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Lorenzo Zanella[*]

Microsystematic revision of the populations of *Abax parallelepipedus* (Piller & Mitterpacher, 1783) occurring in central-western Europe (Coleoptera Carabidae)

Riassunto: *Revisione microsistematica delle popolazioni di* Abax parallelepipedus *(Piller & Mitterpacher, 1783) diffuse in Europa centro-occidentale (Coleoptera Carabidae).*
La variabilità morfologica delle popolazioni europee centro-occidentali di *Abax parallelepipedus* è stata studiata al fine di revisionare la microsistematica di questa specie. Vengono discusse le descrizioni originali e le revisioni sistematiche pubblicate dalla seconda metà del XVIII secolo. Variabili biometriche e indici morfometrici sono stati rilevati in 792 esemplari provenienti da diversi Paesi europei. I dati sono stati sottoposti ad analisi statistica con l'obiettivo di discriminare le popolazioni differenziate in misura significativa rispetto alla forma nominotipica. Vengono discusse anche le caratteristiche dei genitali maschili. I risultati attestano che le variazioni morfologiche divengono più rilevanti tra le popolazioni presenti negli ambienti alpini e quelle italiane mostrano i tratti somatici ed edeagici maggiormente differenziati. Sulla base di questi risultati, *A. p. euganensis* Schatzmayr 1944 viene resuscitato dalla sinonimia con *A. p. inferior*, mentre le seguenti nuove sinonimie vengono proposte:

Abax parallelepipedus parallelepipedus (Piller & Mitterpacher, 1783)
= *A. p. subpunctatus* (Dejean, 1828) **syn. nov.**
= *A. p. audouini* (L. Dufour, 1851) **syn. nov.**
= *A. p. germanus* Schauberger, 1927 **syn. nov.**

Abax parallelepipedus inferior (Seidlitz, 1887)
= *A. p. alpigradus* Schauberger 1927 (*sensu* Schatzmayr, 1944) **syn. nov.**

Alla luce dei dati raccolti viene ipotizzato e discusso uno scenario filogeografico.

Abstract: Morphological variation of central-western European populations of *Abax parallelepipedus* was studied in order to revise the microsystematics of this species. Original descriptions and systematic revisions published since the second half of the 18th century are discussed. Biometric variables and morphometric indexes were evaluated on 792 specimens sampled from several European countries. The data were statistically analysed in order to discriminate the populations significantly differentiated from the nominotypical form. Features of male genitalia are also discussed. The results attest that the morphological variation becomes more relevant among populations inhabiting Alpine environments and the Italian ones show the most distinctive modifications of somatic and/or aedeagic traits. On the basis of these results, *A. p. euganensis* Schatzmayr, 1944 is resurrected from synonymy with *A. p. inferior*, whereas the following new synonymies are proposed:

Abax parallelepipedus parallelepipedus (Piller & Mitterpacher, 1783)
= *A. p. subpunctatus* (Dejean, 1828) **syn. nov.**
= *A. p. audouini* (L. Dufour, 1851) **syn. nov.**
= *A. p. germanus* Schauberger, 1927 **syn. nov.**

Abax parallelepipedus inferior (Seidlitz, 1887)
= *A. p. alpigradus* Schauberger, 1927 (*sensu* Schatzmayr, 1944) **syn. nov.**

A phylogeographical scenario is hypothesized and discussed in the light of the collected data.

Key words: *Abax parallelepipedus*, Subspecies, Microsystematic, Biogeography, Carabidae, Morphology, Geographical variation.

