ventral complex that looks like a stylet formed by two triangular phanerae with their apex in contact; on the sides there are two curved phanerae similar to a parenthesis. In the middle region there are some longitudinal fibres, next to the apical fibres of the «Y»-piece and two external phanerae that also form a kind of parenthesis; in the apical part of the middle region there is an axial piece flanked by two phanerae whose lower end is triangular; the whole set is covered by a striated and scaly tissue. In the apical region there are two reinforcement bands that rest on membranous ligules.

Parameres (Fig. 290.4): Shorter than the median lobe; apex somewhat laminar in appearance, armed with three long, quite robust setae and a dense penicillum inserted in a cavity.

Spermathecal complex (Fig. 291.5): Spermatheca elongated in a regular arch with the apical lobe spherical, the basal lobe elongated and both of them well sclerotized; between them a long hyaline junction duct similar in width to the lobes. The spermatic duct is joined to the spermatheca by a small nodule and to the copulatory bursa in an ill-defined but well-sclerotized basal process. There is a spermathecal gland.

Female uroventrite VIII (Fig. 292.5): Spiculum short, with truncated apex and triangular in shape as a whole.

Discussion. In the phylogenetic tree (Fig. 1C) *Machaeroscelis* stat. nov. is sister of *Bellesia* with support of 99.4/100. Cladogenesis involving the split from its sister genus *Bellesia* has been dated back 10.5 My (Ribera *et al*. 2010) to the Tortonian of the Upper Miocene, this indicates that there was overlapping geographical distribution enableing gene flow between the two populations at the slopes of the Pyrenean moutains ragen prior to that date. During the Eocene-Oligocene transition the orogenesis in the Pyrenean area peaked and in the Aquitanian, of the Lower Miocene, around 23.03 to 20.44 My ago, the Pyrenean folding was already ceasing. Thus, it can be considered that the existence of the proto-*Bellesia-Machaeroscelis* stat. nov. occured while the formation of the Pyrenees was at its height and it is with this confirmed that the mountainous massif did not represent a biogeographical barrier by the time of the cladogenesis. During the Miocene the climate was especially instable, this might have been a positive factor for the occurrence of various cladogenetic events during this period. In the entire early period of the Miocene relatively high temperatures of the Late Oligocene Warming Event are likely to have persisted, although it was interrupted by a relatively short cold period (Mi-1, 23.7 My) that was accompanied by profound geological events concerning the continental plates. However, in the second half of the Miocene a sudden cooling event between 14.2 and 13.8 My is assumed to have occured (Shevenell *et al*. 2004). Subsequently, the end of the period was characeterised by steady thermal cooling, although with important fluctuations causing alternating hot-humid, hot-dry, cold-humid or cold-dry episodes and with this trigger presumably profound changes in the biome. It might have been in this surrounding conditions that the final separation between the Leptodirini of the two sides of the Pyrenees took place. There is evidence that during this period, the cladogenesis of *Speonomus-Paraspeonomus-Ariejasia* gen. nov. (Northern side of the Pyrenees) from *Troglocharinus* (southern side of the Pyrenees) took place. The character to the evolutionary relationship between *Bellesia* and *Machaeroscelis* stat. nov. remained unnoticed, as no obviously divergent morphological characters were found. However, the strikingly similar morphological structures found suggest that there is a close relationship between those genera, and the future molecular studies might confirm this and allow to specify the evolutionary processes involved. Until know only morphological comparisons are possible, showing that it was confirmed that the metendosternites of these two genera are identical, as well as the endophallus has in both of them the basal ventral complex piece in the form of a short stylet. On the other hand, these two characters are also found in other members of their clade (except *Baronniesia*) in

the peculiar shape of the apex of the parameres with the cavity, penicillum and three setae.

Distribution. France. Ariège and Haute-Garonne: high Arbas valley, massif of Lestelas, cavities on the right bank of the Job valley and a single isolated locality west of Saint-Girons, in Rimont.

Species

Machaeroscelis endogaeus (Coiffait, 1963) comb. nov.
S. infernus subsp. ?: Coiffait, 1962: 75.
Speonomus (*Machaeroscelis*) *endogaeus* Coiffait, 1963: 322.

Machaeroscelis infernus (Dieck, 1869) comb. nov.
Machaeroscelis infernus arbasanus (Jeannel, 1924) comb. nov.
Speonomus (*Machaeroscelis*) *infernus* ssp. *arbasanus* Jeannel, 1924a: 148.
Speonomus infernus subsp. *arbasanus* Jeann.: Coiffait, 1959a: 165.
Machaeroscelis infernus cagiranus (Coiffait, 1955) comb. nov.
Speonomus (*Machaeroscelis*) *infernus* subsp. *cagiranus* Coiffait, 1955b: 204.
Speonomus infernus subsp. *cagiranus* Coiff: Coiffait, 1962: 75.
Machaeroscelis infernus infernus (Dieck, 1869) comb. nov.
Adelops infernus Dieck, 1869b: 5.
Bathyscia infernus Dieck: Schaufuss, 1881: xcvii.
Bathyscia (*Bathyscia*) *inferna* Dieck: Reitter, 1885 [1884]: 31.
Speonomus (s. str.) *infernus* Dieck: Jeannel, 1910a: 32.
Speonomus (*Machaeroscelis*) *infernus* Dieck, 1969: Jeannel, 1924a: 148.
Speonomus (*Machaeroscelis*) *infernus* subsp. *infernus* Dieck: Coiffait, 1959a: 165.
Speonomus infernus infernus Dieck: Juberthie-Jupeau & Cazals, 1991a: 25.

Genus ***Vanderberghia*** nov.
https://zoobank.org/NomenclaturalActs/91B00ADA-CA89-4478-BC2B-3E22D1DD26EB

Type species. *Adelops speluncarum* Delarouzée, 1857 by present designation (habitus in Fig. 284.6).

Description. Size ranging between 2.3-2.7 mm. Body very narrow, elongated and slightly convex (Fig. 284.6); females somewhat more robust with the antennae proportionally shorter. Irregular punctation on the pronotum and aligned forming well-defined transverse striolae on the elytra.

Antennae: Almost as long as the elytral suture, with the segments somewhat thickened from the 7th antennomere (with the exception of the 8th).

Pronotum: Transverse, with the widest point slightly before the base, which is as wide as the elytra; lateral margins very tapered forwards and slightly narrowed backwards.

Elytra: Elongated and depressed, with the maximum width located in the proximal quarter, later gradually tapering to the apex, which is broadly rounded; dehiscent apices and absent parasutural stria.

Legs: Slender, moderately elongated and male protarsi thickened; male metafemora with spine or sinuous membranes on posterior margin. Tibiae hairy, with two pectinate internal spurs, two simple external ones, a series of unequal spines between both and distant spines on the external face; protibiae not attenuated, mesotibiae somewhat curved and metatibiae straight.

Mesoventral keel (Fig. 285.6): High and forms an obtuse angle with a pointed vertex; anterior border sinuous and ridged, and the posterior concave with a sharp ridge; it does not extend over the metaventrite.

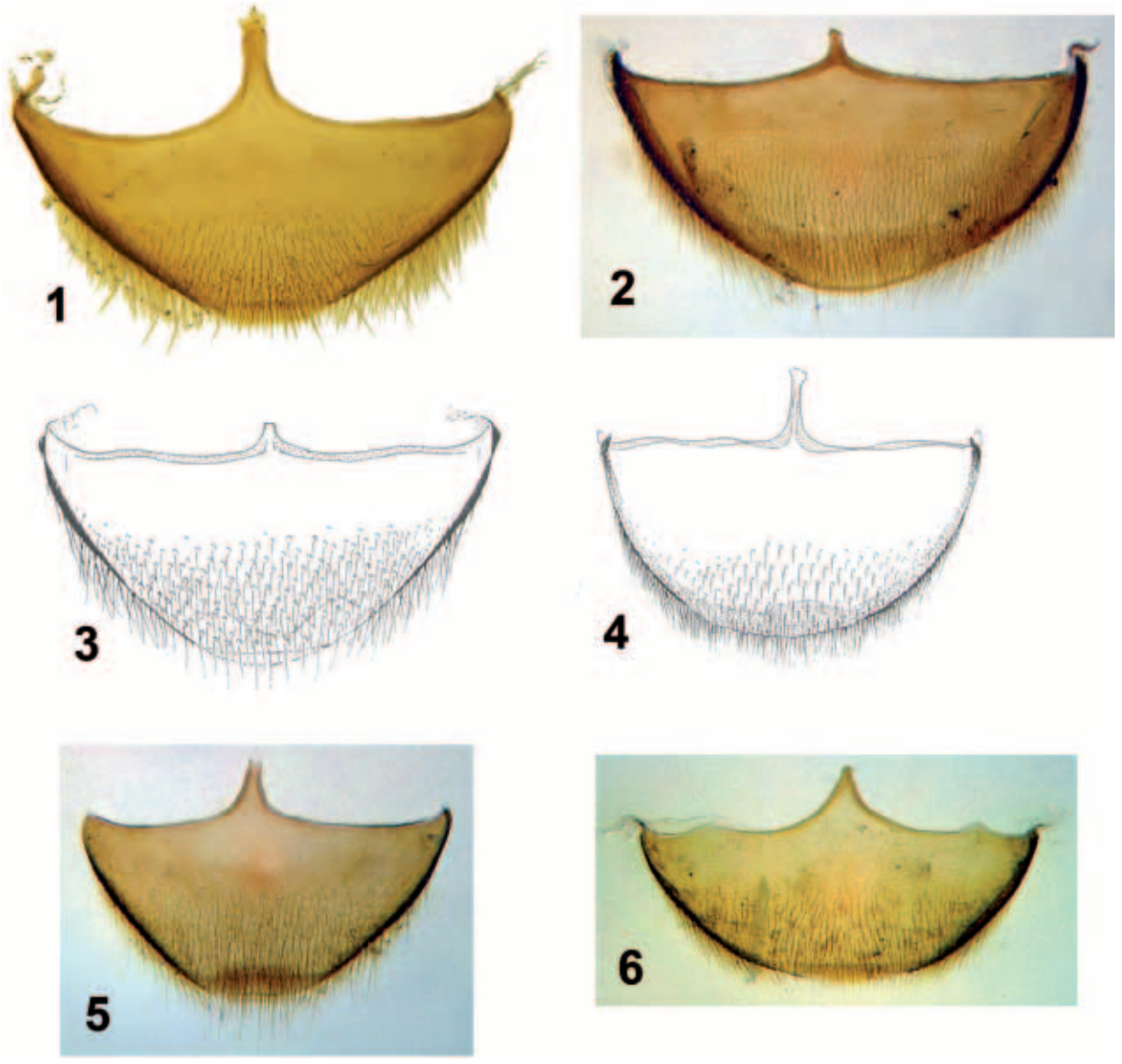
Suture of the metaventrite (Fig. 285.6): Printed at a certain distance from the edge of the mesocoxal cavity so that it delimits an elongated area with a certain width.

Metatergal apparatus (Fig. 286.5): With the metascutum somewhat widened and little elongated and the alacrista reduced, little elongated with apex pointed.

Metendosternite (Fig. 287.6): Furcal arms straight, longer than the furcal trunk, the apex sharp and slightly arched, without terminal apophysis, although a reduced preapical membranous lamina is observed; posterior lamina tapers towards the apical part, with the border almost straight in the middle part. Furcal trunk longer than the area of greatest basal width and the median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 288.6) moderately arched with a marked dorsal depression located in the apical third.

Endophallus (Fig. 289.9): In the basal region, the apical fibres of the «Y»-piece are made up of a highly sclerotized nodule; at the base of the symmetrical arms of the «Y»-piece, some adjoining phanerae are originate and extend in the form of hyaline fibres along the sides of the sac. In the middle region, on



FIGURES 292.1–292.6: *Speonomus* series, *Bathysciella* group. Female uroventrite VIII of: (**1**) *Baronniesia delioti,* (**2**) *Bathysciella jeanneli,* (**3**) *B. fratyi* **comb. nov.**, (**4**) *Bellesia espanyoli,* (**5**) *Machaeroscelis infernus infernus* **comb. nov.**, (**7**) *Vanderberghia ere* **comb. nov.** Figs **3**, **4** modified from Salgado *et al.* (2008).

both sides of the flagellum, there are divergent dorsal and ventral phanerae that seem to be united at their upper end; the whole structure reminds in its appearance of a horseshoe. On both sides of the armor of the axial piece there are muscle bundles that start in the apical region; in this same region, between the reinforcing bands, there are two bags with tegument densely covered with spicules; reinforcing bands rest on unsclerotized ligules.

Parameres (Fig. 290.6): Almost as long as the median lobe and thickened at the apex; in this place there exists an elongated cavity, shaped like an isosceles triangle whose interior is occupied by a penicillum formed by long, numerous and twisted setae; between them there are two or three thick setae. The first two of them, if both are present are inserted on the sides of the base of the cavity; the third somewhat thinner and shorter, inserted at the distal end; sometimes one of

the two strongest ones can be inserted next to the third.

Spermathecal complex (Fig. 291.6): Spermatheca quite rectilinear, since only the basal lobe is bent at an obtuse angle in relation to the middle region; the two lobes are wider than the middle region, especially the apical, which is markedly spherical; also both lobes are sclerotized while the middle region is transparent; at the basal insertion there is a small elongated nodule through which the spermatic duct empties; spermatic duct about 14 times longer than the spermatheca and at the point of insertion with the copulatory bag there is a small sclerotized nodule; there is a spermathecal gland.

Female uroventrite VIII (Fig. 292.6): With the spiculum short and wide, triangular in shape.

ETYMOLOGY. The name of the genus is dedicated to our good friend and collaborator, the biospeleologist Christian Vanderbergh (Les-Clayes-sur-Bois, France). Feminine.

DISCUSSION. In the phylogenetic tree (Fig. 1C), *Vanderberghia* gen. nov. is found at the base of the *Bathysciella* group clade and joins the other genera of the group with high support, 98/100. The endophallus model of *Vanderberghia* gen. nov. differs strongly from *Speonomus*, a genus of which all of its species were included in the analysis. At the apex of the parameres of *Vanderberghia speluncarum* comb. nov. *V. bepmalei* comb. nov. and *V. bourgoini* comb. nov. only two setae were recognised; possibly the third seta is present in other species of the genus or/and is hidden in the penicillum. Also in *V. lopezsellesi* comb. nov. and *V. gaudini* comb. nov. it is difficult to locate that third seta among the dense penicillum, specimens with two or three setae can be found in the same population. The endophallus is very similar to that of the genus *Parvospeonomus* and also the apex of the parameres is similar; the molecular study suggests that there is no close relationship between these two genera; it is still remarkable that their respective distribution areas are located at both ends of the Pyrenean mountain range. As a novelty, it has to be highlighted that the incorporation to this genus of *V. ehlersi* comb. nov., which occupies the most basal position of the clade, has an aedeagus with the dorsal notch (Fig. 288.7) and structures of its endophallus (Fig. 289.6) corresponding exactly to the model described for the genus.

The taxon *asaspensis* was described by Coiffait (1947b) as a subspecies of *Speonomus ochsi*. The molecular phylogeny (Fig. 1C) indicates that this taxon with support of 89.5/100 sister to the clade formed by *V. ochsi ochsi* (AC73) comb. nov. + *V. gaudini arivensis* (IRC18) comb. nov. which are sister species a with support of 100/100. Consequently, *asaspensis* must be changed to the rank of *bona species*: *Vanderberghia asaspensis* stat. nov. comb. nov.

DISTRIBUTION. The genus colonises both the French and Spanish slopes of the Pyrenees mountains. On the northern slope they are distributed in the western half of the massif, from Ariège to Pyrénées-Atlantiques. On the southern slope, three taxa have been described from the mountainous foothills, that separate the Echo and Ansó valleys in Huesca, from the Aezkoa valley at the southern end of the Sierra de Urkulu, and from the Sierra de Labia, both in Navarra.

Species

Vanderberghia alberti (Coiffait, 1947) comb. nov.
Speonomus Alberti Coiffait, 1947a: 70.
Speonomus Ochsi subsp. *Alberti* Coif.: Coiffait, 1959a: 174.

Vanderberghia alticola (Coiffait, 1947) comb. nov.
Speonomus alticola Coiffait, 1947b: 79.

Vanderberghia asaspensis (Coiffait, 1947) stat. nov. comb. nov.
Speonomus Ochsi asaspensis Coiffait, 1947b: 80.

Vanderberghia corbazi sp. nov. (see Appendix New Species)

Vanderberghia bastidea (Coiffait, 1950) comb. nov.
Speonomus (s. str.) *bastideus* Coiffait, 1950a: 63.

Vanderberghia bepmalei (Jeannel, 1908) comb. nov.
Speonomus Bepmalei Jeannel, 1908b: 69.
Speonomus (s. str.) *Bepmalei* Jeannel: Jeannel, 1910a: 33.

Vanderberghia bessoni (Coiffait, 1963) comb. nov.
Speonomus (s. str.) *bessoni* Coiffait, 1963: 322.

Vanderberghia bourgoini (Jeannel, 1947) comb. nov.
Vanderberghia bourgoini bourgoini (Jeannel, 1947) comb. nov.
Speonomus (s. str.) *Bourgoini* Jeannel, 1947a: 89.
Speonomus bourgoini Jeannel: Gers, 1989: 109.
Speonomus (s. str.) *bourgoini bourgoini* Jeannel: Perreau, 2000: 323.

Vanderberghia bourgoini pachycera (Jeannel, 1947) comb. nov.
Speonomus (s. str.) *Bourgoini pachycerus* Jeannel, 1947a: 90.

Vanderberghia cabidochei (Besson, 1968) comb. nov.
Speonomus (s. str.) *cabidochei* Besson, 1968: 219.

Vanderberghia ehlersi (Abeille de Perrin, 1872) comb. nov.
Adelops ehlersi Abeille de Perrin, 1872a: 17.
Bathyscia (*Bathyscia*) *Ehlersi* Abeille: Reitter, 1885 [1884]: 27.
Speonomus Ehlersi Abeille: Jeannel, 1908a: 301.

Vanderberghia ere (Escolà & Fresneda, 2000) comb. nov.
Speonomus ere Escolà & Fresneda, 2000: 36.

Vanderberghia gaudini (Jeannel, 1930) comb. nov.
Vanderberghia gaudini arivensis (Dupré, 1995) comb. nov.
Speonomus gaudini arivensis Dupré, 1995: 3.
Vanderberghia gaudini fouresi (Coiffait, 1947) comb. nov.
Speonomus Gaudini subsp. *Fouresi* Coiffait, 1947b: 79.
Speonomus (s. str.) *gaudini fouresi* Coiffait: Perreau, 2000: 324.
Vanderberghia gaudini gaudini (Jeannel, 1930) comb. nov.
Speonomus (s. str.) *Gaudini* Jeannel, 1930b: 225.
Speonomus gaudini Jeannel: Laneyrie, 1988: 79.
Speonomus (s. str.) *gaudini gaudini* Jeannel: Perreau, 2000: 324.

Vanderberghia lopezsellesi (Español, 1950) comb. nov.
Speonomus lopezsellesi Español, 1950: 108.

Vanderberghia monbulensis (Besson, 1968) comb. nov.
Speonomus (s. str.) *monbulensis* Besson, 1968: 221.

Vanderberghia ochsi (Coiffait, 1947) comb. nov.
Vanderberghia ochsi irenae (Coiffait, 1950) comb. nov.
Speonomus Ochsi subsp. *Irenae* Coiffait, 1950b: 69.
Speonomus (s. str.) *ochsi irenae* Coiffait: Perreau, 2000: 324.
Vanderberghia ochsi ochsi (Coiffait, 1947) comb. nov.
Speonomus Ochsi Coiffait, 1947a: 68.
Speonomus (s. str.) *ochsi ochsi* Coiffait: Perreau, 2000: 324.

Vanderberghia orgibetensis (Gers, 1989) comb. nov.
Speonomus orgibetensis Gers, 1989: 423.

Vanderberghia pierrei (Jeannel, 1947) comb. nov.
Speonomus (s. str.) *Pierrei* Jeannel, 1947a: 90.
Speonomus pierrei Jeannel: Cabidoche, 1961: 424.

Vanderberghia speluncarum (Delarouzée, 1857) comb. nov.
Vanderberghia speluncarum navarica (Jeannel, 1907) comb. nov.
Bathyscia speluncarum navarica Jeannel, 1907d: 247.
Speonomus (s. str.) *speluncarum* subsp. *navaricus* Jeannel: Jeannel, 1910a: 33.
Vanderberghia speluncarum speluncarum (Delarouzée, 1857) comb. nov.
Adelops speluncarum Delarouzée, 1857: xciv.
Bathyscia speluncarum Delar.: Schaufuss, 1881: xcvii.
Speonomus speluncarum Delarouzée: Jeannel, 1908a: 300, 305.

Bathysciella group incertae sedis

Speonomus rudauxi Jeannel, 1909
Speonomus rudauxi Jeannel, 1909a: 18.

France. Pyrénées-Atlantiques, Grotte de Kakouétta on the left bank of the gorges in Sainte-Engrâce. Molecular studies have not been carried out using DNA from these animal, but for the moment it is included in *Bathysciella* group, because *Speonomus rudauxi* lives in the region where only *Vanderberghia* gen. nov. and *Bathysciella* occur.

3.4.8.4 ***Troglophyes*** group

Diagnosis. Pholeuonoid body shape, although there is a bathyscioid species. Reddish yellow colouration, integument entirely covered with a fine, short, flat-lying, whitish pubescence. Depigmented. Integument of the pronotum marked by disordered dots, that of the elytra by transverse striolae.

Head: Occipital carina complete but only slightly marked. Epistomal suture straight and hidden. Last segment of maxillary palps short and conical. Anophthalmous.

Antennae: As long as or longer than the elytral suture; 7th, 9th-11th antennomeres slightly thickened.

Pronotum: Transverse, narrowed or even notched in the basal third or, in bathyscioid species, with regularly curved margins between its two extremities.

Elytra: Elongated with or without parasutural striae.

Male genital segment: Very small, open, with two long peduncles.

Legs: Male protarsi pentamerous, the female ones tetramerous; male protarsomeres dilated, with dilation varying according to genera and species. All tibiae with two pectinate inner spurs, two simple outer spurs and a series of unequal spines between them, densely hairy, with or without a series of spines on the outer surface; protibiae without attenuated apex; mesotibiae curved or not, metatibiae straight.

Mesoventral keel: Mesocoxal cavities separated by a keel, situated on the median line of the mesoventrite, which does not extend into the metaventrite. High keel with a pointed apex, or low and rounded from one end to the other.

Metaventrite: Bifid projecting process or apophysis separating the metacoxal cavities. Half the length of the suture barely separated from the edge of the mesocoxal cavity, delimiting a very narrow area; rest close to the edge.

Metatergal apparatus: Very similar in the three genera of the clade, the metascutum extremely narrow and elongated, the alacrista very reduced.

Metendosternite: Two models, with or without apophysis at the apex of the arms.

Median lobe of aedeagus: Three different models corresponding to the three genera.

Endophallus: Divided into three regions; the basal region with a «Y»-piece; the median region with ventral phanerae which can be highly developed and joined at their upper end, between the two dorsal phanerae inside which the flagellum of the «Y»-piece circulates; the apical region, with the reinforcing bands resting on membranous ligules whose integument may or may not be covered in scales.

Parameres: With a more or less dense penicillum of short setae inserted on one side of the apex or inside a cavity and three differentiated setae of varying insertion.

Spermathecal complex: Spermatheca of «type 1» *sensu* Perreau (1989), with two sclerotized lobes connected by a hyaline tube; the apical smaller and less sclerotized than the basal; spermatic duct inserted by a nodule, with a more or less diffuse sclerotized basal process; spermathecal gland present.

Female uroventrite VIII: Spiculum reduced to a denticle or replaced by two membranous extensions.

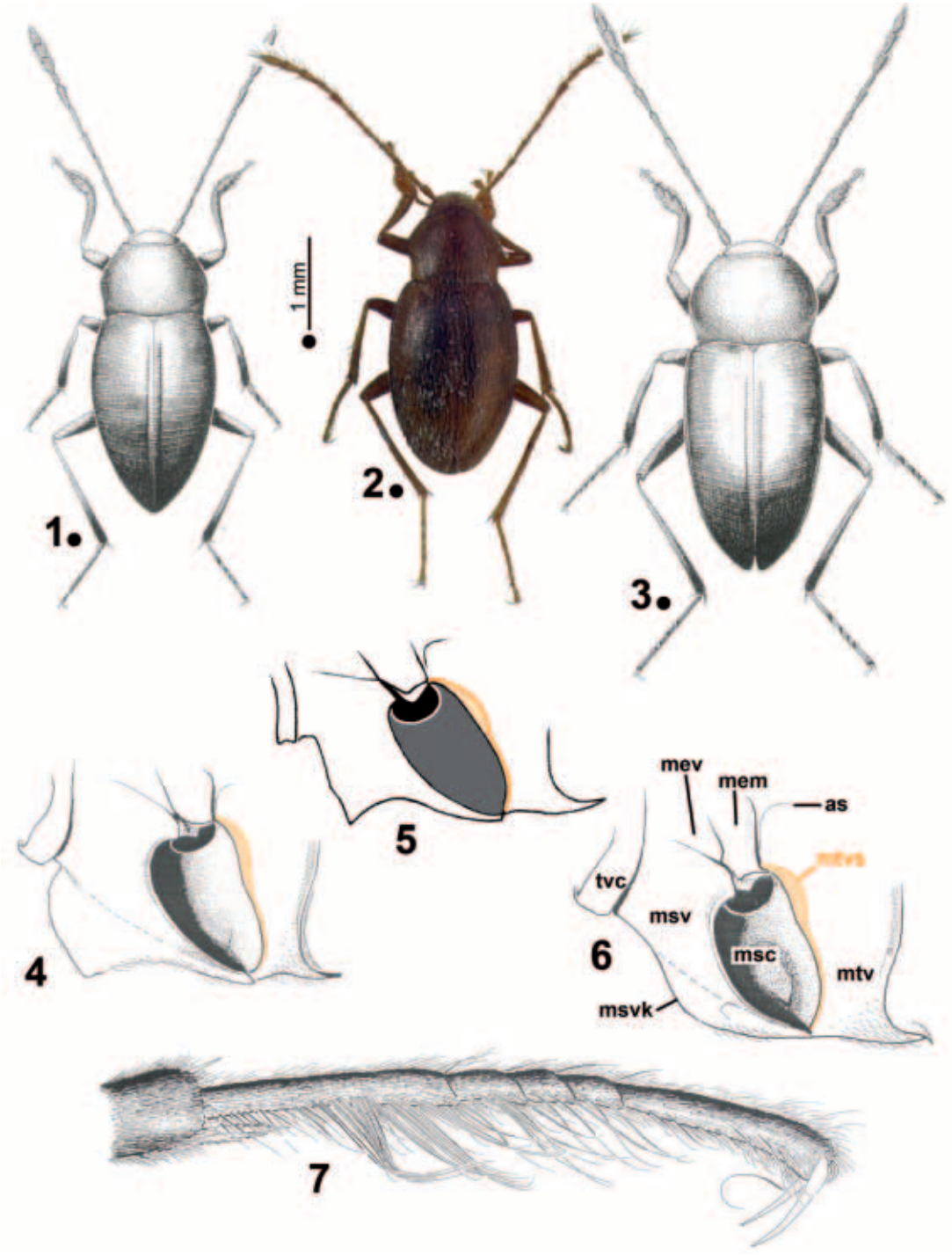
Discussion. In the phylogenetic tree (Fig. 1B), the *Troglophyes* group is supported by 100/100; the clade of the *Troglophye*s group is the sister of the clades of the *Antrocharis* and *Speonomus* groups with a support of 100/100.The conformation of the apex of the parameres, with a cavity occupied by a dense penicillum, appears in the dichotomy of the *Speonomus* series that leads to the *Speonomus* group; it is passed on between the sister clades of the *Parvospeonomus* group, the *Bathysciella* group and the *Troglophyes* group and then changes radically in structure: either all the structures are lost (*Antrocharis* group) or the membranous lamina is developed (*Speonomus* group).

Key to genera

1. Elytra with parasutural striae. Metendosternite with furcal arms much longer than furcal trunk, if as long, there is a terminal apophysis (Figs 294.4, 294.6). Median lobe of aedeagus with or without slight dorsal depression in terminal area (Figs 295.1, 295.3). Apical part of parameres with a cavity and numerous setae forming the penicillum (Figs 295.7, 295.9). Median region of endophallus with absent or very reduced dorsal phanerae and highly developed ventral phanerae that meet at their upper end to form a triangular structure surrounded by striated muscle tissue, sometimes with an axial piece above them (Figs 295.4, 295.6). Basal lobe of spermatheca poorly differentiated, a single sclerotized margin in the area where the spermatic duct joins the copulatory sac (Figs 295.10, 295.12) 2

- Elytra without parasutural stria. Metendosternite with furcal arms as long as furcal trunk and without terminal apophysis (Fig. 294.5). Median lobe of aedeagus with marked dorsal depression in terminal area (Fig. 295.2). Apical part of parameres without cavity, with sparsely furnished penicillum (Fig. 295.8). Median region of endophallus with long, well-developed dorsal phanerae and ventral phanerae that meet at their upper end to form a horseshoe-shaped structure (Fig. 295.6). Basal lobe of spermatheca formed by a truncated cone (Fig. 295.11) ....*Troglophyes*

2. Mesoventral keel high, with pointed, hook-shaped apex (Fig. 293.4). Metendosternite with slender furcal arms, almost twice as long as furcal trunk, and arched, pointed apex without apophysis (Fig. 294.4). Apical



FIGURES 293.1–293.7: *Speonomus* series, *Troglophyes* group. Habitus of: (**1**) *Ceretophyes cenarroi,* (**2**) *Troglophyes gavoyi,* (**3**) *Perriniella faurai.* Pterothorax in lateral view of: (**4**) *C. cenarroi,* (**5**) *T. gavoyi,* (**6**) *P. faurai.* Mesotarsus of: (**7**) *P. bofilli*. Figs **1**, **3**, **4**, **6**, **7** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

area of median lobe of aedeagus straight or slightly curved ventrally (Fig. 295.1). Ventral phanerae of endophallus narrow and joined at upper end to form diffuse triangular structure surrounded by striated muscle tissue; reinforcing bands in apical region resting on basal ligules with integument densely covered with scales (Fig. 295.4). Female uroventrite VIII with a very short spiculum (Fig. 296.1) .....*Ceretophyes*
- Mesoventral keel low, with arched apex (Fig. 293.6). Metendosternite with broad furcal arms, as long as furcal trunk, apex dilated and apophysis developed (Fig. 294.6). Apical area of median lobe of aedeagus curved dorsally (Fig. 295.3). Ventral phanerae of endophallus very wide and surmonted by an axial piece; reinforcing bands of apical region rest on small basal ligules with membranous integument (Fig. 295.5). Female uroventrite VIII with two arched membranous extensions in the median region (Fig. 296.3) ....*Perriniella*

Genus ***Ceretophyes*** Fresneda, 1998
Ceretophyes Comas & Escolà, 1989: 142 (unavailable name).
Ceretophyes Fresneda, 1998: 77.

Type species. *Speophilus cenarroi* Español, 1955 by original designation (habitus in Fig. 293.1).

Diagnosis. Size between 2.5-3.2 mm. Body shape elliptical, elongated, narrowing towards the front and rear (Fig. 293.1). Integument of pronotum marked with fine or granular dots and very pronounced transverse striolae on the elytra.

Head: Anophthalmous.

Antennae: Longer than the elytral suture; antennomeres in the apical third thickened.

Pronotum: Slightly transverse and narrower than the elytra; lateral margins very angular or rounded, maximum width in the middle, always strongly narrowed towards the front; posterior angles straight and receding.

Elytra: Widest just before the middle or nearer the base and very acuminate at the apex; marginal ridge visible in the anterior three quarters; parasutural stria long and well impressed, although it may fade forwards and backwards.

Legs: Proportionally long and slender; male protarsi with first segment quadrangular or rectangular and always a little wider than apical end of protibia; protibiae without spines on outer surface; mesotibiae curved with spines on outer surface; metatibiae straight without spines on outer surface.

Mesoventral keel (Fig. 293.4): Raised, obtuse, with anterior margin convex, not bordered, lower margin concave with sharp edge and vertex pointed.

Suture of the metaventrite (Fig. 293.4): Delimiting a very narrow, arcuate area that is well defined only in the anterior median area.

Metatergal apparatus (Fig. 294.1): Metascutum narrow and thickened outwardly; tips of the alacrista not very prominent and pointed.

Metendosternite (Fig. 294.4): Not «Y»-shaped; furcal arms straight and almost twice as long as furcal trunk, apex arched and pointed, without terminal apophysis; posterior furcal plate of equal width along arm, and smooth arched margin; trunk a little longer than area of greatest basal width and median keel diverging posteriorly.

Median lobe of aedeagus (Fig. 295.1): Elongate and slender in appearance; basal two thirds rectilinear; apical third particularly slender and in contrast to proximal part, although the latter is not particularly robust.

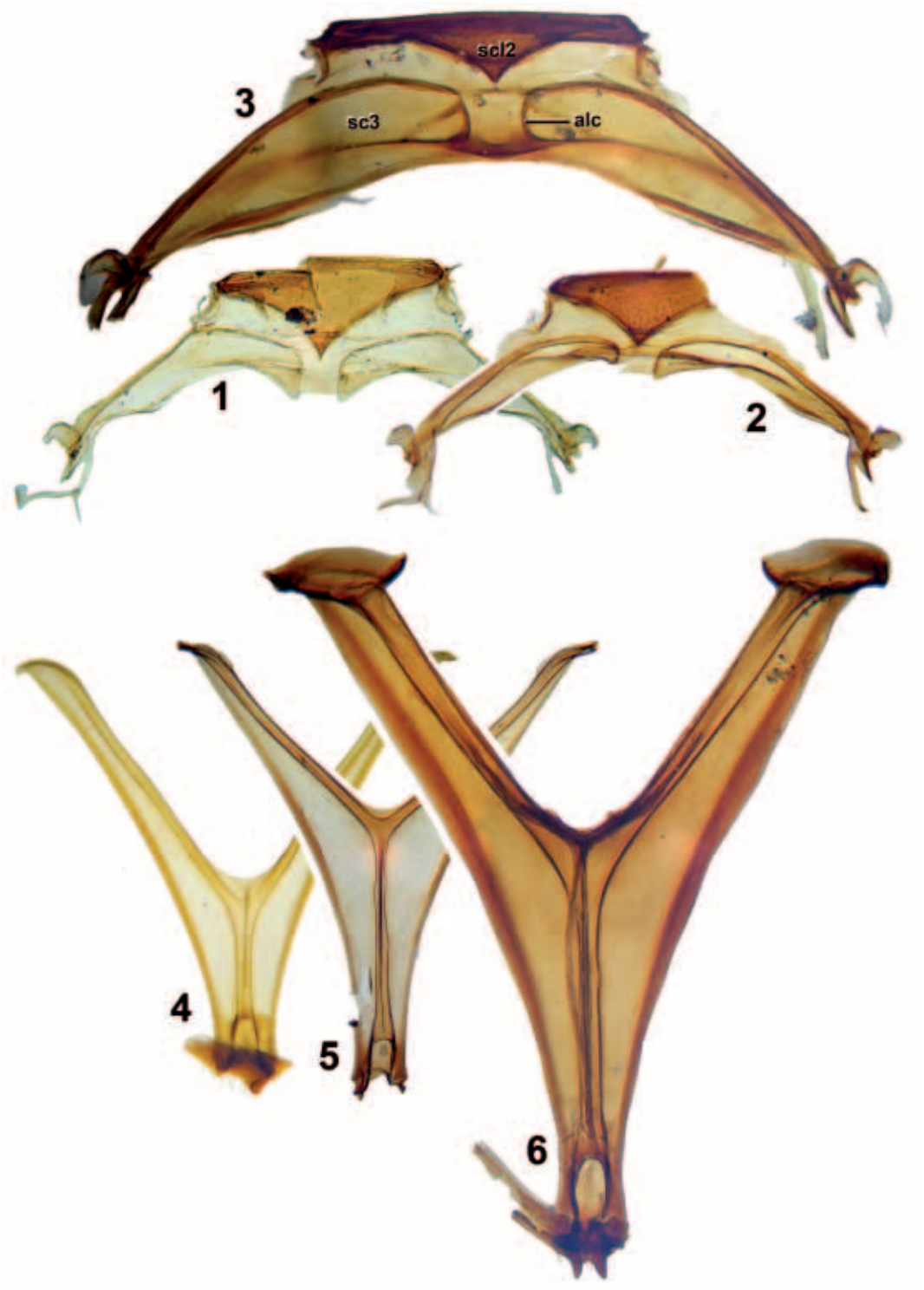
Endophallus (Fig. 295.4): Characterised by a «Y»-piece with symmetrical arms, long and thickened at the distal end; in the median region, some long ventral phanerae extended to the apical region; at its upper end, a diffuse triangular structure surrounded by striated muscle tissue; in the apical region and on both sides of the sac, reinforcing bands fused to the basal ligules forming a unique structure; integument of the basal ligules densely covered with scales.

Parameres (Fig. 295.7): Thickened at the apex, which has a cavity occupied by a dense penicillum and three subequal differentiated setae.

Spermathecal complex (Fig. 295.10): Spermatheca very or slightly curved; the two section lobes a little larger than the median region, both spherical and sclerotized or only the basal one; the median region hyaline; in the basal insertion, presence of a nodule through which the spermatic duct empties, which is about six times as long as the spermatheca, thickening in the vicinity of the copulatory sac and at the point of union with the latter, with a somewhat sclerotized margin; spermathecal gland present.

Female uroventrite VIII (Fig. 296.1): Spiculum very short, reduced to a simple denticle.

Discussion. The model of the endophallus in this genus was described and figured by Comas & Escolà (1989). *Ceretophyes* is related to *Perriniella*, a genus with which it shares the existence of a single pair of phanerae in the median region of the endophallus. The third member of the clade, *Troglophyes*, has two pairs



FIGURES 294.1–294.6: *Speonomus* series, *Troglophyes* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Ceretophyes cenarroi,* (**2**) *Troglophyes gavoyi,* (**3**) *Perriniella bonvouloiri.* Metendosternite of: (**4**) *C. riberai,* (**5**) *T. gavoyi,* (**6**) *P. bonvouloiri.* Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

of phanerae. In the most basal clades of the *Speonomus* series, the presence of two phanerae is not always very clear, there are different hyaline phanerae which can sometimes be identified or which mask each other, resembling folds of a single structure. The existence of two clearly individualised phanerae can be seen in *Troglophyes* and in the genera of the *Speonomus* group. In the molecular phylogeny of the *Troglophyes* group (Fig. 1B), the genus *Ceretophyes* joins the genus *Perriniella* with support 67.3/99.

Distribution. Spain. The genus has two representatives distributed in various cavities in the upper basin of the river Segre, in Cerdanya, provinces of Lleida and Girona.

Species

Ceretophyes cenarroi (Español, 1955)
Speophilus cenarroi Español, 1955: 263.
Troglophyes (*Ceretophyes*) *cenarroi* Español: Comas & Escolà, 1989: 141.
Ceretophyes cenarroi (Español, 1955): Fresneda, 1998: 79.

Ceretophyes riberai (Español, 1967)
Troglophyes riberai Español, 1967: 81.
Troglophyes (*Ceretophyes*) *riberai* Español: Comas & Escolà, 1989: 141.
Ceretophyes riberai (Español, 1967): Fresneda, 1998: 79.

Genus ***Perriniella*** Jeannel, 1910

Perriniella Jeannel, 1910b: 161.

Type species. *Perriniella faurai* Jeannel, 1910 by original designation (habitus in Fig. 293.3).

Diagnosis. Size about 4.0 mm. Body shape (Fig. 293.3) oblong, elliptical, elongate, and slightly convex with an obvious pronotum-elytral angle, although there is also a clearly bathyscioid species. Integument of the pronotum marked by a granular stippling, and transverse striolae on the elytra.

Head: Anophthalmous.

Antennae: As long as the elytral suture; all segments longer than wide and those of the club a little thicker.

Pronotum: A little wider than long and distinctly narrower than the base of the elytra or of equal width; lateral margins regularly curved, with the maximum width situated in the middle or at the base and extended over the elytra; posterior angles acute, with a blunt apex.

Elytra: Broadest at mid-length; the two elytra taken together oval in shape, with the lateral margins evenly arched from base to apex; a marginal edge to near the apex, this margin very finely toothed and curved backwards; a seta in each denticle ; apex of elytra extended separately and, consequently, the suture located at the bottom of the triangular notch it forms; regularly convex, the sutural line in the same plane as the elytral surface; presence of a long, faint parasutural stria.

Legs: Long and stout, covered with very dense fine hairs; first protarsomere of male wider than tibia and subtriangular in shape; mesotarsi densely covered with long hairs and, in two species, on the first four tarsomeres a series of thick, long setae in both sexes (Fig. 293.7); protibiae somewhat curved with spicules along outer margin; meso- and metatibiae straight and in addition to pilosity with spicules on outer surface.

Mesoventral keel (Fig. 293.6): Low, not angular, formed by an arcuate median ridge with setae on margin.

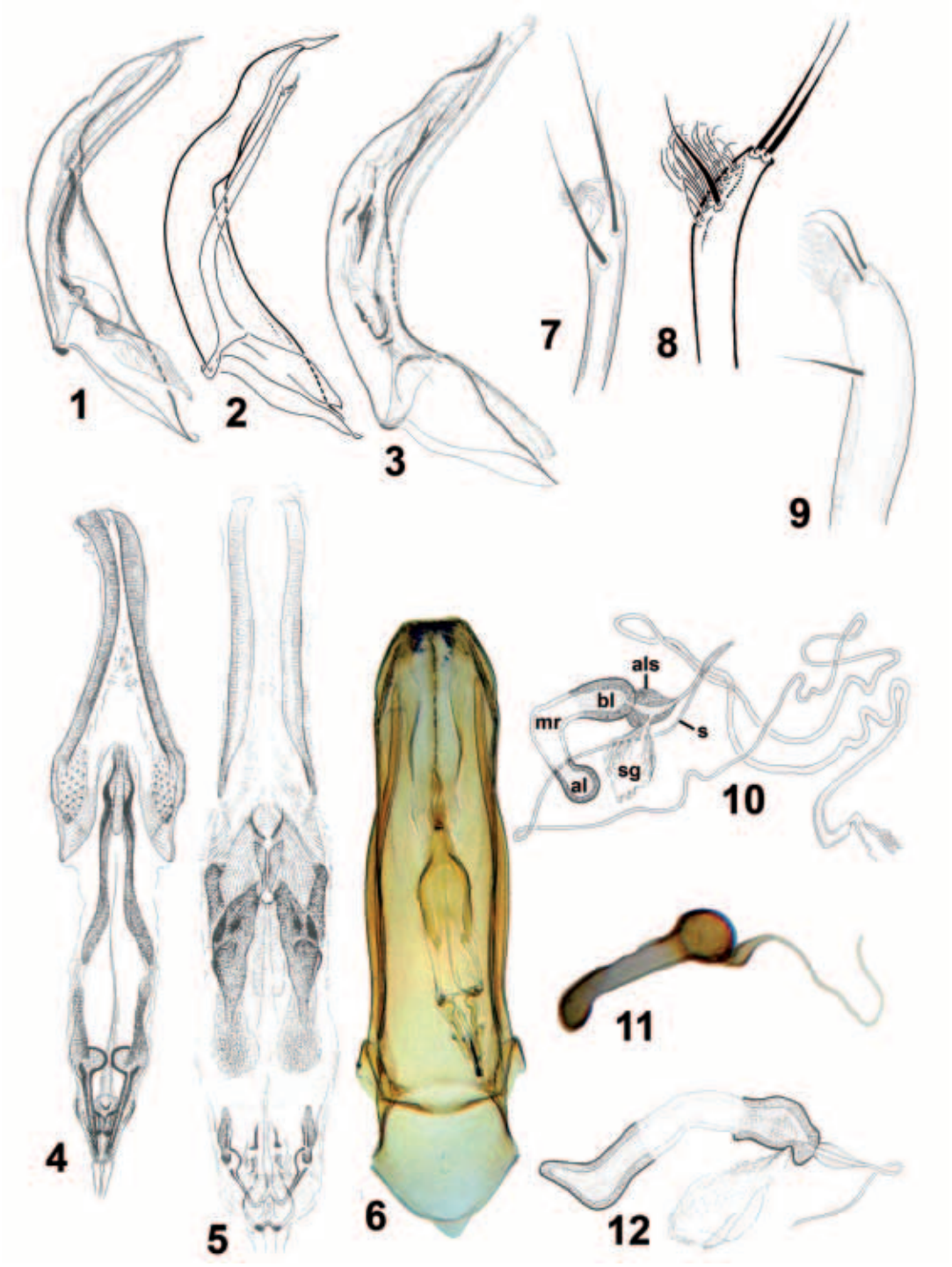
Suture of metaventrite (Fig. 293.6): Similar to that of *Ceretophyes*, although the arcuate area slightly wider.

Metatergal apparatus (Fig. 294.3): Metascutum wider, wings long; alacrista reduced, tips blunter.

Metendosternite (Fig. 294.6): Robust and «Y»-shaped; furcal arms straight and slightly shorter than furcal trunk, with apex not sharp and very dilated, apophysis thick; posterior furcal plate about same width as apex, with smooth arcuate margin; trunk distinctly longer than area of greatest basal width and median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 295.3), arched from base to apex, with marked sinuosity in apical quarter; tip acute and curved posteriorly; basal part much reduced with a ventral thickening in median area.

Endophallus (Fig. 295.5): The «Y»-piece with symmetrical straight arms, the union between them doubly sinuous; by means of a fine tubule, each arm of the «Y»-piece connected to an elliptical piece which does not reach the median region; presence of enormous ventral phanerae in this median region, joined at their upper end and enlarged in the shape of a paddle at the lower end; between them, two tiny dorsal phanerae which, in some of the endophallus studied, seem to be fused to form a tube in which the flagellum of the «Y»-piece circulates; two symmetrical



FIGURES 295.1–296.12: *Speonomus* series, *Troglophyes* group. Aedeagus in lateral view of: (**1**) *Ceretophyes cenarroi,* (**2**) *Troglophyes gavoyi,* (**3**) *Perriniella faurai.* Endophallus of: (**4**) *C. cenarroi,* (**5**) *P. faurai.* Aedeagus in dorsal view of: (**6**) *T. ludovici*. Apex of the paramere of: (**7**) *C. cenarroi,* (**8**) *T. gavoyi.,* (**9**) *P. faurai.* Spermathecal complex of: (**10**) *C. cenarroi,* (**11**) *T. gavoyi,* (**12**) *P. faurai.* Figs **1**, **3**–**5**, **7**, **9**, **10**, **12** modified from Salgado *et al*. (2008). Abbreviations: **als**, apical lobe of the spermiduct; **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

pieces evident at the upper end of the dorsal and ventral phanerae, identified as the axial piece since its armour is clearly seen at its upper end; at the upper end of the median region, two other robust phanerae on both sides; the apical region with long, narrow reinforcing bands resting on diffuse, striated membranous ligules.

Parameres (Fig. 295.9): Longer than the median lobe, stout, except in *P. fresnedai* in which they are shorter and thinner; apex slightly thickened, with a cavity on the dorsal side where, on the apical margin, are two thick, short setae and a dense penicillum; at the lower margin of the cavity, another thick seta arranged perpendicular to the plane of the paramere.

Spermathecal complex (Fig. 295.12): Spermatheca strongly curved at several points in median region, almost straight in *P. fresnedai*; apical lobe not thickened, both more sclerotized than median region; in addition, very evident nodule of basal insertion, through which it empties into spermatic duct; spermathecal gland situated in same place.

Female uroventrite VIII (Fig. 296.3): Spiculum short and broad or non-existent, with, in its anterior or middle anterior area, two arcuate membranous extensions.

Discussion. This model of endophallus has been described and illustrated by Fresneda (1998) and Perreau & Tronquet (2002). *Perriniella* is related to *Ceretophyes*, a genus with which it shares the existence of a single pair of phanerae in the median region of the endophallus; in fact, in *Perriniella* there are two pairs, although the dorsal are very reduced; it also shares with this genus the particular structure of the apex of the parameres, with a cavity, a penicillum and three differentiated setae. The enormous ventral phanerae in the median region of the endophallus make this genus unmistakable. The mesotarsi densely covered with long hairs in both sexes, which does not occur in any other Leptodirini in the *Speonomus* series, was thought to be a character of this genus, but with the discovery of a third species by Perreau & Tronquet (2002) which does not have long setae on the mesotarsus, it has been shown that this is not a generic character. *Speonomus bonvouloiri*, the only species of this clade with a bathyscioid facies, which in this segment is transferred to the genus *Perriniella*, also has long setae on the mesotarsi, although they are only present on the fourth segment; in the phylogenetic tree, it is related to *Perriniella bofilli* and *P. faurai* with a support of 100/100 (Fig. 1B).

Distribution. Spain and France. The genus comprises four species found in different parts of the Puigmal massif and associated mountains; two of them are found in Catalonia, in a number of cavities on the right bank of the upper basin of the River Fresser in Queralbs (Girona); the third species has been found in marmot burrows on the northern slopes of the massif, in France, and the fourth is typical of the underground environment of the Canigou massif, also in France.

Species

Perriniella bofilli Zariquiey, 1924
Perriniella Bofilli Zariquiey, 1924: 14.
Perriniella bofilli Zariquiey: Español, 1956: 119.

Perriniella bonvouloiri (Jacquelin du Val, 1859) comb. nov.
Adelops Bonvouloirii Jacquelin du Val, 1859: 34.
Quaestus Bonvoulviri: Schaufuss, 1861a: 426.
Quaestus Dohrnii Schaufuss, 1862a: 126.
Bathyscia (*Bathyscia*) *Bonvouloiri* Duval: Reitter, 1885a [1884]: 29.
Speonomus Bonvouloiri Duval: Jeannel, 1908a: 301.
Speonomus (s. str.) *bonvouloiri* Jacquelin du Val, 1859: Perreau, 2000: 325.

Perriniella faurai Jeannel, 1910
Perriniella Faurai Jeannel, 1910b: 162.
Perriniella faurai Jeannel: Español, 1956: 119.

Perriniella fresnedai Perreau & Tronquet, 2002
Perriniella fresnedai Perreau & Tronquet, 2002: 482.

Genus ***Troglophyes*** Abeille de Perrin, 1894
Troglophyes Abeille de Perrin, 1894: XXVII.

Type species. *Troglophyes Gavoyi* Abeille de Perrin, 1894 by original designation (habitus in Fig. 293.2).

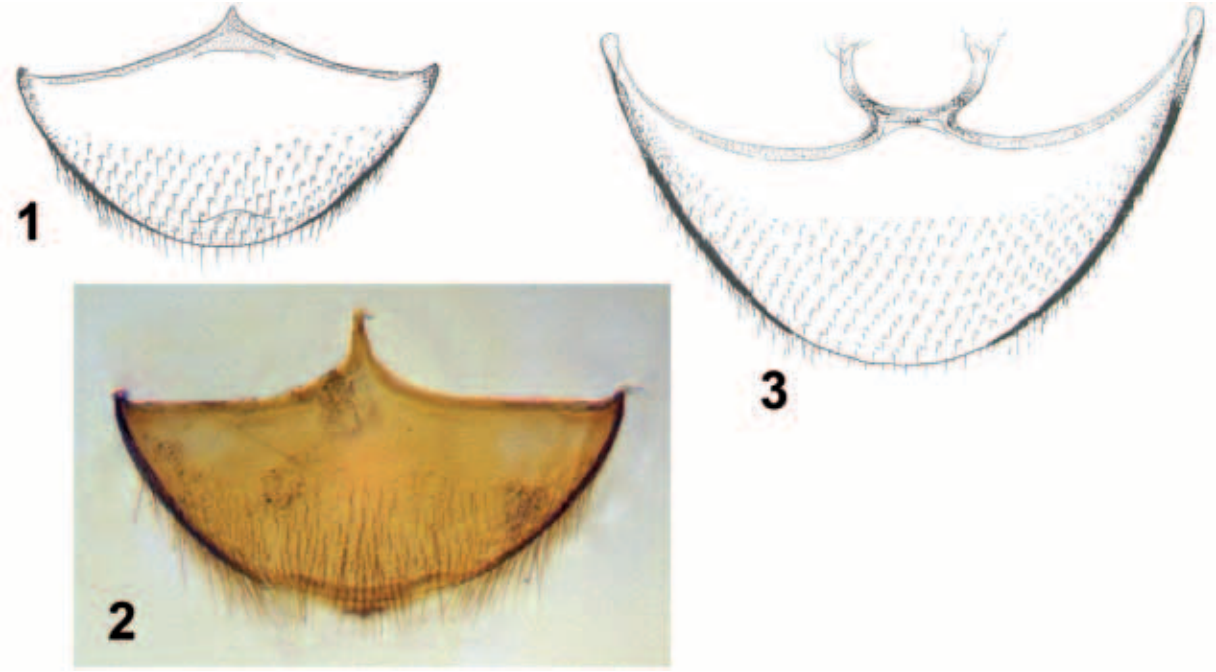
Diagnosis. Size between 2.5-2.7 mm. Body elongated, with the elytral margins regularly curved between its two extremities (Fig. 293.2). Integument of pronotum marked by dots and in the elytra by transverse striolae.

Head: Anophthalmous.

Antennae: Longer than the elytral suture.

Pronotum: Transverse with basal third narrowed and margins subparallel; base straight, narrower than elytra as a whole; posterior angles straight with rounded apex.

Elytra: Relatively short, broad and convex, with



FIGURES 296.1–296.3: *Speonomus* series, *Troglophyes* group. Female uroventrite VIII of: (**1**) *Ceretophyes riberai,* (**2**) *Troglophyes gavoyi,* (**4**) *Perriniella faurai.* Figs **1**, **3** modified from Salgado *et al*. (2008).

maximum width in the median part; very fine marginal ridge; without parasutural stria.

Legs: Long and slender; male protarsi strongly dilated and their first protarsomere heart-shaped and wider than the apical end of the protibia; all tibiae with spines on the outer surface; meso- and metatibiae straight.

Mesoventral keel (Fig. 293.5): High, obtuse, with anterior margin straight, not bordered, the inferior very concave with a sharp edge and the vertex pointed.

Suture of metaventrite (Fig. 293.4): Delimiting a very narrow arcuate part that is well defined only in the anterior median part.

Metatergal apparatus (Fig. 294.5): Metascutum very narrow and elongate; apophysis of alacrista not very prominent.

Metendosternite (Fig. 294.5): «Y»-shaped; furcal arms straight and as long as furcal trunk, apex acute and very slightly sinuate, without obvious terminal apophysis; posterior lamina gradually narrowing in apical area, with broad arched margin. Trunk much longer than area of greatest basal width, median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 295.2), bent at obtuse angle; basal part straight, terminal part strongly sinuate and with marked dorsal depression. In dorsal view (Fig. 295.6), pointed apex with lateral wing.

Endophallus (Fig. 295.6): Characterised by a «Y»-piece with symmetrical, long, rectilinear arms, and after the junction nodule, the apical fibres of the «Y»-piece extending towards the median region; in the median region, some long, narrow, parallel dorsal phanerae, and some ventral phanerae joined at their upper end so as to form a horseshoe; reinforcing bands resting on membranous ligulae.

Parameres (Fig. 295.8): With a penicillum sparse with short setae on one side of the apex and a short preapical insertion seta; two longer setae inserted contiguous to the same apex.

Spermathecal complex: Spermatheca (Fig. 295.11) thin and slightly curved; apical lobe sclerotized and with almost the same cross-section as the median region; basal lobe strongly thickened and sclerotized; spermatic duct inserted into the spermatheca via a small nodule and into the copulatory sac via a truncated, conical and sclerotized basal process; spermathecal gland present.

Female uroventrite VIII (Fig. 296.2): Spiculum short, triangular in shape and pointed.

Discussion. In the phylogenetic tree in Figure 1B, *Troglophyes* appears as sister to *Ceretophyes* and *Perriniella* with very high support 100/100. *Troglophyes gavoyi* (AC114) is the sister species of *T. bedeli* (RA896) with a support of 75.2/100; this group is sister, with a support of 100/100, to *T. gavoyi alluaudi* (RA632) + *T. ludovici* (RA526) with a support of 98.1/100. Consequently, subspecies *alluaudi* must be elevated to the rank of *bona species*. The pronotum, slightly wider than long, and the short, strongly convex elytra with the maximum width in the middle of the length, characterise *Troglophyes alluaudi* stat. nov. compared with *T. gavoyi*.

Distribution. France. In Aude – Coudons, Gesse and Sainte-Colombe-sur-Guette – and Pyrénées-Orientales, subterranean cavities of the Corbières massif.

Species

Troglophyes alluaudi Jeannel, 1911 stat. nov.
Troglophyes Gavoyi subsp. *alluaudi* Jeannel, 1911a: 368.
Troglophyes gavoyi alluaudi Jeannel: Perreau, 2000: 338.

Troglophyes bedeli Jeannel, 1906
Troglophyes bedeli Jeannel, 1906c: 275.

Troglophyes gavoyi Abeille de Perrin, 1894
Troglophyes Gavoyi Abeille de Perrin, 1894: XXVII.
Troglophyes gavoyi gavoyi Abeille de Perrin: Perreau, 2000: 338.

Troglophyes ludovici Chobaut, 1903
Troglophyes Ludovici Chobaut, 1903b: 263.
Troglophyes Gavoyi subsp. *Ludovici* Chobaut: Jeannel, 1911a: 368.
Troglophyes ludovici Chobaut: Perreau, 2000: 338.

Enigmatic species

Troglophyes oblongulus Reitter, 1908
Troglophyes oblongulus Reitter, 1908c: 116.

Both the identity of the species and its origin are dubious. France. Alpes-Maritimes, Grotte de Saint-Cézaire.

3.4.8.5 ***Antrocharis*** group

Diagnosis. Pholeuonoid facies (Figs 297.1-297.3). Yellowish-reddish colouration; pubescence yellowish, thin, short and recumbent. Depigmented. Tegument of pronotum marked by irregular punctation and in elytra by transverse striolae, sometimes ill-defined and of varied conformation.

Head: Small with an occipital carina only slightly marked, or even completely obliterated in the centre. Epistomal suture well defined, straight and darkened. Last segment of maxillary palps short and conical. Anophthalmous.

Antennae: Variable in length and shape of antennomeres, all longer than wide, sometimes with a slightly differentiated club.

Pronotum: Transverse with curved lateral margins or bell-shaped with sinuous sides, or also narrower in the posterior third and with notched margins, even subparallel in the basal half.

Elytra: Short and wide or very elongated and narrow, always convex; in one case, disproportionately longer than the head and pronotum together, giving it a certain «leptodiroid» appearance. No parasutural stria.

Metaventrite: Forming a projecting bifid process or apophysis that separates the metacoxal cavities.

Legs: Very long. Protarsi pentamerous in males and tetramerous in females. All protibiae with two pectinate or bifid inner spurs, two simple outer spurs and a series of asymmetrical spines between them.

Male genital segment: Very small, open and with two long peduncles.

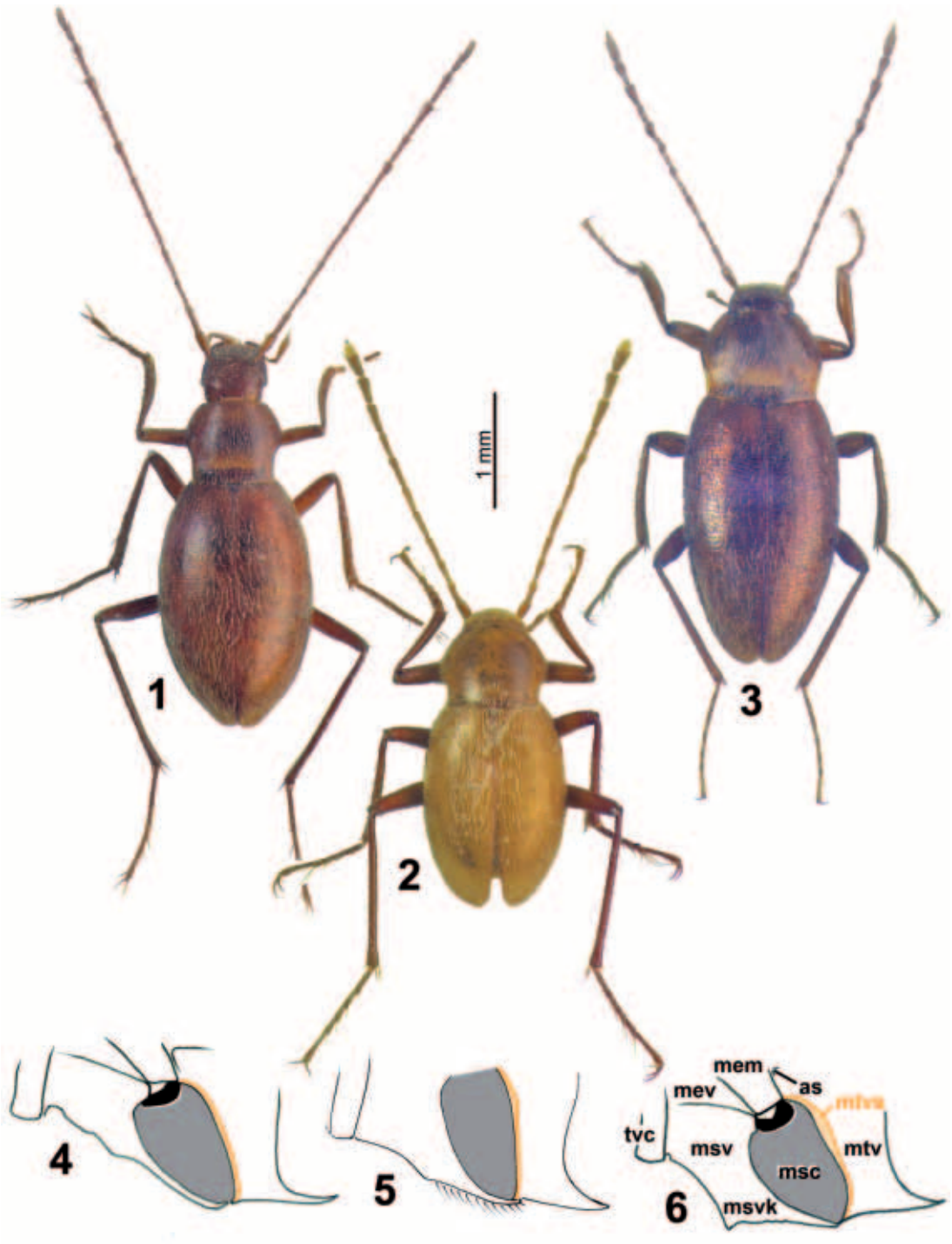
Mesoventral keel (Figs 297.4-297.6): Mesocoxal cavities separated by a high or absolutely reduced keel and limited to a fine, more or less acute ridge situated in the axis of symmetry of the mesoventrite; when present, not extending onto the metaventrite.

Suture of the metaventrite (Figs 297.4-297.6): Completely contiguous and parallel to the edge of the mesocoxal cavity or separated from it by delimiting a small area.

Metatergal apparatus (Figs 298.1-298.3): With a narrow, elongated metascutum and a much reduced alacrista.

Metendosternite (Figs 298.4-298.6): «Y»-shaped, furca with both arms elongated and without terminal apophysis or very reduced.

Median lobe of aedeagus: Very robust. In lateral view (Figs 299.1-299.3), slightly curved and bent at an obtuse angle in the middle or in the apical third and decreasing in size, the apex strongly sinuous. In dorsal



FIGURES 297.1–297.6: *Speonomus* series, *Antrocharis* group. Habitus of: (**1**) *Antrocharis querilhaci querilhaci,* (**2**) *Gesciella delioti,* (**3**) *Paratroglophyes carrerei.* Pterothorax in lateral view of (**4**) *A. q. querilhaci,* (**5**) *G. delioti,* (**6**) *P. carrerei*. Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

view (Figs 299.5, 299.6), straight in the basal two-thirds.

Endophallus (Fig. 299.4): With three regions and numerous sclerotized structures in the median region. A long «Y»-piece, a median region with several pairs of phanerae, and in its terminal part, overlapping the apical region, two sclerotized pieces that form an inverted «V» or «U»; in the apical region, only the reinforcing bands.

Parameres (Figs 299.7-299.9): Shorter than the median lobe and with three setae, two or all three inserted at the apex; no more differentiated structures.

Spermathecal complex (Figs 300.1-300.3): Spermatheca of «type 1» *sensu* Perreau (1989), with the two sclerotized lobes joined by a hyaline tube; spermathecal gland present.

Discussion. In the tree, the *Antrocharis* group is supported by 100/100 and is sister to the clade of the *Speonomus* group with a support of 99.8/100 (Fig. 1B). It is characterised by the following combination of characters:

– Median lobe of the aedeagus, in lateral view, curved at right angle or obtusely, with a strong depression or sinuosity at the level of the third apical part (Figs 299.1-299.3).

– Endophallus: Presence of two additional strongly sclerotized pieces forming an inverted «V» or «U», above the phanerae of the median region (Fig. 299.4; «inverted «V»-piece» of Fresneda *et al*. 2009b); the dorsal sacs of the apex of the median area do not exist.

– Apical part of the «Y»-piece – «fm4, fibres hyalines» of Dupré (1992) or «apical fibres of the «Y»-piece» of Fresneda (1998) –, above the connection nodule («nodule de liaison» of Dupré, 1992), very thin and elongated (Fig. 299.4).

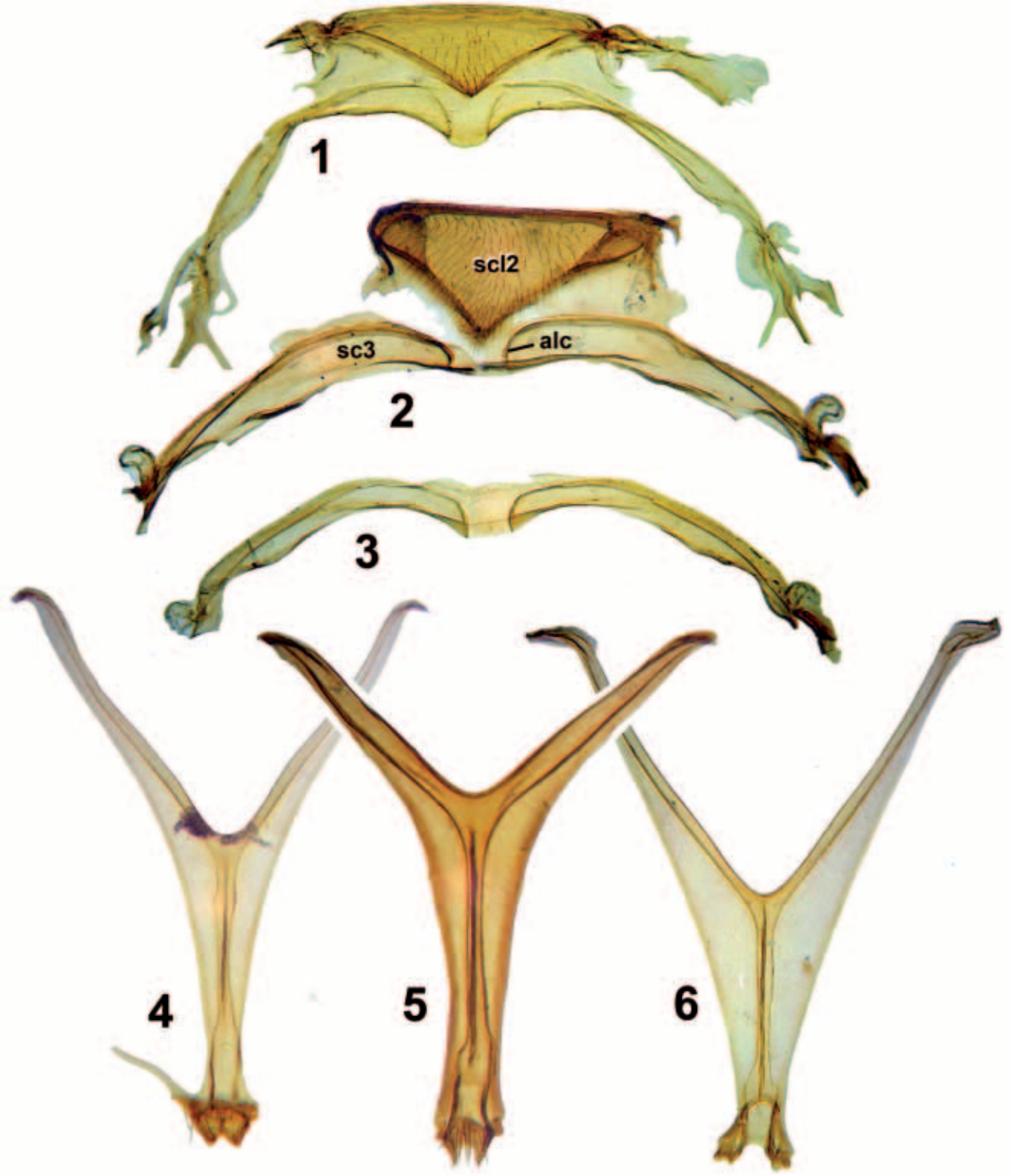
– Parameres of the tegmen shorter than the median lobe, very thin along their entire length and bearing three long setae, two or all three inserted at the apex (Figs 299.7-299.9), and, in the genus *Antrocharis*, a shorter one, without penicillum, cavity or membranous lamina.

The morphological structure of the parameres and the inverted «V»-piece in the median region of the endophallus are also found in *Baronniesia* (Fresneda *et al*. 2009b); the existence of this feature, together with the conformation of the paramere apex, has led to this genus being placed as a sister to the *Antrocharis* clade. Molecular results indicate that the coincidence may be due to convergence or to a derived occurrence that spreads over a few nodes and then disappear: *Baronniesia* is the sister genus of the *Bathysciella-Machaeroscelis-Bellesia* clade. *Pseudospeonomus raholai*, which is in the same clade and sister of *Parvospeonomus*, also lacks a penicillum and a membranous lamina at the apex of the parameres, but the latter has a large penicillum inserted in a more or less large cavity. As already indicated, the absence of these structures could represent the archaic state that has been transmitted to the branches of the tree and which is manifested within clades that already have the derived state of the penicillum and membranous lamina. *Perriniella-Troglophyes-Ceretophyes*, group of genera making up the sister clade to *Antrocharis*, have these derived structures, as do all the representatives of the *Speonomus* group.

Key to genera

1. Elytra with very fine transverse striation only perceptible in the basal area. Mesoventral keel absent (Fig. 297.5). Tibiae totally or partially glabrous and internal spurs bifid. Metendosternite with the trunk of the furca much longer than the arms, which are more robust and with a wider keel (Fig. 298.5). Apical area of median lobe of aedeagus curved dorsally (Fig. 299.2), in lateral view; sharp and narrow (Fig. 299.5), in dorsal view. Median region of endophallus with only two dorsal sclerotized structures and, in upper median area, an inverted «U»-shaped phanera (Fig. 299.5). Spermathecal complex with a small nodule and a basal process (Fig. 300.2) .....*Gesciella*
- Elytra with transverse striation over entire surface. Mesoventral keel low but visible (Figs 297.4, 297.6). Tibiae densely hairy and inner spurs pectinate. Metendosternite with trunk of furca as long as or shorter than arms, which are thinner and with unenlarged keel (Figs 298.4, 298.6). Apical part of median lobe of aedeagus directed ventrally (Figs 299.1, 299.3) in lateral view; in unshrunken arc (Fig. 299.6), in dorsal view. Median region of endophallus with dorsal and ventral phanerae, and in the upper area, between the reinforcing bands, two long sclerotized pieces that join to form an inverted «V»-piece (Figs 299.4, 299.6). Spermathecal complex with only one of the two structures (Figs 300.1, 300.3) 2

2. Mesoventral keel with a small hooked projection in the median part of the mesoventrite (Fig. 297.6). Suture of the metaventrite delimiting a small area towards median part (Fig. 297.6). Metendosternite with the median furcal keel shorter and much stronger than the anterior furcal suture; apical areas of the arms



FIGURES 298.1–298.6: *Speonomus* series, *Antrocharis* group. Metatergal apparatus, ventral view of metanotum and axillaria of: (**1**) *Antrocharis querilhaci querilhaci,* (**2**) *Gesciella delioti,* (**3**) *Paratroglophyes carrerei.* Metendosternite of: (**4**) *A. q. dispar,* (**5**) *G. delioti,* (**6**) *P. carrerei.* Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

slightly dilated and with a reduced apophysis (Fig. 298.6). Median lobe of the aedeagus without dorsal depression in the apical third, sometimes with a slight concavity (Fig. 299.3). Between the two branches of the inverted «V»-shaped part of the endophallus, there is a curved sclerotized structure of transverse arrangement (Fig. 299.6). Spermathecal complex without nodule and with a small basal process (Fig. 300.3). Female uroventrite VIII with a long, wide spiculum, with a slightly wider, notched apex (Fig. 300.5) ....*Paratroglophyes*

- Mesoventral keel with rounded ventral margin (Fig. 297.4). Suture of metaventrite adjoining the coxal cavity (Fig. 297.4). Metendosternite with median furcal keel as long and almost as robust as anterior furcal suture; apical areas of arms curved and with sharp points, without terminal apophysis (Fig. 298.4). Median lobe of aedeagus with marked dorsal depression in apical third (Fig. 299.1). No sclerotized structures between the two branches of the inverted «V»-shaped part of the endophallus (Fig. 299.4). Spermathecal complex with a reduced nodule and no basal process (Fig. 300.1). Female uroventrite VIII with a long, thin and somewhat curved spiculum (Fig. 300.4) ....*Antrocharis*

Genus ***Antrocharis*** Abeille de Perrin, 1878
Antrodietus Abeille de Perrin, 1876: 29.
Antrocharis Abeille de Perrin, 1878: 152 (unjustified new replacement name).

Note. Since 1878, *Antrodietus* Abeille de Perrin, 1876 has been considered a homonym of *Antrodiaetus* Ausserer, 1871 – Arachnida –. However, *Antrodietus* Abeille de Perrin and *Antrodiaetus* Ausserer differ by one letter and according to Article 56.2 of the International Code of Zoological Nomenclature (ICZN, 1999), there is no homonymy and the name of Abeille de Perrin (1876) may be retained. To apply Article 23.9 (ICZN, 1999), reversal of precedence, evidence that Article 23.9.1.2 applies must be provided; Article 23.9.1 of the code must be applied and *Antrodietus* declared *nomen oblitum* and *Antrocharis nomen protectum*. The conditions of Article 23.9.1.2 are not met and the case has been submitted to the Nomenclature Commission; until the case is resolved, the name *Antrocharis* may continue to be used in accordance with Article 23.9.3.

Type species. *Leptoderus querilhaci* Lespès, 1857 by original designation (habitus in Fig. 297.1).

Diagnosis. Size between 3.1-3.3 mm. Pholeuonoid facies (Fig. 297.1).

Head: Occipital carina complete; anophthalmous.

Antennae: Very long, almost twice the length of the elytral suture, the club not or only slightly thickened.

Pronotum: Slightly wider than long, with very narrow sides, subparallel in the basal half.

Elytra: With regularly curved margins, proportionally large compared to the head and pronotum combined, giving the insect a certain «leptodiroid» appearance; fine transverse striolae, clearly visible and close together.

Legs: Male protarsomeres not dilated but with adhesive pilosity. Tibiae with two internal pectinate spurs, two simple external ones and a series of spines spaced on the external surface between the dense pilosity; protibiae without attenuated apex; mesotibiae and metatibiae straight.

Mesoventral keel (Fig. 297.4): Reduced to a thin, inconspicuous, slightly sinuous ridge on the line of contact between the two symmetrical halves of the mesoventrite.

Suture of the metaventrite (Fig. 297.4): Absolutely contiguous and parallel to the margin of the mesocoxal cavity.

Metatergal apparatus (Fig. 298.1): Wings of metascutum long and very narrow; the alacrista very reduced.

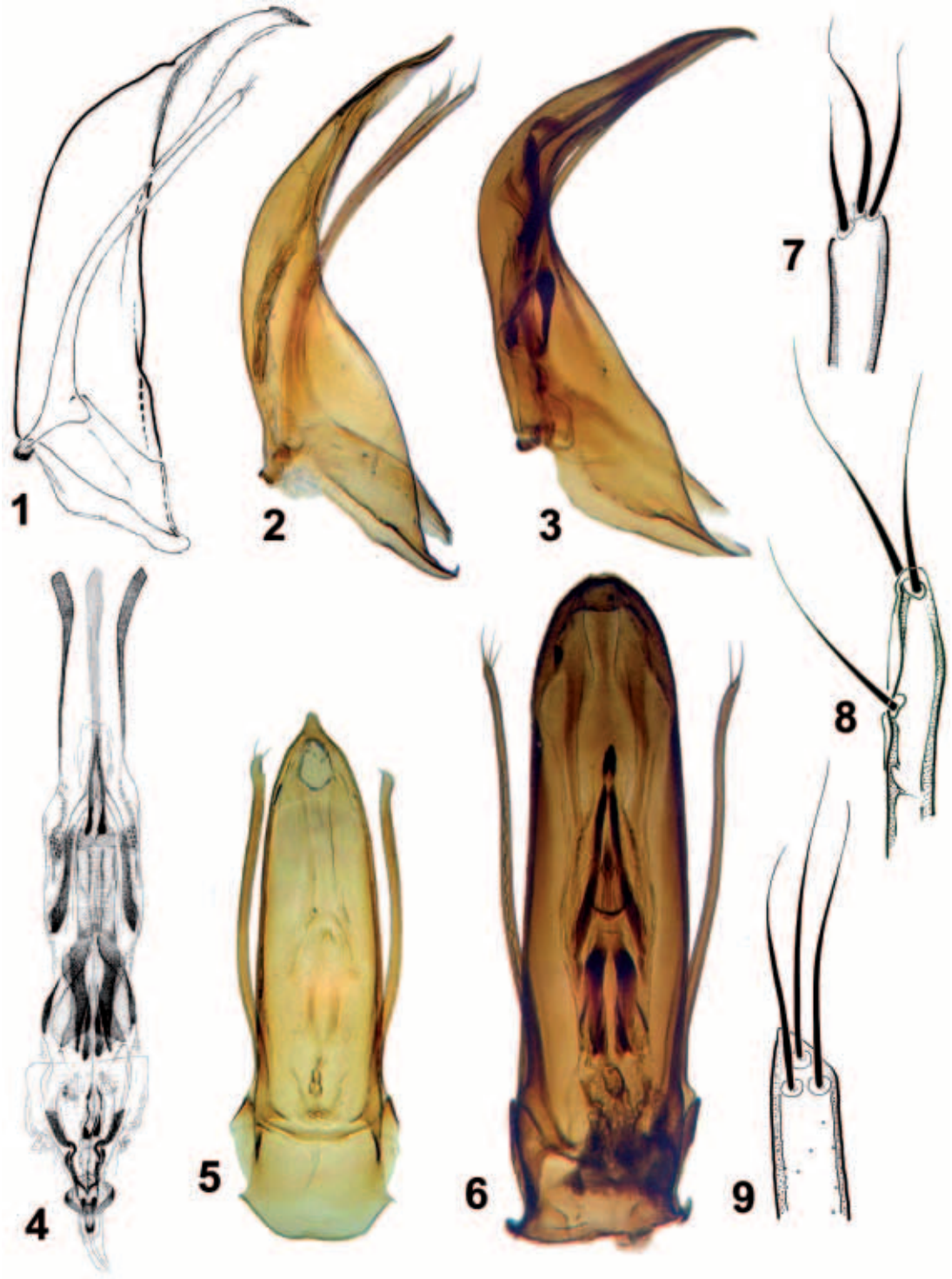
Metendosternite (Fig. 298.4): «Y»-shaped; furcal arms narrow, slightly undulating and as long as furcal trunk, with very curved and acute apex, without terminal apophysis; posterior plate narrow, especially towards apical area of arms, with arched margin; furcal trunk narrow and long, twice as long as area of greatest width and median keel with elongate posterior divergence.

Median lobe of aedeagus: Very robust. In lateral view (Fig. 299.1), ventrally rectilinear in the basal two-thirds and bent at an obtuse angle in the apical third, which decreases in size and has a curved apex facing ventrally; dorsally, a marked depression towards the apical third.

Endophallus (Fig. 299.4): Apical region covered by two sclerotized structures forming an inverted «V».

Parameres (Fig. 299.7): Shorter than median lobe and with three setae inserted exactly at terminal tip of apex, one shorter; no other distinct structures.

Spermathecal complex (Fig. 300.1): Spermatheca elongated with the basal lobe larger than the apical, which is of the same calibre as the median region; in addition, a reduced nodule at the junction between the spermatic duct and spermatheca and no sclerotized basal



FIGURES 299.1–299.9: *Speonomus* series, *Antrocharis* group. Aedeagus in lateral view of: (**1**) *Antrocharis querilhaci querilhaci,* (**2**) *Gesciella delioti,* (**3**) *Paratroglophyes carrerei.* Endophallus of: (**4**) *A. q. querilhaci.* Aedeagus in dorsal view of: (**5**) *G. delioti*, (**6**) *P. carrerei.* Apex of parameres of: (**7**) *A. q. querilhaci,* (**8**) *G. delioti,* (**9**) *P. jeanneli.*

process at the connection with the bursa copulatrix.

Female uroventrite VIII (Fig. 300.4): Spiculum long, thin and slightly curved towards the apex.

Discussion. In the phylogenetic tree (Fig. 1B) the cladogenesis node between *Antrocharis* and *Paratroglophyes*, a sister genus, has a support of 83.8/99. *Paratroglophyes* is a genus with which it has great affinities in terms of both external morphology and aedeagus; the most significant differences are the shape of the pronotum, the mesoventral keel, the metendosternite and certain sclerotized structures of the endophallus. The differences between females are more obvious, being clearly different from those of *Paratroglophyes* as regards the shape of the female uroventrite VIII, the spiculum and the spermathecal complex with a reduced nodule and no basal process.

Distribution. France. Northern slopes of the central Pyrenees in the department of Ariège. It inhabits the underground cavities of the Salat basin, upstream of Saint-Girons, the relief of the Arize basin as far as Le Mas d'Azil and around Foix, and the cavities of the Vicdessos valley not far from Tarascon-sur-Ariège. This species was cited from the island of Menorca by Tenenbaum (1915: p. 51) who also stated that it is a common species on the island: «*na Minorce pospolity*». It is impossible to know which beetle S. Tenenbaum determined to be *A. querilhaci*.

Species

Antrocharis querilhaci (Lespès, 1857)
Antrocharis querilhaci querilhaci (Lespès, 1857)
Leptoderus querilhaci Lespès, 1857: 283.
Drimeotus Querilhaci Lespès: Reiche, 1858: cxcii.
Leptoderus Querilhaci Lespès: Fairmaire, 1859: 31.
Pholeuon Querilhaci: Lespès, 1868: 68.
Antrodietus Querilhaci Lesp.: Abeille de Perrin, 1876: 29.
Antrocharis Querilhaci: Abeille de Perrin, 1878: 152.
Antrocharis Querilhaci Lespès: Reitter, 1885a [1884]: 12.
Antrocharis querilhaci Lespès: Tenenbaum, 1915: 51.
Antrocharis querilhaci querilhaci (Lespès): Perreau, 2000: 302.
Antrocharis querilhaci dispar Abeille de Perrin, 1878
Antrocharis dispar Abeille de Perrin, 1878: 152.
Antrocharis Querilhaci subsp. *dispar* Abeille: Jeannel, 1911a: 380.
Antrocharis querilhaci subsp. *dispar* Ab.: Coiffait, 1962: 77.

Genus ***Gesciella*** Giachino & V.B. Guéorguiev, 1989
Gesciella Giachino & V.B. Guéorguiev, 1989: 403.

Type species. *Gesciella delioti* Giachino & V.B. Guéorguiev, 1989 by original designation (habitus in Fig. 297.2).

Diagnosis. Size between 3.3-3.9 mm. Pholeuonoid facies (Fig. 297.2).

Head: With a complete occipital carina; anophthalmous.

Antennae: As long as or slightly longer than the body; club not very distinct.

Pronotum: Transverse and slightly narrower than the elytra, strongly narrowed after half its length and the sides clearly sinuate in the basal area; posterior vertices acute and protruding.

Elytra: Proportionally short, although longer than wide, and with the margins regularly curved from one end to the other; very fine transverse striation, only defined in the anterior area, the rest covered with disordered dots. Elytral disc very convex.

Legs: Male protarsomeres slightly dilated, narrower than distal end of tibia; claws smooth and very long, reaching two thirds of onychium. Tibiae with bifid inner spurs and with spines on the outer surface; protibiae without attenuated apex, with a hairy inner surface and a glabrous outer surface like the mesotibiae, which are straight; metatibiae also straight and completely glabrous.

Mesoventral keel (Fig. 297.5): Very weak, practically non-existent, limited to an edge situated on the axis of symmetry of the mesoventrite.

Suture of the metaventrite (Fig. 297.5): The area delimiting the suture practically non existent.

Metatergal apparatus (Fig. 298.2): Metascutum narrow and elongated, the alacrista completely reduced and not prominent.

Metendosternite (Fig. 298.5): «Y»-shaped; furcal arms straight and robust, distinctly shorter than furcal trunk and with more dilated keels than in the other two genera of the clade; apical area slightly curved with slightly pointed apex and without differentiated terminal apophysis; posterior furcal plate narrowed and gradually decreasing towards apex, with arched margin. Furcal trunk very long, more than twice as long as area of greatest width and median keel with well-defined posterior divergence.

Median lobe of aedeagus: Slightly arched, short. In lateral view (Fig. 299.2) broad with acute apex, somewhat curved dorsally. In dorsal view (Fig. 299.5), the apical area narrowed, the protruding tip in a sharp arc.

Endophallus (Fig. 299.5): In the basal region, a very thin, elongated «Y»-piece; in the middle, only a pair of sclerotized structures and an inverted «U»-shaped piece are discernible.

Parameres (Fig. 299.8): Shorter than the median lobe, with two setae inserted exactly at the terminal tip of the apex and the other at a proximal insertion; all three setae of equal length.

Spermathecal complex (Fig. 300.2): Spermatheca elongate with both lobes differentiated and sclerotized, the basal a little thicker than the apical; spermiduct short, about three times the length of the spermatheca, connected to it by a minute nodule and with a small sclerotized basal process at the point of attachment to the copulatrix sac; spermathecal gland present.

Female uroventrite VIII: Unknown.

Discussion. It is the sister genus of the *Antrocharis* + *Paratroglophyes* clade to which it is related with a strong support of 100/100 (Fig. 1B). An observation error led the describers to place the genus in the phyletic series of *Cytodromus* with which it shares the absence of transverse striation on the elytra: they observed irregular punctation. It does, however, have very fine transverse striolae on the anterior half of the elytra. Morphologically, the facies of *Gesciella* is very similar to that of *Antrocharis* or *Paratroglophyes*, but, in addition, the endophallus shows the characteristic apomorphy of the group (+ *Baronniesia*): the presence of a sclerotized piece in the upper part of the median region of the endophallus, which has an inverted «U»-shape in *Gesciella* and a «V»-shape with very long arms in the other two genera. The very long claws, bifid spurs and totally or partially glabrous tibiae are synapomorphies of the genus.

Distribution: France. Hypogean endemism of the northern slope of the central Pyrenees known from a single underground cavity near Seix, in the Estours valley, not far from Saint-Girons: the Bordes de Crues underground river. Species uncommon, few specimens known.

Species

Gesciella delioti Giachino & V.B. Guéorguiev, 1989
Gesciella delioti Giachino & V.B. Guéorguiev, 1989: 405.

Genus ***Paratroglophyes*** Fourès, 1954
Paratroglophyes Fourès, 1954: 5.

Type species. *Paratroglophyes carrerei* Fourès, 1954 by original designation (habitus in Fig. 297.3).

Diagnosis. Size between 2.5-3.1 mm. Body oblong (Fig. 297.3), regularly oval in outline, although with a clear pronotum-elytral angle.

Head: With the occipital carina blurred in the central part; anophthalmous.

Antennae: Long and slender, longer than or as long as the elytral suture.

Pronotum: Transverse, a little wider than long; sides with basal third strongly narrowed.

Elytra: Basal third widest and lateral margins evenly arched to apex; apices dehiscent, the end of the suture at the bottom of a deep slit; transverse striation over the whole elytra with fine, separate striae.

Legs: Male protarsomeres enlarged or not, always narrower than the top of the protibiae. Tibiae densely hairy, with pectinate inner spurs, simple outer spurs without spines on the outside; in males, protibiae with a slightly attenuated apex, mesotibiae curved and metatibiae straight. Basal third of the metafemora sometimes greatly narrowed.

Mesoventral keel (Fig. 297.6): Low, hooked, with two sub-rectilinear margins, the anterior one unedged and the lower one with a pointed edge.

Suture of the metaventrite (Fig. 297.6): With a curved line and somewhat detached from the edge of the mesocoxal cavity, delimiting a small but clear area. Metaventrite strongly punctate and rough, the anapleural suture very reduced and practically invisible.

Metatergal apparatus (Fig. 298.3): Narrow and elongated metascutum, a very reduced alacrista with sharp points.

Metendosternite (Fig. 298.6): Not «Y»-shaped; furcal arms very long, straight and slender, distinctly longer than furcal trunk, apex slightly dilated and terminal apophysis reduced; posterior lamina narrowing and tapering towards apex, with rectilinear posterior margin. Furcal trunk slightly longer than the area of greatest basal width, but wider than in the other two genera of the clade, the median keel with a well-defined posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 299.3) abruptly curved at obtuse angle in middle, without dorsal depression in apical third, apex very slightly curved towards ventral side. In dorsal view (Fig. 299.6), margins subparallel and apex rounded.

Endophallus (Fig. 299.6): Median region with dorsal, ventral, and two other very long phanerae joined at the upper end, forming a kind of inverted «V» with the lower branches curved; a thin sclerotized piece slightly curved in a transverse position, between the two branches of the «V»; basal region with a «Y»-piece and a kind of disc at the end of the ventral basal complex.

Parameres (Fig. 299.9): Shorter than median lobe, with three setae inserted exactly at terminal tip of apex, all of equal length.

Spermathecal complex (Fig. 300.3): Spermatheca elongated with the two lobes differentiated, the basal a little wider; spermiduct extremely thin, without a junction nodule in the spermatheca and with a very reduced basal process which joins the bursa copulatrix; spermathecal gland present.

Female uroventrite VIII (Fig. 300.5): Spiculum long and wide, with enlarged and indented apex.

Discussion. *Paratroglophyes* shares with the other genera of the *Antrocharis* group the parameres with three setae, without penicillum (Fourès 1954), no cavity and no membranous lamina; in the median region of the endophallus we find the two very long sclerotized pieces joined at their upper end, which form a sort of inverted «V» (Fresneda *et al*. 2009b, 2011a). However, this genus can be distinguished from other genera by the aedeagus abruptly bent in the middle, in lateral view (Fourès 1954). The very characteristic shape of the meso- and metafemurs mentioned by Fourès (1954) and Coiffait (1955a) has become unusable to characterise the genus within its group since the discovery of *Paratroglophyes orestes* which has them simple. The two *Troglophyes* taxa that inhabit the central Pyrenees, *Troglophyes aubryi aubryi* and *Troglophyes aubryi vallierensis*, have been transferred to the genus *Paratroglophyes*, as indicated by molecular results with a support of 99.9/100 (Fig. 1B). In addition, these two species also show the inverted «V» of the endophallus and the absence of a membranous lamina and a penicillum. An observation error by Coiffait (1953) indicated that *Paratroglophyes aubryi aubryi* comb. nov. has a penicillum at the apex of the parameres, but this was not observed in the numerous specimens studied. On the other hand, the species of the genus *Troglophyes* are typical of the eastern end of the Pyrenees, while *P. aubryi aubryi* comb. nov. and *T. aubryi vallierensis* are distributed in a small area of the central Pyrenees; between the two areas, there are numerous species of various genera of Leptodirini. Synonymy has been established for *Troglophyes aubryi aubryi* comb. nov. and *Troglophyes aubryi vallierensis* syn. nov.

Distribution. France. The species are known from very few localities spread over a small area of Mont-Rouch and Mont-Vallier in Seix, Les-Bordes-sur-Lez and Salau (Port de Salau) in Ariège, on the northern slopes of the central Pyrenees. They inhabit both underground cavities and MSS.

Species

Paratroglophyes aubryi (Coiffait, 1953) comb. nov.
Troglophyes aubryi Coiffait, 1953: 31.
Troglophyes aubryi vallierensis Coiffait, 1953: 31 syn. nov.
Troglophyes Aubryi Coiff, 1953: Coiffait, 1955a: 107.
Troglophyes aubryi aubryi Coiffait: Perreau, 2000: 337.

Paratroglophyes carrerei Fourès, 1954
Paratroglophyes carrerei Fourès, 1954: 5.

Paratroglophyes jeanneli Coiffait, 1955
Paratroglophyes Jeanneli Coiffait, 1955a: 109.
Paratroglophyes jeanneli Coiffait, 1955: Fresneda, Bourdeau & Faille, 2011a: 359.