INTRODUCTION

Few ground beetles have achieved an evolutionary success comparable to that of *Abax parallelepipedus.* Its highly adaptive capacity has allowed this medium-sized Molopina to spread across most of the European continent, often becoming dominant among geophilic carabids of the forestry assemblages (Andersen *et al.*, 1990; Loreau & Nolf, 1993; Varvara & Pilat, 2004; Huidu, 2011, 2012). Its distribution includes (data by Vigna Taglianti, 2014; excepting other references explicitly cited): Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Danish mainland, Estonia, France, Germany, Hungary, Italian mainland, Kaliningrad Region, Kosovo, Latvia

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[*] Lorenzo Zanella, Museo civico di Storia Naturale di Venezia, Santa Croce 1730, 30135 Venezia, Italy.
E-mail: lorenzo.zanella@libero.it

(Telnov, 2004: 23), Liechtenstein, Luxembourg, Republic of Moldova, Montenegro, Norwegian mainland, Poland, Romania, Central Russia, Southern Russia, Serbia (incl. Voivodina), Slovakia, Slovenia, Northern Spanish mainland, Sweden, Switzerland, The Netherlands, Ukraine (Carpathians and Transcarpathia; Kryzhanovskij *et al.*, 1995: 108), United Kingdom.

Rare and local in some regions at the edges of its distribution area, such as Southern Sweden (Lindroth, 1945: 15), *A. parallelepipedus* is abundant in beech forests of central Europe, although it is not tied to any specific tree (Thiele, 1977). This predator is an important contributor to the ecological balance of forest ecosystems (Chaabane *et al.*, 1996) and its reproductive behaviour is of special interest since the female takes care of the eggs (Löser, 1970; Brandmayr, 1977; Brandmayr & Zetto-Brandmayr, 1979), which is quite rare among the Carabidae.

Throughout the process of geographical spread, this species developed morphologically differentiated populations, so that several subspecies were described between the second half of the 18th and the first half of the 20th century, many of which are still formally accepted but ignored by most authors. The morphological variation of *A. parallelepipedus* is consistent with the isolation by distance theory (IBD), which assumes that semi-isolated subpopulations of a continuous population inhabiting a large territory but with short dispersal capacity, tend to develop random and nonadaptive differentiations (Wright, 1943). The short dispersal range of *A. parallelepipedus* was studied by Loreau & Nolf (1993), while Keller *et al.* (2003a, 2004) showed that even the fragmentation of forest habitats due to main roads can interfere with the normal within population gene flow. However, no genetic investigation has yet been performed to verify if the morphological variation observed among the described subspecies has resulted from the casual selection of particular traits caused by IBD, or if it effectively represents an oriented differentiative process, potentially suitable to lead to speciation. The question is not irrelevant, since the recognition of subspecific populations is acceptable only in the latter case.

So far, the genome of this species has been investigated using molecular biology techniques to assess the polymorphism of some microsatellite markers (Keller & Lagardèr, 2003b), the phylogenetic relationships with other Molopina (Düring & Brückner, 2000) and to confirm the taxonomic distinction between *A. parallelepipedus lombardus* and *A. fiorii* (sub *angustatus*; Düring, 2002). However, the only information on the genetic distance among some subspecies can be extracted from a comprehensive phylogenetic study on Molopina by Casale & Ribera (2008), where some data attested to the closer relationship between *A. p. inferior* and *A. p. lombardus* than of either with *A. p. contractus*.

The present work aims to analyse the morphological variation of *A. parallelepipedus* and discuss the validity of its subspecies, hypothesizing the main routes this species might have taken to spread throughout Europe.

HISTORICAL REVIEW

The systematic history of *Abax parallelepipedus* is made very complicated in terms of both taxonomy and nomenclature by the large number of related taxa described since the mid-18th century, often referred to new species and then reduced to subspecies. A perusal of these descriptions is fundamental for a critical analysis of the current taxonomic nomenclature.

Some names, in fact, were probably proposed ignoring the previous ones, while others lack information needed for an unambiguous interpretation.

In order to simplify the overall picture, the cases of *A. fiorii* Jakobson 1907 (= *A. angustatus* Fiori, 1896) and *A. pyrenaeus* (Dejean, 1828) [= *A. grandicollis* (Fairmaire & Laboulbène, 1854)] will not be discussed, despite being considered subspecies of *A. parallelepipedus* throughout some early historical phases and then definitively accepted as valid species.

Abax parallelepipedus parallelepipedus
(Piller & Mitterpacher, 1783)

The description of the nominotypical subspecies (sub *Carabus parallelepipedus*) is due to Piller & Mitterpacher (1783: 105 and pl. VIII), who in 1783 published the results of their entomological survey in the Posega province of the Kingdom of Slavonia (now Požega, eastern Croatia), which at that time was part of the Habsburg Empire. From the environmental notes preceding the description it is possible to guess that the catch zone should be located in the mountains to the south of Kamenska village.

In 1789, the same taxon was again described by Villers (1789: 364) with the junior synonym *Carabus ater*; type locality: southern France. This second description had a wide diffusion among entomologists and, consequently, the name *A. ater* (Villers) remained in use until the end of the 20th century. The description of Piller & Mitterpacher was almost forgotten and, in 1828, the name *Abax parallelepipedus* was even used by Dejean (1828: 382) to describe a new species of *Abax*, creating another obstacle to the re-establishment of the correct nomenclatorial priority. The synonymy with *A. parallelepipedus* (Piller & Mitterpacher) was established by Csiki (1916: 15), that also replaced the junior homonym *A. parallelepipedus* (Dejean) with *A. pilleri* Csiki, 1916. Nevertheless, Jeannel (1942: 776) preferred to maintain the junior name *ater* (Villers) in order not to upset the established usage and to avoid the replacement of the junior homonym *A. parallelepipedus* (Dejean). Only recently, Bousquet (2003: 470) formally accepted the nomenclatorial revision proposed by Csiki.

Description of the Genus *Abax*

In 1810 F.A. Bonelli introduced the genus *Abax* without fixing the type-species; in 1838 Westwood designated *Carabus striola* Fabricius, 1792 [a synonym of *Abax parallelepipedus* (Piller & Mitterpacher, 1783)] as type-species (Madge, 1975). However, throughout most of the 19th century many entomologists considered *Abax* as a subgenus of either *Pterostichus* Bonelli or *Feronia* Latreille, depending on the adopted systematic interpretation.

Abax parallelepipedus subpunctatus (Dejean, 1828)

Described by Dejean (1828: 380) as a subspecies of *Feronia* (*Abax*) *striola* (Fabricius) (currently regarded as a synonym of *A. p. parallelepipedus*) on the basis of specimens from mountains in Croatia that he received already labelled as "*Abax subpunctatus* Ziegler". He described *subpunctatus* as basically similar to the nominotypical subspecies, except for the larger size.

Abax parallelepipedus contractus (Heer, 1841)

Described by Heer (1841: 561) as *Pterostichus contractus* Lasserre; type locality: Monte Generoso and Centovalli (Canton of Ticino, Switzerland). This description raises some problems that a literature search did not resolve. Heer (ibidem) reported that the pronotum is square, while it is transverse in all the subspecies of *A. parallelepipedus*. Furthermore, the indicated type locality falls within the distribution area of *A. p. lombardus,* described 50 years later. Fiori (1896) and Porta (1903), in their early systematic revisions of the genus *Abax*, maintained *A. contractus* distinct from *A. parallelepipedus* (sub *ater*) at species level, reporting the following distribution: central Alps (Grigna, Monte Generoso) and Maritime Alps (with specific reference to Valle Pesio).

Schauberger (1927) reduced *A. contractus* to ssp. of *A. parallelepipedus* (sub *ater*), also providing a new description based on one or more specimens from Valle Pesio (Maritime Alps, Italy). Jeannel (1942: 777) did not make any comment on the description provided by Heer, however, he was the first to report a distribution consistent with that currently accepted for *contractus*: French Hautes-Alpes, Maritime Alps, northern Apennines up to the Apuan Alps.