Paratroglophyes juberthiei sp. nov. (See Appendix New Species)

Paratroglophyes orestes Fresneda, Bourdeau & Faille, 2011
Paratroglophyes orestes Fresneda, Bourdeau & Faille, 2011a: 356.

3.4.8 Series ***Speonomus***

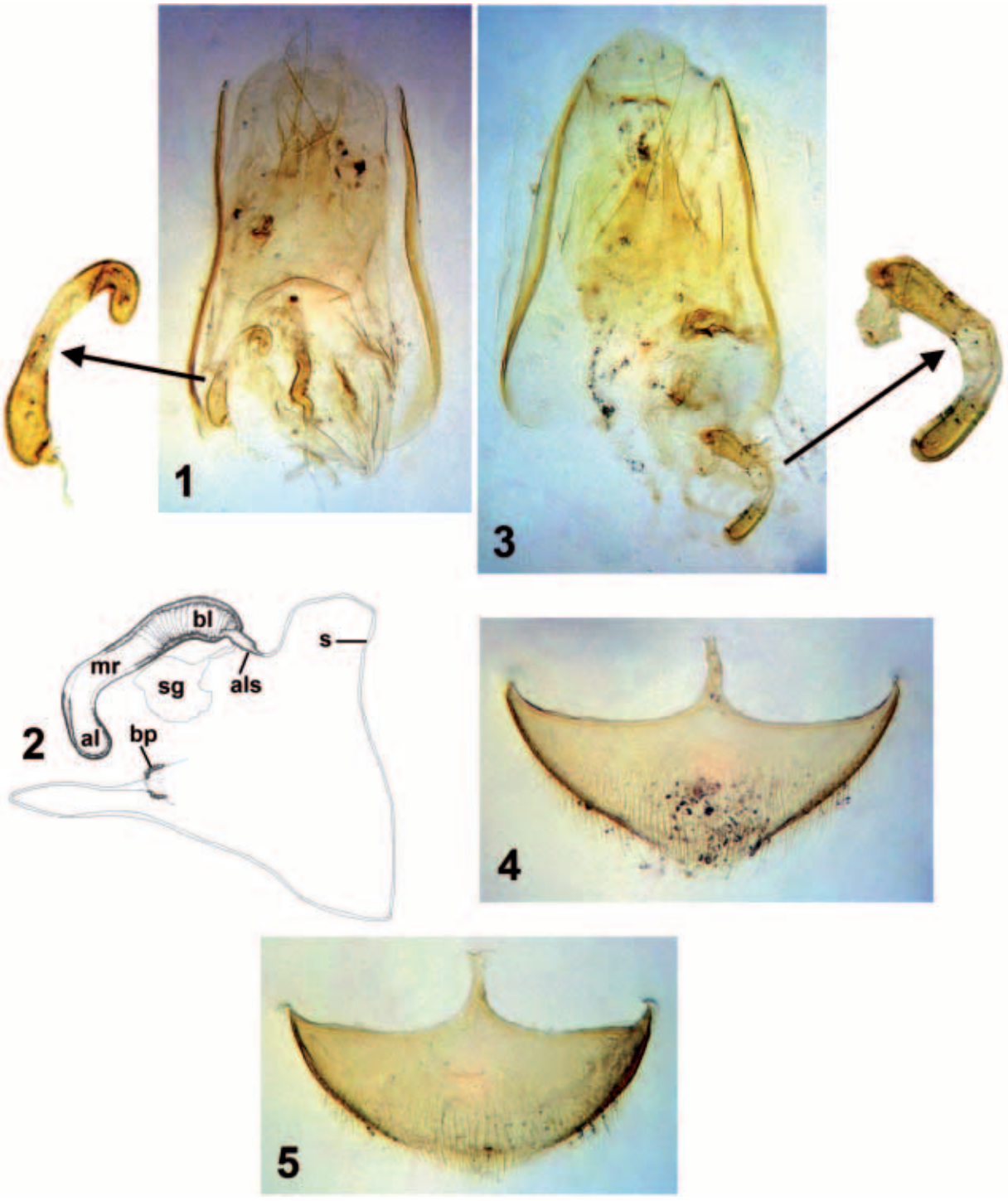
Diagnosis. Elytra with more or less marked transverse striolae, sometimes replaced by isolated or disordered dots; parasutural stria present or absent depending on the group. Anophthalmous and depigmented species.

Mesoventral keel: Short, not extending beyond the metaventrite, high or reduced, sometimes absent.

Suture of metaventrite: Delimiting an arched area, generally small, narrow and more or less elongated.

Median lobe of aedeagus: Arched and thick at the base.

Endophallus: With three regions, and always a «Y»-piece at the base, except in *Pseudospeonomus,* which has a ring-shaped sclerotized part.



FIGURES 300.1-300.5: *Speonomus* series, *Antrocharis* group. Spermathecal complex of: (**1**) *Antrocharis querilhaci querilhaci,* (**2**) *Gesciella delioti* (modified from Giachino & V.B. Guéorguiev 1989), (**3**) *Paratroglophyes carrerei.* Female uroventrite VIII of: (**4**) *A. q. querilhaci,* (**5**) *P. carrerei.* Abbreviations: **als**, apical lobe of the spermiduct; **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland.

Spermatheca: Elongated, generally five times (or more) longer than wide.

Discussion. The series has high support in all analysis, 100/100, in both Tree-1 (Fig. 1C) and Tree-2 (Fig. 2); it is sister to the clade formed by the series *Catopsinus* + *Drimeotus* + *Hittitia* with low support, 81.3/41 in Tree-1 and 74.7/56 in Tree-2.
Two characters of taxonomic importance are present or absent in the different groups of this series: the presence or absence of a penicillum and/or membranous lamina at the apex of the tegmen parameres. Given the topology of the molecular tree, it could be envisaged that:

– The absence of a penicillum is a secondary loss of structure that occurred three times independently.

– Or given that the absence of penicillum is normal in most Leptodirini and that, above all, it is found in the clades with the most basal divergence, even in outgroups, this would then be the ancestral state and the development of penicillum occurred five times independently in the clades: *Parvospeonomus, Vanderberghia* gen. nov., *Bathysciella-Machaeroscelis-Bellesia, Ceretophyes-Perriniella-Troglophyes* and the large clade of the *Speonomus* group.

Given that the sister clade of the entire Pyrenees series – the *Euryspeonomus* group, in the «Basque-Pyrenean» clade (parameres with four setae) – and the sister of the two, the «*Catopsinus series*» (parameres with three setae), do not have a penicillum or membranous lamina, the second hypothesis must be considered more plausible, although it involves more independent occurrences of the same character.

Among the clades with penicillum, two models can be identified:

– Two or three setae, short and fine, and a dense penicillum, inserted in a cavity or depression: *Parvospeonomus, Vanderberghia* gen. nov. clade (ex *Speonomus speluncarum* species group), *Bathysciella* clade, *Machaeroscelis-Bellesia* clade, *Ceretophyes-Perriniella-Troglophyes* clade.

– Three setae of varying thickness, length and curvature, a membranous lamina of varying size and a penicillum that may be denser or rarer: *Speonomites* clade, *Troglocharinus* clade, *Speonomus* clade, *Trapezodirus-Salgadoia-Naspunius-Stygiophyes-Lagariella* clade. In *Troglocharinus orcinus*, there is no penicillum, only a few rare setae, although in this case the structure corresponds to the characteristic pattern of parameres with two large and one fine setae, and a membranous lamina where the penicillum has been lost. In this case, the loss of the penicillum is clearly secondary. *Ariejasia* gen. nov. is also a special case, as this genus has three long setae of varying length and thickness, and the penicillum is formed by long peduncles or bands originating from the margin of the membranous lamina.

Key to groups

1. Parameres without penicillum (Figs 277.11-277.25, 283.6, 290.1, 299.7-299.9) …… 2
- Parameres with penicillum, formed by setae or bands (Figs 283.5, 290.2-290.6, 295.7-295.9, 312.1-312.11) (except *Troglocharinus orcinus*, with pholeuonoid facies, with three setae and membranous lamina in the apical part of the parameres) 5

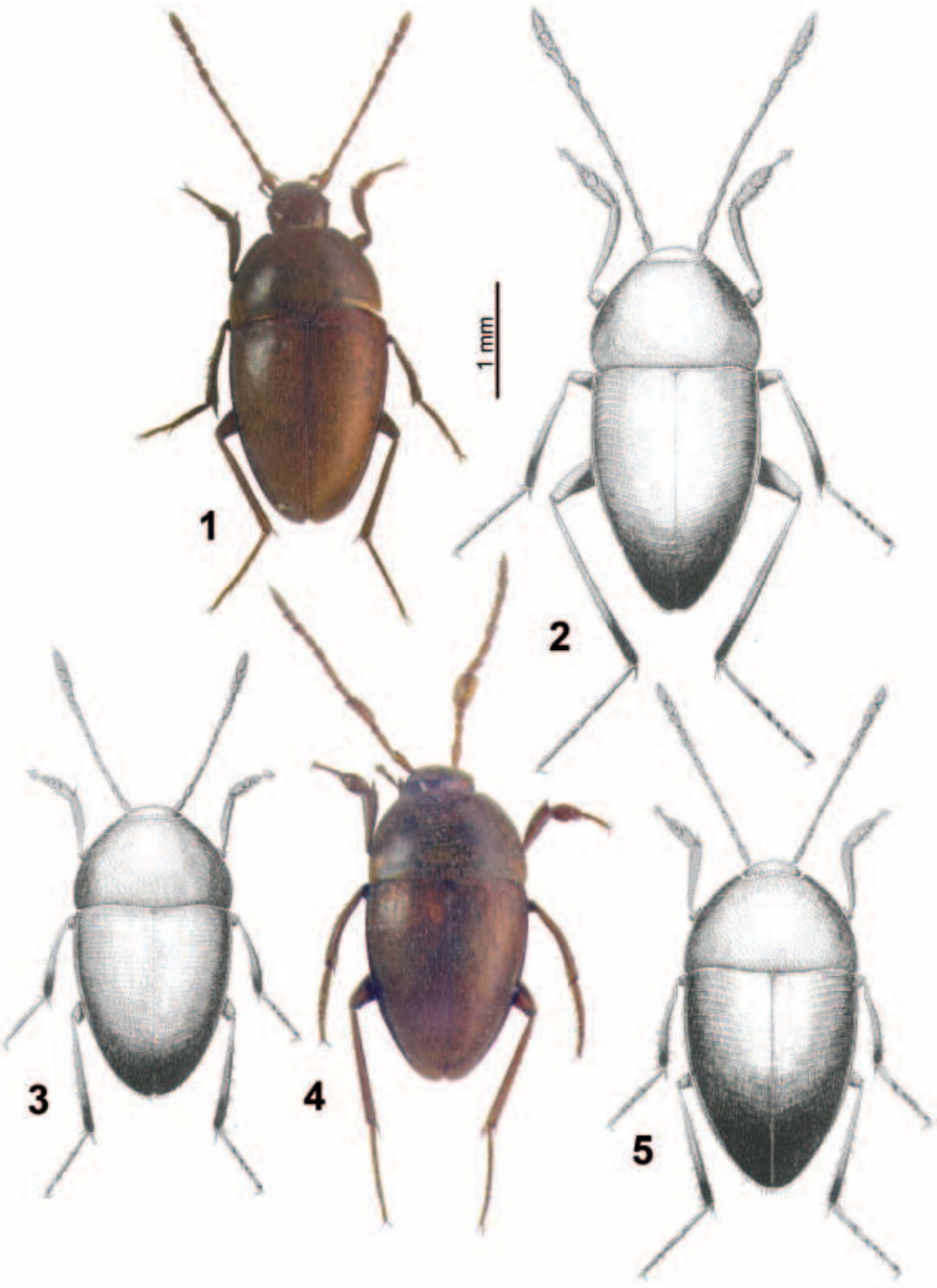
2. Parameres with four setae or spines in the apical part (Figs 277.12-277.20, 277.22-277.25), one case with nine (Fig. 277.21) and another with about 30 setae (Fig. 277.11) .....*Euryspeonomus* group
- Parameres with three setae in the apical part (Figs 283.6, 290.1, 299.7-299.9) 3

3. Pholeuonoid facies (Figs 297.1-297.3) .....
.....*Antrocharis* group
- Bathyscioid facies (Figs 282.1, 282.2, 284.1).....4

4. Elytra without transverse striae. Mesoventral keel high (Fig. 282.4). Metendosternite with furcal arms almost three times as long as the trunk and with a terminal apophysis (Fig. 282.8). Apical area of parameres very sharp (Fig. 283.6); basal region of endophallus with sclerotized ring and teeth on inner margin (Fig. 283.4) .....
.....*Pseudospeonomus* (*Parvospeonomus* group-pars)
- Elytra with visible transverse striae in the basal area. Metendosternite with furcal arms shorter than the trunk and without terminal apophysis (Fig. 287.1). Low mesoventral keel (Fig. 285.1). Apical area of parameres rounded (Fig. 290.1); basal area of endophallus with a «Y»-piece (Fig. 289.1).....
.....*Baronniesia* (*Bathysciella* group-pars)

5. Parameres with a more or less developed membranous lamina (Figs 312.1-312.11) ..*Speonomus* group
- Parameres without membranous lamina (Figs 283.5, 290.2-290.6, 295.7-295.9).....6

6. Elytra without parasutural stria, sometimes with a depression without dots.....7
- Elytra with parasutural stria 8



FIGURES 301.1–301.5: *Speonomus* series, *Speonomus* group. Habitus of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti.* Figs **2**, **3**, **5** modified from Salgado *et al*. (2008).

7. Parameres with a cavity and a dense penicillum with long setae (Figs 290.2-290.6) ....*Bathysciella* group-pars
- Parameres without a cavity and with a sparse penicillum and short setae (Fig. 295.7-295.9) ....*Troglophyes* (*Troglophyes* group-pars)

8. Body short and oval (Fig. 282.1). Protarsi of males slender. Metendosternite with posterior lamina of furca very narrow in arms (Fig. 282.7). Flagellum of the «Y»-piece very long and filiform (Fig. 283.3) ....*Parvospeonomus* group-pars
- Body elongate and elliptical (Figs 293.1-293.3). Protarsi of males dilated, at least as wide as apical end of protibiae. Metendosternite with posterior lamina of furca well developed in arms (Figs 294.4-294.6). Flagellum of the «Y»-piece shorter and more robust (Figs 295.4-295.6) .....*Troglophyes* group-pars

3.4.8.6 ***Speonomus*** group

Diagnosis. Bathyscioid or pholeuonoid body shape, and between the two extremes, all possible intermediate shapes. Depigmented. Yellowish-reddish colouration, the integument entirely covered with a fine pubescence, short or long, recumbent or erect. Punctation of the pronotum marked by disordered dots; that of the elytra generally by transverse striolae, or, in some specific cases, by disordered dots.

Head: Small, with a faint occipital carina, complete or obliterated in its median part. Epistomal suture evident straight or strongly curved and generally dark, although in some cases the same colour as the forehead and epistome. Last segment of maxillary palps short and conical, second segment short and thick or elongated and thin. Anophthalmous.

Antennae: Of 11 antennomeres, very variable in length and shape of segments; generally a little thickened from the 7th antennomere onwards, the 8th reduced; in some cases, no thickening of the apical segments and sometimes a few antennomeres dilated in the basal area.

Pronotum: Transverse with lateral margins arched or bell-shaped with sinuous sides; sometimes very narrow in the posterior third, with strongly notched or subparallel margins in the basal half.

Elytra: Short and wide or very long and narrow, with beaded sides along their entire length; generally without parasutural stria, but sometimes visible, although more or less superficial and blurred, in certain species of the three genera.

Metaventrite: With a protruding bifid process or an apophysis separating the two metacoxal cavities.

Legs: Protarsi pentamerous in males and tetramerous in females; protarsomeres dilated in males. Two inner dorsal and ventral pectinate spurs on all tibiae, sometimes with two simple external spurs; a series of unequal spines between the internal and external spurs; sometimes a series of spines along the outer surface of the tibia. Protibiae not attenuated at distal end, mesotibiae usually arched, but sometimes straight like metatibiae.

Mesoventral keel: Situated on the median line of the mesoventrite, high and forming a triangular lamina in bathyscioid taxa or practically non-existent and reduced to a ridge or simple lash-like tooth in pholeuonoid taxa; not extending onto the metaventrite.

Suture of the metaventrite: In a more or less sinuous arc, extending a short distance from the edge of the mesocoxal cavity and delimiting a small, narrow, more or less elongated area.

Metatergal apparatus: Wings of metascutum elongated and alacrista greatly reduced.

Metendosternite: «Y»-shaped, all arms with an apical apophysis.

Median lobe of aedeagus: In the shape of a pseudo-conical tube, curved regularly from one end to the other or bent at a precise point.

Endophallus: Three regions, the basal one with a «Y»-piece, the median with several sclerotized phanerae and the apical with reinforcement bands.

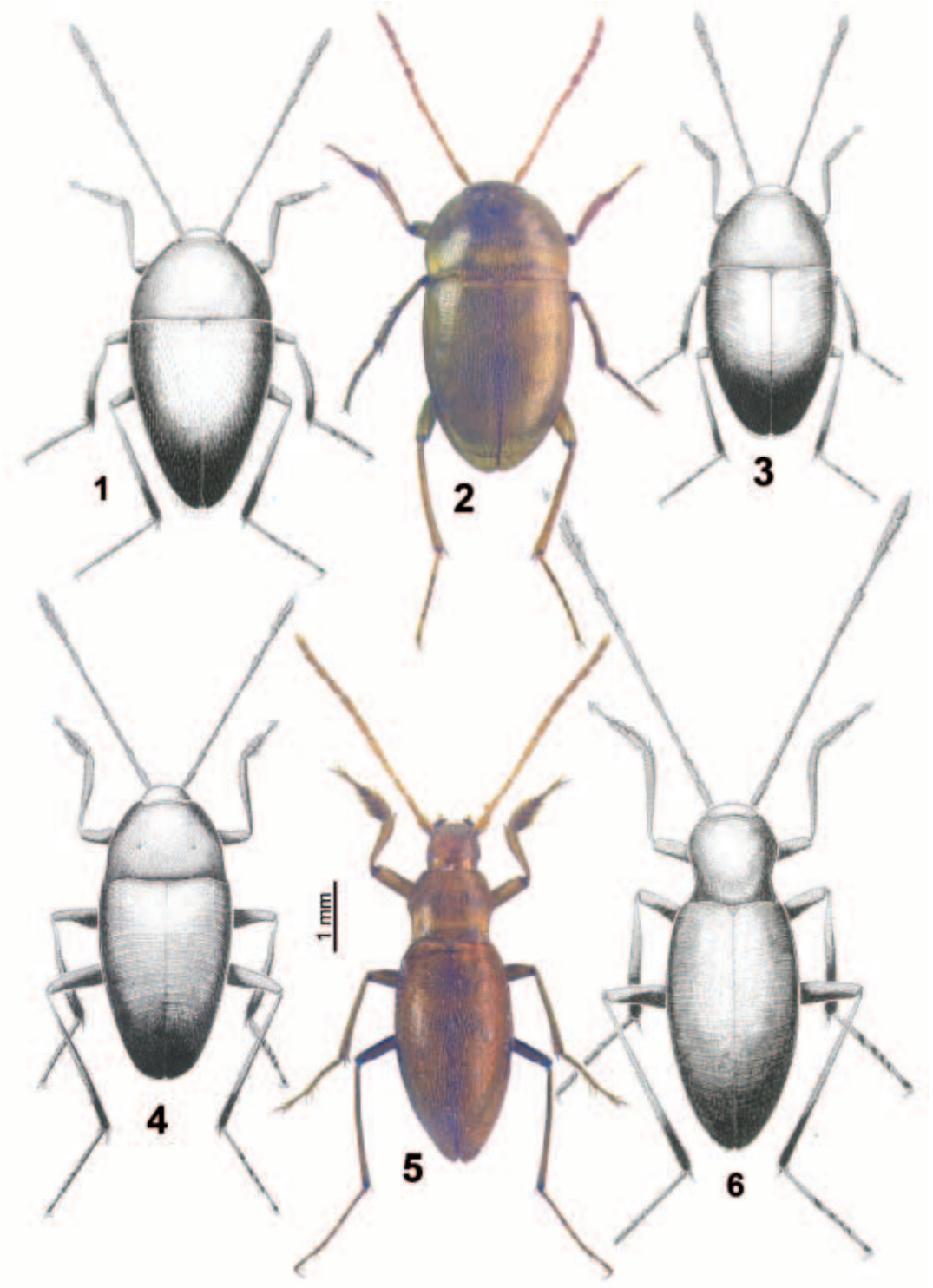
Parameres: With three main setae in apical insertion, only in one case there are two; a membranous lamina attached, although in one case this is an extension of the paramere apex tissue; penicillum formed by numerous setae of variable length, inserted on the side of the apex or on the membranous lamina itself; in one case, no penicillum and in another the setae modified into apparently flat bands.

Male genital segment: Very small, forming an open ring with two long peduncles.

Spermathecal complex: With spermatheca of «type 1» *sensu* Perreau (1989), with two sclerotized lobes joined by a hyaline tube or union duct; a spermatic duct of very variable length, sometimes strongly thickened at the insertion in the basal lobe and presenting a basal piece at the insertion with the copulatory sac; spermathecal gland present.

Female uroventrite VIII: Spiculum long or short, broad or thin, or reduced to two small lobes.

Discussion. The group has a 100/100 support in Tree-1 (Fig. 1C) and Tree-2 (Fig. 2). The internal topology of the clade is constant in both analysis, with the ex-



FIGURES 302.1–302.6: *Speonomus* series, *Speonomus* group. Habitus of: (**1**) *Speonomites velox,* (**2**) *Speonomus pyreneus,* (**3**) *Stygiophyes puncticollis,* (**4**) *Trapezodirus carrodillae,* (**5**) *Trocharanis mestrei,* (**6**) *Troglocharinus ferreri.* Figs **1**, **3**, **4**, **6** modified from Salgado *et al*. (2008).

ception of the position of the genera *Trocharanis* and *Lagariella*, which will be discussed in the sections corresponding to these genera.

Key to genera

1. Mostly pholeuonoid species (Figs 302.5, 302.6), sometimes bathyscioid. Antennae very long, generally longer than the body. Legs very long, especially the metafemora. Mesoventral keel high, low, or absent (Figs 304.10, 304.11). Very long spermatic duct, more than 40 times the length of the spermatheca (Fig. 314.4) 2
- All species bathyscioid (Figs 301.1-301.5, 302.1-302.4, 303.1, 303.2). Antennae shorter, at most slightly longer than the elytral suture. Legs generally shorter and more robust. Mesoventral keel high (Figs 304.1-304.9). Spermatic duct short or long, at most 30 times the length of the spermatheca 3

2. Mesoventral keel high or reduced. Antennae longer than body. Median lobe of aedeagus, in lateral view (Fig. 309.11), with apical region curved ventrally or straight, in dorsal view not sharp. Parameres with a developed membranous lamina and a dense penicillum with long, fine setae (Fig. 312.11) (no penicillum in *T. orcinus*) ..... *Troglocharinus*
- Mesoventral keel reduced to a sharp keel-like projection (Fig. 304.10). Antennae shorter than body. Median lobe of aedeagus, in lateral view (Fig. 309.10), with apical region strongly sinuate and apex directed dorsally, in dorsal view (Fig. 310.4) very sharp. Parameres with a short membranous lamina and an abundant penicillum formed of thick, twisted setae (Fig. 312.10) .....*Trocharanis*

3. Fourth antennomere long and enlarged in a paddle shape in the male (Fig. 301.4), the third very reduced in both sexes. Parameres with three contiguous setae on the same side of the apex, one of the setae being short, thick and robust with a blunt apex (Fig. 312.4) .....*Paraspeonomus*
- Fourth antennomere not enlarged, as long as or slightly longer than the third. Setae of parameres with different insertion and shape (Figs 312.1-312.3, 312.6-312.9) 4

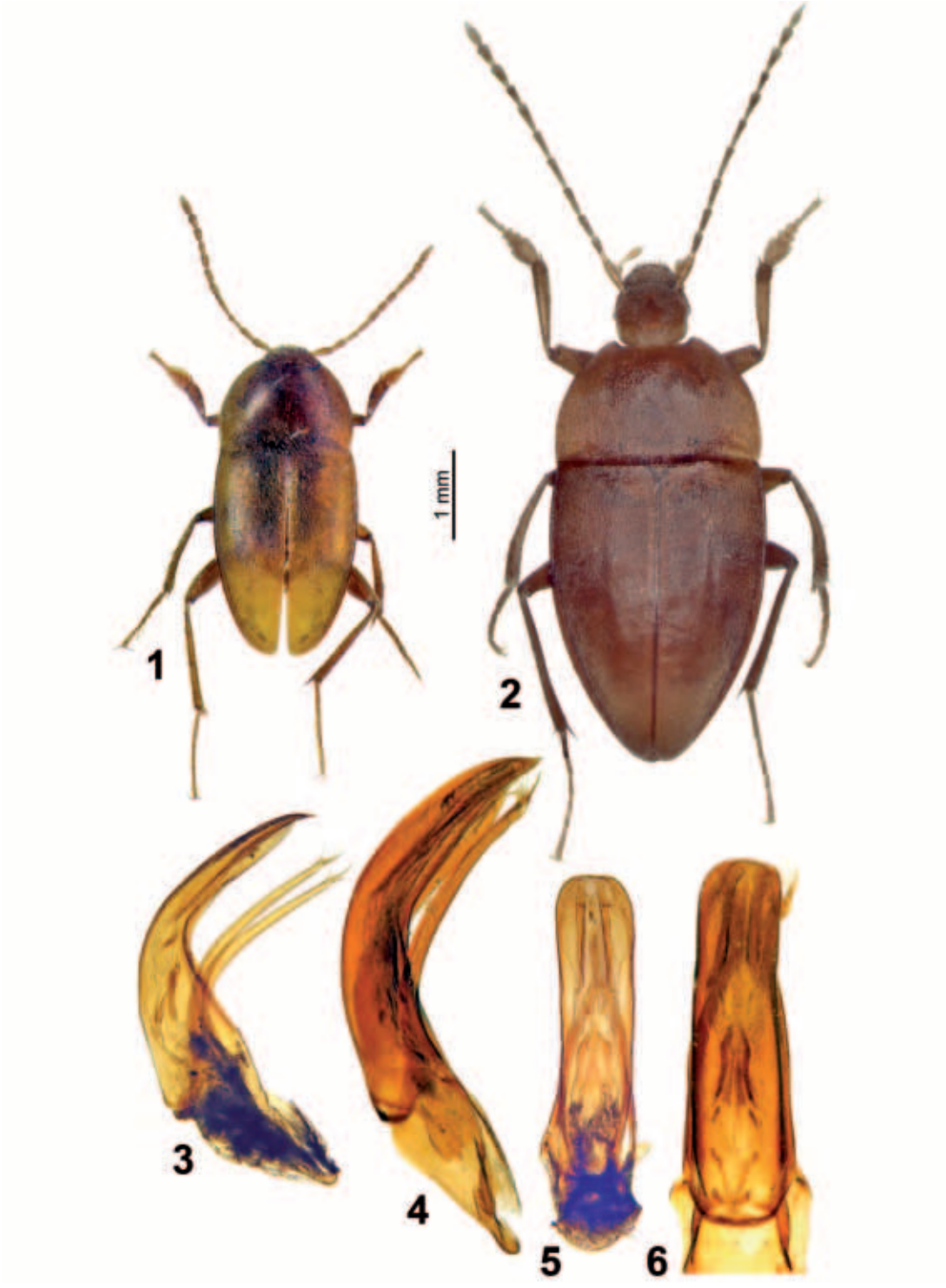
4. Membranous lamina of parameres divided in two; no true penicillum as it consists of bands arranged in two groups (Fig. 312.1).....*Ariejasia* gen. nov.
- When there is a membranous lamina in the parameres, it is entire; penicillum more or less dense and always formed of fine hairs (Figs 312.2, 312.3, 312.6-312.9) 5

5. Metendosternite with furcal trunk longer than arms and posterior plate of arms wide (Fig. 307.5). Parameres with reduced membranous lamina and dense penicillum (Fig. 312.7). Endophallus with a very robust «Y»-piece, with straight and generally short arms (Fig. 310.3) .....*Speonomus*
- Metendosternite with the furcal trunk as long as or shorter than the arms, and when it is longer than the arms, the posterior plate is narrower (Figs 306.5, 307.1, 307.4, 308.1, 308.2). Parameres with the membranous lamina more or less developed and the penicillum with long and numerous setae; if the lamina is reduced, so is the penicillum (Figs 312.2, 312.3, 312.6, 312.8, 312.9). Endophallus with a thinner «Y»-piece, with thin, long and wavy arms (Figs 311.1, 311.2, 311.4-311.6) 6

6. Endophallus with an upper dorsal plate in the median region from which a long and more sclerotized phanera is detached; axial part formed by a tube covered with spicules bearing on its sides sacs which have a sclerotized nodule inside (Fig. 311.4); sac situated between the reinforcement bands of the apical region with the integument without particular relief, with only a wrinkled tissue visible. Basal process of the spermathecal complex in the shape of a disc through which the spermatic duct passes (Fig. 313.6) ....*Speonomites*
- Endophallus with upper dorsal plate in median region where there are no associated phanerae, or when there is a phanerae, it is short; one axial piece, but attached pieces of different shape (Figs 311.1, 311.2, 311.5, 311.6); sac situated between the reinforcement bands of the apical region with the integument covered with scales or spicules, or with sclerotized lateral margins, and in this case, apical sac completed by an apical lamina. Basal process of spermathecal complex undefined or hat- or funnel-shaped (Fig. 313.2, 313.3, 314.1, 314.2) 7

7. Endophallus with disproportionately large dorsal sacs superimposed on two ventral plates (Figs 311.2, 311.3) 8
- Endophallus with small dorsal sacs which may include a phaneroid nodule within or the entire sclerotized inner margin or no differentiated internal structure (Fig. 311.1, 311.5, 311.6) 9

8. Elytra with blurred parasutural stria towards the



FIGURES 303.1–303.6: *Speonomus* series, *Speonomus* group. Habitus of: (**1**) *Speonomus monticola,* (**2**) *S. opisthonoxus* (photo: P. Déliot). Aedeagus in lateral view of: (**3**) *S.* (*M.*) *monticola,* (**4**) *S. opisthonoxus*. Aedeagus in dorsal view of: (**5**) *S.* (*M.*) *monticola,* (**6**) *S. opisthonoxus.*

middle of the apical area. Median lobe of aedeagus, in lateral view, short, gibbous and with a sinuous apical third (Fig. 309.3). Quadrangular membranous lamina at the apex of the parameres (Fig. 312.3). Endophallus (Fig. 311.2) with a «U»-shaped «Y»-piece and the apical region with two phanerae densely covered with spicules situated between the reinforcement bands; dorsal phanerae of the median region divergent, with a slender lower end and a rounded apex. Basal process of spermathecal complex funnel-shaped (Fig. 313.3) .....*Naspunius*

- Elytra without parasutural stria. Median lobe of aedeagus, in lateral view, long, not gibbous and the apical third in an almost rectilinear arc (Fig. 309.5). Membranous lamina at apex of parameres, highly developed and elliptical in shape (Fig. 312.5). Endophallus (Fig. 311.3) with characteristic «Y»-piece and apical region with sclerotized rods and without spicule-covered phanerae ; dorsal phanerae of median region not divergent, with lower end divided into two small lobes. Basal process of spermathecal complex elongate and slightly sclerotized (Fig. 313.5) .....*Salgadoia*

9. Membranous lamina of parameres minute (Fig. 312.2). Endophallus (Fig. 311.1) without differentiated internal structures in the dorsal sacs; between the reinforcing bands a blade extended into two separate tips towards the median region. Spermatic duct of spermathecal complex long, about five to eight times the length of the spermatheca (Fig. 313.2) ....*Lagariella*

- Membranous lamina of the parameres more or less developed (Figs 312.8, 312.9). Endophallus (Figs 311.5, 311.6) with a phaneroid nodule inside, or with strongly striated dorsal sacs; between the apical reinforcement bands, a sac whose integument is covered with scales or spinules. Spermatic duct of the spermathecal complex very long, more than ten times the length of the spermatheca (Figs 314.1, 314.2) 10

10. Generally with a more or less marked parasutural stria. Male metafemora without sinuosity or denticle. Endophallus (Fig. 311.5) with strongly striated dorsal sacs, without phaneroid nodule, ventral phanerae with marked bulge at upper end, and thin, slender phanerae in median region. Parameres with three apically inserted setae, at least one of which is very curved at right angle, the membranous lamina poorly developed and the penicillum with short, sparse setae (Fig. 312.8) .....*Stygiophyes*

- No parasutural stria. Male metafemora with a denticle or sinuosity on the posterior margin. Dorsal endophallus sacs (Fig. 311.6) with phaneroid nodule inside, ventral phanerae without bulge and, at most, upper end slightly thickened; phanerae thicker and more robust from median region. Parameres with three rectilinear or sinuous setae with apical insertion, a developed membranous lamina and a long-hairy penicillum (Fig. 312.9).....*Trapezodirus*

Genus ***Ariejasia*** nov.
https://zoobank.org/NomenclaturalActs/C7F67B25-306A-4685-A5ED-375C0110A6FC

Type species. *Speonomus carrerei* Fourès, 1954 by present designation (habitus in Fig. 301.1).

Diagnosis. Size between 2.4-2.6 mm. Bathyscioid, convex (Fig. 301.1); elytra acuminate towards their apical end in the male and regularly curved in the female. Depigmented.

Head: Without occipital carina; anophthalmous.

Antennae: Shorter than the body.

Pronotum: Transverse with lateral margins regularly arched from base to apex; base sinuous.

Elytra: Short and broad, with well-defined transverse striolae.

Legs: Male protarsomeres short and dilated; first segment as wide as distal end of protibia; protibiae with two simple outer spurs and a series of three or four short, spaced spines on outer face; mesotibiae arcuate with a double series of spines on outer face; metatibiae straight with two or three small spines along outer surface of tibia.

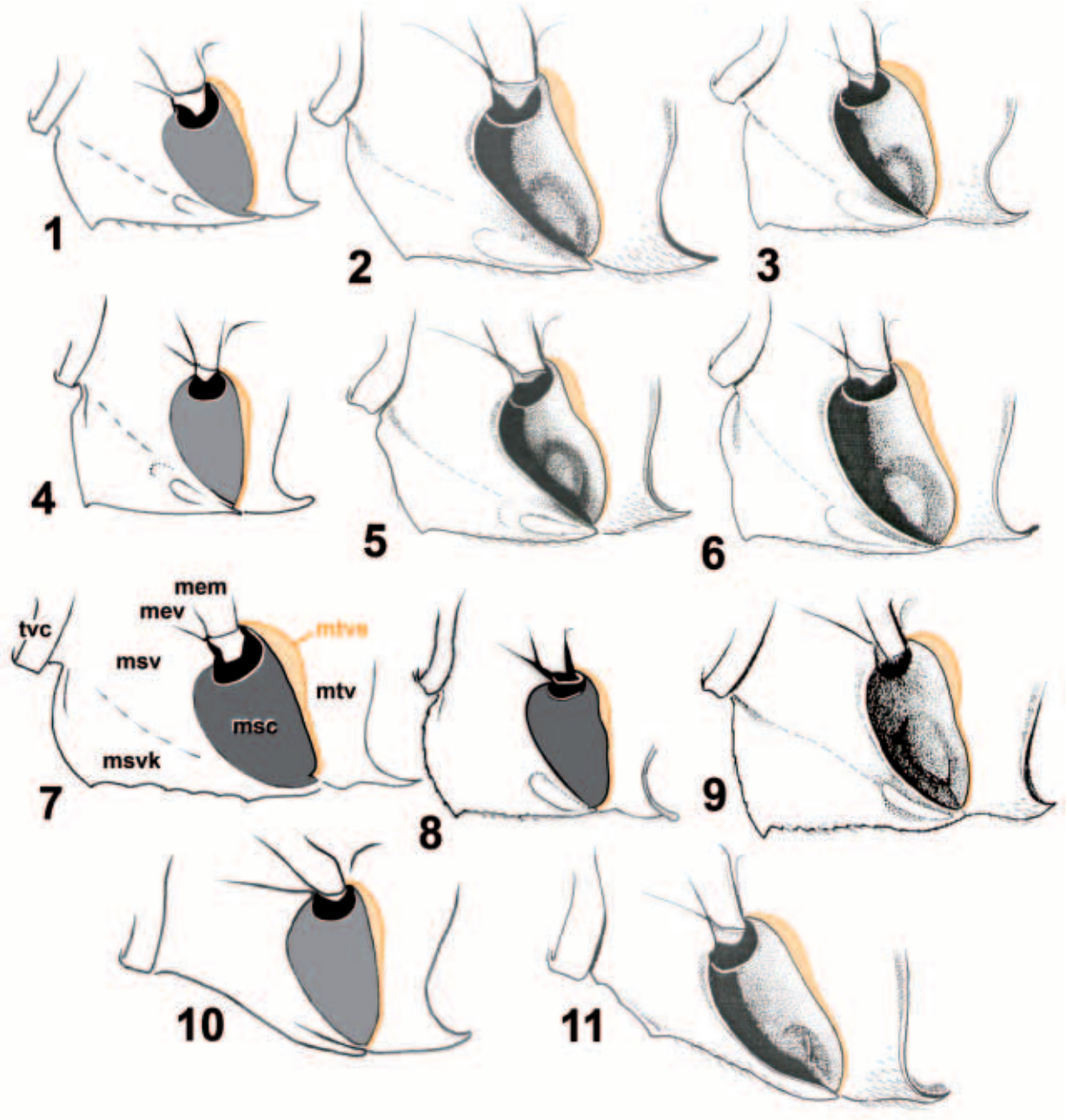
Mesoventral keel (Fig. 304.1): High and forming a slightly obtuse angle with the apex hooked; lower margin straight and rounded where about 15-20 setae are inserted; anterior margin slightly convex and flanged in the basal half, not extending over the metaventrite.

Suture of metaventrite (Fig. 304.1): delimiting a very narrow, arched area that is only well defined in the anterior median part.

Metatergal apparatus (Fig. 305.1): Wings of the metascutum narrow and elongated, apophysis of the alacrista very slightly prominent with very pointed apices.

Metendosternite (Fig. 306.4): Furcal arms a little longer than trunk, apex a little arched and ogival outwards, with apical apophysis; posterior blade a little arched, narrowed along arms; trunk distinctly longer than wide at base and mid-keel with slight posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.1) curved at right angle in middle, apex with small apical thickening and somewhat curved. In dorsal



FIGURES 304.1-304.11: *Speonomus* series, *Speonomus* group. Pterothorax in lateral view of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites crypticola,* (**7**) *Speonomus pyreneus,* (**8**) *Stygiophyes puncticollis,* (**9**) *Trapezodirus carrodillae,* (**10**) *Trocharanis mestrei,* (**11**) *Troglocharinus ferreri.* Figs **2**, **3**, **5**, **6**, **9**, **11** modified from Salgado *et al*. (2008). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

view (Fig. 310.1), sides arched in basal median area, subrectilinear in apical median area, this area narrower, apex broad, slightly depressed in middle. Basal lamina short, with protruding, tapering sides in median region, posterior margin in regular arc, longer and as wide as ventral lamina of tegmen.

Endophallus (Fig. 310.1): Basal region with dorsal and ventral complexes; «Y»-piece with very thin, divergent arms, the apical node joined by a thin tubule; basal lobe present. Median region with dorsal and ventral phanerae thin, rectilinear, divergent and without relief at their lower end; two short intersecting semicircular phanerae at the base of the ventral phanerae; in the upper part, six imbricate leaf-like laminar structures, three on each side of the axis; two membranous ligules where the reinforcement bands of the apical region are inserted; a sac of spiny tissue between the reinforcement bands.

Parameres (Fig. 312.1): Long, slender and curved, their apex slightly exceeding the apex of the median lobe. Three main apically inserted setae, two long on the inner side and one finer and shorter on the outer side. Membranous lamina divided in two: the larger part situated in the prolongation of the apex,the smaller on one side; both parts bordered with anastomosing reliefs that become bands, with about 18-25 long in the larger lamina and about 8-10 shorter in the smaller.

Spermathecal complex (Fig. 313.1): Spermatheca long, with small apical lobe of same calibre as median part, and much larger than basal lobe; basal process short and sclerotized.

Female uroventrite VIII (Fig. 315.1): Spiculum very short, broad and truncated.

ETYMOLOGY. The name refers to the Occitan toponym Arièja, in French Ariège, which gives its name to a river and a department created during the French Revolution by the merger of the counties of Foix and Coserans (Couserans). Feminine name.

DISCUSSION. Sister to *Paraspeonomus* from which it is separated by a significant genetic distance (Fig. 1A); support of 95.2/99. The particular structure of the apex of the parameres with the divided membranous lamina and its edges with anastomosing reliefs that become bands constitutes a synapomorphy of the genus: it is not a true penicillum formed of hairs in the manner of the other genera of the *Speonomus* group.

DISTRIBUTION: France. Ariège, Grotte de Payssa – Salsein –, Grotte de Pétillac – Uchentein –, and a dozen MSS stations in the Orgibet forest massif – Illartein –.

Species

Ariejasia carrerei (Fourès, 1954) comb. nov.
Speonomus carrerei Fourès, 1954: 4.

Genus ***Lagariella*** Fresneda, 2000
Lagaria Fresneda, 1998: 69 (*Nom. praeocc.* Homonymy with *Lagaria* Dallas, 1872 – Hemiptera –).
Lagariella Fresneda, 2000: 147 (Substitution name).

TYPE SPECIES. *Speonomus* (*Speonomites*) *colominasi* Zariquiey, 1924 by original designation (habitus in Fig. 301.2).

DIAGNOSIS. Size of 3.4-3.8 mm. Shape bathyscioid (Fig. 301.2), elliptical, distinctly oblong and convex, with the elytral margins regularly curved from one end to the other. Depigmented.

Head: With a complete but faint occipital carina; anophthalmous.

Antennae: Long and reaching the apical quarter of the elytra or barely exceeding their half.

Pronotum: Transverse, as wide as the elytra, with the greatest width in the middle or posterior third; lateral margins regularly arched; posterior angles acute and rounded, and vertices somewhat prolonged on the elytra.

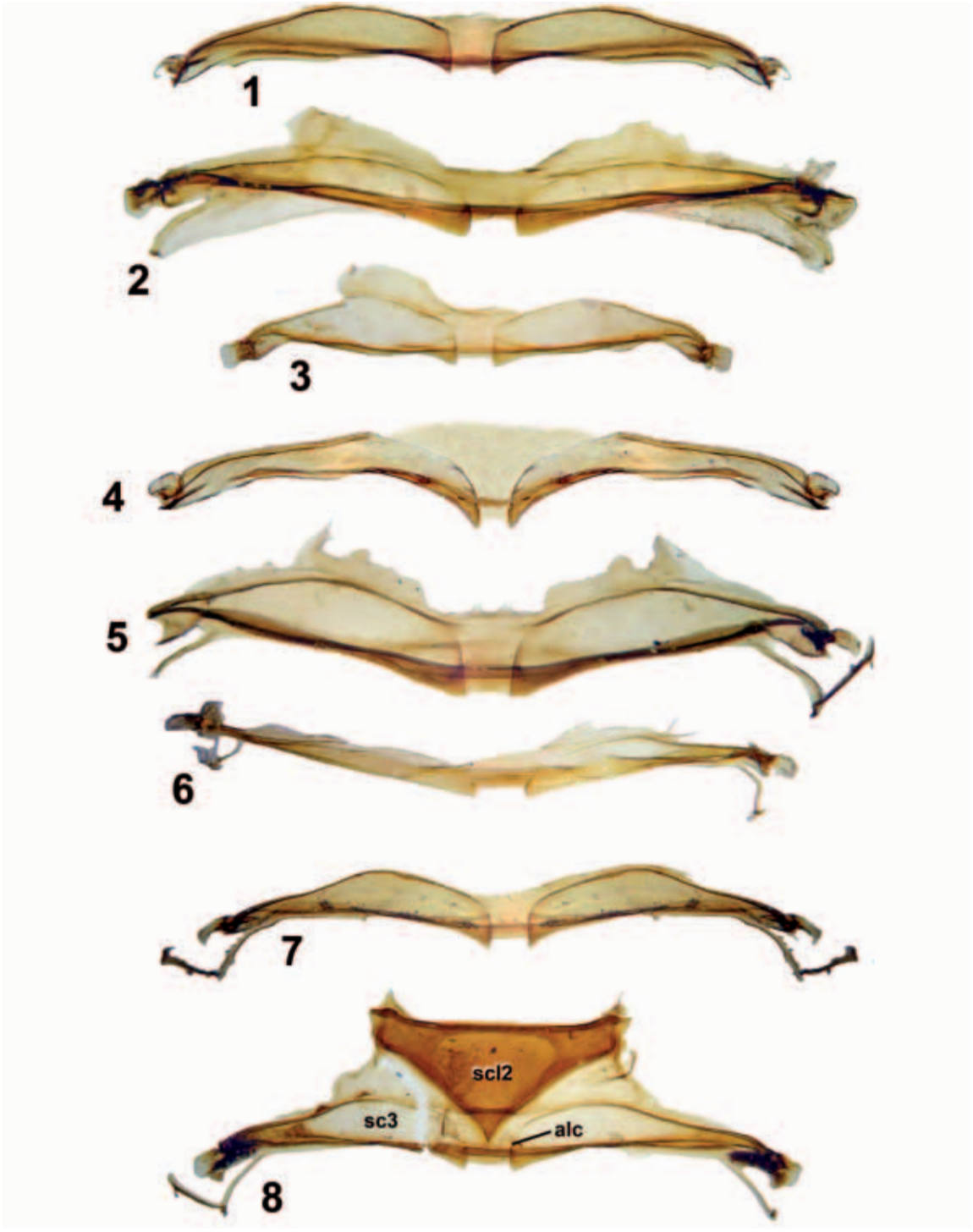
Elytra: Elongated, oval, convex, with subparallel lateral margins in the basal third and with the maximum width situated in the posterior third or at the base; sculpture formed by thick, separate transverse striolae.

Legs: Gracile and proportionally long; the first protarsomere of the male long, rectangular and as wide as or slightly wider than the distal end of the protibia; protibiae with several very small spines that merge with the pilosity, spaced apart on the outer surface; mesotibiae arcuate, with a double series of spines on the outer surface; metatibiae straight, with two or three small spines along the inner and outer surface.

Mesoventral keel (Fig. 304.2): High and forming an obtuse angle with the pointed vertex; lower edge concave in its anterior half, with a marked ridge where some 30-40 long setae are inserted; anterior margin convex in the area of insertion and posteriorly to the straight apex, beaded throughout.

Suture of the metaventrite (Fig. 304.2): Delimiting a very narrow, arcuate part that is only well defined in the anterior median area.

Metatergal apparatus (Fig. 305.2): Wings of metascutum narrow and elongate, apophysis of the



FIGURES 305.1–305.8: *Speonomus* series, *Speonomus* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites velox,* (**7**) *Speonomus normandi,* (**8**) *Stygiophyes puncticollis.* Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

alacrista with rounded apices and only slightly protruding.

Metendosternite (Fig. 306.5): Robust, with furcal arms as long as trunk, apex flattened, not sharpened outward, and apical apophysis sparsely developed; posterior lamina retaining same width on arms to apical area with lateral edge very slightly arched; trunk longer than wide and median keel with long posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.2), bent at an obtuse angle in the apical third; short but very stout, especially the proximal two-thirds which contrast strongly with the apical third; apex sinuous and extending into a fine point.

Endophallus (Fig. 311.1): Characterised by a long «Y»-piece, with the two symmetrical arms slender and slightly divergent, and by the presence of a robust basal lamina. Median region with very thin dorsal phanerae and the apical third curved outwards; ventral phanerae also slightly more robust than the dorsal ones and doubly sinuous; apical part of the median region, in the extension of the phanerae, bearing a tube surmounted by a complex piece with marked sclerotization, the armour of the axial piece; on both sides of the sac, dorsal sacs apparently divided into two compartments and showing a rounded appendage; apical region with reinforcing bands and a central sac extended at its lower end by a distinctive forked hyaline lamina.

Parameres (Fig. 312.2): Apex with three apically inserted setae; two very long, stout and sinuous or strongly curved, the third very thin and rectilinear; tiny membranous lamina protruding very little and inserted in the apex; a discrete penicillum formed of few short hairs arranged on the side of the apex; placoid sensilla visible.

Spermathecal complex (Fig. 313.2): Spermatheca slightly bent at both ends, with the median region almost straight; apical lobe spherical and basal with a slightly larger cross-section than the median region; spermatic duct about six times longer than the spermatheca and emptying into its inner cavity through a small node inserted in the basal lobe where the spermathecal gland is also inserted; at the point of insertion with the copulatory bursa there is a sclerotized basal process shaped like a hat.

Female uroventrite VIII (Fig. 315.2): Spiculum reduced to a simple nodule with two membranous processes.

Discussion. In Tree-1 *Lagariella* is located as a sister to the clade *Stygiophyes* with a support of 95.5/100 (Fig. 1A). In Tree-2 (Fig. 2) *Lagariella* is found as a sister to the clade formed by *Stygiophyes aldomai allomorphus*, *S. saforensis*, *S. ribagorzanus* and *S. akarsticus* with weak support, 78.8/51, but not at the base of the whole genus *Stygiophyes*. In this case, it would be necessary to establish synonymy between these two genera, especially as it has been found that the two lower extensions of the apical sac are also found in *Stygiophyes*, albeit less developed than in *Lagariella*. But this genus has its own characteristics that differentiate it from *Stygiophyes*: its much larger size, its much more robust aedeagus or its female uroventrite VIII with two peduncles attached to the spiculum. This, together with the weak support of its node (Fig. 2: Tree-2) in the clade, justifies its retention as a good genus.

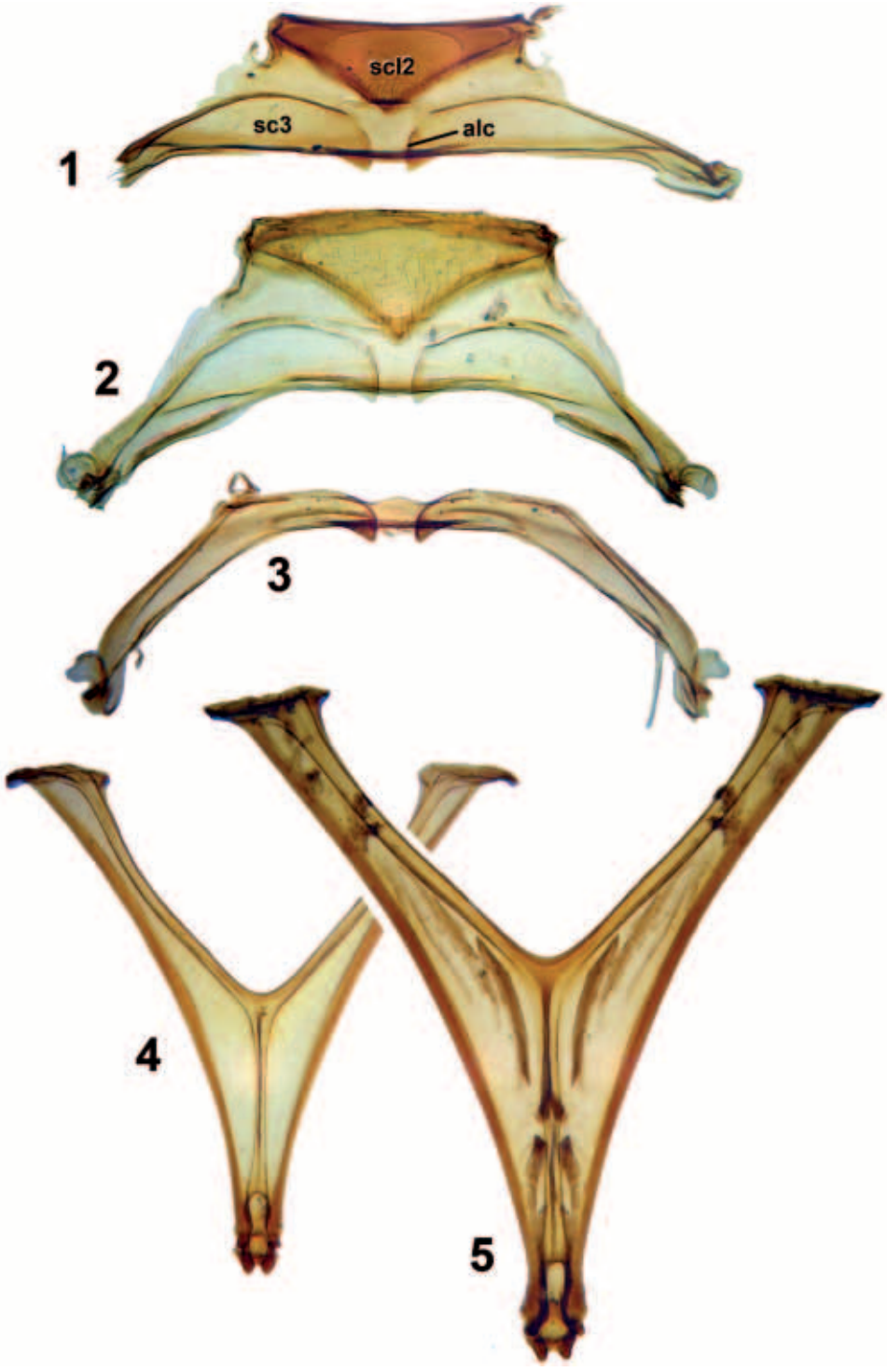
Endophallus was described by Bellés & Comas (1986) and features the three characteristic regions described by Jeannel (1924a). This genus, although related to *Stygiophyes,* is considerably individualized by the very particular facies of the median lobe with the very robust basal part and of the endophallus with a forked hyaline lamina that is also found, although much less developed, in the genus *Stygiophyes*.

Distribution. Spain. The genus currently comprises two species distributed along a line parallel to the Serra del Montsec (Lleida), in the south of this mountain range.

Species

Lagariella colominasi (Zariquiey, 1924)
Speonomus (Speonomites) colominasi Zariquiey, 1924: 6.
Speonomus (Speonomus) colominasi Zariquiey: Bellés, 1977a: 107.
Lagaria colominasi (Zariquiey, 1924): Fresneda, 1998: 69.
Lagariella colominasi (Zariquiey, 1924): Fresneda, 2000: 147.

Lagariella porroiensis (Escolà & Comas, 1983)
Speonomus porroiensis Escolà & Comas, 1983: 259.
Lagaria porroiensis (Escolà & Comas, 1983): Fresneda, 1998: 69.
Lagariella porroiensis (Escolà & Comas, 1983): Fresneda, 2000: 147.



FIGURES 306.1–306.5: *Speonomus* series, *Speonomus* group. Metatergal apparatus, ventral view of the metanotum and axillaria of: (**1**) *Trapezodirus arcticollis,* (**2**) *Trocharanis mestrei,* (**3**) *Troglocharinus senenti.* Metendosternite of: (**4**) *Ariejasia carrerei* **comb. nov.**, (**5**) *Lagariella colominasi*. Abbreviations: **alc**, alacrista; **sc3**, metascutum; **scl2**, mesoscutellum.

Genus ***Naspunius*** Fresneda, Hernando & Lagar, 1994
Speonomus (*Naspunius*) Fresneda, Hernando & Lagar, 1994: 111.

TYPE SPECIES. *Speonomus eseranus* Lagar, 1974 by original designation (habitus in Fig. 301.3).

DIAGNOSIS. Size of 2.0-2.2 mm. Bathyscioid (Fig. 301.3), body elliptical, narrow, slightly convex with elytral margins regularly curved from one end to the other.

Head: Occipital carina complete but only slightly marked; anophthalmous.

Antennae: As long as the elytral suture.

Pronotum: Transverse, with arched sides and greatest width at base, which is sinuous; posterior angles right; no pronotum-elytral angle.

Elytra: Elongated and narrow, with maximum width at base and evenly curved sides; parasutural stria superficial and blurred in apical area; transverse striolae well-defined, fine and even.

Legs: Gracile, with first protarsomere of the male triangular and wider than the distal end of the protibia; protibiae with two very small, simple outer spurs and a series of very small, spaced spines that merge with the hairs on the outer surface; mesotibiae slightly arcuate and metatibiae straight, both without a series of spines on the outer surface.

Mesoventral keel (Fig. 304.3): High and forming an almost right obtuse angle with the hooked vertex; anterior face slightly curved and striate on the basal part; lower margin a little sinuous and keel pointed.

Suture of the metaventrite (Fig. 304.3): Delimiting a very narrow arcuate part that is well defined only in the anterior median area.

Metatergal apparatus (Fig. 305.3): Wings of metascutum narrow and not very elongate; apophysis of alacrista not very prominent, the apices not very sharp.

Metendosternite (Fig. 307.1): Furcal arms long and narrow, longer than trunk, with thick but short apical apophysis; in arms, anterior keel slightly sinuate towards apical area and posterior lamina narrowing, with same width to apical area; furcal trunk longer than wide, median keel with posterior divergence.

Median lobe of aedeagus: Small and, in lateral view (Fig. 309.3), gibbous, folded in the middle; apical third sinuous.

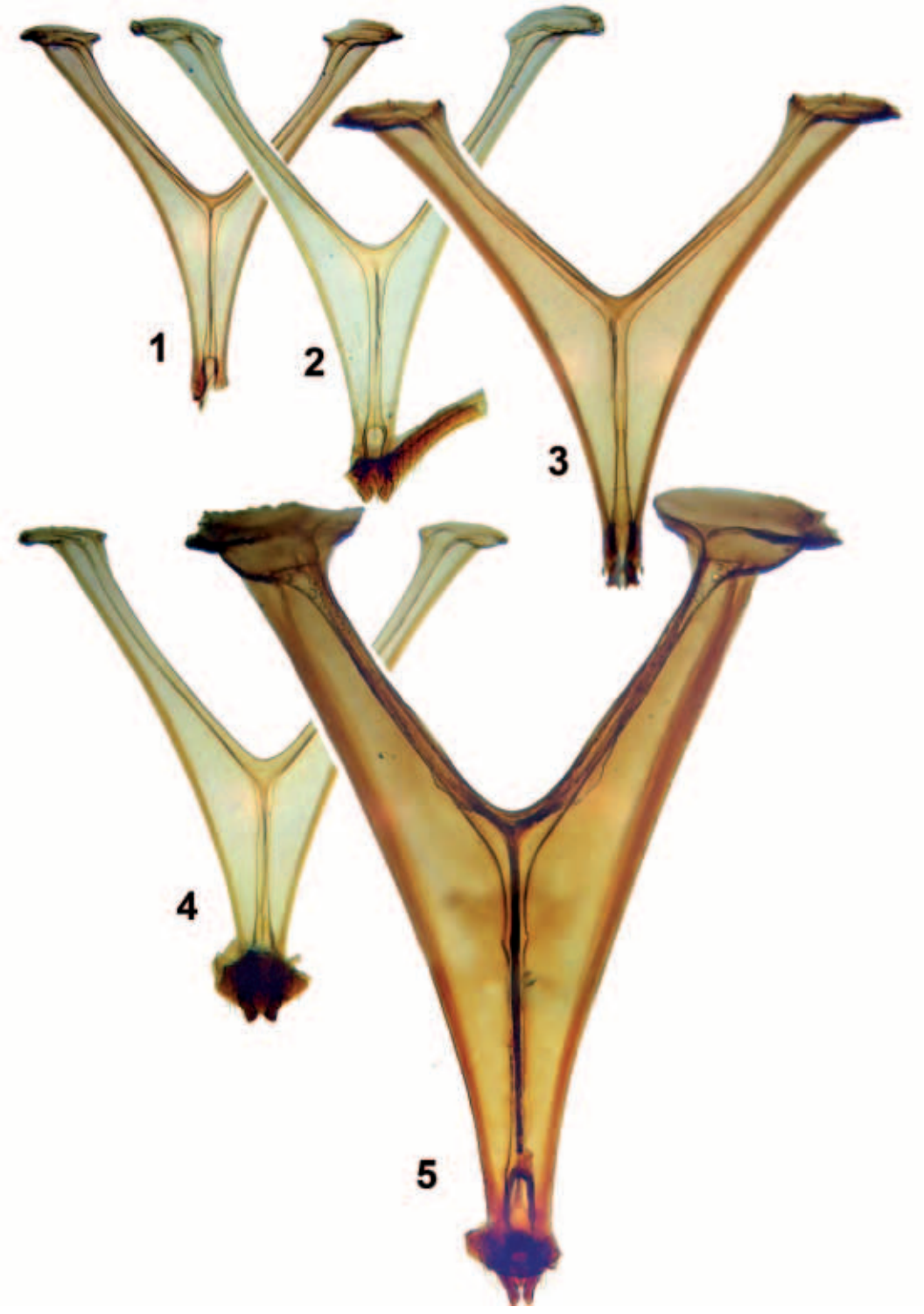
Endophallus (Fig. 311.2): The «Y»-piece with very thin, «U»-shaped arms and adjoining phanerae; in the upper part of the basal region, a sac whose membrane is covered with spicules and transverse wrinkles; very fine, divergent dorsal phanerae, more robust, even more divergent ventral phanerae and a large dorsal plate; apical region with short, thin reinforcing bands, which rest on nodules in the form of two large sacs inside which other, more sclerotized nodules visible; between these structures, presence of a tube covered with spicules, identified as the apical sac.

Parameres (Fig. 312.3): With three apically inserted setae, two robust and sinuous and a third finer, short and rectilinear; a rectangular membranous lamina, a penicillum and a few placoid sensilla visible.

Spermathecal complex (Fig. 313.3): Spermatheca regularly curved from one end to the other; maximum calibre at the basal end of the median region, hyaline, with the basal and apical lobes thinner; at the basal end of the spermatheca and through a nodule the spermatic duct empties, and into this nodule the spermathecal gland is inserted; very fine spermatic duct, about seven times longer than the spermatheca, inserted into the copulatory sac by means of a funnel-shaped sclerotized structure.

Female uroventrite VIII (Fig. 315.3): With short, slender spiculum .

DISCUSSION. In molecular phylogeny *Naspunius* is a sister of *Salgadoia* with a support of 99.6/100 (Fig. 1A). This model of endophallus was studied by Fresneda *et al.* (1994). A first impression reveals an endophallus with a peculiar appearance, as well as various parts that are not found in any other model. The most similar genus is *Salgadoia,* in which the reinforcing bands are also articulated with huge basal nodules consisting of more than one piece. This model is characterised by the presence of disproportionately large phaneroid nodules associated with the dorsal sacs; the dorsal sacs are found in other models of endophallus, but with different shapes and a much smaller size. Also very characteristic are the appendages of the sacs, which in *Naspunius* are particularly rounded and hang from a peduncle separate from the sacs. The rest of the structures in the other regions of the endophallus are also characteristic, but their equivalent can be found in other models. Thus, the ventral phanerae and dorsal plates, although very different from those of the genus *Trapezodirus,* share a common characteristic with it: they are fused at its distal end; in the genus *Stygiophyes,* on the other hand, these phanerae are simple, i.e. there are only ventral phanerae consisting of a single very narrow plate (Bellés 1983a); a similar structure to the ventral phanerae and dorsal plates is found in species of the genus *Speonomites,* but in this case the phanerae are much more complicated and consist of several plates fused in different planes.



FIGURES 307.1–307.5: *Speonomus* series, *Speonomus* group. Metendosternite of: (**1**) *Naspunius eseranus,* (**2**) *Paraspeonomus vandeli,* (**3**) *Salgadoia brieti,* (**4**) *Speonomites velox,* (**5**) *Speonomus diecki.*

DISTRIBUTION: Spain. This species is only known from the type locality, in Foradada del Toscar, Huesca. It appears to be strictly localised to the Naspún point, at the eastern end of the Sierra Ferrera (Lagar 1974a; Fresneda & Salgado 2017).

Species

Naspunius eseranus (Lagar, 1974)
Speonomus eseranus Lagar, 1974a: 25.
Speonomus (*Naspunius) eseranus* (Lagar): Fresneda, Hernando & Lagar, 1994: 111.
Naspunius eseranus (Lagar): Fresneda, 1998: 72.

Genus ***Paraspeonomus*** Coiffait, 1952
Paraspeonomus Coiffait, 1952: 41.

TYPE SPECIES: *Paraspeonomus vandeli* Coiffait, 1952 by original designation (habitus in Fig. 301.4).

DIAGNOSIS. Size of 2.8-3.0 mm. Bathyscioid (Fig. 301.4), body elliptical, narrow, slightly convex, with pronotum-elytral angle and elytral margins regularly curved from one end to the other.

Head: With a complete but only slightly marked occipital carina; anophthalmous.

Antennae: Slightly longer than the elytral suture; not thickened from the 7th antennomere, the 8th not reduced; in the male the 4th antennomere is very long and widened into a pallet (Figs. 9.6, 301.4), and the third reduced, whereas in the female the 4th is long and the third is also very short, and from the 7th a little thickened.

Pronotum: Transverse, with the sides arched and the greatest width along the basal third; base sinuous and posterior angles right-angled.

Elytra: Long and wide, with the greatest width before the base; sides regularly curved and without parasutural stria, but with well-defined transverse striolae.

Legs: Short but slender; first protarsomere of male short and triangular, wider than distal end of protibia; protibiae with two small simple outer spurs and some very small spines on outer surface; mesotibiae arcuate without simple spurs and without series of spines on outer surface; metatibiae straight with two simple spurs on outer surface, and a series of spines along outer surface.

Mesoventral keel (Fig. 304.4): High and forming an almost right obtuse angle with the vertex hooked; anterior margin almost straight and ridged along its entire length; lower margin somewhat serrated, ridge subrectilinear and rounded.

Suture of the metaventrite (Fig. 304.4): Delimiting a very narrow, arched part that is well defined only in the anterior median part.

Metatergal apparatus (Fig. 305.4): Wings of the metascutum narrow and very elongate, with the apophysis of the alacrista not very prominent and the apices arched and pointed.

Metendosternite (Fig. 307.2): Furcal arms long and narrow, longer than trunk and apical apophysis much developed; posterior plate of arms narrow, same width as apical area; furcal trunk longer than wide and median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.4), bent at right angles in the middle of its length and with a dorsal preapical denticle; apex extended into a very fine point. In dorsal view (Fig. 310.2), broad and arched at apex. Basal lamina long, in the median area the sides protruding and a little tapered, then the posterior margin in a regular arc but a little tapered towards the apical area, this lamina a little longer and as wide as the basal lamina of the tegmen.

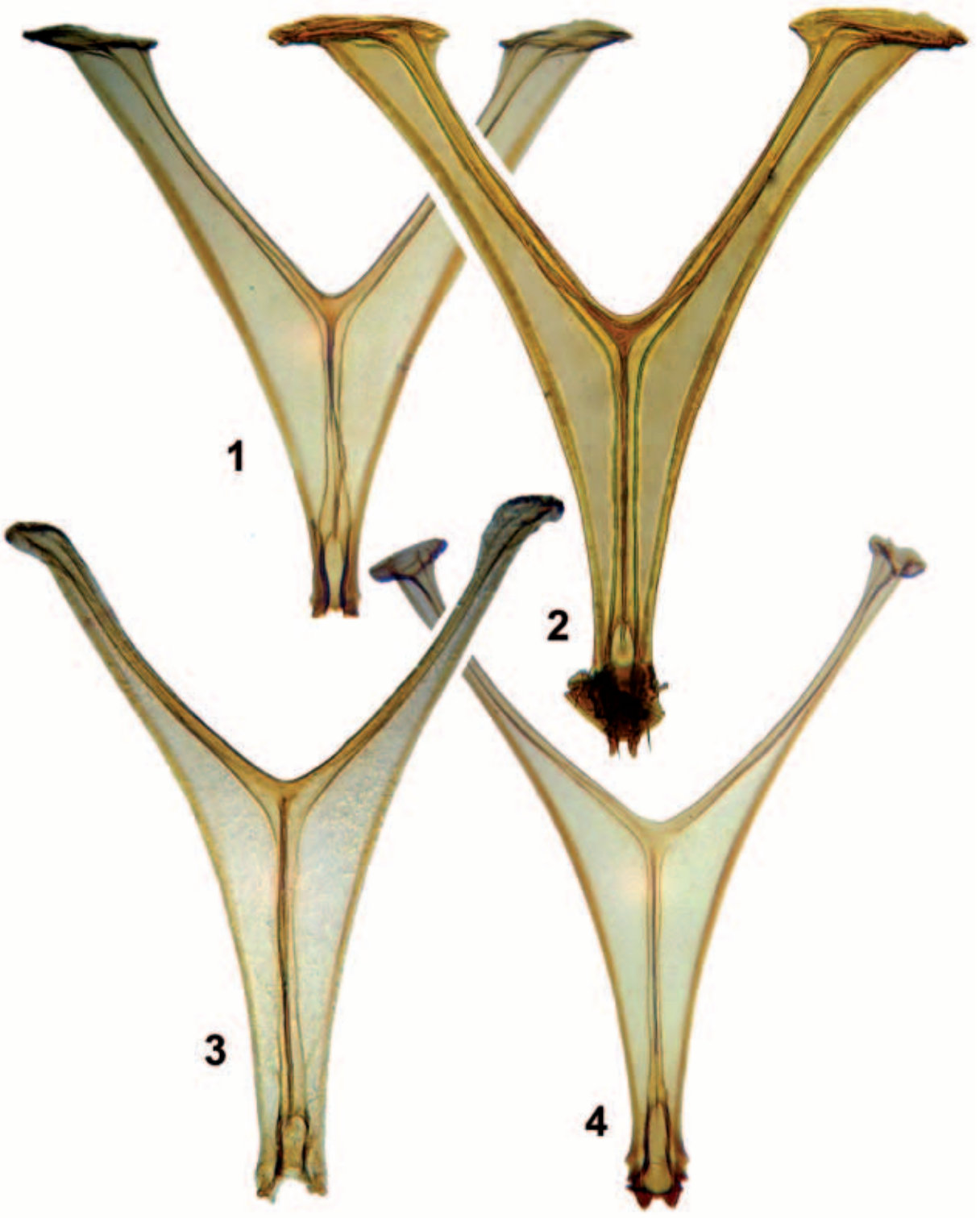
Endophallus (Fig. 310.2): In the basal region, dorsal and ventral complexes with a «Y»-piece with slightly divergent arms and a long, narrow apical nodule; in the median region, dorsal phanerae thickening and diverging towards the apex, ventral phanerae with an external denticle in their median part, and floating pieces 1 and 2; upper end of median region showing axial piece and armour of axial piece enveloped in striated tissue, and two large pedunculated membranous sacs where reinforcement bands of apical region rest.

Parameres (Fig. 312.4): Shorter than the median lobe; apical area armed with a conspicuous penicillum with long setae, a tiny pointed membranous lamina and three contiguously inserted setae on the same side of the apex: the central one short and very thin, one of the laterals very long and sinuous, and the third short and very thick, more than a seta, it could be described as a spine with a blunt apex.

Spermathecal complex: Spermatheca (Fig. 313.4) long, slightly but regularly curved from one end to the other; the two lobes differentiated and well sclerotized, the basal being much larger than the apical.

Female uroventrite VIII (Fig. 315.4): Spiculum short and broad, with enlarged apex.

DISCUSSION. This genus is sister to *Ariejasia* gen. nov. with a support of 95.2/99, and both to the genus *Speonomus* genus with a support of 94.7/86 (Fig. 1A). It is characterised by the particular structure of the dorsal preapical denticle in the median lobe of the aedeagus; the apex of the parameres, with a conspicuous penicil-



FIGURES 308.1–308.4: *Speonomus* series, *Speonomus* group. Metendosternite of: (**1**) *Stygiophyes ribagorzanus,* (**2**) *Trapezodirus bolivari,* (**3**) *Trocharanis mestrei,* (**4**) *Troglocharinus senenti.*

lum accompanied by a tiny pointed membranous lamina; three contiguously inserted setae on the same side of the apex with the central one short and fine, one of the laterals very long and sinuous, and the third short and very thick with a blunt apex; all these characters constitute a synapomorphy of the genus; as does the 4th antennomere of the male enlarged into a paddle (Figs. 9.6, 301.4).

DISTRIBUTION: France: Ariège, in the Estours valley, the cave of Las Souleillos and the Faille de Jouhandet near Seix.

Species

Paraspeonomus vandeli Coiffait, 1952
Paraspeonomus vandeli Coiffait, 1952: 41.

Genus ***Salgadoia*** Fresneda, 1998
Salgadoia Fresneda, 1998: 70.

TYPE SPECIES. *Speonomus brieti* Jeannel, 1911 by original designation (habitus in Fig. 301.5).

DIAGNOSIS. Size 2.8-3.0 mm. Bathyscioid (Fig. 301.5), body oval, very wide, slightly convex and with elytral margins regularly curved from one end to the other.

Head: Occipital carina complete but only slightly marked; anophthalmous.

Antennae: Almost as long as the elytral suture.

Pronotum: Transverse, with arched sides and greatest width in basal quarter; base sinuous and posterior angles right; no pronotum-elytral angle.

Elytra: Considerably broad, with greatest width at base and sides evenly curved; with fine transverse striolae, most evident in the proximal two-thirds.

Legs: Moderately short and slender in appearance; male metafemora with a small denticle in the middle of the hind margin; first protarsomere of male triangular and wider than distal end of protibia; protibiae with two very small, simple outer spurs and a series of very small, spaced spines that merge with the hairs on the outer surface; mesotibiae slightly arched and with two series of thick spines on the outer surface; metatibiae straight, with two simple spurs on the outer part of the apex and a series of spines along the outer surface.

Mesoventral keel (Fig. 304.5): High, with sinuous anterior margin, flanged basal part and a small denticle at apex; lower edge slightly arched and rounded ridge.

Suture of the metaventrite (Fig. 304.5): Delimiting a very narrow, arcuate area that is well defined only in the anterior median part.

Metatergal apparatus (Fig. 305.5): Wings of the metascutum narrow and elongated, the apophysis of the alacrista not very prominent and the apices not very sharp.

Metendosternite (Fig. 307.3): Furcal arms long and broad, slightly longer than trunk, with thick apical apophysis and lateral edge of the blade almost straight; anterior keel slightly sinuate towards apical area and posterior lamina broad, with same width towards apical area; furcal trunk longer than broad and median keel with narrow, elongate posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.5), angle strongly obtuse in middle of its length, gradually tapering from base to apex; apex thickening in preapical area, its tip extending to become very thin.

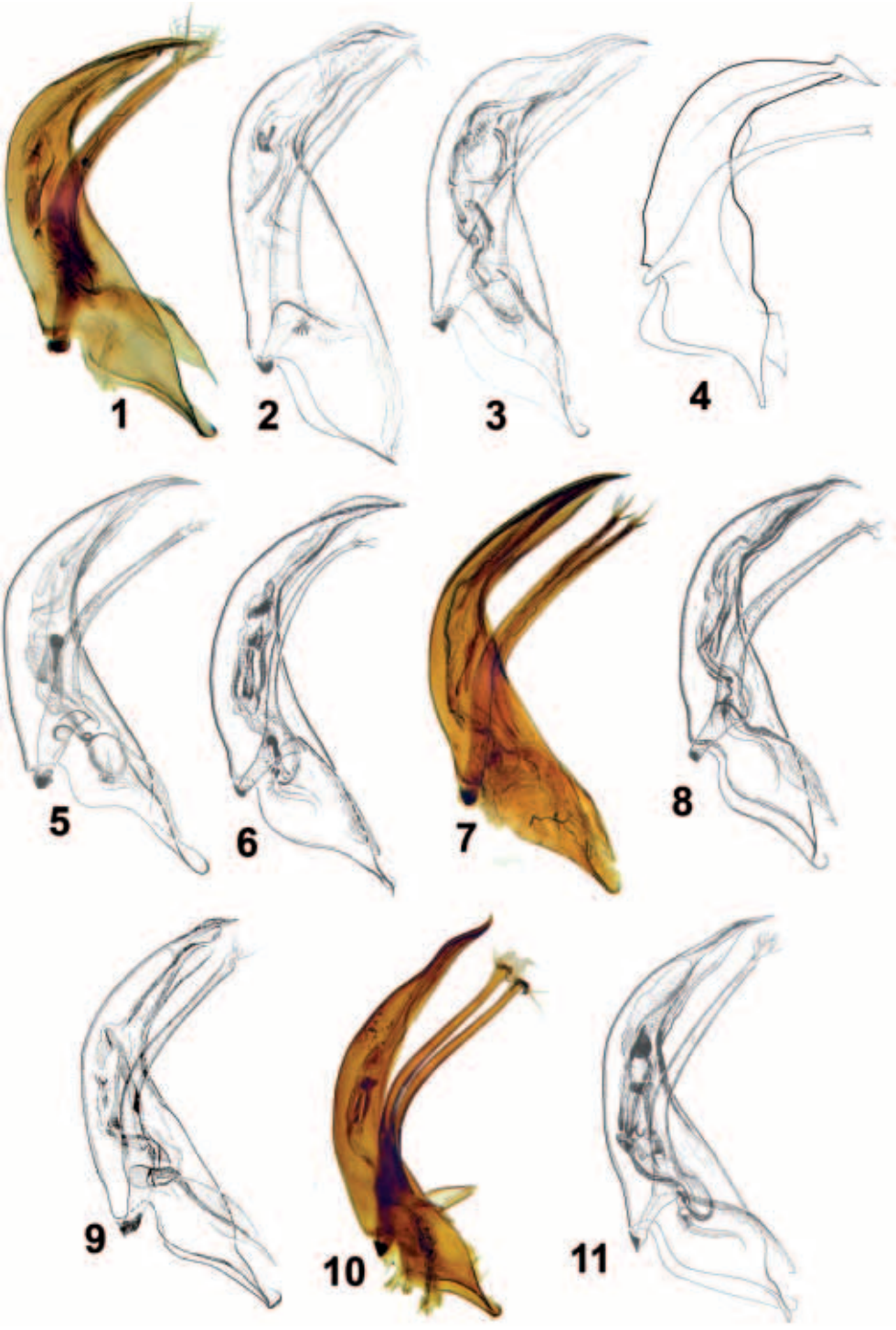
Endophallus (Fig. 311.3): Basal region with arms of «Y»-piece extended towards median region and transformed into hyaline funnels; median region with two ventral phanerae, two dorsal phanerae and a translucent upper dorsal plate with the inner margin strongly sclerotized and curved posteriorly; on both sides of the sac and at the level of the armour of the axial piece, two sacs with an appendix and a huge nodule attached; reinforcing bands in the apical region with two more sclerotized axial rods, with a spiny base and a broad blade.

Parameres (Fig. 312.5): Almost reaching the apex of the median lobe; with three apical setae, two thick and one thin; one membranous lamina, exceptionally developed and elliptical-shaped, and a long, dense penicillum, the setae inserted along the entire margin of the membranous lamina.

Spermathecal complex (Fig. 313.5): Spermatheca long and strongly bent at both ends, almost at a right angle; basal and apical lobes sclerotized, both with a section appreciably larger than the median region; spermatic duct emptying into the internal cavity of the spermatheca through a nodule, to which the membranous spermathecal gland is also inserted, the final area joining the copulatory sac forming an elongated, enlarged and sclerotized basal process.

Female uroventrite VIII (Fig. 315.5): Spiculum short, the apex slightly dilated.

DISCUSSION. From the genital structures, the most similar genus is *Naspunius,* in which the reinforcing bands, as in *Salgadoia,* are articulated with huge basal nodules (endophallus). The clade formed by these two genera has a support of 99.6/100, and is linked to the clade of the genera *Stygiophyes* and *Lagariella* with a support of 97.2/100 (Fig. 1A).



FIGURES 309.1–309.11: *Speonomus* series, *Speonomus* group. Aedeagus in lateral view of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites velox,* (**7**) *Speonomus pyreneus,* (**8**) *Stygiophyes puncticollis,* (**9**) *Trapezodirus carrodillae,* (**10**) *Trocharanis mestrei,* (**11**) *Troglocharinus ferreri.* Figs **2**, **3**, **5**, **6**, **8**, **9**, **11** modified from Salgado *et al*. (2008).

DISTRIBUTION. Spain. Known from only five localities in Huesca, located in the Solana valley, the former district of Burgasé, on the left bank of the river Ara (Jeannel 1911a, 1911b, 1914b, 1924a; Jeannel & Racovitza 1912; Escolà 1980a; Fresneda 1998). The type locality is the Forato de los Moros of Ginuabel (Huesca).

Species

Salgadoia brieti (Jeannel, 1911)
Speonomus Brieti Jeannel, 1911b: 90.
*Salgadoia brieti (*Jeannel): Fresneda, 1998: 72.

Genus ***Speonomites*** Jeannel, 1910
Speonomites Jeannel, 1910b: 150.
Pallaresiella Fresneda, 1998: 68 (Type species: *Speonomus pallaresanus* Jeannel, 1911).

TYPE SPECIES. *Speonomites velox* Jeannel, 1910 by original designation (habitus in Fig. 302.1).

DIAGNOSIS. Size of 2.2-3.0 mm. Bathyscioid (Fig. 302.1), body elliptical or oval. Pubescence yellowish, fine, either long and erect or short and recumbent. Integument with elytra marked with fine transverse or spaced striolae, or dissociated into isolated or disordered dots.

Head: With a complete but faint occipital carina.

Antennae: Long, longer than the elytral suture.

Pronotum: Transverse and more or less convex, as wide as the elytra, with lateral margins regularly arched or very convergent towards the front; maximum width situated in the posterior third or at the base; posterior angles right or acute, the vertex rounded or pointed.

Elytra: Long, cuneiform and regularly convex, proportionally broad and uniformly narrowed towards the back, or subparallel, with the disc depressed; broadest at the base, in the basal quarter or along the anterior half; with a marginal ridge and sometimes a longitudinal depression parallel to the suture in the basal part of the elytra; parasutural stria, if present, blurred.

Legs: Long and slender; protibiae with two very small, simple outer spurs and no series of spines on outer surface; male protarsi generally sparsely thickened; mesotibiae arcuate with a few spines along outer surface; metatibiae straight with two simple spurs on outer part of apex; no series of spines along outer surface.

Mesoventral keel (Fig. 304.6): High, obtusely angled; anterior margin curved and ridged, with a discrete denticle at apex; lower margin sinuous and rounded.

Suture of metaventrite (Fig. 304.6): Delimiting a very narrow, arched area, well defined only in the anterior median part.

Metatergal apparatus (Fig. 305.6): Wings of the metascutum elongated and very narrow, the apophysis of the alacrista very reduced and the apices evanescent.

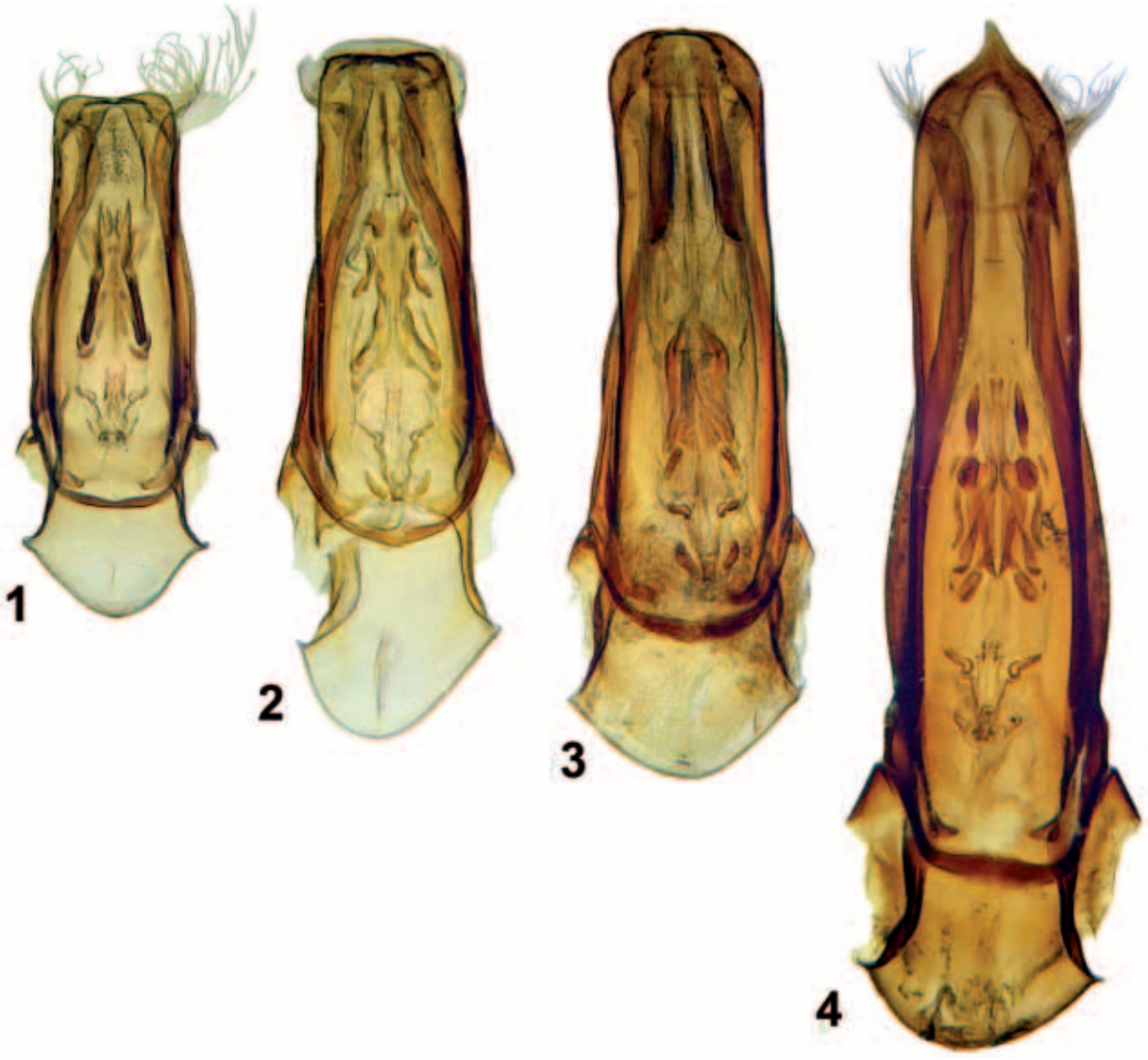
Metendosternite (Fig. 307.4): Furcal arms long and narrow, much longer than trunk, with thick apical apophysis; posterior lamina narrow, same width as apical area; trunk longer than wide and median keel with posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.6), bent at right or obtuse angle, slightly beyond middle or in apical third; distal end thickened by dorsally curved wing-like expansions of lateral margins, with denticle there, or simply extended in thin straight or curved line towards ventral side.

Endophallus (Fig. 311.4): Sinuous «Y»-piece and its funnel-shaped structures seeming to extend in fine muscle fibres along the sides of the sac towards the median region; in this region, some dorsal phanerae bifurcate at its lower end; one of the appendages extended into hyaline fibres towards the basal region; at the same place, some visible floating pieces, which are in contact with the funnel-shaped structures, divergent ventral phanerae and a dorsal plate consisting of two robust phanerae; an axial piece at the apical end of the median region, formed by a tube densely covered with spicules; on both sides of the axial piece, pockets with a thick sclerotized nodule inside and extended at their lower end by an appendix; in the apical region, reinforcement bands with, at the base and overlapping the dorsal bags, an overlying tissue that is densely covered with scales.

Parameres (Fig. 312.6): Very fine and shorter or as long as the median lobe; apex armed with three setae, one sinuous, the other strong and doubly curved, the third much finer and shorter, or of the same length as the others with a membranous lamina which may be very small or well developed; penicillum formed of a few very short setae or numerous and long setae.

Spermathecal complex (Fig. 313.6): Spermatheca long and thin, with lobes of similar cross- section to the median region, or thicker; both lobes in the same plane, or angled from the median region; spermatic duct between 12-14 times as long as the spermatheca, and either very thin or differentiated into two regions of different thickness, very long and very wide in *Speonomites pallaresanus* (Fig. 313.7); at the point of insertion with the copulatory sac, always thicker, more sclerotized, and passing through a disc which may also have a more sclerotized extension.



FIGURES 310.1–310.4: *Speonomus* series, *Speonomus* group. Aedeagus in dorsal view of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Paraspeonomus vandeli,* (**3**) *Speonomus pyreneus,* (**4**) *Trocharanis mestrei.*

Female uroventrite VIII (Fig. 315.6): may have a simple pointed prominence, a short blunt spine or two very short blunt divergent spines.

Discussion. The genus has a high support 96.7/100 (Fig. 1B). This model of endophallus was described and figured by Bellés & Comas (1986). *Speonomites* is morphologically related to *Troglocharinus* due to great similarities in appearance, number and arrangement of structures; however, molecular phylogeny shows that it is the sister group to almost all Pyrenean Leptodirini with support of 100/100. *Speonomites* species have been integrated into three groups according to the sculpture of the elytral integument and the morphology of the spermathecal complex (Fresneda 1998); this grouping is not confirmed by the molecular study and is therefore disregarded.

Distribution. Spain. The species are distributed throughout the province of Lleida. Their southern limit

of dispersal is the Serra de Montroig and the northern slopes of the Serra del Montsec d'Ares and Rubies; they go up through the valleys of the Flamicell and Noguera Pallaresa rivers until they reach the axial Pyrenees (Fresneda & Salgado 2017).

Species

Speonomites andorranus (Comas, 1978)
Speonomus andorranus Comas, 1978a: 73.
Speonomites andorranus (Comas): Fresneda, 1998: 67.

Speonomites antemi (Escolà, 1972)
Speonomus antemi Escolà, 1972: 42.
Speonomites antemi (Escolà): Fresneda, 1998: 67.

Speonomites aurouxi (Español, 1966)
Speonomus (*Speonomus*) *aurouxi* Español, 1966a: 2.
Speonomites aurouxi (Español): Fresneda, 1998: 67.

Speonomites crypticola (Jeannel, 1910)
Speonomus (*Speonomus*) *crypticola* Jeannel, 1910b: 155.
Speonomites crypticola (Jeannel): Fresneda, 1998: 67.

Speonomites kryophilos (Fresneda & Hernando, 1991)
Speonomus (*Speonomus*) *kryophilos* Fresneda & Hernando, 1991: 260.
Speonomites kryophilos (Fresneda & Hernando): Fresneda, 1998: 67.

Speonomites latrunculus (Jeannel, 1910)
Speonomus (*Speonomus*) *latrunculus* Jeannel, 1910b: 157.
*Stygiophyes puncticollis latrunculus (*Jeannel): Fresneda, 1998: 61.
Speonomites latrunculus (Jeannel): Fresneda & Escolà, 2000: 62.

Speonomites nitens Jeannel, 1910
Speonomites nitens Jeannel, 1910b: 152.
Speonomus (*Speonomites*) *nitens* Jeannel, 1910: Jeannel, 1924a: 166.

Speonomites pallaresanus (Jeannel, 1911)
Speonomus pallaresanus Jeannel, 1911b: 83.
Pallaresiella pallaresanus (Jeannel): Fresneda, 1998: 68.
Pallaresiella pallaresana (Jeannel): Salgado, Blas & Fresneda, 2008: 509.
Speonomites pallaresanus (Jeannel, 1911): Fresneda, Rizzo, Comas & Ribera, 2021: 165.

Speonomites tincatincensis (Escolà, Bellés & Comas, 1985)
Speonomus tincatinci Escolà, 1980c: 142 (*Nomen nudum*).
Speonomus tincatincensis Escolà, Bellés & Comas, 1985: 223.
Speonomites tincatincensis (Escolà, Bellés & Comas, 1985): Fresneda, 1998: 68.

Speonomites torresi (Fresneda & Hernando, 1990)
Speonomus torresi Fresneda & Hernando, 1990: 86.
Speonomites torresi (Fresneda & Hernando, 1990): Fresneda, 1998: 67.

Speonomites velox Jeannel, 1910
Speonomites velox Jeannel, 1910b: 151.
Speonomus (*Speonomites*) *velox* Jeannel, 1910: Jeannel, 1924a: 166.

Genus ***Speonomus*** Jeannel, 1908

Speonomus Jeannel, 1908a: 299.
Speonomus (*Metaspeonomus*) Coiffait, 1959: 175 syn. nov. (Type species: *Speonomus* (*Metaspeonomus*) *monticola* Coiffait, 1959).

Type species. *Adelops pyreneus* Lespès, 1857 by subsequent designation (habitus in Fig. 302.2).

Diagnosis. Size from 2.0 to 5.0 mm. Bathyscioid, elliptical shape (Fig. 302.2).