According to Schatzmayr (1944), Heer's description refers to the species that will be successively re-described by Fiori (1896) under the name of *A. angustatus*. Consequently, Schatzmayr considered as valid the description provided by Schauberger (idem), adopting the name *A. ater contractus* Schauberger 1927, which he reported as being in use for a couple of decades. This taxonomical solution, not conform to the International Code of Nomenclature, was accepted by some subsequent authors (Marcuzzi, 1953; Magistretti, 1965) and was maintained until the publication of the checklist of Italian Carabidae by Vigna Taglianti (1993). Nowadays, however, Heer is again considered the author of the subspecific name *contractus* (Bousquet, 2003: 470; Vigna Taglianti, 2014), despite no explanatory contribution being published.

Abax parallelepipedus audouini (L. Dufour, 1851)

Described as *Feronia audouini* by Dufour (1851: 315) following an entomological campaign throughout the eastern Pyrenees (Hautes-Pyrénées and Pyrénées-Atlantiques: from Bagneres Adour to Saint-Jean-de-Luz, from Pic du Midi to La Rhune mountain). Jeannel (1942: 776) reported Le Vernet (Ariége department, France) as type locality, perhaps after examining one or more specimens of the typical series.

Abax parallelepipedus curtulus (Fairmaire, 1856)

An Italian endemism described by Fairmaire (1856: 520) as *Feronia* (*Abax*) *curtula*; type locality:

Maritime Alps and Apennines. Fiori (1896) reduced this taxon to a subspecies of *A. contractus*, followed in this interpretation by Porta (1903). Schauberger (1927) reduced both *curtulus* and *contractus* to subspecies of *parallelepipedus* (sub *ater*), and this was accepted by all later authors.

Abax parallelepipedus inferior (Seidlitz, 1887)

Described by Seidlitz (1887: 37) as a subspecies of *Pterostichus* (*Abax*) *striola,* Dejean, with the following notes:

> *[…] Bei einer südlichen Form aus Spanien, Südfr., Italien, Siebenbürgen sind b. ♂ die Flgd fast 2mal so lang als breit u. die Zwschr. besonders hinten gewölbt, u. das Hls ist auch nach hinten etwas verengt (var. inferior = striola Dej.).*

The characters described by Seidlitz do not allow a reliable diagnosis and he also did not specify the type locality for this subspecies, instead indicating a broad distribution that includes Spain, southern France, Italy and Transylvania.

In a subsequent book (Seidlitz, 1888: 41), this description was slightly reworded by removing Transylvania from the distribution. Despite this minor change, the distribution remains extremely broad and not consistent with that currently accepted. *A. p. inferior* is presently considered endemic to NE Italy, where it is recorded in Trentino Alto Adige, Veneto and Friuli Venezia Giulia (Magistretti, 1965). The original description, therefore, is unsuitable to verify if Seidlitz described with *inferior* the same subspecies currently designated by that name.

Unfortunately, the only specimen labelled as type found in Seidlitz's collection, held at the Zoologische Staatssammlung München, has a label with an unreadable (handwritten) locality and no date. A second specimen collected in 1889, probably from the same locality as the type, also has an indecipherable locality label, while the remaining specimens in the series are just labelled "Sammlung v. Seidlitz".

Thus, neither the description nor the type allow to identify with certainty which population of *Abax* was sampled by Seidlitz when he established the subspecies *inferior*, even if there are no doubts about the systematic interpretation adopted by subsequent authors, starting with the revision by Fiori (1896).

Abax parallelepipedus lombardus Fiori, 1896

Fiori (1896) described *A. ater lombardus*, indicating Monte Grigna (Lecco, Italy) as the type locality and a distribution restricted to the central Alps. Schauberger (1927) reduced this subspecies to a variety of *A. p. inferior*, but this interpretation was not accepted by later authors.

Abax parallelepipedus germanus Schauberger, 1927
Abax parallelepipedus alpigradus Schauberger, 1927

Both described by Schauberger (1927) in his revision of the genus *Abax*. Distinctive characters of *germanus*: broader body and more elliptical elytra than the typical form. Pronotum with inner basal foveae short. Aedeagus apex broader and with pronounced angular expansion of the right side. Distribution: Upper and Lower Austria, Switzerland, Central and Southern Germany.

Distinctive characters of *alpigradus*: smaller in size and more slender than the typical form, similar to *curtulus*. Pronotal base distinctly narrower than elytral base. Distribution: restricted areas of Upper Austria (Sengsengebirge, Warscheneck, Höllengebirge, Sonnwendkogel near Goisern, outskirts of Hallstatt, Gosau).

In his work Schauberger interpreted *alpigradus* as a variety of *germanus*, but the reason for this choice remains unclear since these two subspecies have opposite differential characters from the nominotypical form. In fact, Schatzmayr (1944) and subsequent authors (Marcuzzi, 1953; Magistretti, 1965; Vigna Taglianti, 1993) considered *alpigradus* as a valid subspecies. Schatzmayr (idem) recorded *alpigradus* from the following Italian and Austrian localities: Friuli (east of the Tagliamento river), Dobratsch, Graz, Badgastein.

Abax parallelepipedus athesinus Depoli, 1939
Abax parallelepipedus tridentinus Depoli, 1939
Abax parallelepipedus baldensis Depoli, 1939
Abax parallelepipedus zoldanus Depoli, 1939

Four new subspecies were described by Depoli (1939) on the basis of specimens from localities scattered between Lake Garda and the Kvarner region. The creation of these new names, sometimes based on very few specimens, is an attempt to overcome the problems arising from the morphological variation observed in *A. parallelepipedus*, especially in the ssp. *inferior*. Schatzmayr (1944) did not consider these

Depoli's taxa and they are now considered junior synonyms of *A. p. inferior*.

Abax parallelepipedus euganensis Schatzmayr, 1944

Described by Schatzmayr (1944) on the basis of a series of specimens from the Euganean Hills and a single female from the Berici Hills (Veneto Region, NE Italy). The male has flattened elytral interstriae and less deep elytral striae, similarly to what is normally observed in females. This subspecific taxon was accepted by some later authors (Marcuzzi, 1953; Magistretti, 1965) but finally reduced to a junior synonym of *A. p. inferior* by Vigna Taglianti (1993).

TAXONOMICAL REMARKS

The systematic history of *A. parallelepipedus* spans over two centuries, during which many problems have accumulated. The descriptions of the nominotypical form and ssp. *audouini, i.e*. the oldest ones, do not report characters suitable to separate them from the other geographical subspecies. Subsequent nomenclatorial acts are often affected by uncertain data that make a correct diagnosis difficult. None of the later authors who proposed systematic revisions reported to have examined the typical series, for most of which it has been impossible to trace where they are presently held. However, thanks to the contribution of one reviewer of this paper, the holotypus of *A. p. contractus* (Heer, 1841) has been now traced in the collection of the ETH Zurich (Switzerland) and its taxonomical revision will be proposed in a next work.

This study does not aim to overcome the nomenclatorial problems, which would require solutions designed *ad hoc* for each taxon, instead, it attempts to propose a systematic review based on the examination of body traits and male genitalia morphology of a significant sampling of the different geographical populations. The entomological material was initially classified according to the taxonomy presently accepted by Vigna Taglianti (2014) and Bousquet (2003: 470):