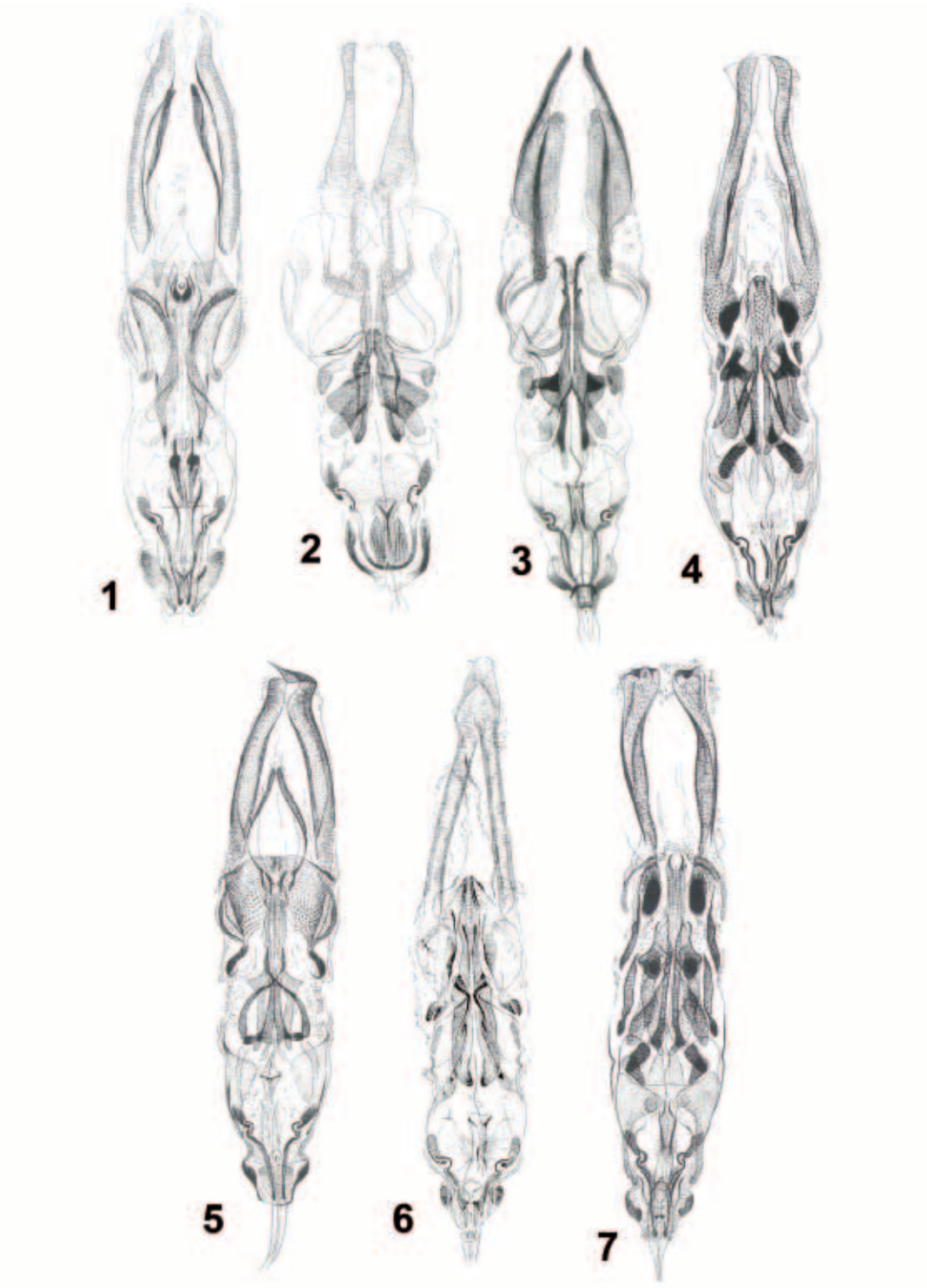
Head: With complete occipital carina; anophthalmous.

Antennae: Slightly shorter than the elytral suture.

Pronotum: Transverse with lateral margins regularly arched from base to apex; maximum width in the basal quarter and sinuous base. Although, in *Speonomus monticola* the lateral margins are a little sinuous in its posterior part, before the vertex: well apparent in the male and somewhat less marked in the female.

Elytra: Long and wide, with fine and close transverse striolae or well marked and more widely spaced.

Legs: Protibiae with two simple external spurs and a series of thick spines on the external face; mesotibiae slightly arched with a double series of spines on the external face; metatibiae straight with a series of spines along the external face.



FIGURES 311.1–311.7: *Speonomus* series, *Speonomus* group. Endophallus of: (**1**) *Lagariella colominasi,* (**2**) *Naspunius eseranus,* (**3**) *Salgadoia brieti,* (**4**) *Speonomites velox,* (**5**) *Stygiophyes puncticollis,* (**6**) *Trapezodirus carrodillae,* (**7**) *Troglocharinus ferreri.* Figs **1**–**7** modified from Salgado *et al*. (2008).

Mesoventral keel (Fig. 304.7): High, obtusely angled, with curved anterior border, apex toothed, and sinuous rim; ventral edge serrated, not flat, laterally serrated and ventrally fine, sharp.

Suture of the metaventrite (Fig. 304.7): It delimits an area very narrow and arched that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 305.7): With the metascutum narrow and elongated, and the apophysis of the alacrista very little protruding and apices very pointed.

Metendosternite (Fig. 307.5): Quite robust, with the furcal arms somewhat shorter than the trunk and the terminal apophysis very thick; posterior furcal blade broad on the arms and trunk, with slightly arched posterior edge; trunk distinctly longer than wide at the base and mid-keel (mfk) with marked posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.7), bent at an obtuse angle between the apical third and fourth; progressively tapering from the base to the apex that is prolonged into a finetip. In dorsal view (Fig. 310.3), sides of basal half subrectilinear or slightly sinuous, then tapering to almost straight and parallel in apical half, both sides joining to form a broad regular arc. Basal lamina rather long, the sides ending with the basal edge in regular arc to form sharp projections; ventral lamina of tegmen shorter and with similar width.

Endophallus (Fig. 310.3): In the basal region in the dorsal complex there is a very robust «Y»-piece with straight arms that connect to the apical fibres of the «Y»-piece which in turn seem to be extended by kind of floating pieces; these floating pieces apparently do not come into contact with the dorsal phanerae of the mid-region; in the ventral complex the central canal exhibits an elongated apical crown; in the middle region there are the dorsal phanerae, that are long and widened at their lower end; robust and parallel ventral phanerae are present and dorsal plates joint with the appearance of fine and divergent phanerae; at the upper end of these structures, a tube surrounded by muscular tissue is observed, at which an apex, with a differentiated structure, is insinuated. On both sides of the axial piece and the upper end of the ventral and dorsal phanerae, bag-like structures covered with scales are present, with a more sclerotized inner rim and an extension at its lower end; the bag-like structures seem to flexibly bound to the reinforcing bands of the apical region; in the apical region, very robust reinforcing bands are observed, which show interlocking extensions at the basal end.

Parameres (Fig. 312.7): They do not reach the tip of the median lobe. Equipped with three setae with a gently curved tip: one being longer and considerably more robust than the others, and with the point of insertion adjoining to each other at the apical end of the style; the third, finer one that inserts a little before the distal end. Membranous lamina poorly developed and on the outer margin there is a dense penicillum with some setae as long as the main ones.

Spermathecal complex: Spermatheca (Fig. 313.8) with the apical lobe thickened and bent at an obtuse angle with respect to the middle region. The middle region hyaline with the somewhat smaller section in the vicinity of the apical lobe; basal lobe with a larger section and arranged—in relation to the middle region—at an obtuse angle somewhat more closed than that of the apical lobe. Both lobes are more sclerotized than the middle region. In basal part there is a tiny nodule in which the spermathecal duct and a membranous gland are originating from; the spermiduct joints the copulatory bag in a somewhat widened basal process in the area of junction, also somewhat funnel-shaped and slightly sclerotized.

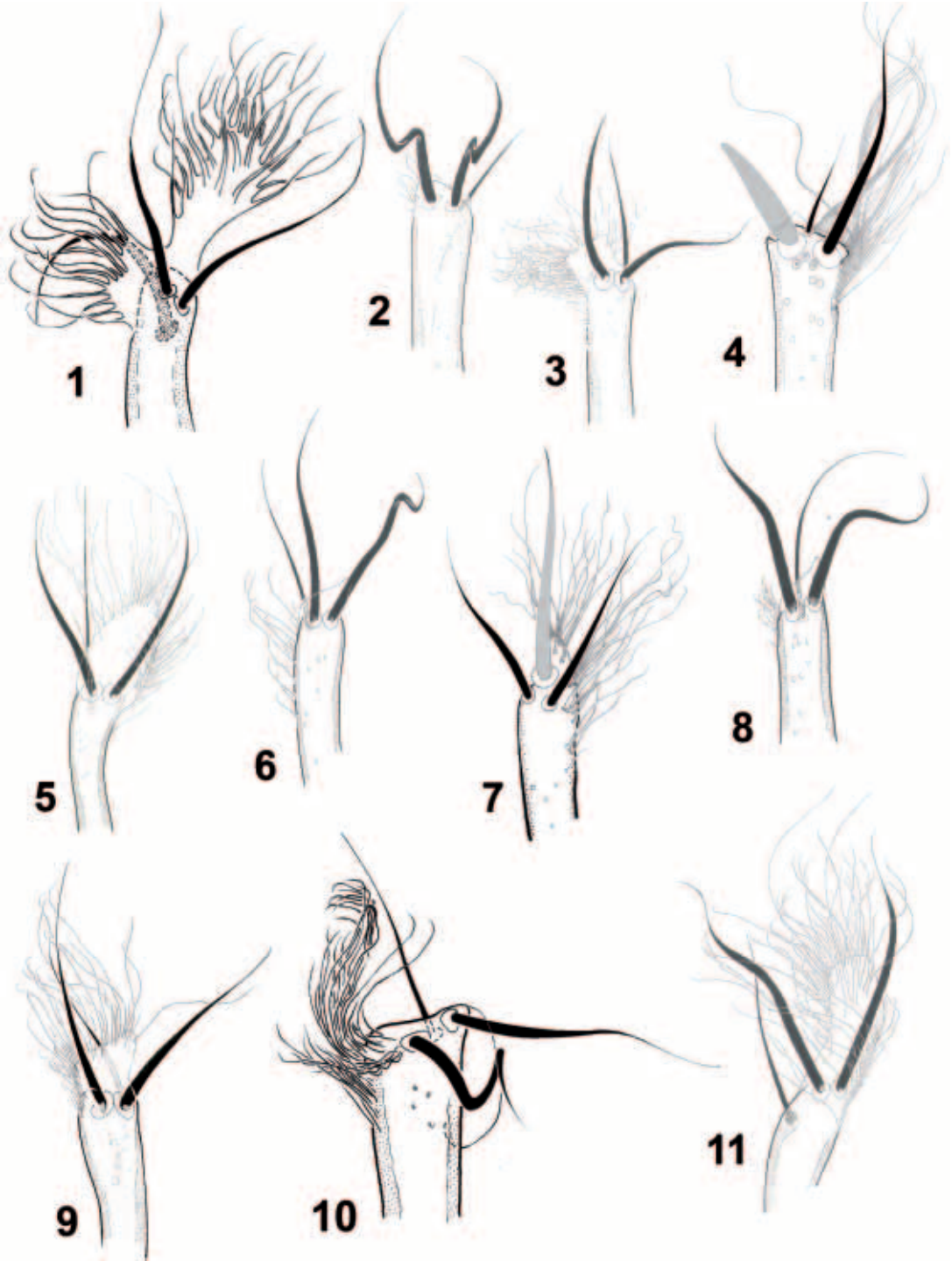
Female uroventrite VIII (Fig. 315.7): With a short and wide spiculum with rounded apex.

DISCUSSION. It worth noticing that *Speonomus opisthonoxus* (Fig. 303.2) has been included in this genus, despite the fact that the species was not included in the molecular study. It used to be part of its own group together with *Speonomus ehlersi* – «Groupe *ehlersi*» of Perreau (2000) – and therefore did not belong to the *Speonomus pyreneus* group. Its aedeagus and endophallus structures (Figs 303.4, 303.6) correspond exactly to the model described for *Speonomus.* The other species in the group, *S. ehlersi,* has been transferred to the genus *Vanderberghia* gen. nov. and where it is found to be at the base of this clade.

In the analysis the genus *Speonomus* is consisting of three clades that do not correspond to the groups of Perreau (2000) and therefore these classification is not maintained. The topology of the clade is as follows (Fig. 1A):

– it is sister to all others with support of 91.5/99 for the clade of *S. zophosinus*: *S. abeillei abeillei, S. normandi* and *S. zophosinus.* The clade is also supported well by values of 95.3/100.

– the clade of *S. stygius* is well supported by 96.4/86, and found to be to the clade of *S. pyreneus* with the species *S. abeillei bouilloni, S. chardonis, S. leleupi, S. proserpinae,* and *S. stygius*, sister with high support, 100/100,.



FIGURES 312.1–312.11: *Speonomus* series, *Speonomus* group. Apex of the paramere of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites velox,* (**7**) *Speonomus curvipes subcurvipes,* (**8**) *Stygiophyes ptuncticollis,* (**9**) *Trapezodirus carrodillae,* (**10**) *Trocharanis mestrei,* (**11**) *Troglocharinus ferreri.* Figs **2**, **3**, **5**, **6**, **8**, **9**, **11** modified from Salgado *et al*. (2008).

– the clade of *S. pyreneus* is well supported by values of 94.6/97, consisting of the species *S. curvipes, S. diecki*, *S. fagniezi, S. longicornis, S. piochardi* and *S. pyreneus*.

In the sense of Perreau (2000) defined the «*pyreneus*» group it was composed of the species: *S. chardonis, S. curvipes, S. fagniezi, S. longicornis, S. piochardi, S. proserpinae, S. pyreneus* and *S. stygius*. The «*zophosinus*» group of Perreau (2000) was composed of the species: *S. abeillei, S. colluvii, S. leleupi, S. normandi, S. zophosinus, S. bonvouloiri* (transferred to the genus *Perriniella)* and *S. carrerei,* which had been included in the new genus *Ariejasia* gen. nov., and this sister of *Paraspeonomus.*

Other consequences:

– *Speonomus abeillei bouilloni* RA758 is sister of *S. stygius tisiphone* RA801 (both from type locality) with support of 97.5/95 and is not in the same clade as *S. abeillei abeillei* RB2. Consequently, it must be raised to the rank of a good species: *Speonomus bouilloni*. *Speonomus stygius tisiphone* RA801*,* is a sister species of *S. bouilloni* RA758 and is not found in the clade of *S. stygius stygius* AI529 (from type locality); but there are other previously described subspecies that have not been studied. If any of them were synonymous with *tisiphone,* their name would prevail. Consequently, no taxonomic act is proposed.

– *Speonomus pyreneus major* AI535 is the sister of *S. diecki* AI536 (both from type locality) with no genetic differences and support of 99.1/100; the synonymy between both is established and the morphology is consistent with this taxonomic change. Sister of both species is *Speonomus pyreneus nadari* AF57, which was also obtained from the type locality with support of 80.3/100. But there are other previously described subspecies that have not been studied. If any of them were synonymous with *nadari,* their name would prevail. Consequently, no taxonomic act is proposed.

– *Speonomus longicornis fauveaui* RA667 appears as a sister of *S. fagniezi* AF125 + *S. curvipes s. l.* HI24/AC168 with a support of 100/100. *Speonomus longicornis longicornis* AI531 is sister of *S. piochardi* with support of 90/94; so *fauveaui* should be considered as a good species. But there are three other previously described subspecies that have not been studied: *Speonomus longicornis perieri*, *S. longicornis hermensis* and *S. longicornis pandellei*; if any of them were synonymous with *fauveaui,* their name would prevail. Consequently, no taxonomic act is proposed.

– *Speonomus normandi normandi* AI532 (from type locality) is sister of *S. normandi hydrophilus* AI528 + *S. abeillei abeillei* RB2 with support of 100/100, which in turn amongst them show a support of 85.6/100. *S. hydrophilus* should be considered as a good species, but there is one other previously described subspecies that has not been studied: *Speonomus normandi bergesi*. Consequently, no taxonomic act is proposed.

– *Speonomus stygius crassicornis* RB8 (from type locality) with support of 87.6/96 is a sister of (*S. leleupi* AN414 (*S. stygius stygius* AI529 – from type locality – + *S. stygius saulcyi* RB9)). Given the great morphological differences of *S. leleupi* with respect to the others and its position in the phylogram, we must consider *S. crassicornis* as a good species. But there are one other previously described subspecies that have not been studied: *Speonomus stygius brevicornis*. Consequently, no taxonomic act is proposed.

– DNA sequences of the subgenus *Metaspeonomus* have not been available. The appearance of *Speonomus* (*Metaspeonomus*) *monticola* (Fig. 303.1) is very similar to that of *Speonomus pyreneus*. Also the aedeagus (Figs 303.3, 303.5) of *Speonomus monticola* is practically identical to that of *S. pyreneus,* the type species of the genus: the endophallus of these two species cannot be differentiated. Is established the synonymy of *Metaspeonomus* Coiffait, 1959 syn. nov. = *Speonomus* Jeannel, 1908.

All these changes have been included in the list of species: it seems that a molecular and morphological review of the entire genus is required.

DISTRIBUTION. Northern slope of the Pyrenean massif in its eastern half, France.

Species

Speonomus abeillei (Saulcy, 1872)
Adelops Abeillei Saulcy, 1872: 20.
Bathyscia (*Bathyscia*) *Abeillei* Saulcy: Reitter 1885 [1884]: 30.
Speonomus Abeillei Saulcy: Jeannel, 1908a: 300.
Speonomus (*Speonomus*) *abeillei* (Saulcy): Perreau, 2000: 325.

Speonomus monticola (Coiffait, 1959)
Speonomus (*Metaspeonomus) monticola* Coiffait, 1959: 176.

Speonomus bouilloni Coiffait, 1959 stat. nov.
Speonomus abeillei bouilloni Coiffait, 1959: 173.

Speonomus chardonis (Abeille de Perrin, 1875)

Speonomus chardonis aletinus (Abeille de Perrin, 1883)
Bathyscia aletina Abeille de Perrin, 1883: 3.
Bathyscia (*Bathyscia*) *aletina* Abeille de Perrin: Reitter 1885 [1884]: 31.
Bathyscia Chardoni aletina Abeille de Perrin: Jeannel, 1907c: 64.
Speonomus (*Speonomus) Chardoni aletina* Abeille de Perrin: Jeannel, 1910a: 32.
Speonomus (*Speonomus) chardonis aletinus* (Abeille de Perrin): Perreau, 2000: 317.
Speonomus chardonis chardonis (Abeille de Perrin, 1875)
Adelops Chardonis Abeille de Perrin, 1875c: 215.
Bathyscia (*Bathyscia) Chardonis* Abeille de Perrin: Reitter 1885 [1884]: 31.
Bathyscia Chardoni Abeille de Perrin: Jeannel, 1907a: 133.
Speonomus Chardoni Abeille de Perrin: Jeannel, 1908a: 300.
Speonomus (*Speonomus*) *Chardoni* Subsp. *Chardoni* Abeille de Perrin: Jeannel, 1924a: 150.
Speonomus (*Speonomus*) *chardonis chardonis* (Abeille de Perrin): Perreau, 2000: 317.
Speonomus chardonis hecatae (Abeille de Perrin, 1878)
Adelops Hecatae Abeille de Perrin, 1878: 154.
Bathyscia (*Bathyscia*) *Hecate* Abeille de Perrin: Reitter 1885 [1884]: 30.
Bathyscia stygia ssp. *Hecate* Abeille de Perrin: Jeannel, 1907c: 64.
Speonomus (*Speonomus*) *Chardoni* Subsp. *Hecate* Abeille de Perrin: Jeannel, 1910a: 32.
Speonomus (*Speonomus*) *chardonis hecatae* (Abeille de Perrin, 1878): Perreau, 2000: 317.
Speonomus chardonis pueli (Chobaut, 1903)
Bathyscia Pueli Chobaut, 1903a: 221.
Bathyscia Chardoni subsp. *Pueli* Chobaut: Jeannel, 1907c: 64.
Speonomus (*Speonomus*) *Chardoni* subsp. *Pueli* Chobaut: Jeannel, 1910a: 32.
Speonomus (*Speonomus*) *chardonis pueli* (Chobaut): Perreau, 2000: 317.

Speonomus colluvii Delay, Juberthie & Ruffat, 1983
Speonomus colluvii Delay, Juberthie & Ruffat, 1983: 249.

Speonomus curvipes (Piochard de la Brûlerie, 1872)
Speonomus curvipes curvipes (Piochard de la Brûlerie, 1872)
Adelops curvipes Piochard de la Brûlerie, 1872: 444.
Bathyscia (*Bathyscia*) *curvipes* Piochard de la Brûlerie: Reitter 1885 [1884]: 29.
Speonomus curvipes La Brûlerie: Jeannel, 1908a: 300.
Speonomus (*Speonomus*) *curvipes* Supsp. *curvipes* La Brûlerie: Jeannel, 1924a: 152.
Speonomus curvipes subcurvipes (Abeille de Perrin, 1878)
Adelops subcurvipes Abeille de Perrin, 1878: 154.
Speonomus (*Speonomus*) *curvipes* subsp. *subcurvipes* Abeille: Jeannel, 1910a: 33.
Speonomus curvipes subrectipes (Abeille de Perrin)
Adelops subrectipes Abeille de Perrin, 1878: 154.
Speonomus (*Speonomus*) *curvipes* subsp. *subrectipes* Abeille: Jeannel, 1910a: 33.

Speonomus diecki (Saulcy, 1872)
Adelops Diecki Saulcy, 1872: 18.
Bathyscia (*Bathyscia*) *Diecki* Saulcy: Reitter 1885 [1884]: 27.
Speonomus Diecki Saulcy: Jeannel, 1908a: 301.
Speonomus diecki Saulcy: Fourès, 1947: 256.
Speonomus pyrenaeus major Coiffait, 1959: 168 syn. nov.
Speonomus (s. str.) *diecki* (Saulcy): Perreau, 2000: 318.

Speonomus fagniezi Jeannel, 1910
Speonomus Fagniezi Jeannel, 1910e: 49.
Speonomus (s. str.) *fagniezi* Jeannel: Perreau, 2000: 318.

Speonomus leleupi Coiffait, 1953
Speonomus leleupi Coiffait, 1953: 28.

Speonomus longicornis (Saulcy, 1872)
Speonomus longicornis fauveaui (Jeannel, 1907)
Bathyscia Fauveaui Jeannel, 1907d: 245.
Speonomus (s. str.) *longicornis* subsp. *Fauveaui* Jeannel: Jeannel, 1910a: 32.
Speonomus (s. str.) *longicornis fauveaui* (Jeannel): Perreau, 2000: 319.
Speonomus longicornis fuxeensis Jeannel, 1908
Speonomus longicornis ssp. *fuxeensis* Jeannel, 1908b: 64, 71.
Speonomus (s. str.) *longicornis* subsp. *fuxeensis* Jeannel: Jeannel, 1910a: 32.
Speonomus longicornis hermensis (Abeille de Perrin, 1873)
Adelops Hermensis Abeille de Perrin, 1873: XCVIII.
Bathyscia hermensis Abeille, 1873: Jeannel, 1907c: 63.
Speonomus hermensis Abeille: Jeannel, 1908a: 300.
Speonomus (s. str.) *longicornis* subsp. *hermensis* Abeille: Jeannel, 1910a: 32.

Speonomus longicornis longicornis (Saulcy, 1872)
Adelops Longicornis Saulcy, 1872: 19.
Bathyscia (*Bathyscia*) *longicornis* Saulcy: Reitter 1885 [1884]: 28.
Speonomus longicornis Saulcy: Jeannel, 1908a: 300.
Speonomus (s. str.) *longicornis* Subsp. *longicornis* Saulcy, 1872: Jeannel, 1924a: 153.
Speonomus longicornis pandellei (Abeille de Perrin, 1883)
Bathyscia Pandellei Abeille de Perrin, 1883: 2.
Bathyscia (*Bathyscia*) *Pandellei* Ab.: Reitter 1885 [1884]: 30.
Speonomus Pandellei Abeille: Jeannel, 1908a: 300.
Speonomus (s. str.) *longicornis* subsp. *pandellei* Abeille: Jeannel, 1910a: 32.
Speonomus longicornis perieri (Piochard de la Brûlerie, 1872)
Adelops Perieri Piochard de la Brûlerie, 1872: 446.
Bathyscia (*Bathyscia*) *Perieri* Pioch.: Reitter 1885 [1884]: 28.
Bathyscia Perieri var. *gracilis* Jeannel, 1907d: 245.
Speonomus Perieri La Brûlerie: Jeannel, 1908a: 300.
Speonomus (s. str.) *longicornis* subsp. *Perieri* La Brûlerie: Jeannel, 1910a: 32.
Speonomus (s. str.) *longicornis* subsp. *Perieri* var. *gracilis* Jeannel: Jeannel, 1911a: 336.

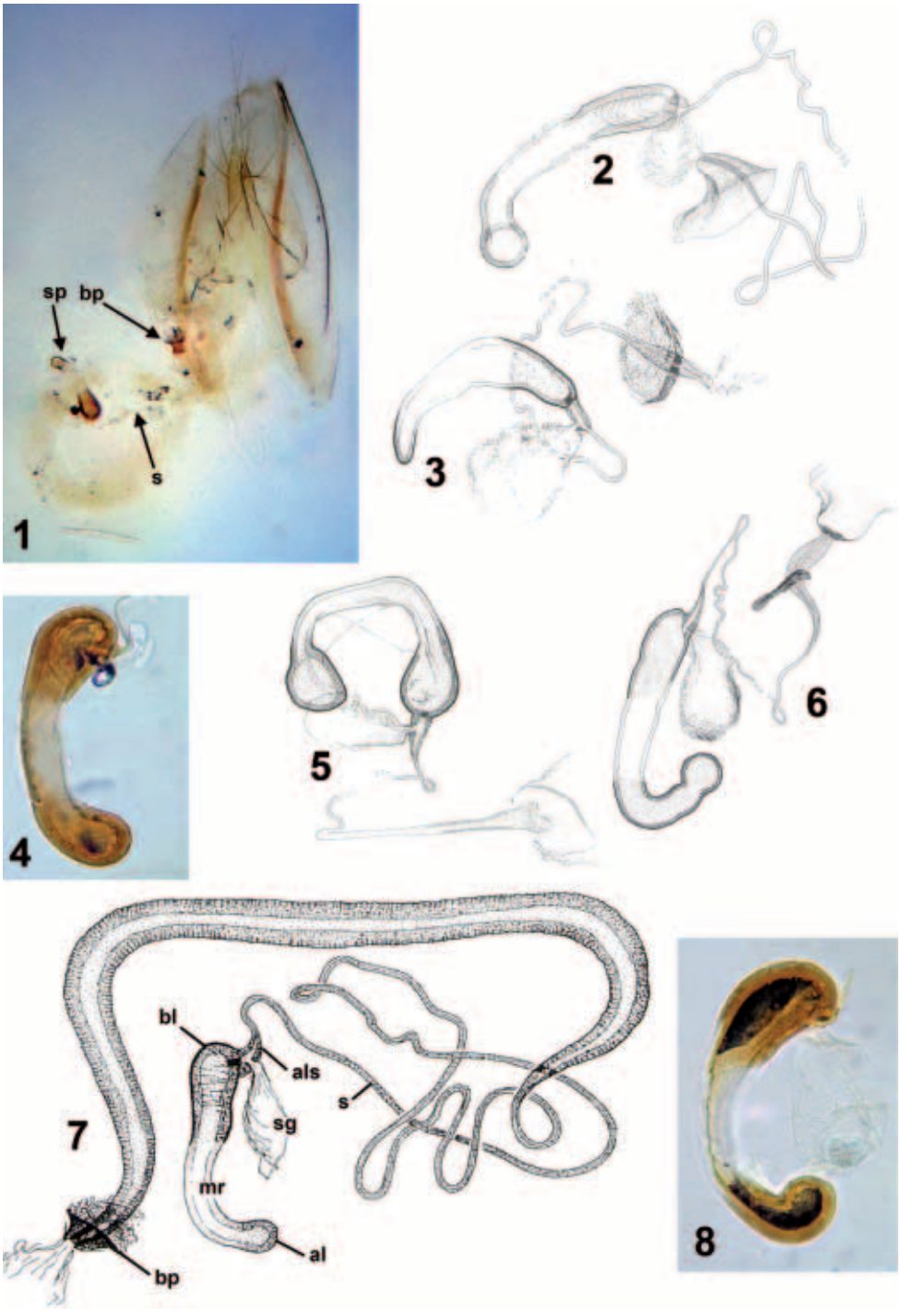
Speonomus normandi (Jeannel, 1906)
Speonomus normandi bergesi Coiffait, 1959
Speonomus hydrophilus bergesi Coiffait, 1959: 172.
Speonomus (s. str.) *normandi bergesi* Coiffait: Perreau, 2000: 326.
Speonomus normandi hydrophilus (Jeannel, 1907)
Bathyscia hydrophila Jeannel, 1907a: 127, 131.
Speonomus hydrophilus Jeannel: Jeannel, 1908a: 300.
Speonomus (s. str.) *hydrophilus* Jeannel: Jeannel, 1910a: 33.
Speonomus (s. str.) *hydrophilus* Subsp. *hydrophilus* Jeannel: Jeannel, 1924a: 156.
Speonomus (s. str.) *normandi hydrophilus* (Jeannel): Perreau, 2000: 326.
Speonomus normandi normandi (Jeannel, 1906)
Bathyscia Normandi Jeannel, 1906b: 246.
Bathyscia hydrophila subsp. *Normandi* Jeannel: Jeannel, 1907c: 64.
Speonomus (s. str.) *hydrophilus* subsp. *Normandi* Jeannel: Jeannel, 1910a: 33.
Speonomus hydrophilus subsp. *Normandi* Jeannel: Coiffait, 1959: 171.
Speonomus hydrophilus normandi Jeannel: Coiffait, 1963: 31.
Speonomus (s. str.) *normandi normandi* (Jeannel): Perreau, 2000: 327.

Speonomus opisthonoxus Gers & Dupuy, 1988
Speonomus opisthonoxus Gers & Dupuy, 1988: 168.

Speonomus piochardi (Abeille de Perrin, 1873)
Adelops Piochardi Abeille de Perrin, 1873: XCVIII.
Bathyscia (*Bathyscia*) *Piochardi* Ab.: Reitter 1885 [1884]: 29.
Speonomus Piochardi Abeille: Jeannel, 1908a: 300.
Speonomus (s. str.) *Piochardi* Abeille: Jeannel, 1911a: 334.
Speonomus (s. str.) *piochardi* (Abeille de Perrin): Perreau, 2000: 320.

Speonomus proserpinae (Abeille de Perrin, 1878)
Adelops proserpinae Abeille de Perrin, 1878: 155.
Bathyscia (*Bathyscia) Proserpinae* Ab.: Reitter 1885 [1884]: 31.
Bathyscia proserpina Abeille: Jeannel, 1907a: 133.
Speonomus Proserpina Abeille: Jeannel, 1908a: 300.
Speonomus (s. str.) *Proserpina* Abeille: Jeannel, 1910a: 32.
Speonomus (s. str.) *proserpina* Abeille: Jeannel, 1924a: 28.

Speonomus pyreneus (Lespès, 1857)
Speonomus pyreneus discontignyi (Saulcy, 1872)
Adelops Discontignyi Saulcy, 1872: 18.
Bathyscia (*Bathyscia*) *Discontignyi* Saulcy: Reitter 1885 [1884]: 28.
Speonomus Discontignyi Saulcy: Jeannel, 1908a: 301.
Speonomus (s. str**.)** *pyrenaeus* subsp. *Discontignyi* Saulcy: Jeannel, 1910a: 33.
Speonomus pyrenaeus subsp. *discontignyi* Saulcy: Fourès, 1947: 255.
Speonomus pyrenaeus subsp. *Discontignyi* Saulcy: Coiffait, 1959: 167.
Speonomus (s. str**.)** *pyreneus discontignyi* (Saulcy): Perreau, 2000: 320.
Speonomus pyreneus hustachei Coiffait, 1959
Speonomus pyrenaeus subsp. *Hustachei* Coiffait, 1959: 168.
Speonomus (s. str**.)** *pyreneus hustachei* Coiffait: Perreau, 2000: 320.
Speonomus pyreneus maurasi Coiffait, 1955
Speonomus (s. str.) *pyrenaeus* subsp. *maurasi* Coiffait, 1955b: 203.
Speonomus (s. str.) *pyreneus maurasi* Coiffait: Perreau, 2000: 321.
Speonomus pyreneus nadari (Jeannel, 1906)
Bathyscia Nadari Jeannel, 1906b: 244.
Bathyscia pyrenaea subsp. *Nadari* Jeannel: Jeannel, 1907c: 63.



FIGURES 313.1–313.8: *Speonomus* series, *Speonomus* group. Spermathecal complex of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites velox,* (**7**) *Speonomites pallaresanus,* (**8**) *Speonomus pyreneus.* Figs **2**, **3**, **5**–7 modified from Salgado *et al*. (2008). Abbreviations: **als**, apical lobe of the spermiduct; **al**, apical lobe; **bl**, basal lobe; **bp**, basal piece; **mr**, middle region; **s**, spermiduct; **sg**, spermathecal gland; **sp**, spermatheca.

Speonomus (s. str.) *pyrenaeus* subsp. *Nadari* Jeannel: Jeannel, 1910a: 33.
Speonomus pyrenaeus subsp. *Nadari* Jeannel: Coiffait, 1959: 167.
Speonomus pyrenaeus nadari Jeannel: Bernasconi, 1964: 563.
Speonomus (s. str.) *pyreneus nadari* (Jeannel): Perreau, 2000: 321.
Speonomus pyreneus nerzici Coiffait, 1959
Speonomus pyrenaeus subsp. *Nerzici* Coiffait, 1959: 169.
Speonomus (s. str.) *pyreneus nerzici* Coiffait: Perreau, 2000: 321.
Speonomus pyreneus novemfontium (Piochard de la Brûlerie, 1872)
Adelops Novem-Fontium Piochard de la Brûlerie, 1872: 445.
Bathyscia (*Bathyscia*) *novemfontium* Pioch: Reitter 1885 [1884]: 28.
Bathyscia pyrenaea subsp. *novemfontium* La Brûlerie: Jeannel, 1907c: 63.
Speonomus (s. str.) *pyrenaeus* subsp. *novemfontium* La Brûlerie: Jeannel, 1910a: 33.
Speonomus pyrenaeus subsp. *novemfontium* La Brûlerie: Coiffait, 1959: 167.
Speonomus (s. str.) *pyreneus novemfontium* (Piochard de la Brûlerie): Perreau, 2000: 321.
Speonomus pyreneus pratensis Coiffait, 1959
Speonomus pyrenaeus subsp. *pratensis* Coiffait, 1959: 169.
Speonomus (s. str.) *pyreneus pratensis* Coiffait: Perreau, 2000: 321.
Speonomus pyreneus pyreneus (Lespès, 1857)
Adelops Pyreneus Lespès, 1857: 283.
Adelops pyrenaeus Lespès: Fairmaire, 1859: 32.
Adelops Barnevillei Saulcy, 1872: 18.
Bathyscia (*Bathyscia*) *pyrenaeus* Lespès: Reitter 1885 [1884]: 27.
Bathyscia (*Bathyscia*) *Barnevillei* Saulcy: Reitter 1885 [1884]: 27.
Bathyscia pyrenaea Lespès: Jeannel, 1907c: 63.
Speonomus pyrenaeus Lespès: Jeannel, 1908a: 301.
Speonomus (s. str.) *pyrenaeus* Lespès: Jeannel, 1910a: 33.
Speonomus pyrenaeus pyrenaeus Lespès: Crouau-Roy & Bakalowicz, 1993: 549.
Speonomus (s. str.) *pyreneus pyreneus* (Lespès): Perreau, 2000: 321.

Speonomus stygius (Dieck, 1869)
Speonomus stygius brevicornis Coiffait, 1952
Speonomus stygius ssp. *brevicornis* Coiffait, 1952: 43.
Speonomus (s. str.) *michaeli* Fourès, 1954: 4.
Speonomus stygius crassicornis (Piochard de la Brulerie, 1872)
Adelops crassicornis Piochard de la Brûlerie, 1872: 447.
Bathyscia (*Bathyscia*) *crassicornis* Pioch.: Reitter 1885 [1884]: 31.
Bathyscia stygia subsp. *crassicornis* La Brûlerie: Jeannel, 1907a: 132.
Speonomus stygius subsp. *crassicornis* La Brûlerie: Jeannel, 1911a: 332.
Speonomus (s. str.) *stygius* subsp. *crassicornis* La Brûlerie: Jeannel, 1914b: 29.
Speonomus stygius saulcyi (Abeille de Perrin, 1872)
Adelops Saulcyi Abeille de Perrin, 1872a: 19.
Bathyscia (*Bathyscia*) *Saulcyi* Ab.: Reitter 1885 [1884]: 30.
Bathyscia stygia subsp. *Saulcyi* Abeille: Jeannel, 1907c: 64.
Speonomus stygius subsp. *Saulcyi* Abeille: Jeannel, 1911a: 332.
Speonomus (s. str.) *stygius saulcyi* (Abeille de Perrin): Perreau, 2000: 322.
Speonomus stygius stygius (Dieck, 1869)
Adelops stygius Dieck, 1869a: 5.
Adelops Clavatus Saulcy, 1872: 20.
Bathyscia (*Bathyscia*) *stygia* Dieck: Reitter 1885 [1884]: 30.
Bathyscia (*Bathyscia*) *clavata* Saulcy: Reitter 1885 [1884]: 29.
Bathyscia stygia Dieck: Jeannel, 1907c: 63.
Speonomus stygius Dieck: Jeannel, 1908a: 300.
Speonomus (s. str.) *stygius* subsp. *stygius* Dieck: Jeannel, 1924a: 151.
Speonomus stygius thibali Coiffait, 1959
Speonomus stygius subsp. *Thibali* Coiffait, 1959: 167.
Speonomus (s. str.) *stygius thibali* Coiffait: Perreau, 2000: 322.
Speonomus stygius tisiphone Jeannel, 1908
Speonomus stygius subsp. *Tisiphone* Jeannel, 1908b: 62.
Speonomus (s. str.) *stygius* subsp. *tisiphone* Jeannel: 1924: 151.

Speonomus zophosinus (Saulcy, 1872)
Adelops Zophosinus Saulcy, 1872: 21.
Adelops oviformis Piochard de la Brûlerie, 1872: 447.
Bathyscia (*Bathyscia*) *cophosina* Saulcy: Reitter 1885 [1884]: 32.
Bathyscia oviformis Piochard de la Brûlerie: Abeille de Perrin, 1905: 209.
Bathyscia zophosina Saulcy: Jeannel, 1907a: 132.
Speonomus zophosinus Saulcy: Jeannel, 1908a: 300.

Genus ***Stygiophyes*** Fresneda, 1998
Stygiophyes Fresneda, 1998: 60.

Type species. *Speonomus puncticollis* Jeannel, 1910 by original designation (habitus in Fig. 302.3).

Diagnosis. Size of 2.5-3.2 mm. Bathyscioid (Fig. 302.3), with the body elongated, subparallel, depressed, ovoid and convex, or very wide and slightly convex.

Head: With occipital carina vanished in the central part; anophthalmous.

Antennae: Moderately to distinctly long.

Pronotum: Transverse as wide as elytra, or in some cases much wider; lateral margins uniformly arched or with the anterior two thirds strongly converging towards the front and the posterior with the accentuated curvature; maximum width at the base or in the posterior third.

Elytra: Elongated, convex or depressed; parasutural stria, which occurs in almost all species, more or less visible; transverse striolae, in general fine, with a regular arrangement and very close to each other.

Legs: Moderately long, always slender; protibiae with two very small simple external spurs and a series of very small spaced spines that are mixed up with the hair on the external face; sparsely arched mesotibiae with two small simple spurs on outer side and two series of thick spines on outer side; metatibiae straight, with two simple spurs on outer part of apex and a series of spines along outer face of tibia; male protarsi are thickened.

Mesoventral keel (Fig. 304.8): High, with the anterior margin nearly straight or sharply curved and ridged and hooked at the apex; lower margin sinuous, with rounded ridge.

Suture of the metaventrite (Fig. 304.8): It delimits an area very narrow and arched that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 305.8): With wings of the metascutum narrow and elongated; apophysis of the alacrista not very apparent and apices not very pointed.

Metendosternite (Fig. 308.1): Furcal arms as long as trunk, with thick terminal apophysis; posterior furcal blade fairly wide on arms and trunk, arms around the same width up to apex and posterior edge slightly arched; furcal trunk distinctly longer than wide at base and median keel diverging posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 309.8), curved at an obtuse angle but close to 90°; progressively tapering towards the apex, which, however, is thickened shortly before the distal end and the two sides form a sort of curved wings towards the back.

Endophallus (Fig. 311.5): «Y»-piece with symmetrical arms and double sinuosity; the apical fibres of the «Y»-piece appear triple and one of the prolongations resembles a floating piece that comes into contact with the dorsal phanera of the middle region; in this region two dorsal phanerae with their internal margins in contact are present; each of them bifurcates in their lower region and one of the prolongations connects with the floating pseudo-piece, while the other is prolonged and insinuates an appendage of the dorsal phanera; there are some ventral phanerae with an prominent thickening in the middle of their length; two upper dorsal plates can also be seen within the inner margin being somewhat more sclerotized and a very apparent outer phanerae; apical region with two reinforcing bands and a central bag that may be densely covered with spicules and that contains also two prolongations towards the middle region of the bag, in the same way as seen in the genus *Lagariella;* the bands are implanted on striated membranous ligules.

Parameres (Fig. 312.8): Shorter than the median lobe with three setae of apical insertion: the first two of equal length, robust and sinuous, while the third - finer one- is short and rectilinear, and its point of insertion is separated from that of the other two; poorly developed membranous lamina and a penicillum at the junction point of the membranous lamina, formed by short and scarce setae, numerous placoid sensilla can be observed.

Spermathecal complex: Spermatheca (Fig. 314.1) with the apical lobe spherical and more or less bent at an angle with respect to the middle region that presents a regular section; basal lobe as wide as mid-region and may be bent relative to mid-region at same angle as apical lobe; both lobes more sclerotized than the middle region; in the basal part, a minute nodule is usually seen in which the spermatic duct and a membranous gland are inserting; long, very thin spermatic duct this is inserted into the copulatory bag through a hat-shaped sclerotized piece.

Female uroventrite VIII (Fig. 315.8): With short and pointed spiculum.

Discussion. In the molecular phylogeny (Fig. 1A), here named Tree-1, the sister genus of *Stygiophyes* is *Lagariella* this node has a high support of 95.5/100. In Tree-2 (Fig. 2) *Lagariella* as a sister to the clade formed by *Stygiophyes aldomai allomorphus*, *S. saforensis*, *S. ribagorzanus* and *S. akarsticus* with low

support, 78.8/51, and not at the base of the entire genus *Stygiophyes*. The validity of the two genera is maintained according to the results of Tree-1, with much better support; the case has been commented in the discussion section of the genus *Lagariella*. *Stygiophyes* + *Lagariella* together are sister with a high support of 97.2/100 of the clade formed by *Salgadoia* and *Naspunius*.

The endophallus model was described by Bellés (1983); in this study, the two pairs of phanerae of the median region were commented on and included, structures that allowed the author to establish the specific independence of two taxa, *S. puncticollis* and *S. espinosai*. This genus is related to *Lagariella* because it has striated membranous ligules without an internal nodule and a plate located between the apical reinforcement bands that have extensions that penetrate the middle region; there are also certain similarities with *Trapezodirus* due to the structure of the middle region of the endophallus with the ventral and dorsal phanerae straight and parallel to each other, not at all divergent; however, in *Stygiophyes* the dorsal bags do not present an interior sclerotized nodule and the mid-region phanerae are much finer and more slender than in the genus *Trapezodirus*. The genus *Stygiophyes* has been the subject of a study by Fresneda & Escolà (2000), where the geonemia is updated and a distribution map is included, taxonomic data is provided and the dispersal processes of its species are pondered.

DISTRIBUTION: It colonises an extensive region extending from the outer pre-Pyrenean mountains, almost bordering the Ebro depression of the Serra del Montsec all the was to relatively high altitudes, already within the Pyrenean massif, in the municipalities of El Pont de Suert, Vall de Boí (Lleida) and Bonansa (Huesca). In the southern limits of its distribution area, it extends along both banks of the Noguera Pallaresa and Noguera Ribagorçana rivers, while to the north it only colonises a narrow strip on both sides of the Noguera Ribagorçana; possibly the dispersal through the northern territories has occurred gradually following the retreat of the upper Pleistocene glacial phenomenon, to colonise azoic regions; as this process took place, significant taxonomic diversification occurred. Several cases of coexistence between species of *Stygiophyes* and *Trapezodirus* are found at the limit of their respective distribution areas, which therefore overlap a little, and the same happens with *Stygiophyes* and *Speonomites*. Species of the genus *Stygiophyes* probably enter the Pyrenees following the Ribagorçana basin and come into contact with species of the genus *Trapezodirus,* which has clearly cryophilic species and which is likely to have preceded the dispersion of *Stygiophyes*; the same happened to *Troglocharinus*. The second route of dispersion of the species of *Stygiophyes* in the Pyrenees must have been along the Noguera Pallaresa basin; however, along this path the extension of the distribution area has been minimal since territories colonised by representatives of the genus *Speonomites,* with markedly cryophilic taxa are present (Fresneda & Hernando 1991) this then must also have preceded the dispersion of *Stygiophyes*.

Species

Stygiophyes akarsticus (Escolà, 1980)
Speonomus akarsticus Escolà, 1980a: 27.
Stygiophyes akarsticus (Escolà): Fresneda, 1998: 61.

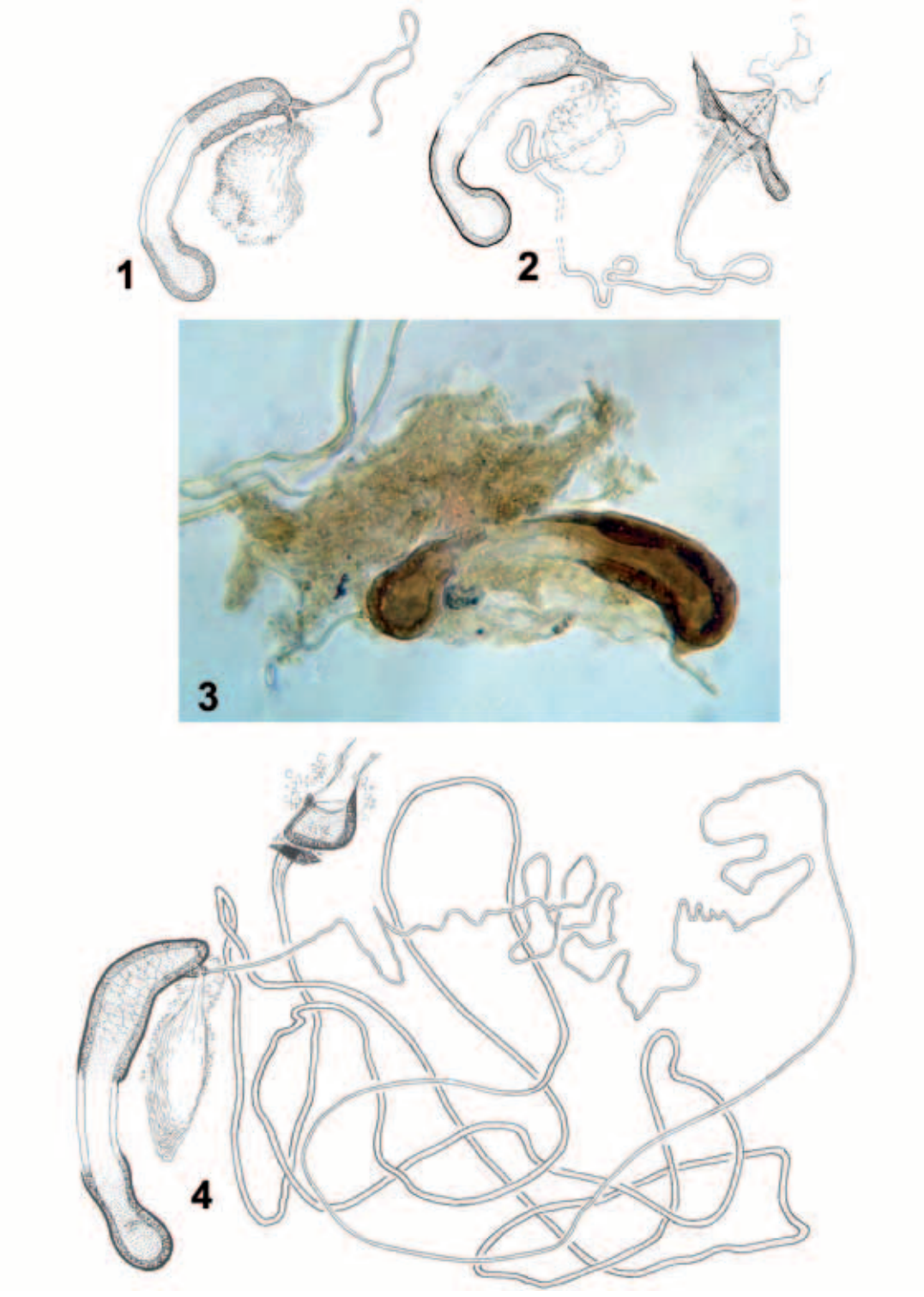
Stygiophyes aldomai (Fresneda & Hernando, 1988)
Stygiophyes aldomai aldomai (Fresneda & Hernando, 1988)
Speonomus aldomai Fresneda & Hernando, 1988: 164.
Stygiophyes aldomai aldomai (Fresneda & Hernando): Fresneda, 1998: 61.
Stygiophyes aldomai allomorphus Fresneda & Escolà, 2000
Stygiophyes aldomai allomorphus Fresneda & Escolà, 2000: 56.

Stygiophyes spinosai (Bellés, 1983)
Speonomus spinosai Bellés, 1983: 105.
Stygiophyes spinosai (Bellés): Fresneda, 1998: 61.

Stygiophyes hansferyi Fresneda & Escolà, 2001
Stygiophyes hansferyi Fresneda & Escolà, 2001: 71.

Stygiophyes latebricola (Jeannel, 1911)
Stygiophyes latebricola elongatus (Jeannel, 1911)
Speonomus latebricola elongatus Jeannel, 1911b: 87.
Stygiophyes latebricola elongatus (Jeannel): Fresneda, 1998: 61.
Stygiophyes latebricola latebricola (Jeannel, 1911)
Speonomus latebricola Jeannel, 1911b: 86.
Stygiophyes latebricola latebricola (Jeannel): Fresneda, 1998: 61.

Stygiophyes puncticollis (Jeannel, 1910)
Speonomus puncticollis Jeannel, 1910b: 155.
Speonomus troglodytes Jeannel, 1910b: 158.
Speonomus troglodytes angustior Jeannel, 1910b: 160.



FIGURES 314.1-314.4: *Speonomus* series, *Speonomus* group. Spermathecal complex of: (**1**) *Stygiophyes puncticollis,* (**2**) *Trapezodirus carrodillae,* (**3**) *Trocharanis mestrei,* (**4**) *Troglocharinus ferreri.* Figs **1**, **2**, **4** modified from Salgado *et al*. (2008).

Stygiophyes puncticollis (Jeannel): Fresneda, 1998: 61.

Stygiophyes ribagorzanus (Jeannel, 1911)
Speonomus ribagorzanus Jeannel, 1911b: 85.
Stygiophyes ribagorzanus (Jeannel): Fresneda, 1998: 61.

Stygiophyes saforensis (Escolà, Bellés & Comas, 1985)
Speonomus saforensis Escolà, Bellés & Comas, 1985: 225.
Stygiophyes saforensis (Escolà, Bellés & Comas): Fresneda, 1998: 61.

Stygiophyes sanctigervasi (Jeannel, 1911)
Speonomus Sancti-Gervasi Jeannel, 1911b: 84.
Stygiophyes sanctigervasi (Jeannel): Fresneda, 1998: 61.

Stygiophyes zariquieyi (Jeannel, 1924)
Speonomus (s. str.) *Zariquieyi* Jeannel, 1924a: 159.
Stygiophyes zariquieyi (Jeannel): Fresneda, 1998: 62.

Genus ***Trapezodirus*** Jeannel, 1924
Speophilus (*Trapezodirus*) Jeannel, 1924a: 172.
Trapezodirus Jeannel: Fresneda, 1998: 58.

TYPE SPECIES. *Speophilus carrodillae* Jeannel, 1911 by original designation (habitus in Fig. 302.4).

DIAGNOSIS. Size of 1.9-4.8 mm. Bathyscioid (Fig. 302.4), with the body oblong or oval, narrow or wide, slightly convex and with the elytral margins regularly curved from one end to the other or strongly tapered.

Head: With a poorly marked complete occipital carina; anophthalmous.

Antennae: Long and slender, almost equal in length to the body.

Pronotum: Slightly wider or slightly narrower than elytra and pronotum-elytral angle may be apparent in some cases or absent in others; transverse with arched sides, much more in the posterior third although in some cases they may be somewhat low-cut; posterior angles right or slightly acute, somewhat prolonged or not, depending on the species, and with the vertex rounded or acute and projecting; base more or less sinuous, also depending on the species and the maximum width in the posterior third.

Elytra: Widest in proximal third and margins regularly arched to apex or subparallel in first third and sharply narrowing towards the apex; finely denticulate rim and the existence of a parasutural stria is not detectable; transverse striolae well marked, fine, regular and generally somewhat rough and close together; epipleurae covered by fine transverse striolae and by pilosity in the style of the rest of the elytra.

Legs: Long and slender in appearance; male metafemora with a small denticle or sinuosity on posterior margin; first article of male protarsus as wide as apical end of tibia, triangular or heart-shaped to subrectangular in shape; protibiae with two very small simple outer spurs and no series of spines on outer surface; mesotibiae slightly arched, without simple spurs on the outer side, and with two series of small spines along the outer side; metatibiae straight, with two simple spurs on the outer part of the apex and a series of fine spines along the outer face of the tibia.

Mesoventral keel (Fig. 304.9): High, with evenly curved and flanged anterior border, and a small denticle at apex; anterior and bottom edges slightly serrated, the latter straight with rounded ridge.

Suture of the metaventrite (Fig. 304.9): It delimits an area very narrow and arched that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 306.1): With wings of the metascutum narrow and elongated; apophysis of the alacrista not very prominent and apices not very pointed.

Metendosternite (Fig. 308.2): Furcal arms as long as its trunk, with thick apical apophysis; posterior blade furcal slightly tapered towards middle, with slightly arched posterior edge; furcal trunk nearly twice as long as wide at base and mid-keel diverging posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 309.9), sharply curved at mid-length, then progressively tapering from the basal part to the tip, which also becomes progressively narrower and somewhat thickened preapically.

Endophallus (Fig. 311.6): The «Y»-piece with symmetrical arms extended towards the middle region and transformed into hyaline funnels; the fibres at the apex of the «Y»-piece connect to the floating pieces or extend to become the mid-region; the middle region is very complex due to the profusion of pieces arranged at different levels inside the bag or inside its walls; it consists of two ventral phanerae, two dorsal ones and a translucent upper dorsal plate with two of its margins very sclerotized so that they resemble two phanerae; at the base of the ventral phanerae there are two floating pieces; on both sides of the sac, at the level of the armor of the axial piece, there are two bags that show an appendix and an internal sclerotized nodule; on

both sides of the apical region there are reinforcing bands and between them, in an axial position, a apical bag densely covered with spicules.

Parameres (Fig. 312.9): They practically reach the apex of the median lobe; with three apical setae: two robust ventral ones, one of them regularly arched to the apex and the other doubly sinuous, and the third, dorsally inserted, finer and rectilinear; well-developed membranous lamina, with the penicillum not very dense, but with long setae, and placoid sensilla.

Spermathecal complex (Fig. 314.2): Spermatheca with distinct and clearly spherical apical lobe; median region hyaline and basal lobe slightly larger in diameter and more sclerotized than median; in basal situation, there is a tiny nodule in which the spermatic duct is originating, which is about 18-20 times longer than the spermatheca and is inserted into the copulatory bag by means of a sclerotized piece in the shape of a hat; there is a spermathecal gland.

Female uroventrite VIII (Fig. 315.9): With a short and very fine spiculum.

Discussion. In Tree-1 *Trapezodirus* is the sister of *Trocharanis* with support of 80.6/40, and these in turn belong to the clade that includes the genera *Lagariella*, *Stygiophyes, Salgadoia* and *Naspunius* with support of 90.6/40 (Fig. 1A); both nodes show poor support (see *Trocharanis* discussion).

The species of which this genus consists have been subject to a taxonomic review published in the study by Fresneda *et al.* (1998). *Trapezodirus* is closely related to *Stygiophyes* the structure of the middle region of the endophallus, with the ventral and dorsal phanerae straight and parallel to each other, is fairly similar; however, in *Stygiophyes* the dorsal bags do not present an internal sclerotized nodule and the phanerae of the middle region are much finer and more slender, unlike the genus *Trapezodirus*. In *Trapezodirus* a very apparent sexual dimorphism is manifest and there is a curious secondary sexual character since they are not only different in the general shape, the protarsi and the antennal structure in both sexes, but also the males have a spiniform prolongation in the middle of the margin posterior of the metafemora, which is missing in females; this character is especially developed in *T. escollae.*

Distribution: Spain. The eight species of the genus are distributed throughout the Pyrenees and pre-pyrenees province of Huesca: in the foothills located between the River Ara to the west and the Noguera Ribagorçana to the east; from the Monte Perdido massif, near the Pyrenees watershed, to the north to the Sierra de la Carrodilla to the south (the last pre-pyrenean branch that precedes the Ebro depression). Auroux & Bellés (1974a) and Fresneda *et al.* (1998) provided two distribution maps of the genus.

Species

Trapezodirus altimontanus (Bellés, 1975)
Speonomus bolivari altimontanus Bellés, 1975: 49.
Trapezodirus altimontanus (Bellés): Fresneda, 1998: 59.

Trapezodirus arcticollis (Jeannel, 1911)
Speonomus cerberus arcticollis Jeannel, 1911b: 90.
Trapezodirus arcticollis (Jeannel): Fresneda, 1998: 59.

Trapezodirus bolivari (Martínez de la Escalera, 1898)
Bathyscia bolivari Martinez de la Escalera, 1898: 38.
Speonomus bolivari Escalera: Jeannel, 1908a: 300, 306.
Speonomus bolivari luciani Jeannel, 1911b: 92.
Trapezodirus bolivari (Martínez de la Escalera): Fresneda, 1998: 59.

Trapezodirus carrodillae (Jeannel, 1911)
Speophilus Carrodillae Jeannel, 1911b: 94.
Speophilus (*Trapezodirus) Carrodillae* Jeannel: Jeannel, 1924a: 173.
Speophilus carrodillae Jeannel: Español, 1966b: 20.
Troglocharinus (*Speophilus*) *carrodillae* (Jeannel): Escolà & Comas, 1983: 257.
Trapezodirus carrodillae (Jeannel): Fresneda, 1998: 59.

Trapezodirus cerberus (Jeannel, 1911)
Speonomus Cerberus Jeannel, 1911b: 88.
Trapezodirus cerberus (Jeannel): Fresneda, 1998: 59.

Trapezodirus escollae (Fresneda & Hernando, 1994)
Speonomus escollae Fresneda & Hernando, 1994a: 63.
Trapezodirus escollae (Fresneda & Hernando): Fresneda, 1998: 60.

Trapezodirus gimenezi (Fresneda, Hernando & Lagar, 1998)
Speonomus gimenezi Fresneda, Hernando & Lagar, 1998: 143.
Trapezodirus gimenezi (Fresneda, Hernando & Lagar): Fresneda, 1998: 60.

Trapezodirus orobios (Fresneda, Hernando & Lagar, 1998)
Trapezodirus orobios orobios (Fresneda, Hernando & Lagar, 1998)
Speonomus orobios Fresneda, Hernando & Lagar, 1998: 146.
Trapezodirus orobios orobios (Fresneda, Hernando & Lagar): Fresneda, 1998: 60.
Trapezodirus orobios robustus (Fresneda, Hernando & Lagar, 1998)
Speonomus orobios robustus Fresneda, Hernando & Lagar, 1998: 150.
Trapezodirus orobios robustus (Fresneda, Hernando & Lagar): Fresneda, 1998: 60.

Genus ***Trocharanis*** Reitter, 1885
Trocharanis Reitter, 1885a [1884]: 12.

Type species. *Antrocharis mestrei* Abeille de Perrin, 1878 by monotypy (habitus in Fig. 302.5).

Diagnosis. Size 4.0 mm. Pholeuonoid facies (Fig. 302.5), oblonged body-shape, slightly convex and with elytral margins regularly curved from one end to the other.

Antennae: Longer than the elytral suture and not thickened from the 7th antennomere.

Pronotum: As wide as long, with the greatest width in its middle part; it is very narrow in the basal half and with notched and subparallel lateral margins; straight base, with right posterior angles and protruding vertices.

Elytra: Narrow and elongated, with the maximum width located in the middle part, sides regularly curved and strongly acuminate towards the apices that are dehiscent; no parasutural stria; transverse striolae well marked and close.

Legs: Very long and slender in appearance; male protarsomeres very dilated, the first article being triangular and much wider than the distal end of the protibia; protibiae with two small simple outer spurs and very dense hair on inner side; mesotibiae and metatibiae straight, the latter with two simple spurs on the outer part of the apex; all tibiae without series of spines along outer side.

Mesoventral keel (Fig. 304.10): Reduced to a protrusion in the form of a sharp and narrow ridge located at the end of the middle part of the mesoventrite.

Suture of the metaventrite (Fig. 304.10): It delimits an area very narrow and arched that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 306.2): With the wings of the metascutum elongated and slightly widened in the middle, slightly protruding apophysis of the alacrista and pointed apices.

Metendosternite (Fig. 308.3): Furcal arms thin and somewhat shorter than the trunk, with the internal apical area somewhat arched and the apophysis poorly developed; posterior lamina of furca narrows sharply towards apical area of arms; furcal trunk nearly twice as long as wide at base and median keel diverging posteriorly.

Median lobe of aedeagus: In lateral view (Fig. 309.10), regularly curved, and with the apical region strongly sinuous and pointed with the tip oriented towards the dorsal face; in dorsal view (Fig. 310.4), sides in the basal half in regular arcs tapering in the apical half to almost straight, then in the apical area forming a small, somewhat curved, subtriangular blade with sharp apex. Basal lamina long and with narrower, arched sides ending at the junction of the basal margin in pointed apices; ventral lamina of tegmen somewhat shorter and broader.

Endophallus (Fig. 310.4): «Y»-piece with straight and divergent branches and its funnel-shaped structures seem to extend into fine muscle fibres along the sides of the sac towards the middle region; in this region there are some bifurcated dorsal phanerae at its lower end; one of the appendages extends into hyaline fibres towards the basal region; in the same place some floating pieces are present that are in contact with the funnel-shaped structures and there are also divergent ventral phanerae and a dorsal plate consisting of two robust phanerae; at the apical end of the middle region there is an axial piece formed by a tube; on both sides of the axial piece there are bags with an elongated sclerotized nodule inside; in the apical region there are reinforcement bands at the base of which, and overlapping with the dorsal bags, there is a tissue that covers them and that is densely covered with scales.

Parameres (Fig. 312.10): Somewhat thickened at apex, shorter than the median lobe; three setae are inserted at the apex, two long curved and a third finer rectilinear, one located on the opposite side to the others; membranous lamina short and inserted on the side; there is a dense penicillum of twisted setae.

Spermathecal complex: Long spermatheca (Fig. 314.3), with a spherical apical lobe and almost in the same layer than the middle region, which is hyaline and clearly inferior in section to that of the lobes; basal lobe long and somewhat thicker than apical lobe; both lobes clearly sclerotized; in the basal area of this lobe the duct and the spermathecal gland are inserted, no

nodule is observed; very long and thin spermatic duct with slightly thicker final section.

Female uroventrite VIII (Fig. 315.10): With the spiculum short, slightly widened and the apex truncated.

Discussion: In Tree-1 (Fig. 1A) *Trocharanis* is sister of *Trapezodirus* with a support of 80.6/40, and these in turn belong to the clade that includes the genera *Lagariella*, *Stygiophyes, Salgadoia* and *Naspunius* with support of 90.6/40. In Tree-2 (Fig. 2) this genus is sister of the clade *Ariejasia* gen. nov., *Paraspeonomus* and *Speonomus*, the main line of Leptodirini from the northern slope of the Pyrenees, although the node support is fairly low with 44.3/45. Although the position of *Trocharanis* is uncertain, there is indirect evidence that the Tree-2 topology may be somewhat more plausible:

– The geographical criterion: it is a genus from the northern Pyrenees just like the others. However, there are some isolated cases of trans-Pyrenean phylogenetic relationships among the Leptodirini such as *Bellesia* + *Machaeroscelis* or in the case of the Trechini (Carabidae) as shown by Faille *et al*. (2023) for *Aphaenops leschenaulti* Bonvouloir, 1862 + *Aphaenops linderi* Jeannel, 1938 + *Aphaenops catalonicus* Escolà & Canció, 1983.

– It seems that this genus was undergoing a similar radiation as it was found for *Aphaenops leschenaulti* Bonvouloir, 1862 (Carabidae, Trechini), the second most diverse hypogean group in this region. *Aphaenops* (*Pyreneotrechus*) *aldensis* (Jeannel 1955) is sister to all other *Aphaenops* species (Faille *et al*. 2023) and an endemic species of the Belesta area (France, Ariège) as is *Trocharanis*: *Aphaenops* (*Pyreneotrechus*) *aldensis* and *Trocharanis mestrei* cooccur in several caves. It could be that this region is the origin of all the hypogean coleoptera fauna, e.g. Leptodirini and Trechini of the northern slope of the Pyrenees. This fact indirectly supports the Tree-2 topology.

The differences in external morphology to *Trapezodirus* are very profound, but the same is not ture for the genital structures that is similar with the endophallus practically identical. The differences lie in the conformation of the apex of the parameres and in the shape of the median lobe of aedeagus. This is the second case that shows the existence of close evolutionary relationships between the northern and southern slopes of the Pyrenees. The here sister groups are found to be distributed in geographically distant regions with a territory separating them that is inhabited by other apparently unrelated Leptodirini. The other case is that of *Machaeroscelis* and *Bellesia.*

Distribution. France. Cavities of the massifs between the Aude and Hers rivers: Coudons and Rivel (Aude), and Bélesta (Ariège).

Species

Trocharanis mestrei (Abeille de Perrin, 1878)
Antrocharis Mestrei Abeille de Perrin, 1878: 152.
Trocharanis Mestrei Abeille: Reitter 1885 [1884]: 12.
Trocharanis mestrei (Abeille): Perreau, 2000: 331.

Genus ***Troglocharinus*** Reitter, 1908

Perrinia Reitter, 1885a [1884]: 16 (*Nom. praeocc*. by *Perrinia* Adams, 1853—Mollusca—) (Type species: *Adelops Kiesenwetteri* Dieck, 1869).
Troglophyes (*Troglocharinus*) Reitter 1908: 116.
Troglocharinus Reitter, 1908: Jeannel, 1910a: 34.
Antrocharidius Jeannel, 1910h: 283 (Type species: *Antrocharidius orcinus* Jeannel, 1910).
Speophilus Jeannel, 1911b: 93 (Type species: *Adelops kiesenwetteri* Dieck, 1869).

Type species. *Troglophyes ferreri* Reitter, 1908 by monotypy (habitus in Fig. 302.6).

Diagnosis. Size of 2.5-4.5 mm. Pholeuonoid or bathyscioid form with all intermediate stages. Fine, dense, tight and lying pubescence or sometimes longer and more erect setae can be found, especially in the terminal portion of the elytra.

Head: With a poorly marked complete occipital carina and the epistomal suture does not show any darker colouration.

Antennae: Very long, with the first six thin antennomeres, the 7th with a thick apex, the 8th again thin, and the last three thick.

Pronotum: Can be very narrow in the posterior third, having sinuous lateral margins, somewhat notched and subparallel in the basal half or regularly arched.

Elytra: Very long compared to the pronotum, in the pholeuonoid species, and proportionally shorter, in the bathyscioids; always more or less convex; there may be a faint obliterated parasutural stria on posterior half of elytra; integument marked by transverse striolae that can be rough and distant or thin and close together.

Legs: Very long; protibiae with two very small simple outer spurs and no series of spines on outer

side; mesotibiae straight and have two series of fine spines on the outer side; metatibiae straight, with two simple spurs on the outer part of the apex and a series of fine spines along the outer side.

Mesoventral keel: High in bathyscioid species, the anterior border being convex and the apex hooked, and absent or reduced to a small, more or less sharp prominence in pholeuonoid species (Fig. 304.11).

Suture of the metaventrite (Fig. 304.11): It delimits a very narrow and arched area that is only well defined in the anterior middle area.

Metatergal apparatus (Fig. 306.3): Very reduced, with the wings of the metascutum very narrow and without sutures; alacrista without apical nodule and very short basal apophysis with pointed apices.

Metendosternite (Fig. 308.4). Furcal arms very thin and as long as the trunk, with a short but well-developed apophysis; posterior lamina of the furca narrows so extremely that it almost disappears at apical area and arched posterior border; furcal trunk twice as long as wide at base and median keel with elongated posterior divergence.

Median lobe of aedeagus: In lateral view (Fig. 309.11), with a sharp obtuse or right-angled curve between the middle and apical third, although the curve may also be regular from one end to the other; it tapers progressively from the basal portion to the apex, which is pointed; there may be a slight preapical thickening and on the dorsal side a depression in the distal third with a very fine and prolonged end; the apical third of the sternal part may be somewhat sinuous. These structures adopt the shape of a funnel with the floating pieces at their upper end and accommodating the appendages of the dorsal phanerae of the middle region.

Endophallus (Fig. 311.7): In the basal region, the «Y»-piece is sinuous with divergent arms and, through a nodule, they articulated with the apical fibres of the «Y»-piece; these structures adopt funnel-shaped, with the floating pieces at their upper end and accommodating the appendages of the dorsal phanerae of the middle region; in the latter there are two thickened and bifurcated dorsal phanerae at its lower end; one of these appendages extends until it is touching the funnel-shaped structure, here a floating piece is accommodated in the cavity formed between both appendages that also contacts the same structure; there are also two ventral phanerae thickened at the bottom and divergent; two upper dorsal plates can be seen and each one of them has a thin and long outer phanera and an inner, more robust one, with the upper end bifurcated and each thickening folded in a different layer and very sclerotized; on both sides of the axial piece there are two large bags inside this are two highly sclerotized nodules and a long appendage at its lower end; in the apical region there are only the reinforcing bands and a bag located between them, furrowed with longitudinal wrinkles and thickened margins.

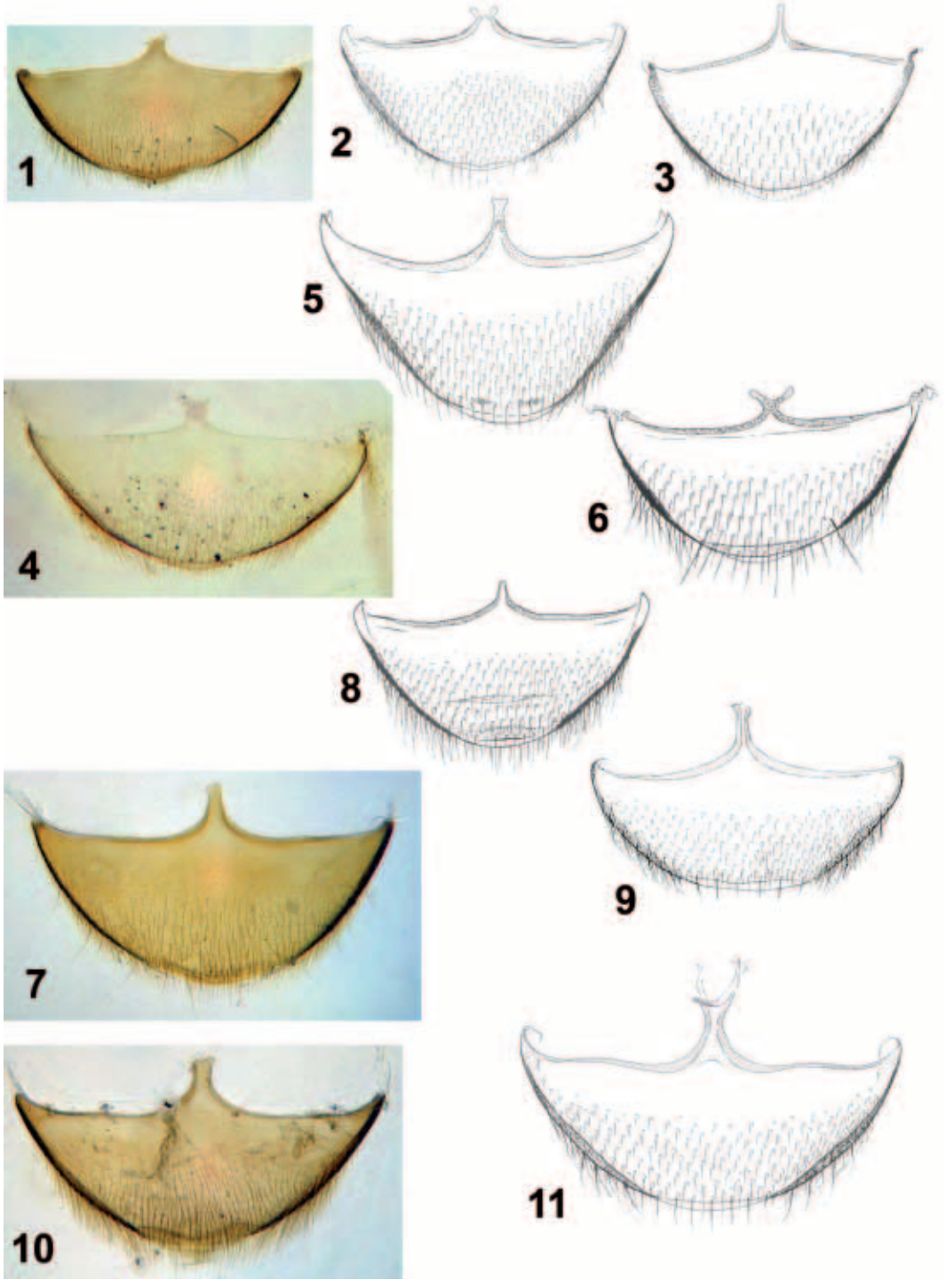
Parameres (Fig. 312.11): They do not reach the apex of the middle lobe; with two apical and one preapical insertion setae, the first two being long, robust and straight or arched and gently sinuous or sharply curved at different points; the third finer and can be as long as the others or much shorter and gently sinuous or subrectilinear; a highly developed membranous lamina also stands out, as long as half of the first two main setae, or short and trapezoidal; on the surface of the lamina, but especially on the margins, there is a highly developed penicillum that is only missing in *Troglocharinus orcinus;* near the apex some placoid sensilla are found.

Spermathecal complex (Fig. 314.4): The spermatheca can be long or very long, with the apical lobe spherical and folded or arranged in the same layer as the middle region; mid-region hyaline and clearly inferior in section to that of the lobes; basal lobe thick and progressively folded with respect to the middle region; both lobes sclerotized; in the basal part, the spermathecal gland and the spermatic duct are inserted, which is very long, between 40 and 70 times the length of the spermatheca, depending on the species; In general, both halves of the duct are differentiated but to a different degree with distinct diameters and the basal process of the copulatory bag is showing a different degree of development .

Female uroventrite VIII (Fig. 315.11): Spiculum wide and not very long; it may have a truncated or bifurcated apex.

Discussion. In the phylogenetic tree (Fig. 1B) the genus is well-supported with values of 95.3/100 and equally well suppported (95.4/100) it is found to be sister to the clade formed by *Ariejasia* gen. nov., *Lagariella*, *Naspunius*, *Paraspeonomus*, *Salgadoia*, *Speonomus*, *Stygiophyes*, *Trapezodirus*, and *Trocharanis*. This group includes most of the Pyrenean Leptodirini described so far. Partial phylogenies of the genus already existed and a large part of the sequences used come from those studies (Rizzo & Comas 2015; Rizzo *et al*. 2013, 2017; Fresneda *et al*. 2021). The trees provided in this study are consistent with these previous results.

This is a widely distributed genus with known representatives in many regions. This has led to the de-



FIGURES 315.1–315.11: *Speonomus* series, *Speonomus* group. Female uroventrite VIII of: (**1**) *Ariejasia carrerei* **comb. nov.**, (**2**) *Lagariella colominasi,* (**3**) *Naspunius eseranus,* (**4**) *Paraspeonomus vandeli,* (**5**) *Salgadoia brieti,* (**6**) *Speonomites velox,* (**7**) *Speonomus pyreneus,* (**8**) *Stygiophyes puncticollis,* (**9**) *Trapezodirus carrodillae,* (**10**) *Trocharanis mestrei,* (**11**) *Troglocharinus ferreri.* Figs **2**, **3**, **5**, **6**, **8**, **9**, **11** modified from Salgado *et al*. (2008).

scription of numerous infraspecific taxa in some species, most of them based on characters that are difficult to observe. This genus, defined by a specific model of the endophallus (Fresneda 1998), brings together the ancient *Troglocharinus, Speophilus, Antrocharidius* and a species that was described as *Speonomus*. Regarding these characters of the endophallus it is likely to be closely related to the genus *Speonomites*. The discovery of *T. (T.) ferreri pallaresi*, which exhibits a bell-shaped pronotum, was the first evidence that made Bellés (1973a) suspect that the relationship between the genera *Troglocharinus* and *Speophilus* were such that they should be possibly merged into one genus, subsequently Bellés *et al.* (1978) included *Speophilus* into the genus *Troglocharinus,*however, Escolà (1992) insisted on the «*Speophilus* and *Troglocharinus problem*» questioning the classification, finally Fresneda (1998) established the synonymy of both genera. Rizzo & Comas (2015) established the synonymy of *Antrocharidius* and later Fresneda *et al.* (2020) transfered to this genus several species of *Speonomites* that are located in the most basal cladogenesis of the genus. Zariquiey (1917) carried out the first comprehensive study of the genus when only four taxa were known. Alegre & Escolà (1983) provided a cytogenetic study of five species. The phylogenetic tree shows that the bathyscioid elements derive from the most basal cladogenesis of the genus. In the most basal position is *T. mengeli* (95.3/100), followed by *T. sendrai* (99.9/100), sister of *T. fadriquei* (100/100), followed by *T. mercedesi* (78.1/95) sister of *T. vinyasi* (93.9/96); later is the great pholeuonoid radiation of *Troglocharinus* with its two main clades (Rizzo *et al.* 2013):

- The Pyrenean clade: *T. fonti schuttei*, *T. fonti zariquieyanus*, *T. hustachei*, *T. impellitierii*, *T. quadricollis*, *T. senenti*, *T. subilsi*, *T. vivesi* and *T. bellesi* sp. nov.; presumably also *T. ludovici* and *T. rizzoae* sp. nov. for which there are no molecular data. *Troglocharinus fonti fonti* sister of *T. quadricollis* (100/100) is the sister of all the Mediterranean clade (76.5/100)

- The Mediterranean clade: *T. elongatus*, *T. espanoli*, *T. ferreri*, *T. jacasi*, *T. kiesenwetteri*, *T. olerdolai*, *T. orcinus*, *T. pallisei* and *T. patracoi*, several of them with different subspecies described; morphologically *T. schibii* also belong to this clade, species for which to date are no molecular data available.

Troglocharinus rovirai from the Huesca Pyrenees is a species only known from the holotype of which there are serious doubts about its origin. Type locality: Cueva de Don Macario in Burgasé, Huesca.

Two apomorphies have been identified:

– The antennae are longer than the body. This characteristic also occurs in *Speocharidius* of the Basque clade and other Leptodirini outside the Pyrenean-Catalan fauna.

– The legs are very long and this is especially apparent in the metafemora. This characteristic also occurs in *Speocharidius* from the Basque clade and other Leptodirini outside the Pyrenean-Catalan fauna.

Two synapomorphies have been found:

– At the apex of the parameres is a highly developed membranous lamina, as long as half of the first two main setae, and a highly developed penicillum with numerous long setae, except for *Troglocharinus orcinus* which lacks penicillum, only with few dispersed setae.

– The spermatic duct of the spermathecal complex is very long, between 40 and 70 times the length of the spermatheca, depending on the species; two parts of different diameter and a basal process with a more or less developed copulatory bag is present.

Given the topology of the phylogenetic tree, all the subspecies of *Troglocharinus elongatus* and even some of its synonyms (Bellés & Martínez 1980; Salgado *et al.* 2008; Fresneda & Salgado 2017) must be rearranged to recover the groups monophyly. All these taxa have independent geographical distribution areas which are clearly limited to different karstic massifs (Bellés & Martínez 1980); morphological differences between them exist and each morphological model can be attributed to a defined distribution area (Bellés & Martínez 1980). Depending on the personal criteria of each author, these differences have been assigned a certain value, representing the individual opinion. Consequently, they have been considered a species at one time or subspecies or synonym depending on the investigators view. A conservative ordination is proposed based on the study of Bellés & Martínez (1980) and on the phylogenetic tree (Fig. 1B):

– *Troglocharinus jacasi* VR22 (from type locality) it is the sister species of all the *Troglocharinus* of the Mediterranean ridges with high support, 99.8/100. *Troglocharinus elongatus arlai* VR15 (from type locality) + *T. elongatus pinyareti* VR38 (from type locality) are not included in the clade of the nominotypical subspecies and the morphological differences are evident (Zariquiey 1950; Lagar 1966), also the genetic distance between these last two is considerable, and being well supported in our analysis (98.3/100). It is proposed to change both taxa to the rank of good species: *T. arlai* and *T. pinyareti.* The remaining taxa of the *elongatus* complex are found to form a clado-

genic succession line, with little support, and incorporating species normally considered outside the complex such as *T. olerdolai* VR102; *T. roselli*.was described as a subspecies, at the when it was considered synonymous with *T. portai*. *T. roselli* AN139 in the new analysis was found to be sister to the clade formed by *T. portai* RA1176 + *T. ollai* VR17 (90.9/100, both from type locality) with a support of 94.8/100. Morphological differences among all these taxa are evident (Zariquiey 1950; Lagar 1952). It is proposed to conserve these taxa at the rank of subspecies, maintaining in part the classification of Bellés & Martínez (1980): *T. elongatus elongatus*, *T. elongatus mateui, T. elongatus olerdolai*, *T. elongatus ollai, T. elongatus portai* and *T. elongatus roselli.*

– *Trogloch*arinus *fonti s. l*. complex. *Trogloch*arinus *fonti schuttei* VR37 (from type locality) is the sister species of *T. impellitierii* IRC22 (from type locality) (96.8/100) and not of *T. fonti fonti* IRC26 (from type locality) which seems fairly unrelated and is included in another distant clade. The morphological differences between *T. fonti* and *T. schuttei* are evident (Español 1955) and *T. impellitierii* is considerably different from both. Consequently *Trogloch*arinus *schuttei* is raised to the rank of *bona species.* The same happens with *T. fonti zariquieyanus* AF30, which is at the base of the previous two with 68.2/100 support; this taxon is also elevated to the rank of *bona species*: *Trogloch*arinus *zariquieyanus*.

– *Trogloch*arinus *kiesenwetteri s. l.* complex. *Trogloch*arinus *kiesenwetteri andresi* VR13 is the sister species (95/100) of *T. kiesenwetteri sanllorensi* VR11 + (*T. patracoi* VR16,from type locality + T. *kiesenwetteri kiesenwetteri* VR39,from type locality) (support 49.4/100). Given that the morphological differences are evident and especially striking in *T. patracoi* with respect to the others, they will therefore all be treated with the rank of *bona species*: *T. andresi, T. kiesenwetteri, T. sanllorensi* and *T. patracoi*. All these changes are referred to in the list of species.

Distribution. Spain. They colonise Catalunya, basically in two well-defined and distant areas. One of them, relevant due to the high density of karstic phenomena and high number of taxa in this group, is located in the Garraf massif (Catalan coastal mountains), the mountains that extend to the north of the Penedés depression, between the lower Llobregat river and upper Gaià river,in addition the cluster of massifs including the Sant Llorenç del Munt, Serra de l'Obac and Montserrat. The second part extends through higher altitude foothills in the Pre-Pyrenees and includes the Serra del Montsec de Rubies, the northern areas of the Serra del Boumort, the region of Alt Urgell to the east and the Serra de Lleràs to the west, all of these foothills are located in the province of Lleida. Lastly, there is a species considerably isolated to the west from the rest of species related to it, which inhabits a cavity in upper Aragon, *T. rovirai*; however, there are serious doubts about the origin of this insect. Escolà (1974) also announced the discovery of a species close to *T. fonti* in foothills near Escuaín, Huesca; here also the author expressed doubts about the origin of these insect.

Species

Troglocharinus abenzai (Lagar, 1972)
Speophilus abenzai Lagar, 1972: 38.
Troglocharinus variabilis abenzai (Lagar): Bellés & Martínez, 1980: 228.
Troglocharinus (*Troglocharinus*) *variabilis abenzai* (Lagar): Fresneda, 1998: 64.
Troglocharinus (*Troglocharinus*) *elongatus abenzai* (Lagar): Salgado, Blas & Fresneda, 2008: 657.

Troglocharinus andresi (Escolà, 1966) stat. nov.
Speophilus kiesenwetteri andresi Escolà, 1966: 200.
Troglocharinus (*Troglocharinus*) *kiesenwetteri andresi* (Escolà): Fresneda, 1998: 63.

Troglocharinus arlai Zariquiey, 1950: 199 stat. nov.
Troglocharinus españoli arlai Zariquiey, 1950: 199.

Troglocharinus bellesi sp. nov. (see Appendix New Species)

Troglocharinus elongatus Zariquiey, 1950
Troglocharinus elongatus elongatus Zariquiey, 1950
Troglocharinus españoli elongatus Zariquiey, 1950: 200.
Troglocharinus españoli Zariquiey, 1950: 192 (non Jeannel, 1930).
Troglocharinus (*Troglocharinus*) *variabilis* Bellés, 1978: 17 (*Nomen novum*).
Troglocharinus (*Troglocharinus*) *variabilis elongatus* Zariquiey: Bellés, 1978: 17.
Troglocharinus (*Troglocharinus*) *elongatus elongatus* Zariquiey: Salgado, Blas & Fresneda, 2008: 653.
Troglocharinus elongatus mateui Zariquiey, 1950
Troglocharinus españoli mateui Zariquiey, 1950: 200.
Troglocharinus (*Troglocharinus*) *variabilis mateui* Zariquiey: Bellés, 1978: 17.
Troglocharinus (*Troglocharinus*) *elongatus mateui*

Zariquiey: Salgado, Blas & Fresneda, 2008: 657.
Troglocharinus elongatus olerdolai Lagar, 1952
Troglocharinus espanoli olerdolai Lagar, 1952: 79.
Troglocharinus (*Troglocharinus*) *olerdolai* Lagar: Fresneda, 1998: 63.
Troglocharinus elongatus ollai Zariquiey, 1950
Troglocharinus español ollai Zariquiey, 1950: 199.
Troglocharinus (*Troglocharinus*) *variabilis ollai* (Zariquiey): Bellés, 1978: 17.
Troglocharinus (*Troglocharinus*) *elongatus ollai* Zariquiey: Salgado, Blas & Fresneda, 2008: 657.
Troglocharinus elongatus portai Zariquiey, 1950
Troglocharinus español portai Zariquiey, 1950: 197.
Troglocharinus (*Troglocharinus*) *variabilis portai* (Zariquiey): Bellés, 1978: 17.
Troglocharinus (*Troglocharinus*) *elongatus portai* Zariquiey: Salgado, Blas & Fresneda, 2008: 657.
Troglocharinus elongatus roselli Lagar, 1952
Troglocharinus espanoli roselli Lagar, 1952: 77.

Troglocharinus espanoli (Jeannel, 1930)
Speophilus (s. str.) *Español* Jeannel, 1930a: 91.
Troglocharinus (Speophilus) *espanoli* (Jeannel): Escolà, 1982: 187.
Troglocharinus (*Troglocharinus*) *espanoli* (Jeannel): Fresneda, 1998: 63.

Troglocharinus fadriquei Fresneda, Rizzo, Comas & Ribera, 2020
Troglocharinus fadriquei Fresneda, Rizzo, Comas & Ribera, 2020: 166.

Troglocharinus ferreri (Reitter, 1908)
Troglocharinus ferreri abadi Lagar, 1981
Troglocharinus Ferreri Abadi Lagar, 1981: 28.
Troglocharinus ferreri abadi Lagar: Fresneda, 1998: 63.
Troglocharinus ferreri ferreri (Reitter, 1908)
Troglophyes (*Troglocharinus*) *Ferreri* Reitter, 1908c: 116.
Troglocharinus Ferreri Codinai Zariquiey, 1917: 291.
Troglocharinus Ferreri Jeanneli Zariquiey, 1917: 289.
Troglocharinus Ferreri Fonti Zariquiey, 1924: 17 (*Nom. praeocc.* by *Troglocharinus fonti* (Jeannel, 1910). Since it is a molecularly proven synonym, no replacement name is proposed.
Troglocharinus Ferreri Zariquieyi Jeannel, 1924b: 17.
Troglocharinus (*Troglocharinus*) *ferreri ferreri* (Reitter): Fresneda, 1998: 63.
Troglocharinus ferreri pallaresi Bellés, 1973
Troglocharinus ferreri pallaresi Bellés, 1973a: 45.
Troglocharinus (*Troglocharinus*) *ferreri pallaresi* Bellés: Fresneda, 1998: 63.

Troglocharinus fonti (Jeannel, 1910)
Troglocharinus fonti fonti (Jeannel, 1910)
Perrinia fonti Jeannel, 1910b: 160.
Speophilus fonti (Jeannel): Jeannel, 1911b: 93.
Speophilus (*Trapezodirus*) *fonti* (Jeannel): Jeannel, 1924a: 172.
Troglocharinus fonti (Jeannel): Bellés, 1987: 159.
Troglocharinus (*Troglocharinus*) *fonti fonti* (Jeannel): Fresneda, 1998: 63.
Troglocharinus fonti infernus (Jeannel, 1911)
Perrinia Fonti inferna Jeannel, 1911a: 364.
Speophilus Fonti infernus (Jeannel): Jeannel, 1914b: 30.
Speophilus (*Trapezodirus*) *Fonti infernus* (Jeannel): Jeannel, 1924a: 172.
Troglocharinus (*Troglocharinus*) *fonti infernus* (Jeannel): Fresneda, 1998: 63.

Troglocharinus hustachei Jeannel, 1911
Troglocharinus Hustachei Jeannel, 1911b: 96.
Troglocharinus (*Troglocharinus*) *hustachei* Jeannel: Fresneda, 1998: 63.

Troglocharinus impellitierii Español, 1955
Troglocharinus hustachei impellitierii Español, 1955: 270.
Troglocharinus impellitierii Español: Español, 1966a: 7.
Troglocharinus (*Troglocharinus*) *impellitierii* Español: Fresneda, 1998: 63.

Troglocharinus jacasi (Lagar, 1966)
Speophilus jacasi Lagar, 1966: 29.
Troglocharinus (*Speophilus) jacasi* (Lagar): Escolà, 1982: 187.
Troglocharinus (*Troglocharinus*) *jacasi* (Lagar): Fresneda, 1998: 63.

Troglocharinus kiesenwetteri (Dieck, 1869)
Adelops Kiesenwetteri Dieck, 1869b: 350.
Perrinia Kiesenwetteri (Dieck): Reitter, 1885a [1884]: 16.
Speophilus Kiesenwetteri (Dieck): Jeannel, 1911b: 93.
Troglocharinus kiesenwetteri (Dieck): Bellés, 1987: 159.
Troglocharinus (*Troglocharinus*) *kiesenwetteri kiesenwetteri* (Dieck): Fresneda, 1998: 63.

Troglocharinus ludovici Bellés & Déliot, 1983
Troglocharinus ludovici Bellés & Déliot, 1983: 241.
Troglocharinus (*Troglocharinus*) *ludovici* Bellés & Déliot: Fresneda, 1998: 63.

***Trogloch**arinus mengeli* (Jeannel, 1910)
Speonomus (*Speonomus*) *mengeli* Jeannel, 1910b: 154.
Speonomites mengeli (Jeannel): Fresneda, 1998: 67.
*Trogloch**arinus mengeli* Fresneda, Rizzo, Comas & Ribera, 2020: 169.

***Trogloch**arinus mercedesi* (Zariquiey, 1922)
Speonomus mercedesi Zariquiey, 1922: 161.
*Trogloch**arinus mercedesi* Fresneda, Rizzo, Comas & Ribera, 2020: 176.

***Trogloch**arinus orcinus* (Jeannel, 1910)
***Trogloch**arinus orcinus acevedoi* (Español, 1953)
Antrocharidius orcinus acevedoi Español, 1953: 94.
*Trogloch**arinu*s (*Antrocharidius*) *orcinus acevedoi* (Español): Fresneda, 1998: 65.
*Trogloch**arinus orcinus acevedoi* (Español): Rizzo & Comas, 2015: 109.
***Trogloch**arinus orcinus figuerai* (Lagar, 2011)
Antrocharidius orcinus figuerai Lagar, 2011 [2010]: 89.
*Trogloch**arinus orcinus figuerai* (Lagar): Rizzo & Comas, 2015: 109.
***Trogloch**arinus orcinus lagari* (Español, 1953)
Antrocharidius orcinus lagari Español, 1953: 93.
*Trogloch**arinus* (*Antrocharidius*) *orcinus lagari* (Español): Fresneda, 1998: 65.
*Trogloch**arinus orcinus lagari* (Español): Rizzo & Comas, 2015: 109.
***Trogloch**arinus orcinus orcinus* (Jeannel, 1910)
Antrocharidius orcinus Jeannel, 1910h: 284.
*Trogloch**arinus* (*Antrocharidius*) *orcinus orcinus* (Jeannel): Fresneda, 1998: 65.
*Trogloch**arinus orcinus orcinus* (Jeannel): Rizzo & Comas, 2015: 109.

***Trogloch**arinus pallisei* Rizzo & Comas, 2015
*Trogloch**arinus pallisei* Rizzo & Comas, 2015: 3.

***Trogloch**arinus patracoi* (Zariquiey, 1922)
Speophilus Kiesenwetteri Patracoi Zariquiey, 1922: 162.
*Trogloch**arinus patracoi* (Zariquiey): Bellés, 1987: 159.
*Trogloch**arinus* (*Trogloch**arinus*) *patracoi* (Zariquiey): Fresneda, 1998: 63.

***Trogloch**arinus pinyareti* Zariquiey, 1950 stat. nov.
*Trogloch**arinus españoli pinyareti* Zariquiey, 1950: 201.
*Trogloch**arinus* (*Trogloch**arinus*) *variabilis pinyareti* (Zariquiey): Bellés, 1978: 17.
*Trogloch**arinus* (*Trogloch**arinus*) *elongatus pinyareti* Zariquiey: Salgado, Blas & Fresneda, 2008: 656.

***Trogloch**arinus quadricollis* (Jeannel, 1911)
Speophilus quadricollis Jeannel, 1911b: 95.
*Trogloch**arinus quadricollis* (Jeannel): Bellés, 1987: 159.
*Trogloch**arinus* (*Trogloch**arinus*) *quadricollis* (Jeannel): Fresneda, 1998: 63.

***Trogloch**arinus rizzoae* sp. nov. (see Appendix New Species)

***Trogloch**arinus rovirai* Lagar, 1975
*Trogloch**arinus rovirai* Lagar, 1975: 45.
*Trogloch**arinus* (*Trogloch**arinus*) *rovirai* Lagar: Fresneda, 1998: 63.

***Trogloch**arinus schibii* (Español, 1972)
Speophilus schibii Español, 1972a: 56.
*Trogloch**arinus* (*Speophilus*) *schibii* (Español): Bellés, 1978: 17.
*Trogloch**arinus* (*Trogloch**arinus*) *schibii* (Español): Fresneda, 1998: 64.

***Trogloch**arinus sanllorensi* (Zariquiey, 1924) stat. nov.
Speophilus kiesenwetteri San Llorensi Zariquiey, 1924: 10.
Speophilus Kiesenwetteri Castellsaperai Zariquiey, 1924: 10.
*Trogloch**arinus* (*Trogloch**arinus*) *kiesenwetteri sanllorensi* (Zariquiey): Fresneda, 1998: 63.

***Trogloch**arinus sendrai* Fresneda, Rizzo, Comas & Ribera, 2020
*Trogloch**arinus sendrai* Fresneda, Rizzo, Comas & Ribera, 2020: 165.

***Trogloch**arinus senenti* Escolà, 1967
*Trogloch**arinus senenti* Escolà, 1967: 85.
*Trogloch**arinus* (*Trogloch**arinus*) *senenti* Escolà: Fresneda, 1998: 64.

***Trogloch**arinus schuttei* (Español, 1955) stat. nov.
Speophilus fonti schüttei Español, 1955: 268.
*Trogloch**arinus* (*Trogloch**arinus*) *fonti schüttei* (Español): Fresneda, 1998: 63.

***Trogloch**arinus subilsi* (Español, 1966)
Speophilus subilsi Español, 1966a [1965]: 5.
*Trogloch**arinus subilsi* (Español): Bellés, 1987: 159.

Troglocharinus (*Troglocharinus*) *subilsi* (Español): Fresneda, 1998: 64.

Troglocharinus vinyasi (Escolà, 1971)
Speonomus vinyasi Escolà, 1971: 32.
Troglocharinus (*Troglocharinus*) *vinyasi* (Escolà): Fresneda, 1998: 64.

Troglocharinus vivesi Comas, 2023
Troglocharinus vivesi Comas, 2023: 143.

Troglocharinus zariquieyanus Salgado, Blas & Fresneda, 2008 stat. nov. (*Nom. praeocc*. by *Troglocharinus fonti zariquieyi* (Jeannel, 1924). Replacement name by homonymy of *T. fonti zariquieyi* Jeannel, 1924 with *T. ferreri zariquieyi* Jeannel, 1924.
Speophilus (*Trapezodirus*) *Fonti Zariquieyi* Jeannel, 1924a: 172.
Troglocharinus (*Troglocharinus*) *fonti zariquieyi* (Jeannel): Fresneda, 1998: 63.
Troglocharinus (*Troglocharinus*) *fonti zariquieyanus* Salgado, Blas & Fresneda, 2008: 665.

Enigmatic species

Speonomus ellipticus Jeannel, 1924
Speonomus (s. str.) *ellipticus* Jeannel, 1924b: 15.

Type locality. «*forat La Bou, à Serradell, partido de Tremp, prov de Lerida*» (Jeannel 1924b). Only the female holotype is known of this species; since the year of its description it has not been found again and its identity and affinities are uncertain.

Speonomus fugitivus (Reitter, 1885)
Bathyscia (*Bathyscia*) *fugitiva* Reitter, 1885a [1884]: 35.
Speonomus fugitivus Reitter: Jeannel, 1908a: 300.
Speonomus (s. str.) *fugitivus* Reitter: Jeannel, 1910a: 34.

Type locality. «*Catalonien, in den Grotten des Montserrat*» (Reitter 1885). Jeannel (1911a) having studied the type, he indicates that it should be included in section 3 of the genus *Speonomus* of French distribution. In his review it is mentioned and doubts are expressed about the origin of the insect. Reitter's data (1885) have been repeatedly cited by different authors: Martínez de la Escalera (1898, 1899), Jeannel (1911a, 1914, 1924a), Codina (1924), Fuente (1925), Español (1956), Escolà (1986, 1998), Perreau (2000) or Salgado *et al*. (2008).

Leptodirini *Nomen nudum*

Adelops hispanus Abeille de Perrin, 1878
Adelops Hispanus Abeille de Perrin, 1878: 146 (*Nomen nudum*).

It is impossible to know which Coleoptera E. Abeille de Perrin is referring to, since he did not offer a formal description of this taxon. The type locality «South of Spain» suggests that it is likely not to be a Leptodirini.

Cholevinae *Incertae Sedis*: Genera *Coreobathyscia* and *Proleptodirina*

There are two further poorly known non-Mediterranean genera currently included in Leptodirini, both of them from Palaearctic East Asia: *Coreobathyscia* and *Proleptodirina*. The hypothesis of Fresneda *et al*. (2011b) is that the subtribe Leptodirini (excl. Platycholeina) comprises mostly subterranean species geographically restricted to the north Mediterranean basin, with the eastern-most species occuring in the north of Iran. Such a hypothesis is consistent with the biogeographic pattern suggested for the blind Raymondionymidae weevils (Grebennikov 2010).

But the hypothesis of Fresneda *et al*. (2011b) apparently is not confirmed by the results of this molecular phylogeny, since *Sinobathyscia*, also from the eastern Palaearctic, is a Leptodirini, sister genus to the *Drimeotus* clade (Apuseni mountains in Romania) with high support 97.9/100 (Fig. 1D), however, doubts have been expressed about the origin of these specimens (see the discussion section on *Sinobathyscia*). The other presumed Leptodirini from the eastern Palaearctic, *Fusi* Perkovsky, 1989 and *Sciaphyes* Jeannel, 1910, were already excluded from the tribe showing that the former must be included in Cholevini and the latter gives its name to a sister tribe of Anemadini (Fresneda *et al*. 2011b), or a set of genera from various other tribes: in Tree-1 (Fig. 1D) *Sciaphyes* is sister of *Fusi* + Cholevini + Eunemadina + Paracatopina with support 97.8/99. These exclusions have stimulated the study of the other two genera, *Coreobathyscia* and *Proleptodirina*, for which to us their affiliation to the Leptodirini is doubtful. The detailed study of the original descriptions reveals characters which have gone unnoticed e.g. which might not have been sufficiently taken into account, that clearly distinguish them from this tribe. Even so, summarised descriptions from the papers of Szymczakowski (1975) and Perkovsky (1998) are provided. It has not been possible to study specimens of these species morphologically or obtain material for molecular analysis.

Genus ***Coreobathyscia*** Szymczakowski, 1975
Coreobathyscia Szymczakowski, 1975: 464.

Type species. *Coreobathyscia solivaga* Szymczakowski, 1975 by original designation.

Diagnosis (Szymczakowski 1975**)**. Small size of 2.0-2.2 mm. Body broad, ovoid and slightly convex; bathyscioid facies. Brownish, dark colouration. Golden, fine, short, dense and lying down pubescence. Apterous. Integument with a fine and diffuse microsculpture.

Head: Small, very finely dotted with blurred occipital carina, especially in the middle area; last two maxillary palpomeres of subequal in length; anophthalmous.

Antennae: Quite short with the first two antennomeres subequal, the 1st being slightly thicker; 1st and 2nd antennomere as thick as the 3rd, 4th and 5th; the 3rd somewhat longer than each of the 4th, 5th and 6th antennomere, this one transverse like the 8th; slightly thickened club, being the 9th and 10th antennomeres subquadrate and the 11th as long as the sum of lengths of the 9th and 10th.

Pronotum: Short and very transverse, almost twice as wide as long, with the greatest width near the base that is as wide as the basal area of the elytra; sides regularly arched, the basal margin being very slightly concave; posterior vertices blunt and somewhat protruding backward, and angles acute; very fine punctation.

Elytra: Ovoid, not welded, slightly convex and quite elongate, one-third as long as wide, with greatest width near the base; sides slightly arched, tapering gradually towards apical area which is somewhat sinuous and the apices subtruncated; sculpture formed by fine and close transverse striolae, more evident in the lateral areas; there is no parasutural stria.

Legs: Slender and quite long. Males with pentamerous protarsi slightly dilated; protibiae provided with a simple internal spur, another ventral and three external ones, of which the middle one is highly developed, as well as spines on the distal half of the external edge, but there is no apical comb, not even on the external edge; mesotibiae somewhat arched and metatibiae straight, on both the external edges with pubescence and between the hairs short and fine spines, in addition to four simple spurs, two external and two internal; no apical basket; simple, long and thin claws.

Mesoventral keel (Szymczakowski 1975: Fig. 3): High and triangular, with the anterior border convex in the basal part and rectilinear in the apical part, the vertex being sharp and the angle a little obtuse; the posterior or ventral border is wide, straight, not crenulated and with setae; the mesoventral process is continuous with the metaventrite, with a suture in the junction area.

Suture of the metaventrite, *metatergal apparatus* and *metendosternite*: Unknown.

Median lobe of aedeagus (Szymczakowski 1975: Fig. 4): Small. In lateral view, slightly arched. In dorsal view, broad with parallel sides that strongly taper at the top, forming a triangular structure with a blunt apical vertex. Basal lamina clearly shorter than the median lobe, with parallel sides up to the distal area, which appears widened.

Endophallus (Szymczakowski 1975: Fig. 4): Unarmed, without sclerotized pieces.

Parameres (Szymczakowski 1975: Fig. 4): Longer than the median lobe, slightly curved inwards and slightly dilated throughout the apical third, the apex attenuated; armed with five long setae that are inserted in the distal area, one at the apex, two inserted very close by, one on the outside and one on the inside, the other two distant, the closest to the apical area on the outer surface and the one furthest in the interior. Ventral lamina of tegmen somewhat shorter and broader than the basal lamina.

Female: Unknown.

Discussion. Szymczakowski (1975) pointed out that it is difficult to establish which are the closest relatives of this genus as it does not appear to be related to the genera it was considered to be related to by that time, which were Bathysciinae, *Sciaphyes* (Sciaphyini) and *Platycholeus* (Leptodirini). Szymczakowski (1975) indicated that *Coreobathyscia* should be included in the Bathysciini tribe and the Euryscapes group, as the first antennomere is as long as the second, the males protarsi pentamerous, the protibiae without a comb and the meso- and metatibiae without a apical crown. For their part, Casale *et al*. (1991a) associated five genera found outside the western Palaearctic region with subtribes of Leptodirini, these were: *Sciaphyes*, *Coreobathyscia* and *Fusi*, from eastern Asia; *Platycholeus*, from western North America; and *Neotropospeonella*, from Venezuela. Newton (1998), based on the original description, places *Coreobathyscia* in the subtribe Pholeuina, as did Perreau (2000).

The original description did not indicate what characters link *Coreobathyscia* to the Leptodirini, it is assumed that it is possibly due to its general appearance and the characters that allow it to be placed

within the tribe were used ignoring other characters contradicting this classification. Just like the characters that coincide with Leptodirini-typical characters have not been described, there were also two characters that indicate that this genus could belong to the Cholevini:

– The maxillary palps with the last two palpomeres of subequal length. The last palpomere is shorter than the penultimate in Anemadini, Leptodirini, Ptomaphagini and Sciaphyini, while in Cholevini the last two palpomeres are subequal or the last one is only slightly shorter than the second one.

– All tibial spurs, internal and external, are simple. The bifid, pectinate, or polydentate inner spur is characteristic and exclusive to the tribe Leptodirini excluding *Platycholeus*, the most basal element with a plesiomorphic status in numerous characters, and *Anthroherpon* whose spurs are simple (a character reversal in a highly derived genus with numerous strongly divergent characters with all other Leptodirini).

In conclusion, it is very probable that this genus does not belong to the Leptodirini tribe but to the Cholevini tribe. One Anemadini – *Micronemadus pusillimus* (Kraatz, 1877) –, 11 Cholevini (two *Sciodrepoides* Hatch, 1933, eight *Catops* Paykull, 1798, one *Catopodes* Portevin, 1914 (Nishikawa & Cho 2000), and one Ptomaphagini – *Ptomaphagus* (*Ptomaphagus*) *sibiricus* Jeannel, 1934 – (Wang *et al*. 2016) are known from South Korea.

Distribution. South Korea. Only the data of the Kungkolgul cave is known.

Species

Coreobathyscia solivaga Szymczakowski, 1975
Coreobathyscia solivaga Szymczakowski, 1975: 464.

Genus ***Proleptodirina*** Perkovsky, 1998
Proleptodirina Perkovsky, 1998: 9.

Type species. *Proleptodirina kurbatovi* Perkovsky, 1998 by original designation.
Diagnosis (Perkovsky 1998). Small size 1.6-2.0 mm. Broad, ovoid and highly convex body shape; bathyscioid facies. Dark reddish colouration. Yellowish pubescence, made up of short, lying hairs. Thick head, slightly wider than long, without occipital carina and weak microsculpture.

Head: With small and pigmented eyes.

Antennae: Short, not reaching the base of the pronotum; first antennomere longer and as thick as the second; differentiated club with 8th, 9th and 10th antennomeres transverse; the 11th antennomere as long as the sum of 9th and 10th lengths.

Pronotum: Very convex and very transverse, almost twice as wide as long; sides regularly arched with greatest width at base as wide as the elytra; posterior vertices blunt and somewhat rearward on sides of the elytra; acute angles; surface with fine curved streaks and small granules between them.

Elytra: Convex, ovoid and short, 1.1-1.2 times longer than wide overall; maximum width towards the basal part; lateral margins regularly rounded and not narrowed apically, apices subtruncated; stronger transverse striolation on front half of the elytra; without parasutural stria.

Legs: Short and quite robust. Males protarsi pentamerous and slightly dilated, tetramerous and gracile in females; protibiae with external and internal spurs and without a comb on the apical and external edges but with spines; meso- and metatibiae with internal and external spurs and spines on external edges, longer in metatibiae.

Mesoventral keel: High and triangular; narrow edges, the anterior straight and the ventral rectilinear, somewhat thicker in the middle part; the posterior process does not exceed the mesocoxae.

Median lobe of aedeagus (Perkovsky 1998: Figs. 2-3): Relatively long with around 0.6 mm and robust. In lateral view thick, with the dorsal edge in a smooth regular arc and the more sinuous ventral edge with a distinctive concavity towards the middle; the apical area short and not very pointed. In dorsal view has subparallel sides up to the apical area that narrows to form a beak or trapezoidal prolongation with subarched sides and a rounded apex. The basal lamina short and the posterior margin in a regular arc.

Endophallus (Perkovsky 1998: Fig. 2): Basal region with a sclerotized «U»-shaped piece and a small flagellum oriented upwards and inserted at the base of the piece; in the middle region there are small grouped spines.

Parameres (Perkovsky 1998: Fig. 2): Thin with the apical area slightly arched inwards, shorter than the median lobe, without a distinct club and armed with two very short setae inserted at the apex.

Spermathecal complex (Perkovsky 1998: Fig. 4): Small spermatheca, 0.1 mm. With three well differentiated regions, the apical lobe well sclerotized and formed by two rings; the junction part short, hyaline, but well differentiated; the thickest basal lobe, well sclerotized, and formed by three rings; spermathecal gland not seen.

Suture of the metaventrite, *metatergal apparatus*, *metendosternite* and *female uroventrite VIII*: Unknown.

Discussion. *Proleptodirina* is a monotypic genus known from specimens collected from leaf litter in the Ussuri Reserve, Primorsky Krai, Russian Far East. The author limited himself to comparing the species with *Fusi* (Cholevini) and *Coreobathyscia*, the geographic neighbours of *Proleptodirina*, at that time belonging to the Bathysciinae. The combination of pentameric male and tetrameric female protarsi, and the lack of a lateral row of spines on the protibiae or an apical crown of spines on the mesotibiae and metatibiae, suggests its possible placement in the subtribe Pholeuina (*sensu* Perreau 2000) in the case that it really is a Leptodirini. But there are characters, which until now have gone unnoticed, which suggest that it should be excluded from this tribe. Their affinities are uncertain.

– The third maxillary palpomere is cone-shaped, equal in length to the second but much narrower. Only in Cholevini the last two palpomeres are equal in length or else the last is only slightly shorter than the second; in the other tribes, including Leptodirini, the last palpomere is clearly shorter than the penultimate. On the other hand, the last long palpomere, but much thinner than the penultimate one, associates this species with Ptomaphagini.

– Figure 2 of Perkovsky (1998) shows, not without difficulty, that there seem to be transverse striolae on the pronotum: they can be seen in the photograph in the lower left corner of the pronotum. This characteristic is specified in the description of the pronotum: «Поверхность с тонкими изогнутыми черточками и мелкими бугорками между ними» [«Surface with fine, curved streaksand small tubercles between them»] (Perkovsky 1998), the first of the characters unequivocally associates *Proleptodirina* with Ptomaphagini. In Leptodirini only in *Purkynella* the pronotum disc is transversally striolated in the basal part.

– The spermatheca is ringed (Perkovsky 1998: Fig. 4) with an exclusive structure and totally different from «type 1» of Perreau (1989), universally found in Leptodirini; in fact, it does not correspond to any of the models proposed by this author and it does not seem as if it can be associated with Leptodirini. However, there is a certain similarity with the spermatheca of *Baryodirus hammondi* Perreau, 2000 (Ptomaphagini), which is also ringed but not divided into three regions (Perreau 2000: Fig. 41).

Everything leads to the exclusion of *Proleptodirina* from the Leptodirini and its inclusion in the Ptomaphagini, and given the structure of the aedeagus apparently not coincident (from the figures of Perkovsky 1998: (Figs. 2-3) with the generalized pattern in Ptomaphagini, possibly for this genus a new subtribe would have to be established. But given that the spermatheca closely resembles that of *Baryodirus*, the genus for which Perreau (2000) established the Baryodirina subtribe, and that this species was described on a single female specimen, so the aedeagus of the male of the species is unknown, it could be that *Proleptodirina* would have to be included in Baryodirina. Therefore, until a male of *Baryodirus hammondi* is studied, it is not possible to know if *Proleptodirina* should be included in Baryodirina or if a new subtribe should be established.

Distribution. Genus monotypic. The specimens were collected from forest leaf litter in Kamenushka village at southern part of the Russian Far East (Perkovsky 1998).

Species

Proleptodirina kurbatovi Perkovsky, 1998
Proleptodirina kurbatovi Perkovsky, 1998: 10.

Sister and outgroups: other Leiodidae

The phylogenetic tree provided (Figs 1J, 1K) contains relevant data on the classification of the family and should be commented on. There are not enough data on sister or outgroups of Leptodirini to address taxonomic changes at the tribal or subfamily level. Even isolated genera change places in the phylogenetic tree leaving the tribe or subfamily to which they had been assigned to join other tribes or subfamilies.

The most evident taxonomic inconsistencies observed are the following:

1. *Catops americanus* Hatch, 1928, it must be transferred to the genus *Cholevinus* Reitter, 1901; the node between the sister species *Cholevinus pallidus pallidus* (Ménétriés, 1832) and *Catops americanus* is well supported: 91.6/90.

2. *Catops ventricosus rotundatus* Szymczakowski, 1963 is the sister species of *Catops tristis* (Panzer, 1794) with support 99.9/100; in consequence is a good species clearly independent of *Catops ventricosus* (Weise, 1877); taxonomic status changed: *Catops rotundatus* Szymczakowski, 1963 *bona species*.

3. *Sciodrepoides* Hatch, 1933 is a derived group within the large *Catops* clade with support 100/100;

therefore these two genera are synonymous or *Sciodrepoides* could be preserved, but in this case a genus would have to be described for *Catops angustitarsis* (Reitter, 1896) + *Catops geomysi* Peck & Skelley, 2001; a second option is transferred this species to the genus *Sciodrepoides*. The genus *Catops* has more than 140 species, of which only 21 have been used in molecular analysis. Adding those not studied would most likely lead to changes in the topology of the clades. For this reason, no taxonomic change is proposed. With sufficient data it might be possible, and perhaps even advisable, to break *Catops* into a few genera.

4. The long genetic distance between *Sciodrepoides watsoni watsoni* (Spence, 1815) (RA572) and *Sciodrepoides watsoni hornianus* (Blanchard, 1915) AN936 (with high support: 97.9/100) from Canada shows that the latter is a good species that has already been described with the name *Choleva horniana* Blanchard, 1915: 294 (USA: Tyngsboro, Massachusetts) and currently considered a subspecies of *S. watsoni* (Perreau 2000; Peck & Skelley 2001) or a synonym of this species (Peck & Cook 2002; Majka & Langor 2008). It is restored to species status as *Sciodrepoides hornianus* (Blanchard, 1915).

5. The clade formed by *Nargus* (*Nargus*) *algiricus* Portevin, 1903 (AI574-AN672), *N*. (*Nargus*) *velox* (Spence, 1815) (AI927), the nominotypical species of the genus *Nargus*, and *N*. (*Demochrus*) *armeniacus* (Reitter, 1884) (AN530) is the sister group, with support 100/100, to the clade *Choleva* Latreille, 1796, *Attaephilus* Motschulsky, 1844, *Nargus* (*Demochrus*) *brunneus* (Sturm, 1839) (GBKKF492873), *N*. (*Demochrus*) *cavazzutii* Giachino & Vailati, 2000 (AN286), *N*. (*Demochrus*) *transcaucasica* Giachino & Vailati, 2000 (RA468), *N*. (*Demochrus*) *wilkini* (Spence, 1815) (RA532) and *N*. (*Nargus*) *badius* (Sturm, 1839) (RA807).

It might seem justified to elevate *Demochrus* Thomson, 1867 to the status of a good genus, but the presence of a *Demochrus* among the *Nargus* (*s. str*.) and of a *Nargus* (*s. str*.) among the *Demochrus* makes it seem more prudent to wait for a more complete representation of the genus; furthermore, it is not known to which of the two *Nargus* clades the type species of *Demochrus*, *Choleva anisotomoides* Spence, 1815, would be incorporated:

– If it were incorporated into the clade of *N*. (*Nargus*) *velox*, synonymy could be established or maintained as a subgenus.

– In this case, the clade *brunneus-cavazzutii-transcaucasica-wilkini-badius* would not have a generic name or if the type species of *Eunargus* Perreau, 1996 were incorporated, it would take this name.

– If it were incorporated into the clade of *brunneus-cavazzutii-transcaucasica-wilkini-badius*, *Demochrus* could be elevated to the rank of a good genus.

6. The genetic distance between the Algerian *Nargus* (*Nargus*) *algiricus* (AN672) from the type locality and the Iberian *N*. (*Nargus*) *algiricus* (AI574) indicates that the latter probably belongs to an unnamed species. In the tree this constatation is highly supported (100/100). No significant differences have been found between the two specimens that allow the description.

7. Fresneda *et al*. (2011) excluded *Fusi* Perkovsky, 1989 from Leptodirini although in that article it was derived from a polytomy with Cholevina and Catopina. With more data, its position becomes more precise: it derives from the basal cladogenesis of the Catopina + Cholevina + Eunemadina + *Mesocolon* but with support 82.7/99.

8. The Eunemadina (Anemadini) *Dissochaetus* Reitter, 1884, *Falkonemadus* Szymczakowski, 1961, *Nemadiopsis* Jeannel, 1936 and *Falkocholeva* Hatch, 1828 are not in the clade of *Anemadus* Reitter, 1884 and therefore should not be included among the Anemadini. Together with *Mesocolon* Brown, 1880 (Paracatopina), sister genus to *Falkonemadus* (Eunemadina), they are the sister clade of Cholevina (*Choleva* Latreille, 1796 + *Nargus* + *Attaephilus* Motschulsky, 1870) with high support 99.1/97. On the other hand, *Nemadus* Thomson, 1867, a Nemadina, joins the Anemadina with high support 98.3/100. To highlight is a new species of *Anemadus* AN854 sister of *Anemadus hajeki* RA187 with 100/100 support and not a great genetic distance. Its description has not been carried out because the only specimen studied is a female and because this specimen implies biogeographical reconsiderations: AN854 comes from Cameroon, in the Ethiopian region or Afrotropical ecopart. The only Anemadini known from Africa belong to the genus *Speonemadus* (Fresneda *et al*. 2019) and are of North-Saharian origin from the Palaearctic region.

9. The most uncertain position is that of *Prionochaeta* Horn, 1880, a Cholevina, with very low support 0/14, ranked as sister to the Leptodirini tribe.

10. Sciaphyini are the sister group of *Fusi* + Catopina + Paracatopina + Eunemadina + Cholevina with high support 97.8/99. In the partial phylogeny of Fresneda *et al*. (2011) Sciaphyini was found to be a sister to Anemadini, a position apparently consistent with the morphology of the genital structures.

11. Ptomaphagini is the sister group of the Anemadina + Nemadina with support 88/99.

12. From the unifiying node with the external groups (Staphylinidae) from the most basal to the most derived the following was found:

– *Colon* Herbst, 1797, Coloninae, sister group of all the rest of Leiodidae with support 89.3/100, that should also be excluded from Cholevinae.

A large clade where representatives of various subfamilies are found such as:

– As sister group to the whole group, with support 88.2/68, are *Oritocatops* Jeannel, 1921 (AN893) and *Afrocatops basilewskyi* (Jeannel, 1960) (AN520), both Oritocatopini that should also be excluded from Cholevinae. Probably the subfamily Oritocatopinae should be constituted.

– *Chelagyrtodes* Szymczakowski, 1973 + *Chiliopelates* Jeannel, 1964, both Camiarinae Agyrtodini, as sister group to the rest of the clade with support 80.3/51.

A subclade consisting of:

– In basal position with support 94.8/61, *Eucatops* Portevin, 1903 (AF220 + RA342), a Cholevinae Eucatopini that would have to be excluded from the tribe Cholevinae.

– The other Camiarinae studied *Dictydiella* Jeannel, 1936, Agyrtodini, is sister with low support 40.1/62 of other Leiodinae such as *Colenis* (*Colenodes*) *bonnairii* Jacquelin du Val, 1859 (RA639), a Pseudoliodini plus an indeterminate Leiodinae (AN856) appear as a sister group to *Agathidium* Panzer, 1797 (AI1305-RA249), Agathidiini, with 95.6/94 support. Only molecular studies will make it possible to point out the position of the diverse Camiarinae studied, as well as those for *Agyrtodes* Portevin, 1907, *Camiarus* Sharp, 1876, and *Neopelatops* Jeannel, 1936, molecular data on these three nominotypical genera of the Camiarinae tribes are needed to provide sufficient information to confirm the validity of these names and the distribution of various genera of this tribes.

And the sister subclade formed by:

– The Platypsyllinae Ritsema, 1869 subfamily is the sister group of some Leiodinae Leiodini such as *Leiodes dilutipes* Sahlberg, 1903 (AN556) + *Leiodes* sp. AN299 with a support of 89.8/87.

13. Perreau (2000) considered that Platypsyllinae, in the sense given by this author, is the sister group of Cholevinae. It should be noted that the sister group of Cholevinae is a clade formed by an pool of genera belonging to different subfamilies (Fig. 1K) among which a are Platypsyllinae also included, as it was suggested by Perreau (2000),as are Agathidiini, Leiodini and Pseudoliodini (Leiodinae), Eucatopini and Oritocatopini (Cholevinae), Agyrtodini (Camiarinae) and Coloninae.

The scarce representation of the subfamilys, tribes and their subtribes of the Leiodidae does not allow to confidently introduce the necessary taxonomic changes, but the paraphyly or polyphyly of most of the subfamilys, tribes and subtribes is evident. The taxonomic arrangement in use of the Leiodidae is revealed to be obsolete, it does not correspond to what appears to be the natural arrangement following evolutionary criteria. As has been seen, a complete revision and reordering of the family is required, although it seems that it will not be easy to find the necessary morphological characters to define the new groupings.

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On April 15th 2020 during the writing process of this article, our friend and co-author Ignacio Ribera died in Barcelona. We want to pay him a modest tribute from these pages that would not have existed without his fundamental contribution. This is therefore one other of his posthumous publications. It may seem strange that I. Ribera signs this article four years after his death; it is certainly evident that it cannot be said that he agrees with the final wording. But he is responsible for all the molecular work, for part of the sample collection, for part of the proposal for the new organization of the tribe and for a part of the final writing.

The authors declare no competing or conflicts of interest. All relevant data are included in this manuscript; additional data may be provided under request.

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Spelaeodromus Reitter, 1885 195
Spelaetes Apfelbeck, 1907 (see *Spelaites*)
Spelaites Apfelbeck, 1907 222
Speocharidius Jeannel, 1919 668
Speocharinus Español & Escolà, 1977 499
Speodiaetus Jeannel, 1908 441
Speogeus Salgado, 1985 (see *Quaestus*)
Speonesiotes Jeannel, 1910 333
Speonomidius Jeannel, 1924 162
Speonomites Jeannel, 1910 753
Speonomus Jeannel, 1908 755
Speophilus Jeannel, 1911) (see *Troglocharinus*)
Speophyes Jeannel, 1910 421
Speoplanes G. Müller, 1911 199
Sphaerobathyscia G. Müller, 1917 170
Stagobius F.J. Schmidt, 1832 (see *Leptodirus*)
Stoppaniola Vailati, 2017 629
Stygiophyes Fresneda, 1998 764
Tamaniniella Giachino & Vailati, 2019 632
Tartariella Nonveiller & Pavićević, 1999 338
Tismanella Jeannel, 1928 103
Tranteeviella Pretner, 1958 (see *Bulgariella*)
Trapezodirus Jeannel, 1924 767
Trichopharis Knirsch, 1925 583
Trocharanis Reitter, 1885 769
Troglocharinus Reitter, 1908 770
Troglodromus Sainte Claire Deville, 1901 442
Troglophyes Abeille de Perrin, 1894 723
Uhagoniella gen. nov. 165
Uludagites Casale, Giachino, Vailati & Rampini, 1991 567
Urbasolus Español, 1948 672
Valdesiella gen. nov. 645
Vallespirana gen. nov. 685
Vanderberghia gen. nov. 713
Velebitodromus Casale, Giachino & Jalzić, 2004 184
Viallia Pavan, 1950 363
Vratzaniola Duprè, 2000 (see *Radevia*)
Weiratheria Zariquiey, 1927 339
Zariquieyella Jeannel, 1928 687
Zoiana gen. nov. 619

APPENDIX 1: NEW SPECIES (in alphabetical order)

Aphaobius gorenjskanus sp. nov.
(Figs. 216.1, 317.1, 317.5, 317.9, 318.1, 318.3)
https://zoobank.org/NomenclaturalActs/D8E860B6-DC90-461A-A5C7-672374B2C785

Type locality. Slovenia, Kamnik, Velika Špica, Jama v Kamnolomu (a cave in a quarry), 46°13'N 14°37'E, 619 m.

Type series. Holotype ♂ (in col. Kofler): labelled [JAMA V KAMNOLOMU / VELIKA SPICA, KAMNIK / 26.II.2012-17.III.2013 / Leg B. KOFLER], [HOLOTYPUS / *Aphaobius* / *gorenjskanus* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on a transparent card mounted on the same pin as the holotype. Paratypes: with same collection data as holotype, 9 ♂♂, 45 ♀♀, with paratype label [Paratypus / *Aphaobius* / *gorenjskanus* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, CDV, SMNS).

Diagnosis. A species of genus *Aphaobius* belonging to group *kraussi* (*sensu* Bognolo & Vailati 2010); closely related to *A. angusticollis* in body shape and shape of median lobe of aedeagus. From this species well distinguished by less elongated transverse pronotum, by different structure of endophallus and by more elongated parameres.

Description. Holotype ♂. Total length: 2.8 mm. Facies slightly pholeuonoid (Fig. 316.1). Body shape elliptical, broad and moderately elongated; coloration brownish-testaceous, with legs, antennae and palpi of same colour; pronotum and elytra uniformly covered with yellow, sparse, moderately long pubescence, semi-erect along middle of elytra.

Head: Retractile, anophthalmous; with evident occipital carina; long and semi-erect pubescence on frons and clypeus.

Antennae: Long, slender, not reaching apical fourth of elytra. All antennomeres filiform, markedly longer than wide; 1st as long as 2nd; 3rd to 6th similar in length, with 4th somewhat longer; antennomere 11th in middle somewhat compressed, being longest of all and about as long as 9th and 10th together. Antennal formula: see Table 2.

Pronotum: Transverse (ratio maximum width/maximum length: 1.6), maximum width near middle, disk not flattened near basal angles; lateral margins regularly curved anteriorly and slightly sinuate or concave just before base; base of pronotum slightly narrower than base of elytra; angles acute strongly pointed and facing somewhat outwards. Pronotal disc slightly granulose with evident microsculpture.

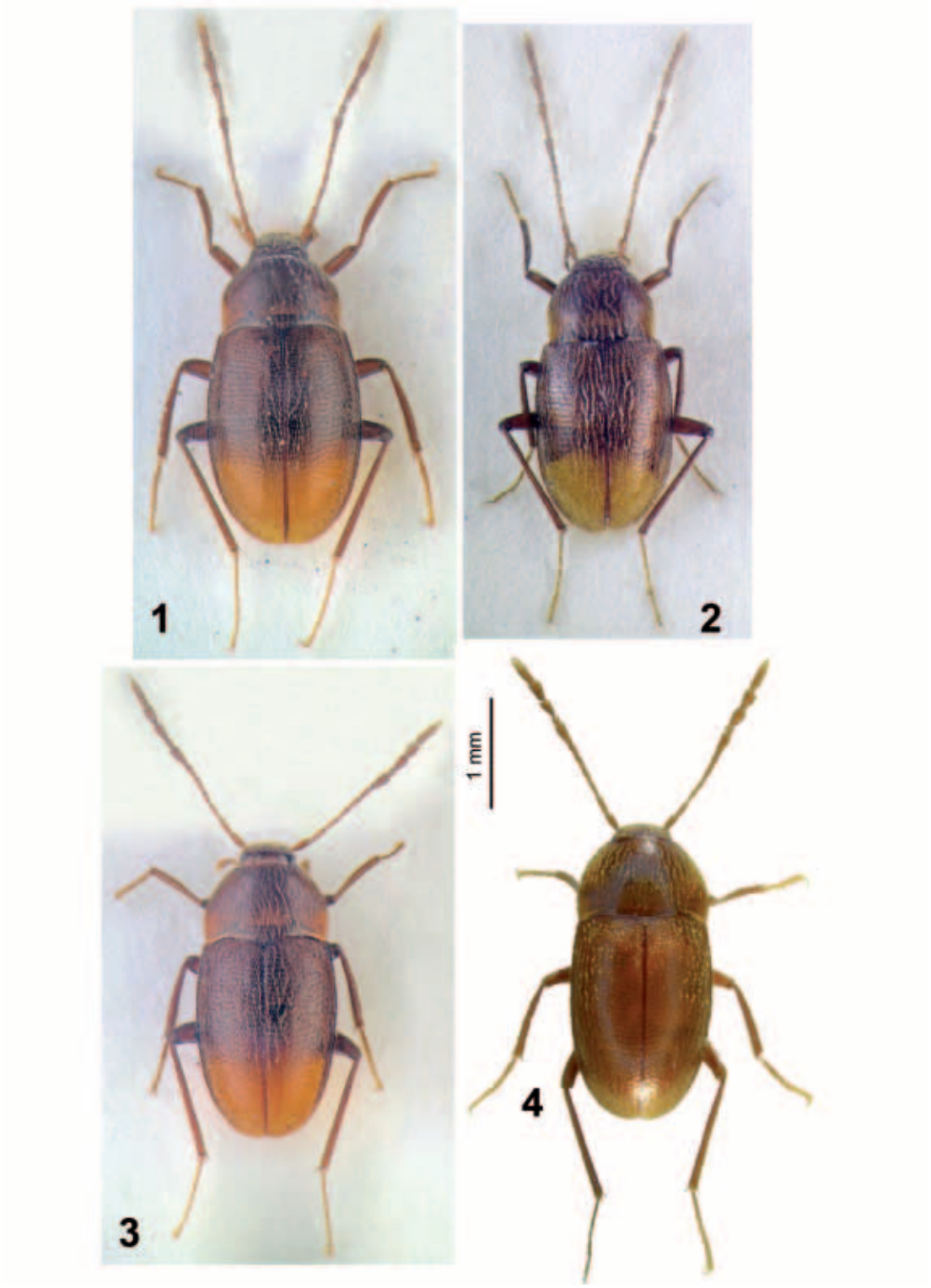
Elytra: Elliptical, elongate (ratio maximum width/máximum length: 0.72), with largest width very close to middle; each elytron rounded apically. Elytral disc convex, slightly depressed along suture near base; parasutural stria absent; disc with transverse striation.

Legs: Relatively long and slender, with tarsal claws simple; protarsi four-segmented and not dilated; protibiae gently arcuate outwards, without external comb of bristles; meso- and metatibiae straight, with two outer apical spurs.

Mesoventral keel: Tall and lamellar, anteriorly widely rounded, not reaching metaventrite.

Median lobe of aedeagus: Large and robust. In lateral view (Fig. 317.1) regularly arched, apex very little curved and tapering; basal part thickened. In dorsal view (Fig. 317.5) broad, sides slightly curved from base to apical fifth, then with soft concavity to end in a broad apical margin very slightly convex or subrectilinear. Basal lamina long, as wide as median lobe, with curved sides tapering progressively to apex in rounded arc.

Parameres (Fig. 317.9): Slender, longer than median lobe, not curved inwards, apically narrowed. Chaetotaxy consisting of three setae of similar length: first one in apical position, second one oriented inwards and equidistant from other two, third one subapical and oriented outwards.



FIGURES 316.1–316.4: *Aphaobius* spp. Habitus of: (**1**) *A. gorenjskanus* **sp. nov.**, (**2**) *A. angusticollis*, (**3**) *A. luckae* **sp. nov.**, (**4**) *A. kaplai* (modified from Giachino 2023).

Endophallus (Fig. 317.5): Consisting of two parts: basal part formed like an inverted «Y»-piece; provided with two pairs of slightly sclerotized, symmetrical, overlapping phanerae, shaped like an arcuate lamellae and separated by a median stylus. Apical part formed by two weakly robust reinforcement bands, apparently part of apical lamellae.

Female. Somewhat broader than males, more globular; antennae shorter than in males, with slightly thicker antennomeres; elytra more convex.

Spermathecal complex: Spermatheca small (Fig. 318.1), with three differentiated parts: apical lobe ovoid, well sclerotized, being broadest and most developed part; hyaline union duct longer and slightly narrower than basal part; basal lobe very short and well sclerotized. Spermatic duct joining this lobe, here lobe dilated and well sclerotized. Small spermathecal gland present.

Female uroventrite VIII (Fig. 318.3): Shaped like a quarter-moon, spiculum atrophied, only very little prominent.

Variability. Length of paratypes 2.6-3.1 mm.

Etymology. *A. gorenjskanus* relates to the type locality of this species, the Gorenjska, which is the historical Upper Carniola in Slovenian language (slovenski jezik). Region of Slovenia located in the mountainous northern part of the greater Carniola region.

Discussion. *Aphaobius gorenjskanus* sp. nov. fits perfectly into the group of *A. kraussi* (*sensu* Bognolo & Vailati 2010) by its body shape which tends to pholeuonoid, by the pronotum being narrower than the elytral base and by the shape of the aedeagus, with its preapically sinuated sides. Within this group is *A. angusticollis* the most similar species by the slender shape of the body (albeit with a less transverse pronotum) (Fig. 316.2), the shape of the aedeagus (Figs. 317.2, 317.6) and the shape of the endophallus (Fig. 317.6). The discovery of a new species of *Aphaobius* in previously unexplored region, after other recent discoveries (Faille *et al*. 2016; Giachino 2023), invites us to reflect on the completeness of the data on a genus wrongly believed to be well known. In biogeographical terms arise always problems if in the area of a widely distributed species another species is found which has only are rather restricted distribution area.

Distribution. The new species is only known from the type locality in Slovenia, a cave in a small quarry next to the road that goes up to Velika Špica, in the vicinity of Kamnik (Fig. 318.5). The specimens were collected with pitfall traps that were placed for thirteen months. The long sampling period and the relatively small number of specimens demonstrate the rarity of this species.

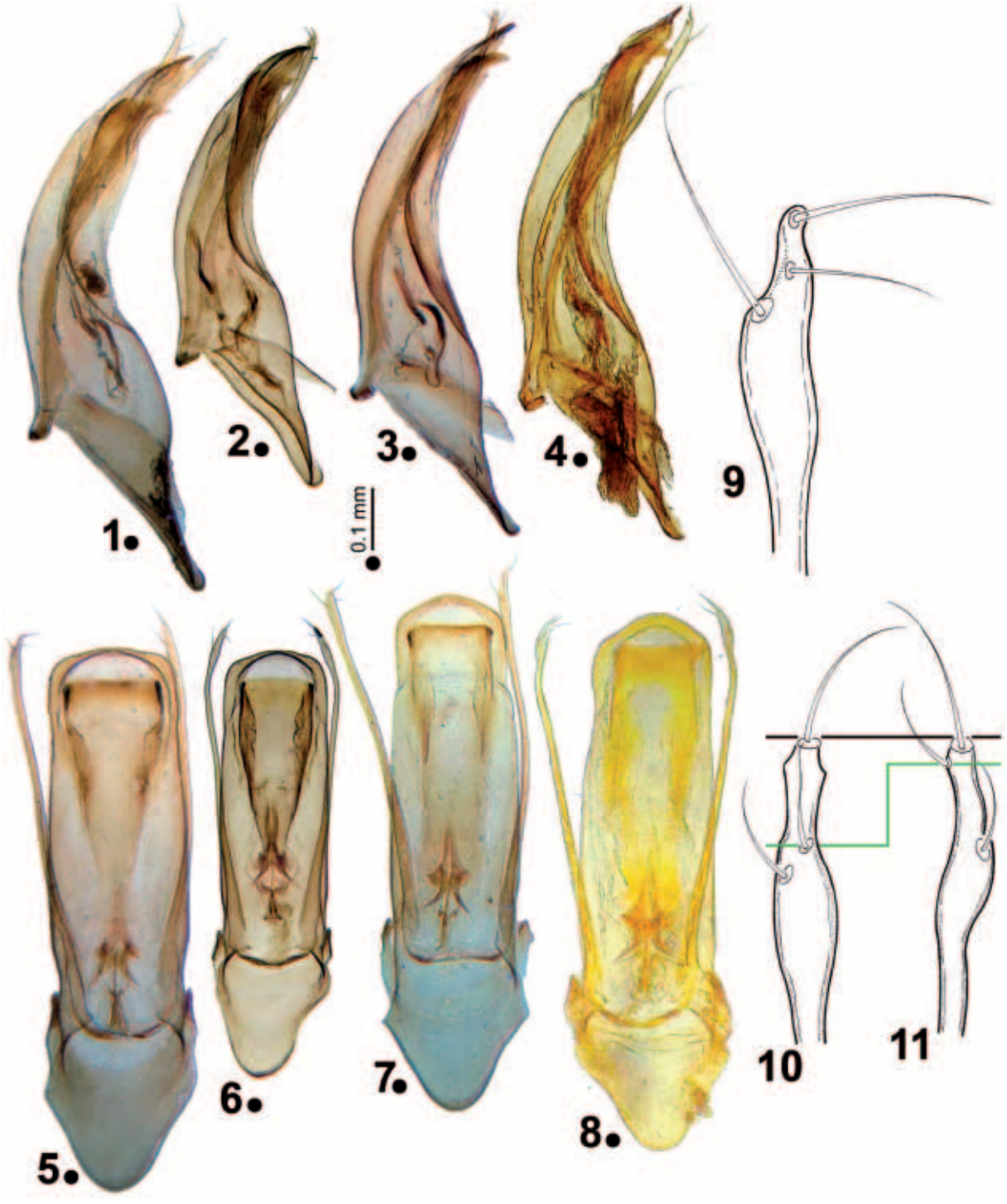
Segment	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**
Length	0.19	0.18	0.18	0.13	0.15	0.14	0.28	0.10	0.21	0.23	0.40
Width	0.06	0.06	0.04	0.04	0.04	0.05	0.09	0.06	0.08	0.09	0.06

TABLE 2. Measurements of antennomeres of the holotype of *Aphaobius gorenjskanus* sp. nov. (mm).

Aphaobius luckae sp. nov.
(Figs. 316.3, 317.3, 317.7, 317.10, 318.2, 318.4)
https://zoobank.org/NomenclaturalActs/8DFE1660-9774-4A17-BE17-708C3680D480

Type locality. Slovenia, Železniki, Navihana Malina cave (Slovene Cave Cadastre No. 9663), WGS84: 46.250670ºN 14.017760ºE, 1,325 m.

Type series. Holotype ♂ (in col. Kofler): labelled [NAVIHANA MALINA / SORISKA PL, SLO / 10.6–7.10.2023 / Leg. Bojan Kofler], [HOLOTYPUS / *Aphaobius* / *luckae* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on a transpa-



FIGURES 317.1–317.11: *Aphaobius* spp. Aedeagus in lateral view of: (**1**) *A. gorenjskanus* **sp. nov.**, (**2**) *A. angusticollis*, (**3**) *A. luckae* **sp. nov.**, (**4**) *A. kaplai*. Aedeagus in dorsal view of: (**5**) *A. gorenjskanus* **sp. nov.**, (**6**) *A. angusticollis*, (**7**) *A. luckae* **sp. nov.**, (**8**) *A. kaplai*. Apex of paramere of: (**9**) *A. gorenjskanus* **sp. nov.**, (**10**) *A. luckae* **sp. nov.**, (**11**) *A. kaplai*.

rent card mounted on same pin as holotype. Paratypes: with same collection data as holotype, 8 ♂♂, 9 ♀♀ (Kofler, CPMG, CFL, CDV); with same collection data as holotype, except 27.V.2015-23.VIII.2016, 14 ♀♀ (Kofler, CPMG); with same collection data as holotype, except 1.VIII.2017-8.VIII.2018, 2 ♀♀ (Kofler, CPMG); with same collection data as holotype, except 1.VI.2019-19.IX.2020, 5 ♀♀ (Kofler, CPMG); with same collection data as holotype, 5.VII.2013-6.VI.2014, 1 ♀ (Kofler); with same collection data as holotype, except 7.X.2023-25.V.2024, 3 ♀♀ (Kofler, CPMG); with same collection data as holotype, except 8.VIII.2018-1.VI.2019, 1 ♀, (Kofler). All specimens with paratype label [Paratypus / *Aphaobius* / *luckae* sp. n. / Fresneda *et al*. 2024] (rl).

Diagnosis. An *Aphaobius* of group *milleri* (sensu Bognolo & Vailati 2010) closely related to *A. kaplai* in body shape and shape of median lobe of aedeagus. From this species well distinguished by broader body, by different shape of pronotum and by different position of setae on parameres.

Description. Holotype ♂. Total length: 2.7 mm. Facies bathyscioid (Fig. 316.3) Body shape elliptical, broad and moderately elongated; coloration brownish-testaceous, with legs, antennae and palpi of same colour. Pronotum and elytra uniformly covered with yellow, sparse, moderately long pubescence, semi-erect along middle of elytra.

Head: Retractile, with evident occipital carina; long and semi-erect pubescence on frons and clypeus. Anophthalmous.

Antennae: Long, slender, reaching apical third of elytra. All antennomeres filiform, markedly longer than wide; 1st as long as 2nd; 3rd to 6th similar in length, with 5th somewhat longer; antennomere 11th somewhat compressed in middle, being longest of all and about as long as 9th and 10th together. Antennal formula: see Table 3.

Pronotum: Transverse (ratio maximum width/maximum length: 1.44), maximum width in basal third, disk not flattened near basal angles; lateral margins regularly curved anteriorly and subrectilinear before base; pronotal base slightly narrower than elytral base; angles pointed and facing somewhat outward. Pronotal disc slightly granulose with evident microsculpture.

Elytra: Elliptical, elongate (ratio maximum width/máximum length: 0.69), with largest width very close to middle, each elytron rounded apically. Elytral disc convex, slightly depressed along suture near base; parasutural stria absent; disc with transverse striation.

Legs: Relatively long and slender, with tarsal claws simple; protarsi four-segmented and not dilated; protibiae gently arcuate outwards, without external comb of bristles; meso- and metatibiae straight, with two outer apical spurs.

Mesoventral keel: Tall and lamellar, anteriorly widely rounded, not reaching metaventrite.

Median lobe of aedeagus: Large and robust. In lateral view (Fig. 317.3), in regularly arched, apex very little curved and tapering; dorsal preapical saddle absent. In dorsal view (Fig. 317.7), broad, sides slightly curved from base to apical fifth, then abruptly narrowing, followed by rectilinear sides, ending in a broad and convex apical margin. Basal lamina long, as wide as median lobe, with curved sides tapering progressively to apex and ending in rounded arc.

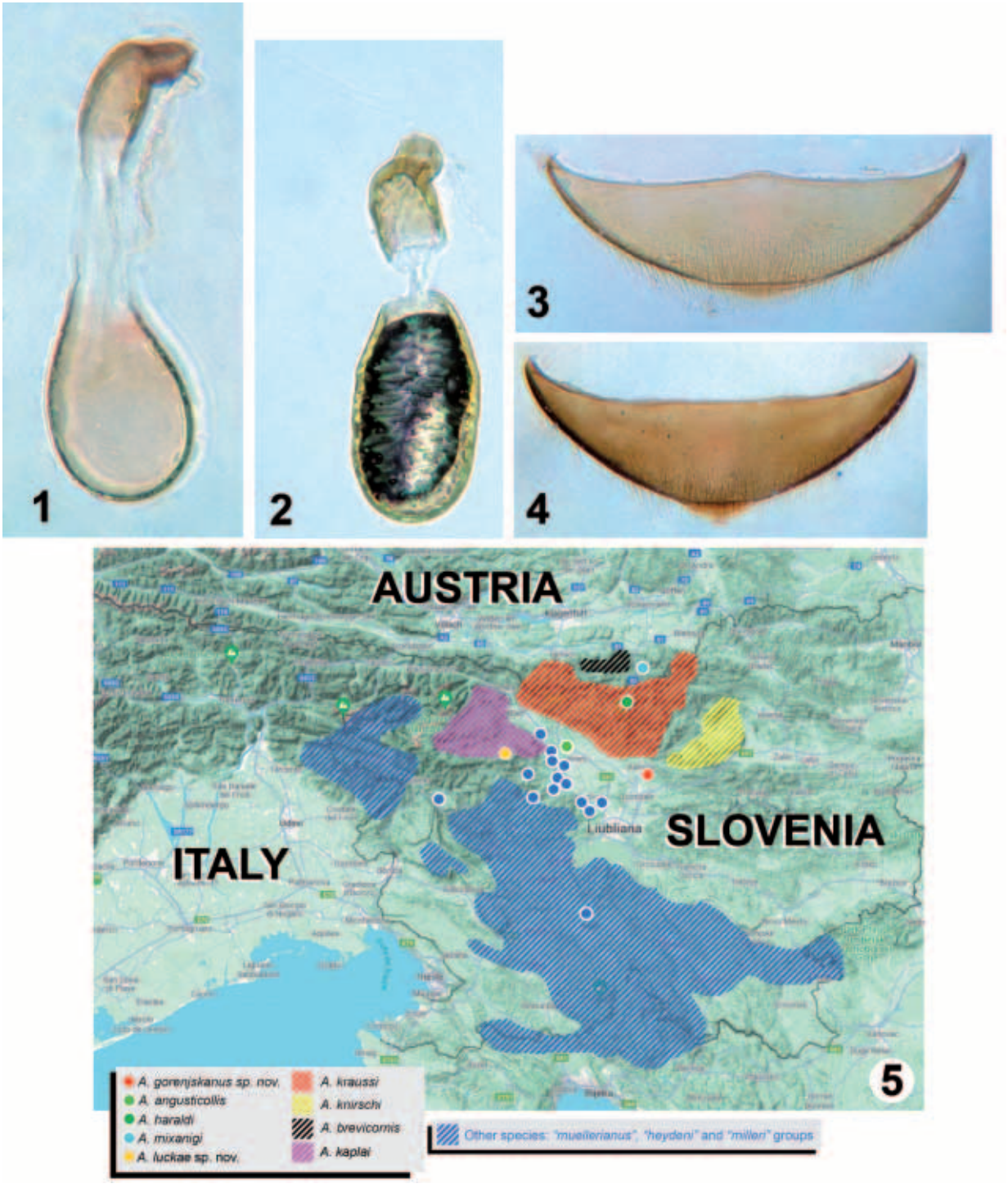
Parameres (Fig. 317.10): Slender, longer than median lobe, not curved inwards, apically narrowed. Chaetotaxy consisting of three setae of similar length: first one in apical part, second one oriented inwards and closest to third; third one subapical and oriented outwards.

Endophallus (Fig. 317.7): Formed by two parts: basal part formed like an inverted «Y»-piece, provided with two pairs of slightly sclerotized, symmetrical, overlapping phanerae, shaped like an arcuate lamellae and separated by a median stylus. Apical part formed by two weakly robust posteriorly convergent reinforcement bands, apparently part of the pair of apical lamellae.

Female. Somewhat broader than males, more globular; antennae shorter than in males with slightly thicker antennomeres; elytra more convex.

Spermathecal complex: Spermatheca small (Fig. 318.2), with three differentiated parts; apical lobe ovoid, well sclerotized, being widest and most developed part; hyaline union duct longer and slightly narrower than basal part; basal lobe very short and well sclerotized. Spermatic duct joining this lobe, here lobe dilated and well sclerotized. Small spermathecal gland present.

Female uroventrite VIII (Fig. 318.4): Shape like a quarter-moon, spiculum atrophied, only very little prominent.



FIGURES 318.1–318.5: *Aphaobius* spp. Spermathecal complex of: (**1**) *A. gorenjskanus* **sp. nov.**, (**2**) *A. luckae* **sp. nov.** Female uroventrite VIII of: (**3**) *A. gorenjskanus* **sp. nov.**, (**4**) *A. luckae* **sp. nov.** (**5**) Distribution map of the genus *Aphaobius*.

Variability. Length of paratypes 2.6-3.0 mm.

Etymology. We are pleased to dedicate this new species to Lučka Kobal, the youngest granddaughter and most active member of «Bojan Kofler's entomological family».

Discussion. *Aphaobius luckae* sp. nov. fits perfectly into the group of *A. milleri* (sensu Bognolo & Vailati 2010) by its narrow and elongate body shape, by a pronotum narrower than the elytra base and by the shape of the aedeagus, with its preapically sinuated sides and the straight proximal edge margin of the apical orifice. Within this group is *A. kaplai* the most similar species by the slender shape of the body (Fig. 316.4), the shape of the aedeagus (Figs. 317.4, 217.8) and the shape of the endophallus (Fig. 317.8). Among other characters these two species can be easily distinguished by the different insertion points of the setae at the apex of the parameres: one apical and two pre-apical in *A. luckae* sp. nov. (Fig. 317.10), two apical and one pre-apical in *A. kaplai* (Fig. 317.11). In biogeographical terms arise always problems if in the area of a widely distributed species another species is found which has only are rather restricted distribution area small. *Aphaobius luckae* sp. nov. appears in fact as a peripheral isolate with respect to *A. kaplai*, a species with a wider distribution. The discovery of a new species of *Aphaobius*, after other recent discoveries (Faille *et al*. 2016; Giachino 2023), invites us to reflect on the completeness of the current data about this genus.

Distribution (Fig. 318.5). The new species is known only from the type locality, a cave in the vicinity of the Soriška Planina ski resort in Železniki, Slovenia. The Navihana Malina cave is 38 m long and 10 m deep. In this cave *A. luckae* sp. nov, was found in sympatry with *Pretneria soriscensis* and collected using pitfall traps.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.16	0.16	0.16	0.12	0.14	0.14	0.21	0.09	0.16	0.19	0.28
Width	0.05	0.04	0.03	0.03	0.03	0.04	0.09	0.05	0.09	0.09	0.07

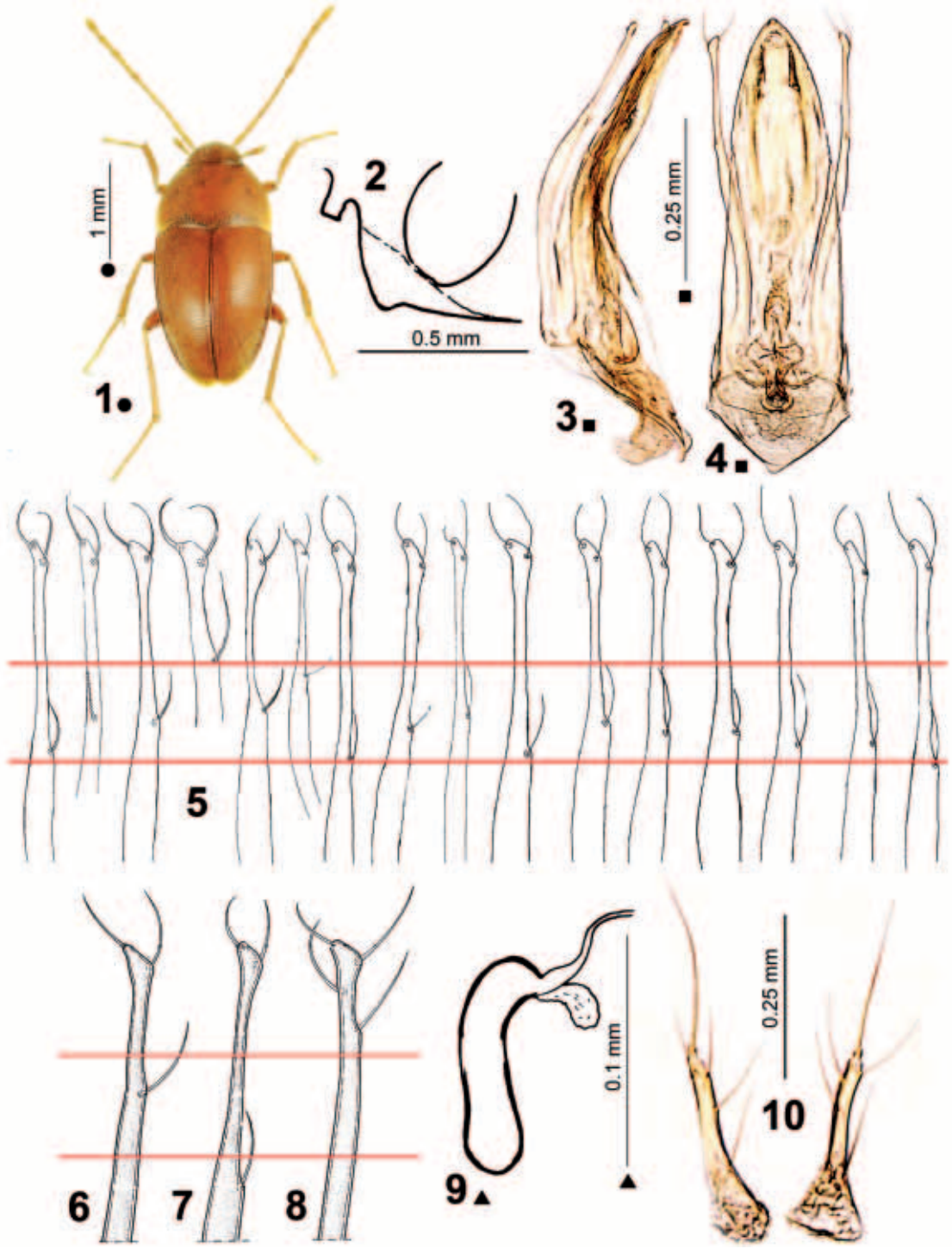
TABLE 3. Measurements of antennomeres of the holotype of *Aphaobius luckae* sp. nov. (mm).

Archeoboldoria martinottii sp. nov.
(Figs. 319.1-319.5, 319.9, 319.10)
https://zoobank.org/NomenclaturalActs/E9C1E439-B282-465D-A352-5954BD34B358

Type locality. Italy, Piemonte, Biella, Bioglio upper Val Sessera, Rondolere, Pietra Bianca 2 mine (CAPI 5008), 45°40'47.12''N 8°02'41.99''E, 1,270 m.

Type series. Holotype ♂ (CPMG): Italia, Piemonte, Biella, Bioglio, alta Val Sessera, Rondolere, ex Miniera Pietra Bianca 2, 1,270 m, 28.IV.2002, P.M. Giachino leg., with holotype label [Holotypus / *Archeoboldoria* / *martinottii* n. sp./ Fresneda *et al*., 2024] (hw, rl), genitalia mounted on transparent card inserted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 107 ♂♂, 247 ♀♀, (CPMG, CAC, CDV, CFL); Italia, Piemonte, Biella, Bioglio, alta Val Sessera, Rondolere, ex Miniera Pietra Bianca 2, 1,270 m, 24.VI.2001, T. Pascutto leg., 38 ♂♂, ♀♀ (CPMG, CVA, CFL); with same collection data, 3.VIII.2023, E. Lana leg., 1 ♂ (CPMG); with same collection data, 2.VI.2020, P.M. Giachino leg., 4 ♂♂, 4 ♀♀ (CPMG); with same collection data, 8 ♂♂ (all spares in ethanol except one 1 ♂ mounted with DNA extraction code «SMNS-M339»), 13♀♀ (SMNS); Val Sessera, Ital., 24.IX.1963, Biella, vers. 1,800 m, 1 ♂ (CPMG). All specimens with paratype label [Paratypus / *Archeoboldoria* / *martinottii* sp. n. / Fresneda *et al*., 2024] (hw, rl).

Diagnosis. *Archeoboldoria martinottii* sp. nov. show only three setae on parameres (four in *A. pascuttoi*) with median seta very variable in position from the apex (Fig. 319.5). Median lobe of aedeagus acuminate in dorsal view and dorsally not sinuated in lateral view. Externally show a tapered elytral apex, and evident microsculpture on elytral disk.



FIGURES 319.1–319.10: *Archeoboldoria martinottii* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Variability of the insertion point of median seta of parameres in different specimens. Apex of parameres of: (**6**) *A. doderona*, (**7**) *A. lanai*, (**8**) *A. pascuttoi*. *Archeoboldoria martinottii* **sp. nov.**: (**9**) Spermatheca, (**10**) Female styles.

Description. Holotype ♂. Medium-small sized, 2.5 mm with bathyscioid habitus (Fig. 319.1), elliptical in shape, with large pronotum as wide as elytra; uniformly covered by golden pubescence, short and lying. Anophthalmous.

Antennae: Antennae long, surpassing middle of elytra. First antennomere much shorter as second one; 8th longer than wide; 11th ogival and as long as the previous one. Antennal formula: see Table 4.

Pronotum: Sides little rounded, broad and sub-belly-shaped. As wide as elytra, with maximum width just ahead of the acute basal angles and facing backwards due to accentuated sinuosity of pronotal base, little narrow as well. Disc punctation scattered and slightly accentuated, giving integuments a brilliant appearance.

Elytra: Elongated, oval, with maximum width in anterior third; parasutural stria almost complete and well marked; transverse striolae fine and not very tight, more very evident on the disk.

Legs: Moderately elongated and thin. Protarsi never dilated, less wide than apex of protibiae. Metafemora simple, with unarmed posterior margin. Apex of tibiae with combed internal spurs. Meso- and metatibiae with incomplete apical basket of spines.

Mesoventral keel (Fig. 319.2): Tall, but not anteriorly prominent. Anterior profile slightly curved, and ventral one slightly sinuous; form an obtuse angle, inferiorly equipped with tooth, pronounced but blunted. Without posterior apophysis prolonged on metaventrite.

Metaventrite suture: Unknown.

Metatergal apparatus: Large, with posterior apophysis approximately one fifth of the elytra length.

Metendosternite: Not «V»-shaped, with furcal arms triangular and wide at base.

Median lobe of aedeagus: Relatively large, elongated. In lateral view (Fig. 319.3) little and regularly curved (not sinuated pre-apically), slender, with apex slightly facing downwards. In dorsal view (Fig. 319.4) converging sides from base to apex, which is subtriangular and blunt.

Endophallus (Fig. 319.4): Basal «Y»-piece large and well-sclerotized. Median phanera slightly sclerotized, small and complex, formed by spiny bands; with two apical lists long and parallel, moderately sclerotized.

Parameres (Fig. 319.5): Long and slender, clearly shorter than median lobe, with apex simple in dorsal view. Chaetotaxy consisting of three setae: two long, one apical and another subapical; and another one long, internal, placed just at base of anterior third of paramere.

Female

Spermathecal complex: Spermatheca (Fig. 319.9) small, elongate, with proximal and distal lobes of same dimension. Ductus distally enlarged and sclerotized at insertion on spermatheca.

Female styles: In figure 319.10.

Female uroventrite VIII: Identical to nominotypical species, as in genus *Archeoboldoria* diagnosis section.

Variability. Length 2.1-3.1 mm. As shown in figure 319.5: position of middle seta on paramere very variable and cannot be used to separate *Archeoboldoria martinottii* sp. nov. from other congeneric species.

Etymology. We are pleased to dedicate this new species in memory of our friend Antonio (Nino) Martinotti, who, in 1968, published the first catalog of the subterranean fauna of Piedmont, Italy.

Discussion. *Archeoboldoria martinottii* sp. nov. (M339) is the sister species of *Archeoboldoria pascuttoi* (M413) + *Archeoboldoria doderona* (RA511) with moderate support, 62.5/100 (Fig. 1D). Differs from *A. pascuttoi* mainly for the number of setae (3 vs. 4) of the parameres, and by the shape of the median lobe of aedeagus in dorsal view. The position of the median seta of the parameres is too variable (Fig. 319.5) in *A. martinottii* sp. nov. to be used to separate this species from currently known *Archeoboldoria* species: *Archeoboldoria doderona* (Fig. 319.6), *Archeoboldoria lanai* (Fig. 319.7), *Archeoboldoria pascuttoi* (Fig. 319.8).

Distribution (Fig. 320). Italy. Is known from a single site in the Sessera Valley, Pennine Alps (Piedmont), where it was collected in an old mine of magnetite of 67-length m, at altitude of 1,270 m. On the map (Fig. 320), the distribution data of *Archeoboldoria* species have been obtained from: Casale & Giachino (2010); Giachino & Vailati (1997); Giachino *et al*. (2001); Vailati (1988).

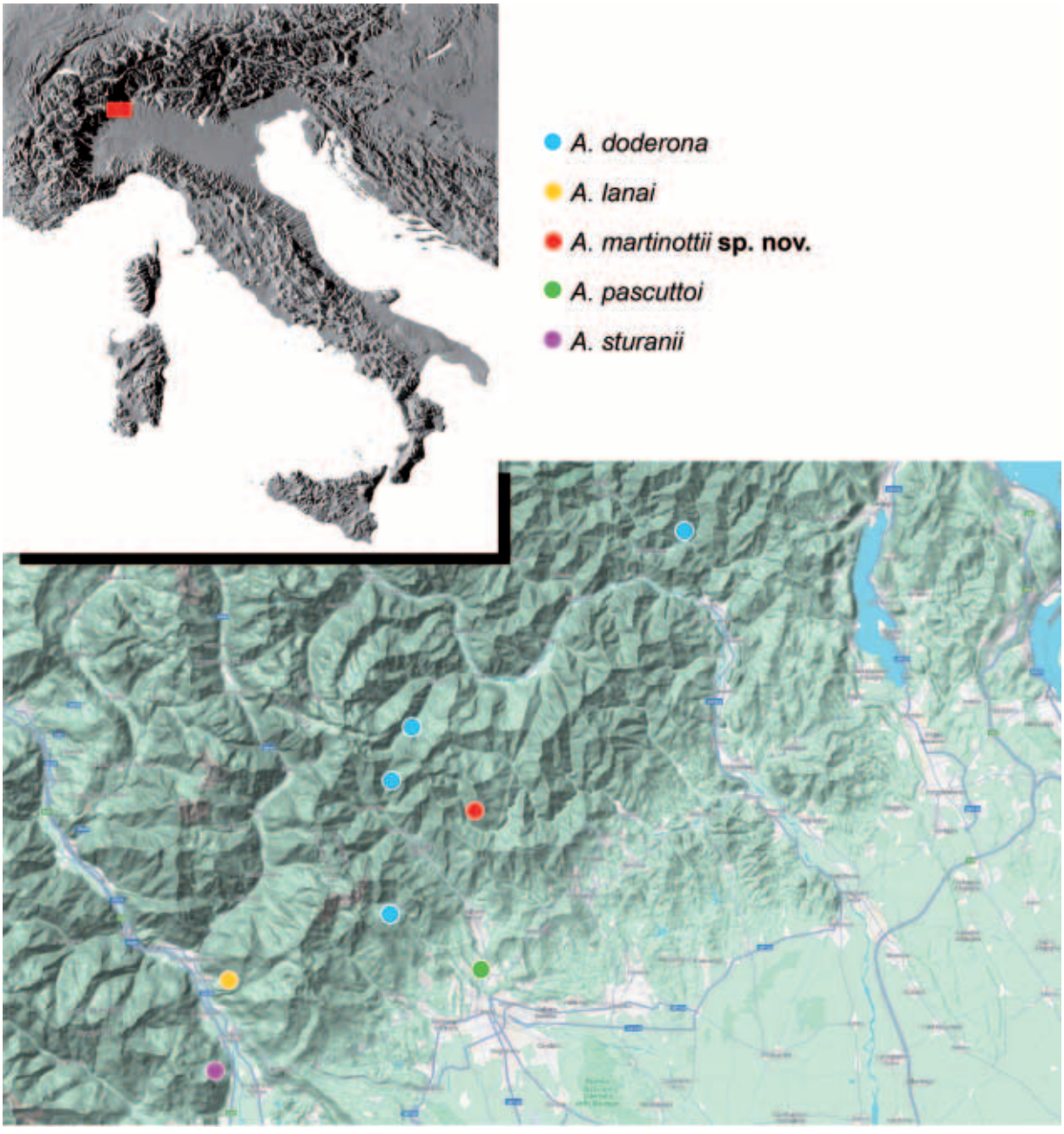


FIGURE 320: Distribution map of *Archeoboldoria* spp.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.17	0.19	0.12	0.10	0.12	0.12	0.15	0.09	0.20	0.18	0.23
Width	0.03	0.03	0.02	0.02	0.02	0.02	0.05	0.02	0.05	0.05	0.06

TABLE 4. Measurements of antennomeres of the holotype of *Archeoboldoria martinottii* sp. nov. (mm).

Bathyscidius* (*Bathyscidius*) *crnagorensis sp. nov.
(Figs. 321.1-321.5)
https://zoobank.org/NomenclaturalActs/E694F985-6202-41F9-B7E5-8AC674CB9DCF

Type locality. Montenegro, Lovcen, UTM 34T 32 469.

Type series. Holotype ♂ (CPMG): labelled [Lovcen – Geb. / April 1916] (white printed label), [ex. Collezione / V. B. GUEORGUIEV / 1990] (green printed label), [HOLOTYPUS / *Bathyscidius* / *crnagorensis* sp. n. / Fresneda *et al*. 2024] (rl); aedeagus on transparent card mounted on the same pin as the holotype.

Description. Holotype ♂. Very small size 1.2 mm; bathyscioid facies (Fig. 321.1); body oval and very convex. Pubescence without order, more abundant on elytra, fine, short, yellowish and lying down. Depigmented, colour weak dark reddish. Sculpture consisting of punctation fine and disordered on the head and pronotum, which on elytra forms transverse striolae quite separated and strong, particularly in basal-median part.

Head: Retractable, somewhat wider than long, with transverse occipital carina weakly-defined. Anophthalmous.

Antennae: Quite thick and short, not reaching pronotal base. Second antennomere longest, distinctly longer and more robust than first; 3rd antennomere longer than antennomeres 4th to 6th; antennomeres of club flattened and very transverse, 11th being widest of all; 11th also short, apically truncate and as long as 9th and 10th together. Antennal formula: see Table 5. Note: The left antenna of the holotype is damaged, it has only six antennomeres.

Pronotum: Strongly convex and transverse, 1.8 times wider than long, with regularly rounded lateral margins, maximum width before base, as wide as elytra; posterior basal margin bisinuated; posterior angles acute and somewhat prolonged over elytra.

Elytra: Elongated-oval, 1.15 times longer than wide, basal apex largely rounded with maximum width on anterior part decreasing in regular curve to rounded apices; striation on elytra aligned transversally, missing on apical part, and in lateral rows slightly undulating; without parasutural stria. Scutellum wide triangular,

Legs: Moderately short and robust; protarsi with four undilated tarsomeres. Protibiae flattened, without external spurs but with comb of strong spines extending at entire apical edge and part of lateral and on internal apical side with one smaller and one larger; spurs strong and polydentate. Meso- and metatibiae straight and cylindrical with numerous spines near distal half; periapical ring of spines of unequal length (basket) and two toothed spurs large and strong on internal apical side.

Mesoventral keel (Fig. 321.2): Tall, well-developed and moderately thick; anterior margin convex, vertex widely rounded and very obtuse angle. Posterior border slightly concave in the middle part and ventrally flattened and widened; the posterior apophysis extends to the middle of the metaventrite.

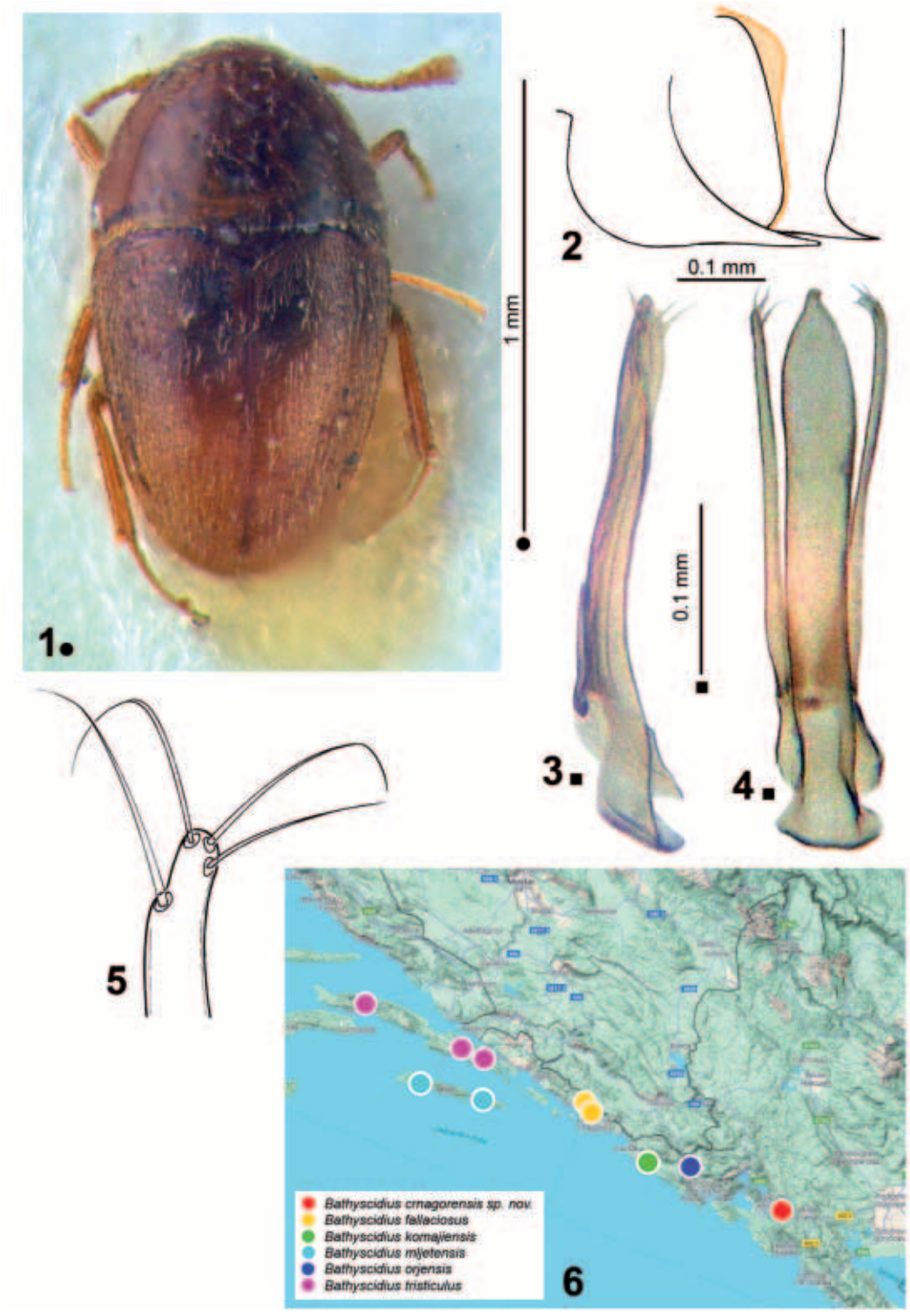
Suture of the metaventrite (Fig. 321.2): In the lower half it runs very close to the coxal cavity and in the upper half it delimits an arched área.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: Elongated, very small and thin. In lateral view (Fig. 321.3) narrow, with ventral face slightly curved and shallow depression in middle of the dorsal face. In dorsal view (Fig. 321.4) slender, with subrectilinear sides; apical part progressively narrowing into slightly arched sides, tip like small lobe in shape and somewhat right oriented. Basal lamina narrow, almost parallel with median lobe, relatively short, with final part broad, curved and not invaginated backwards on its apical part.

Endophallus: Unarmed, without visible sclerotized pieces.

Parameres (Fig. 321.5): Sides almost parallel, somewhat shorter than median lobe, without differentiated club and somewhat narrowed near rounded apex; with four setae, three apical ones with insertion pores close and one



FIGURES 321.1–321.6: *Bathyscidius crnagorensis* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Distribution map of species of the genus *Bathyscidius* (s. str.).

preapical, thicker than others. Ventral blade of tegmen with part of maximum width in a arc, as broad as basal lamina, but shorter.

Female. Unknown.

Etymology. Named after Crna Gora (Montenegro in montenegrin or cmogorski dialect), due to its relevance in the large number of taxa located in the karst systems of this country. Feminine name.

Discussion. The only specimen, which is currently in col. Giachino, comes from ex col. V.B. Guéorguiev (Sofia, Bulgaria). It must be included in the subgenus *Bathyscidius* because the basal lamina of the aedeagus is not prolonged, and because its distribution also coincides with that of this subgenus. Its aedeagus is similar to that of *Bathyscidius komajiensis,* but it is more slender, gracile, elongate and sinuous; moreover, the minute apical lobe of the aedeagus observed in the new species is not present in *B. komajiensis* (Polak & Jalžić 2019: Fig. 38). The geographically closest species is *Bathyscidius orjensis* from the northern area of Boka Kotorska (Montenegro), but its aedeagus is considerably shorter and more robust (Polak & Jalžić 2019: Fig. 54). The tiny apical lobe of the apex of the aedeagus, in dorsal view, is reminiscent of that present in some species of the subgenus *Ionobathyscidius*, with a much more southern distribution (southern Albania). However, the basal lamina of the aedeagus is short and therefore cannot be included in this subgenus, as it has already been noted. The existence of four setae inserted at the apex of the parameres distinguishes *Bathyscidius crnagorensis* sp. nov. of all other species of *Bathyscidius* as they all have three apical setae. A similar feature has also been observed in the genus *Quaestus*, in which all species have three apical setae in the parameres, except *Quaestus incognitus* which has four. There is also a similar insertion to *Bathyscidius crnagorensis* sp. nov. three apical and one preapical setae, more distant and more robust. There are also other genera in which the number of parameres setae is different among each species.

Distribution (Fig. 321.6). This species is only known from the type locality, an undetermined location in the Lovcen massif (Nationalni Park Lovcen), Montenegro. There is no further information about the circumstances of its discovery. Its origin is consistent with the distribution area of the subgenus *Bathyscidius* (Polak & Jalžić 2019): *Bathyscidius crnagorensis* sp. nov. is the southernmost species of the subgenus *Bathyscidius*.

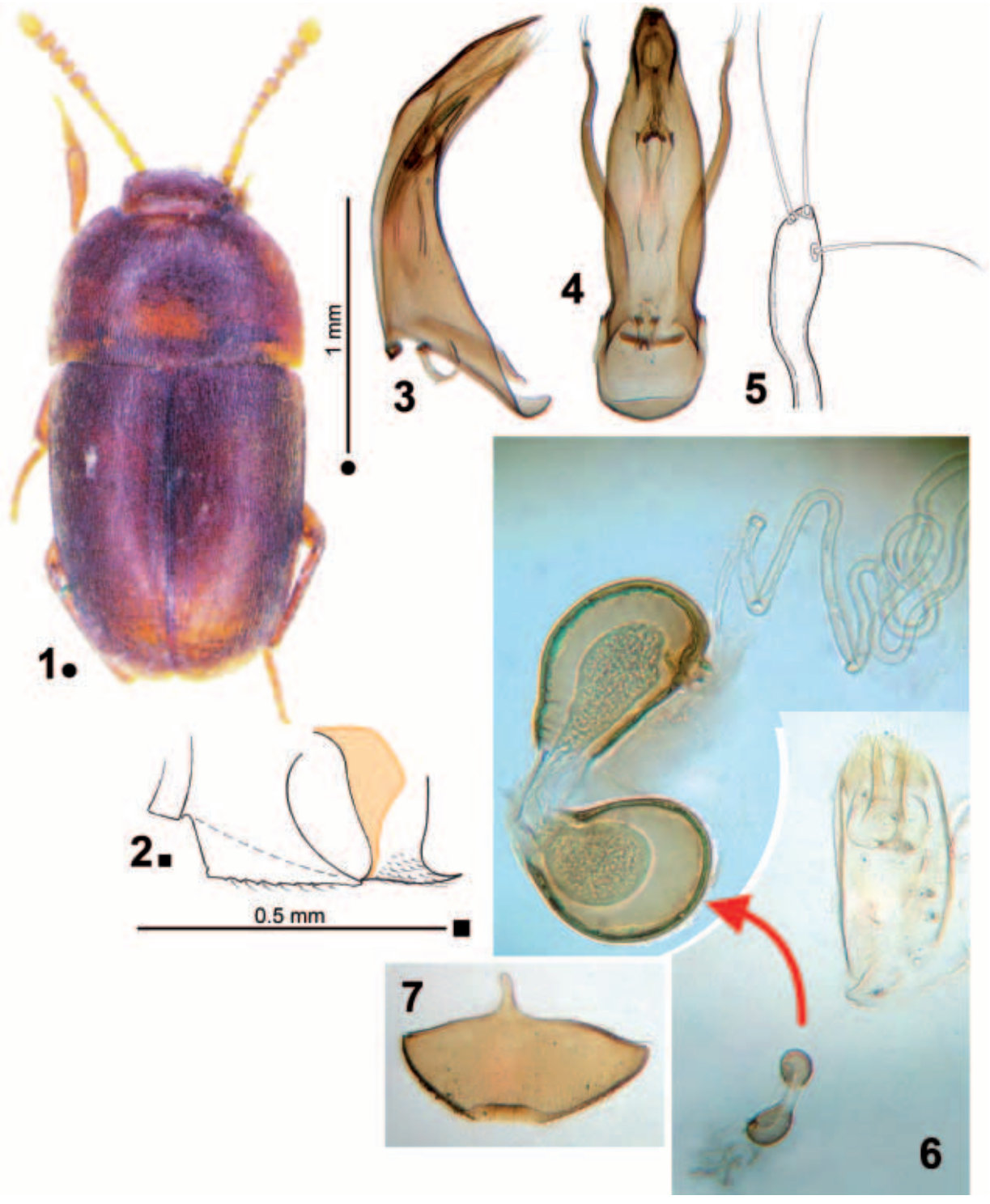
Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.05	0.07	0.04	0.03	0.03	0.02	0.04	0.02	0.03	0.04	0.07
Width	0.02	0.03	0.02	0.02	0.02	0.03	0.04	0.02	0.03	0.04	0.03

TABLE 5. Measurements of antennomeres of the holotype of *Bathyscidius crnagorensis* sp. nov. (mm).

Bathysciola balestrae sp. nov.
(Figs. 322.1-322.7)
https://zoobank.org/NomenclaturalActs/3AA42FC5-DAA9-4B21-9D46-1D148BA0EF2E

Type locality. Italy, Piemonte (CN), Ormea, M.te Antoroto, Cima Ciuaiera, 44°11’27N 7°53’12 E, 2,110 m.

Type series. Holotype ♂ (CPMG): labelled [Italia, Piemonte (CN), Ormea, Cima Ciuaiera, m 2110, 17.VIII.2009/10.VIII.2010 / P.M. Giachino leg.], [HOLOTYPUS / *Bathysciola* / *balestrae* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 7 ♂♂, 9 ♀♀, one specimen with code voucher DNA extraction RA193 (CFL); with the same collection data as the holotype, 2.IX.2015, 2 ♂♂, 14 ♀♀; 24.VIII.2008/17.VIII.2019, P.M. Giachino leg., 1 ♀. Italia, Piemonte (CN), Ormea, M.te Antoroto, strada per Colla dei Termini, 1,515 m, 2.X.2010/19.VII.2011, P.M. Giachino leg, 5 ♂♂, 5 ♀♀ (CPMG, CFL). All the specimens with paratype label [Paratypus / *Bathysciola* / *balestrae* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, CDV, MNCN).



FIGURES 322.1–322.7: *Bathysciola balestrae* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of the paramere, (**6**) Spermathecal complex and magnification of the spermatheca, (**7**) Female uroventrite VIII.

Diagnosis. A species of *Bathysciola* of size about 2.0 mm, similar to *Bathysciola monregalensis* in shape of median lobe of aedeagus, but from this well distinguished by body shape, more elongated, and by structure of endophallus.

Description. Holotype ♂. Medium size, 2.2 mm, habitus bathyscioid (Fig. 322.1).

Head: Retractile, with complete occipital carina; eyes absent.

Antennae: short. Not reaching the pronotal base; first antennomere as long as the second, but more robust; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th shorter than 9th and 10th together. Antennae formula: see Table 6.

Pronotum: Transverse, broadest at base, regularly curved towards anterior angles and less curved near posterior angle, base bisinuate. Posterior angles acute and prominent.

Elytra: Without transverse striolae but with a parasutural stria.

Legs: Apex of tibiae on the inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia; metatibiae straight.

Mesoventral keel (Fig. 322.2): Tall, rectilinear anteriorly, with apex toothed; inferior margin serrated, not reaching metaventrite.

Metaventrite suture (Fig. 322.2): First half curved with a big area delimited by two angles, and subsequently alongside laterals of mesocoxal cavity. Suture reaching very close to lower edge of metaventrite.

Median lobe of aedeagus: Slightly curved in lateral view (Fig. 322.3), up to the tip that is uncurved. In dorsal view slender, (Fig. 322.4), with sides convergent in apical part; apex regularly rounded and not lanceolate.

Endophallus (Fig. 322.4): With internal armature formed by two sclerotized pieces differentiating two parts (basal and medial). «Y»-piece and flagellum in basal area present. Median part with two sclerotized phanerae superposed, cup-shaped, and upside down.

Parameres (Fig. 322.5): Shorter than median lobe. Not enlarged at apex. Apex bearing three setae, two long apical, and another one shorter, subapical on inner side.

Female. With habitus more stocky, antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex (Fig. 322.6): Spermatheca, small and stout, with basal lobe bigger than apical one, well sclerotized, with median part short and less sclerotized. Spermatic duct very long without any expanded area. Spermathecal gland present.

Female uroventrite VIII (Fig. 322.7): Distally rounded with apical dimple. Proximal edge slightly convex. Spiculum long, digitiform, with apex rounded.

Variability. Length of paratypes 1.9-2.3 mm.

Etymology. The new species is dedicated to Valentina Balestra, one of the new recruits of Piedmontese biospeleology, companion of numerous excursions.

Discussion. As mentioned in the diagnosis, *Bathysciola balestrae* sp. nov. is, morphologically, closely related to *Bathysciola monregalensis* from Val Casotto which, at the time of the original description (Giachino 1988) appeared geographically isolated from congeneric species. The discovery of this new species, together with the others described here, partially fills the existing hiatus between *Bathysciola casalei* known from Limone, Piemonte (CN), and these more southern species.

Distribution (Fig. 325.8). Italy. This new species is known from some sites located all in the slopes of the mountain that ends with Cima Ciuaiera, above the village of Ormea (CN), Piedmont. In these sites it was collected under large stones by means of subterranean traps.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.08	0.08	0.04	0.03	0.04	0.04	0.05	0.03	0.05	0.05	0.09
Width	0.04	0.03	0.02	0.02	0.03	0.03	0.04	0.04	0.06	0.07	0.08

TABLE 6. Measurements of antennomeres of the holotype of *Bathysciola balestrae* sp. nov. (mm).

Bathysciola chestai sp. nov.
(Figs. 323.1-323.7)
https://zoobank.org/NomenclaturalActs/C806D117-25BD-4204-8CAA-00BC084E0B74

Type locality. Italy, Cuneo, Vinadio, Valle Stura di Demonte, Tana Neraissa 1, Cave Cadastre No. 1074 Pi/CN, UTM: 32T 354296 4908574, 1,030 m.

Type series. Holotype ♂ (CPMG): labelled [Italia, Vinadio (CN), Grotta sulla strada di Neirassa, 26.VII.2019, M. Chesta & E. Lana leg.], [HOLOTYPUS / *Bathysciola* / *chestai* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 3 ♂♂, 2 ♀♀; 25.X.2013, E. Lana & M. Chesta, 2 ♂♂, 4 ♀♀, one female with code voucher DNA extraction AN681 (CFL); 30.X.2013, P.M. Giachino leg., 4 ♂♂. All the specimens with paratype label [Paratypus / *Bathysciola* / *chestai* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, CDV).

Diagnosis. A *Bathysciola* of small size, 1.6 mm, similar to *B. casalei* in shape of median lobe of aedeagus, but from this well distinguished by body shape, with elytra more elongated, and by structure of endophallus.

Description. Holotype ♂. Small size, 1.6 mm, habitus bathyscioid (Fig. 323.1).

Head: Retractile, with complete occipital carina; eyes absent.

Antennae: Short. Just reaching, stretching backward pronotal base; first antennomere shorter, and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th as long as 9th and 10th together. Antennal formula: see Table 7.

Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved, subrectilinear near posterior angles; base bisinuate; posterior angles acute and prominent.

Elytra: Without transverse striolae, with parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia; metatibiae hardly curved; metafemora toothed (Fig. 323.3).

Mesoventral keel (Fig. 323.2): Short, curved anteriorly, with apex untoothed and largely rounded, with inferior edge not serrated and not reaching metaventrite.

Median lobe of aedeagus: Slightly arched in lateral view (Fig. 323.4) up to uncurved tip. In dorsal view slender (Fig. 323.5), with sides not convergent in apical part, but emarginated at apical third, after protruded in an apex shaped like a beak, subtruncated and not lanceolate.

Endophallus (Fig. 323.5): Endophallus with an internal armature consisting of two sclerotized pieces, differentiating two different parts (basal and medial). «Y»-piece and flagellum in basal area present. Median part with one phanera sclerotized, «Y»-shaped, and upside down.

Parameres (Fig. 323.6): Shorter than median lobe. Not enlarged at apex, but sinuated in dorsal view. Apex with three setae, two long apical, and another one shorter, subapical on inner side.

Female. With antennae shorter and protarsomeres tetramerous non-dilated.