Abax parallelepipedus parallelepipedus (Piller & Mitterpacher, 1783)
  = *Carabus ater* Villers, 1789
  = *Carabus clavipes* Bergstrasser, 1778
  = *Carabus depressus* Olivier, 1795
  = *Carabus dubius* Cuvier, 1833
  = *Abax podolicus* Motschulsky, 1850
  = *Carabus striola* Fabricius, 1792
Abax parallelepipedus alpigradus Schauberger, 1927
Abax parallelepipedus audouini (L. Dufour, 1851)
Abax parallelepipedus contractus (Heer, 1841)
Abax parallelepipedus curtulus (Fairmaire, 1856)
Abax parallelepipedus germanus Schauberger, 1927
Abax parallelepipedus inferior (Seidlitz, 1887)
  = *Abax ater athesinus* Depoli, 1939
  = *Abax ater athesinus var. anaunus* Depoli, 1939
  = *Abax ater athesinus var. dolomiticola* Depoli, 1939
  = *Abax ater baldensis* Depoli, 1939
  = *Abax ater euganensis* Schatzmayr, 1944
  = *Abax ater tridentinus* Depoli, 1939
  = *Abax ater tridentinus var. bondonensis* Depoli, 1939
  = *Abax ater zoldanus* Depoli, 1939
Abax parallelepipedus lombardus A. Fiori, 1896
  = *Abax ater lombardus var. lessinicus* Depoli, 1939
Abax parallelepipedus subpunctatus (Dejean, 1828)
  = *Abax ater subpunctatus var. istrianus* Depoli, 1939

MATERIALS AND METHODS

The morphological variation of *Abax parallelepipedus* was assessed by studying 792 specimens from several European regions, especially from Italy. As pointed out in the historical review, most of the oldest subspecies descriptions (or species then reduced to subspecies) do not provide useful diagnostic characters, therefore the material examined was classified on the basis of the descriptions by Schauberger (1927), Jeannel (1942) and Schatzmayr (1944).

All specimens were photographed and their images analysed to detect the following biometric variables: total length (TL), pronotal length (PL), maximum pronotal width (MPW), pronotal base width (PBW), elytral length (EL), maximum elytral width (MEW) and elytral base width (EBW). The reference points adopted to measure the biometric variables are shown in Fig. 1. All variables were detected using NIH Image software v. 1.45s (http://rsb.info.nih.gov/nih-image) and measurements are reported in millimetres.

Some morphometric indexes were calculated from the biometric data in order to point out the variation of shape in pronotum and elytra. These indexes are as follows:

- PWI (Pronotum Wideness Index) – MPW:PL ratio that varies proportionally with the transversal shape;

- PRI (Pronotum Roundness Index) – MPW:PBW ratio that varies proportionally with the narrowing of the pronotum base in comparison to its maximum diameter (positioned at around the middle);
- ESI (Elytra Slenderness Index) – EL:MEW ratio that varies proportionally with the slenderness of the elytra;
- ERI (Elytra Roundness Index) – MEW:EBW ratio that varies proportionally with the oval shape of the elytra, due to an increased difference between its maximum width around the middle and the width at the base.

The normal distribution of biometrical data and related morphometric indexes was assessed using the Kolmogorov-Smirnov test, while the assumption of equivalency of variances was verified by using the Bartlett's test (WinSTAT for MS-Excel v. 2007.1, provided by Robert K. Fitch). Despite the data resulting as normally distributed, the data related to *A. p. curtulus*, and sometimes also those related to *A. p. contractus*, showed non-homogenous variances (heteroschedastic data). Since one of the assumptions required to perform the Analysis of Variance (ANOVA) was violated, the statistical significance of the differences between the observed sample means was evaluated by the Kruskal-Wallis test. The statistical difference between the subspecific groups and the typical *parallelepipedus* was evaluated by means of the Games-Howell test, which is a non-parametric ANOVA *post-hoc* test designed to treat data sets having unequal variances and unbalanced sizes (Real-Statistics software, provided by Charles Zaiontz; http://www.real-statistics.com).

The morphological study was completed by dissecting and examining some male genitalia. The inner sac (membranous extension of the aedeagus) of some aedeagi was everted by injecting toothpaste (Berlov, 1992) or silicon glue (Brandmayr & Algieri, 1994) through the median foramen at the base of the aedeagus using a syringe.

The examined material is held in the following institutional and private collections: Natural History Museum of Venice, Natural History Museum of Trieste, Natural History Museum of Milan, Museum of Zoology of the University "La Sapienza" of Rome, private collection L. Zanella.