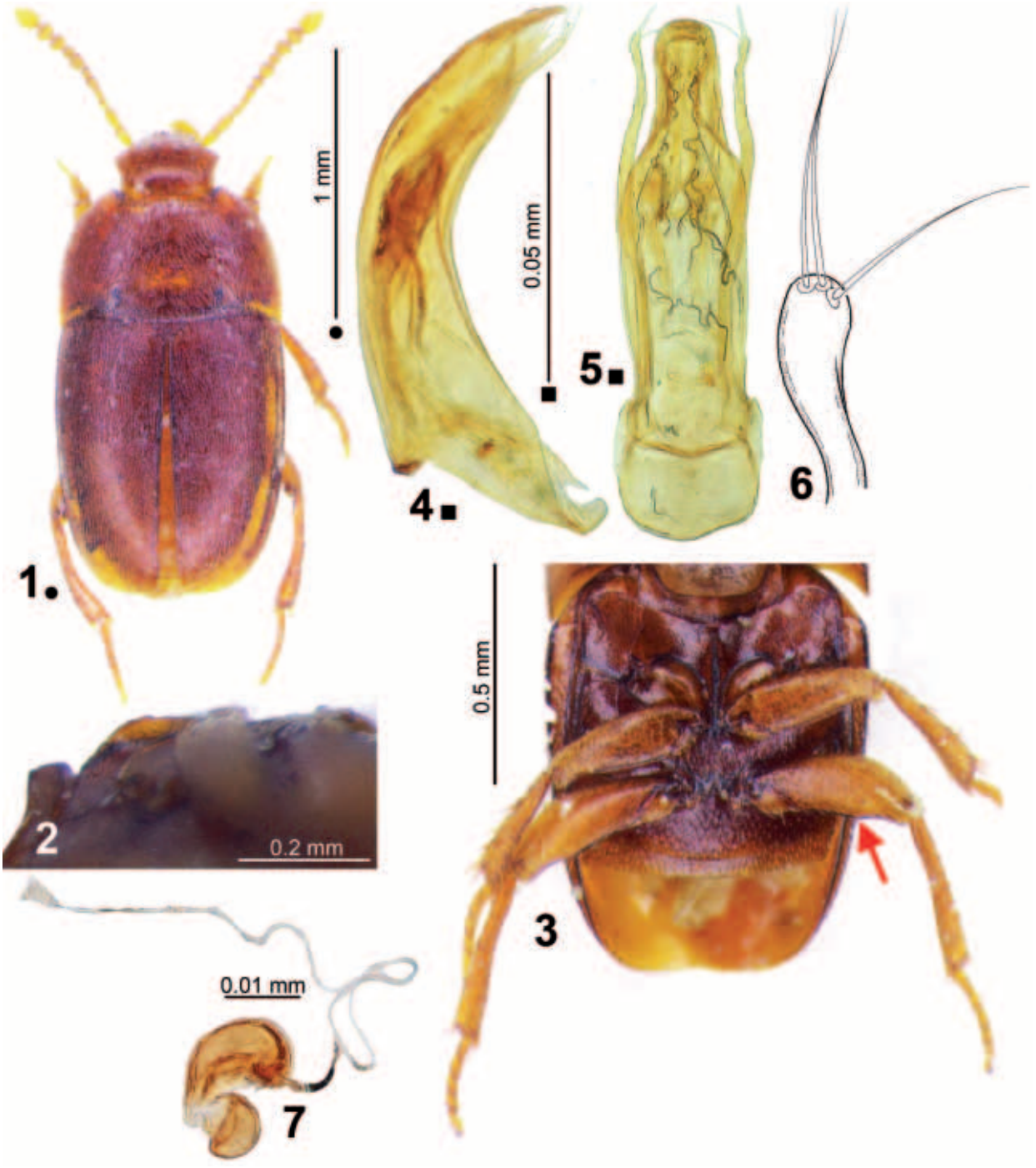
Spermathecal complex (Fig. 323.7): Spermatheca, small and stout, with basal lobe bigger than apical one, well sclerotized, with median part short and less sclerotized. Spermatic duct very long without any expanded area. Spermathecal gland present.

Female uroventrite VIII: Unknown.

Variability. Length of paratypes 1.6-1.7 mm.

Etymology. The new species is dedicated to Michelangelo (Mike) Chesta, Piedmontese biospeleologist, companion of numerous excursions.

Discussion. As mentioned in the diagnosis, *Bathysciola chestai* sp. nov. is, morphologically and molecularly, closely related to *Bathysciola casalei* from Limone, Piemonte, which, at the time of the original description (Giachino 1988)



FIGURES 323.1–323.7: *Bathysciola chestai* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Ventral view, (**4**) Aedeagus in lateral view, (**5**) Aedeagus in dorsal view, (**6**) Apex of paramere, (**7**) Spermathecal complex.

appeared geographically isolated from congeneric species. The discovery of this new species, together with the others described here, partially fills the existing hiatus between *Bathysciola casalei* and *Bathysciola guedeli* from Crissolo (Po Valley).

Distribution (Fig. 325.8). The new species *Bathysciola chestai* sp. nov. is known only from the type locality, the Tana Neraissa 1 cave, near Vinadio (CN), in Stura di Demonte valley. This site is located at 1,030 m.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.07	0.08	0.04	0.03	0.03	0.03	0.05	0.02	0.04	0.04	0.09
Width	0.04	0.03	0.02	0.02	0.02	0.02	0.04	0.03	0.04	0.05	0.06

TABLE 7. Measurements of antennomeres of the holotype of *Bathysciola chestai* sp. nov. (mm).

Bathysciola lanai sp. nov.
(Figs. 324.1-324.7)
https://zoobank.org/NomenclaturalActs/BA6CCF09-D887-4263-A328-CBB67B7BAFF1

Type locality. Italy, Cuneo, Fabrosa Soprana, Faggeta davanti allo Grotta di Bossea, UTM: 32T 407520 4899525, 830 m.

Type series. Holotype ♂ (CPMG): labelled [Italy, Cuneo, Fabrosa Soprana, Faggeta davanti allo Grotta di Bossea, UTM: 32T 407520 4899525, 830 m. 19.VI/7.VII.2012, E. Lana], [HOLOTYPUS / *Bathysciola* / *lanai* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 3 ♂♂, 4 ♀♀; same collection data, 24.6.2012, 4 ♂♂, 3 ♀♀, one male with DNA extraction code voucher AN678 (CFL); same collection data, 14.VI.2013, 3 ♂♂, 2 ♀♀; Italia, Piemonte, Roburent (CN), Case Il Torno 1,074 m, Pozzo Innominato, 2.IX.2022, Chesta & Lana, 1 ♂. All the specimens with paratype label [Paratypus / *Bathysciola* / *lanai* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, CDV, MNCN).

Diagnosis. A *Bathysciola* of size about 2.0 mm, similar to *Bathysciola monregalensis* in shape of median lobe of aedeagus, but from this well distinguished by body shape more elongated and by structure of endophallus.

Description. Holotype ♂. Medium size, 1.9 mm, bathyscioid body (Fig. 324.1).

Head: Retractile, with complete occipital carina; eyes absent.

Antennae: Short. Reaching, stretching backward pronotal base; first antennomere as long as the second but more robust. Antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th as long as 9th and 10th together. Antennal formula: See Table 8.

Pronotum: Transverse, broadest just before base, regularly curved towards anterior angles and less curved towards posterior angle; base bisinuate; posterior angles acute and prominent.

Elytra: Without transverse striolae, with parasutural stria.

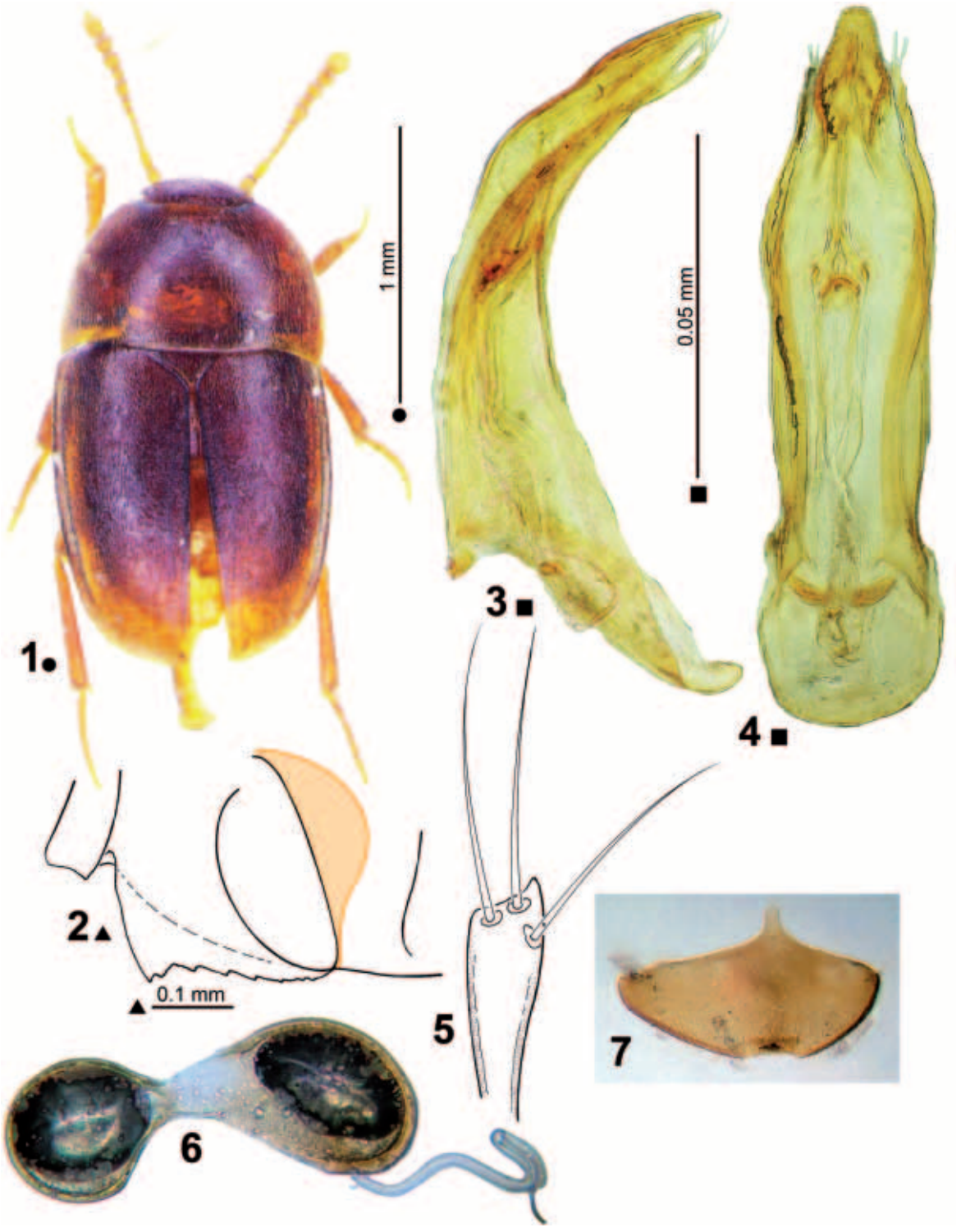
Legs: Apex of tibiae on the inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia; metatibiae straight.

Mesoventral keel (Fig. 324.2): Tall, rectilinear anteriorly, with a large tooth at apex and inferior edge serrated, not reaching metaventrite.

Metaventrite suture (Fig. 324.2): In sinuous curve, distant in upper two thirds so it covers a broad curved area, very close to coxal cavity in lower third.

Median lobe of aedeagus: In lateral view slightly curved (Fig. 324.3) up to uncurved tip. In dorsal view slender (Fig. 324.4), with sides convergent in apical part; apex subtruncate, not lanceolate.

Endophallus (Fig. 324.4): With internal armature consisting of two sclerotized pieces, differentiating two regions (basal and medial). «Y»-piece and flagellum in basal area present. Median part with two sclerotized phanerae superposed, cup-shaped and upside down.



FIGURES 324.1–324.7: *Bathysciola lanai* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Spermatheca, (**7**) Female uroventrite VIII.

Parameres (Fig. 324.5): Shorter than median lobe. Not enlarged at apex. Apex with three setae, two long apical, and another one shorter, subapical, on inner side.

Female. With body stockier, with antennae shorter and protarsomeres tetramerous and non-dilated.

Spermathecal complex: Spermatheca (Fig. 324.6) small and stout, with basal lobe bigger than apical one, well sclerotized; median part short and less sclerotized. Spermatic duct without any expanded area. Spermathecal gland present.

Female uroventrite VIII (Fig. 324.7): Distally rounded with an apical dimple. Proximal edge subrectilinear, convergent. Spiculum long, digitiform, with rounded apex.

Variability. Length of paratypes 1.8-2.2 mm.

Etymology. This new species is dedicated to Enrico Lana, biospeleologist, as a sign of friendship.

Discussion. As mentioned in the diagnosis, *Bathysciola lanai* sp. nov. is, morphologically, closely related to *Bathysciola monregalensis* from Val Casotto and *Bathysciola balestrae* sp. nov. *Bathysciola monregalensis* at the time of the original description (Giachino 1988) appeared geographically isolated from congeneric species. The discovery of this new species, together with the others described here, partially fills the existing hiatus between *Bathysciola casalei* known from Limone (Piemonte, CN) and these more southern species.

Distribution (Fig. 325.8). This new species is known for two sites located near the entrance of the Bossea Cave, Frabosa Soprana (CN), Piedmont. It was collected under stones in *Fagus* wood at 830 m. A single specimen was collected also in Pozzo Innominato cave, located on the right slope of the same valley (Corsaglia Valley) at 1,070 m.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.09	0.09	0.04	0.05	0.04	0.04	0.06	0.03	0.05	0.05	0.1
Width	0.04	0.03	0.02	0.02	0.02	0.03	0.05	0.04	0.05	0.05	0.05

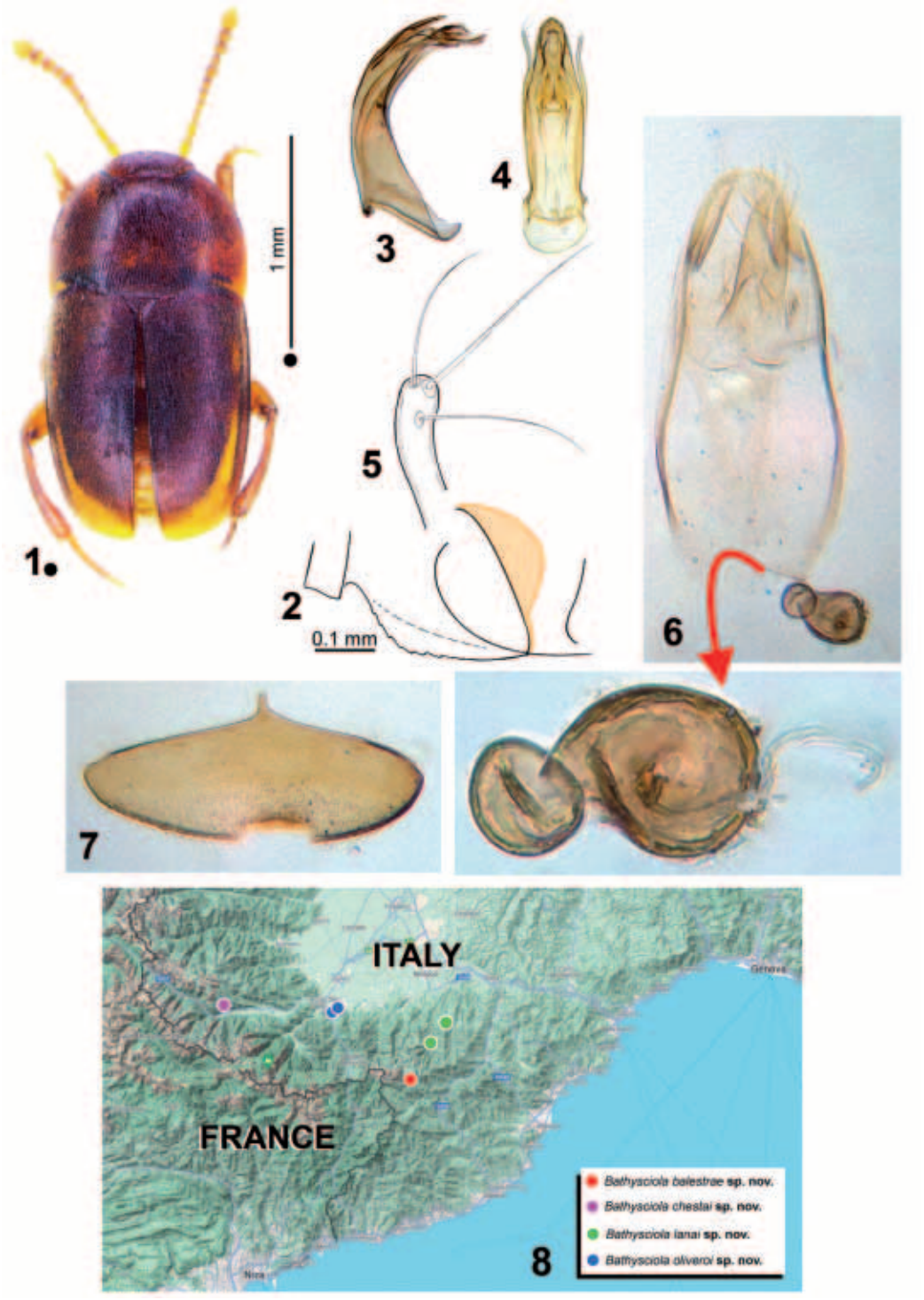
TABLE 8. Measurements of antennomeres of the holotype of *Bathysciola lanai* sp. nov. (mm).

Bathysciola oliveroi sp. nov.
(Figs. 325.1-325.7)
https://zoobank.org/NomenclaturalActs/F58896E9-36E9-4A9B-8E34-E0311C606530

Type locality. Italy, Cuneo, Robilante, Valle Vermenagna, Riparo I sotto Tetti Pignuna, Cave Cadastre No. 210 Pi/CN, UTM: 32T 381695 4906656, 688 m.

Type series. Holotype ♂ (in col. Giachino): labelled [Italy Cuneo Robilante / Valle Vermenagna / Riparo I sotto Tetti / Pignuna, 210 Pi/CN], [UTM: 32T 381695 / 4906656, 688 m / 23.8.2013 / E. Lana & M. Chesta], with holotype label [HOLOTYPUS / *Bathysciola* / *oliveroi* sp. n. / Fresneda *et al*. 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 11 ♂♂, 3 ♀♀, one male with DNA extraction code voucher AN679 (CFL); same data except 27.VII.2019, 11 ♂♂, 17 ♀♀; same data except 16.VIII.2013, 4 ♀♀; Piemonte, Boves (CN), Grotta della Bercia Pi 3034, 961 m, 15.X.2022, M. Chesta & E. Lana leg., 11 ♂♂, 21 ♀♀ (CPMG, CFL, CDV); with the same data except 9.IX.2022, M. Chesta & E. Lana leg., 1 ♂ (CPMG). ; I – Cuneo, Entracque / SE, Gias d'Ischietto / leg. Kahlen, 1.360 m Buchenwald / Quellhorizont / BF 31.5-20.7.2009 FERDINANDEUM / INNSBRUCK / SLG. KAHLEN 4 ♂♂ and 9 ♀♀; same data 7.10.2009-24.5.2010, 6 ♂♂ and 4 ♀♀ (Coll. Kahlen, Museum Ferdinandeum Innsbruck, CPMG). All the specimens with paratype label [Paratypus / *Bathysciola* / *oliveroi* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, CDV, MNCN).

Diagnosis. A *Bathysciola* of small size, about 1.5 mm, similar to *Bathysciola guerzoi* and *Bathysciola chestai* sp. nov. in shape of median lobe of aedeagus, but from this well distinguished by body shape more elongated, and by structure of endophallus.



FIGURES 325.1–325.8: *Bathysciola oliveroi* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Spermathecal complex and magnification of the spermatheca, (**7**) Female uroventrite VIII. (**8**) Distribution map of *Bathysciola balestrae* **sp. nov.**, *B. chestai* **sp. nov.**, *B. lanai* **sp. nov.** and *B. oliveroi* **sp. nov.**

Description. Holotype ♂. Small size, 1.5 mm, habitus bathyscioid (Fig. 325.1).

Head: Retractile, with complete occipital carina; eyes absent.

Antennae: Short. Just reaching pronotal base; first antennomere shorter, and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th as long as 9th and 10th together. Antennal formula: see Table 9.

Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved, subrectilinear, near posterior angles; base bisinuate; posterior angles acute and prominent.

Elytra: Without transverse striolae, with parasutural stria.

Legs: Apex of tibiae on inner side with spurs polydentate; apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia; metatibiae curved.

Mesoventral keel (Fig. 325.2): Short, largely rounded anteriorly, with apex untoothed, and inferior edge smooth, not reaching metaventrite.

Metaventrite suture (Fig. 325.2): In sinuous curve, distant in upper two thirds so it covers a broad curved area, very close to coxal cavity in lower third.

Median lobe of aedeagus: In lateral view slightly curved (Fig. 325.3), up to uncurved tip. In dorsal view slender (Fig. 325.4), with sides convergent in apical part; apex regularly rounded and not lanceolate.

Endophallus (Fig. 325.4): With an internal armature consisting of two sclerotized pieces, differentiating two parts (basal and medial). «Y»-piece and flagellum in basal area present. Median part with one phanera sclerotized «H»-shaped.

Parameres (Fig. 325.5): Shorter than median lobe. Not enlarged at apex. Apex with three setae, two long apical, and another one shorter, subapical, on inner side.

Female. With body more stocky, antennae shorter, metatibiae straight and protarsomeres tetramerous non-dilated.

Spermathecal complex (Fig. 325.6): Spermatheca, small and stout, with basal lobe bigger than apical one, well sclerotized; with median part short and less sclerotized. Spermatic duct long without any expanded area. Spermathecal gland present.

Female uroventrite VIII (Fig. 325.7): Distally rounded with an apical dimple. Proximal edge slightly convex. Spiculum long, digitiform, with apex rounded.

Variability. Length of paratypes 1.4-1.8 mm.

Etymology. The new species is dedicated to Dario Olivero, one of the new recruits of Piedmontese biospeleology, companion of numerous excursions.

Discussion. As mentioned in the diagnosis, *Bathysciola oliveroi* sp. nov. is, morphologically and molecularly, closely related to *Bathysciola guerzoi* from San Martino Canavese (TO) which, at the time of the original description (Giachino 1988) appeared geographically isolated from congeneric species. *Bathysciola oliveroi* sp. nov. appears less closely related to the two geographically closest species *Bathysciola casalei* and *Bathysciola chestai* sp. nov.

Distribution (Fig. 325.8). Italy. Is known only from three localitys in Piedmont: the Cave Riparo I sotto Tetti Pignuna, near Robilante in Vermenagna Valley, Grotta della Bercia in Boves, and Gias d'Ischietto near Entracque.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.09	0.09	0.04	0.03	0.04	0.04	0.05	0.03	0.04	0.04	0.08
Width	0.04	0.03	0.02	0.02	0.02	0.02	0.04	0.04	0.05	0.05	0.06

TABLE 9. Measurements of antennomeres of the holotype of *Bathysciola oliveroi* sp. nov. (mm).

Batinoscelis degiovannii sp. nov.
(Figs. 326.2, 326.4, 326.7, 327.2, 327.5)
https://zoobank.org/NomenclaturalActs/CB836C7A-D57A-4395-9033-AD5ED0B92894

Type locality. Italy, Sardinia, Ogliastra, Monte Tonneri.

Type series. Holotype ♂ (CPMG): labelled [I. Sardegna / Ogliastra / Monte Tonneri / 20.III.2014, A. Degiovanni leg.], [HOLOTYPUS / *Batinoscelis* / *degiovannii* sp. n. / Fresneda *et al*. 2024] (rl); aedeagus on transparent card mounted on the same pin as the holotype. Paratype: Same data as the holotype, 1,100 m, 1 ♀ (CPMG), with paratype label [Paratypus / *Batinoscelis* / *degiovannii* sp. n. / Fresneda *et al*. 2024] (rl).

Description. Holotype ♂. Size 2.2 mm. Facies bathyscioid (Fig. 326.2); body slightly elongated and oval, slightly acuminate backwards and slightly convex. Pubescence yellowish, thin, short, lying down and most numerous on elytra. Coloration dark reddish.

Head: Quite thick, wider than long, with occipital carina complete but poorly marked; punctation thin and sparse, with integument shiny; without eyes.

Antennae: Relatively long, reaching anterior third of elytra; 1st antennomere shorter than 2nd, the longest of all; 3rd and 5th antennomeres somewhat longer than 4th and 6th, being equal to each other; club well differentiated, with the 8th antennomere ovoid, as long as wide; 9th and 10th slightly longer than wide, the 11th pointed and somewhat shorter than the sum of two preceding ones. Antennal formula: see Table 10.

Pronotum: Slightly convex and very transverse, twice as wide as long, with lateral margins regularly curved; maximum width at base, being as wide as elytra; posterior angles slightly tapering facing backwards and slightly covering elytra sides; angles acute. Punctation fine, with points distant and shallow.

Elytra: Slightly convex and little elongated, 1.3 times longer than wide; sides parallel in anterior half, then decrease in a regular arc until apices. Rounded and without transverse striae, with points larger than those of pronotum, somewhat rough and aligned transversely in basal half of elytra; parasutural stria blurry.

Legs: Short and not very thick; protibiae on the inner side with spurs polydentate, protarsi pentamerous and clearly narrower than apical part of protibiae; meso- and metatibiae straight, both armed with robust spines and bristly on outer part.

Mesoventral keel (Fig. 326.4): High, with apex pointed or toothed, angle subrectilinear; posterior process not reaching metaventrite; anterior edge arched with flange, posterior edge serrated and slightly concave.

Metaventrite suture (Fig. 326.4): A single suture between mesoventrite and anteromedian process of metaventrite delimiting an area curved in upper half and remaining close to coxal cavity in lower half.

Metatergal apparatus and *Metendosternite*: Unknown.

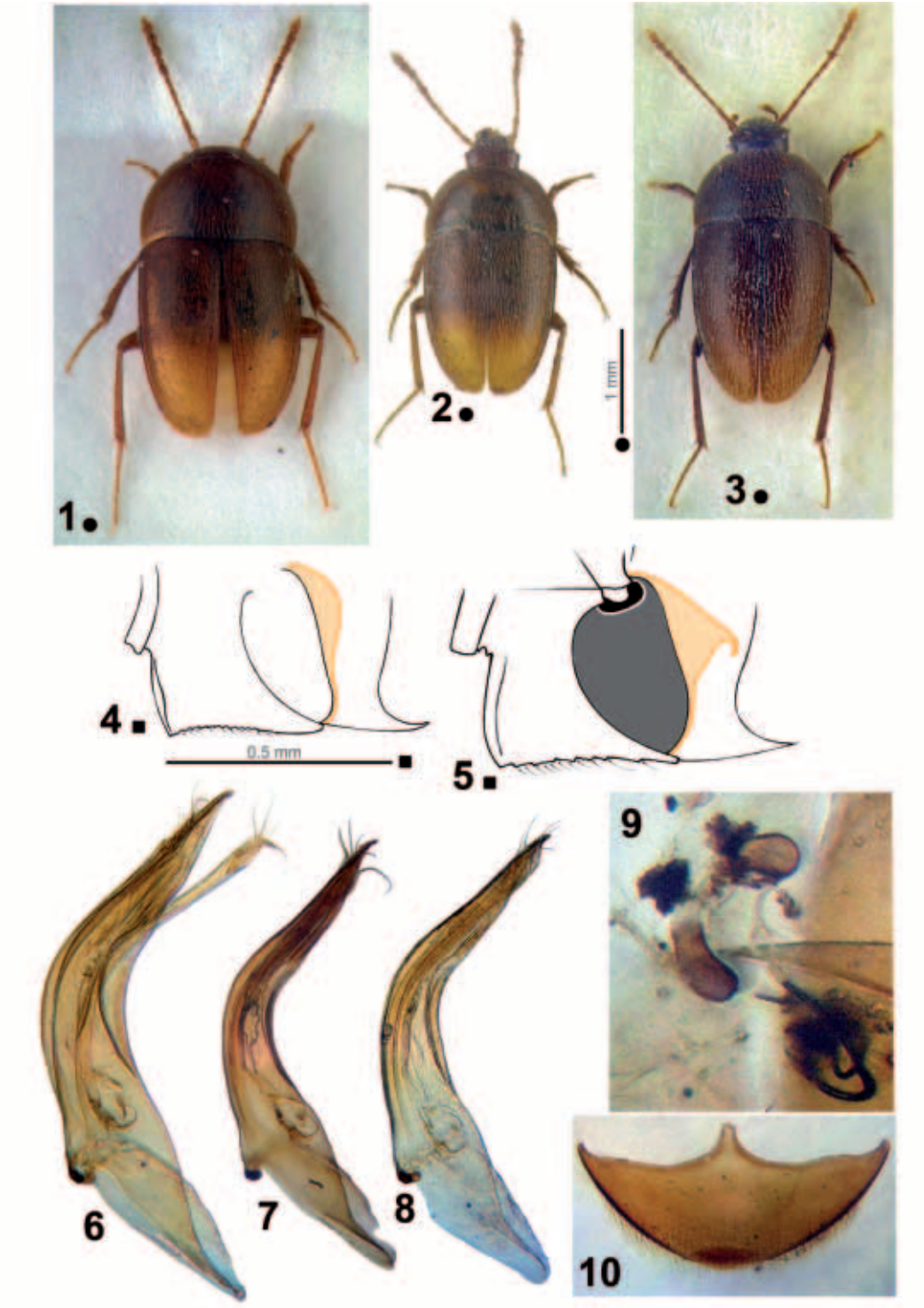
Median lobe of aedeagus: Slender. In lateral view (Fig. 326.7) basal two thirds regularly arched and in apical third the dorsal face straight until the final area that curves in arc towards ventral face; tip not very pointed and ventrally beveled. In dorsal view (Fig. 327.2), sides of basal two-thirds in slightly sinuous arc, then progressively narrowing to apex regularly rounded. Basal lamina longer and somewhat narrower than ventral lamina of the tegmen, with apical area arched.

Endophallus (Fig. 327.2): Three well-differentiated parts. Basal part with the arms of «Y»-piece short, thin and recurved, between them a flagellum short and diffuse; middle region with a pair of bars parallel and elongate in the upper part and curved in the lower part, and higher up two pairs of small sclerotized pieces; apical part with pair of short reinforcing bands.

Parameres (Fig. 327.5): Little curved and somewhat shorter than median lobe; apical part not widened, with three apical setae with close insertion pores, lower seta somewhat recurved; on subapical inner side a penicillum of numerous setae inserted into a short cavity, rather deep and oval.

Female. Female paratype entered our availability after revision was already completed so it was not possible to provide iconography. Length of paratype 2.3 mm. Female with body stockier, with antennae shorter, protarsomeres tetramerous non-dilated.

Etymology. The species is dedicated to its collector, Augusto Degiovanni – Bubano (BO), Italy –.



FIGURES 326.1–326.10: *Batinoscelis* spp. Habitus of: (**1**) *B. diabolicus*, (**2**) *B. degiovannii* **sp. nov.**, (**3**) *B. onnisi* **sp. nov.** Mesoventral keel of: (**4**) *B. degiovannii* **sp. nov.**, (**5**) *B. onnisi* **sp. nov.** Aedeagus in lateral view of: (**6**) *B. diabolicus*, (**7**) *B. degiovannii* **sp. nov.**, (**8**) *B. onnisi* **sp. nov.** *B. onnisi* **sp. nov.** (**9**) Spermathecal complex and (**10**) Female uroventrite VIII.

Discussion. *Batinoscelis* species are characterized by four setae in the apical part of the parameres and a cavity with penicillum. Of them, one species has three setae, *B. degiovannii* sp. nov. (Fig. 327.5). Undoubtedly, the closest species is *B. diabolicus* comb. nov. both in body facies (Fig. 326.1) and aedeagus (Fig. 326.6, 327.1); it coincides with this species in the existence of a single sinuous metaventral suture that delimits a hemicircular area in its anterior half and runs adjacent to the mesocoxal cavity in its posterior half; both *B. lostiae* comb. nov. (Fig. 158.2) like *B. onnisi* sp. nov. (Fig. 326.5) have two sutures that delimit a triangular area.

From *B. diabolicus* comb. nov. it differs because *B. degiovannii* sp. nov. is smaller in size, the antennae are a little longer with the 9th and 10th antennomeres somewhat longer than wide and the ventral margin of the mesoventral keel is slightly more concave and serrated; also the median lobe of aedeagus, in dorsal view, the apical third is less narrowed and the parameres are less arched with a different shape of the penicillum pit, and especially because in *B. diabolicus* comb. nov. they have four setae (Fig. 327.4).

Distribution (Fig. 327.7). This species is only known from the type locality, on Mount Tonneri, which is located about nine kilometers, as the crow flies, from the locality of *B. diabolicus* comb. nov. on Mount Arqueri (Casale *et al*. 2009). The environment and circumstances of its discovery are unknown.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.12	0.15	0.10	0.08	0.10	0.08	0.13	0.07	0.11	0.08	0.15
Width	0.06	0.05	0.03	0.04	0.04	0.04	0.07	0.06	0.09	0.09	0.09

TABLE 10. Measurements of antennomeres of the holotype of *Batinoscelis degiovannii* sp. nov. (mm).

Batinoscelis onnisi sp. nov.
(Figs. 326.3, 326.5, 326.8-326.10, 327.3, 327.6)
https://zoobank.org/NomenclaturalActs/1D07EFFE-B6E3-49B1-A238-FDE916A16EFF

Type locality. Italy, Sardinia, Nurri, Grotta N. 5.

Type series. Holotype ♂ (CPMG): labelled [I. Sardegna / Nurri / Grotta N. 5 / 19.IV.2011 Onnis], [HOLOTYPUS / *Batinoscelis* / *onnisi* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: 3 ♀♀, same data as the holotype; 1 ♂ and a rest labelled [I. Sardegna / Gr. Sa Lilla / 14.5.2011 / C. Onnis]; 5 ♂♂, 2 ♀♀ labelled [I. Sardegna (CA) / Miniera Sa Lilla / 28.11.2010 / C. Onnis]; Sardinia, Villasalto (SU), Sa Rutta 'e Scusi, 14.III.2010, A. Casale leg., 1 ♂ (DNA code voucher RA267); 1 ♀ labelled [Italia, Sardegna, Grotta Sa Foxi 'e s'Abba (0728 SA/NU), 39.816 9.489, 22.II.2022, M. Isaia - G. Nicolosi leg.]. All paratypes with a red label [PARATYPUS / *Batinoscelis* / *onnisi* sp. n. / Fresneda *et al*. 2024] (CPMG, CFL, CDV, CAC).

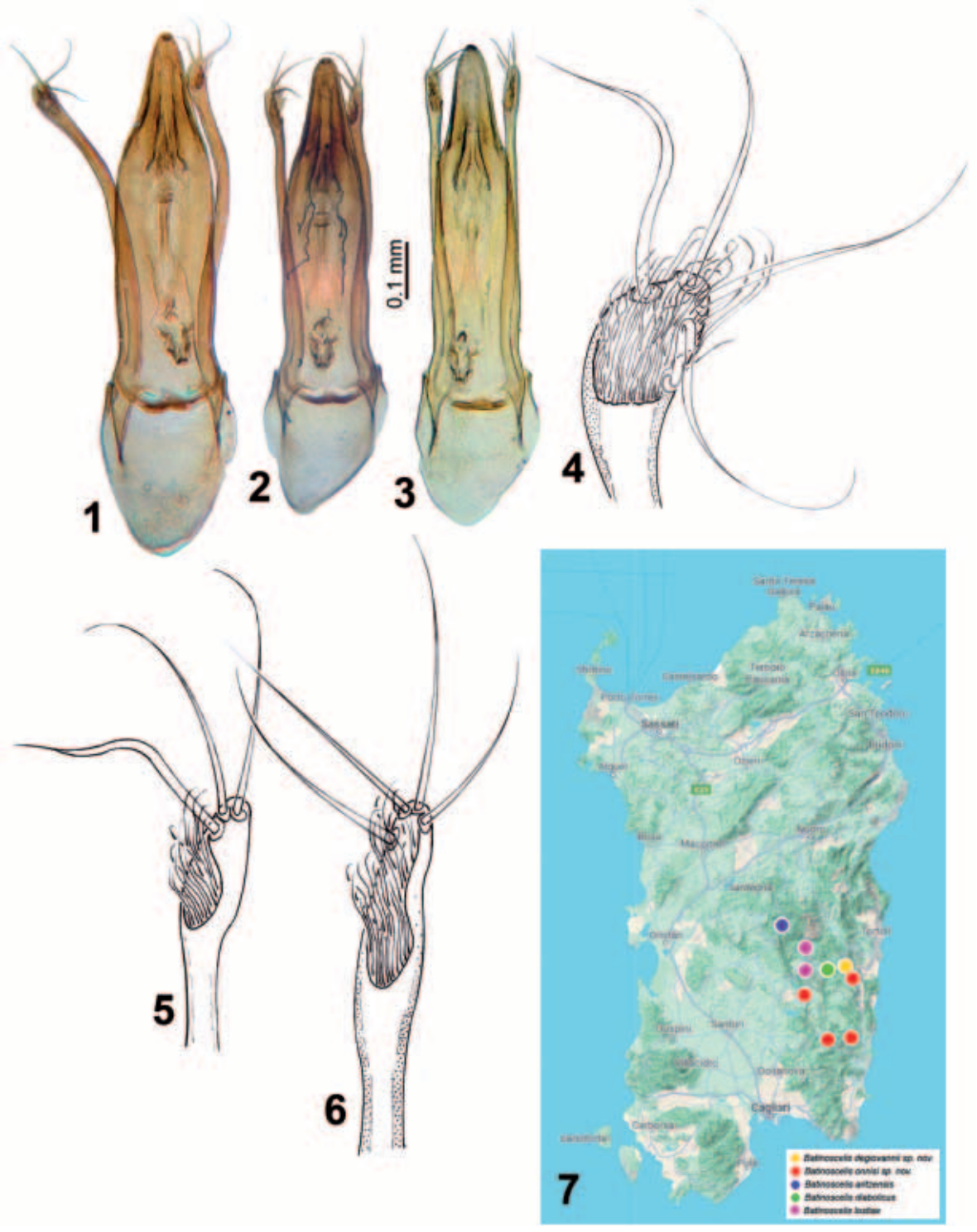
Description. Holotype ♂. Medium size, 2.5 mm. Habitus bathyscioid (Fig. 326.3); ovoid, lateral margins regularly curved and body poorly convex. Uniformly covered by golden pubescence, short and lying.

Head: Retractile, with complete occipital carina, although somewhat blurred; punctation fine and superficial; eyes absent.

Antennae: Antennae quite long reaching elytral third; all antennomeres longer than wide; first antennomere somewhat shorter and more robust than second; 2nd and 11th antennomeres longest and of equal length; 9th and 10th together longer than 11th. Antennal formula: see Table 11.

Pronotum: Very transverse, 1.9 times wider than long, with regularly curved sides; maximum width near base, as wide as maximum width of elytra; posterior vertexes not very pointed with angles acute; basal margin very slightly bisinuate.

Elytra: Elongated and oval, with maximum width in anterior third, from here they decrease regularly until rounded apex; without transverse striolae, covered with irregular punctation; parasutural stria present, more marked along median part.



FIGURES 327.1–327.7: *Batinoscelis* spp. Aedeagus in dorsal view of: (**1**) *B. diabolicus*, (**2**) *B. degiovannii* **sp. nov.**, (**3**) *B. onnisi* **sp. nov.** Apex of paramere of: (**4**) *B. diabolicus*, (**5**) *B. degiovannii* **sp. nov.**, (**6**) *B. onnisi* **sp. nov.** (**7**) Distribution map of species of the genus *Batinoscelis* **stat. nov.** in Sardinia.

Legs: Quite long and thin; apex of tibiae on inner side with spurs polydentate; protarsi pentameres little dilated, less wide than apex of protibiae; apical baskets of meso- and metatibiae incomplete; mesotibiae somewhat curved and metatibiae straight, both armed with bristly spines, longer than internal spurs in mesotibiae.

Mesoventral keel (Fig. 326.5): Tall and short, with an obtuse angle and apex forming a small tooth; anterior edge rounded and flanged; posterior edge slightly concave, finely serrated, silky and posterior apophysis slightly exceeds mesoventrite.

Sutures of the metaventrite (Fig. 326.5): Upper half delimited in a triangular area by both sutures with junction vertex elbowed; lower suture in its basal half borders coxal cavity.

Median lobe of aedeagus: In lateral view (Fig. 326.8) slender; ventral margin in regular curve and dorsal margin with basal half convex and distal half rectilinear with apex curved towards ventral face and tip rounded. In dorsal view (Fig. 327.3) with subparallel sides in basal 2/3, then concave forming a subtriangular apical part and apex regularly rounded.

Endophallus (Fig. 327.3): Internal armature allows differentiating three regions. Basal part with «Y»-piece, thin arms and corkscrew apical area; middle part with two narrow pieces in elongated arches; apical part with two reinforcing bands and between them in basal part with two short sclerotized pieces.

Parameres (Fig. 327.6): Slender, slightly sigmoid and a little shorter than median lobe. Apical club elongated but poorly differentiated, with four long setae, three apical and one subapical, and on inner side with a pit elongated and shallow into which fine, short setae are inserted, forming a penicillum.

Female.

Spermathecal complex (Fig. 326.9): Spermatheca with three well differentiated parts; two lobes well sclerotized, distal lobe more elongated and as wide as proximal one, latter more globose; hyaline joining duct as long as distal lobe; spermatic duct short, about 2-3 times length of spermatheca. Small spermathecal gland present that converges with spermiduct to flow into inferior and posterior part of proximal lobe.

Female uroventrite VIII (Fig. 326.10): Distal part in regular arc; short spiculum with apex rounded.

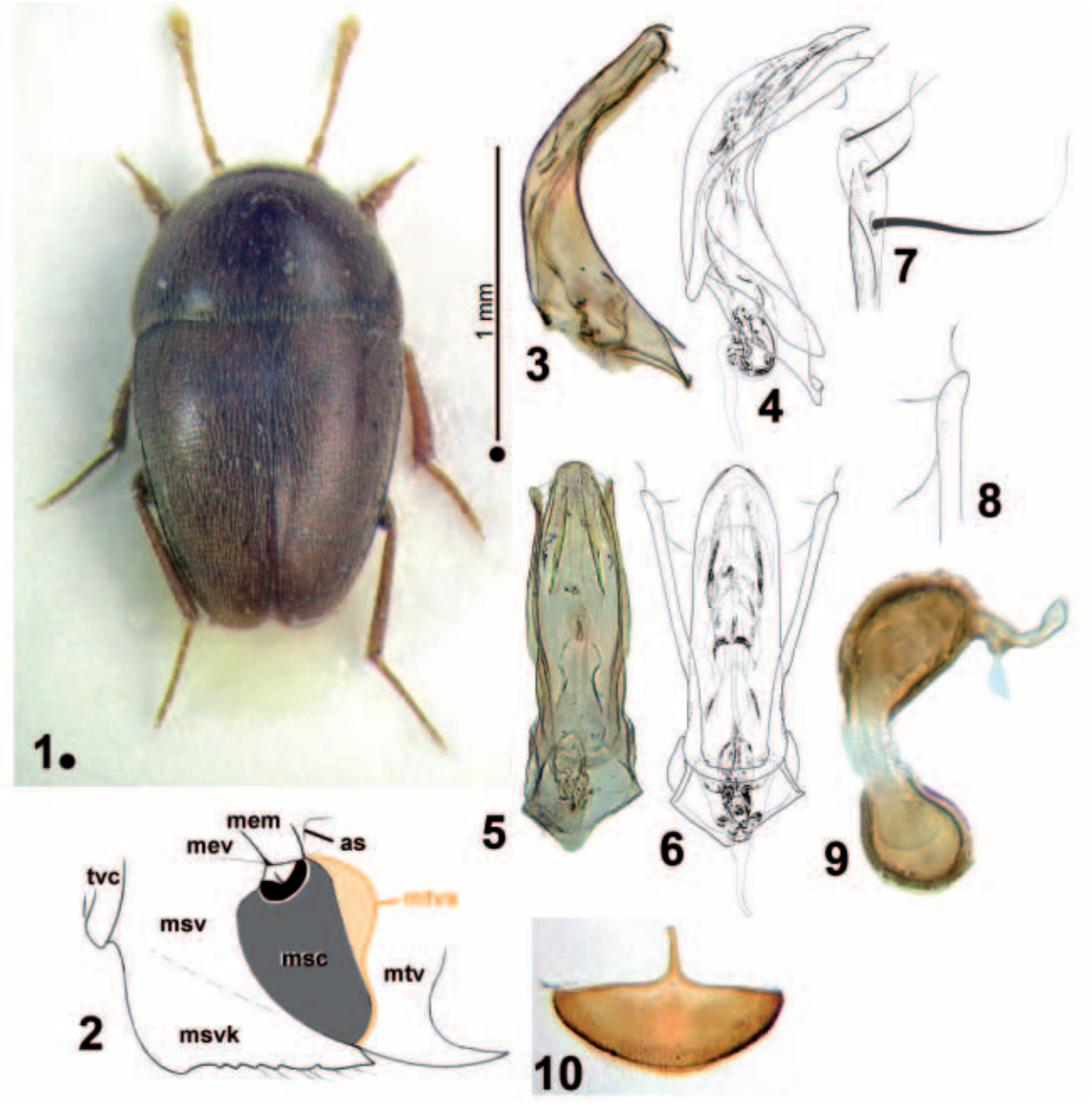
Etymology. The new species is dedicated to the collector, the biospeleologist Carlo Onnis (Sardinia, Italy).

Discussion. Of the four species treated here we have molecular data from two, while those of *B. aritzensis* comb. nov. and *B. diabolicus* comb. nov. are lacking. The two species with molecular data are: *B. lostiae* comb. nov. and *B. onnisi* sp. nov. In the phylogenetic tree (Fig. 1G) the genetic distance between them is very clear and the morphological differences between *B. lostiae* and *B. onnisi* sp. nov. should be observed in the penicillum pit, which is more elongated and shallower in *B. onnisi* sp. nov. and also in this species the reinforcing bands are longer and narrower, in addition to the differently sclerotized pieces.

Distribution. Italy. Southeast of Sardinia. Four scattered localities in low-lying mountainous areas between the Fiume Flumendosa and the Tyrrhenian Sea, south of mount Perda ‘e Liana.

Segment	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**
Length	0.12	0.17	0.12	0.10	0.11	0.11	0.16	0.08	0.11	0.11	0.17
Width	0.06	0.05	0.04	0.04	0.04	0.05	0.07	0.06	0.07	0.08	0.08

TABLE 11. Measurements of antennomeres of the holotype of *Batinoscelis onnisi* sp. nov. (mm).



FIGURES 328.1–328.10: *Catopsinus* spp. Habitus of: (**1**) *C. rudoyi* **sp. nov.** Pterothorax in lateral view of: (**2**) *C. rudoyi* **sp. nov.** Aedeagus in lateral view of: (**3**) *C. rudoyi* **sp. nov.**, (**4**) *C. pusillus*. Aedeagus in dorsal view of: (**5**) *C. rudoyi* **sp. nov.**, (**6**) *C. pusillus*. Apex of paramere of: (**7**) *C. rudoyi* **sp. nov.**, (**8**) *C. pusillus*. *Catopsinus rudoyi* **sp. nov.**: (**9**) Spermatheca, (**10**) Female uroventrite VIII. Figs **4**, **6**, **8** modified from Zoia & Rampini (1994). Abbreviations: **as**, anapleural suture; **mem**, mesoepimere (mesothoracic epimere); **mev**, mesoepiventrite (mesothoracic epiventrite); **msc**, mesocoxal cavity; **msvk**, mesoventral keel; **msv**, mesoventrite; **mtv**, metaventrite; **mtvs**, metaventral suture; **tvc**, transverse collar.

Catopsinus rudoyi sp. nov.
(Figs. 328.1-328.3, 328.5, 328.7)
https://zoobank.org/NomenclaturalActs/7BB30A3B-1753-49AB-858C-BAFB51E1227A

Type locality. Azerbaijan, Qax [Kakh], Kashkachay, forest litter *Fagus* next to road, 41°23'40.9»N 47°3'0.1»E, 1,160 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): Azerbaijan, Qax [Kakh], Kashkachay, forest litter Fagus next to road, 41°23'40.9»N 47°3'0.1»E, 1,160 m, 5.V.2014, A. Faille, J. Fresneda, I. Ribera & A. Rudoy leg., with holotype label [HOLOTYPUS / *Catopsinus* / *rudoyi* sp. n. / Fresneda *et al*., 2023] (pr, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 2 ♂♂, 2 ♀♀ (CFL, CPMG), 1 ♂ with DNA extraction code voucher: AN62, 1 ♂ in Jena (Germany) for SEM photographys, 1 ex. (MNCN), 1 ex. (code voucher: ZSM-AFM101) and 1 ex. (ZSM), with paratype labels [PARATYPUS / *Catopsinus* / *rudoyi* sp. n. / Fresneda *et al*., 2023] (pr, rl).

Description. Holotype ♂. Size 1.6 mm. Habitus rounded with margins regularly curved (Fig. 328.1). Microphthalmous, with eyes composed of half a dozen pigmented ommatidia.

Antennae: Short with thickened antennomeres from 7th; the 8th is as long as it is wide, shorter than 10th and this in turn also shorter than 9th. Antennal formula: see Table 12.

Pronotum: Transverse, 0.9 mm broad by 0.5 mm long; strongly attenuated forwards, hemispherical in shape; greatest width little before base, which is as wide as elytra; posterior angles straight with apex rounded; base bisinuated; integument microreticulate and hair insertion pores invisible.

Elytra: Short and wide, with margins regularly curved; greatest width near base; apex of each elytra separately rounded; elytral sculpture formed by transverse striolae thick and granular; parasutural stria present with more blurred in basal and apical areas.

Mesoventral keel (Fig. 328.2): Tall, forming a right angle with apex broadly rounded; anterior edge straight, without a ridge, and lower edge somewhat sinuous and toothed.

Suture of the metaventrite (Fig. 328.2): Strongly curved in anterior half, delimiting a well-defined area, and adjoining mesocoxal cavity in posterior half.

Legs: Short, with mesotibiae somewhat curved and metatibiae straight; first three protarsomeres dilated, as wide as distal end of protibia; simple meso- and metafemora with a series of minute spicules on proximal part of posterior margin.

Median lobe of aedeagus: In lateral view (Fig. 328.3) bent at an obtuse angle about half way; gracile and apex prolonged and strongly curved towards ventral part. In dorsal view (Fig. 328.5) with sinuous lateral margins near basal bulb, posteriorly thickens and then regularly decreases to widely curved apex.

Endophallus (Fig. 328.5): Presents three parts. Basal part with «Y»-piece with reduced apical nodules. Middle part with two hyaline dorsal phanerae, two finer ones doubly curved with inverted curves apparently joined at their upper end, and an axial piece consisting of two elongated pieces very close to each other. Apical part with reinforcing bands resting on membranous ligulae and between them other two, finer and hyaline.

Parameres (Fig. 328.7): Shorter than median lobe with basal third strongly curved inwards; apex thickened to form a paddle with a depression or cavity in its inner part, with three setae with distant insertion.

Female. Slightly more robust than male, with elytra somewhat broader and more convex; protarsi not thickened and tetramerous.

Spermathecal complex: Spermatheca (Fig. 328.9) short with basal lobe slightly larger than apical one. Spermathecal gland present, inserted in ductus.

Female uroventrite VIII (Fig. 328.10): With spiculum long and slender.

Etymology. The new species is dedicated to the entomologist Andrey Rudoy, fellow of the expedition to the Caucasus of Azerbaijan in May 2014. The specific name is a noun in the genitive singular.

Discussion. This species is close to *Catopsinus pusillus* with which it shares an identical endophallus structure (Figs. 328.5, 328.6). But the median lobe, both in dorsal and lateral views, and the apex of the parameres of both species



FIGURES 329.1–329.3: *Catopsinus* spp. (**1**) Distribution map of: *C. rudoyi* ***sp. nov.*** (red circle) and *C. pusillu*s (blue circle). (**2**) Detail of the capture point. (**3**) Mixed forest near Kashkachay, bed of a tributary stream of the Alazani River, *locus typicus* of *C. rudoyi* **sp. nov.**

are considerably different. In *Catopsinus pusillus* the apex of the median lobe, in lateral view (Fig. 328.4) is straight and, in dorsal view (Fig. 328.6), the lateral margins are subrectilinear and the apex slightly pointed; while in *C. rudoyi* sp. nov., in lateral view (Fig. 328.3) the apex curves towards the ventral side and, in dorsal view (Fig. 328.5), the lateral margins are more sinuous and curved and the apex is broadly rounded. The parameres, in *Catopsinus pusillus* (Fig. 328.8), are straight along the median part and the apical part is narrower and without a defined cavity on the inner face, while in *C. rudoyi* sp. nov. they are curved in the median region and the apical part is more dilated, with a cavity in which the three setae are inserted (Fig. 328.7).

Distribution (Fig. 329.1). *Catopsinus rudoyi* sp. nov.: Forest litter in a mixed forest next to road near Qax, Kashkachay, in Azerbaijan. The place in question is located a few meters above the bed of a tributary of the great Alazani River (Fig. 329.2). The specimens were found by sifting leaf litter with a Winkler sieve in mixed hardwood forest whose predominant species in the region is *Fagus orientalis* (Fig. 329.3). *Catopsinus pusillus*: Georgia: Ananur (type locality) and Darial (Motschulsky 1840); Marktopi and Gombori (Zoia & Rampini 1994); Dumaniss and Katharinenfeld (Schneider & Leder 1878). Azerbaijan: Araxesthal (Zoia & Rampini 1994). The locality of «Araxesthal», valley of the river Aras, appears in old harvest labels; the region is located in the Nakhchivan Autonomous Republic, an enclave now belonging to Azerbaijan that borders Armenia, Turkey and Iran. This locality is considerably further south than where *Catopsinus pusillus* collection localities are concentrated, including, of course, the type locality. It is very likely that the «Araxesthal» specimens belong to another species.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.06	0.08	0.04	0.04	0.04	0.03	0.06	0.03	0.04	0.05	0.09
Width	0.04	0.04	0.02	0.02	0.03	0.02	0.03	0.03	0.04	0.05	0.07

TABLE 12. Measurements of antennomeres of the holotype of *Catopsinus rudoyi* sp. nov. (mm).

Lakedemoniana mizerakisi sp. nov.
(Figs. 213.1, 213.3, 213.5, 213.7)
https://zoobank.org/NomenclaturalActs/A005E29E-9A7A-48C9-8716-84817445C65B

Type locality. Greece, Peloponnese, Lakonia, Trypi, Caladas cave, 37.09552°N 22.34055°E.

Type series. Holotype ♂ (in col. SMNS): labelled [Greece, Peloponnisos, Lakonia, Trypi, 37.09552 22.34055, «VLOC.24», Caladas cave, VM125], [HOLOTYPUS / *Lakedemoniana* / *mizerakisi* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype; with DNA extraction code voucher SMNS-M475.

Description. Holotype ♂. Length 1.9 mm, facies bathyscioid (Fig. 213.1) regularly oval in shape, with very wide and short appearance.

Head: Occipital carina absent. Punctation thick and spaced. Anophthalmous.

Antennae: As long as half body. Antennal formula: See Table 13.

Pronotum: Broad, transverse and convex with punctation thick and spaced.

Elytra: Very short, barely longer than pronotum, with maximum width at base. Punctation thick, spaced and disordered over the entire surface. Parasutural stria absent.

Legs: Short, protarsi pentameres dilated.

Median lobe of aedeagus: In lateral view (Fig. 213.3) regularly curved, with a very slight dorsal depression in apical quarter and apex somewhat curved near ventral side. In dorsal view (Fig. 213.5) regular, with a constant width until near rounded apex.

Endophallus (Fig. 213.5): With three regions. «Y»-piece in the basal part present with a stylet/flagellum and two adjoining phanerae. Middle part with four two-by-two symmetrical phanerae: upper ones broad and sub-triangular, and lower ones thin and curved; together forming an «H». Apical part with two reinforcing bands.

Parameres (Fig. 213.7): Thick and as long as median lobe. Apex armed with four setae: two apical, one pre-apical and fourth, also apically inserted, on a lateral membranous lamina.

Female. Unknown.

Etymology. The new species is dedicated to Vangelis Mizerakis (State Museum of Natural History, Stuttgart, Germany), the collector of the only specimen. The specific name is a noun in the genitive singular.

Discussion. See Description and Discussion sections of the genus *Lakedemoniana* gen. nov.

Distribution. Greece. Only known from the type locality, Caladas cave in Trypi, western slope ot the Taygetos mountains, in Peloponnese.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.09	0.12	0.07	0.06	0.07	0.05	0.11	0.06	0.09	0.09	0.14
Width	0.04	0.04	0.03	0.03	0.04	0.04	0.05	0.04	0.06	0.06	0.06

TABLE 13. Measurements of antennomeres of the holotype of *Lakedemoniana mizerakisi* sp. nov. (mm).

Latellana benellii sp. nov.
(Figs. 330.1-330.7)
https://zoobank.org/NomenclaturalActs/5244C827-5A48-45E2-9C23-05E2F24DC9A2

Type locality. Italy, Lazio, Formia (LT), Maranola, Monte Sant'Angelo, 41°19'0.8»N 13°38'54.2»E, 1,200 m.

Type series. Holotype ♂ (CPMG): Italia, Lazio, Formia (LT) Maranola, Monte Sant'Angelo, 1,200 m, 14.V.2022, A. Benelli leg., with holotype label [Holotypus / *Latellana* / *benellii* n. sp./ Fresneda *et al*., 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 1 ♀ (CPMG); with the same collection data as the holotype, 11.V.2017, 1,227 m, A. Faille, J. Fresneda, I. Ribera leg., with DNA extraction code voucher AN785, 1 ♂ (CFL); Lazio (FR), Monte Sant'Angelo, 1,200 m, 14.V.2022, A. Benelli & A. Petrioli leg., 1 ♂, 14 ♀♀. Lazio, Monti Aurunci, Formia (LT), Monte Sant'Angelo, Grotta n.c., 14.V.2022, A. Benelli & A. Petrioli leg., 5 ♂♂, 6 ♀♀. Monte Sant'Angelo, (LT), 1,100 m, 2.V.2008, M. Bastianini leg., 2 ♂♂, 2 ♀♀ (CPMG, CFL, CMB, CDV); Lazio, Mt. Aurunci (LT), Spino Saturnia, Mount Sant'Angelo, 1,300 m, 11.V.2024, A. Degiovanni leg., 12 ♂♂, 5 ♀♀ (CPMG). All specimens with paratype label [Paratypus / *Latellana* / *benellii* sp. n. / Fresneda *et al*., 2024] (rl).

Diagnosis. A medium-sized *Latellana* gen. nov. characterized by presence of parasutural stria and by shape of median lobe of aedeagus and parameres, very dilated at apex.

Description. Medium size, 2.5 mm, habitus bathyscioid (Fig. 330.1).

Head: Retractile, with occipital carina complete; eyes absent.

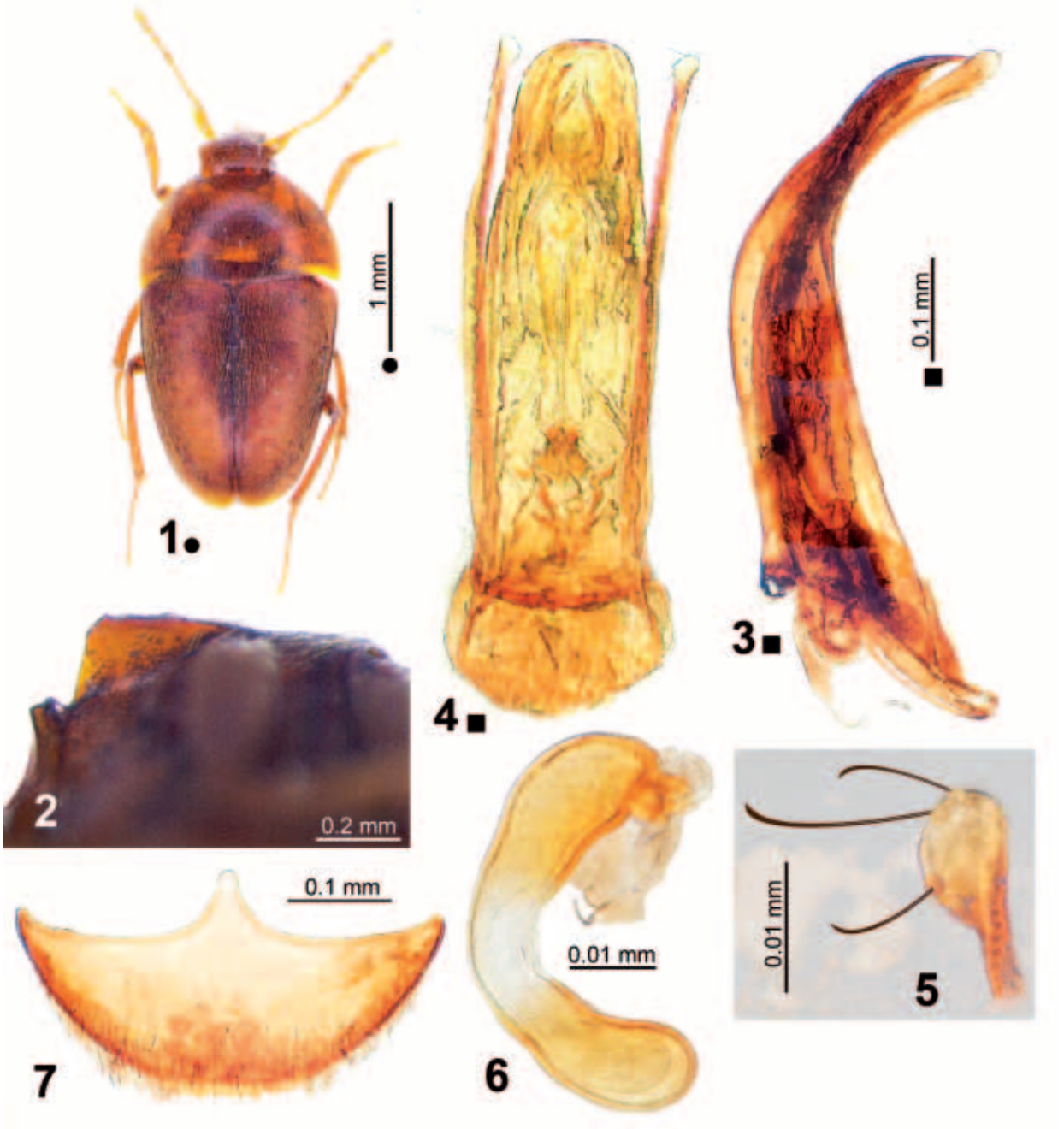
Antennae: Medium short. Just reaching pronotal base; first antennomere shorter and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th slightly longer than wide; 11th shorter than 9th and 10th together. Antennal formula: See Table 14.

Pronotum: Transverse, broadest just before base, regularly curved near anterior angles and less curved near posterior angle; base weakly bisinuate; posterior angles acute.

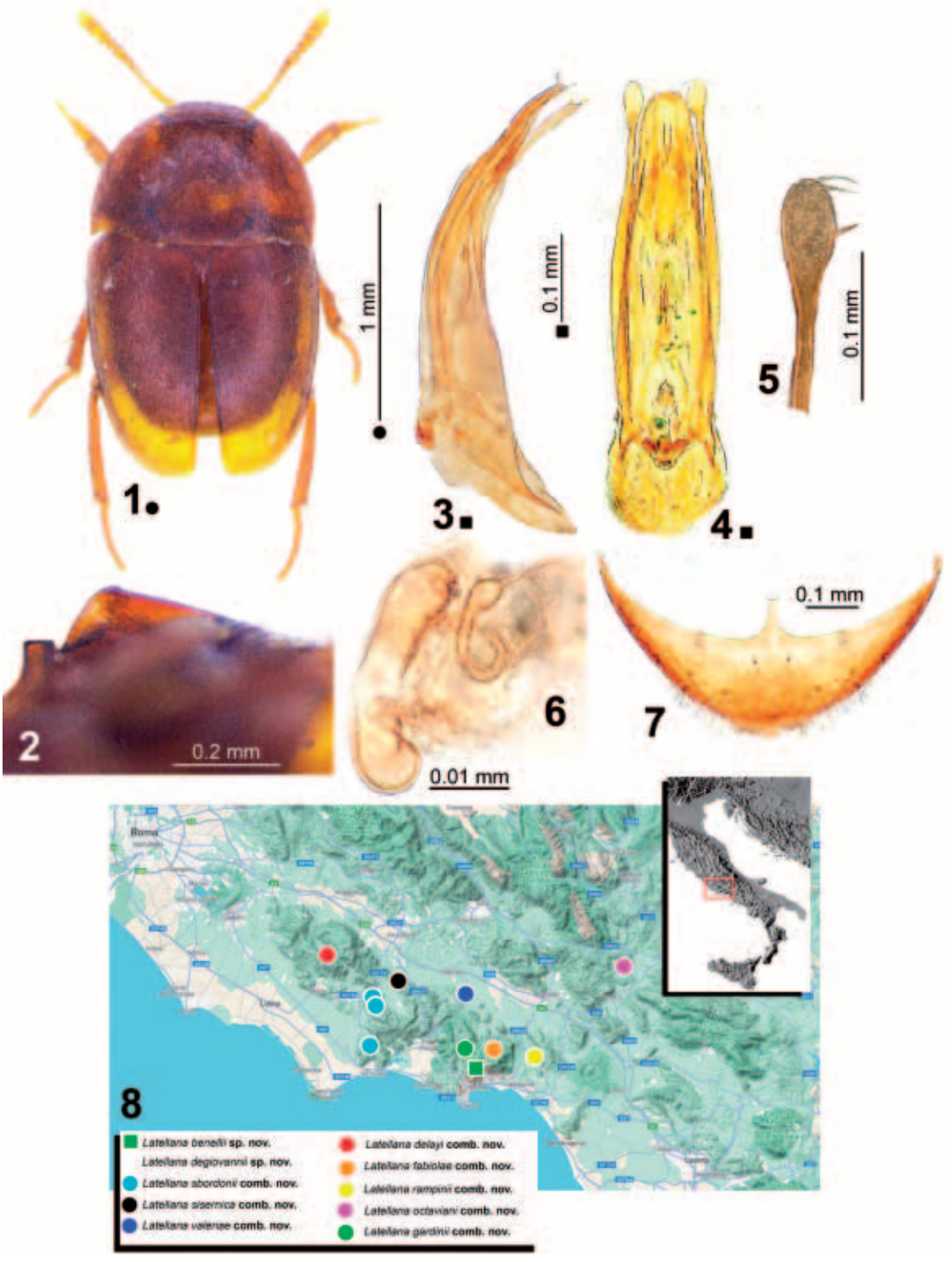
Elytra: Without transverse striolae and with parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs. Apical baskets of meso- and metatibiae incomplete; protarsi dilated, as broad as anterior part of protibia.

Mesoventral keel (Fig. 330.2): Tall, subrectilinear anteriorly, with apex toothed, with inferior edge straight, not reaching metaventrite.



FIGURES 330.1–330.7: *Latellana benellii* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Spermatheca, (**7**) Female uroventrite VIII.



FIGURES 331.1–331.8: *Latellana degiovannii* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Aedeagus in lateral view, (**4**) Aedeagus in dorsal view, (**5**) Apex of paramere, (**6**) Spermatheca, (**7**) Female uroventrite VIII. (**8**) Distribution map of *Latellana* **gen. nov.** spp. from the mountains of the Aurunci range.

Metaventrite suture (Fig. 330.2): Arched throughout mesocoxal cavity, demarcating a well-defined area.

Median lobe of aedeagus: Slender, with lateral edges in basal and median parts subrectilinear, not convergent, gently convergent in apical one. In lateral view (Fig. 330.3) subrectilinear in basal 2/3, after slightly curved up to tip, curved in ventral part. Apex, in dorsal view (Fig. 330.4), regularly rounded.

Endophallus (Fig. 330.4): With internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two bundles slightly sclerotized, with central cup-shaped phanera. Apical reinforcement bands long and apically convergent.

Parameres (Fig. 330.5): Slightly longer than median lobe. At apex decidedly enlarged, spoon shaped. Three setae at apex of parameres: first one apical, second one subapical, and third one lower.

Female. With stockier body, with antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex (Fig. 330.6): Spermatheca with basal and apical lobes of same dimension, well sclerotized, and median part long and hyaline. Expanded area of spermatic duct present, elongated. Spermathecal gland present.

Female uroventrite VIII (Fig. 330.7): Distally rounded, with a proximal edge slightly convex. Spiculum short, triangular, with apex rounded.

Variability. Length paratypes between 2.0-2.6 mm. Position of setae at apex of parameres substantially devoid of variability.

Etymology. We dedicate this interesting new species to one of its collector, our friend Alessio Benelli, well-known collector of subterranean beetles.

Discussion. This species is characterized by the presence of a parasutural stria (as in *Latellana magrinii* sp. nov. and *Latellana degiovannii* sp. nov.) and the parameres, very dilated at the apex (Fig. 330.5) (as in *Latellana petruzzielloi* sp. nov. and *Latellana petruzziellana* sp. nov.). In the phylogenetic tree it is found (Fig. 1G), with good support of 94.5/100, at the base of the clade formed by *Latellana sisernica* comb. nov., *Latellana valeriae* comb. nov., *Latellana rampinii* comb. nov. and *Latellana delayi* comb. nov.

Distribution (Fig. 331.8). Italy. *Latellana benellii* sp. nov. is known, now, only from two sites on Sant'Angelo Mount, near Formia (LT) on Aurunci Mounts (Lazio). It was collected shifting litter in forest *Fagus* and in a small cave at 1,200 m on Sant'Angelo Mount. It is syntopic with *Latellana degiovannii* sp. nov.

Segment	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**
Length	0.11	0.14	0.07	0.07	0.08	0.07	0.10	0.04	0.07	0.07	0.13
Width	0.05	0.04	0.02	0.02	0.03	0.03	0.06	0.04	0.05	0.06	0.06

TABLE 14. Measurements of antennomeres of the holotype of *Latellana benellii* sp. nov. (mm).

Latellana degiovannii sp. nov.
(Figs. 331.1-331.8)
https://zoobank.org/NomenclaturalActs/F876D7E0-D70D-4E38-9862-FEA538E1EC0C

Type locality. Italy, Lazio, Monti Aurunci, Formia (LT), Maranola, Mount Sant'Angelo, 41°19'0.8»N 13°38'54.2»E, 1,200 m.

Type series. Holotype ♂ (CPMG): Italy, Lazio, Monti Aurunci, Formia (LT), Maranola, Mount Sant'Angelo, 1,200 m, 14.V.2022, P. Magrini leg., with holotype label [Holotypus / *Latellana* / *degiovannii* sp. n. / Fresneda *et al*., 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 5 ♂♂, 6 ♀♀ (CPMG, CFL, CDV); Mount Sant'Angelo, 1,227 m, 11.V.2017, A. Faille, J.

Fresneda, I. Ribera leg., 1 ♂ with DNA extraction code voucher AN786 (CFL); Mount Sant'Angelo, 1,299 m, 15.IX.2002, A. Degiovanni leg., 1 ♀ (CPMG); Mount Sant'Angelo, 1,200 m, 25.X.2021, P. Magrini leg., 5 ♂♂, 3♀♀ (CPMG); Mount Sant'Angelo, 1,100 m, 2.V.2008, M. Bastianini leg., 2 ♂♂ (CPMG); same data except 1.V.2003, 5 ♂♂ (CPMG, CMB); Lazio, Mt. Aurunci (LT), Spino Saturnia, Mount Sant'Angelo, 1,100 m, 11.V.2024, A. Degiovanni leg., 2 ♂♂, 1 ♀ (CPMG). All specimens with paratype label [Paratypus / *Latellana* / *degiovannii* sp. n. / Fresneda *et al*., 2024] (rl).

Diagnosis. A small-sized *Latellana* gen. nov. characterized by presence of parasutural stria and by shape of the median lobe of aedeagus and parameres, very dilated at apex.

Description. Holotype ♂. Small size, 1.5 mm, habitus bathyscioid (Fig. 331.1).

Head: Retractile, with occipital carina complete; eyes absent.

Antennae: Short. Not reaching, stretching backward pronotal base; first antennomere shorter and less robust than second; antennomeres 1st to 7th moderately longer than wide; 8th to 10th slightly transverse; 11th shorter as 9th and 10th together. Antennal formula: See Table 15.

Pronotum: Transverse, broadest just before base, regularly curved near anterior angles and less curved near posterior angles; base weakly bisinuate. Posterior angles acute.

Elytra: Without transverse striolae and parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs. Apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia.

Mesoventral keel (Fig. 331.2): Tall, gently curved anteriorly, with apex toothed, with inferior edge straight not reaching metaventrite.

Metaventrite suture: Arched throughout mesocoxal cavity and describing a well-defined area.

Median lobe of aedeagus: Slender, with lateral edges regularly convergent, slightly curved in lateral view (Fig. 331.3) up to tip, curved in ventral part. Apex, in dorsal view (Fig. 331.4), regularly rounded, not truncate.

Endophallus (Fig. 331.4): With internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two bundles slightly sclerotized and without central phanera. Apical reinforcement bands long and apically convergent.

Parameres (Fig. 331.5): Slightly longer than median lobe. At apex, decidedly enlarged, spoon shaped. Three setae at apex of parameres: first one apical, second one subapical, and third one lower.

Female. With stockier body, shorter antennae and protarsomeres tetramerous non-dilated.

Spermathecal complex: Spermatheca (Fig. 331.6) with basal and apical lobes of same dimension, well sclerotized, and the median part long and hyaline. Expanded area of spermatic duct present, rounded, and well away from spermatheca. Spermathecal gland present.

Female uroventrite VIII (Fig. 331.7): Distally rounded, with a proximal edge very convex. Spiculum short, not triangular, with apex truncate.

Variability. Length paratypes between 1.4-1.7 mm. Position of setae at apex of parameres substantially devoid of variability.

Etymology. We dedicate this interesting new species to one of its collectors, our friend Augusto Degiovanni, well-known collector of subterranean beetles.

Discussion. This species is characterized by the presence of parasutural stria (as in *Latellana magrinii* sp. nov. and *Latellana benellii* sp. nov.) and by the shape of the median lobe of aedeagus and parameres, very dilated at the apex (as in *Latellana benellii* sp. nov., *Latellana petruzzielloi* sp. nov. and *Latellana petruzziellana* sp. nov.) It is found at the base of the entire *Latellana* gen. nov. clade (Fig. 1G) with very good support 95.3/100.

Distribution (Fig. 331.8) and ecology. Italy. It is known, now, only for its type locality on Sant'Angelo Mount, near Formia (LT) on Aurunci range mountains (Lazio). It was collected shifting litter in forest *Fagus* at 1,200-1,299 m. In this site *Latellana degiovannii* sp. nov. is syntopic with *Latellana benellii* sp. nov.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.08	0.09	0.04	0.03	0.04	0.04	0.05	0.02	0.04	0.04	0.10
Width	0.03	0.04	0.02	0.02	0.02	0.03	0.05	0.04	0.05	0.06	0.06

TABLE 15. Measurements of antennomeres of the holotype of *Latellana degiovannii* sp. nov. (mm).

Latellana magrinii sp. nov.
(Figs. 332.1-332.7)
https://zoobank.org/NomenclaturalActs/CC574D40-776E-42DE-87A8-956B7D7FD8E2

Type locality. Italy, Campania, Letino (CE), Grotta dei 7 Diavoli, 1,000 m.

Type series. Holotype ♂ (CPMG): Italy, Campania, Letino (CE), Grotta dei 7 Diavoli, 18.VIII.2018, P. Magrini leg., with holotype label [Holotypus / *Latellana* / *magrinii* sp. n. / Fresneda *et al*., 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 1 ♂, 1 ♀ (CPMG, CPM); same data except 31.VIII.2018, 5 ♂♂, 4 ♀♀ (CPMG, CFL, CPM); same data except 23.X.2021, 2 ♂♂, 2 ♀♀ (CPM); same data except 2.IV.2024, 10 ♂♂, 13 ♀♀ (CPM); same data except 26.VI.1986, 1 ♂, 4 ♀♀ (CDV, CMG). Campania, Miralago (CE), Inghiottitoio di Campo Braca, CP 45, 1,140 m, 28.VII.2019, P. Magrini leg., 2 ♂♂, 8 ♀♀ (CPMG, SMNS); same data except 24.X.2021, 2 ♀♀ (CPMG). All specimens with paratype label [Paratypus / *Latellana* / *magrinii* sp. n. / Fresneda *et al*., 2024] (rl).

Diagnosis. A medium-sized *Latellana* gen. nov., characterized by a parasutural stria evident (lacking in *Latellana petruzzielloi* sp. nov. and *Latellana petruzziellana* sp. nov.), by shape of median lobe of aedeagus and parameres, slightly dilated at apex (very dilated in *Latellana petruzzielloi* sp. nov. and *Latellana petruzziellana* sp. nov.).

Description. Holotype ♂. Medium size, 2.1 mm, habitus bathyscioid (Fig. 332.1).

Head: Retractile, with occipital carina complete; eyes absent.

Antennae: Medium short. Not reaching, stretching backward pronotal base; first antennomere shorter and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th as long as 9th and 10th together. Antennal formula: See Table 16.

Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved near posterior angles; base weakly bisinuate. Posterior angles acute.

Elytra: Without transverse striolae and with parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, wider than anterior part of protibia.

Mesoventral keel (Fig. 332.2): Tall, gently curved anteriorly, with apex toothed, with inferior edge straight, not reaching metaventrite.

Metaventrite suture (Fig. 332.3): Arched throughout mesocoxal cavity and demarcating a well-defined area.

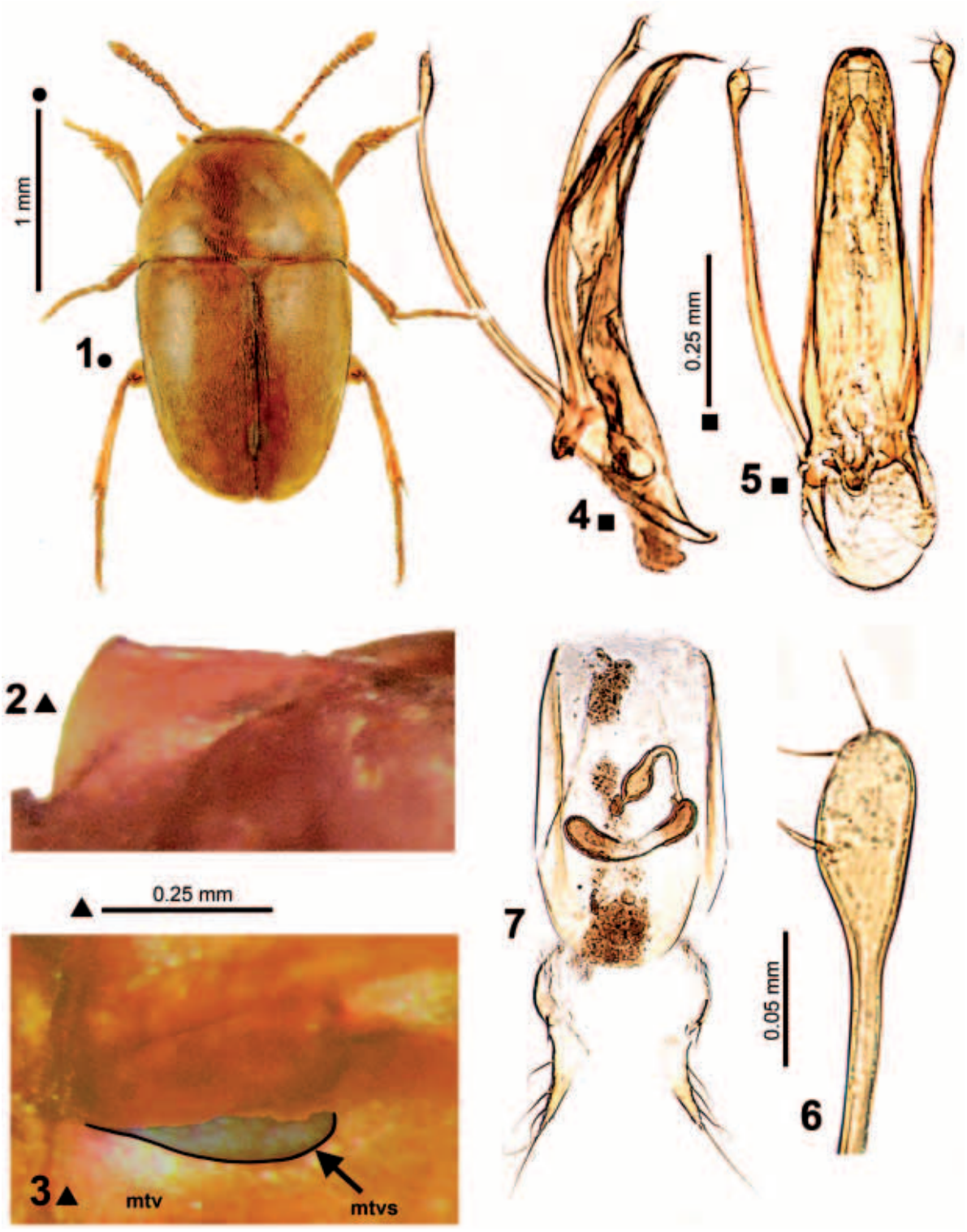
Median lobe of aedeagus: Slender, with lateral edges regularly convergent, slightly curved in lateral view (Fig. 332.4) up to tip, curved in ventral part. Apex, in dorsal view (Fig. 332.5), regularly rounded and slightly truncate.

Endophallus (Fig. 332.5): With internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two bundles slightly sclerotized, and without central upside down phanera. Apical reinforcement bands long and apically convergent.

Parameres (Fig. 332.6): Slightly shorter than median lobe. Decidedly enlarged, spoon shaped at apex. Three setae at apex: first one apical, second one subapical, and third one lower.

Female. With stockier body, antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex (Fig. 332.7): Spermatheca with basal and apical lobes of same dimension, well sclerotized, and median part long and hyaline. Expanded area of spermatic duct present, rounded, and well away from spermatheca. Spermathecal gland present.



FIGURES 332.1–332.7: *Latellana magrinii* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Metaventral suture, (**4**) Aedeagus in lateral view, (**5**) Aedeagus in dorsal view, (**6**) Apex of the paramere, (**7**) Spermathecal complex.

Variability. Length paratypes between 2.0-2.2 mm. Position of setae at apex of parameres substantially devoid of variability.

Etymology. We dedicate this interesting new species to its collector, our friend Paolo Magrini, well-known specialist of subterranean beetles.

Discussion. There is no molecular data available for this species; *Latellana magrinii* sp. nov. appears morphologically not so strictly related to *Latellana petruzziellana* sp. nov. from Cigno Mount (geographically nearby).

Distribution and ecology. Italy. It is known, now, only for two localities: its type locality, the Grotta dei 7 Diavoli, located near Letino (CE), and the cave Inghiottitoio di Campo Braca, located near Miralago (CE). In the 7 Diavoli cave it was collected with an interesting subterranean associated fauna as: *Duvalius carchinii* Vigna Taglianti, Magrini & Vanni, 1993 and *Typhloreicheia usslaubi* (Saulcy, 1870) (Coleoptera Carabidae); *Vulda benellii* Bordoni & Magrini, 2020 and *Lathrobium angelae* Bordoni & Magrini, 1996 (Coleoptera Staphylinidae); and *Neobisium petruzzielloi* Gardini, 2023 (Pseudoscorpiones).

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.08	0.09	0.04	0.03	0.04	0.04	0.05	0.02	0.04	0.04	0.10
Width	0.03	0.04	0.02	0.02	0.02	0.03	0.05	0.04	0.05	0.06	0.06

TABLE 16. Measurements of antennomeres of the holotype of *Latellana magrinii* sp. nov. (mm).

Latellana petruzziellana sp. nov.
(Figs. 333.1-333.8)
https://zoobank.org/NomenclaturalActs/E42AF651-C414-419B-A83B-BBBE875F1B39

Type locality. Italy, Campania, Cusano Mutri (BN), Grotta dei Briganti n° CP46, UTM: 41,3030650 14,5409848, 478 m.

Type series. Holotype ♂ (CPMG): Italy, Campania, Cusano Mutri (BN), Grotta dei Briganti n° CP46, 478 m, 25.VII.2022, L. Petruzziello leg., with holotype label [Holotypus / *Latellana* / *petruzziellana* sp. n. / Fresneda *et al*., 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 17 ♂♂, 11 ♀♀ (CPMG, CFL, CDV); same data except 5.V.2024, 51 ♂♂, 69 ♀♀ (CPMG, CFL, CDV, CLP, CMP, SMNS); same data except 27.XII.2022, 57 ♂♂, 45 ♀♀ (CPMG, CFL, CDV, CLP, CMP, CAC, CLL, CAF). Campania, Cusano Mutri (BN), Grotta delle Fate, 315 m, 27.XII.2022, L. Petruzziello leg., 1 ♂, 1 ♀ (CPMG). All specimens with paratype label [Paratypus / *Latellana* / *petruzziellana* sp. n. / Fresneda *et al*., 2024] (rl).

Diagnosis. A medium-sized *Latellana* gen. nov., similar to *Latellana petruzzielloi* sp. nov. in shape of median lobe of aedeagus and parameres very dilated at the apex (slightly dilated in *Latellana magrinii* sp. nov.) and lack of parasutural stria (present in *Latellana magrinii* sp. nov.).

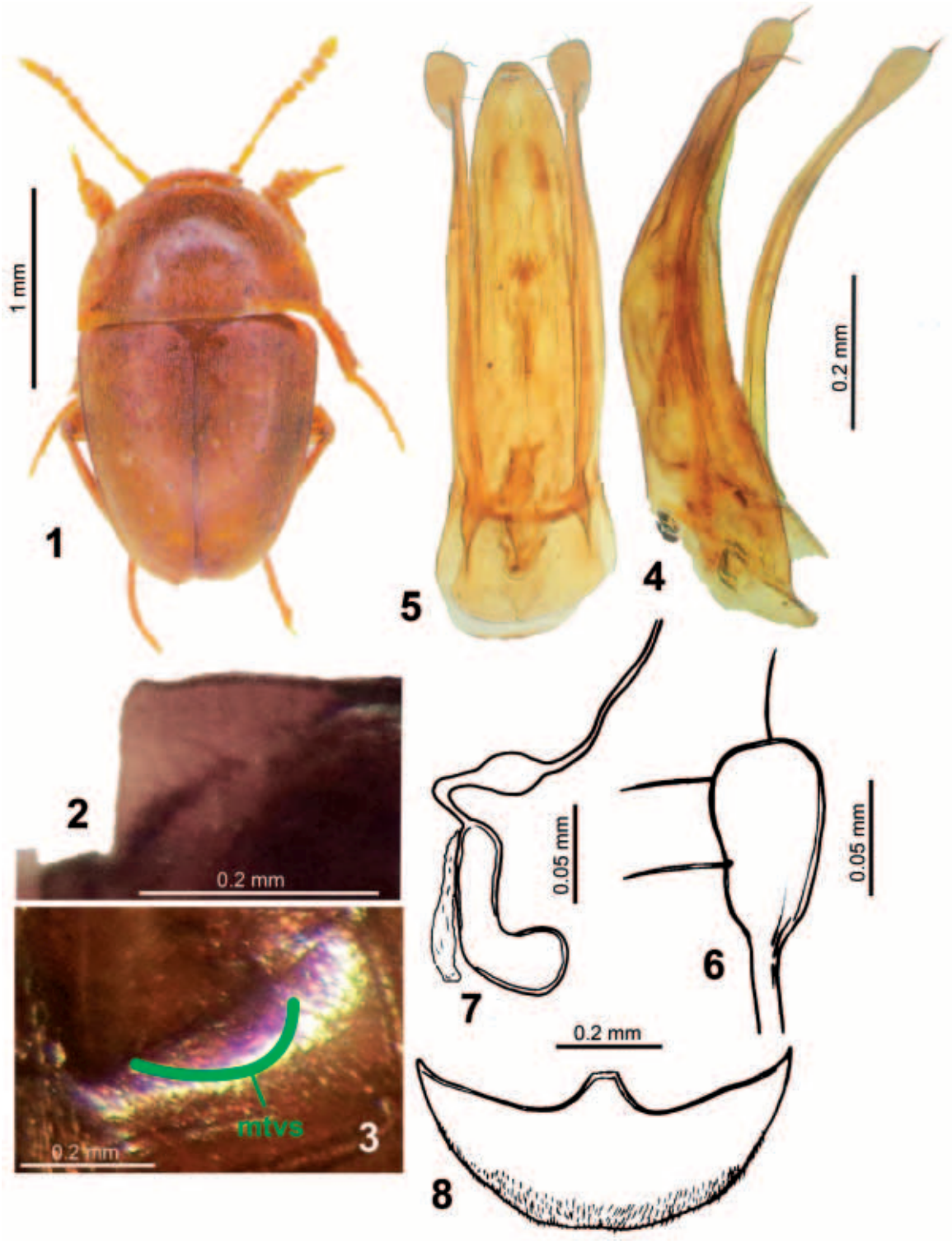
Description. Holotype ♂. Medium size, 2.0 mm, body bathyscioid (Fig. 333.1).

Head: Retractile, with occipital carina complete; eyes absent.

Antennae: Short. Just reaching, stretching backward pronotal base; first antennomere shorter and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th shorter than 9th and 10th together. Antennal formula: See Table 17.

Pronotum: Transverse, broadest at base, regularly curved from anterior angles to posterior ones, base weakly bisinuate. Posterior angles acute.

Elytra: Without transverse striolae and parasutural stria.



FIGURES 333.1–333.8: *Latellana petruzziellana* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Metaventrite suture, (**4**) Aedeagus in lateral view, (**5**) Aedeagus in dorsal view, (**6**) Apex of paramere, (**7**) Spermatheca, (**8**) Female uroventrite VIII.

Legs: Apex of tibiae on inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, wider than anterior part of protibia.

Mesoventral keel (Fig. 333.2): Tall, rectilinear anteriorly, with apex toothed, with inferior edge slightly sinuate, not reaching metaventrite.

Metaventrite suture (Fig. 333.3): Arched throughout mesocoxal cavity describing a well-defined area.

Median lobe of aedeagus: Slender, with lateral edges slightly curved and convergent. In lateral view (Fig. 333.4) slightly curved in basal part, subrectilinear in apical part, up to tip, curved in ventral part. Apex, in dorsal view (Fig. 333.5), regularly rounded and slightly truncate.

Endophallus (Fig. 333.5): With internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two bundles slightly sclerotized and central «W»-shape upside down phanera. Apical reinforcement bands short and apically convergent.

Parameres (Fig. 333.6): Slightly longer than median lobe. At apex widely enlarged, spoon shaped. In dorsal view, truncate at apex. Three setae at apex: first one apical, second one subapical, and third one lower.

Female. With stockier body, antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex: Spermatheca (Fig. 333.7) with basal and apical lobes of same dimension, well sclerotized, and median part long and hyaline. Expanded area of spermatic duct present, rounded, and well away from spermatheca. Spermathecal gland present.

Female uroventrite VIII (Fig. 333.8): Distally rounded, with a proximal edge slightly convex. Spiculum short, triangular, with apex truncate.

Variability. Length paratypes between 1.7-2.2 mm. The position of setae at apex of parameres substantially devoid of variability.

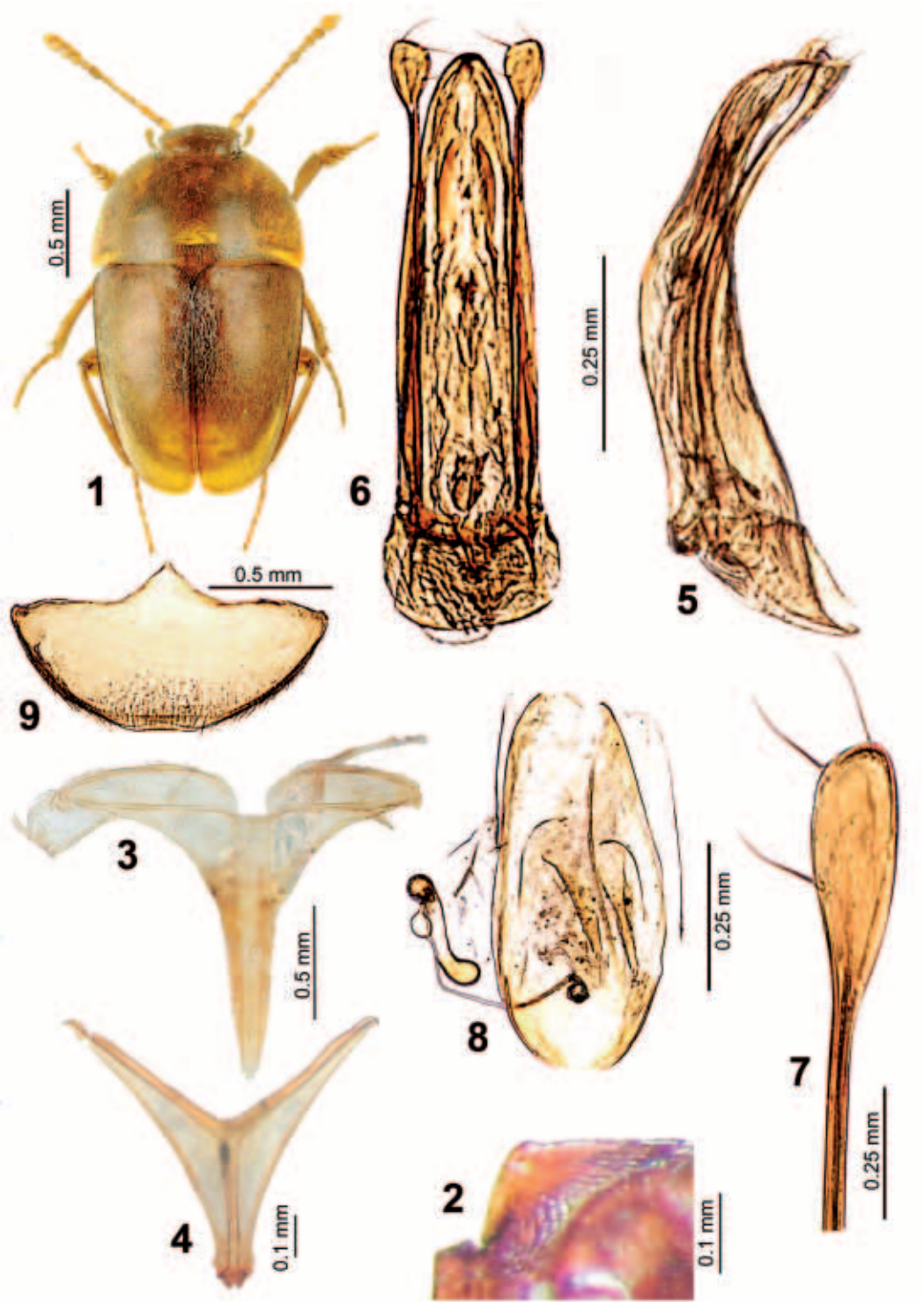
Etymology. We dedicate this interesting new species to its collector, our friend Luigi Petruzziello, tireless investigator of the subterranean fauna of Campania.

Discussion. There are no molecular data available for this species. *Latellana petruzziellana* sp. nov. appears strictly morphologically related to *Latellana petruzzielloi* sp. nov. from Picentini Mounts (geographically away) rather than with *Latellana magrinii* sp. nov. from Matese Plateau (geographically nearby).

Distribution and ecology. Italy. It is known, now, only for two caves located on Monte Cigno, a mountain massif at southeast of the Matese Plateau, the Caves Grotta dei Briganti and Grotta delle Fate, located a few hundred meters away from each other. The cave Grotta dei Briganti (or Grotta di Monte Cigno), located at an altitude of 467 m, has a difference in height of 38 m and a planimetric development of 240 m. The cave Grotta delle Fate (not stacked and of artificial origin, excavated in 1960 to look for water), is located at 315 m and has a planimetric development of a few tens of meters. In both localities *Latellana petruzziellana* sp. nov. has been collected either directly on sight or with the help of pitfalls traps.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.08	0.12	0.06	0.05	0.05	0.06	0.07	0.04	0.06	0.06	0.11
Width	0.05	0.03	0.02	0.02	0.03	0.03	0.05	0.05	0.07	0.06	0.07

TABLE 17. Measurements of antennomeres of the holotype of *Latellana petruzziellana* sp. nov. (mm).



FIGURES 334.1–334.9: *Latellana petruzzielloi* **sp. nov.**: (**1**) Habitus, (**2**) Mesoventral keel, (**3**) Metatergal apparatus, (**4**) Metendosternite, (**5**) Aedeagus in lateral view, (**6**) Aedeagus in dorsal view, (**7**) Apex of paramere, (**8**) Spermathecal complex, (**9**) Female uroventrite VIII.

Latellana petruzzielloi sp. nov.
(Figs. 334.1-334.9)
https://zoobank.org/NomenclaturalActs/351C44AE-5B72-4A7F-B667-74F7FC7C29C7

Type locality. Italy, Campania, Acerno (SA), Grotta degli Angeli, n 588 CpSA, 1,075 m.

Type series. Holotype ♂ (CPMG): Italy, Campania, Acerno (SA), Grotta degli Angeli, n 588 CpSA, 1,075 m, 25.07.2020, L. Petruzziello leg., with holotype label [Holotypus / *Latellana* / *petruzzielloi* n. sp./ Fresneda *et al*., 2024] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 34 ♂♂, 42 ♀♀ (CPMG, CLP, CFL, CDV, CAC, SMNS); same data except 31.VII.2021, 35 ♂♂, 43 ♀♀ (CPMG, CLP, CFL, CDV); same data except 13.VIII.2019, 8 ♂♂, 12 ♀♀ (CPMG). Campania, Acerno (SA), miniera di Lignite 584 m, 21.XII.2023, L. Petruzziello leg., 1 ♂, 2 ♀♀ (CPMG). Campania, Acerno (SA), Grotta Strazzatrippa n 598 CpSA, 1,125 m, 21.VII.2021, L. Petruzziello leg., 2 ♂♂, 1 ♀ (CPMG); with the same collection data, 23.VII.2020, 1 ♂, 1 ♀ (CPMG). Campania, (AV) Bagnoli Irpino, grotta di Strazzatrippa, 1,150 m, Monte Cervialto, 18.VII/17.VIII.15, L. Petruzziello leg., 1 ♂ (CLL). Campania, Moltella (AV), Grotta del Caprone, CP 56, 860 m, 31.XII.2015, L. Petruzziello leg., 16 ♂♂, 23 ♀♀ (CPMG, CLP); with the same collection data, 6.VIII.2018, 19 ♂♂, 29 ♀♀ (CPMG, CLP, CDV, CFL); same data except 6.VII.2018, 5 ♂♂, 11 ♀♀ (CLP, CDV, CFL); same data except VIII.2016/VIII.2017, 12 ♂♂, 12 ♀♀ (CPMG, CLP). Campania (AV) Montella, Grotta del Caprone, 830 m, VII.2014, Petruzziello leg., 3 ♂♂, 3 ♀♀ (CMG); in trappole a caduta con fegatino di pollo, 6.VII/14.VIII.2014, L. Petruzziello leg., 1 ♂, 1 ♀ (CLL). Campania (AV), Montella, Grotta del Caprone, 27.XII.2014, 850 m, L. Petruzziello leg., 2 ♂♂ (CLL). Campania (AV), Bagnoli Irpino, Monte Cervialto (Monti Picentini), 1,100 m, 27.XII.2014/18.VII.2015, L., Petruzziello leg., 6 ♂♂, 10 ♀♀ (CLL). Acerno (SA), M. Cervialto, grotta degli Angeli, 18.VII.2016, Petruzziello leg., 2 ♂♂, 2 ♀♀ (CMG). All specimens with paratype label [Paratypus / *Latellana* / *petruzzielloi* sp. n. / Fresneda *et al*., 2024] (rl).

Diagnosis. A medium-sized *Latellana* gen. nov., similar to *Latellana petruzziellana* sp. nov. by the lack of parasutural stria (present in *Latellana magrinii* sp. nov.), by the shape of the median lobe of aedeagus and parameres, very dilated at the apex (slightly dilated in *Latellana magrinii* sp. nov.).

Description. Holotype ♂. Medium size, 2.1 mm, habitus bathyscioid (Fig. 334.1).

Head: Retractile, with occipital carina complete; eyes absent.

Antennae: Medium short. Not reaching, stretching backward pronotal base; first antennomere shorter and more robust than second; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th as long as 9th and 10th together. Antennal formula: See Table 18.

Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved near posterior angles; base weakly bisinuate. Posterior angles acute.

Elytra: Without transverse striolae and with parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, wider than anterior part of protibia.

Mesoventral keel (Fig. 334.2): Tall, with apex toothed, with inferior edge straight and anterior one slightly curved, not reaching metaventrite.

Metaventrite suture: Arched throughout mesocoxal cavity and describing a well-defined area.

Metatergal apparatus (Fig. 334.3): With wings of metascutum long and large; alacrista apophysis long.

Metendosternite (Fig. 334.4): Not «V»-shaped, with furcal arms slightly longer than furcal trunk. Anterior furcal plate lacking; furcal plate progressively reduced along furcal arms. Arm apophysis very reduced.

Median lobe of aedeagus: Slender, with lateral edges regularly convergent, slightly bisinuated in lateral view (Fig. 334.5) up to tip, curved in ventral part. Apex, in dorsal view (Fig. 334.6), short rounded and not truncate.

Endophallus (Fig. 334.6): Endophallus with internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two sclerotized bundles. Apical reinforcement bands long, slightly curved and apically convergent.

Parameres (Fig. 334.7): As long as median lobe. Decidedly enlarged, spoon shaped, at apex. Three setae at apex: first one apical, second one subapical, and third one lower.

Female. With stockier body, with antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex (Fig. 334.8): Spermatheca with basal and apical lobes of same dimension, well sclerotized, and median part long and hyaline. Expanded area of spermatic duct present, rounded, and close to spermatheca. Spermatic duct two times longer than spermatheca. Spermathecal gland present.

Female uroventrite VIII (Fig. 334.9): Distally rounded, with slightly convex proximal edge. Spiculum short, broad, triangular, very enlarged at basis.

Variability. Length paratypes between 1.8-2.4 mm. Position of setae at apex of parameres substantially devoid of variability.

Etymology. We dedicate this interesting new species to its collector, our friend Luigi Petruzziello, well-known collector of subterranean beetles.

Discussion. No molecular data are available for this species; *Latellana petruzzielloi* sp. nov. appears morphologically strictly related to *Latellana petruzziellana* sp. nov. from Cigno Mount, and less with *Latellana magrinii* sp. nov. from Matese Plateau.

Distribution and ecology. Italy. At the moment, this species is known for several caves and artificial cavities of the Picentini Mountains in Campania: the Grotta Strazzatrippa (speleological registry no. 598 Cp/Sa), the Grotta degli Angeli (speleological registry no. 588 Cp/Sa) and the Grotta del Caprone (speleological registry no. 56 Cp/Av) where it was collected on sight or with the use of traps for different periods of time. The first two caves open in the municipality of Acerno in the province of Salerno; are part of the same karst complex, and are communicating with each other (Bordoni 2018). The associated fauna is represented by *Anemadus petruzzielloi* Giachino & Vailati, 2018, *Choleva sturmi* Brisout, 1863, *Choleva angustata* (Fabricius, 1781), *Choleva reitteri* Petri, 1915, *Catops subfuscus* Kellner, 1846, *Catops tristis* (Panzer, 1793) (Leiodidae Cholevinae) and *Lathrobium petruzzielloi* Bordoni, 2018 (Staphylinidae). The Caprone cave opens at an altitude of 850 m in the municipality of Montella in the province of Avellino and has a development of just 35 m.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.07	0.12	0.06	0.06	0.04	0.07	0.09	0.03	0.06	0.06	0.10
Width	0.04	0.03	0.02	0.02	0.02	0.03	0.05	0.04	0.06	0.08	0.08

TABLE 18. Measurements of antennomeres of the holotype of *Latellana petruzzielloi* sp. nov. (mm).

Nafarroa ericduprei sp. nov.
(Figs. 335.1, 335.3, 335.5, 336.1)
https://zoobank.org/NomenclaturalActs/3263D86F-3477-451F-8516-FD8FD1B60B43

Type locality. Spain, Navarra, Elizondo, Beartzun de Baztan, Sima de Belaun (= Sima Franclona), 43° 6' N 1°27'W, 700 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): labelled [HISP - NA, Elizondo / Gfre. Franclona / Dupré leg. 18.7.85], [Franclona gfe. / Elizondo Espagne // 18/7/85 931B / Eric Dupré] (hw E. Dupré), [HOLOTYPUS / *Nafarroa* / *ericduprei* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype.

Description. Holotype ♂. Length 2.2 mm from anterior edge of pronotum to apex of elytra; outline oval, stocky, with slightly wider pronotum than elytra (Fig. 335.1); depigmented; all surface covered by yellowish pubescence, short, thin and lying down.

Head: Without occipital keel; punctation well-marked and dense; anophthalmous.

Antennae: Length 0.9 mm; first antenomere longer than second; antennomeres gradually dilated from 3rd to 6th; third being longest; 7th big and well-differentiated club; 9th, 10th and 11th antennomeres of same thickness, 11th being longest. Antennal formula: See Table 19.

Pronotum: Strongly transverse (length 0.7 mm x width 1.2 mm), with sides very curved and maximum width at base; punctation fine, slightly marked, but very dense.

Elytra: Slightly longer (1.4 mm) than wide (1.3 mm), depressed with lateral margins regularly curved up to apexes, these in regular arc little narrowed. Strongly punctated; dots broad and rough, without transverse striolae and parasutural stria.

Legs: Relatively short; protarsomeres pentameres with 1-3 segments dilated, first wider than apex of protibia; onychium as long as protarsomeres 1-2 combined; mesotibiae arched and spiny, metatibiae straight.

Mesoventral keel: Tall, forming a right angle with vertex rounded, and posterior process not reaching metaventrite.

Median lobe of aedeagus: Short and quite robust. In lateral view, slightly bent (Fig. 335.3), with terminal region sinuate. In dorsal view (Fig. 335.5), width decreasing from base to apex; apex rounded; lateral margins regularly curved. Basal part relatively reduced.

Endophallus (Fig. 335.5): With three parts typical of *Speonomus* series. In apical part reinforcement bands, long and reaching base, pointed and inserted on membranous ligulae. Median part with flagellum – with origin in «Y»-piece –, short axial piece with sclerotized armour, and dorsal and ventral phanerae. In basal area with phanerae associated to «Y»-piece.

Parameres (Fig. 336.1): More longer that median lobe; very robusts through their entire length; apex rounded, with four setae.

Female. Unknown.

Etymology. The new species is dedicated to Eric Dupré, excellent biospeleologist and companion who passed away on January 21 of 2023. He collected the holotype of this species. The specific name is a noun in the genitive singular.

Discussion. The most significant morphological differences between *Nafarroa sorogainensis* and *Nafarroa ericduprei* sp. nov. are:

– Antennae: The lengths and widths of antennomeres are similar to *Nafarroa sorogainensis*, although the first is longer than the second in *N. ericduprei* sp. nov.

– Mesoventral keel: It forms an obtuse angle with a pointed vertex in *Nafarroa sorogainensis*, and in *N. ericduprei* sp. nov. it forms a right angle with rounded vertex.

– Protarsi: Noticeably narrower than the apex of the protibia, only slightly enlarged in *Nafarroa sorogainensis*, and with the same width as the apex of the protibia, well dilated in *N. ericduprei* sp. nov.

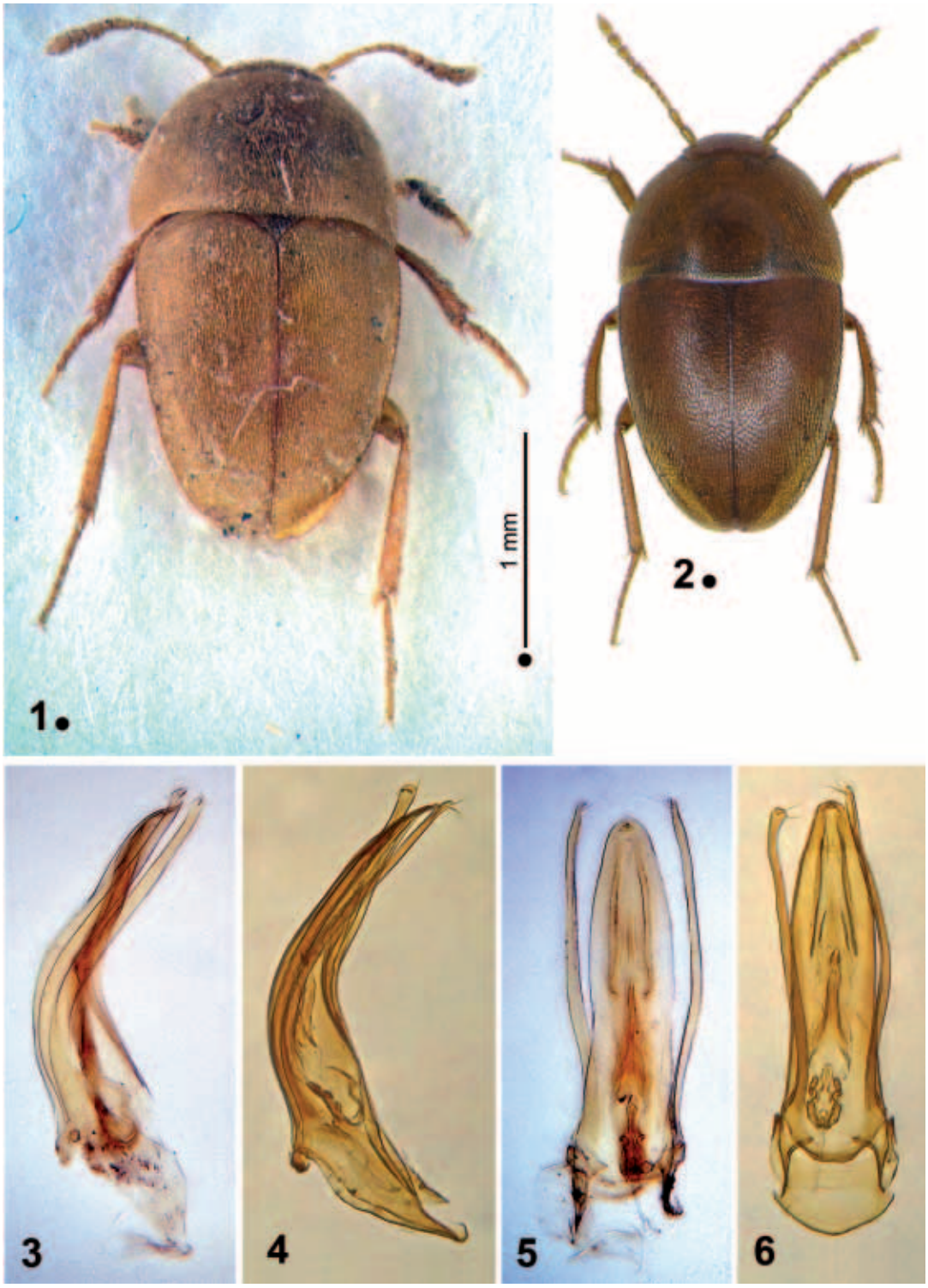
– Median lobe of aedeagus in lateral view: It is slightly bent, forming an obtuse angle in *Nafarroa sorogainensis* (Fig. 335.4) or with the terminal region sinuate in *N. ericduprei* sp. nov. (Fig. 335.3).

– Median lobe of aedeagus in dorsal view: Width decreasing from base to apex, with apex rounded and lateral margins sinuate in *Nafarroa sorogainensis* (Fig. 335.6), or width decreasing from base to apex, with apex rounded and lateral margins regularly curved in *N. ericduprei* sp. nov. (Fig. 335.5).

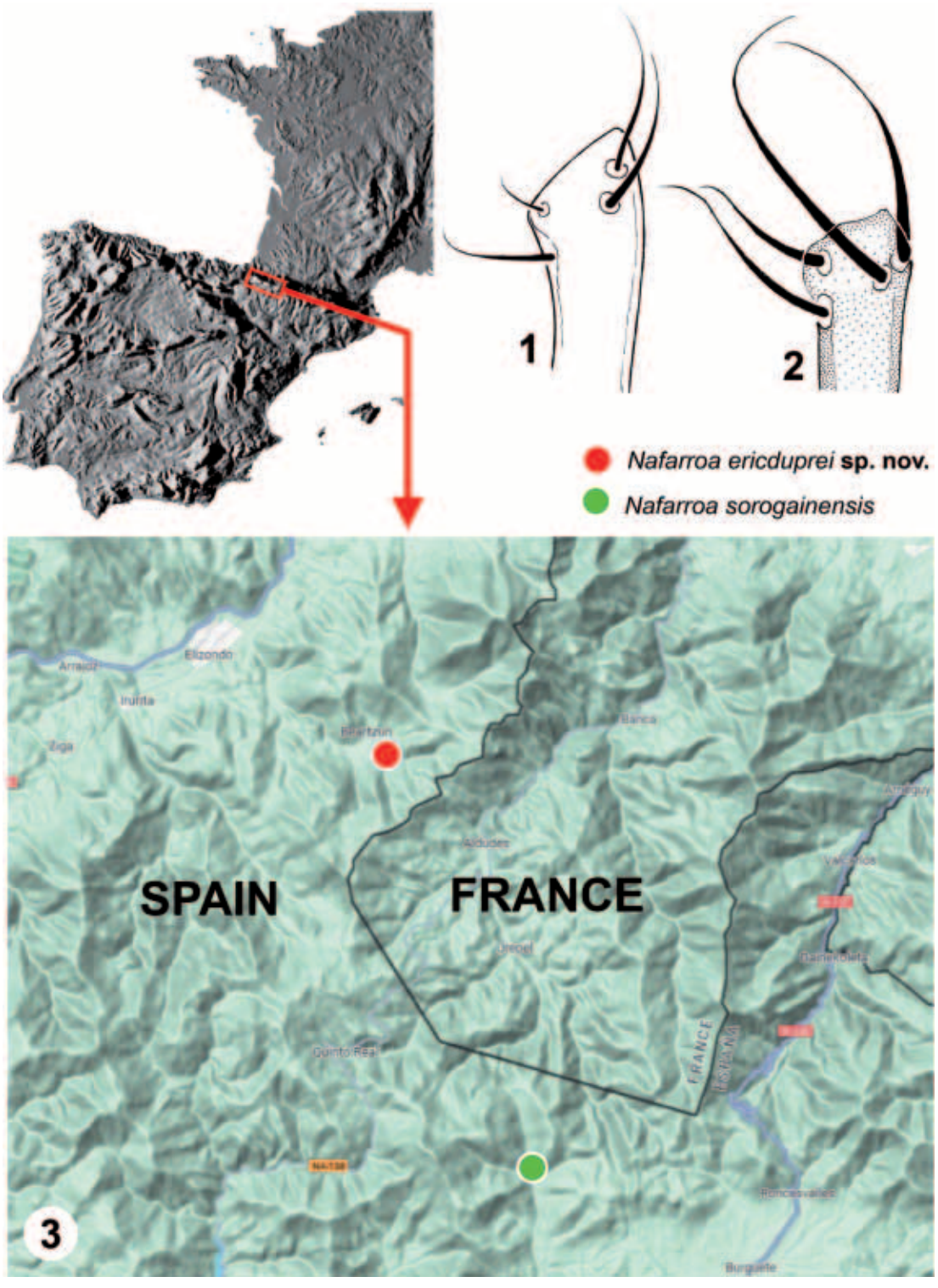
– Parameres: The apical setae are shorter and finer in *Nafarroa ericduprei* sp. nov. (Fig. 336.1) than in *Nafarroa sorogainensis* (Fig. 336.2).

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.15	0.13	0.08	0.07	0.06	0.06	0.10	0.05	0.10	0.08	0.14
Width	0.06	0.05	0.03	0.03	0.03	0.04	0.06	0.06	0.09	0.09	0.09

TABLE 19. Measurements of antennomeres of the holotype of *Nafarroa ericduprei* sp. nov. (mm).



FIGURES 335.1–335.6: *Nafarroa* spp. Habitus of: (**1**) *N. ericduprei* **sp. nov.**, (**2**) *N. sorogainensis***.** Aedeagus in lateral view of: (**3**) *N. ericduprei* **sp. nov.**, (**4**) *N. sorogainensis*. Aedeagus in dorsal view of: (**5**) *N. ericduprei* **sp. nov.**, (**6**) *N. sorogainensis*.



FIGURES 336.1–336.3: *Nafarroa* spp. Apex of paramere of: **(1)** *N. ericduprei* **sp. nov.**, (**2**) *N. sorogainensis***.** (**3**) Distribution map of *N. ericduprei* **sp. nov.** and *N. sorogainensis*.

Paratroglophyes juberthiei sp. nov.
(Figs. 337.1, 337.2, 338.1, 338.6, 339.1, 339.3)
https://zoobank.org/NomenclaturalActs/7DC1C140-FC15-4E6B-BF33-F652A93A7025

Type locality. France, Ariège, Forêt de Balmiou, MSS.

Type series. Holotype ♂ (in col. Fresneda-Lagar): France, Ariège, Forêt de Balmiou, MSS S74, 20.V.1981, CNRS Moulis, with holotype label [HOLOTYPUS / *Paratroglophyes* / *juberthiei* sp. n. / Fresneda *et al*., 2023] (pr, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: France, Ariège, Forêt de Balmiou, MSS S78, CNRS Moulis, 1 ♂; 20.III.1980, CNRS Moulis, 1 ♂; with paratype label [PARATYPUS / *Paratroglophyes* / *juberthiei* sp. n. / Fresneda *et al*., 2023] (pr, rl) (CFL, CPMG). The three specimens of the type series are in poor condition; the holotype is complete although one antenna is separated from the head; the paratypes are incomplete.

Description. Holotype ♂. Size 2.4 mm. Body elongated, pholeuonoid (Fig. 337.1), reddish-yellowish in colour, with pubescence short and lying.

Antennae: Long, more than length of body, with antennomeres somewhat thickened from 7th; 8th three times its width in length and shorter than 10th; 9th and 10th of equal length. Antennal formula: See Table 20.

Pronotum: Transverse, a little wider than long, attenuated forwards and strongly narrowed in its basal half; widest in middle and base as wide as elytral base; posterior angles acute and divergent, base regularly curved; integument dotted.

Elytra: Elongated, with margins regularly curved throughout their length; maximum width in middle; apices regularly curved with little indentation in area of suture; elytral sculpture formed by transverse striolae widely separated; without parasutural stria.

Legs: Delicate, very long with first four protarsomeres dilated and first, being widest, narrower than apex of protibia; meso- and metafemora simple.

Mesoventral keel: Short, forming a dihedral very obtuse, with anterior margin somewhat shorter than inferior and apex strongly hooked.

Median lobe of aedeagus: In lateral view (Fig. 338.1) bent at an obtuse angle a little more near apex than midway; dorsal face presents a strong curvature marked by a depression in basal third; gradually reduced in apical third with a slight dorsal depression; apex fine, prolonged and slightly curved near ventral part. In dorsal view (Fig. 338.6) with lateral margins markedly sinuous and distal area pointed, although apex broadly rounded.

Endophallus (Fig. 339.3): Formed by three parts. Basal part provided with a «Y»-piece and a ventral tubular complex from which a flagellum emerges. Middle part with two thick ventral phanerae and upper part with two thick and strongly sclerotized phanerae forming an inverted «V»; axial piece forming a nodule covered with some imbricate spicules. Reinforcing bands resting on membranous ligulae in apical part.

Parameres: Much shorter than median lobe (Fig. 339.1), arched near middle, with a fine apex with three differentiated setae, one shorter than others and with point of insertion a little displaced near base.

Female. Unknown.

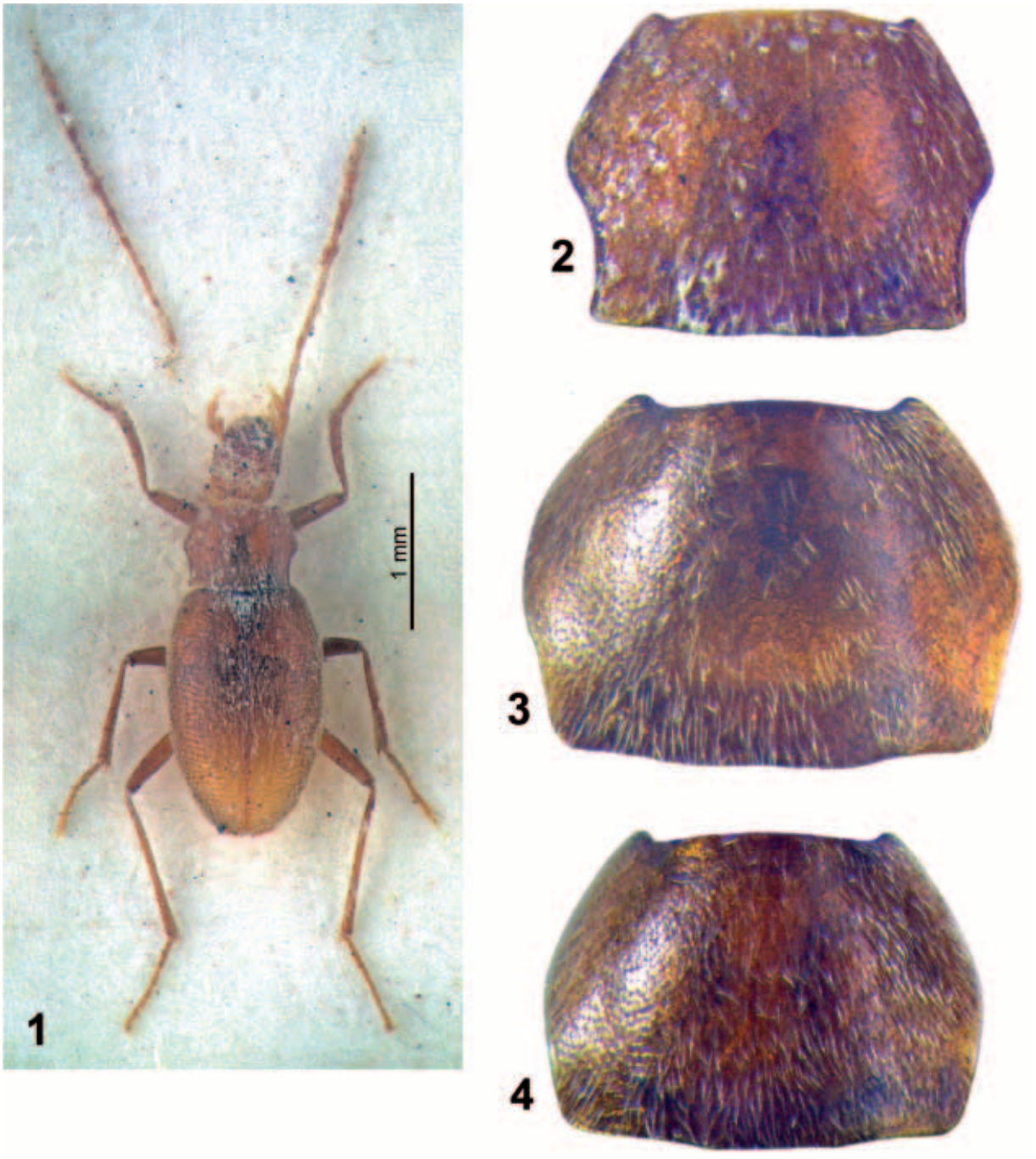
Etymology. This species is honored to Christian Juberthie who for years directed the Laboratoire Souterrain de Moulis of the CNRS (Saint-Girons, France) and collected the specimens of the type series. The specific name is a noun in the genitive singular.

Discussion. *Paratroglophyes juberthiei* sp. nov. is closely related to *P. aubryi* comb. nov., but differs from this species in the following characters:

– The pronotum is strongly narrowed in the basal third (Fig. 337.2), very similar to the Mediterranean *Troglocharinus*; in *P. aubryi* with regularly curved margins (Fig. 337.4) or also somewhat sinuous near the posterior vertices (Fig. 337.3).

– The male protarsi are very narrow, narrower than distal end of the protibia; in *P. aubryi* they are wide, somewhat more than the distal end of the protibia and often much wider.

– The aedeagus in lateral view (Fig. 338.1) tapers regularly to the apex having a slight dorsal depression, and in



FIGURES 337.1–337.4: *Paratroglophyes* spp. Habitus of the holotype of: (**1**) *P. juberthiei* **sp. nov.** Pronotum of: (**2**) *P. juberthiei* **sp. nov.**, (**3**) *P. aubryi* **comb. nov.** from Bethmale, (**4**) *P. aubryi* **comb. nov.** from Route de Gérac.



FIGURES 338.1–338.10: *Paratroglophyes* spp. Aedeagus in lateral view of: (**1**) *P. juberthiei* **sp. nov.**, (**2**) *P. aubryi* **comb. nov.**, (**3**) *P. orestes*, (**4**) *P. carrerei*, (**5**) *P. jeanneli*. Aedeagus in dorsal view of: (**6**) *P. juberthiei* **sp. nov.**, (**7**) *P. aubryi* **comb. nov.**, (**8**) *P. orestes*, (**9**) *P. carrerei*, (**10**) *P. jeanneli*.

dorsal view it has sinuous lateral margins (Fig. 338.6); in *P. aubryi* it is gibbous, the apical third is drastically reduced to a point from which it maintains the dimensions to the tip (Fig. 338.2), and in dorsal view it looks more robust, with the lateral margins in a regular curve (Fig. 338.7).

– The endophallus has an axial piece with imbricated spicules at the upper end of the middle part (Fig. 339.3); in *P. aubryi* it has a bundle with numerous divergent spicules (Fig. 339.4).

It has been possible to study three females from another nearby locality that do not belong to the type series. They are more robust than the male, with the elytra somewhat broader and more domed; the narrowing of the basal part of the pronotum is less pronounced; the protarsi are not thickened and are tetramerous.

The other *Paratroglophyes* are different (Fresneda *et al*. 2011), larger, with differences in the median lobe of aedeagus, which is larger and angled, the two halves of similar length (Figs. 338.3-338.5); the endophallus has a very long, fine inverted «V» and at the bottom of each branch a curved thickening (Figs. 338.8-338.10); there is sexual dimorphism in the meso- and metafemora, although it is little marked in *P. orestes*.

On *Paratroglophyes aubryi aubryi* comb. nov. and *P. aubryi vallierensis*. In the study of a large series of specimens from different localities, it has been found that the slight sinuosity of the basal part of the lateral margins of the pronotum can be more or less pronounced, even in the two margins of the same specimen; furthermore, in the two localities of the Cirque d'Anglade, in the cave (type locality) the pronotum is not sinuous (Coiffait 1953), while in MSS S47 (see Material studied) it is sinuous. Each one of the forms does not seem to have a determined distribution (Fig. 339.5). The specimens of (see Material studied) MSS S47, S48, S52 nº 1, S53 nº 2, S83, S88 and Lameza-Grotte des Hommes Morts have a sinuous pronotum (Fig. 339.5). The specimens of MSS S84, Grotte du Trapech, Grotte du Bois d'Arros and Grotte du Cirque d'Anglade (Coiffait 1953) have a non-sinuous pronotum (Fig. 337.4). It is not known what the pronotum of the males of MSS S54 is like, a locality from which only one female has been studied. But not only the shape of the pronotum has an irregular distribution, but also the width of the male protarsi or the shape of the mesoventral keel. There are no significant differences in the aedeagus of each of the populations studied. It is probable that Coiffait described the subspecies *vallierensis* due to the marked sexual dimorphism that he found in *P. aubryi* comb. nov., very moderate in the other subspecies. Later, he discovered that what he had believed to be female *P. aubryi* comb. nov. were actually of another species, *P. jeanneli*, which he later described (Coiffait 1955) and corrected the characterization of *P. aubryi* comb. nov. For all of the above, it is established the synonymy *Troglophyes aubryi* Coiffait, 1953 = *Troglophyes aubryi vallierensis* Coiffait, 1953 syn. nov.

Material studied and bibliographical references. Part of the material studied was donated by Ch. Juberthie to one of the authors (JF) around 1990. It forms part of the collections of the CNRS study campaign in superficial subterranean environment (MSS) in the Ariège region (France). Each locality is labeled with the place name and an identification number of the sampling station; accurate information has only been found for «S52 No. 1», which is given in detail by Juberthie & Bouillon (1983).

Paratroglophyes juberthiei sp. nov. In addition to the type series, three females have been studied: France, Ariège, Candails sup., 12.VI.1983, CNRS Moulis, 2 ♀♀; 13.VI.1983, CNRS Moulis, 1 ♀. All the specimens were collected by means of traps placed in MSS. It inhabits the reliefs of the Arac river basin and its tributary the Liers, between Massat and Col de Port (Ariège, France).

Paratroglophyes aubryi (Coiffait, 1953) comb. nov. Mont-Rouge and Mont-Vallier, in the southern reliefs of Seix up to the line of maximum altitude of the Pyrenees (France):

– Ariège, Bethmale, MSS S52 nº 1, 31.X.1979, CNRS Moulis, 6 ♂♂, 15 ♀♀ (CFL). S52 nº 1 = X: 498,27; Y: 3063,55 (coordinates Lambert), 1,020 m (Juberthie & Bouillon 1983).

– Ariège, Bethmale, MSS S53 nº 2, 23.X.1979, CNRS Moulis, 1 ♀ (CFL).

– Ariège, Bethmale, Lameza-Grotte des Hommes Morts (Coiffait 1953), G26, CNRS Moulis, 1 ♀ (CFL).

– Ariège, Bois de Rames, MSS S88, 2.X.1980, CNRS Moulis, 3 ♂♂ (CFL).

– Ariège, Bordes-sur-Lez, Grotte du Trapech, pièges 2002, Bourdeau leg., 3 ♂♂, 3 ♀♀ (CFL).

– Ariège, Campuls, MSS S83, 30.X.1980, CNRS Moulis, 2 ♂♂, 2 ♀♀ (CFL).

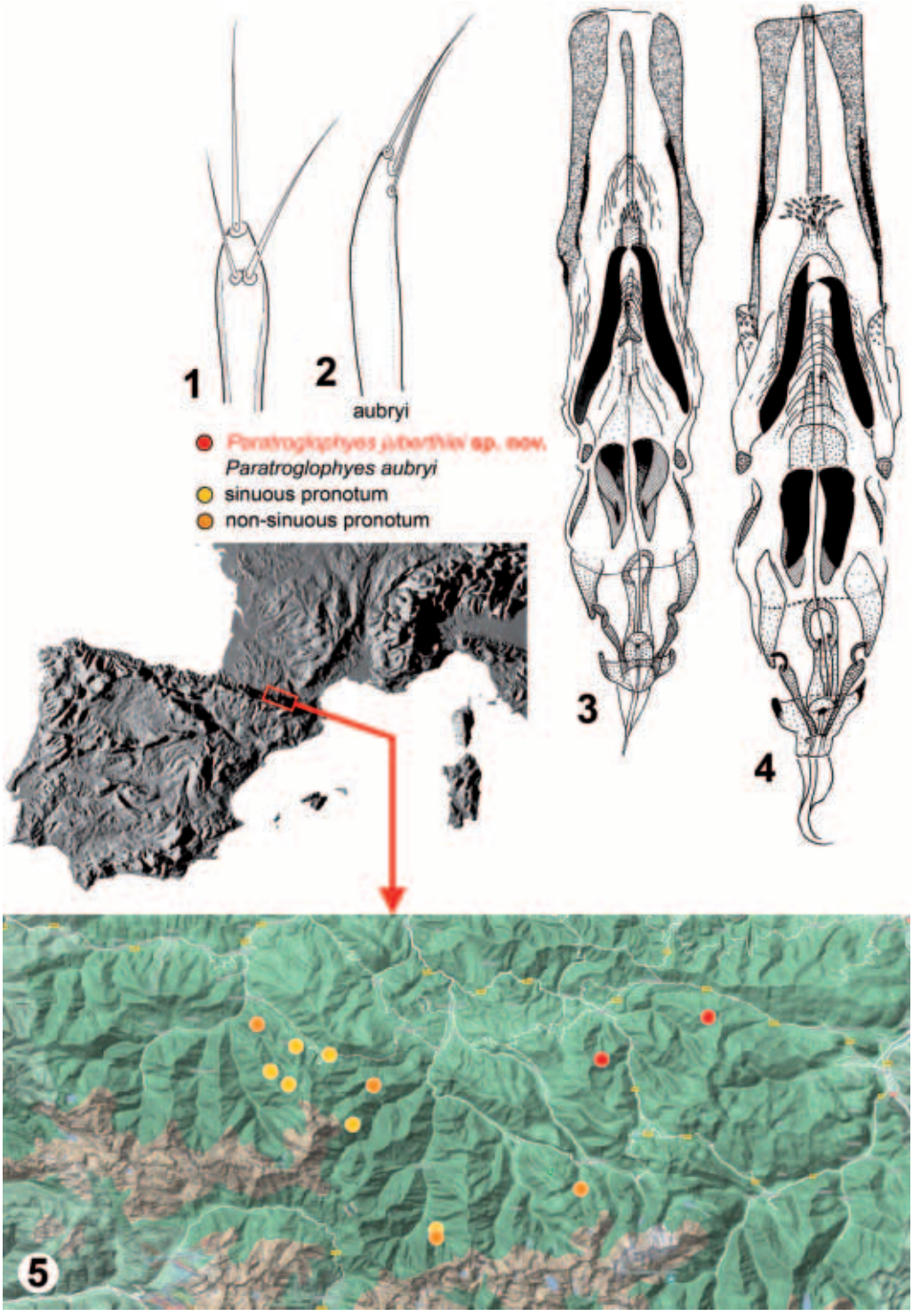
– Ariège, Pas de la Core, Grotte du Bois d'Arros, VI.2006, Bourdeau leg., 28 exx. (CFL).

– Ariège, Col de la Core, MSS S54, 22.VIII.1980, CNRS Moulis, 1 ♀ (CFL).

– Ariège, Route de Gérac, 1750 m, MSS S84, CNRS Moulis, 8 ♂♂, 3 ♀♀ (CFL).

– Ariège, Salau, Cirque d'Anglade, 1,500 m, MSS S47, 6.9.1979, CNRS Moulis, 1 ♂, 3 ♀♀ (CFL).

– Ariège, MSS S48, CNRS Moulis, 1 ♀ (CFL) – unknown location –.



FIGURES 339.1–339.5: *Paratroglophyes* spp. Apex of paramere of: (**1**) *P. juberthiei* **sp. nov.**, (**2**) *P. aubryi* **comb. nov.** Endophallus of: (**3**) *P. juberthiei* **sp. nov.**, (**4**) *P. aubryi* **comb. nov.** (**5**) Distribution map of *P. juberthiei* **sp. nov.** and *P. aubryi* **comb. nov.** with sinuate pronotum (yellow circle) and non-sinuate pronotum (light brown circle).

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.17	0.17	0.17	0.18	0.19	0.23	0.24	0.15	0.2	0.2	0.29
Width	0.07	0.05	0.06	0.05	0.05	0.05	0.10	0.06	0.08	0.10	0.09

TABLE 20. Measurements of antennomeres of the holotype of *Paratroglophyes juberthiei* sp. nov. (mm).

Perreauia dalmatica sp. nov.
(Figs. 110.2, 112.2, 114.2, 114.8, 115.2, 116.2, 116.10)
https://zoobank.org/NomenclaturalActs/AA01D138-E3F5-4DAA-B373-4489EDB7AD16

Type locality. Croatia, Makarska, Bast, Kukor Spilja, UTM: 4801742 6418672, 430 m.

Type series. Holotype ♂ (CPMG): labelled [CROATIA Biokovo Mt. / Makarska, Bast / Kukor Spilja 23.IX.1999 / P.M. Giachino leg], [HOLOTYPUS / *Perreauia* / *dalmatica* gen. n. sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: 1 ♂, 3 ♀♀, same data as the holotype. All the paratypes with red label [PARATYPUS / *Perreauia* / *dalmatica* gen. n. sp. n. / Fresneda *et al*. 2024] (CMNH, CPMG, CFL).

Description. Holotype ♂. Total length 1.6 mm and maximum width 0.9 mm. Body oval, elongated, moderately convex and clearly narrowed backwards (Fig. 110.2). Coloration reddish-brown. Pubescence fairly long, yellowish, shiny, fine and lying.

Head: Retractile, almost twice as wide as long; with occipital carina little marked but evident; punctation well-marked and clearly distant dots. Anophthalmous.

Antennae: Short and robust not exceeding pronotal base. First antennomere shorter than second one. Club differentiated, with antennomeres slightly flattened; antennomere 3rd longer than each of 4th, 5th and 6th; 8th globose and transverse; 9th and 10th transverse and as thick as 11th, being 11th slightly longer than 9th and 10th together. Antennal formula: See Table 21.

Pronotum: Transverse, 1.7 times wider than long; attenuated forwards, slightly arched sides widening progressively backwards; with very small and fine dots scarcer and finer than on the head; maximum width just at the base, which is as wide as elytra; posterior angles acute with pointed vertices, somewhat prolonged on the base of the elytra in dorsal view; bisinuate base.

Elytra: Oval-elongated and convex; length 0.8 width of both elytra; with arched lateral margins in anterior half; widest near base; apex of each elytra rounded; dorsal surface clearly microreticulate; elytral sculpture formed by well marked and well separated transverse striolae; without parasutural stria. Scutellum small and triangular.

Legs: Relatively long and delicate; protibiae with internal spur and with comb at the apical and outer edges, there are no external spurs; protarsi pentameres widened with the first tarsomere narrower than the widest part of the protibia and as wide as long; meso- and metatibiae thin and straight, both without apical basket of spines.

Mesoventral keel (Fig. 112.2): Tall, with convex anterior and posterior margins, the latter smooth and with some setae; rounded vertex and very obtuse angle; posterior process extends over middle of metaventrite.

Suture of the metaventrite (Fig. 112.2): It runs a short distance from the edge of mesocoxal cavity and delimits a small arched area in the upper half.

Median lobe of aedeagus: Long and narrow. In lateral view (Fig. 114.2) not arcuated, with dorsal and ventral sides parallel along the basal and middle areas; dorsal side straight and without any depression, with a very curved, narrow apical area and a very pointed tip. In dorsal view (Fig. 114.8), with sides slightly arched, with a soft concavity in the middle, near the apical area tapering which thins abruptly to form a long extension bent towards ventral surface. Basal blade long, narrow, with concave sides and arcuate apical margin.

Endophallus (Fig. 114.8): Armed with sclerotized structures in three regions; in basal part with a long inverted stylet that reaches the middle part; in the middle part and in the centre a narrow, well sclerotized lamina, sigmoid in lateral view; in apical part two bands joining in an inverted «Y»-piece with two spongy structures on both sides of the base of this piece.

Parameres (Fig. 115.2): Very robust, wide and flattened to apical area, as long as median lobe; apical area elbow-shaped facing outward, with rounded apex; three setae inserted in this area, two apical with the inner one longer and much thicker, the third subapical inserted in the elbow area. Ventral blade of tegmen wider and as long as basal blade of median lobe.

Female.

Spermathecal complex (Fig. 116.2) and *female uroventrite VIII* (Fig. 116.10): See genus description.

Variability. The studied specimens maintain constant characters, there are no significant differences between them. Sexual dimorphism is only visible in the protarsi, which are pentamerous and dilated in males, tetramerous not dilated in females.

Etymology. The specific name refers to Dalmatia and indicates the capture area in this region of Croatia.

Discussion. See under the Discussion section of the genus *Perreauia* nov.

Distribution. Only known from the type locality, the cave Kukor Spilja in Bast, near Makarska, Biokovo mountains, Croatia.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.07	0.10	0.05	0.03	0.04	0.03	0.04	0.03	0.04	0.04	0.10
Width	0.04	0.04	0.03	0.03	0.03	0.03	0.04	0.04	0.06	0.07	0.07

TABLE 21. Measurements of antennomeres of the holotype of *Perreauia dalmatica* sp. nov. (mm).

Proleonhardella epimikes sp. nov.
(Figs. 340.1, 340.3, 341.1, 341.3, 341.4, 342.1, 342.2)
https://zoobank.org/NomenclaturalActs/240D2C67-79C5-4E07-9AB1-9A621484DFAB

Type locality. Bosnia-Herzegovina, Foča, Toplica, 43°59'N 19°26'E.

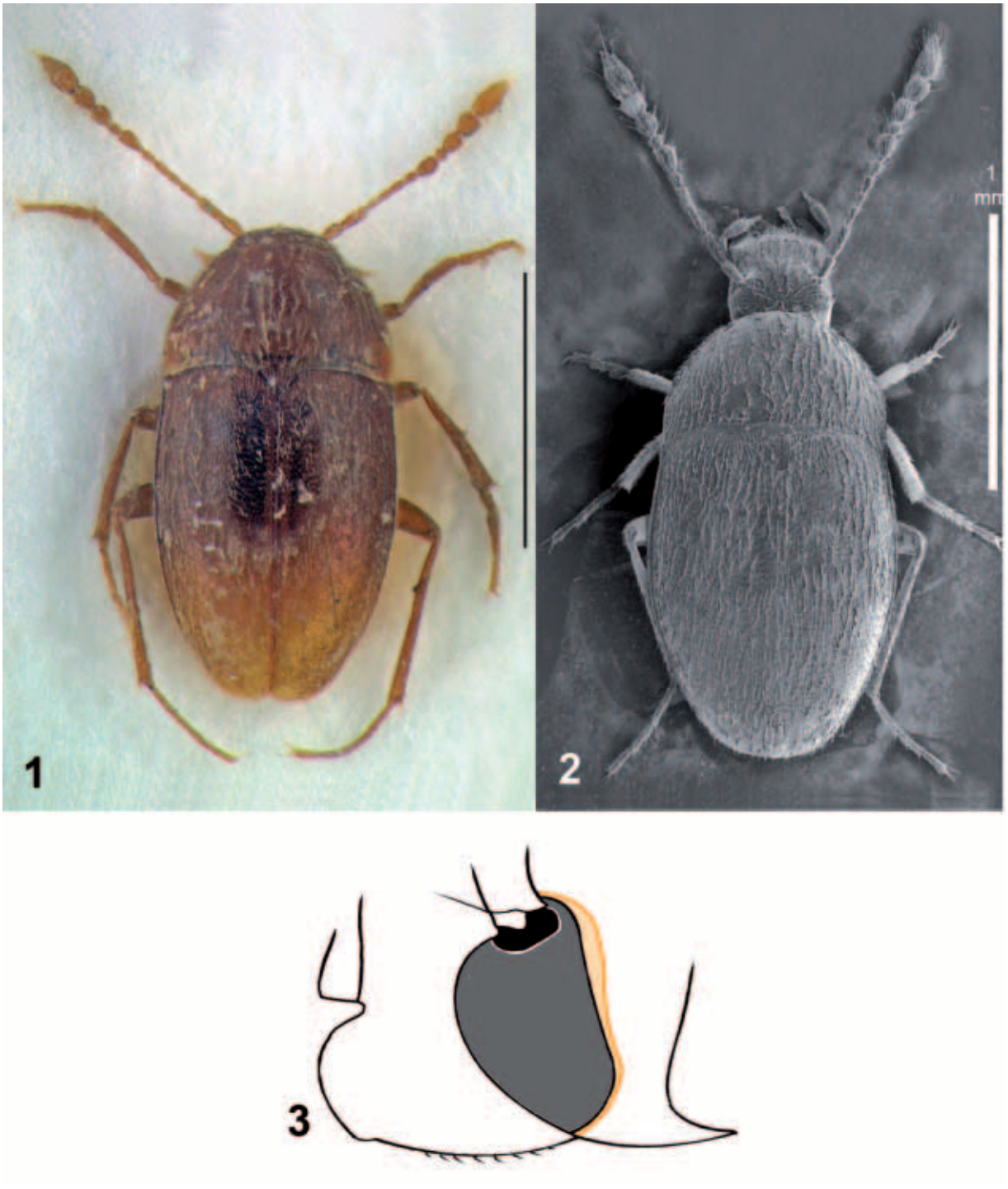
Type series. Holotype ♂ (CPMG): labelled [Yougosl Bosnia / Foca, Toplica, D Bud. / 21.7.1969, Eg Pretner], [HOLOTYPUS / *Proleonhardella* / *epimikes* sp. n. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: 45 exx. ♂♂ and ♀♀, with the same collection data as the holotype, with paratype label [Paratypus / *Proleonhardella* / *epimikes* sp. n. / Fresneda *et al*. 2024] (rl) (CPMG, CFL, SMNS).

Diagnosis. *Proleonhardella* characterized by a body elongated and oval; pronotum narrower than elytra and lateral margins weakly rounded backwards; elytral punctation fine; mesoventral keel elevated and angled; elytra long, slightly convex and at least twice as long as length of pronotum and in basal half parallel or subparallel; aedeagus elongated.

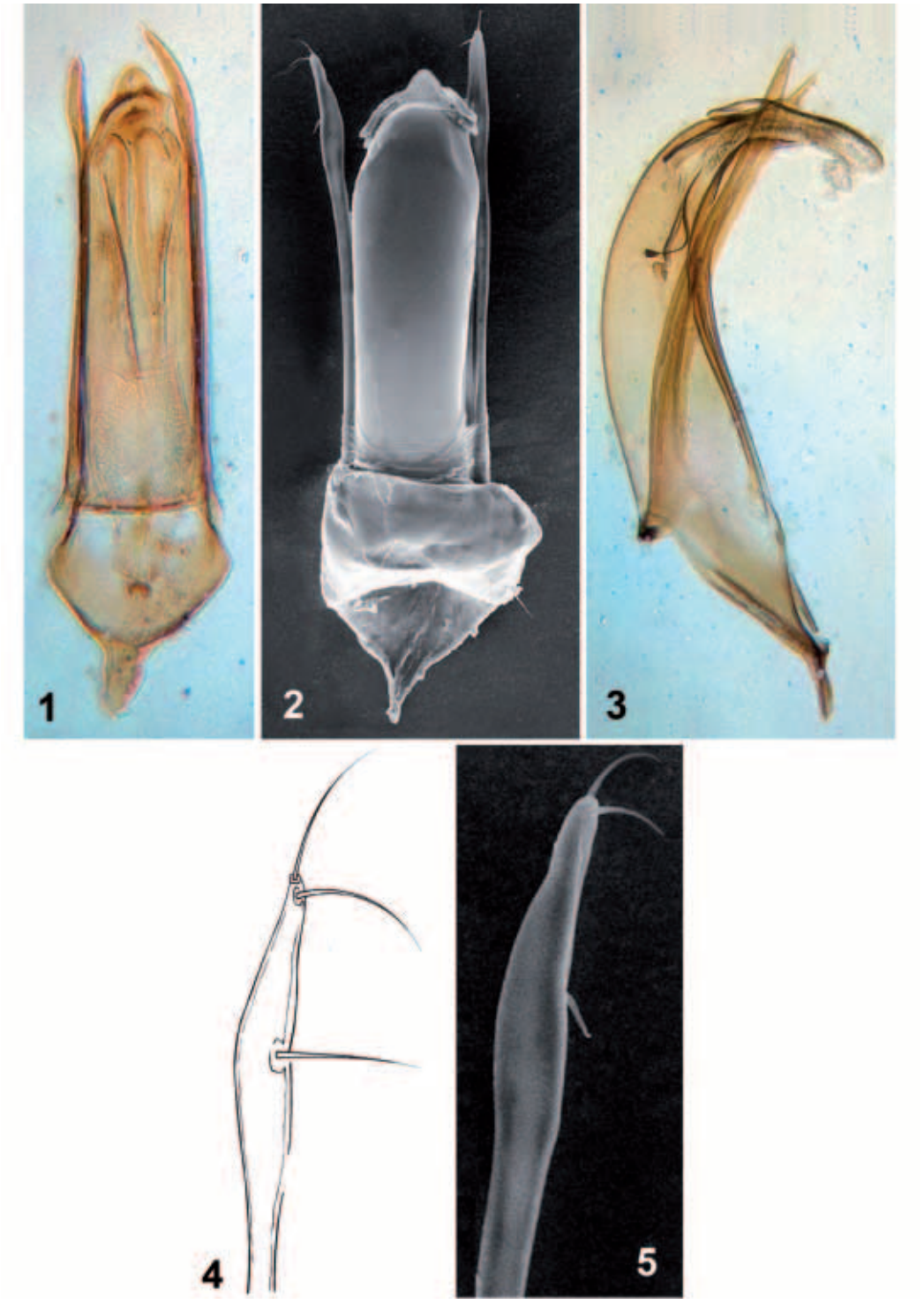
Description. Holotype ♂. Small size, 1.75 mm; maximum width 0.89 mm. Body shape oval elongated, convex, moderately broadened, with slightly curved lateral margins and little acuminate near back (Fig. 340.1); facies bathyscioid; reddish-brown colour. Pubescence yellowish, short, thin and recumbent. Depigmented.

Head: Retractile, short, moderately broad, slightly longer than wide; sculpture made of sparse dots densely arranged; occipital carina poorly marked; anophthalmous.

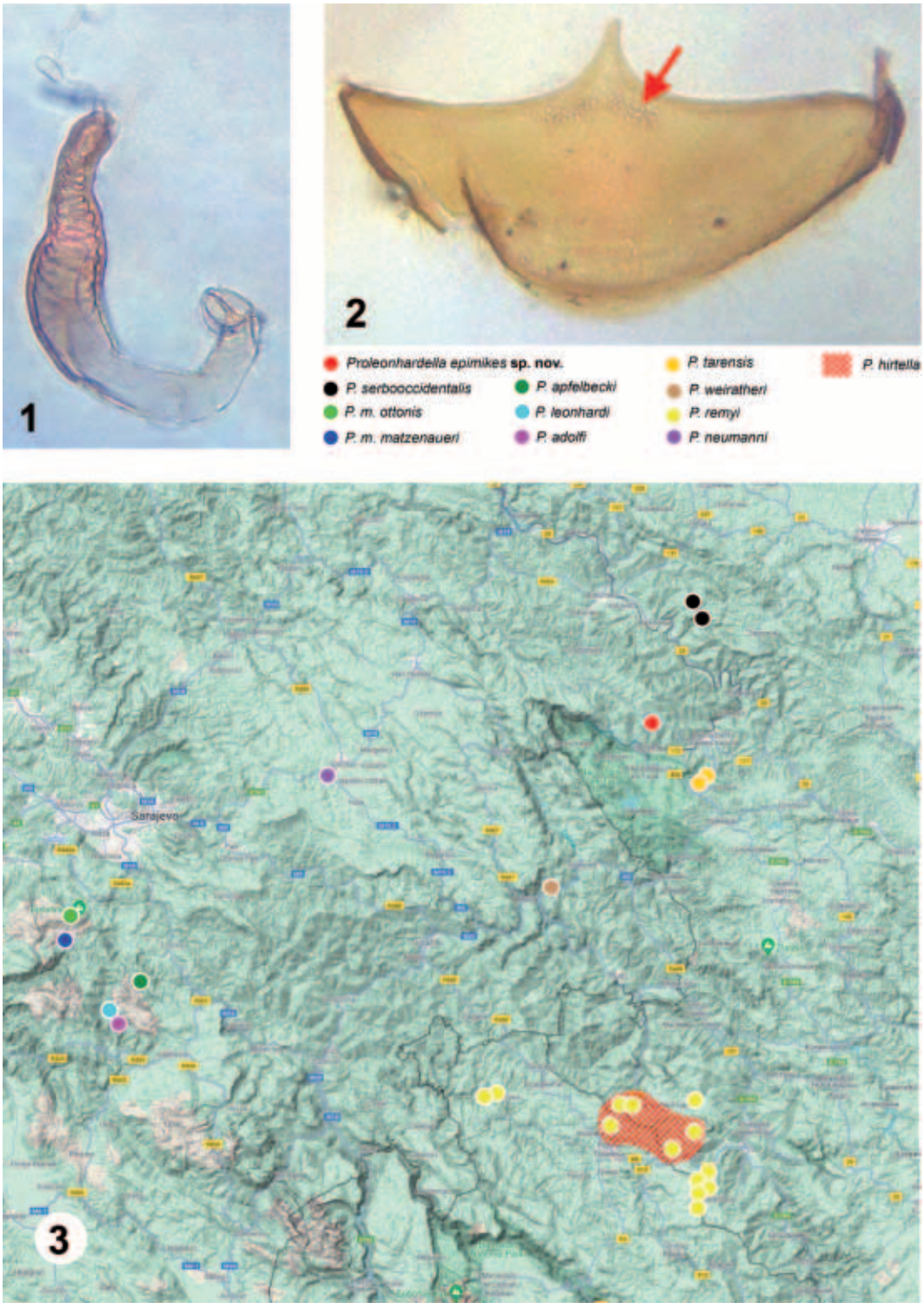
Antennae: Long (1 mm) and narrow, reaching basal third of elytra; antennomeres of club broad; 2nd longer than 1st; 3rd to 6th longer than wide, similar in length and width; 7th apically widened and twice as long as wide; 8th oval and very slightly longer than wide; 10th slightly longer and wider than 9th and both slightly longer than wide; 11th twice as wide as long and almost as long as 9th and 10th together. Antennal formula: See Table 22.



FIGURES 340.1–340.3: *Proleonhardella* spp. Habitus of: (**1**) *P. epimikes* **sp. nov.**, (**2**) *P. tarensis* (modified from S. Ćurčić *et al*. 2021). Mesoventral keel of: (**3**) *P. epimikes* **sp. nov.**



FIGURES 341.1–341.5: *Proleonhardella* spp. Aedeagus in dorsal view of: (**1**) *P. epimikes* **sp. nov.** (**2**) *P. tarensis*. Aedeagus in lateral view of: (**3**) *P. epimikes* **sp. nov.** Apex of the paramere of: (**4**) *P. epimikes* **sp. nov.** (**5**) *P. tarensis*. Figs **2**, **5** modified from S. Ćurčić *et al*. (2021).



FIGURES 342.1–342.3: *Proleonhardella* spp. *P. epimikes* **sp. nov.**: (**1**) Spermathecal complex, (**2**) Female uroventrite VIII, (**3**) distribution map of species of the genus *Leonhardella*. Red arrow pointing to the « field of pores».

Pronotum: Transverse, 1.7 times wider than long, maximum width near base and this as wide as basal area of elytra; sides slightly curved in anterior half and more curved in posterior half; angles acute and not very pointed vertices.

Elytra: Elongated, 2.5 times longer than pronotum and 1.4 times longer than wide; in basal third narrower and subparallel, then more curved being part of maximum width, with final third slightly tapered backward and curved apices. Microsculpture of pronotum formed by large isodiametric meshes. Dots numerous, fine and irregular, without transverse striation. Parasutural stria absent.

Legs: Relatively elongated and thin, with hairs; protibiae slightly curved inwards, meso- and metatibiae very slightly curved inwards in proximal third then straight, both with few spines laterally. Protarsi tetramerous and dilated in males but narrower than distal part of protibia.

Mesoventral keel (Fig. 340.3): Tall and short. Prominent front edge very convex, very obtuse-angled, vertex forms a tooth broad and very slightly protruding; posterior edge in broad and smooth curvature with hairs and ventral area not grooved. Posterior process not exceeding mesocoxal cavities.

Suture of the metaventrite (Fig. 340.3): Simple suture sinuously arched near basal third, close to mesocoxal cavity delimiting an elongated and reduced area, slightly broader in upper half.

Metatergal apparatus and *metendosternite*: Unknown.

Median lobe of aedeagus: In lateral view (Fig. 341.3) half of basal area of ventral margin straight, then in very marked curve to apical area; dorsal margin almost regularly arched to strong distal depression, this area narrow and pointed. In dorsal view (Fig. 341.1), elongated, narrow, subparallel-sides ending in bulging projection in middle part, followed by apical part narrowing into a triangle shape with apical vertex rounded. Basal lamina broader than median lobe and in posterior half with an elongated subtriangular projection.

Endophallus (Fig. 341.1): Copulatory pieces weakly sclerotized, consisting of a small basal phanera resembling a slender flagellum dilated at base, similar to that of species of genus *Quaesticulus*; basal median part with a broad band of spinules lining inner wall of sac and in apical part two reinforcing bands long and narrow reaching middle part of sac.

Parameres (Fig. 341.4): In lateral view, broadened at base and then progressively narrowing to elongated club, somewhat broadened in middle part and very narrowed at apex, consisting of three medium-length setae, two apical with insertion pores very close and another internal subapical very distant from previous ones. In dorsal view, slender, longer than median lobe, with apical parts directed inward.

Female.

Spermathecal complex (Fig. 342.1): Spermatheca small, curved or stick-shaped; well sclerotized and externally banded basal part, that area of attachment to spermiduct being narrower, then broader; median part or joining duct, long, membranous and narrower; apical part somewhat more sclerotized, in form of a small bonnet; thin spermatic duct joining directly to spermatheca; no spermathecal gland observed.

Female uroventrite VIII (Fig. 342.2): Large, transverse, setose both medially and distally, with band of points arranged in arc behind short spiculum, triangular in shape and apical part somewhat curved, with apex slightly tapering.

Etymology. From classic Greek *επίμηκες*, epímikes = elongated, oblong. Relating to the body shape of new species.

Discussion. *Proleonhardella epimikes* sp. nov. is characterized by an elongated oval body; the pronotum being narrower than the elytra and the lateral margins weakly rounded backwards; the elytral punctation is fine; the mesoventral keel is elevated and angled; the elytra long, slightly convex and at least twice as long as the length of the pronotum and in the basal half parallel or subparallel; the aedeagus is elongated. All these characteristics are shared with its closest relatives *Proleonhardella hirtella*, *P. neumanni*, *P. tarensis* and *P. weiratheri*. Of these four species, the morphologically most similar is *P. tarensis*, from which it is clearly differentiated by:

– *Proleonhardella epimikes* sp. nov.: The contour is more regular without pronotal-elytral angle (Fig. 340.1); the mesoventral keel (Fig. 340.3) has the anterior edge more prominent forward, the ventral edge more convex, the angle more obtuse and the tooth more blurred; the female uroventrite VIII (Fig. 342.2) has a band of dots arranged in an arc behind the spiculum; the aedeagus in dorsal view (Fig. 341.1) with the apex of the triangular apical part more rounded and the structures of the endophallus are different, especially the shape of the flagellum and the wide

band of spinules on the internal wall of the sac; also, the setae at the apex of the parameres are somewhat longer (Fig. 341.4).

– *Proleonhardella tarensis*: It has pronotal-elytral angle marked (Fig. 340.2); the mesoventral keel has the anterior edge more prominent forward, the ventral edge less convex, the angle less obtuse and the tooth less blurred (S. Ćurčić *et al*. 2021: Fig. 5c); the female uroventrite VIII (S. Ćurčić *et al*. 2021: Fig. 5i) does not present a band of dots arranged in an arc behind the spiculum; the aedeagus in dorsal view (Fig. 341.2) with the apex of the triangular apical part less rounded and the structures of the endophallus different; the setae at the apex of the parameres are somewhat shorter (Fig. 341.5).

Distribution (Fig. 342.3). Only known from the type locality an unspecified place in Toplica (Foča, Bosnia-Herzegovina), near the Serbian border. There is no information on the circumstances of its discovery.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.07	0.10	0.05	0.03	0.04	0.03	0.04	0.03	0.04	0.04	0.10
Width	0.04	0.04	0.03	0.03	0.03	0.03	0.04	0.04	0.06	0.07	0.07

TABLE 22. Measurements of antennomeres of the holotype of *Proleonhardella epimikes* sp. nov. (mm).

Salfia angelinii sp. nov.
(Figs. 343.3, 343.6-343.8, 344.3, 343.6, 343.9)
https://zoobank.org/NomenclaturalActs/573EF695-CADE-48F0-A171-5DEA93F50D36

Type locality. Italy, Lucania, Accettura (MT), 700 m.

Type series. Holotype ♂ (CPMG): Italy, Lucania, Accettura (MT), 700 m, 25.IX.1991, P.M. Giachino leg., with holotype label [Holotypus / *Salfia* / *angelinii* n. sp./ Fresneda *et al*., 2024] (hw, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 1 ♀ (CPMG). Basilicata (MT), foresta di Accettura, 800 m, 23.V.2018, P. Magrini leg., 2 ♀♀ (CPMG, CFL). All paratypes with label [Paratypus / *Salfia* / *angelinii* sp. n. / Fresneda *et al*., 2024] (hw, rl).

Diagnosis. A small-sized *Salfia* stat. nov., without parasutural stria (present in *Salfia ruffoi* comb. nov.), and dilated male protarsomeres (less dilated in *Salfia laudis* sp. nov.), shape of the median lobe of aedeagus with apex not lanceolate (lanceolate in *Salfia ferdinandi* comb. nov.) and parameres only slightly dilated at the apex (more dilated in *Salfia laudis* sp. nov. and *Salfia ruffoi* comb. nov.)

Description. Holotype ♂. Small size, 1.6 mm, habitus bathyscioid (Fig. 343.3).

Head: Retractile, with occipital carina complete; eyes absent.

Antennae: Short. Not reaching, stretching backward pronotal base; first antennomere as long as the second, but more robust; antennomeres 1st to 7th longer than wide; 8th to 10th transverse; 11th shorter than 9th and 10th together. Antennal formula: See Table 23.

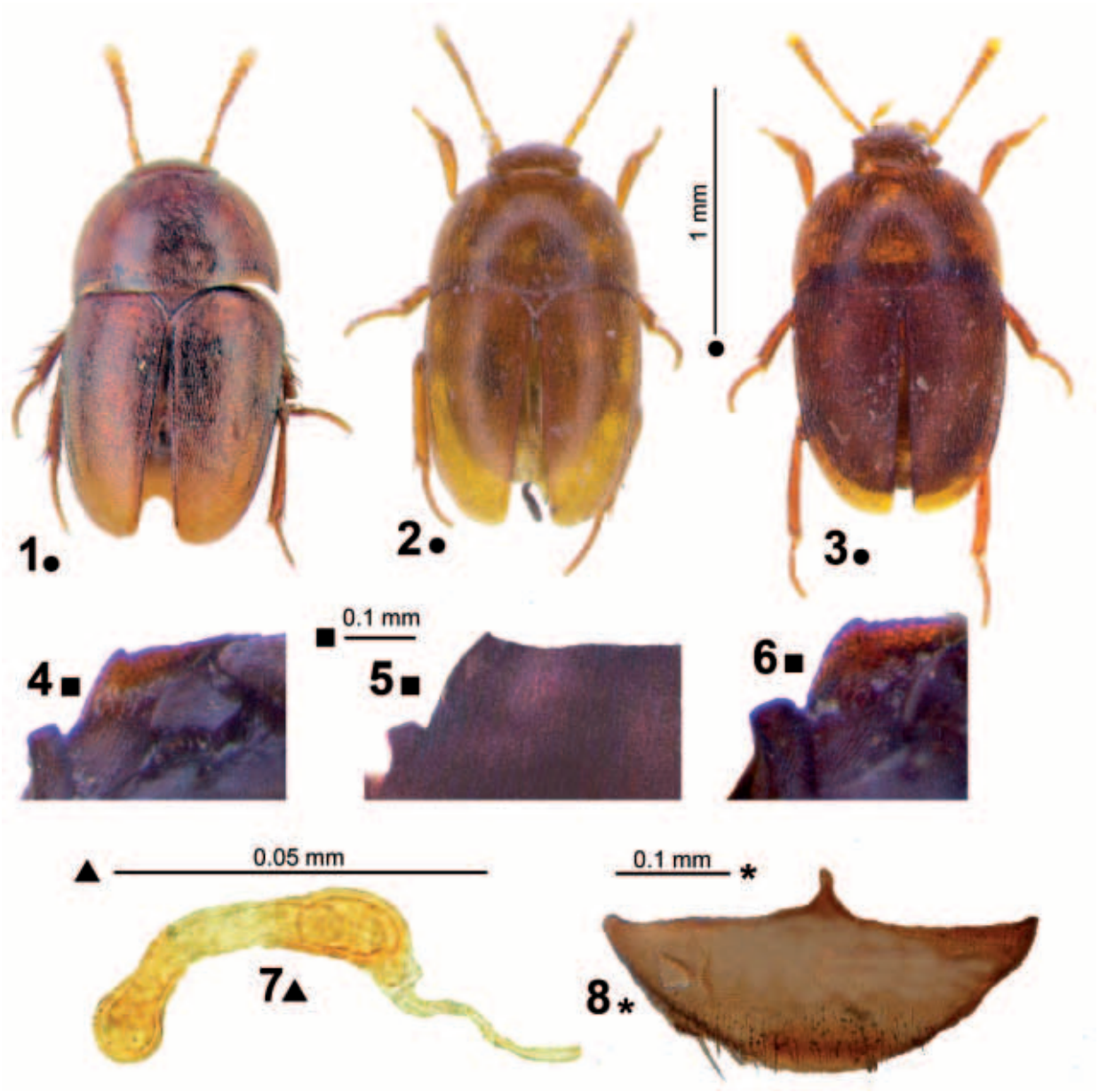
Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved near posterior angles; base weakly bisinuate. Posterior angles acute and prominent.

Elytra: Without transverse striolae and lacking of parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs; apical baskets of meso- and metatibiae incomplete; protarsi dilated, as broad as anterior part of protibia.

Mesoventral keel (Fig. 343.6): Tall, slightly curved anteriorly, with toothed apex, with inferior edge nocked and not reaching metaventrite.

Median lobe of aedeagus: Slightly curved in lateral view (Fig. 344.3) up to tip, not curved. In dorsal view (Fig. 344.6) slender, with subparallel sides in basal half, convergent in apical part; apex regularly rounded, slightly subtruncate but not lanceolate.



FIGURES 343.1–343.8: Habitus of: (**1**) *Salfia ruffoi* **comb. nov.**, (**2**) *S. laudis* **sp. nov.**, (**3**) *S. angelinii* **sp. nov.** Pterothorax in lateral view of: (**4**) *S. ruffoi* **comb. nov.**, (**5**) *S. laudis* **sp. nov.**, (**6**) *S. angelinii* **sp. nov.** Spermatheca and Female uroventrite VIII of: (**7**, **8**) *S. angelinii* **sp. nov.**

Endophallus (Fig. 344.6): With internal armature formed by three sclerotized pieces, differentiating three regions (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with one slightly «U»-shaped sclerotized phanera. Apical reinforcement bands short and not apically convergent.

Parameres (Fig. 344.9): Slightly longer than median lobe and not enlarged at apex. Three setae sickle-shaped at apex.

Female. With stockier body, antennae shorter and protarsomeres tetramerous non-dilated.

Spermathecal complex: Spermatheca (Fig. 343.7) large and elongate, with basal and apical lobes of same dimension, well sclerotized, and median part long and less sclerotized. Expanded area of spermatic duct absent. Spermathecal gland present.

Female uroventrite VIII (Fig. 343.8): Posterior margin broadly arched; sides of anterior margin subrectilinear meeting in middle area forming a spiculum, short, pointed and more or less triangular-shaped.

Variability. Length of female paratype 1.7 mm.

Etymology. We dedicate this new species to the memory of Fernando Angelini, an appreciated coleopterologist who pointed out the interesting site of Accettura to one of the authors (PMG).

Discussion. No molecular data are available for this species; *Salfia angelinii* sp. nov. appears morphologically strongly related to *Salfia ruffoi* comb. nov. from Pollino Mount:

– *Salfia angelinii* sp. nov.: without parasutural stria (Fig. 343.3) and parameres only slightly dilated at the apex (Fig. 344.9).

– *Salfia ruffoi* comb. nov.: with parasutural stria (Fig. 343.1) and parameres more dilated (Fig. 344.7).

Distribution. Italy. It is known, now, only for the type locality, an oak forest near the village of Accettura (MT); it was collected by shifting oak litter.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.06	0.06	0.03	0.03	0.03	0.04	0.05	0.03	0.04	0.04	0.06
Width	0.03	0.03	0.01	0.02	0.01	0.02	0.04	0.04	0.05	0.06	0.06

TABLE 23. Measurements of antennomeres of the holotype of *Salfia angelinii* sp. nov. (mm).

Salfia laudis sp. nov.
(Figs. 343.2, 343.5, 344.2, 344.5, 344.8)
https://zoobank.org/NomenclaturalActs/D541C370-EFC2-4B08-B38E-4EE87A91D0D2

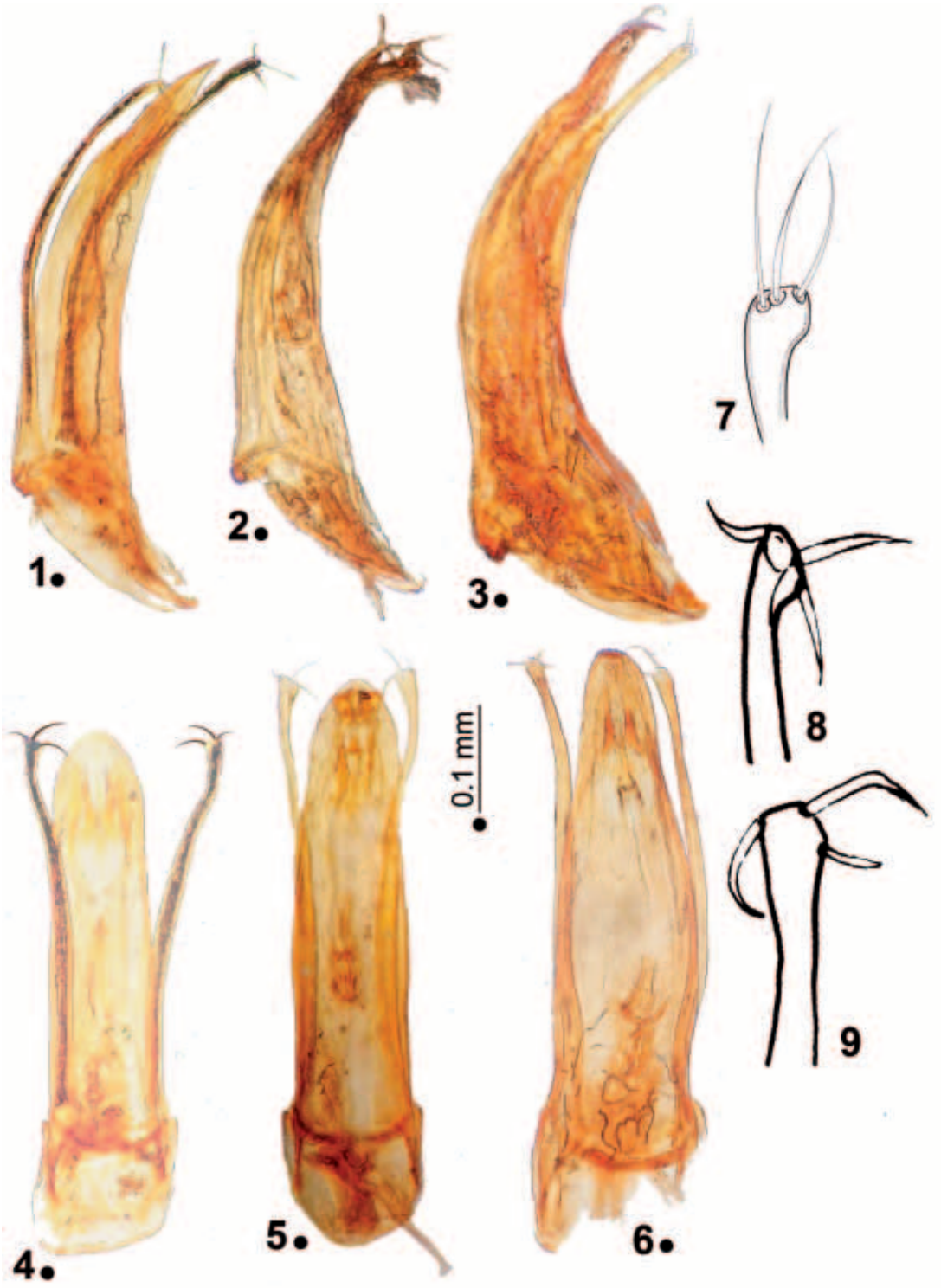
Type locality. Italy, Lucania, Lagonegro (PZ), Monte Sirino, 1,230 m.

Type series. Holotype ♂ (CPMG): Italy, Lucania, Lagonegro, Monte Sirino, 1,230 m, 26.IX.1991, P.M. Giachino leg., with holotype label [Holotypus / *Salfia* / *laudis* n. sp./ Fresneda *et al*., 2024] (hw, rl), genitalia on transparent card mounted on the same pin as the holotype.

Diagnosis. A small-sized *Salfia* stat. nov., without parasutural stria (present in *Salfia ruffoi* comb. nov.), and male protarsomeres slightly dilated (more dilated in *Salfia angelini* sp. nov.), shape of the median lobe of aedeagus with apex not lanceolate (lanceolate in *Salfia ferdinandi* comb. nov.) and parameres dilated at apex (less dilated in *Salfia angelinii* sp. nov. and *Salfia ruffoi* comb. nov.)

Description. Holotype ♂. Small size, 1.5 mm, body bathyscioid (Fig. 343.2).

Head: Retractile, with occipital carina complete; eyes absent.



FIGURES 344.1–344.9: Aedeagus in lateral view of: (**1**) *Salfia ruffoi* **comb. nov.**, (**2**) *S. laudis* **sp. nov.**, (**3**) *S. angelinii* **sp. nov.** Aedeagus in dorsal view of: (**4**) *S. ruffoi* **comb. nov.**, (**5**) *S. laudis* **sp. nov.**, (**6**) *S. angelinii* **sp. nov.** Apex of the paramere of: (**7**) *S. ruffoi* **comb. nov.**, (**8**) *S. laudis* **sp. nov.**, (**9**) *S. angelinii* **sp. nov.**

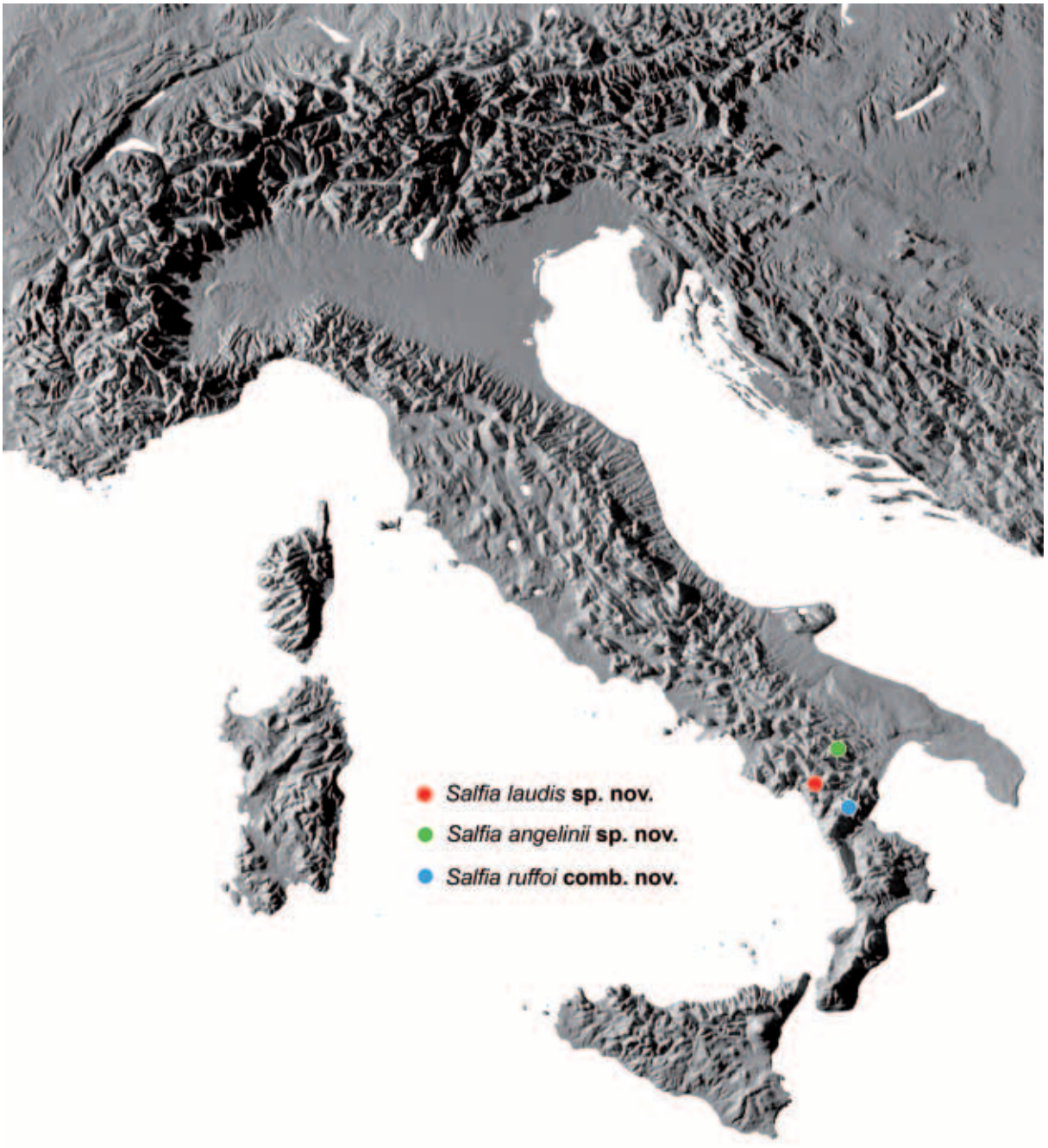


FIGURE 345: Distribution map of: *Salfia ruffoi* **comb. nov.**, *Salfia laudis* **sp. nov.** and *S. angelinii* **sp. nov.**

Antennae: Medium short. Not reaching, stretching backward pronotal base; first antennomere as long as the second, but more robust; antennomeres 1st to 7th longer than wide; 8th and 10th as long as wide; 11th as long as 9th and 10th together. Antennal formula: See Table 24.

Pronotum: Transverse, broadest at base, regularly curved near anterior angles and less curved near posterior angles; base weakly bisinuate. Posterior angles acute and prominent.

Elytra: Without transverse striolae and lacking of parasutural stria.

Legs: Apex of tibiae on inner side with polydentate spurs. Apical baskets of meso- and metatibiae incomplete; protarsi dilated, narrower than anterior part of protibia.

Mesoventral keel (Fig. 343.5): Tall, slightly curved anteriorly, with apex toothed, with inferior edge straight and not reaching metaventrite.

Median lobe of aedeagus: Slightly curved in lateral view (Fig. 344.2) up to tip, not curved. In dorsal view (Fig. 344.5) slender, with subparallel sides in basal half and slightly convergent in apical part; apex regularly rounded and not lanceolate.

Endophallus (Fig. 344.5): With internal armature formed by three sclerotized pieces, differentiating three parts (basal, medial and apical). «Y»-piece and flagellum in basal area present. Median part with two phanerae slightly sclerotized «U»-shaped. Apical reinforcement bands short and not apically convergent.

Parameres (Fig. 344.8): Slightly longer than median lobe. Apex enlarged, club-shaped. At apex three sickle-shaped setae .

Female. Unknown.

Etymology. From the Latin *laus-laudis* (praise, glory), the name recalls Lake Laudemio (*Laudemium* in Medieval Latin), located on Sirino Mount.

Discussion. No molecular data are available for this species; *Salfia laudis* sp. nov. appears strictly morphologically related to *Salfia ruffoi* comb. nov. from Pollino Mount:

– *Salfia laudis* sp. nov.: without parasutural stria (Fig. 343.2), aedeagus in lateral view less robust (Fig. 344.2), in dorsal view more pointed (Fig. 344.5) and parameres more dilated at the apex (Fig. 344.8).

– *Salfia ruffoi* comb. nov.: with parasutural stria (Fig. 343.1), aedeagus in lateral view more robust (Fig. 344.1), in dorsal view more rounded (Fig. 344.5) and parameres less dilated at the apex (Fig. 344.7).

Distribution. Italy. Currently, it is known only from the type locality, the Sirino Mount, located near Lagonegro (PZ); it was collected by shifting beech litter.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.08	0.08	0.05	0.03	0.03	0.04	0.05	0.03	0.04	0.04	0.08
Width	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.04	0.04

TABLE 24. Measurements of antennomeres of the holotype of *Salfia laudis* sp. nov. (mm).

Schaufussia sinuatipenis sp. nov.
(Figs. 346.1-346.3, 346.5, 346.7, 346.8, 346.10)
https://zoobank.org/NomenclaturalActs/243921AE-B81F-4369-8049-23CC2DE94E52

Type locality. Spain, Asturias, Llandellena de Arriba, Cueva del Prau de la Sierra, UTM 2703 47968, 377 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): Spain, Asturias, Llandellena de Arriba, Cueva del Prau de la Sierra, 18.6.1988, J.M. Salgado leg., with holotype label [Holotypus *Schaufussia* / *sinuatipenis* sp. n. / Fresneda *et al.* det. 2023] (rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, 50 ♂♂, 110 ♀♀, with paratype label [Paratypus *Schaufussia* / *sinuatipenis* sp. n. / Fresneda *et al.* det. 2023] (rl) (CFL, CPMG, SMNS).

Description. Length 2.2 mm and maximum width 1.1 mm. Body oval, elongated, convex and slightly narrowed backward (Fig. 346.1). Pubescence fairly long, grayish and shiny, fine and lying. Sculpture very fine, almost imperceptible, formed by scattered dots both in pronotum and in elytra, in these closer and more abundant.

Head: Moderately broadened, with occipital carina somewhat blurred in middle area, lateral angles of forehead very prominent and pointed.

Antennae: Short (0.95 mm) and quite robust, slightly exceeding posterior edge of pronotum; antennomeres thickened from 7th; 3rd antennomere somewhat longer than 4th to 6th, being equals; 8th to 10th very slightly longer than wide; 11th widest, twice as long as 10th, and as long as 2nd. Antennal formula: See Table 25.

Pronotum: Transverse almost twice as wide as long (ratio: 1.8); narrowed at front and slightly narrowed backward, with sides regularly curved; widest a little before base, as wide as elytra; posterior angles rounded and very little prolonged on elytra, with a sub-rectilinear base.

Elytra: Short and broad – 1.25 times as long as wide –, with regularly curved margins and united at elytral suture very weakly, unattached; parasutural stria formed by parallel points along entire suture; apex of each elytra separately rounded.

Legs: Relatively long and delicate; protarsi almost as wide as maximum width of protibia (ratio: 0.95), with first tarsomere little longer than wide; mesotibiae somewhat curved and metatibiae straight; mesofemora with somewhat sinuate posterior margin and metafemora widened near middle and with minute prominence or spine on posterior margin.

Mesoventral keel (Fig 346.2): Tall and long, forming a curved apex with a right angle; two edges slightly convex, anterior one smoothly beaded and posterior one finely serrated in area near apex and somewhat broadened in middle area, but without a groove.

Suture of the metaventrite (Fig 346.2): Delimiting an arched area in its first half and subsequently running parallel to edge of mesocoxal cavity.

Median lobe of aedeagus: Long 0.6 mm. In lateral view (Fig. 346.3) with a sinuate profile, bent at an obtuse angle near middle of its path on ventral margin, with apical area curved near ventral face and apex pointed; on dorsal margin with a marked concavity near apical third delimiting two arches, one short apical and other broad basal; basal lamina forming a spoon-like structure in final part. In dorsal view (Fig. 346.5) presenting an apical area narrow and pointed, with area located near middle and sub-rectilinear lateral margins progressively decreasing until beginning of long basal lamina.

Endophallus (Fig. 346.5): With a stylet fairly robust and rather short, not reaching half the length of median lobe; surrounded by bags of membranous tissue with two bands of more visible lateral spicules in its apical part, without basal plate. Mid-apical part with two long reinforcing bands.

Parameres (Fig. 346.7): Slender, shorter than median lobe, without differentiated club and apex with three long setae inserted in very close insertion pores, two apical ones of similar length and basal one shorter.

Female. With same shape, size and punctation characteristics as males; most significant differences found in protarsi not dilated and tetramerous; posterior medial area of metafemora not broadened and without a spine; club of antennae with shortest and transverse antennomeres.

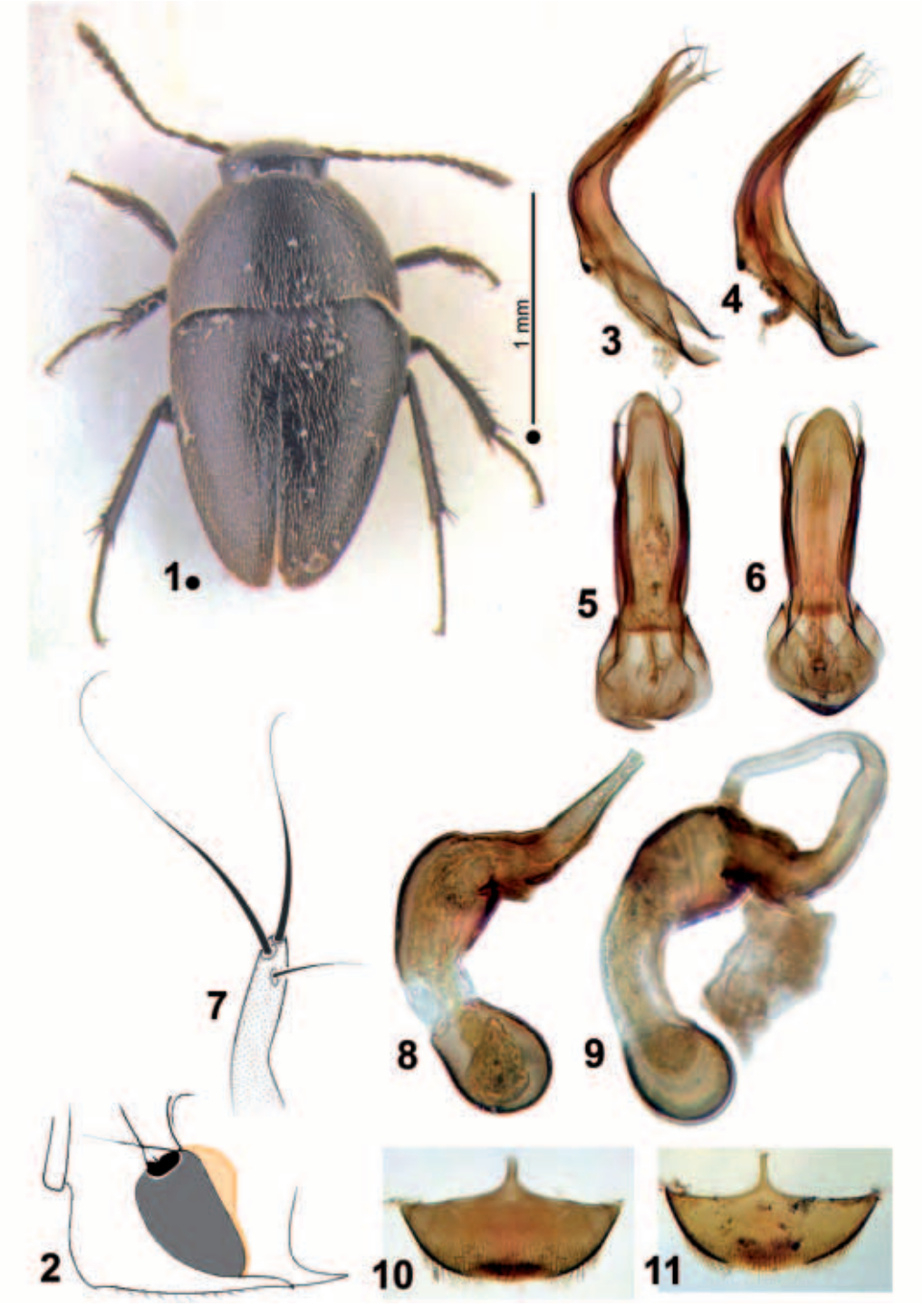
Spermathecal complex: Spermatheca (Fig. 346.8) with almost spherical apical lobe and oblong basal, both of similar width, and junction duct short and hyaline; spermiduct short, about three to four times longer than spermatheca; in its area of attachment to basal lobe very dilated, then narrowing progressively until forming a filiform duct emptying into copulatory bag without any sclerotized structure; spermathecal gland well-developed, emptying into broadened area of duct.

Female uroventrite VIII (Fig. 346.10): Apical margin slightly notched in middle area and with a narrow dark spot; spiculum long, narrow, straight and with a curved tip.

Variability. Variation only found in length and width of specimens studied: 2.2-2.3 mm and 1.1-1.2 mm respectively.

Etymology. This specific name is an adjective referring to the marked sinuosity of the aedeagus in lateral view.

Discussion. *Schaufussia sinuatipenis* sp. nov. shares with all the species of the genus a similar external morphology



FIGURES 346.1–346.11: *Schaufussia* spp. Habitus of the holotype of: (**1**) *S. sinuatipenis* **sp. nov.** and (**2**) Mesoventral keel. Aedeagus in lateral view of: (**3**) *S. sinuatipenis* **sp. nov.**, (**4**) *S. pachecoi* **comb. nov.** Aedeagus in dorsal view of: (**5**) *S. sinuatipenis* **sp. nov.**, (**6**) *S. pachecoi* **comb. nov.** Apex of paramere of: (**7**) *S. sinuatipenis* **sp. nov.** Spermathecal complex of: (**8**) *S. sinuatipenis* **sp. nov.**, (**9**) *S. pachecoi* **comb. nov.** Female uroventrite VIII of: (**10**) *S. sinuatipenis* **sp. nov.**, (**11**) *S. pachecoi* **comb. nov.**

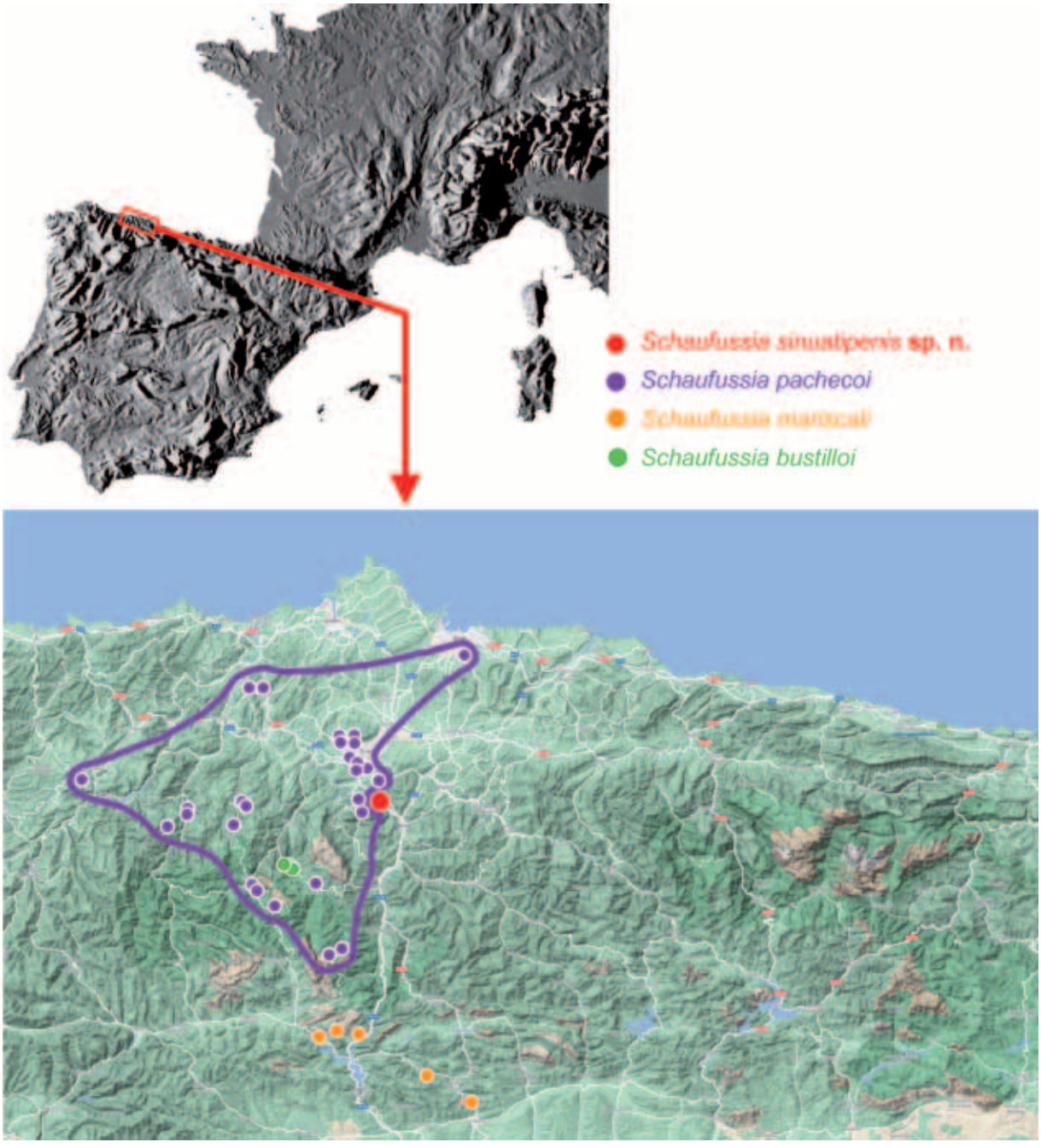


FIGURE 347: Distribution map of species of the genus *Schaufussia* **nov.**

in antennae and protarsi; in the antennae there should be observed small differences in the 4th to 6th antennomeres and in the 8th to 10th antennomeres of the club (see Table 25); in the protarsi the first tarsomere is slightly narrower than the apical end of the protibia, as in *Schaufussia mariscali* (until now a synonym of *Schaufussia pachecoi* and that has been rehabilitated in our work) (Salgado 1979; Salgado *et al*. 2008), while *Schaufussia bustilloi* comb. nov. and *Schaufussia pachecoi* comb. nov. (from type locality) (Bolívar 1915; Salgado & Fresneda 2009) are as or somewhat wider. Undoubtedly, the most significant differences can be found in the aedeagus, median lobe and parameres; the median lobe, in lateral view (Fig. 346.3) is clearly sinuous with a marked concavity near the middle on the dorsal margin, while in the other species (Fig. 346.4: *Schaufussia pachecoi* comb. nov.) the dorsal and ventral margins are curved and without concavity; and in dorsal view (Fig. 346.6: *Schaufussia pachecoi* comb. nov.), the apical area is much more pointed and narrower than in any other species of the genus; the differences in the parameres are presented in the shape of the apical part and in the three setae: in *Schaufussia sinuatipenis* sp. nov. the apical part is gracile and of the three setae the basal one is significantly shorter, while in the other species the apical part is more dilated or curved and the three setae are of similar length. The basal lobe of the spermatheca and the thickening of the ductus are more developed in *Schaufussia pachecoi* comb. nov. (Fig. 346.9) than in the new species; the spiculum of the female uroventrite VIII is longer and more slender in *Schaufussia pachecoi* comb. nov. (Fig. 346.11) than in *Schaufussia sinuatipenis* sp. nov. (Fig. 346.10).

Distribution. Hypogean Iberian endemism. This species is only known from the type locality, Cueva del Prau de la Sierra, which is «surrounded» by numerous caves in which *Schaufussia pachecoi* comb. nov. inhabits. *Schaufussia bustilloi* comb. nov. lives in two nearby caves which are also «surrounded» by more western caves in which *S. pachecoi* comb. nov. also lives (Fresneda & Salgado 2017) (Fig. 347). *Schaufussia mariscali* comb. nov. is known from caves located south of Peña Ubiña, in the last mountainous reliefs before the Duero river depression, in León.

Segment		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Schaufussia	**length**	0.12	0.15	0.09	0.09	0.08	0.09	0.12	0.07	0.1	0.07	0.18
pachecoi	**width**	0.05	0.05	0.03	0.03	0.04	0.04	0.06	0.05	0.06	0.07	0.09
Schaufussia	**length**	0.11	0.13	0.08	0.07	0.07	0.07	0.09	0.06	0.07	0.06	0.13
sinuatipenis	**width**	0.06	0.04	0.03	0.03	0.03	0.03	0.06	0.05	0.06	0.06	0.08
Schaufussia	**length**	0.12	0.13	0.08	0.07	0.07	0.07	0.09	0.04	0.07	0.07	0.14
bustilloi	**width**	0.05	0.04	0.03	0.03	0.03	0.03	0.06	0.04	0.07	0.07	0.08

TABLE 25. Length and width of the antennomeres of *Schaufussia pachecoi* comb. nov., *Schaufussia sinuatipenis* sp. nov. and *Schaufussia bustilloi* comb. nov. All measurements in mm.

Serbiana latitarsis sp. nov.
(Figs. 111.3, 112.7, 114.6, 114.14, 115.8, 116.8, 116.16)
https://zoobank.org/NomenclaturalActs/F04EA23D-6402-42EE-B54F-417A7CD8D31D

Type locality. Serbia, Tutin, cave near Godovo, UTM: 34T 442 4755.

Type series. Holotype ♂ (CPMG): labelled [YU: Serbien / Pecina b.Godovo / (b.Tutin) 17.7. / leg. Deeleman 1971] (white printed label), [ex. Collezione / V. B. GUEORGUIEV / 1990] (green printed label), [HOLOTYPUS / *Serbiana* / *latitarsis* n. gen. n. sp. / Fresneda *et al*. 2024] (rl); genitalia on transparent card mounted on the same pin as the holotype. Paratypes: 4 ♀♀ same data as the holotype, with the red label [PARATYPUS / *Serbiana* / *latitarsis* n. gen. n. sp. / Fresneda *et al*. 2024] (CPMG, CFL).

Description. Holotype ♂. Length 1.5 mm and maximum width 0.8 mm. Body oval, elongated, convex and clearly narrowed backward (Fig. 111.3). Pubescence fairly long, grayish and shiny, fine and lying. Sculpture fine, not very evident, formed by scattered points in pronotum and elytra, in these more marked, closer and more abundant.

Head: Large, wider than long, with occipital carina blurred; lateral angles of forehead very prominent and pointed, with very small eyes located at tip of a peduncle.

Antennae: Short, slightly exceeding pronotal base. First antennomere shorter than second one. Club differentiated, although antennomeres slightly flattened; antennomere 3rd longer than each of 4th, 5th and 6th; 8th globose and transverse; 9th and 10th transverse and as thick as 11th, being 11th slightly shorter than 9th and 10th together. Antennal formula: See Table 26.

Pronotum: Transverse, almost twice as wide as long (ratio: 1.85); narrowed at front, with sides regularly curved; maximum width at base, as wide as elytra; posterior angles pointed, with basal angles acute and apex prolonged on elytra, with base curved.

Elytra: Short, elongated and convex – both elytra 1.25 times as long as wide –, with maximum width very close to base; sub-rectilinear lateral margins tapering progressively backwards and apices rounded; transverse striolation slightly marked, formed by few striae thin and close visible between middle and basal area of elytra; punctation formed by small dots; without parasutural stria.

Legs: Relatively long and delicate; protibiae with internal spur and with comb at apical and outer edges, no outer spurs present; protarsi pentameres widened with first tarsomere clearly wider than apical area of protibia (ratio = 1.25) and slightly wider than long; mesotibiae straight and metatibiae slender, somewhat curved, both without apical basket of spines.

Mesoventral keel (Fig. 112.7): Tall, with anterior edge convex, apex rounded, very slightly toothed and angle obtuse; posterior edge straight, smooth and reaching middle of metaventrite.

Suture of the metaventrite (Fig. 112.7): Lower half running very close to coxal cavity and delimiting in upper half an arched area.

Median lobe of aedeagus: Relatively long. In lateral view (Fig. 114.6) thickened in basal part and then slightly and uniformly widened in middle part; all regularly curved, with a marked depression near apical fifth of dorsal margin; apex pointed and curved towards ventral side, although tip slightly oriented towards the dorsal side. In dorsal view (Fig. 114.14), with sub-rectilinear sides that gradually widen slightly to apical fifth, narrowing into slightly curved sides ending in a pointed apex. Basal blade well-developed, narrowed anteriorly and gradually widening to apical margin.

Endophallus: Since being totally evaginated, not clearly distinguishable which pieces compose it and their disposition. No «Y»-piece observed and teeth in middle and apical parts present.

Parameres (Fig. 115.8): As long as median lobe; very thick until apical area, narrowing and forming a club with a triangular appearance with tip pointed consisting of four setae on the inner margin, two apical and other two equidistant, basal one slightly longer. Ventral blade of tegmen well-developed and wider, as long as basal blade.

Female. Protarsi tetramerous and not dilated. Larger, measuring between 1.7 and 1.8 mm, being 1.5 mm in male; elytra laterally more rounded and not as acuminate as those of male.

Spermathecal complex (Fig. 116.8): Spermatheca small, curved, crook-shaped or hook-shaped, with basal and apical lobes well sclerotized; basal lobe much longer and wider than apical lobe with posterior area very slightly ringed; apical lobe with parallel sides and slightly curved with apical area rounded and somewhat dilated; joint duct short and hyaline, as wide as posterior area of apical lobe.

Female uroventrite VIII (Fig. 116.16): Apical margin widely arched; spiculum long and narrow, with apex rounded.

Etymology. The specific name points out to one of the most striking characteristics, the width of the male protarsomeres. From the Latin *latus-i*, wide and *tarsus-i* (from the Greek *ταρσός*), part of the foot or by extension simply foot.

Discussion. See Discussion section of the genus *Serbiana* nov.

Distribution. Only known from the type locality. An indeterminate cave (probably Godovska Pećina) near Godovo village, municipality Tutin, southwestern Serbia, close to Montenegro's border.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.07	0.07	0.05	0.03	0.03	0.03	0.05	0.02	0.04	0.04	0.08
Width	0.03	0.04	0.03	0.03	0.03	0.03	0.04	0.04	0.05	0.06	0.07

TABLE 26. Measurements of antennomeres of the holotype of *Serbiana latitarsis* sp. nov. (mm).

Tamaniniella pivai sp. nov.
(Figs. 348.1-348.5, 348.7-348.11)
https://zoobank.org/NomenclaturalActs/A13FE8AE-B20E-420D-9AB8-974E0E6E9E70

Type locality. Italy, Trentino, Lessini Mt., Sega di Ala (TN), 45°40'58''N 10°58'45''E, 1,400 m.

Type series. Holotype ♂ (CDV): M. Lessini, Sega d'Ala (TN), 27.V.2000, M. Grottolo leg., DV1800, with holotype label [Holotypus / *Tamaniniella* / *pivai* sp. n. / Fresneda *et al*., 2024] (hw, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same collection data as the holotype, DV1801, 1 ♂, (CDV); M.ti Lessini, P.so Fittanze, 1,400 m., 1.VII.1988, Grottolo leg., DV3481 and DV3482, 2 ♂♂ (CDV); Trentino, TN, Sega d'Ala, 1,400 m, passo Fittanze, 7.VII.1989, Grottolo leg., 1 ♂ DV3422, 5 ♀♀ (CDV); M. Lessini (VR), Boscochiesanuova, 1.VI.1980, R. Monguzzi leg., 1 ♀ (CDV); Veneto, Monti Lessini, Roverè Veronese (VR), località Malga Bagorno, 1,430 m, 28.IX.2012, D. Bianco & E. Piva leg., 2 ♂♂ (CDB); Veneto, Monti Lessini, Roverè Veronese (VR), 2ª faggeta residua a sud di Malga Bagorno, 1,430-1,460 m ca., 28.IX.2012, D. Bianco & E. Piva leg., 3 ♂♂, 3 ♀♀ (CDB, CPMG); same data, 1 ♂ (EP 19H) (CEP); same data except 15.V.2013, E. Piva leg., 2 ♂♂, 2 ♀♀ (CDB, CEP); Veneto, Monti Lessini, Roverè Veronese (VR), 1ª faggeta residua a sud di Malga Bagorno, ca. 1,430-1,460 m, 28.IX.2012, D. Bianco & E. Piva leg., 30 ♂♂ (E.P. 20H- 29H and E.P. 04P- 07P), 62 ♀♀ (CDB, CEP, CPMG); same data except 15.V.2013, E. Piva leg., 3 ♂♂, 3 ♀♀ (CDB, CEP); Veneto, Monti Lessini, Crespadoro (VI), scavo in dolina sulla Cima di Lobbia, ca. 1,600 m, 24.VII.1993, E. Piva leg., 1 ♂ (758B), 1 ♀ (CEP); Veneto, Lessini, San Giorgio, tr. V/17.IX.1986, Casale-Giachino leg., 2 ♂♂ (DV2733), 3 ♀♀ (DV2734 and DV3414) (CPMG, CAC); M. Lessini, Roverè (VR), dint. Buso d. Rena, 17.IX.1992, Monguzzi leg., 2 ♂♂, 19 ♀♀ (CPMG); Veneto (Vr), Marano di Valpolicella, 650 m, dint. E loc. Ca' Nuova presso str. per loc. Baiaghe, 18.III.2007, A. Zanetti leg., 1 ♀ (CPMG); Veneto, Monti Lessini, Rovere Mille, Cova del Monte Capriolo (VR), 11.XI.2011, E. Lana & A. Faille leg., 1 ex. (DNA extraction code voucher: RA785) (CFL). All specimens with paratype label [Paratypus / *Tamaniniella* / *pivai* sp. n. / Fresneda *et al*., 2024] (hw, rl).

Diagnosis. *Tamaniella pivai* sp. nov. has the median seta on parameres very far from apex, the elytra tapering to apex sharply pointed and pronotal surface shiny.

Description. Holotype ♂. Medium-small sized, 2.05 mm with habitus bathyscioid (Fig. 348.1), oval in shape, with large pronotum, wider than elytra; anophthalmous. Uniformly covered by pubescence golden, short and tightly fitting to surface..

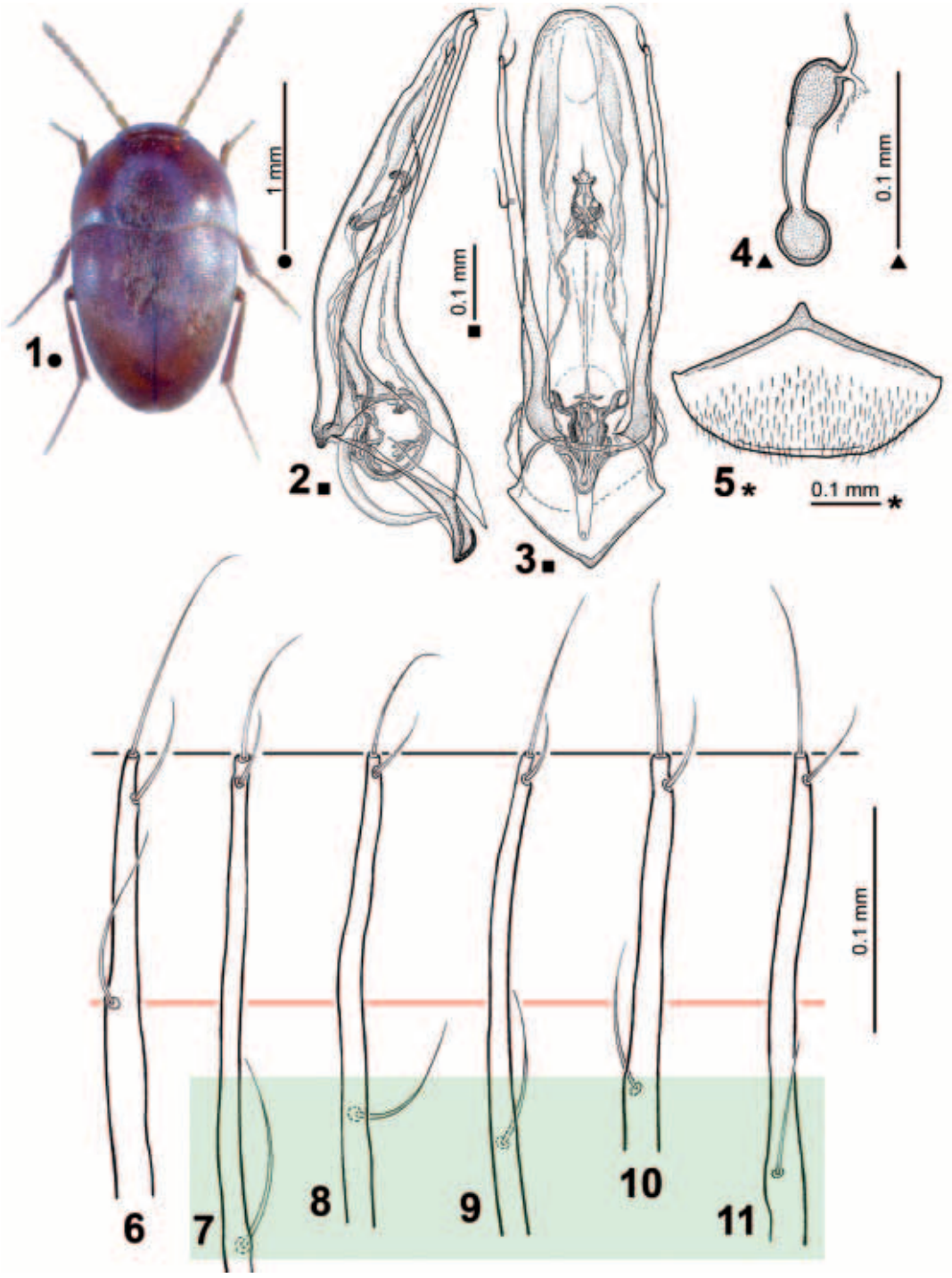
Antennae: Antennae short, if stretched backwards just reaching behind pronotal base. First antennomere much shorter than second one; 8th wider than long; 11th ogival and about twice as long as previous one. Antennal formula: See Table 27.

Pronotum: With regularly rounded sides, broad and globular. Wider than elytra, with maximum width just ahead of basal angles; basal angles acute and facing backwards due to accentuated sinuosity of pronotal base, also slightly narrow. Disc with punctation scattered and slightly accentuated such as to give integuments a brilliant appearance.

Elytra: Elongated oval, with maximum width in anterior third; with a parasutural stria almost complete and well marked, anteriorly evanescent; transverse striolae fine and not very tight.

Legs: Short and stout; protarsi never dilated, less wide than apex of protibiae; metafemora simple, with posterior margin unarmed; apex of tibiae with internal spurs polydentate; meso- and metatibiae with incomplete apical baskets; spines short and sparse.

Mesoventral keel: Tall, but not prominent forward. Anterior profile, obliquely and rectilinearly elusive, and ventral one, slightly sinuous; forming an obtuse angle, equipped inferiorly with a pronounced tooth. Without posterior apophysis reaching metaventrite.



FIGURES 348.1–348.11: *Tamaniniella pivai* **sp. nov.**: (**1**) Habitus, (**2**) Aedeagus in lateral view (**3**), Aedeagus in dorsal view, (**4**) Spermatheca, (**5**) Female uroventrite VIII. Apex of paramere of *T. vallarsae* from (**6**) Bocchetta Gabellele and *Tamaniniella pivai* **sp. nov.** from: (**7**) Sega di Ala, (**8**) Passo Fittanze, (**9**) San Giorgio, (**10**) Cima di Lobbia, (**11**) Malga Bagorno. The black line marks the apex of the paramere, the red line marks the insertion level of the median seta in *T. vallarsae*, and the green area marks the variability in the insertion point of the same seta in *T. pivai* **sp. nov.**

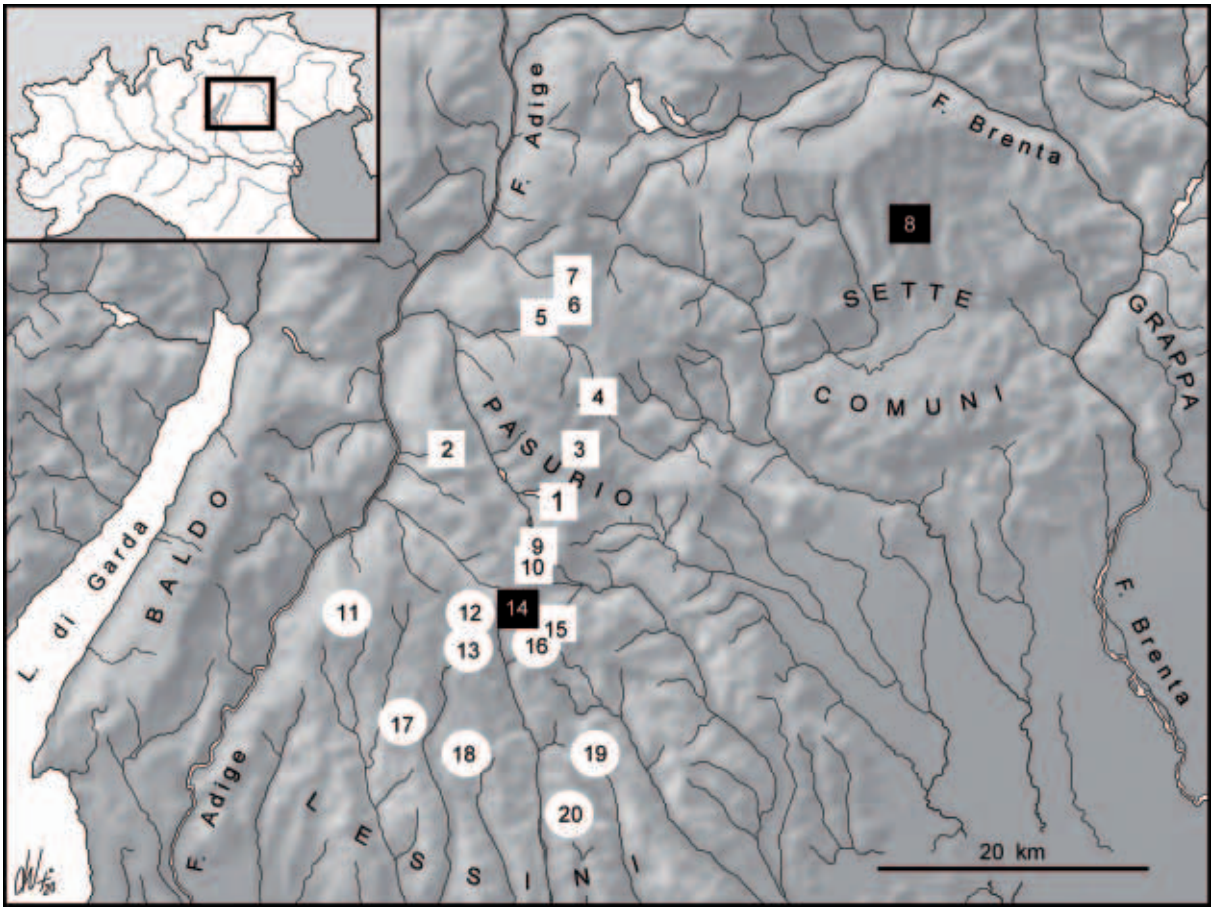


FIGURE 349: Distribution map of *Tamaniniella* spp. *T. vallarsae* (white circles), *T. pivai* **sp. nov.** (white squares), *Tamaniniella* sp. (black squares): (**1**) Pian delle Fugazze, (**2**) Coni Zugna, (**3**) Corno del Pasubio, (**4**) Passo della Borcola, (**5**) Lont del Laché cave, (**6**) Malga Parisa, (**7**) Mezzaselva m 1200, (**8**) Caséra Zingarella (Zoia & Latella, 2005), (**9**) Malga Storta, (**10**) M. Obante, (**11**) Sega di Ala, Passo delle Fittanze, (**12**) San Giorgio, (**13**) Malga Bagorno, (**14**) M. Zevola, (**15**) Bocchetta Gabellele, (**16**) Cima di Lobbia, (**17**) Bosco Chiesanuova, (**18**) Cova del Monte Capriolo, (**19**) Pesciaia di Bolca, (**20**) Damati Cave.

Metatergal apparatus: Large, with posterior apophysis approximately one third of elytra Length.

Metendosternite: Not «V»-shaped, with furcal arms triangular, wide at base.

Median lobe of aedeagus: Relatively large, elongated. In lateral view (Fig. 348.2) little and regularly curved, slender, with apex slightly facing downwards. In dorsal view (Fig. 348.3) with sides subparallel in 2/3 basal, therefore slightly converging near apex; apex ogivate and largely rounded.

Endophallus (Fig. 348.3): With basal «Y»-piece large and well-sclerotized. Median phanera small and complex; two apical lists present, long, parallel, twisted at base and moderately sclerotized.

Parameres (Figs. 348.7–348.11): Long and slender, clearly shorter than median lobe, with apex, in dorsal view, simple. Bearing three setae: one long, apical; one short, subapical and internal; another one long, internal, placed just over half of paramere.

Female

Spermathecal complex: Spermatheca (Fig. 348.4) small, with proximal lobe smaller and elongated, and distal one globular. Ductus distally not enlarged nor sclerotized at insertion on spermatheca.

Female uroventrite VIII (Fig. 348.5): With spiculum little developed in length, stocky, triangular. Front edge of ventrite with clearly converging sides.

Variability. Length paratypes between 1.5-2.9 mm.

Etymology. We are pleased to dedicate this new species to our friend Erminio Piva from Vicenza (Italy), a very active biospeleologist and excellent Leptodirini specialist.

Discussion. *Tamaniella pivai* sp. nov. is the sister species of *T. vallarsae* with very high support, 100/100 (Fig. 1D). It differs from *T. vallarsae* mainly in the different position of the median seta of the parameres, which is much more far from the apex: Sega di Ala (Fig. 348.7), Passo Fittanze (Fig. 348.8), San Giorgio (Fig. 348.9), Cima di Lobbia (Fig. 348.10) and Malga Bagorno (Fig. 348.11). The median seta of *Tamaniniella vallarsae* is always inserted closer to the apex: Bocchetta Gabellele (Fig. 348.6). The apical seta of *Tamaniniella pivai* sp. nov. are somewhat shorter than in the other species. Externally, *Tamaniella pivai* sp. nov. show a more tapered elytral apex, which is pointed, and also brighter integuments on the pronotum.

Distribution (Fig. 349). Italy. Is known from several sites in the Veronese Lessini mountains (Veneto), where it was collected in caves and MSS at altitudes varying between 650 and 1,600 m. On the map (Fig. 349), the distribution data of *Tamaniniella vallarsae* has been taken from: Giachino (1993a), Giachino & Vailati (2005a; 2019), Zoia & Latella (2007).

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.10	0.11	0.06	0.06	0.06	0.04	0.15	0.04	0.06	0.06	0.11
Width	0.05	0.04	0.03	0.03	0.03	0.04	0.04	0.04	0.05	0.05	0.03

TABLE 27. Measurements of antennomeres of the holotype of *Tamaniniella pivai* sp. nov. (mm).

Troglocharinus bellesi sp. nov.
(Figs: 350.1, 351.1, 351.5, 352.1, 352.3, 352.5)
https://zoobank.org/NomenclaturalActs/10E82E90-B55C-475D-80FA-BAFE0D3C1B28

Type locality. Spain, Lleida, Peramola, Avenc de la Roca del Corb, UTM: 31N 3563 46594, 852 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): Spain, Lleida, Peramola, Avenc de la Roca del Corb, 22.IV.2017, Fadrique leg., with holotype label [HOLOTYPUS / *Troglocharinus* / *bellesi* sp. n. / Fresneda *et al*., 2023] (pr, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same data as the holotype, 32 ♂♂, 41 ♀♀; 2 exx. with DNA code voucher RA1136 and RA1137; with paratype label [PARATYPUS / *Troglocharinus* / *bellesi* sp. n. / Fresneda *et al*., 2023] (pr, rl) (CFL, CPMG, SMNS).

Description. Holotype ♂. Length 3.0 mm; maximum width 1.3 mm. Body shape (Fig. 350.1) elliptical, convex, rather broad, moderately elongated and gradually narrowed; sub-bathyscioid facies, presenting basal area of pronotum slightly sinuous or concave. Coloration yellow-red. Pubescence yellowish, short, slender and lying, somewhat denser on elytra than on pronotum. Sculpture on head consisting of very fine dots, little impressed and distant; on pronotum by dots small, shallow, somewhat rough and irregularly arranged; on elytra dots transversely aligned, forming transverse striolae well-marked and differentiated, somewhat rough. Depigmented.

Head: Moderately broadened, with occipital carina visible but poorly marked; anophthalmous.

Antennae: Long (2.4 mm) and delicate, exceeding two thirds of length of body, with 7th, 9th and 10th antennomeres dilated in apical area; in them, 1st, 2nd, 3rd and 11th antennomeres of equal length, 1st being thickest; 5th longest of all; 8th five times as long as wide; 8th and 9th with same length and slightly longer than 10th, and each of these three somewhat shorter than 11th. Antennal formula: See Table 28.



FIGURES 350.1–350.5: *Trogloharinus* spp. Habitus of: (**1**) *T. bellesi* **sp. nov.**, (**2**) *T. rizzoae* **sp. nov.**, (**3**) *T. hustachei*, (**4**) *T. fonti fonti*, (**5**) *T. vivesi*.

Pronotum: Slightly transverse (width/length ratio: 1.4); anterior apical part clearly narrower than basal part, with sides in anterior two thirds slightly and regularly curved, being in basal third slightly concave and divergent; widest before concavity and base sinuous, somewhat narrower than basal area of elytra; posterior angles slightly projecting and rounded, almost right.

Elytra: One and a half times longer than wide overall and convexity uniform, although throughout suture area a little sunken; humeral angles rounded; maximum width in basal third; lateral margins gently curved throughout their length, with a fine rim along entire length of elytra, apices progressively decreasing backwards and rounded; without parasutural stria.

Legs: Slender, very long and delicate; first protarsomere rectangular almost twice as long as wide, slightly broader than distal end of protibia (width/length ratio: 1.08); mesotibiae slightly sinuous and metatibiae straight.

Mesoventral keel: Tall and short. Anterior border convex with apex hooked and angle obtuse; posterior margin narrow, concave in anterior third, then straight with setae along entire margin. Posterior process not reaching mesocoxal cavities.

Suture of the metaventrite: Slightly sinuously arched in basal third, close to mesocoxal cavity and delimiting an area elongated and curved.

Median lobe of aedeagus: In lateral view (Fig. 351.1) regularly curved from base to apex; prolonged in a point fine and straight. In dorsal view (Fig. 351.5) broad, with sides slightly sinuous tapering a little near apical area; apex broadly curved with a slight median depression.

Endophallus (Fig. 351.5): With three sections as defined by Jeannel (1924a). Basal part with an «Y»-piece with arms divergent and sinuous, articulated with apical membranous extension through a nodule; these structures forming a funnel with floating pieces and appendixes of dorsal phanerae of medial part in upper part. Medial region with two phanerae enlarged, bifurcated at base; one of bifurcations extented until funnel-like structure of basal part; with a floating piece in between both arms of bifurcated phanerae also in contact with funnel-like structure. With two ventral phanerae enlarged and divergent at their base, with a nodule of variable shape in apex; with two upper dorsal plates, each of them with a outer phanerae long and slender, and another internal more robust, latter with apex bifurcated and area enlarged folded in a different orientation, very sclerotized. With two large bags at both sides of axial piece, with internal nodules very sclerotized and a long appendix at base. Apical region with reinforcement bands with a bag in between them, with longitudinal stripes and margins engrossed.

Parameres (Fig. 352.1): Robust and shorter than median lobe, with a double curvature more marked at apical part; whose apex oriented outwards and without a differentiated club; apical area with three long setae of similar length and two apical somewhat thicker, in addition to a highly developed membranous lamina with a penicillium with numerous setae.

Female. Similar in length to male, but generally more robust, with maximum width of 1.4 mm. Antennae slightly shorter and antennomeres rlatively thicker. Antennal formula: See Table 28). Pronotum with lateral margins of basal part less sinuous, almost curved. Protarsi slender and tetramerous.

Spermathecal complex: Spermatheca very long (Fig. 352.3) with apical lobe spherical and in same plane as hyaline middle part, very long, with a section inferior to lobes; basal lobe thicker than apical and elongated sac in shape and slightly curved; both lobes sclerotized. Basal bottom of spermatheca with spermathecal gland and spermatic duct open, latter being slender and very long, without a nodule in area of insertion to spermatheca but thicker and sclerotized in area of insertion into copulatory bag.

Female uroventrite VIII (Fig. 352.5): With apical margin in a broad regular arc; medial basal area with spiculum short and broad with a truncated apex.

Variability. Measurements taken in six specimens chosen at random. Total length, between 2.8-3.1 mm; maximum width of body, between 1.3-1.4 mm. Width/length ratio pronotum, between 1.37-1.43. Elytra length/width ratio, between 1.45-1.55. One specimen showing a lobe-like extension in middle basal area of the pronotum that hides the scutellum.

Etymology. The new species is dedicated to Dr. Xavier Bellés in gratitude for his research work in the field of biospeleology, with a very specific contribution to the knowledge of the genus *Troglocharinus*. The specific name is a noun in the genitive singular.

Discussion. This species is a Leptodirini that both Escolà (1973, 1980) and Bellés (1973) determined as *Trogloch*arinus fonti*. Actually, the morphological characters mean that at first sight it could be confused with this species. However, the phylogenetic tree (Fig. 1B) shows that it is sister to *Trogloch*arinus hustachei* with support, 44.2/100; and sister of these two, *Trogloch*arinus senenti* with support 98.2/100. Geographical criteria support this relationship: its area of distribution is close to that of its sister species, and it is, together with these, considerably further south than where the subspecies of *Trogloch*arinus fonti* are found. The examination of the habitus shape of *Trogloch*arinus bellesi* sp. nov. allows us to easily differentiate it from its sister species. Both *Trogloch*arinus hustachei* (Fig. 350.3) and *Trogloch*arinus senenti* are markedly pholeuonoid, very oblong, with the pronotum strongly constricted in its basal half, with the same facies as the type species of the genus, *Trogloch*arinus ferreri*, while *Trogloch*arinus bellesi* sp. nov. is shorter, more stocky, with a certain tendency to the bathyscioid shape and with a slightly bell-shaped pronotum (Fig. 350.1). Although they are not in the same clade, it is not easy to distinguish this new species from *Trogloch*arinus fonti*; in *Trogloch*arinus bellesi* sp. nov. the pronotum is somewhat less transverse, with the basal half of the sides a little notched and the antennomeres shorter, slender, but with the apical half strongly thickened: this is especially evident in the 7th antennomere. In *Trogloch*arinus fonti* (Fig. 350.4) the pronotum is more transverse, with the sides curved regularly from one end to the other and the antennomeres are longer, very slender, with the apical half slightly thickened: the antennae are generally more slender.

The bathyscioid form seems to be the plesiomorphic state of the character; it is very marked in the sister *Trogloch*arinus* of the entire genus – *Trogloch*arinus fadriquei*, *Trogloch*arinus mengeli*, *Trogloch*arinus mercedesi*, *Trogloch*arinus sendrai* and *Trogloch*arinus vinyasi* – with support 98.1/100 (Fig. 1B); the shape is elongated, it becomes more oblong and the pronotum is deformed, narrowing its basal part, in the following clades with *Trogloch*arinus bellesi* sp. nov., *Trogloch*arinus schuttei* or *Trogloch*arinus subilsi*, and *Trogloch*arinus fonti* and *Trogloch*arinus quadricollis*, this second sister of all the markedly pholeuonoid *Trogloch*arinus* with 76.5/100 support (Fig. 1B). This derived state appears independently twice in the *Trogloch*arinus hustachei* clade, once in the *Trogloch*arinus ferreri* clade, and once in the *Trogloch*arinus elongatus*-*Trogloch*arinus orcinus* clade.

*Trogloch*arinus bellesi* sp. nov. also bears some resemblance to *Trogloch*arinus vivesi* (Fig. 350.5), but the latter is somewhat larger, with longer antennae, a broader and more bulging body and a pronotum that is narrower at the base. Furthermore, the two clades *Trogloch*arinus fonti* + *Trogloch*arinus fonti* complex, including *Trogloch*arinus bellesi* sp. nov., are distributed along the western reliefs of the Segre River; the sister species of the entire clade, *Trogloch*arinus subilsi*, inhabits the eastern reliefs, as does *Trogloch*arinus vivesi*. The median lobe of aedeagus and the endophallus of these species follow the same pattern but have small but constants differences: *Trogloch*arinus bellesi* sp. nov. (Figs. 351.1, 351.5), *Trogloch*arinus fonti* (Figs. 351.3, 351.7), *Trogloch*arinus vivesi* (Figs. 351.4, 351.8).

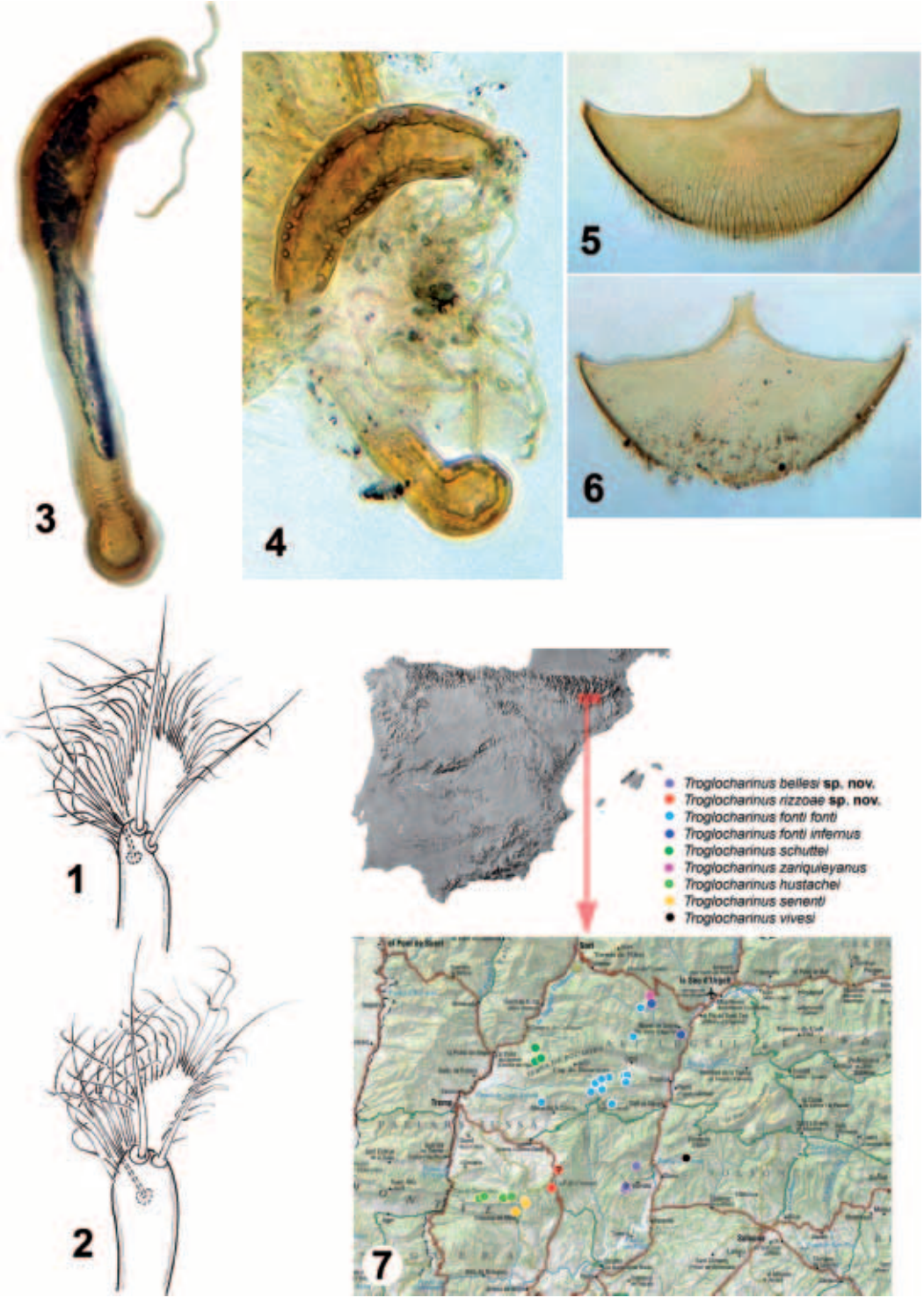
Distribution (Fig. 352.7). This species is known from four underground cavities in the Serra d'Aubens and Massís de Sant Honorat in Peramola, Lleida: Avenc de la Roca del Corb, Pou del Dring (= Avenc de Pau Esteve), Avenc del Mort and Avenc d'en Viladric. Hypogean species of the deep subterranean environment that coexists in all localities with the rare Leptodirini *Trogloch*arinus vinyasi*.

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
♂ **length**	0.21	0.21	0.21	0.24	0.29	0.26	0.26	0.18	0.18	0.17	0.21
♂ **width**	0.07	0.05	0.04	0.04	0.04	0.04	0.07	0.03	0.06	0.06	0.05
♀ **length**	0.19	0.19	0.19	0.20	0.23	0.22	0.22	0.17	0.18	0.16	0.19
♀ **width**	0.07	0.05	0.04	0.04	0.04	0.04	0.07	0.04	0.06	0.06	0.05

TABLE 28. Measurements of antennomeres of the holotype and female paratype of *Trogloch*arinus bellesi* sp. nov. (mm).



FIGURES 351.1–351.8: *Troglocharinus* spp. Aedeagus in lateral view of: (**1**) *T. bellesi* **sp. nov.**, (**2**) *T. rizzoae* **sp. nov.**, (**3**) *T. fonti fonti*, (**4**) *T. vivesi*. Aedeagus in dorsal view of: (**5**) *T. bellesi* **sp. nov.**, (**6**) *T. rizzoae* **sp. nov.**, (**7**) *T. fonti fonti*, (**8**) *T. vivesi*.



FIGURES 352.1–352.7: *Troglocharinus* spp. Apex of paramere of: (**1**) *T. bellesi* **sp. nov.**, (**2**) *T. rizzoae* **sp. nov.** Spermatheca of: (**3**) *T. bellesi* **sp. nov.**, (**4**) *T. rizzoae* **sp. nov.** Female uroventrite VIII of: (**5**) *T. bellesi* **sp. nov.**, (**6**) *T. rizzoae* **sp. nov.** (**7**) Distribution map of the *T. fonti* species complex.

Troglocharinus rizzoae sp. nov.
(Figs: 350.2, 351.2, 351.6, 352.2, 352.4, 352.6)
https://zoobank.org/NomenclaturalActs/D181DB4F-CB92-4AFA-ABF7-AF744714E8C4

Type locality. Spain, Lleida, Artesa de Segre, Avenc de Comiols (= Pou del Curs), UTM: 31N 342062 4655899, 1,021 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): Spain, Lleida, Artesa de Segre, Avenc de Comiols, 1,021 m, 10.VI.2018, Fadrique leg., with holotype label [HOLOTYPUS / *Troglocharinus* / *rizzoae* sp. n. / Fresneda *et al*., 2023] (pr, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same data as the holotype, 7 ♂♂, 11 ♀♀, with paratype labels [PARATYPUS / *Troglocharinus* / *rizzoae* sp. n. / Fresneda *et al*., 2023] (pr, rl) (CFL, CPMG).

Description. Holotype ♂: Length 2.8 mm; maximum width 1.3 mm. Body shape elliptical, convex, broad, moderately elongated and gradually tapering near back (Fig. 350.2); facies sub-bathyscioid; lateral margins of basal part of pronotum slightly concave. Colour orange. Pubescence yellowish, short, slender and recumbent, somewhat denser on elytra than on pronotum. Head sculpture made of sparse dots densely arranged; pronotum with dots very small and shallow, with arrangement irregular; on the elytra there are well marked transverse striolae. Depigmented.

Head: Moderately broad, with occipital carina visible but slightly marked; anophthalmous.

Antennae: Long (2.6 mm) and delicate, exceeding ¾ of length of body, with 7th, 9th, 10th and 11th antennomeres dilated in apical area; in them, 2nd and 3rd of equal length, 1st being thickest; 5th longest of all; 8th four times as long as wide; 8th and 10th with same length and slightly short than 9th, and each of these three somewhat shorter than 11th. Antennal formula: See Table 29.

Pronotum: Little transverse (width/length ratio: 1.4); anterior apical part clearly narrower than basal part, with sides in anterior two thirds slightly and regularly curved, being in basal third slightly concave and divergent; widest before concavity and sinuous base, somewhat narrower than elytral basal area; posterior angles slightly prominent and rounded, with angles right.

Elytra: 1.6 times as long as wide and convexity uniform; humeral angles rounded; maximum width in basal third; lateral margins gently curved along their entire length; with a fine edge throughout of elytra, tapering backwards and apices rounded, with elytral suture at bottom of junction of apices; without parasutural stria.

Legs: Slender, very long and graceful; first protarsal segment rectangular almost twice as long as wide, narrower than distal end of protibia (width/length ratio: 2); mesotibiae very slightly sinuous and metatibiae straight.

Mesoventral keel: Tall and short. Front edge convex with apex hooked and angle obtuse; posterior edge narrow, concave in anterior third, then straight with setae along entire edge. Posterior process not reaching mesocoxal cavities.

Suture of the metaventrite: Slightly sinuously arched in basal third, close to mesocoxal cavity, delimiting an elongated arched area.

Median lobe of aedeagus: In lateral view (Fig. 351.2) regularly curved from base to apex; prolonged in a fine tip, sinuous and straight. In dorsal view (Fig. 351.6), broad, with sides slightly sinuous tapering a little near apical area; apex broadly curved with a slight median depression.

Endophallus (Fig. 351.6): With three parts as defined by Jeannel (1924a). Basal part with an «Y»-piece with arms divergent and sinuous, articulated with apical membranous extension through a nodule; these structures forming a funnel with floating pieces and appendixes of dorsal phanerae of medial part in upper part. Medial region with two enlarged phanerae, bifurcated at base; one bifurcation extending until funnel-like structure of basal part; with a floating piece in between both arms of bifurcated phanerae also in contact with funnel-like structure. With two ventral phanerae enlarged and divergent at base, with a nodule notched in its upper and lower part; with two upper dorsal plates, each of them with a outer phanerae long and slender , and another more robust internal, latter with apex bifurcated and area enlarged folded in a different orientation, very sclerotized. With two large bags at both sides of axial piece, with very sclerotized internal nodules and a long appendix at base. Apical region with reinforcement bands with a bag in between, with longitudinal stripes and margins engrossed.

Parameres (Fig. 352.2): Robust and shorter than median lobe, with a double curvature more marked at apical part, whose apex oriented outwards and without a differentiated club; apical area with three long setae of similar length and two apical somewhat thicker, in addition to a membranous lamina highly developed with a penicillium with numerous setae.

Female. Length similar to that of male, but generally more robust, with a maximum width of 1.4 mm; antennae slightly shorter than in male. Antennal formula: See Table 29. Pronotum with lateral margins of basal part less sinuous, almost curved; protarsi filiform and tetramerous.

Spermathecal complex: Long spermatheca (Fig. 352.4) with apical lobe spherical bent at right angles to hyaline middle part, very long, with a section inferior to lobes; basal lobe thicker than apical, shaped like a sac, elongated and strongly curved; both lobes sclerotized. At basal bottom of spermatheca, spermathecal gland and spermatic duct open, latter being slender and very long, without a nodule in area of insertion to spermatheca but with an area thicker and sclerotized in area of insertion into copulatory bag; basal process present.

Female uroventrite VIII (Fig. 352.6): With apical margin in a broad regular arc; in mid-basal part spiculum short and width with apex truncated.

Variability. Measurements in six specimens of each sex taken at random:

– Males: Length between 2.72 and 2.84 mm; maximum width between 1.28 and 1.34 mm; length/width ratio between 2.08 and 2.14.

– Females: Length between 2.78 and 2.90 mm; maximum width between 1.36 and 1.46 mm; length/width ratio between 1.97 and 2.07.

Etymology. The new species is dedicated to our friend, Dr. Valeria Rizzo (Rome, Italy), a specialist in the genus *Troglocharinus*, in gratitude for her research work. The specific name is a noun in the genitive singular.

Discussion. The specimens of this provenance were determined by Escolà (1970) as *Troglocharinus fonti*. Indeed, its external morphology means that it could be confused with this species: both the habitus and the proportions of the antennary antennomeres are very similar. It has not been possible to sequence DNA from *Troglocharinus rizzoae* sp. nov., but the fact of having discovered *Troglocharinus bellesi* sp. nov., largely thanks to a molecular study, has stimulated the study of other populations in the same geographical area. The range of *Troglocharinus rizzoae* sp. nov. is close to that of *Troglocharinus bellesi* sp. nov., and, specifically, it is located between the area of distribution of this species and its sister species, *Troglocharinus hustachei* and *Troglocharinus senenti*; together with all these populations, the population of *Troglocharinus rizzoae* sp. nov. is found considerably further south than where *Troglocharinus fonti* is distributed. Based exclusively on the morphological study, it seems clear that it would have to be incorporated into the clade (*Troglocharinus subilsi* (*Troglocharinus bellesi* sp. nov. (*Troglocharinus hustachei* + *Troglocharinus senenti*))), as sister to this clade excluding *Troglocharinus subilsi*, as sister to *Troglocharinus bellesi* sp. nov. or as sister to *Troglocharinus hustachei* + *Troglocharinus senenti*.

The shape of the bathyscioid body with the slightly bell-shaped pronotum (Fig. 350.2) allows differentiating *Troglocharinus rizzoae* sp. nov. from *Troglocharinus hustachei* and *Troglocharinus senenti*, markedly pholeuonoid species, by the pronotum strongly narrowed in its basal half. It shares with *Troglocharinus bellesi* sp. nov. the shape of the pronotum, less transverse, with the basal half of the sides slightly notched against the pronotum more transverse, with the sides regularly curved from one end to the other of *Troglocharinus fonti*. *Troglocharinus rizzoae* sp. nov. differs from *Troglocharinus bellesi* sp. nov. in the proportions of the antennary segments, due to the longer and slender antennomeres, with the apical half slightly thickened: the antennae are generally more graceful than in *Troglocharinus bellesi* sp. nov. and similar to those of *Troglocharinus fonti*. The first protarsomere of the male of *Troglocharinus rizzoae* sp. nov. is considerably narrower than that of *Troglocharinus bellesi* sp. nov. But, it clearly differs from all the species of its clade and from *Troglocharinus fonti* in the shape of the nodule of the ventral phanerae of the median part («nfvm» of Fresneda *et al*. 2021) of the endophallus: this nodule is notched in its upper and lower part being in the remaining species more or less rounded or more or less quadrangular; the appearance of this nodule is reminiscent of that described for *Troglocharinus mercedesi* (Fresneda *et al*. 2021). The apex of the median lobe of aedeagus in lateral view is much finer and more sinuous in *Troglocharinus rizzoae* sp. nov. (Fig. 351.2) what is *Troglocharinus bellesi* sp. nov. (Fig. 351.1).

Distribution. At the moment, this species is only known from the type locality, in the Serra de Comiols, at the eastern end of the pre-Pyrenean mountain range of Montsec, Lleida, Spain. It is more than likely that it also inhabits other nearby cavities of which *Troglocharinus fonti* has been cited: Pou dels Graells (Baronia de Rialb) and Forat del Lladre (Benavent de la Conca) (Escolà 1970).

Segments	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
♂ length	0.25	0.22	0.22	0.26	0.29	0.27	0.28	0.20	0.21	0.20	0.24
♂ width	0.08	0.05	0.04	0.03	0.03	0.03	0.08	0.05	0.08	0.08	0.09
♀ length	0.24	0.22	0.24	0.21	0.24	0.25	0.24	0.16	0.20	0.19	0.26
♀ width	0.07	0.04	0.04	0.03	0.04	0.04	0.07	0.04	0.08	0.08	0.08

TABLE 29. Measurements of antennomeres of the holotype and female paratype of *Troglocharinus rizzoae* sp. nov. (mm).

Vanderberghia corbazi sp. nov.
(Figs. 353.1, 353.2, 353.6)
https://zoobank.org/NomenclaturalActs/447B6A99-DFCA-4B6E-9174-9DD6013ADF5C

Type locality. France-65, Ferrère, Chalets Saint-Nérée, Fontaine de Pousseillac, 42º 55' N 0º 30' E, 815 m.

Type series. Holotype ♂ (in col. Fresneda-Lagar): F-65, Ferrère, Fontaine de Pousseillac, captage d'eau, 815 m, 24.X.1987, G. Corbaz leg., with holotype label [Holotypus / *Vanderberghia* / *corbazi* sp. n. / Fresneda *et al*., 2023] (hw, rl), genitalia on transparent card mounted on the same pin as the holotype. Paratypes: with the same data as the holotype, 3 ♂♂, 10 ♀♀, with paratype label [Paratypus / *Vanderberghia* / *corbazi* sp. n. / Fresneda *et al*., 2023] (hw, rl) (CFL, CAF, CCB, CPMG).

Description. Size of 2.7 mm. Body elongated with subparallel margins (Fig. 353.1). Depigmented.

Head: Anophthalmous.

Antennae: Short and robust with antennomeres slightly thickened from 7th; 8th length twice its width, shorter than 10th and latter being longer than 9th. Antennal formula: See Table 30.

Pronotum: Transverse, twice as wide as long; strongly attenuated forwards and slightly tapered backward; widest width just before base, as wide as elytra; posterior angles rounded, slightly acute and somewhat prolonged on elytra; base bisinuate; integument sculpture grainy.

Elytra: Elongated, with subparallel margins in anterior half; widest near base; apex of each elytra separately rounded; elytral sculpture consisting of transverse striolae thick and rough; finer secondary striolae present; without parasutural stria.

Legs: Delicate, moderately long with first protarsomere dilated, but narrower than apex of protibia; metafemora simple, without any special relief (Fig. 353.6).

Mesoventral keel: Very tall forming a right angle with vertex hooked.

Median lobe of aedeagus: In lateral view (Fig. 353.2) bent to an obtuse angle approximately halfway; dorsal face presenting a curve from base to apex, but at beginning of apical third a rounded notch present prior to a marked terminal thickening; apex slender, prolonged and curved near back.

Parameres: As long as median lobe with apex thickened; with a cavity with interior occupied by a penicillum consisting of numerous and long setae; three thicker setae differentiated.

Endophallus: Consisting of three parts. Apical fibres of basal «Y»-piece made up of a nodule highly sclerotized; base of symmetrical arms of «Y»-piece with some phanerae attached arising and extending in form of hyaline fibres throughout sides of bag. Middle part, on both sides of flagellum, with divergent dorsal phanerae, and ventral ones seeming to be united at their upper end, whole taking on appearance of a horseshoe; armour of axial piece is made up consisting of two pieces symmetrical and elongated, with upper end thickened; muscle bundles on both sides of armor of axial piece starting in apical part. Apical region with reinforcing bands resting on membranous ligulae.

Female. Slightly more robust than male, with elytra somewhat broader and more domed; protarsi not thickened and tetramerous.

Etymology. This new species is amicably named in honour of Gabriel Corbaz (Boucou, Sauveterre-de-Comminges, France), for his contribution to the knowledge of the cave beetle fauna of Haute-Garonne and for being the collector of the specimens of the Fontaine de Pousseillac. The specific name is a noun in the genitive singular.



FIGURES 353.1–353.9: *Vanderberghia* spp. Habitus of the holotype of(**1**) *V. corbazi* **sp. nov.** Aedeagus in lateral view of: (**2**) *V. corbazi* **sp. nov.,** (**3**) *V. orgibetensis* **comb. nov.**, (**4**) *V. bourgoini* **comb. nov.**, (**5**) *V. bastidea* **comb. nov.** Metafemur of: (**6**) *V. corbazi* **sp. nov.,** (**7**) *V. orgibetensis* **comb. nov.**, (**8**) *V. bourgoini* **comb. nov.**, (**9**) *V. bastidea* **comb. nov.** Red arrow pointing to the femoral teeth.

Discussion. *Vanderberghia corbazi* sp. nov. must be located in the basal part of the *Vanderberghia* gen. nov. clade, in the subclade of *Vanderberghia orgibetensis* comb. nov. and *Vanderberghia bourgoini* comb. nov. (Fig. 1C). This group of species have the westernmost distribution of their clade:

– *Vanderberghia ehlersi* comb. nov. derives from most basal cladogenesis with 100/100 support.

– *Vanderberghia bastidea* comb. nov. derives from the following cladogenesis with support 44.8/88; adding more sequences could change places and this would be likely, given that the geographic sequence from east to west is *Vanderberghia ehlersi* comb. nov., *Vanderberghia orgibetensis* comb. nov., *Vanderberghia bourgoini* comb. nov. and finally *Vanderberghia bastidea* comb. nov.; it is believed to be consistent that it could move to cladogenesis after *Vanderberghia bourgoini* comb. nov.-*Vanderberghia orgibetensis* comb. nov.

– As a third cladogenesis we find the group of sister species *Vanderberghia bourgoini* comb. nov.-*Vanderberghia orgibetensis* comb. nov., the latter being the one that presents the greatest affinities with *Vanderberghia corbazi* sp. nov.

Vanderberghia corbazi sp. nov. shares with *Vanderberghia orgibetensis* comb. nov. the dorsal part of the median lobe of aedeagus with a rounded notch prior to a marked terminal thickening (Figs. 353.3), this thickening being greater in *Vanderberghia corbazi* sp. nov. as it corresponds to a considerably more robust aedeagus (Fig. 353.2); in *Vanderberghia corbazi* sp. nov. the ventral part of the basal lobe of the aedeagus is rectilinear (Fig. 353.2), thickened in *Vanderberghia orgibetensis* comb. nov. (Fig. 353.3). The metafemora of the male of *Vanderberghia corbazi* sp. nov. does not show any special relief (Fig. 353.6) while in *Vanderberghia orgibetensis* comb. nov. there is a thickening or sinuosity in the posterior part of the middle part (Fig. 353.7). With the other species of the region, the morphological relationships are less evident, *Vanderberghia bourgoini* comb. nov. also has a notch on the dorsum of the median lobe but the posterior thickening diminishes strongly near the apex (Fig. 353.4) and the metafemora shows a thick femoral spine nearby to the base (Fig. 353.8); *Vanderberghia bastidea* comb. nov. does not have the dorsal notch of the median lobe of aedeagus but a thickening prior to the apex (Fig. 353.5) and its metafemora is simple (Fig. 353.9).

It is suspected that *Vanderberghia bepmalei* comb. nov. and *Vanderberghia bastidea* comb. nov. are two names of the same species. Not only are the typical localities of both very close (Fig. 354), but also the shapes of their aedeagus coincide. *Vanderberghia bepmalei* comb. nov. could not be studied, it is a rare species only known by the holotype.

The only locality of *Vanderberghia corbazi* sp. nov. is practically «surrounded» by localities inhabited by *Vanderberghia bourgoini* comb. nov., in the western reliefs of the Garonne river (Fig. 354). The closest species, *Vanderberghia orgibetensis* comb. nov., is instead found at a considerable distance on the eastern reliefs of the same river, in the same region inhabited by *Vanderberghia ehlersi* comb. nov. Therefore, it seems that *Vanderberghia corbazi* sp. nov. and *Vanderberghia orgibetensis* comb. nov. are vicariant species isolated by the river course that, probably at some point in the Pleistocene, were able to cross the river, during a period of drought or under the ice during some glacial stage. There is a certain defect in the region in the sampling of species of this genus: they are species that are rarely found in caves (a biotope exhaustively studied in the central Pyrenees) and instead seem to be abundant in limestone MSS.

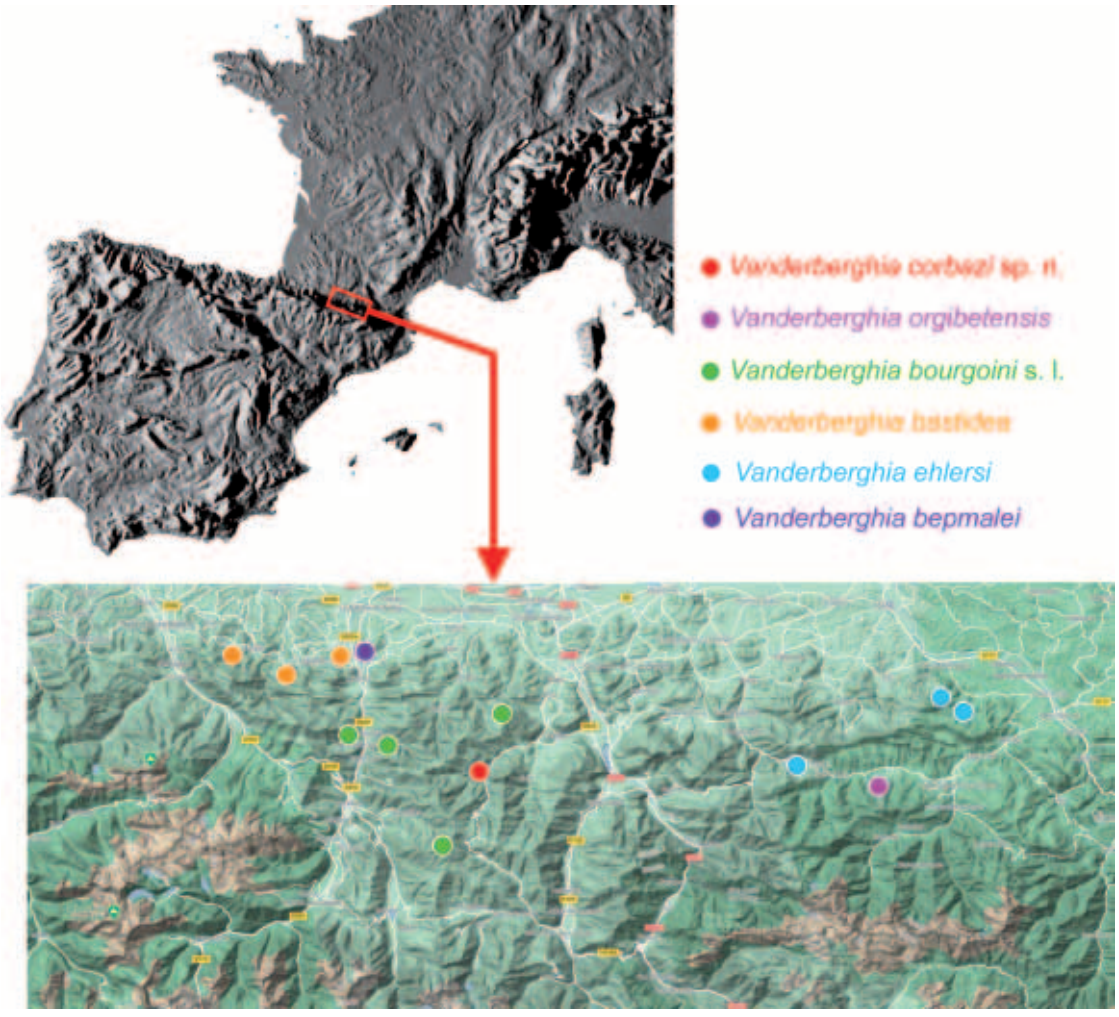
Distribution. France. Only known from the type locality in Barousse valley, north slope of Central Pyrenees: the upwelling of Fontaine de Pousseillac.

Material studied and bibliographical references.

– *Vanderberghia bastidea* comb. nov.: F-65, Esparrós, rivière souterraine d'Artigaléou-Arodets, 19.III.2009, Bourdeau & Fresneda leg., 7 exx. (CFL). References: Coiffait (1950); Cabidoche (1961); Perreau (2000); Löbl & Smetana (2004).

– *Vanderberghia bepmalei* comb. nov.: References: Jeannel (1908b, 1910a, 1911a, 1914b, 1924a, 1947a); Dupré (1989); Perreau (2000); Löbl & Smetana (2004).

– *Vanderberghia bourgoini* comb. nov.: F-31, Ourde, Grotte de Péne Toué, 20.XI.2012, Bourdeau leg., 5 exx. (CFL); F-65, Ferrère, Tuto de la Cigalero, 19.VIII.2004, Déliot & Faille leg., 4 exx. (CFL); F-65, Sarrancolin, Grotte de la Cascade, VI.2007, Bourdeau leg., 7 exx. (CFL). References: Jeannel (1947a, 1947b); Gers (1989); Perreau (2000); Löbl & Smetana (2004).



FIGURES 354: *Vanderberghia* spp. Distribution map of: *V. corbazi* **sp. nov.**, *V. orgibetensis* **comb. nov.**, *V. bourgoini* **comb. nov.**, *V. bastidea* **comb. nov.**, *V. ehlersi* **comb. nov.** and *V. bepmalei* **comb. nov.**

– *Vanderberghia bourgoini pachycera* comb. nov.: References: Jeannel (1947a); Perreau (2000); Löbl & Smetana (2004).

– *Vanderberghia ehlersi* comb. nov.: F-31, Couledoux, MSS Grotte de la Bouhadère, traps: 14.V/30.X.2009, 1 ex. (CFL). References: Abeille de Perrin (1872a-b); Reitter (1885); Jeannel (1908, 1910, 1911, 1914, 1924); Fagniez (1927); Perreau (2000); Löbl & Smetana (2004).

– *Vanderberghia orgibetensis* comb. nov.: F-09, Illartein, Ravin de la Tire, Bourdeau leg., numerous specimens. (CFL).

Segment	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length	0.16	0.17	0.11	0.12	0.15	0.15	0.15	0.11	0.14	0.12	0.17
Width	0.06	0.06	0.04	0.05	0.05	0.05	0.07	0.05	0.08	0.07	0.08

TABLE 30. Measurements of antennomeres of the holotype of *Vanderberghia corbazi* sp. nov. (mm).

APPENDIX 2: Material used in the molecular phylogeny, with code voucher, locality, date, collector and GenBank accession numbers (newly obtained sequences in green; in yellow gen., sp., stat. and comb. nov.)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Adelopsella bosnica	AN774	Bosnia-Herzegovina, Ljubovcici, sifting in coniferous forest, 43°45'41.1"N 18°9'16.9"E, 859 m, 6.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Adelopsis coronaria	AF221	Ecuador, Pichincha, Unión de Toachi, 10.3.2009, J.M. Salgado	x	HE572801	HE576704		HE572834	HE572856
Afrocatops basilewskyi	AN520	Tanzania, South Pare, Mts., Kwizu For., 4.12924º S 37.88445ºE, 1629 m, 7.1.2013, V.V. Grebennikov		x		x	x	x
Agathidium sp.	AI1305	Spain, Córdoba, Cabra, Via Verde, 5.11.2006, A. Castro		GU356849	GU356744	x	GU356903	
Agathidium sp.	RA249	China, Yunnan, E slope Cangshan at Dali., 25º40'13.2"N 100º07'54.8"E, 2728 m, 13.5.2010, V.V. Grebennikov		x	x	x	x	x
Amphogeus angustitarsis **comb. nov.**	RA760	Spain, Vizcaya, Dima-Indusi, Cueva del Craneo, 43.1282N 2.73618W, 20.6.2011, A. Weigand	x	x	x	x		x
Amphogeus bolivari bolivari **comb. nov.**	AF15	Spain, Cantabria, Bustablado, Cueva la Cañuela, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x
Amphogeus bolivari monacatus **comb. nov.**	RA662	Spain, Cantabria, Montehano-Escalante, Cueva del Convento, 22.1.2010, J.M. Salgado & C. González Luque		x	x		x	x
Amphogeus cantabricus **comb. nov.**	AF8	Spain, Vizcaya, San Pedro de Galdames, Cueva de la Magdalena, 4.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak		HG915385	HG915688	HG915607	HG915458	HG915532
Amphogeus cisnerosii **comb. nov.**	AI524	Spain, Madrid, Patones, Cueva del Reguerillo, 19.11.2005, V.M. Ortuño		x	x		x	x
Amphogeus escalerai **comb. nov.**	AF9	Spain, Cantabria, Rasines, Cueva del Valle, 5.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak		HG915386	HG915690		HG915459	HG915533
Amphogeus filicornis **comb. nov.**	AC91	Spain, Cantabria, Andina-Guriezo, Cueva de los Tocinos, 25.10.2008, J.M. Salgado		x	x	x	x	x
Amphogeus intermedius **stat. & comb. nov.**	AF100	Spain, Cantabria, Cueva Nobre de Casa Caravia, 1.11.2008, C.G. Luque	x	x	x	x	x	x
Amphogeus luquei **comb. nov.**	AN191	Spain, Cantabria, Santoña, Barrio del Dueso, Cueva del Polvorín, 31.5.2003, J.M. Salgado	x	GU356864	GU356760	GU356814	GU356914	GU356956
Amphogeus nigricans **stat. & comb. nov.**	AC92	Spain, Cantabria, Puente Viesgo, Cueva de los Murciélagos, 17.9.2008, J.M. Salgado	x	HG915390	HG915692	HG915611	HG915462	HG915537
Amphogeus noltei **comb. nov.**	IRC3	Spain, Gipuzkoa, Olatz, Sima Kobeta, 15.7.1998, J. Fresneda		HE572816	HE576716	HE572887	GU356928	HE572869
Amphogeus oxypterus **comb. nov.**	AF21	Spain, Cantabria, Sámano, Cueva de la Lastrilla, 5.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x
Amphogeus seeboldi **stat. & comb. nov.**	AF13	Spain, Vizcaya, San Pedro de Galdames, Cueva de la Magdalena, 4.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Amphogeus sharpi **comb. nov.**	AN231	Spain, Cantabria, Suauces, Cueva de las Brujas de Ongayo, 6.3.2010, C.G. Luque		x	x	x	x	x
Amphogeus vasconicus **comb. nov.**	AF12	Spain, Burgos, Llorengoz, Cueva de Albia, 4.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak		HG915388	HG915689	HG915609	HG915461	HG915535
Anemadus hajeki	RA187	China, Yunnan, E slope Cangshan at Dali., deep soil, 25º39'54.7"N 100º06'04.5"E, 3815 m, 19.5.2010, V.V. Grebennikov		HE572819	HE576718	LS999499	LS999477	LS999486
Anemadus **sp. nov.**	AN854	Cameroon, Mt. Cameroon, 4.0935N 9.0573E, 524 m, 28.12.2015, V.V. Grebennikov	x	x	x	x	x	x
Anillochlamys aurouxi	IRC24	Spain, Castelló, Ain, La Covatilla, 8.7.2001, J. Fresneda		x	x	x		x
Anillochlamys bueni	AF174	Spain, Alacant, Beniarbeig, Cova del Bolumini, 30.1.2009, A. Faille & C. Andújar	x	HG915337		HG915562	HG915410	HG915482
Anillochlamys cullelli	RA673	Spain, Castelló, Serra d'Engarcerà, Cova Santa, 7.2.2010, S. Teruel & A. Sendra	HG915308	HG915338	HG915638	HG915563	HG915411	HG915483
Anillochlamys lencinai	RA674	Spain, Valencia, Cortes de Pallàs, Cueva Hermosa, 27.5.2007, S. Teruel & A. Sendra	x	x	x	x	x	x
Anillochlamys moroderi	RA31	Spain, Valencia, Llombai, Cova Meravelles, 8.7.2009, P. Barranco	HG915309	HG915339	HG915637	HG915564	HG915412	HG915484
Anillochlamys sendrai	RA675	Spain, Valencia, Siete Aguas, Cova de l'Orao, 5.4.2008, S. Teruel & A. Sendra	x	x	x	x	x	x
Anillochlamys subtruncata	IRC1	Spain, Castelló, Montan, Cova Cirat, 19.12.1998, J. Fresneda	ON109503	GU356850	GU356745	GU356802	GU356904	GU356941
Anillochlamys tropica	IRC28	Spain, Valencia, Alzira, Cova de les Meravelles, 10.7.2001, J. Fresneda		x	x	x		x
Anthroherpon charon	VA34	Bosnia-Herzegovina, Pale, Ravna pl, Omladinska pecina (Njunjić 2016)	KX121088	KX121109		MH368212	KU980188	KX121059
Anthroherpon cylindricolle cylindricolle	IE3	Bosnia-Herzegovina, Pale, Rogatica, Golubovica pecina (Njunjić 2016)			KX719890	KX719833		KX719928
Anthroherpon ganglbaueri ganglbaueri	AN773	Bosnia-Herzegovina, Nevesinje, Novakusa pecina, 43°14'58.0"N 18°4'34.8"E, 1030 m, 5.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Anthroherpon harbichi	IB3	Bosnia-Herzegovina, Sarajevo, Crepoljsko, Kecina stena (Njunjić 2016)	KX121091	KX121112		MH368213	KU980191	KX121060
Anthroherpon hoermanni ssp.	AN779	Bosnia-Herzegovina, Jelaska, Mamutova jama, 43°29'28.6"N 18°29'37.6"E, 1118 m, 7.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Anthroherpon latipenne latipenne	IE13	Montenegro, Orjen, Ericova jama (Njunjić 2016)	KX121093	KX121114	KX719897	KX719840	KU980184	KX121062
Anthroherpon matulici	I5	Bosnia-Herzegovina, Gubar Mt, Bukova rupa (Njunjić 2016)		KX121115	MH368219	MH368214	KU980186	KX121056
Anthroherpon matzenaueri matzenaueri	IB13	Montenegro, Golija, Laticno, Jama u Rudinskom dolu (Njunjić 2016)	KX121086	KX121116	KX719900	KX719843	KU980193	KX121057

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Anthroherpon primitivum primitivum	IE39	Bosnia-Herzegovina, Turica, Motka, Mravinja (Njunjić 2016)	KX121094	KX121117	KX719901	KX719844	KU980187	KX121063
Anthroherpon pygmaeum pygmaeum	IE25	Bosnia-Herzegovina, Bjelasnica, Opancak, Ledenjaca (Njunjić 2016)	KX121085	KX121118	MH368220	MH368215	KU980178	KX121064
Anthroherpon shtarensis	AN1278	Albania, Vrana e Madhe, Shpella Shtares cave, 1427 m, 42.31766°N 19.85403°E, 23.8.2019, A. Lacirignola, M. G. Mastronardi, M. Pastore		x	x			
Anthroherpon sinjajevina	VA6	Montenegro, Sinjajevina, Rudnica, Blazova pecina, I. Njunjić leg. (Njunjić 2016)	KX121095		KX719904	KX719847	KU980194	KX121065
Anthroherpon stenocephalum stenocephalum	IE44	Bosnia-Herzegovina, Olovo, Bijambar (Njunjić 2016)	KX121096	KX121119	KX719907	KX719850	KU980195	KX121066
Anthroherpon taxi taxi	IE55	Montenegro, Kameno more, Dvestotka (Njunjić 2016)	KX121097	KX121120		MH368216	KU980185	KX121067
Anthroherpon weiratheri	IE21	Bosnia-Herzegovina, Sarajevo, Crepoljsko, Kecina stena (Njunjić 2016)	KX121098	KX121121	KX719911	KX719854	KU980179	KX121068
Anthroherpon zariquieyi	IE37	Montenegro, Durmitor, Vodeni krs, Vodena pecina (Njunjić 2016)	KX121099	KX121122	KX719912	KX719855	KU980196	KX121069
Antrocharis querilhaci dispar	AI588	France-09, Aigües Juntes, Grotte Les Cloutets, 18.5.2004, A. Faille	x	GU356851	GU356746	GU356803	GU356905	GU356942
Antrocharis querilhaci querilhaci	AC118	France-09, Suc et Sentenac, Trou du Rantou, 9.8.2009, C. Vanderbergh	MT521293	LN849262		LN849304		
Aphaobius brevicornis	RA957	Austria, Obir, Stollen unter dem Rainier Schmitzhaus, trap propylen, 16.9.2012, H. Mixaning	LT602646	LT602637	LT602707	LT602699	x	LT602677
Aphaobius haraldi	RA629	Austria, Kärnten, Bad Bellach, MSS, 20.8.2011, H. Mixaning & A. Faille	LT602649	LT602636	LT602714	LT602694	LT602660	LT602671
Aphaobius kraussi cf	RA870	Austria, Windischbleiberg, Singernerg, Stollen 1, 4.5.2012, A. Faille & H. Mixaning	LT602648	LT602642	LT602701	LT602698	x	LT602676
Aphaobius milleri	RA505	Slovenia, Mt. Krim, Jama Velika Pasica, 3.9.2010, E. Lana	LT602650	LT602644	LT602713	LT602687	LT602661	LT602672
Aphaobius mixanigi	RA633	Austria, Kärnten Bag Eisenkappel, Lobnigschacht, 20.8.2011, H. Mixaning & A. Faille	LT602653	LT602635	LT602705	LT602686	LT602659	LT602670
Apholeuonus nudus nudus	AN778	Bosnia-Herzegovina, Kalinovik, Krbljine pecina, 43°34'3.3"N 18°29'55.1"E, 1169 m, 7.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Apholeuonus nudus sturanyi	IAP3	Bosnia-Herzegovina, no data (Genbank: Njunjić *et al.* 2016)	KX121100				KU980171	KX121082
Aranzadiella leizaolai	IRC17	Spain, Gipuzkoa, Mendaro, Cueva del Viento, 18.7.2000, J. Fresneda		GU356852	GU356747	GU356804	GU356906	GU356943
Archeoboldoria doderona	RA511	Italy, Biella, Böcca d'la Bussa Pitta - 2517 Pi/VC, Sabbia, 1, UTM: 32T 442304 5080457, 1120 m, 28.4.2011, E. Lana	x		x	x	x	x
Archeoboldoria martinottii **sp. nov.**	M339	Italy, Piemonte (Bi) Val Sessera, Miniera Pietrabianca 2, 2.6.2020, P.M. Giachino			x			
Archeoboldoria pascuttoi	M413	Italy, Miniera "Vittorio Amedeo" 2, Sagliano Micca, 700 m, Oneglie, 1.6.2020, E. Lana			x		x	

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Archeoboldoria sturanii	AN677	Italy, Brosso, Torino, Buca del Ghiaccio della Cavallaria, 1609 Pi/TO, UTM: 32T 405988 5041431, 1150 m, 25.6.2013, E. Lana	x	x	x	x	x	x
Ariejasia carrerei **gen. nov. comb. nov.**	AI530	France-09, Illartein, Ravin de la Tire, MSS, 3.6.2004, Ph. Déliot & A. Faille	MT521311	GU356895	GU356793	GU356840	GU356937	GU356985
Astagobius angustatus	RA501	Slovenia, Mt. Nanos, Volcja Jama nº 743, 28.7.2010, P.M. Giachino, A. Casale, E. Lana, P. Marcia, F. Gasparo	HG915310	x	HG915639	HG915565	HG915413	HG915485
Attaephilus sp.	RA469	Turkey, Erzurum, Yesildere, little cave 1, 40º06'42.4"N 41º24'22.2"E, 1863 m, 12.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x
Baronniesia delioti	AF188	France-65 , Esparros-Arrodets, rivière souterraine d'Artigaléou, 18.8.2009, C. Bourdeau	x	HG915340	HG915640	HG915566	HG915414	HG915486
Bathysciella alexinae **comb. nov.**	RA858	France-64, Camou-Cihigue, Gte d´Oxibar infèrieure, 11.4.2012, C. Bourdeau & A. Faille	x	x	x	x	x	x
Bathysciella bordei **comb. nov.**	RA262	France-64, Saint-Etienne-de-Baïgorry, Grotte Astate, 16.4.2010, E. Dupré	x	x	x	x	x	x
Bathysciella duprei **comb. nov.**	AI912	France-64, Esterencuby, Grotte du Renard, 4.5.2006, C. Bourdeau	x	HE572814	x	x	x	x
Bathysciella fratyi **comb. nov.**	IRC23	Spain, Navarra, Villanueva de Aezkoa, Sima Ilaraldea, 12.10.2001, J. Fresneda	x	GU356879	GU356775	GU356827	x	GU356969
Bathysciella ittanus **comb. nov.**	AI595	France-64, Arbailles, Grotte d'Istaurdy, 4.6.2004, C. Bourdeau	x	GU356878	GU356774	GU356826	GU356925	GU356968
Bathysciella jeanneli	AI540	France-64, Arbailles, Grotte d'Istaurdy, 25.5.2004, A. Faille		GU356853	GU356748	HG915567	GU356907	
Bathysciella mascarauxi **comb. nov.**	RA754	France-64, Ahusquy, Doline d'Arangaysca, 22.9.2011, C. Bourdeau	x	x		x	x	x
Bathysciella sioberi **comb. nov.**	AF27	France-64, Barlanès, Grotte de Barlanès, no data, E. Dupré		HE572784	HE576690	HE572874	HE572821	HE572843
Bathyscimorphus byssinus acuminatus	AF131	Slovenia, Trebnje (central south Slovenia), Velika jama nad Trebnjem, kat. No. 104, 3.3.2007, S. Polak	x	HG915341	HG915641		HG915415	HG915487
Bathysciola balestrae **sp. nov.**	RA193	Italy, Piemonte (CN), Ormea, Cima Ciuaiera, 44°11'27N 7°53'12 E, 2110 m., 10.8.2010, E. Lana	x	x	x	x	x	x
Bathysciola brevicollis	RA630	France-06 Roquebilliere, Font de Gordolon, 13.7.2011, A. Faille & J. Raffaldi	x	x	x	x	x	x
Bathysciola casalei	AN675	Italy, CN, Piemonte, Limone, Buco di Napoleone, no data, E. Lana & M. Chesta	x	x	x	x	x	x
Bathysciola chestai **sp. nov.**	AN681	Italy, Cuneo, Vinadio, Valle Stura di Demonte, Tana Neraissa 1, 1074 Pi/CN, UTM: 32/ 354296 4908574, 1030 m, 25.10.2013, E. Lana & M. Chesta	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Bathysciola guedeli	AN1256	Italy, Valle Po, Crissolo, Grotta Buco di Valenza, 8.7.2019, M. Chesta & E. Lana leg.	x	x	x	x	x	x
Bathysciola guerzoi	AN1230	Italy, Piemonte, San Martino Canavese (TO), 385 m, 15.6.2019, P.M. Giachino	x	x	x		x	x
Bathysciola lanai **sp. nov.**	AN678	Italy, Cuneo, Fabrosa Soprana, Faggeta davanti allo Grotta di Bossea, UTM: 32T 407520 4899525, 830 m, 24.6.2012, E. Lana	x	x	x	x	x	x
Bathysciola monregalensis	AN1232	Italy, CN, Piemonte, Serradi Pamparato, 900 m, 21.6.2019, P.M. Giachino	x	x	x	x	x	x
Bathysciola nicaeensis	RA402	France-06, Tende, Gorges de Paganin, 9.7.2010, J. Fresneda	HG915311	HG915343	HG915643	HG915569	x	HG915488
Bathysciola oliveroi **sp. nov.**	AN679	Italy, Cuneo, Robilante, Valle Vermenagna, Riparo I sotto Tetti Pignuna, 210 Pi/CN, UTM: 32T 381695 4906656, 688 m, 23.8.2013, E. Lana & M. Chesta	x	x		x	x	x
Bathysciotes khewenhuelleri khewenhuelleri	RA506	Slovenia, Orecca, Zeguana jama, 29.8.2010, P.M. Giachino	HG915318	HG915357	HG915660	HG915583	HG915432	HG915503
Bathysciotes khewenhuelleri tergestinus	AC54	Slovenia, Storje (southern Slovenia), Belinca jama, kat. No. 950, 26.3.2007, S. Polak	x	x	x	x	x	x
Batinoscelis lostiae **(genus stat. nov.)**	GBK-AY012698	Sardinia (Isl.), Nuoro, Sadali, Margiani Ghiana cave (Caccone & Sbordoni, 2001)		AY012698				
Batinoscelis onnisi **sp. nov. (genus stat. nov.)**	RA267	Sardinia (Isl.), Villasalto, La Rutta le Scusi, 14.3.2010, A. Casale	x	x	x	x	x	x
Baudiola tarsalis	AN1255	Italy, Piemonte, Biella, Oropa, MSS, 1280 m, 13.7.2019, P.M. Giachino	x	x	x	x	x	x
Bellesia espanyoli	IRC21	Spain, Huesca, Sercué, Cueva de Aso, 28.10.2001, J. Fresneda		GU356858	GU356754	GU356809	GU356910	GU356948
Besuchetiola priapus	RA497	Turkey, Artvin, Arhavi-Arılıköyü, 41°16'29.6"N 41°22'28.5"E, 289 m, 13.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x
Breuilia triangulum	AF2	Spain, Asturias, Porrúa, Cueva Verde, 6.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HG915358	HG915661	x	HG915433	HG915504
Breuilites eloyi	AI662	Spain, Asturias, Caravia Alta-Arriondas, Cueva de Entrecuevas, 21.1.2006, J.M. Salgado	ON109504	GU356859	GU356755	GU356810	GU356911	GU356949
Cacciamalia glacialis	AN1146	Italy, Lombardia-Brescia, Vobarno, Rècia de Mar, nº 211 Lo, 1065 m, 19.12.2014-23.10.2015, D. Vailati		x				
Canapiciella angeli	AN1233	Italy, Piemonte, Ronco Canavese (TO), Bivio per Soanolosia, 900 m, 23.6.2019, P.M. Giachino	x	x	x	x	x	x
Canavesiella lanai	RA805	Italy, Piemonte, Torino, Vasario, Sparone, I Grotta "La Custreta", 1593, UTM: 32T, 386340 5033760, 1350 m, 22.8.2011, E. Lana, & A. Pastorelli	x	x	x	x	x	x
Cansiliella servadeii	AN181	Italy, Tramonti di S (PN), Grotta Foos di Campone (507/229 FR), Sala B, 23.9.2012, L. Dorigo	LT602651	LT602643	LT602710	LT602697	LT602658	LT602685
Cantabrogeus antimachus	RA34	Spain, Cantabria, Carcabal-Merilla, San Roque de Rio Miera, Cueva de Covallarco, 6.6.2009, J.M. Salgado & C.G. Luque	x	HE663496	HE663535	HE663506	HE663512	HE663520

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Cantabrogeus cultellus	AC83	Spain, Cantabria, Solares, Cueva de la Matorra IV, 23.8.2008, C.G. Luque	x	x	x	HE663507	HE663513	HE663521
Cantabrogeus fresnedai	RA241	Spain, Cantabria, Esles-St. Ma. De Cayón, Cueva de la Peña Caborco, 9.4.2010, C.G. Luque	HG915319	HE663498	HE663529	HE663508	HE663515	HE663523
Cantabrogeus luquei	AF3	Spain, Cantabria, Llanos-Penagos, Cueva del Encinar, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HE663499	HE663530	HE663509	HE663516	HE663524
Cantabrogeus nadali	AF4	Spain, Cantabria, Bustablado, Cueva la Cañuela, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HE663500	HE663531	HE663510	HE663517	HE663525
Casalella finismillennii **gen. & comb. nov.**	RA525	France-09, Eycheil, Grotte de Sabouche sup., 12.12.2009, C. Bourdeau & J. Fresneda	HG915312	HG915346	HG915647	HG915571	HG915419	HG915491
Casalella liqueana **gen. & comb. nov.**	RA523	France-09, Moulis, Grotte de Liqué inf., 19.11.2009, C. Bourdeau & J. Fresneda	HG915315	HG915351	HG915653	HG915575	HG915425	HG915496
Casalella meridionalis **gen. & comb. nov.**	RA797	France-09, Aigües Juntes, Grotte Les Cloutets, 12.5.2012, J. Fresneda & A. Cieslak	x	HG915342	HG915642	HG915568	HG915416	x
Catalaniana madoni **gen. & comb. nov.**	AC76	Spain, Girona, Sant Joan de les Abadesses, Coll Santigosa, beech forest, 42°12'37.5"N 2°20'12.3"E, 1100 m, 11.9.2008, I. Ribera, C. Hernando & C. Andújar	x	HG915352	HG915654	HG915576	HG915426	HG915497
Catalaniana penicillata **gen. & comb. nov.**	RA800	Spain, Lleida, Navés, St. Pere de Graudescales, 3.4.2012 J. Fresneda	HG915316	HG915356	HG915658	HG915580	HG915430	x
Catalaniana zariquieyi **gen. nov. comb. nov.**	AI1255	Spain, Barcelona, Sant Celoni, Serra de Montnegre, Roureda d'en Preses, Sot del Til.ler, 650m, 21.10.2006, C. Hernando	x	GU356857	GU356753	HG915582	x	GU356947
Catops americanus	RMNH-INS-63170	GBK-KF604717, no data (Genbank: Schilthuizen, M.)	KF604717					
Catops andalusicus	AF72	Spain, Córdoba, Cabra, La Nava, 28.4.2007, M. Baena		HE572791	HE576694		HE572826	HE572848
Catops angustitarsis	RMNH-INS-546058	GBK-KF604723, no data (Genbank: Schilthuizen, M.)	KF604723					
Catops basilaris	AN933	Canada, Ontario, Leeds-Grenville Co., Peck's Beetle Acres, 22.5.2010, S. Peck	x	x	x	x	x	x
Catops chrysomeloides	RMNH-INS-549300	GBK-KF492887, no data (Genbank: Schilthuizen, M.)	KF492887					
Catops coracinus	RMNH-INS-549274	GBK-KF492836, no data (Genbank: Schilthuizen, M.)	KF492836					
Catops fuliginosus	AF32	Spain, Huesca, Seira, MSS 002, C.N. 260 entre el PK 396 y PK 397, 750 m, 18.5.2008, J. Fresneda		HE572786	HE576692		HE572822	HE572844
Catops fuscus fuscus	AN462	Spain, Huesca, Villanúa, Cueva de Esjamundo, 28.9.2009, C. Bourdeau, A. Faille & J. Fresneda	x	x	x			x
Catops geomysi	AN932	USA, Florida, Leon Co., Tall Timbers Res. Stn., 27.4.2010, S. Peck	x	x	x		x	x
Catops grandicollis	BC-97	GBK-KF492826, no data (Genbank: Schilthuizen, M.)	KF492826					
Catops hilleri	RMNH-INS-546060	GBK-KF604711, no data (Genbank: Schilthuizen, M.)	KF604711					
Catops kirbyi	BC-103	GBK-KF492871, no data (Genbank: Schilthuizen, M.)	KF492871					
Catops nigricans	BC-90	GBK-KF492853, no data (Genbank: Schilthuizen, M.)	KF492853					
Catops nigriclavis	BC-87	GBK-KF492893, no data (Genbank: Schilthuizen, M.)	KF492893					

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Catops picipes	RA806	France-27, La Saussaye, Forêt d'Elbeuf, piège terrier de Renard, 2,80 m, 4/30.4.2010, A. Faille		x	x	x	x	x
Catops rotundatus **stat. nov.**	AF30	Spain, Cantabria, Bustablado, Cueva la Cañuela, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HE572785	HE576691	x		HE572865
Catops simplex	AN934	USA, Florida, Leon Co., Tall Timbers Res. Stn., 27.4.2010, S. Peck	x	x	x	x	x	x
Catops sp.	AN531	Turkey, Erzincan, Sipikor, wolf's lair, 395323.6N 393507E, 2291 m, 19.6.2011, A. Faille, J. Fresneda & I. Ribera		x				
Catops subfuscus	RA531	France-27, La Saussaye, terrier de renard, 1,80 m, 4/30.4.2010, A. Faille	x	x	x	x	x	x
Catops tristis	RMNH-INS-549234	GBK-KF492880, no data (Genbank: Schilthuizen, M.)	KF492880					
Catops ventricosus	RA472	Turkey, Gümüşhane, Arılı Mağarasi, 40°26'50.8"N 39°19'19.1"E, 1777 m, 16.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x
Catopsinus rudoyi **sp. nov.**	AN62	Azerbaijan, Qax [Kakh], Kashkachay, forest litter Fagus next to road, 41°23'40.9"N 47°3'0.1"E, 1160 m, 5.5.2014, A. Faille, J. Fresneda, I. Ribera, A. Rudoy	x	x	x	x	x	x
Ceretophyes cenarroi	RA463	Spain, Lleida, Bellver de Cerdanya, Fou de Bor, 17.5.2011, C. Bourdeau & J. Fresneda	HG915320	HG915359	HG915662	HG915584	HG915434	HG915505
Ceretophyes riberai	AI597	Spain, Girona, Olopte, Cova d'en Manent, 7.7.2004, Ph. Déliot & A. Faille	MT521341	GU356862	GU356758	GU356812	GU356913	GU356952
Charonites sp.	IO33	Bosnia-Herzegovina, Pale, Omladinsca pecina (Njunjić 2016)	KX121101	KX121123		KX719859	KU980172	KX121083
Chelagyrtodes davidi	AN256	New Zealand (Isl.), South Island Buller (BR) Rahu Scenic Reserve, Springs Junction, Nothofagus fusca forest, NZ144, 42°19'56.1'S' 172°10'16.6"E, 437m , 31.1.2003, C. D'Haese	x	x	x	x	x	x
Chiliopelates nigrus	AN144	Chile, Huinay biol.st., Notophagus forest "catedrales"; 42°22'12.9"S 72°24'13.5"W, 88 m, 8.12.2014, I. Ribera	x	x	x	x	x	
Choleva agilis	RMNH-INS-549317	GBK-KF492883, no data (Genbank: Schilthuizen, M.)	KF492883					
Choleva angustata	AF144	France-31, Izaut de l'Hôtel, Grotte de la Maouro, 10.10.2003, A. Faille		HE572794	HE576697		HE572828	HE572850
Choleva bosnica	AN777	Bosnia-Herzegovina, Kalinovik, Krbljine pecina, 43°34'3.3"N 18°29'55.1"E, 1169 m, 7.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Choleva cisteloides	AF197	France-31, Tibiran, Grotte de Tignahuste, 19.5.2009, C. Bourdeau & J. Fresneda	x	HE572795	HE576698	HE572878	HE572829	HE572851
Choleva elongata	RA530	France-27, La Saussaye, mare au rivier, 30.4.2010, A. Faille	x	x	x	x	x	x
Choleva fagniezi	RA752	France-09, Saurat, Rivière souterraine de Siech, 17.8.2010, C. Vanderbergh	x	x	x	x		
Choleva kocheri	AF216	Morocco, Aït Mohammed, Ifri N'Caid, 10.9.2009, A. Faille	x	HE572797	HE576700		HE572831	HE572853
Choleva oblonga	RMNH-INS-550279	GBK-KF492815, no data (Genbank: Schilthuizen, M.)	KF492815					
Choleva sp.	RA473	Turkey, Ordu, Kulakköy Mağarasi, 40°55'25.0"N 37°28'34.1"E, 44 m, 17.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Choleva sturmi	RMNH-INS-550288	GBK-KF492829, no data (Genbank: Schilthuizen, M.)	KF492829					
Cholevinus pallidus pallidus	AN864	Kazakhstan, lake Inder, 48.5575 52.0450, 13 m, in cave "Ledyanoy Paporotnik", 22 m deep of max. 25 m and 62m from entrance, 2.5.2017, I. Golovachev	x	x	x	x	x	x
Closania winkleri winkleri	RA558	Romania, Gorj, Closani, Pestera de Closani, 26.7.2011, J. Fresneda	x	x	x	x	x	x
Colenis bonnairii	RA639	Spain, Jaén, Hornos, Sima de la Tubería, 28.8.2011, GEV	x	x	x	x		
Colon (Platycolon) sp.	AN715	Tanzania, W Usambara Mts., Kkusu For., 4.76585ºS 38.36022ºE, 1576 m, 14.1.2013, V.V. Grebennikov	x	x	x	x	x	x
Colon (Platycolon) sp.	AN894	Tanzania, Mt. Meru, above Miriakamba Huts, 3.22201ºS 36.78352ºE, 3178 m, 2.12.2012, V.V. Grebennikov		x				
Colon sp.	AN855	China, Yunnan, E slope Cangshan at Dali.,25º40'14.7"N 100º06'12.0"E, 3827 m, 17.5.2010, V.V. Grebennikov		x	x			
Croatodirus bozicevici	C3048	Croatia, Kaverna u tunelu Učka, Učka, Opatija (Polak *et al*. 2016)	KX223671	KX223659	KX223624			KX223635
Cytodromus ambiguus	RA1030	France-26, St. Laurent en Royans, Scialet Grail, 17.3.2012, C. Alonso	x	x	x	x	x	x
Cytodromus dapsoides	AC22	France-26, Vassieux-en-Vercors, Baume Cervière, 8.7.2007, J. Fresneda	x	HG915360	HG915663	HG915585	HG915435	HG915506
Dellabeffaella roccae	RA191	Italy, Piemonte (TO), Mazzanile, Grotta del Pugnetto, 21.8.2010, E. Lana	x	x	x	x	x	x
Diaprysius andreae	RA521	France-34, La Vacquerie, Aven de Vitalis, 2.9.2009, C. Alonso	x	x	x	x	x	x
Diaprysius caudatissimus	AC148	France-07, Vallon Pont d'Arc, Grotte du Dèroc, 18.8.2009, C. Alonso	x	x	x	x	x	x
Diaprysius caudatus	RA522	France-07, Saint Montan, Grotte de Pascaloune, 20.10.2009, C. Alonso	HG915321	HG915361	HG915664	HG915586	HG915436	HG915507
Diaprysius fagniezi	RA520	France-30, St. Prives de Champelos, Grotte du Serre de Berri, 13.10.2009, C. Alonso	HG915322	HG915362	HG915665	HG915587	HG915437	HG915508
Diaprysius gezei	RA519	France-30, Montclus, Aven du Capitan, 20.10.2009, C. Alonso	x	x	x	x	x	x
Diaprysius mazaurizi	AC149	France-30, Lussan, Aven du Camelié, 19.10.2009, C. Alonso	x	x	x	x	x	x
Diaprysius serullazi alberti	RA1031	France-07, Ruoms, Grotte de Baume Grenas, 6.7.2010, C. Alonso	x	x	x		x	x
Diaprysius serullazi muelleri	RA26	France-07, Labeaume, Grotte de Peyroche, 6.7.2009, J. Fresneda	HG915323	HG915363	HG915666	HG915588	HG915438	HG915509
Diaprysius serullazi peyerimhoffi	AN682	France-07, Event Gournier, Aigueze (30), VII.2013, A. Faille	x	x	x	x		x
Diaprysius sicardi	RA28	France-34, Coupiac, rd D986, grotte du Bois de Long, 43º53'07"N 03º41'22.4"E, 322 m, 2.8.2008, J. Fresneda, I. Ribera & A. Cieslak	HG915324	HG915364	HG915667	HG915589	HG915439	HG915510

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Dictydiella leleupi	RA585	South Africa, EC, Leaf litter @ Storms River Mouth, Tsitiskama, 24.9.2008, D.T. Bilton		x	x			
Dissochaetus chiapensis	RA341	Ecuador, Pichincha, Unión de Toachi, 10.3.2009, J.M. Salgado	x	x	x	x	x	x
Dissochaetus hetschkoi	AF219	Ecuador, Orellana, Reserva Nacional de Yasuni, Estación Biológica, 19.3.2009, J.M. Salgado	x	HF912461	HF912611	HF912508	HF912581	HF912593
Dissochaetus oblitus	AN938	USA, Florida, Leon Co., Tall Timbers Res. Stn., 27.4.2010, S. Peck	x	x	x	x	x	x
Drimeotus kraatzi	RA680	Romania, Ferice cave Da/Da, R. Bucur	x	x	x	x	x	x
Drimeotus viehmanni	RA559	Romania, Bihor, Remeti, Pestera cu Apa din Valea Lesului, 16.7.2011, J. Fresneda	x	x	x	x	x	x
Dupreia beruetei **gen. nov. comb. nov.**	IRC15	Spain, Navarra, Donamaria, Cueva de Iguntsoro, 22.7.2000, J. Fresneda		GU356865	GU356761	GU356815	GU356915	GU356957
Epiroella acharnanis	AN187	Greece, nom. etolía-Akarnanía, o. Sérekas, Gr. Megálo Spilió, 1000 m, 23.5.2013, H. Mixaning				x		x
Espanoliella cuneus	AF5	Spain, Cantabria, Límpias, Cueva de Seña, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HG915365	HG915668	HG915590	HG915440	HG915511
Espanoliella jeanneli	IRC4	Spain, Cantabria, Sámano, Cueva de la Lastrilla, 12.7.1998, J. Fresneda	ON109505	GU356863	GU356759	GU356813	ON117155	GU356955
Espanoliella tibialis	AF6	Spain, Cantabria, Rasines, Cueva de San Roque de Liebe, 5.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak		x	x	x	x	x
Espanoliella urdialensis	AC90	Spain, Cantabria, Santullán, Cueva de los Peines II, 17.10.2008, J.M. Salgado		HG915366	HG915669	HG915591	HG915441	HG915512
Eucatops incognitus	RA342	Ecuador, Orellana, Reserva Nacional de Yasuni, Estación Biológica, 19.3.2009, J.M. Salgado	x	x	x	x	x	x
Eucatops rossii	AF220	Ecuador, Pichincha, Unión de Toachi, 10.3.2009, J.M. Salgado	x	HE572800	HE576703	HE572879	HE572833	HE572855
Euryspeonomus (Euryspeonomus) breuili	IRC20	Spain, Navarra, Alli, Cueva de Akelar, 30T: 590288 4760052, 625 m, 17.7.2000, J. Fresneda	x	HG915367	HG915670	HG915592	x	HG915513
Euryspeonomus (Urbasolus) ciaurrizi	IRC16	Spain, Navarra, Atalo, Cueva Malkorrandi, 21.7.2000, J. Fresneda		GU356866	GU356762	GU356816	x	GU356958
Euryspeonomus (Urbasolus) eloseguii	HI22	Spain, Navarra, Urbasa, Larraona, Cueva de los Cristinos, 19.6.2006, C. Bourdeau	x	x	x	x	x	x
Falkocholeva falklandica	GBK-BMNH673230	Falkland (Isl.), no data (Papadopoulou *et al.* 2009)			FM994861			
Falkonemadus sp.	GBK-BMNH673231	Falkland (Isl.), no data (Papadopoulou *et al.* 2009)	FM994514	FM994499	FM994862			
Fresnedaella lucius	RA188	Spain, Cantabria, Selaya, Cueva de La Canal de la Cubia, 15.6.2010, C.G. Luque	x	HE663501	HE663534	HG915593	HE663518	HG915514
Fusi cf *nyujwa*	AF67	Russia, Primorsky Kr., Anisimovka vil., soil traps, 43º07'25"N 132º47'43"E, 500 m, 9-11.7.2008, V.V. Grebennikov	x	HE572789	HE576693	x	HE572824	HE572846
Galliana linderi linderi **gen. nov. comb. nov.**	AF224	France-07, Labeaume, Grotte de Peyroche, 6.7.2009, J. Fresneda		HG915350	HG915652		HG915424	HG915495

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Georgiana brignolii **gen. nov. comb. nov.**	RA496	Turkey, Artvin, Cankurtaran Geçidi, 41°23'30.6"N 41°32'14.3"E, 680 m, 13.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x
Georgiana suramensis **gen. nov. comb. nov.**	M503	Georgia, Racha-Lechkhumi-Kvemo Svaneti region, Ambrolauri district, Racha karst massif, Dolabistavi Cave N42°27'03.9" E043°10'39.5" 1202m , 25.5.2022 , Barjadze, Faille, Maghradze			x		x	x
Gesciella delioti	AI525	France-09, Seix, Bordes de Crues, 16.10.2004, J. Fresneda	MT521295	GU356867	GU356763	GU356817	GU356916	GU356959
Graciliella apfelbecki apfelbecki	VA43	Croatia, Bobani, Brabovica (Njunjić 2016)	KX015840	KX011091		MH368217	KU980180	KX121070
Graciliella kosovaci	IE63	Croatia, Tunel Konavle, Kaverna 781 (Njunjić 2016)		KX121124	KX719916	KX719862	KU980181	KX121071
Graciliella metohijensis	IB15	Bosnia-Herzegovina, Nevesinje, Balabani, Drvendzina pecina (Njunjić 2016)	KX015829	KX011080	KX719917	KX719863	KU980182	KX121058
Graciliella ozimeci	VA44	Croatia, Dubrovnic, Tocionik, Vranja, pecina (Njunjić 2016)	KX015841	KX011092		KX719864	KU980183	KX121072
Gueorguievella petrovi	AN141	Bulgaria, Smilyan, Kraypatnata caves, 41°30'44.5"N 24°45'36.4"E, 800 m, 26.5.2015, A. Faille, J. Fresneda & I. Ribera	x	x	x		x	x
Hadesia asamo	MP01	Bosnia-Herzegovina, Trebinje, Zupci, Bravenik (Njunjić 2016)		KX121125	KX719918	KX719865	KU980174	KX121073
Hadesia lakotai	MP03	Bosnia-Herzegovina, Korita, Kobilja glava, Datlo (Njunjić 2016)	KX121102	KX121126	KX719919	KX719866	KU980175	KX121074
Hadesia vasiceki	IH1	Bosnia-Herzegovina, Popovo polje, Vjeternica (Njunjić 2016)	KX121103	KX121127	KX719920	KX719867	KU980176	KX121075
Hadesia weiratheri	IH2	Montenegro, Orjen, Kameno more, PT4 (Njunjić 2016)	KX121104	KX121128	KX719921	KX719868	KU980177	KX121076
Hadesia zetae	C4263	Montenegro, Lipska pećina, Lipa, Cetinje (Polak *et al.* 2016)	KX223668	KX223656	KX223621			KX223643
Halbherria zorzii	RA25	Italy, Veneto, Verona , Bosco Chiesanuova, Grotta dell'Arena, 23.7.2009, J. Fresneda	x	x	x	x	x	x
Hartigiella baldensis	AN1145	Italy, Trentino-Trento, Brentonico - M. Altissimo di Nago cavernetta militare c/o Rif. D. Chiesa, 1860 m, 5.5.2017, A. Carlin		x		x		
Hittitia schuelkei **comb. nov.**	RA499	Turkey, Ordu, Yenikent-Kendirlik, 40°56'03.3"N 37°06'47.5"E, 925 m, 18.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x		x	x
Hypogesia minos **gen. nov. comb. nov.**	AF14	Spain, Cantabria, Rasines, Cueva del Valle, 5.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x
Isereus colasi	AC3	France-06, Parc de la Moulière, Gouffre de La Glacière, 43°45'21.0"N 6°45'43.9"E, 1347 m, 4.7.2007, A. Cieslak & J. Fresneda	x	HG915368	HG915671	HG915594	HG915442	HG915515
Isereus giordani	AN748	France-06, Caussols, Aven de la Charogne, 5.3.2017, P. Balart	x	x	x		x	x
Josettekia mendizabali	IRC19	Spain, Gipuzkoa, Aia, Cueva de Pagoeta, 18.7.2000, J. Fresneda		GU356868	GU356764	GU356818	GU356917	GU356960
Karadeniziella omodeoi	RA498	Turkey, Ordu, Çarkili, 40°39'26.3"N 37°20'49.8"E, 1300 m, 17.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x	x	x	x
Kircheria dritae	AN1280	Albania, Vrana e Madhe, Shpella Shtares cave, 1427 m, 42.31766°N 19.85403°E, 23.8.2019, A. Lacirignola, M. G. Mastronardi, M. Pastore		x	x			

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Lagariella colominasi	IRC30	Spain, Lleida,Os de Balaguer, Cova Joan d'Os, 1.8.2001, J. Fresneda		GU356869	GU356765	GU356819	GU356918	GU356961
Lakedemoniana mizerakisi **gen. nov. sp. nov.**	M475	Greece, Peloponnisos, Lakonia, Trypi, 37.09552 22.34055 "VLOC.24", Caladas cave, VM125 , 28.8.2021 , V. Mizerakis					x	
Latellana benellii **gen. nov. sp. nov.**	AN785	Italy, Maranola, Mt. St. Angelo, sifting in beech forest, 41°19'0.8"N 13°38'54.2"E, 1227 m, 11.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x		x	x
Latellana degiovannii **gen. nov. sp. nov.**	AN786	Italy, Maranola, Mt. St. Angelo, sifting in beech forest, 41°19'0.8"N 13°38'54.2"E, 1227 m, 11.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x			x	x
Latellana delayi **comb. nov.**	ARN	Italy, Cave on the Carrozzabile per il Monte Semprevisa (Carpineto Romano, Roma, Latium, Central Italy) (Latella *et al.* 2017)		KY934141	KY934117			
Latellana fabiolae **comb. nov.**	GDS	Italy, Grava dei Serini Cave (Esperia, Frosinone, Latium, Central Italy) (Latella *et al.* 2017)		KY934150	KY934126			
Latellana fortesculpta **comb. nov.**	RA783	Sardinia (Isl.), Lula, Nuoro, Grotta "Sos Omines Agrestes" 68 Sa/UN, 800 m, 26.9.2011, A. Pastorelli & E. Lana	HG915313	HG915347	HG915648	HG915572	HG915420	x
Latellana partenii **gen. nov. comb. nov.**	AN1257	Italy, Campania, Avella, Grotta degli Sportiglioni, 450 m, 8.8.2019, L. Petruzziello	x	x	x		x	x
Latellana rampinii **gen. nov. comb. nov.**	GAR	Italy, Arnale Cave (Coreno Ausonio, Frosinone, Latium, Central Italy) (Latella *et al.* 2017)		KY934136	KY934112			
Latellana sbordonii **gen. nov. comb. nov.**	ARE	Italy, Aretino Cave (Pisterzo, Frosinone, Latium, Central Italy) (Latella *et al.* 2017)		KY934137	KY934113			
Latellana sisernica **gen. nov. comb. nov.**	GPAs1	Italy, Pozzo l'Arcaro Cave (Amaseno, Frosinone, Latium, Central Italy) (Latella *et al.* 2017)		KY934143	KY934119			
Latellana valeriae **gen. nov. comb. nov.**	GSG	Italy, Cave on the Carrozzabile per il Santuario della Madonna della Guardia (S. Giovanni in Carico, Frosinone, Latium, Central Italy) (Latella *et al.* 2017)		KY934135	KY934111			
Leiodes dilutipes	AN556	Kazakhstan, Kuluktau, Mts., Kegen, 43.1159ºN 79.1009ºE, 2029 m, KZ87, sweeping, 26.6.2016, S. Kolov	x	x	x	x	x	x
Leiodes sp.	AN299	Bulgaria, Smilyan, Kraypatnata caves, 41°30'44.5"N 24°45'36.4"E, 800 m, 26.5.2015, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Leiodinae	AN856	Cameroon, Mt. Cameroon, 4.0935N, 9.0573E, 524 m, 28.12.2015, V.V. Grebennikov		x				
Leonesiella bergidi	AC59	Spain, León, Sanvitul, Cueva Moroucedi, 22.9.2007, J.M. Salgado	x	HG915369	HG915672	HG915595	HG915443	HG915516
Leonhardella antennaria	IO37	Montenegro, Durmitor, Savin kuk, Vodena pecina (Njunjić 2016)	KX671648	KX671678	KX719922	KX719869		

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Leptinillus validus	AN925	Canada, Ontario, Westport, Peck's Beetle Acres, 44°37'34.9"N, 76°21'38.9"W, 28.10.2017, S. Peck & V.V.Grebennikov	x	x	x	x	x	x
Leptinus orientoamericanus	AN926	USA, Florida, Leon Co., Tall Timbers Res. Sta., 1-27.4.2010, S. Peck	x	x	x	x	x	x
Leptinus testaceus	AF82	Spain, Cantabria, El Bosque, Entrambasaguas, Cueva de las Enjanas, 1.9.2007, C.G. Luque	x	HE572792	HE576695	HE572877	HE572827	HE572849
Leptinus vaulogeri	AN497	Spain, Jaén, Siles, sima GEV-2000, 11.4.2015, GEV	x	x	x	x	x	x
Leptodirini Euboea gen. sp. 1	AN535	Greece, Euboea island, Pit in Dirfis mountain, 25.5.2011, P.M. Giachino	x	x	x	x	x	x
Leptodirini Euboea gen. sp. 2	RA512	Greece, Euboea island, Pit in Dirfis mountain, 25.5.2011, P.M. Giachino	x	x		x	x	x
Leptodirus hochenwartii hochenwartii	RA504	Slovenia, Mt. Nanos, Volcja Jama nº 743, 28.7.2010, P.M. Giachino, A. Casale, E. Lana, P. Marcia, F. Gasparo		HG915370	x	HG915596	HG915444	HG915517
Leptodirus hochenwartii reticulatus	AC51	Slovenia, Kozina (Southern Slovenia), Cikova jama, Kat no. 971, 22.3.2007, S. Polak		x	x		x	x
Leptomeson bujasi	IL4	Croatia, Brac, Jama kot, Matesica stana (Njunjić 2016)	KX121105	KX121129		MH368218	KU980200	KX121080
Leptomeson dombrowskii dombrowskii	IL2	Croatia, Dalmacija, Mosor, Vranjaca spilja kod Dugopolja (Njunjić 2016)	KX121106	KX121130		KX719871	KU980198	KX121078
Leptomeson radjai	IL1	Croatia, Sibenik, Perkovic, Zvekaca (Njunjić 2016)	KX121107	KX121131		KX719872	KU980197	KX121081
Leptomeson raguzi	IL3	Bosnia-Herzegovina, zapadna Herzegovina, Grude, Drinovci, Majica Ponor (Njunjić 2016)		KX121132		KX719873	KU980199	KX121079
Lotharia angulicollis	AFM-ZSM-Lot	Austria, Kärnten, Gitter Stollen - Schaidassattel, trap propylen (Faille *et al*. 2016), 4.11.2011, A. Faille			LT602711		LT602667	LT602674
Luquesia pasensis **gen. nov. comb. nov.**	AC97	Spain, Cantabria, Ocejo-Luena, Cueva del Rellano, 23.8.2008, C.G. Luque	x	HE663503	HE663533	x	x	HE663527
Machaeroscelis infernus arbasanus	AI533	France-09, Galey, Grotte d'Escarchein, 3.6.2004, Ph. Déliot & A. Faille		GU356893	GU356791	x	GU356936	GU356984
Machaeroscelis infernus cagiranus	AF196	France-31, Juzet d'Izaut, Gouffre du Béguet, UTM, WGS84 31T 0316608 4761810, 16.5.2009, C. Bourdeau & J. Fresneda		x	x			
Machaeroscelis infernus infernus	RB11	France-09, Liqué, Grotte de Liqué, no data, Ph. Déliot & A. Faille		x				
Mesocolon crenatellum	RA552	New Zealand (Isl.), South Island Buller (BR) St Arnaud, Rotoiti lake, Brunner peninsula sifter+berlese Leaf litter+moss, NZ140 41°48'28.9"S 172°50'09.8"E, 629 m, 30.1.2003, C. D'Haese	x	x	x	x	x	x
Micropeplinae Micropeplus sp.	AI521	Bhutan, Mo Chhu [river], ca. 30 m wide, large gravel banks, springfed and residual pools; JDNP, at suspension bridge to Chhephu, ca. 16 km NW of Punakha; Punakha Prov., Timphu Prov.; ca. 1450, 27°41'54"N 89°46'01"E, 28.11.2005, M.A. Jäch		HE572804	HE576707		HE572837	HE572859
Nafarroa sorogainensis	AF26	Spain, Navarra, Sorogain, Cueva del Carlista, 26.5.2008, E. Dupré	x	HG915371	HG915673	HG915597	HG915445	HG915518

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Nanobathysciola catalana **gen. nov. comb. nov.**	AI663	France-31, Ganties, La Spugus de Ganties, 29.9.2004, A. Faille	x	x	x	x	x	x
Nanobathysciola ovata **gen. nov. comb. nov.**	AI598	Spain, Huesca, Bonansa, Cova de Sant Salvador, 14.11.2004, J. Fresneda	x	HG915354	HG915656	HG915579	GU356908	HG915500
Nanobathysciola simonis **gen. nov. comb. nov.**	AN136	France-81 Grésigne Montoulieu, Fagus, tamisage, 17.12.2014, E. Cateau	x	x				
Nanobathysciola talpa **gen. nov. comb. nov.**	AN229	France-09, Bedeillhac, MSS, 28.1.2013, C. Bourdeau	x	x	x	x	x	x
Nargus algiricus	AN672	Algeria, Djurjura, small cave in road RN30, ex. loc 212, 25.5.2012, Aït Moulout & A. Faille		x			x	x
Nargus algiricus cf	AI574	Spain, Málaga, Antequera, Sierra de las Cabras, N331 Km 133, 14.2.2004, M. Baena	x	GU356871	GU356767	GU356820	GU356919	GU356962
Nargus armeniacus	AN530	Azerbaijan, Ax Ox Ay (Az) Sift. 40º52'07.5"N 48º09'05"E, 4.5.2014, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Nargus badius	RA807	Italy, Serle, Altipiano di Cariadeghe, Buco del Budrio, 14.7.2010, A. Casale, E. Lana, D. Vailati & A. Faille	x	x	x	x	x	x
Nargus brunneus	GBK-RMNH.INS.550290	no data (Genbank: Schilthuizen, M.)		KF492873				
Nargus cavazzutii cf	AN286	Azerbaijan, muddy pond, btw Budzhakah & Bash-Dashagyi, 41°8'50.6"N 47°24'53.6"E, 1020 m, 5.5.2014, A. Faille, J. Fresneda, I. Ribera & A. Rudoy	x	x	x	x	x	x
Nargus transcaucasicus	RA468	Turkey, Erzurum, Yesildere, little cave 1, 40º 06' 42.4"N 41º 24' 22.2"E, 1863 m, 12.6.2011, J. Fresneda, A. Faille & I. Ribera	x	x	x			x
Nargus velox	AI927	Spain, Albacete, E-No. 10, N Sierra de Segura, 10 km N Yeste, Rio Tús, 38º25'N 02º19W, 10.4.2003, V. Assing & P. Wunderle	x	GU356870	GU356766	x	x	x
Nargus wilkinii	RA532	France-27, La Saussaye, Forêt d'Elbeuf, piège terrier de Renard, 2,80 m, 4/30.4.2010, A. Faille	x	x	x	x	x	x
Naspunius eseranus	IRC29	Spain, Huesca, Foradada del Toscar, Inflas de Naspún, 11.9.2001, J. Fresneda		GU356872	GU356768	GU356821	GU356920	GU356963
Nemadiopsis sp.	AN285	Chile, Huinay biol. st., pitfall in meadow, 42°22'46.6"S 72°24'50.0"W, 13.12.2014, I. Ribera	x	x	x	x	x	x
Nemadus horni	AN939	USA, Florida, Alachua Co., NW Gainesville, 22.2.2020, S. Peck	x	x	x	x	x	x
Neobathyscia mancinii	RA770	Italy, Roverè Veronese (VR), Contrada Capraia, Grotta di Monte Capraiolo, 11.11.2011, E. Lana & A. Faille	x		x	x	x	x
Neobathyscia pasai	RA202	Italy, Veneto, Verona, Velo Veronese, Tana delle Sponde, ED50 5053105N 665380E, 19.7.2010, J. Fresneda & A. Cieslak	x	x	x		x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Notidocharis calabrezi	AC79	Spain, Asturias, Caravia Alta, Cueva de Entrecuevas, 5.10.2008, J.M. Salgado	x	x			x	x
Notidocharis uhagoni	AC80	Spain, Cantabria, Suano, hayedo proximo a la cueva de Hornucos, 11.10.2008, J.M. Salgado	x	HG915373		HG915598	HG915447	HG915520
Ochsiella bucheti **comb. nov. (genus stat. nov.)**	RA634	France-06, Saint Jean de la Riviere Vésubie, Grotte 151-J, 12.07.2011, A. Faille	HG915327	x	HG915694	HG915614	HG915466	HG915542
Omalinae Lesteva sp.	AI450	Spain, Ávila, Puerto Pico de Gredos, N. side, rd. N502 pk 53, stream on left, 1280 m, 40º20'14"N 5º00'48"W, 15.5.2005, I. Ribera		HE572803	HE576706		HE572836	HE572858
Oritocatops sp.	AN893	Tanzania, W. Usambara Mts., Shume For., 4.73129ºS 38.25688ºE, 1863 m, 16.1.2013, V.V. Grebennikov		x				
Orostygia doderoi bucciarellii	RA960	Italy, Lombardia, Montello, Bus delle Fade sup., E. Lana, G. Colombetta & A. Faille	x	LT602654	LT602708	LT602696	x	LT602681
Orostygia rossii	RA784	Italy, Friuli-Venezia Giulia, Pordenone, Valcellina, Grotta della Vecchia, Diga 786/327 fr/PN, 500 m, 2.10.2011, E. Minuzzco & E. Lana	LT602652			LT602688	LT602663	LT602680
Orostygia tibialis	RA959	Italy, Friuli-Venezia Giulia, Pordenone, Montereale Valcellina, Inghio Ititoio del Val di Pai, 30.6.2012, Fornasier & A. Faille	x	LT602641	LT602716	x		
Oryotus dreoni cf	AN182	Italy, Friuli-Venezia Giulia, Pordenone, Tramonti di Sopra, Grotta close to Foos di Campone (507/229 FR) , no data, E. Ruzzier	x	LT602640	LT602709	LT602693	LT602666	LT602684
Oryotus ravasinii	RA803	Italy, Veneto, Treviso, Fregona, Pinn Consiglio, Bus da la Genciana, 12.11.2011, E. Lana, A. Faille & Fornasier	LT602655	LT602639		LT602689	LT602664	LT602682
Oryotus schmidti ssp.	RA503	Slovenia, Mt. Nanos, Volcja Jama nº 743, 28.7.2010, P.M. Giachino, A. Casale, E. Lana, P. Marcia, F. Gasparo		x	LT602715	LT602690	LT602665	LT602683
Ovobathysciola castrimedusae	AN348	Sardinia (Isl.), Cagliari, Villaputzu, Monte del Castello di Quirra, Grutta de Giuanniccu Mene (735 Sa/CA), 7 m, 20.4.2014, P. Marcia & C. Onnis	x	x			x	x
Ovobathysciola cogonii **comb. nov.**	AN1140	Sardinia (Isl.), 2944 Sa/OR - Cuglieri (Cavaleddu) Grotta di Turaghile, 30.9.2017, R. Cogoni	x	x	x	x	x	x
Ovobathysciola deleddae	AN236	Sardinia (Isl.), NV, Galtelli, M. Tuttavista, pozzo C, 16.3.2008, P. Marcia	x	x	x	x	x	x
Ovobathysciola gestroi	AF229	Sardinia (Isl.), Grotta Ulassai 2, "SA FOXI 'E S'ABBA", Catasto Speleologico 728 SA/NU, Tacco di Ulassai, 39º49'02.2"N 9º29'26"E, 22.8.2009, A. López-Pancorbo & E. Planas	x	HG915375	HG915676		HG915449	HG915522
Ovobathysciola gestroi cplx	AN349	Sardinia (Isl.), Cagliari, Monte Taccu, Grotta Risorgente di Sa Turru (2521 Sa/ CA), 21.4.2014, P. Marcia & C. Onnis		x	x	x	x	x
Ovobathysciola grafittii	GBK-AY012690	Sardinia (Isl.), Sassari, Pozzomaggiore, Badde cave (Caccone & Sbordoni 2001)		AY012690				

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Ovobathysciola majori	AF79	Sardinia (Isl.), Dorgali, Grotta del Bue Marino, 24.5.2008, A. Casale & P. Marcia	x	HG915376	HG915677	x	HG915450	HG915523
Ovobathysciola sardoa cf **comb. nov.**	RA631	Sardinia (Isl.), Oliena, Grotta Nurra é Pradu, 8.3.2009, P. Marcia			x			x
Ovobathysciola supramontana	AN347	Sardinia (Isl.), Nuoro, Urzulei, Grotta su Cardu, 26.6.2005, A. Casale	x	x	x		x	x
Oxytelinae Thinodromus sp.	AI554	Switzerland, Pfyn, stream in village, 408 m, 47º35'43.8"N 8º57'17.4"E, 2.8.2005, I.Ribera & A.Cieslak		HE572807	HE576709		HE572839	HE572861
Paederinae Domene pastori	RA919	Spain, GenBank: LN624390; LN624388; LN624389		LN624390			LN624388	LN624389
Paederinae Paederus sp.	AI552	Italy, Liguria, lat. rd SS28, 2Km E Cosio di Arriscia, stream, 819 m, 44º04'41.6"N 7º50'41.5"E, 31.7.2005, I.Ribera & A.Cieslak		HE572806	HE576708		HE572838	HE572860
Parabathyscia dematteisi dematteisi	RA192	Italy, Piemonte, Cuneo, Rossana (EW), Grotta dei Partigiani, 21.8.2010, E. Lana	HG915325	HG915377	HG915678	x	HG915451	HG915524
Parabathyscia gracilicornis	AH187	France-2B, Corsica (Isl.), Venaco, Aven de Venaco, 5.4.2008, J.M. Lemaire	x	x	x	x	x	x
Parabathyscia grouvellei	RA524	France-06, Contes, Vallon du Destey, 22.11.2009, J.M. Lemaire	x	x	x	x	x	x
Parabathyscia oodes	AN908	Italy, Piemonte (CN), Crissolo, Cumbal Brusà, Buco di Valenza, 19.7.2016, A. Faille & E. Lana	x	x	x	x	x	x
Parabathyscia remyi	AH188	France-2B, Corsica (Isl.), Sisco, Grotte de Buttone, 7.4.2008, J.M. Lemaire	x	x	x	x	x	x
Parabathyscia spagnoloi devillei	AF1	France-06, Sospel, Grotte de l'Albarea, 7.5.2008, J.M. Lemaire	x	HG915378	HG915679	HG915600	HG915452	HG915525
Parabathyscia spagnoloi spagnoloi	RA508	Italy, Liguria Pigna (IM), loc. Marellae n. 3 Li/IM, Tana della Giacheira, 5.2.2011, A. Pastorelli	x	x	x		x	x
Parabathyscia wollastoni	RA751	France-50, La Manche, Les Roquettes (lavage), 20.10.2011, R. Ancellin	x	HG915379	HG915680	HG915601	HG915453	HG915526
Paranillochlamys catalonica	RA30	Spain, Tarragona, Torre del Espanyol, Mina del Horts Nº 2, 13.7.2009, F. Fadrique	x	HG915380	HG915681	HG915602	HG915454	HG915527
Paranillochlamys urgellesi	AF69	Spain, Tarragona, Sant Carles de la Ràpita, Cova del Tendo, 14.12.2008, C. Andujar, J. Comas, A. Faille & F. Fadrique	x	x	x	x	x	x
Paranillochlamys velox	IRC37	Spain, Tarragona, Hospitalet de l'Infant, Avenc de la Júlia, 16.12.2001, F. Fadrique		GU356874	GU356770	GU356823	GU356922	GU356965
Parapropus pfeiferi	IE34	Bosnia-Herzegovina, GBK-KX719874 (Njunjić *et al*. 2016)	KX671647	KX671679		KX719874	KY397774	KY397810
Parapropus sericeus muelleri	IO26	Bosnia-Herzegovina, Sanski most, Hrustovacka pecina (Njunjić 2016)	KX121087	KX121133		KX719875	KU980173	KX121084
Parapropus sericeus sinuaticollis	AC52	Bosnia-Herzegovina, Kljuc, Sitnica, Mackica pecina, (north central Bosnia), 20.7.2004, S. Polak & P. Trontelj	x	HG915381	HG915682	HG915603	HG915455	HG915528
Paraspeonomus vandeli	AI539	France-09, Seix, Grotte Les Souleillos, 17.10.2004, C. Bourdeau & A. Faille	MT521344	GU356875	GU356771	HE572881		HE572867

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Paratroglophyes aubryi comb. nov.	AC72	France-09, Seix, Grotte d'Esbints, 22.7.2007, A. Faille	x	x	x	x	x	x
Paratroglophyes carrerei	AF184	France-09, Bordes-sur-Lez, Aven du Trapech d'en Haut, 2.10.2003, J. Fresneda	MT521294	HF912460	MT571466	HF912507	HF912580	HF912592
Parvospeonomus canyellesi	AI1066	Spain, Barcelona, Gualba de Dalt, Avenc de les Pedreres, 8.9.2006, J. Fresneda	x	HG915382	HG915683	HG915604	HG915456	HG915529
Parvospeonomus delarouzeei catalonicus	IRC10	Spain, Girona, Queralbs, Coves de Rialb, 22.4.2000, J. Fresneda		GU356876	GU356772	GU356824	GU356923	GU356966
Parvospeonomus delarouzeei delarouzeei	AN271	Spain, Girona, Susqueda, cova del Far, 30.4.2014, J. Comas	x	x	x		x	x
Parvospeonomus delarouzeei guimjuani	IRC32	Spain, Girona, Terrades, Cova Bora Major, 2002, F. Fadrique	x	HG915383	HG915684	HG915605	x	HG915530
Parvospeonomus urgellesi	AF110	Spain, Barcelona, Caldes de Montbui, Cova de Solanes, 20.12.2008, L. Auroux	x	x	x	x	x	x
Parvospeonomus vilarrubiasi	AN15	Spain, Girona, Susqueda, cova del Far, 30.4.2014, J. Comas	x	x	x		x	x
Perriniella bofilli	IRC40	Spain, Girona, Queralbs, Coves Encantades, 8.12.2001, F. Fadrique		GU356877	GU356773	GU356825	GU356924	GU356967
Perriniella bonvouloiri **comb. nov.**	AC111	France-66, Villeneuve de Conflent, Grotte de Fuilla 2.8.2009, C. Vanderbergh	x	LN849259	x	LN849301	LN849333	LN849343
Perriniella faurai	AC101	Spain, Girona, Queralps, Coves de Rialb, 6.7.2009, J. Comas		LN849257	MT571482	LN849299		
Phaneropella lesinae	M469	Croatia, Markova Spilja, N43°11'27.0" E016°24'10.1", 57m , 5.4.2022 , I. Čupić, A. Faille, B. Jalžić, V. Mizerakis, N. Sudar		x	x		x	
Phloeocarinae Phloeocharis diecki	AI880	Spain, Gipuzkoa, Aia, Pagoeta, pista a Legarrola,10.5.2006		HE572813	HE576714		HE572842	HE572864
Pholeuon gracile	RB14	Romania, Apuseni Mountains, Padurea Craiului Mountains, Stanu Ciutii cave, R. Bucur			GU356776			GU356970
Pholeuon knirschi proserpinae	RB15	Romania, Apuseni Mountains, Bihorului Mountains, Aven Sesuri cave, R. Bucur			GU356777			GU356971
Pholeuon leptodirum leptodirum	RA560	Romania, Bihor, Sighistel, Pestera de la Fanate, 17.7.2011, J. Fresneda	x	x	x	x	x	x
Pholeuonella erberi erberi	AN784	Bosnia-Herzegovina, Trebinje, Matulica pecina, sifting outside, 42°41'31.4"N 18°21'41.4"E, 586 m, 10.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Pholeuonidius halbherri	RA604	Italy, Venezia Tridentina, Gruppo del Carega-Piccole Dolomiti -Pasubio, Vallarsa (TN), loc. Pian delle Fugazzetestata, Val della Busa, 1150 m, 26.7.2011, E. Diva	x	x	LT602702	LT602691	LT602668	LT602678
Pholeuonopsis grabowskii	AN772	Bosnia-Herzegovina, Nevesinje, Novakusa pecina, 43°14'58.0"N 18°4'34.8"E, 1030 m, 5.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Platycholeus opacellus	AF217	USA, California, Calaveras Co., Stanislaus, N.F., For. Rd. 7N09 to Pumpkin Hollow, Abies concolor forest, under bark conifer logs, 38º25.301'N 120º09.303'W, 2103 m, FIELD MUSEUM NAT.HIST., 11.6.2006, A. Newton & M. Thayer	x	HE572798	HE576701			HE572866
Platycholeus **sp. nov.**	AF218	USA, Oregon, Hood River Co., Mt. Hood, N.F., Pacific Crest Tr. N of Barlow Pass, old-growth Pseudotsuga, Tsuga-Abies procera forest, under bark conifer logs, site ANMT 1209, 45º17.23'N 121º41.06'W, 1336 m, FIELD MUSEUM NAT. HIST., 26.6.2006, A. Newton & M. Thayer	x	HE572799	HE576702		HE572832	HE572854
Platypsyllus castoris	RA660	Russia, Voroneath Distr., vil. Troitskoye, Lake 1.5 km from river Don, 9.6 m, V. Budaev	x	x	x	x	x	x
Platypsyllus castoris	AN928	USA, Maryland, Carroll Co, 5 km N Finksburg, 13.12.2008, W. Steiner, J. Swearingen, J. Worthley et al. [via S. Peck]	x	x	x	x	x	x
Prionochaeta harmandi	GBK-RMNH.INS.549245	no data (Genbank: Schilthuizen, M.)	KF492859					
Prionochaeta opaca	AN937	Canada, Ontario, Leeds-Grenville Co., Peck's Beetle Acres, 22.5.2010, S. Peck	x	x	x	x	x	x
Proleonhardella remyi	I7	Serbia, Kamena gora, Guvniste, Mujova jama (Njunjić 2016)		KX671680	KX719924	KX719876		
Protopholeuon hungaricum	RB20	Romania, Apuseni Mountains, R. Bucur						x
Pseudoboldoria bergamasca bergamasca	RA200	Italy, Bérgamo, Rota Imagna, Tomba dei Polacchi, 13.7.2010, A. Faille	x	x	x	x	x	x
Pseudospeonomus raholai	IRC41	Spain, Girona, Roses, Cau del Lliri, 21.12.2001, F. Fadrique		GU356880	GU356778	GU356828	GU356926	GU356972
Ptomaphagus consobrinus	AN929	USA, Florida, Levy Co., Rosewood, 16 km NE Cedar Key, 1-14.3.2011, S. Peck	x	x	x	x	x	x
Ptomaphagus pyrenaeus	RA261	France-64, Iriberri, MSS, E. Dupré		HE572820	x	x	x	HE572872
Ptomaphagus schwarzi	AN931	USA, Florida, Leon Co., Tall Timbers Res. Stn., 27.4.2010, S. Peck		x	x	x	x	x
Ptomaphagus tenuicornis tenuicornis	AI760	Spain, Lleida, El Pont de Suert, Llesp, 5.4.2006, J. Fresneda	x	GU356881	GU356779	GU356829	GU356927	GU356973
Ptomaphagus texanus	AN930	USA, Florida, Leon Co., Tall Timbers Res. Stn., 27.4.2010, S. Peck	x	x	x	x	x	x
Ptomaphagus troglodytes	IRC33	Spain, Granada, Gualchos, Cueva de las Campanas, 27.3.2002, J. Fresneda	x	GU356882	GU356780	GU356830	x	GU356974
Pyrenaeola (Garunnia) convena **subgen. nov. comb. nov.**	AF185	France-65, Tibiran, Grotte de Tignahuste, 19.5.2009, C. Bourdeau & J. Fresneda		HG915345	HG915646	HG915570	HG915418	HG915490
Pyrenaeola (Garunnia) larcennei **subgen. nov. comb. nov.**	RA755	France-65, Nistos, Arize, Tute du Chef, 17.11.2011, C. Bourdeau	HG915314	x	HG915651	HG915574	HG915423	HG915494
Pyrenaeola (Pyrenaeola) rectipes **gen. nov. stat. nov. comb. nov.**	AF198	France-31, Juzet d'Izaut, Gouffre du Béguet, UTM: WGS84 31T 0316608 4761810, 16.5.2009, C. Bourdeau & J. Fresneda		HG915349	HG915650	HG915573	HG915422	HG915493

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Pyrenaeola (Pyrenaeola) simplex **gen. nov. stat. nov. comb. nov.**	RA666	France-31, Coulédoux, MSS Grotte de la Bouhadère, traps: 14.5/30.10.2009, C. Bourdeau & J. Fresneda	x			x		
Quaesticulus adnexus	AF11	Spain, Cantabria, Llanos-Penagos, Cueva del Encinar, 3.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	HE663502	HE663532		HE663519	HE663526
Quaesticulus autumnalis autumnalis **comb. nov.**	RA243	Spain, Cantabria, Rioseco-Santiurde de Torazo, Cueva de las Arrigueras, 14.11.2007, C.G. Luque		HG915387	HG915687	HG915608	HG915460	HG915534
Quaesticulus autumnalis brevicornis **comb. nov.**	RA661	Spain, Cantabria, San Felices de Buelna, Cueva de Hornos de la Peña «B» (small cave that is above the typical locality), 6.2.2010, J.M. Salgado & C.G. Luque		x	x	x	x	x
Quaesticulus canis **comb. nov.**	AC93	Spain, Cantabria, Viaña, Cueva del Perro o del Coviezo, 11.10.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus acuminatus	AF76	Spain, Asturias, Tospe, Cueva la Xiana, 12.5.2007, J.M. Salgado	ON109507	ON421530	ON386256	ON420827	ON117156	ON146576
Quaestus amicalis	AI1078	Spain, León, Oseja de Sajambre, Cueva de Buseco, 24.6.2006, J.M. Salgado	x	x	x	x	x	x
Quaestus arcanus	PB32	Spain, Cantabria, Alfoz de Lloredo, Cueva de la Rogeria de Oreña, C.G. Luque & L. Labrada	ON109509		ON386257	ON420828	ON117157	ON146577
Quaestus asturicus	RA35	Spain, Asturias, Riensena-Nueva, Cueva de Cuetu Lluengu, 3.10.2009, J.M. Salgado	x	x	x	x	x	x
Quaestus avicularis	RA33	Spain, Asturias, Soto de Agues, Cueva del Troncu, 1.10.2009, J.M. Salgado		x	x	x	x	x
Quaestus breuili	AC61	Spain, Asturias, Pimiango, Cueva Tina I, 21.7.2007, J.M. Salgado	x	x	x	x	x	x
Quaestus diegoi	AC69	Spain, Asturias, Peón, Cueva del Lloviu, 17.7.2007, J.M. Salgado	x	x	x		x	x
Quaestus dilatatus **stat. nov.**	AF22	Spain, Asturias, Las Cuevas, Cueva del Agua, 28.6.2008, J.M. Salgado	x	HG915391	HG915685	HG915612	HG915464	HG915539
Quaestus espanoli	AC62	Spain, Asturias, Pando-Ribadesella, Cueva del Foyu, 2.6.2007, J.M. Salgado	x	x	x	x		x
Quaestus incognitus	AF10	Spain, Asturias, Puente de Piedra-Buspria, Cueva del Prau, 21.6.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus jaspei	AF7	Spain, Asturias, Covadonga, Cueva del Reguerín, 24.4.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus jeannei	AC99	Spain, Asturias, Covadonga, Cueva de la Vega de Teón, 7.11.2008, J.M. Salgado	ON109510	ON421532	ON386258	ON420829	ON117158	ON146578
Quaestus jubilationis	AF225	Spain, Asturias, Pando-Villaviciosa, Cueva de Covallos, 17.10.09, J.M. Salgado	ON109512	ON421533	ON386259	ON420826	ON117159	ON146579
Quaestus littoralis	AC70	Spain, Asturias, Torre, Cueva de Barredo, 24.7.2007, J.M. Salgado	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Quaestus longicornis	AF17	Spain, Asturias, Puente de Piedra-Buspriz, Cueva del Prau, 21.6.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus luctuosus	AF18	Spain, Asturias, Las Cuevas, Cueva del Agua, 28.6.2008, J.M. Salgado	x	x	x	x		x
Quaestus mermejaensis	AF23	Spain, Asturias, Puente de Piedra-Buspriz, Cueva del Prau, 21.6.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus nietoi	RA32	Spain, Asturias, San Pedro de Tolivia, Cueva del Sierru, 19.9.2009, J.M. Salgado		x	x	x	x	AC
Quaestus nuptialis	AI1079	Spain, León, Oseja de Sajambre, Cueva de Buseco, 24.6.2006, J.M. Salgado	ON109513	ON421534	ON386260	ON420830	ON117160	ON146580
Quaestus occidentalis	AF19	Spain, Asturias, Porrúa, Cueva Verde, 6.7.2008, J.M. Salgado, A. Faille, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x
Quaestus olajensis	AC63	Spain, León, Santa Olaja de la Varga, Cueva del Carrascal, 15.5.2007, J.M. Salgado	ON109514	ON421535	ON386262		ON117161	ON146582
Quaestus perezi	AC96	Spain, Cantabria, Riclones, Cueva de la Cuevona, 6.9.2008, J.M. Salgado	x	x	x	x	x	x
Quaestus pongai **stat. nov.**	AI1075	Spain, Asturias, Viboli, Cueva de los Moros, 24.6.2006, J.M. Salgado	ON109511	GU356884	GU356782	HE663511	GU356929	GU356976
Quaestus pseudoccidentalis	AC64	Spain, Asturias, Villobal-Borines, Cueva del Sidrón, 23.6.2007, J.M. Salgado	ON109515	ON421536	ON386263	ON420831	ON117162	ON146583
Quaestus recordationis	AF20	Spain, Asturias, Las Cuevas, Cueva del Agua, 28.6.2008, J.M. Salgado	ON109516	ON421537	ON386264	ON420832	ON117167	ON146585
Quaestus riberai	AF77	Spain, Asturias, Tospe, Cueva la Xiana, 12.5.2007, J. M. Salgado	ON109517	ON421538	ON386265	ON420833		ON146575
Quaestus sajaensis	RA663	Spain, Cantabria, Saja-Los Tozos, Cueva del Poyo, 16.12.2008, J.M. Salgado	x	x	x		x	x
Quaestus sellai	AC65	Spain, Asturias, Nueva, Cueva del Penicial, 21.7.2007, J.M. Salgado	ON109518	ON421539	ON386266	ON420825	ON117164	ON146586
Quaestus spinulosus	AC66	Spain, Asturias, Piñera-Sevares, Cueva les Xianes, 23.6.2007, J.M. Salgado	ON109519	ON421540	ON386267	ON420834	ON117163	ON146584
Quaestus suevensis	AC67	Spain, Asturias, Bodes, Cueva de la Carretera o de Pitufos, 12.5.2007, J.M. Salgado	ON109520	ON421541	ON386268	ON420824	ON117165	ON146587
Quaestus valenzuelai	AC71	Spain, Asturias, Piñera-Sevares, Cueva les Xianes, 23.6.2007, J.M. Salgado	ON109521	ON421542	ON386261		ON117166	ON146581
Quaestus variabilis	AC68	Spain, Asturias, Bodes, Cueva del Queso, 12.5.2007, J.M. Salgado	x	x	x	x	x	x
Reitteriola pumilio	RA510	Italy, Piemonte (CN), Val Varaita Brossasco, Gr. Pertus d'la Tunda, 19.9.2010, E. Lana	x	x	x	x	x	x
Remyella javorensis	IR14	Serbia, Donje Lopize, Usacka pecina (Njunjić 2016)	KX671642	KX671685			KY397788	KY397824

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Remyella scaphoides hussoni	IR20	Serbia, Pester Derekare, Sjera jama (Njunjić 2016)	KX671644	KX671683			KX755498	
Remyella scaphoides propiformis	IE8	Serbia, Pester, Lopuzina jama (Njunjić 2016)	KX671640	KX671686			KY397785	KY397821
Remyella sp.	IR16	Serbia, Pester Derekare, Vrelo Derekarske reke (Njunjić 2016)	KX671646	KX671681		KX719877	KY397775	KY397811
Rhodopiola cavicola	AN142	Bulgaria, Belitsa, Shepran dupka, cave, 41°49'58.9"N 24°52'58.9"E, 885 m, 27.5.2015, A. Faille & J. Fresneda	x	x	x	x	x	x
Riberius stillicidii	AN1279	Albania, Vrana e Madhe, Shpella Shtares cave, 1427 m, 42.31766°N 19.85403°E, 23.8.2019, A. Lacirignola, M. G. Mastronardi, M. Pastore		x	x			
Rondolinia adelinae	AN1198	Italy, Valduggia, Fenera, Vercelli, Bell'Ingresso-2539 Pi/VC, UTM: 32T 447489 5062303, 754 m, 7.4.2012, E. Lana	x		x		x	x
Royerella tarissani ferrierensis	AC24	France-26, Vassieux-en-Vercors, Baume Cervière, 8.7.2007, J. Fresneda	x	HG915392	HG915693	HG915613	HG915465	HG915540
Royerella tarissani gaveti	RA1033	France-38, Lausen, Grotte Eymards, 18.3.2012, C. Alonso		x	x	x		x
Royerella tarissani henroti	RA1043	France-38, Presles, Grotte de Pré l'étang, 18.3.2012, C. Alonso	x		x	x		x
Royerella tarissani vertacomicora	RA1029	France-26, St. Sulien en Quiat, Grotte du Bec Pointu, 16.3.2012, C. Alonso	x	x	x	x	x	x
Rozajella deelemani	IRO8	Montenegro, Berane, Petnjic, Grada pecina (Njunjić 2016)	KX671637	KX671689		KX719886	KY397802	KY397838
Rozajella madzgalji	IRO3	Montenegro, Berane, Gorazde, Velika pecina na Gareskom krsu (Njunjić 2016)			KX719925	KX719887		KX719980
Salfia damryi **comb. nov.**	AN676	Sardinia (Isl.), M. Orbai, Villarassargia, 17.4.2012, C. Onnis	x	x	x	x	x	x
Salfia derosasi **comb. nov.**	RA201	Italy, Toscana, Orbetello, Grotta della Punta degli Stretti, 27.7.2010, J. Fresneda	x	x		x		x
Salfia georgii **comb. nov.**	GPAg15	Italy, Pozzo l'Arcaro Cave (FR, Latium, Central Italy) (Latella *et al*. 2017)		KY934153	KY934129			
Salfia ruffoi **comb. nov.**	AN1231	Italy, Maddona del Pollino, PZ in faggeta, 1500 m, 3.6.2019, P. Magrini	x	x	x	x	x	x
Salfia sarteanensis **comb. nov.**	ADA	Italy, Villa Ada live oak wood (Rome, Latium, Central Italy) (Latella *et al*. 2017)		KY934151	KY934127			
Salgadoia brieti	AI587	Spain, Huesca, Santa Olaria de Ara, Ginuabel, Forato de los Moros, 1.5.2002, J. Fresneda	MT521296	GU356885	GU356783	GU356832	GU356930	GU356977
Schaufussia bustilloi **gen. nov. comb. nov.**	AF16	Spain, Asturias, Toriezo-Quirós, Cueva de la Peña de Cotrutes, 3.5.2008, J.M. Salgado	x	x	x	x	x	x
Schaufussia pachecoi **gen. nov. comb. nov.**	AI665	Spain, Asturias, San Tirso-San Román de Candamo, Cueva del Ferradal, 15.10.2005, J.M. Salgado	x	HG915389	HG915691	HG915610	x	HG915536
Sciaphyes shestakovi	AF66	Russia, Primorsky Kray, Chuquevskiy r-n., sifting litter, 44º02'N 134º13'E, 650 m, 21-25.5.2008, V.V. Grebennikov	x	HE572788	x	HE572875	HE572823	HE572845
Sciaphyes sibiricus	AF68	Russia, Primorsky Kray, Anisimovka vil., soil traps, 43º07'25"N 132º47'43"E, 500 m, 9-11.7.2008, V.V. Grebennikov	x	HE572790	x	HE572876	HE572825	HE572847

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Sciodrepoides fumatus	RMNH-INS-63164	GBK-KF604727 (Genbank: Schilthuizen, M.)	KF604727					
Sciodrepoides hornianus	AN936	Canada, Ontario, Leeds-Grenville Co., Peck's Beetle Acres, 22.5.2010, S. Peck	x	x	x	x	x	x
Sciodrepoides terminans	AN935	Canada, Ontario, Leeds-Grenville Co., Peck's Beetle Acres, 22.5.2010, S. Peck	x	x	x	x		x
Sciodrepoides tsukamotoi	RMNH-INS-546062	GBK-KF604725, no data (Genbank: Schilthuizen, M.)	KF604725					
Sciodrepoides watsoni	RA562	Romania, Bistrita-Nasaud, Telciu, *Fagus* forest, 21.7.2011, J. Fresneda	x	x	x	x	x	x
Silphopsyllus desmanae	RA265	Russia, Lipetsk distr., Plavitsariv, *Desman* sp. [male], 27.3.2007, A. Zemlanukhin			HE576719	x	x	HE572873
Sinobathyscia tianma	AN789	China, Shanghai: Songjiang District, Tianmashan (天马山), 40 m, 31°04'35.95"N 121°08'45.45"E, sifted from rotten wood (Paratypus), 19.12.2016, Xiao-Bin Song leg.	x		x	x	x	x
Sophrochaeta oltenica	RA794	Romania, Cioaca cu Brebenei Cave, 31.3.2012, R. Bucur	x	x	x	x	x	x
Spelaeochlamys ehlersi	IRC31	Spain, Alacant, Cocentaina, Cova de les Meravelles, 30.3.2002, J. Fresneda		GU356886	GU356784	GU356833	GU356931	GU356978
Speocharidius (Kobiella) galani	AI580	Spain, Gipuzkoa, Usurbil, Guardetxe Aurre ko Leizia, 24.6.2002, I. Zabalegui	x	GU356887	GU356785	GU356834	GU356932	HG915541
Speocharidius (Speocharidius) breuili	IRC11	Spain, Gipuzkoa, Albiztur, Cueva de Mendikute, 15.7.1998, J. Fresneda	x	GU356888	GU356786	GU356835	x	GU356979
Speodiaetus galloprovincialis	RA641	France-83, Mazaugues, Mines de Tourves, 43º22.28'N 05º53.73'E, 4.10.2011, Y. Leroy	HG915328	HG915393	HG915695		HG915467	HG915543
Speonemadus angusticollis	AI551	Spain, Jaén, Siles, Cueva Nacimiento de San Blas, 7.7.2002, M. Baena	x	GU356889	GU356787	GU356836	GU356933	GU356980
Speonemadus bolivari	AF34	Spain, Málaga, Antequera, Cueva del Yeso III, 29.3.2008, GEV		LS999468	LS999470		LS999478	LS999487
Speonemadus breuili	AN464	Spain, Cádiz, Jeréz-Cortes de la Frontera, Cueva Motilla Parralejo (Complejo Motillas), 13.9.2009, GIEX	LS999460	LS999465	LS999471	LS999496	LS999479	LS999488
Speonemadus brusteli	AN489	Morocco, Rif, Talembote, Talamssemtane, Sapinière, 13.11.2015, H. Brustel	LS999459	LS999464	LS999473	LS999500	LS999482	LS999491
Speonemadus clathratus	HI21	Spain, Jaén, Sierra de Cazorla, alrededores de Linarejos, 1.11.2006, M. Baena	x	HE572815	HE576715	HE572886	x	x
Speonemadus gracilis	RA638	Spain, Jaén, Hornos, Sima de la Tubería, 28.8.2011, GEV	LS999461	LS999462	LS999474		LS999484	LS999493
Speonemadus maroccanus	AF215	Morocco, Taza, Ghar Chiker, 4.9.2009, A. Faille	x	HE572796	HE576699	x	HE572830	HE572852
Speonemadus vandalitiae	AC110	Spain, Huesca, Villanúa, Cueva de Esjamundo, 28.9.2009, C. Bourdeau, A. Faille & J. Fresneda	x	LS999469	x	LS999497	LS999485	x
Speonesiotes (Kulzeria) muelleri	AN783	Bosnia-Herzegovina, Trebinje, Matulica pecina, 42°41'31.4"N 18°21'41.4"E, 586 m, 10.5.2017, A. Faille, J. Fresneda & I. Ribera	x	x	x	x	x	x
Speonesiotes (Speonesiotes) gobanzi	M457	Croatia, Isl. Mljet-Spilja kod Nerezinog dola, N42°45'30.4" E017°26'09.9" 193m , 6.4.2022 , I. Čupić, A. Faille, B. Jalžić, V. Mizerakis, N. Sudar			x		x	

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Speonemadus pulchellus	AN306	Sicily (Isl.), Ficuzza, 25.5.2013, C. Bourdeau, A. Faille, J. Fresneda & I. Ribera	LS999457	LS999466	LS999476	LS999498	LS999480	LS999489
Speonemadus tenuipes	AN671	Algeria, Djurdjura, Aït Abd El Ali, Ifri Semedane, 23.5.2012, A. Moulout & A. Faille		LS999467	LS999475	LS999495	LS999483	LS999492
Speonomidius crotchi aitzquirrensis	RA756	Spain, Gipuzkoa, Oñate, Cueva Arrikurtz, 43.28290N 3.25877W, no data, A. Jochum	x	x			x	x
Speonomidius crotchi crotchi	AI1067	Spain, Navarra, Zegama, Cueva de Orobe, 29.7.2006, J. Fresneda	x	GU356890	GU356788	GU356837	GU356934	GU356981
Speonomidius crotchi oberthuri	AF127	Spain, Gipuzkoa, Zegama, Cueva de San Adrián, UTM: 30T 0555845 4753819, 988 m, 3.5.2009, C. Bourdeau & J. Fresneda	x	x				x
Speonomites antemi	AI1074	Spain, Lleida, Gerri de la Sal, Baen, Cova dels Porredons, 12.8.2006, J. Fresneda	MT521319	GU356891	GU356789	HG915615	GU356935	GU356982
Speonomites aurouxi	AC170	Spain, Lleida, Sant Miquel de la Vall, Avenc de Sant Gervàs, 1.4.2010, J. Fresneda		MT542160	x	LN849307	LN849336	LN849346
Speonomites crypticola	RA27	Spain, Lleida, Serradell, Forat Negre, 12.8.2009, J. Fresneda	HG915329	HG915394	HG915696	HG915616	HG915468	HG915544
Speonomites latrunculus	IRC8	Spain, Lleida, Santa Linya, Cova del Lladre, 14.11.1998, J. Fresneda	MT521320	LN849288	LN849381	LN849320	MT586236	LN849354
Speonomites nitens	IRC5	Spain, Lleida, Camarasa, Cova del Tabaco, 1.8.2001, J. Fresneda	MT521321	LN849287	LN849380	LN849319	MT586237	LN849353
Speonomites pallaresanus	AF123	Spain, Lleida, Sort, Cova Saverneda, 29.3.2009, J. Fresneda, C. Bourdeau & A. Faille	MT521323	HF912455	HF912607	HF912505	HF912578	MT586256
Speonomites tincatincensis	IRC6	Spain, Lleida, Altron, Forat del Tincatinc, 9.7.1999, J. Fresneda	MT521324	GU356892	GU356790	GU356838	MT586239	GU356983
Speonomites velox	AI586	Spain, Lleida, Vilanova de Meià, Querant del riu Merlé, 2.7.2002, J. Fresneda	MT521322	LN849275	LN849370	LN849314	MT586238	LN849349
Speonomus abeillei	RB2	France-09, Le Mas d'Azil, Grotte de Peyrounard, Ph. Déliot & A. Faille		GU356894	GU356792	GU356839		
Speonomus alticola	RA266	France-64, Gères-Belesten, Gouffre Damoclés, 28.5.2010, C. Bourdeau & A. Faille	x	x	x	x		
Speonomus bouilloni	RA758	France-09, Saurat, Rivière souterraine de Siech, 17.8.2010, C. Vanderbergh	MT521304	MT542152	LN849365	LN849325	MT586229	LN849358
Speonomus chardonis aletinus	AN178	France-11, Alet-les-Bains, Grotte de la Valette, 15.3.2010, C. Bourdeau	x	x	x	x	x	x
Speonomus chardonis chardonis	AC172	France-11, Axat, Grotte des Gorges de l'Aude, 21.11.2009, C. Bourdeau		MT542154	LN849361	LN849308		
Speonomus curvipes curvipes	HI24	France-11, Rivel, Grotte de l'Home Mort, 10,2006, C. Bourdeau	MT521306	LN849285	MT571469	LN849318	LN849339	MT586251
Speonomus curvipes subcurvipes	AC168	France-11, Coudons, Grotte du Bac de Lacaune, 9.11.2009, C. Bourdeau			HG915700	HG915620	HG915471	

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Speonomus diecki	AI536	France-09 Moulis, Grotte d'Aubert, 22.7.2004, A. Faille	MT521345	GU356896	GU356794	GU356841	GU356938	GU356986
Speonomus diecki	AI535	France-09, Rogalle, Grotte d'Ardet, 8.1.2004, C. Bourdeau	x	HG915403	HG915706	HG915626	x	HG915553
Speonomus fagniezi	AF125	France-11, Saint-Paul-de-Fenouillet, Gorges de Galamus, Grotte de la Madeleine, 11.3.2009, C. Bourdeau	MT521307	HF912456	HF912608	HF912506	HF912579	HF912591
Speonomus leleupi	AN414	France-09 Seix, Grotte de Lameza, 1.11.2015, H. Brustel		MT542153	MT571470	MT551102	MT586231	MT586252
Speonomus longicornis fauveaui	RA667	France-09, Freychenet, Grotte des Capètes, 11.2009, C. Bourdeau	x	HG915399		HG915622	HG915473	HG915549
Speonomus longicornis longicornis	AI531	France-09, Aigües Juntes, Grotte de Pigaï, 18.5.2004, A. Faille	MT521308	HG915400	HG915702	HG915623		HG915550
Speonomus normandi hydrophilus	AI528	France-09, Riverenert, 7.6.2004, A. Faille	x	HG915401	HG915703	HG915624	HG915474	HG915551
Speonomus normandi normandi	AI532	France-09, Alzen, Grotte de Férrobach, 11.7.2004, A. Faille	MT521309	HG915402	HG915704	HG915625	HG915475	HG915552
Speonomus piochardi	AC119	France-09, Unjat, Grotte de la Garosse, 20.8.2009, C. Vanderbergh		MT542155		LN849305	LN849335	LN849345
Speonomus proserpinae	HI25	France-11, Rivel, Grotte de l'Home Mort, 10,2006, C. Bourdeau	MT521305	LN849286	LN849376		MT586230	MT586250
Speonomus pyreneus discontigny	AI668	France-09, Massat, Grotte du Ker, 1.2006, C. Bourdeau	x	HG915404	HG915705	HG915627	x	HG915554
Speonomus pyreneus hustachei	RA670	France-09, Eycheil, Grotte de Sabouche inf., 19.11.2009, C. Bourdeau & J. Fresneda	x	LN849292	x	x	x	x
Speonomus pyreneus nadari	AF57	France-09, Tourtouse, Grotte de Tourtouse, 13.02.2008, A. Faille & C. Bourdeau	x	LN849265		LN849309		
Speonomus pyreneus pyreneus	AC55	France-09, Ussat, Grotte de Lombrives, 29.11.2006, A. Faille	MT521346	MT542156	MT571485	LN849298		LN849342
Speonomus stygius crassicornis	RB8	France-09, Le Mas d'Azil, Grotte de Peyrounard, Ph. Déliot & A. Faille			x	x		
Speonomus stygius saulcyi	RB9	France-09, Taurignan, Grotte de la Touasse Peyrous, Ph. Déliot & A. Faille			LN849385	LN849332		
Speonomus stygius stygius	AI529	France-09, Moulis, Grotte d'Aubert, 22.7.2004, A. Faille		GU356898	GU356797	GU356844		GU356989
Speonomus stygius tisiphone	RA801	France-09, Malarnaud-Montseron, 5.4.2011, C. Bourdeau	x	x	x	x	x	x
Speonomus zophosinus	AI667	France-09, Massat, Grotte du Ker, 1.2006, C. Bourdeau	MT521310	HF912500	HF912616	HF912513	HF912584	HF912598
Speophyes lucidulus	RA1020	France-34 Laroque, Grotte du Maire, 10.4.2012, C. Alonso	x	x	x	x	x	x
Speoplanes biocovensis	VS11b	Croatia, Rašćane Gornje, Bebeci, Baba pecina (Mizerakis *et al*. 2022)	OP105158					OP106438
Speoplanes giganteus	VS9b	Croatia, Mosor, Gornje Sitno, Jama Velika Gajna (Mizerakis *et al*. 2022)	OP105156					OP106437
Sphaerobathyscia hoffmanni	M464	Italy, Duino-Aurisina, Caverna Moser, N45°44'50.5" E013°42'16.8" 207m , 1.4.2022 , A. Faille, V. Mizerakis			x		x	

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	trnL+trnL+nad1	cytb	SSU	LSU
Staphylininae Coprophilus striatulus	AI839	England, Norfolk, Ludham How Hill Marsh, 6.5.2006, Balfour Browne Club meeting		HE572812	HE576713		HE572841	HE572863
Stygiophyes akarsticus	IRC7	Spain, Lleida, Altron, Forat del Tincatinc, 9.7.1999, J. Fresneda		GU356899	GU356798	GU356845	GU356940	GU356990
Stygiophyes aldomai allomorphus	AI1077	Spain, Lleida, El Pont de Suert, Forat d'Irgo, 25.7.2006, J. Fresneda	MT521297	HG915406	x	HG915630	HG915477	HG915557
Stygiophyes hansferyi	IRC39	Spain, Lleida, El Pont de Suert, Cova de la Carretera, 2.2.2002, J. Fresneda	MT521303	GU356900	GU356799	GU356846	MT586228	GU356991
Stygiophyes latebricola elongatus	AI596	Spain, Lleida, El Pont de Suert, Graller de Sant Roc, 12.8.2004, J. Fresneda	x	LN849279	LN849373	LN849316	LN849338	x
Stygiophyes latebricola latebricola	AN339	Spain, Lleida, Tremp, Espluga de Serra, Esplugallorna, 12.7.2015, R. Sendra & J. Pallisé	MT521340	MT542173	MT571481			MT586265
Stygiophyes puncticollis	RA932	Spain, Lleida, Llimiana, Forat de l'Or, 42º02'21"N 0º53'05"E, 350 m, 22.9.2012, J. Fresneda & I. Ribera	MT521300	LN849294	MT571468	LN849326	MT586226	LN849359
Stygiophyes ribagorzanus	AI575	Spain, Huesca, Bonansa, Cova des Toscllasses, 22.5.2004, J. Fresneda	MT521298	LN849272	LN849368	LN849313	MT586225	LN849348
Stygiophyes saforensis	AC105	Spain, Huesca, Santorens, Cova del Garrabero, 12.8.2009, J. Fresneda	MT521299	LN849258	MT571467	LN849300		MT586249
Stygiophyes sanctigervasi	AI863	Spain, Lleida, Tremp, Mines de Canal de Llastarri, 15.5.2006, J. Fresneda	MT521302	LN849282	LN849374		MT586227	LN849351
Stygiophyes zariquieyi	AF187	Spain, Lleida, Ager, Cova Colomera de Corsà, 30.5.2009, J. Fresneda	MT521301	LN849268	LN849364	LN849311	LN849337	LN849347
Tachyporinae Tachyporus hypnorum	AI555	Switzerland, Pfyn, stream in village, 408 m, 47º35'43.8"N 8º57'17.4"E, 2.8.2005, I.Ribera & A.Cieslak		HE572808	HE576710		HE572840	HE572862
Tamaniniella pivai **sp. nov.**	RA785	Italy, Veneto, Monti Lessini, Rovere Mille (VR), Grotta di Monte Capriolo, 11.11.2011, E. Lana & A. Faille	x	x	x	x		
Tamaniniella vallarsae	RA603	Italy, Venezia Tridentina, Gruppo del Carega-Piccole Dolomiti-Pasubio, Vallarsa (TN), loc. Pian delle Fugazzetestata, al della Busa, 1150 m, 26.7.2011, E. Piva	x	x	x	x	x	x
Tismanella chappuisi chappuisi	RA561	Romania, Gorj, Tismana, Pestera de la Manastirea Tismana, 27.7.2011, J. Fresneda	x	x	x	x	x	x
Trapezodirus altimontanus	RA958	Spain, Huesca, Escuaín, Revilla, B15, 8.8.2012, A. Faille	x	x	LN849366	LN849327	x	LN849360
Trapezodirus arcticollis	AI576	Spain, Huesca, Bonansa, Cova de Sant Salvador, 16.3.2003, J. Fresneda	MT521312	LN849273	LN849369	MT551103	MT586234	MT586253
Trapezodirus bolivari	IRC27	Spain, Huesca, Sercué, Cueva de Aso, 28.10.2001, J. Fresneda	MT521315	MT542157	LN849378	LN849322	LN849340	LN849355
Trapezodirus carrodillae	IRC9	Spain, Huesca, Estadilla, Grallera de Estadilla, 4.8.1999, J. Fresneda	MT521316	GU356901	GU356800	GU356847	MT586232	GU356992
Trapezodirus cerberus	AI600	Spain, Huesca, Bonansa, Esplluga des Tosses, 31.7.2004, J. Fresneda	MT521313	HF912499	HF912615	HF912512	HF912583	HF912597

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Trapezodirus escollae	AF129	Spain, Huesca, Seira, MSS 002, C.N. 260 entre el PK 396 y PK 397, 750 m, 10.5.2009, J. Fresneda, A. Faille & C. Bourdeau		LN849266	LN849363	LN849310		
Trapezodirus orobios orobios	AF59	Spain, Huesca, Barbaruens, Cotiella-Armeña, Sima A332, 25.10.2008, J. Fresneda, A. Faille & C. Bourdeau	MT521314	HG915407	HG915709	HG915631	HG915478	HG915558
Trocharanis mestrei	AC169	France-11, Coudons, Grotte du Bac de Lacaune, 9.11.2009, C. Bourdeau		LN849263	HF912604		HF912576	MT586262
Troglocharinus andresi **stat. nov.**	VR13	Spain, Barcelona, Esparreguera, Avenc del Clast, 11.2.2010, V. Rizzo & J. Comas	LT799421	HF912466	HF912623	HF912520		x
Troglocharinus arlai **stat. nov.**	VR15	Spain, Barcelona, Albinyana, Cova de Vallmajor, 21.1.2010, V. Rizzo & J. Comas		HF912468	HF912625	HF912522		
Troglocharinus bellesi **sp. nov.**	RA1137	Spain, Lleida, Peramola, Avenc de la Roca del Corb, 11.7.2013, J. Pastor	x	x	x	x		x
Troglocharinus elongatus elongatus	AN413	Spain, Barcelona, Querol, Cova del Mandil, 7.11.2015, J. Pallisé	MT521325	MT542161				
Troglocharinus elongatus mateui	VR4	Spain, Tarragona, Querol, Cova del Garrofet, 1.10.2009, J. Comas	x	x	x	x		x
Troglocharinus elongatus ollai	VR17	Spain, Barcelona, Aiguaviva, Cova de la Olla, J.Comas & V.Rizzo	LT799422	HF912470	HF912627	HF912524		
Troglocharinus elongatus portai	RA1176	Spain, Barcelona, Pontons, Mines de Pontons, Cova de les Calaveres,P. Balart	LT797303	LT797308				
Troglocharinus elongatus roselli	AN139	Spain, Barcelona, Torrelles de Foix, Cova Freda, 23.4.2015, F. Fadrique	MT521327	MT542162	MT571473	MT551107	MT586240	MT586257
Troglocharinus espanoli	VR23	Spain, Tarragona, Pla de Cabra, Cova del Traça, 17.04.2010, F. Fadrique	LT797300	HF912475	HF912630	HF912529		LT797443
Troglocharinus fadriquei	AN1239	Spain, Lleida, Figols d'Organya, Forat de Casanova, 30.9.2017, J. Pallissé	MT521339	MT542171				
Troglocharinus ferreri ferreri	AI1065	Spain, Barcelona, Begues, Avenc del Sant Roc, 9.9.2006, J. Fresneda	LT797272	HF912496	HF912612		HF912582	HF912594
Troglocharinus ferreri pallaresi	VR3	Spain, Barcelona, Corbera, Avenc de Can Montmany, 12.11.2009, J. Comas	HG915334	HF912480	HF912632	HF912531		HF912601
Troglocharinus fonti fonti	IRC26	Spain, Lleida, Montanisell, Cova d'Ormini, 1.11.2001, J. Fresneda	MT521328	GU356902	GU356801	GU356848	HF912585	GU356993
Troglocharinus hustachei	VR36	Spain, Lleida, Vilanova de Meià, Forat del Gel, 26.5.2010, A.Meseguer		HF912487	HF912635	HF912533	LT797435	
Troglocharinus impellitierii	IRC22	Spain, Lleida, Taús, Cova Palomera, 1.11.2001, J. Fresneda	MT521332	HF912501	HF912617	HF912514		HF912599
Troglocharinus jacasi	VR22	Spain, Barcelona, La Llacuna, Cova de les Rondes, 18.04.2010, J.Comas & V.Rizzo	LT799423	HF912474	MT571474	HF912528		
Troglocharinus kiesenwetteri	VR39	Spain, Barcelona, Collbatò, Cova Freda, 20.5.2010, J. Comas	MT521333	HF912490	HF912637	HF912536		

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Troglocharinus mengeli	RA672	Spain, Lleida, Toloriu, Coves Encantades, 17.10.2009, C. Bourdeau, A. Faille, M. Escoll & J. Fresneda	MT521317	MT542158	MT571471	MT586233	MT551104	MT586254
Troglocharinus mercedesi	AN696	Spain, Barcelona, Berguedà, Montmajor, Bofia de St. Jaume, 11.2.2017, J. Fresneda & I. Ribera	MT521334	x	x	MT551108	MT586243	MT586258
Troglocharinus olerdolai	VR102	Spain, Barcelona, Olèrdola, Avenc d'Olèrdola, 20.03.2011, J.Comas, V.Rizzo & J. Pastor	MT521326					
Troglocharinus orcinus acevedoi	VR20	Spain, Tarragona, La Riba, Cova d'en Cartanyà, F. Fadrique	x	HF912472	LT797428	HF912527	LT797433	LT797436
Troglocharinus orcinus figuerai	VR89	Spain, Tarragona, Montblanc, Avenc de la Figuera, 4580735N 0345152E, 540 m, 20.3.2011, V. Rizzo	x	x	x	x		x
Troglocharinus orcinus lagari	AN263	Spain, Tarragona, l'Albiol, La Petita de Bonretorn, UTM: ED50 0343265 4568130, 525 m, 10.4.2011, F. Fadrique	x	x				
Troglocharinus orcinus orcinus	VR9	Spain, Tarragona, La Febró, Cova de la Febró, UTM: 333922 4570285, 17.12.2009, V. Rizzo	HG915332	HF912495	HF912642	HF912540	HF912590	LT797444
Troglocharinus pallisei	RA1190	Spain, Tarragona, La Riba, Cova de la Riba del Talc, 28.7.2013, J. Pallisé	LT797282	LT797309	LT797426	MT551106	LT797431	LT797440
Troglocharinus patracoi	VR16	Spain, Barcelona, Esparreguera, Cova del Patracó, 19.1.2010, V. Rizzo & J. Comas		HF912469	HF912626	HF912523		MT586263
Troglocharinus pinyareti **stat. nov.**	VR38	Spain, Tarragona, Aiguaviva, Avenc dels Pinyarets, 27.05.2010, J.M.Victoria	LT797284	HF912489	HF912636	HF912535		LT797442
Troglocharinus quadricollis	AI578	Spain, Lleida, Tremp, Graller de Castellet, 8.11.2003, J. Fresneda	MT521329	HF912497	HF912613	HF912510	MT586241	HF912595
Troglocharinus sanllorensi **stat. nov.**	VR11	Spain, Barcelona, Sant Llorenç, Coves de Mura, 9.1.2010, V. Rizzo	LT797306	HF912464	HF912621	HF912518	HF912587	x
Troglocharinus schuttei **stat. nov.**	VR37	Spain, Lleida, Hortoneda de la Conca, Cova de la Font Mentidora, 1.6.2010, J. Fresneda, I. Ribera & V. Rizzo	x	HF912488	x	HF912534		x
Troglocharinus sendrai	AN351	Spain, Lleida, La Vansa i Fornols, Mina Coll d'Arnat, 16.10.2015, J. Comas & V. Rizzo	MT521338	MT542169	MT571478	MT551112	MT586246	MT586261
Troglocharinus senenti	VR6	Spain, Lleida, Vilanova de Meià, Querant Gran de Paús, 2.7.2002, J. Fresneda	MT521330	HF912493	HF912640	HF912538	MT586242	HF912603
Troglocharinus subilsi	RA1189	Spain, Lleida, Alinyà, Grallera de Cambrils, 7.7.2012, J. Fresneda & V. Rizzo	MT521331	MT542163	LT797424	LT799425	LT797430	LT797439
Troglocharinus vinyasi	AN790	Spain, Lleida, Peramola, Avenc de la Roca del Corb, 31T 4659411 356378, 866 m, 19.3.2017, F. Fadrique		MT542172	MT571480	x		MT586264
Troglocharinus zariquieyanus **stat. nov.**	AF130	Spain, Lleida, La Guardia d'Ares, Avenc del Pla Fornesa, 9.5.2009, J. Fresneda, A. Faille & C. Bourdeau		x	HF912609			
Troglodromus bucheti poenitens	AC1	France-06, Caussols, Aven de la Vieille Poste, 43°44'38.3"N 6°56'40.0"E, 1079 m, 3.7.2007, A. Cieslak & J. Fresneda	x	x	x	x	x	x

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Troglophyes alluaudi **stat. nov.**	RA632	France-11, Bugarach, Réseau Bufo Fret, 7.7.2010, M. Meissonier	MT521343	MT542176	MT571484	MT551115	MT586248	MT586267
Troglophyes bedeli	RA896	France-66, Opoul, Barranc Gran del Plà de Perillós, 17.2.2012, J. Pastor	MT521342	MT542174		MT551114	MT586247	MT586266
Troglophyes gavoyi	AC114	France-11, Sainte-Colombe/Guette, Grotte de Majestier, 5.8.2009, C. Vanderbergh	x	LN849260	x	LN849302	LN849334	LN849344
Troglophyes ludovici	RA526	France-11, Coudons, Grotte du Bac de Lacaune, 9.11.2009, C. Bourdeau	HG915336	MT542175	MT571483	HG915634	HG915481	HG915561
Uhagoniella franzi **gen. nov. comb. nov.**	AN564	Spain, Picos de Europa, Cueva Camplengo, 30T 343311 4792439, 28.7.2016, E. Valenzuela	x	x			x	x
Uhagoniella laurae **gen. nov. comb. nov.**	AI664	Spain, Asturias, San Tirso-San Román de Candamo, Cueva del Ferradal, 15.10.2005, J.M. Salgado	x	GU356873	GU356769	GU356822	GU356921	GU356964
Uhagoniella meregallii **gen. nov. comb. nov.**	AC77	Spain, Asturias, Campo de Caso, Bueres, Hayedo en la Collada de Arnicio, 25.9.2008, J.M. Salgado	x	HG915372	HG915674		HG915446	HG915519
Uhagoniella ovoidea **gen. nov. comb. nov.**	AC60	Spain, Asturias, Oballo-Boal, Cova Fonte das Covas, 5.10.2007, J.M. Salgado		x		x	x	x
Uhagoniella zariquieyi **gen. nov. comb. nov.**	AN563	Spain, Asturias, Somiedo, Pozos promedio, 29T 733606 4770564, 7.6.2014, E. Valenzuela		x	x	x	x	x
Uludagites minuta **comb. nov.**	AN301	Turkey, Bursa prov., Uludag, mix beech-conifer forest, 40°6'40.5"N 29°4'38.8"E, 1400 m, 30.7.2014, I. Ribera & A. Cieslak	x	x	x	x	x	x
Valdesiella olmii **gen. nov. comb. nov.**	AN1197	Italy, Torino, Angrogna, Ghieisa d'Ia Tana - 1538 Pi/TO UTM: 32T 359364 4967937, 842 m, 3.5.2012, E. Lana				x	x	x
Vallespirana grenieri **gen. nov. comb. nov.**	RA1220	France-66, Prats de Molló, beech forest 1 km W La Preste, 42º24'29.6"N 2º23'22.3"E, 1177 m, 1.11.2013, J. Fresneda, I. Ribera & A. Cieslak	x	x	x	x	x	x
Vanderberghia asaspensis **gen. nov. comb. nov.**	AN547	France-64, Husse de Mirassou, Sarrance, 18.7.2015, H. Brustel	x	x	x	x	x	x
Vanderberghia bastideus **gen. nov. comb. nov.**	AF186	France-65, Esparros-Arrodets, rivière souterraine d'Artigaléou, 19.5.2009, C. Bourdeau & J. Fresneda	x	HG915396	HG915698	HG915618	HG915470	HG915546
Vanderberghia bessoni **gen. nov. comb. nov.**	RA551	France-64, Arthez-d'Asson, Grotte de Nabails, 20.6.2009, C. Bourdeau, A. Faille & J. Fresneda	HG915330	x	HG915707	HG915628	HG915476	HG915555
Vanderberghia bourgoini bourgoini **gen. nov. comb. nov.**	AI538	France-65, Sarrancolin, Grotte de la Cascade, 10.6.2004, A. Faille	x	HG915397	HG915699	HG915619	x	HG915547
Vanderberghia ehlersi **gen. nov. comb. nov.**	RA671	France-31, Coulédoux, MSS Grotte de la Bouhadère, traps: 14.5/30.10.2009, C. Bourdeau & J. Fresneda	x	x		x		
Vanderberghia gaudini arivensis **gen. nov. comb. nov.**	IRC18	Spain, Navarra, Arive, Cueva de Mendia Landa, 13.4.2001, J. Fresneda	x		GU356795	GU356842	x	GU356987
Vanderberghia ochsi alberti **gen. nov. comb. nov.**	AF28	France-64, Ste. Engrâce, Kakoueta, Grotte Zagitete, 4.6.2008, E. Dupré	x	HG915395	HG915697	HG915617	HG915469	HG915545

APPENDIX 2. (Continued)

Species	Voucher	Locality, date & collector	cox 1-5'	cox 1-3'	rrnL+trnL+nad1	cytb	SSU	LSU
Vanderberghia ochsi ochsi **gen. nov. comb. nov.**	AC73	France-64, Barlanès, Aven de Licié Etsaut, 8.5.2007, A. Faille	x	x	x	x	x	x
Vanderberghia orgibetensis **gen. nov. comb. nov.**	AI526	France-09, Illartein, Ravin de la Tire, MSS, 3.6.2004, Ph. Déliot & A. Faille	x	GU356897	GU356796	GU356843	GU356939	GU356988
Vanderberghia pierrei **gen. nov. comb. nov.**	AC106	France-64, Sainte Engrâce, Kakouetta, Grotte du Mouton, 5.10.2009, C. Bourdeau	x	x	x	x	x	x
Vanderberghia speluncarum speluncarum **gen. nov. comb. nov.**	AC104	France-65, Saint-Pé-de-Bigorre, Grotte de la Pale, 20.6.2009, C. Bourdeau, A. Faille & J. Fresneda	x	x	x	x		x
Zariquieyella bigerrica **comb. nov.**	AC201	France-64, Gères-Bellesten, Cinq Monts, 21.6.2009, C. Bourdeau, A. Faille & J. Fresneda	x	x	HG915644	x		x
Zariquieyella breuili **comb. nov.**	AF126	Spain, Gipuzkoa, Rentería, Cueva de Landarbaso, 2.5.2009, C. Bourdeau & J. Fresneda		HG915344	HG915645		HG915417	HG915489
Zariquieyella diegoi **comb. nov.**	IRC14	Spain, Navarra, Arive, Cueva de Mendia Landa, 20.7.2000, J. Fresneda	x	x	GU356749	GU356805		GU356944
Zariquieyella fadriquei **comb. nov.**	AF195	Spain, Huesca, Villanua, Cueva de Esjamundo, 6.6.2009, J. Fresneda	x	HG915353	HG915655	HG915578	HG915428	HG915499
Zariquieyella grandis cplx. **comb. nov.**	AC74	France-64, Barlanès, Aven de Licié Etsaut, 8.5.2007, A. Faille	x	HG915348	HG915649		HG915421	HG915492
Zariquieyella mystica **comb. nov.**	AI581	Spain, Lleida, Vielha-Mitjaran, Plan Batalher, 22.10.2002, J. Fresneda	x	GU356856	GU356752	GU356808	GU356909	GU356946
Zariquieyella obermaieri **comb. nov.**	AN239	Spain, Huesca, Villanúa, Cueva del Camino, 6.6.2009, J. Fresneda	x	x	x		x	x
Zariquieyella parallela **comb. nov.**	AF73	France-40, St. Cricq du Gave, Grotte des Fées, 11.7.2007, C. Vanderbergh	x	HG915355	HG915657		HG915429	HG915501
Zariquieyella rugosa **comb. nov.**	IRC12	Spain, Navarra, Zegama, Dolina de Orobe, 16.7.1998, J. Fresneda	x	GU356855	GU356751	GU356807	x	x
Zariquieyella schiodtei **comb. nov.**	RA529	France-65, Bagnères-de-Bigorre, Grotte de Castelmouly, pierres, mousse, 21.01.2010, C. Bourdeau & A. Faille	HG915317	x	HG915659	HG915581	HG915431	HG915502
Zoiana kociani **gen. nov. comb. nov.**	M502	Georgia, Martvili, Inchkhuli cave, 427 m, N42º27'24.5'' E42º24'15.2'', 18.V.2022, Barjadze, Faille, Maghradze		x	x		x	x