Results and Discussion

External characters. Length between 16 and 22 mm, robust parallel-sided shape, dorso-ventrally flattened body, shiny black colour. Head (including eyes) approximately 2/3 of the pronotum in width; frons de-

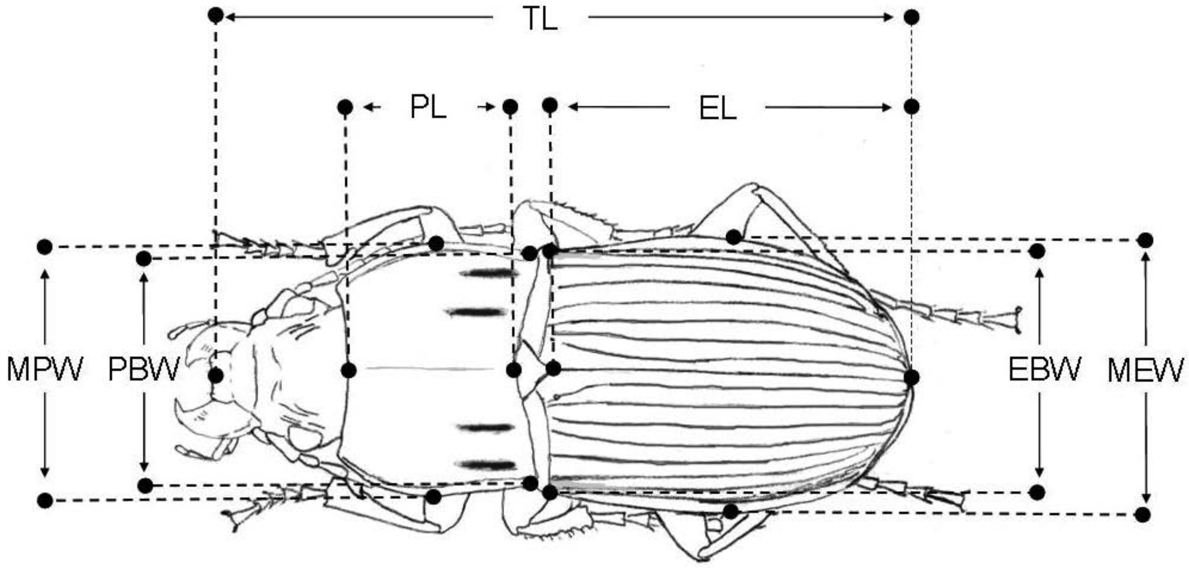

Fig. 1. Somatic position of the reference points adopted to detect the biometric variables.

limited by doubled and wrinkled furrows. Pronotum wider than long, with maximum diameter in the middle or just ahead, sides behind this almost straight and converging to rectangular hind angles. Pronotum lateral margins thick and marked by a deep furrow that fades at the hind angles. Pronotum base concave along its central margin and with two basal foveae each side, unpunctured but transversally wrinkled. Thin transversal wrinkles are scattered on head and pronotum, very superficial and sometimes only visible under the microscope by orienting the light source. Elytral shoulders toothed. Base of the seventh interstria raised in a sharp keel. Scutellary pore almost always present. Male elytra shiny and deeply striated, with interstriae slightly convex; female elytra dull and finely striated, with flat interstriae. Striae may be finely punctured, or all smooth. Brachypterous. A summary of the measurements is given in Tab. 1.

Male aedeagus. Length of the median lobe 5.5-6.5 mm. The apex (the part between the anterior margin of the median orifice and the tip of the lobe) forms a moderately flattened lamina, slightly asymmetric, with a small angular expansion along the right margin, in sub-terminal position (Figs. 2-4) which is reduced or absent in some subspecies. The terminal margin of the apex tip is bent towards the ventral side and looks as if it were cut transversally. Hereinafter, this abrupt termination is termed “truncation”. The arrows in Fig. 5A point to the angles that delimit this “tip truncation”, observable in dorsal vision by tilting the aedeagus apex at 45° towards the observer. The shape of the tip can vary markedly among the subspecies: in the nominotypical form it is broadly truncated as shown in Fig. 5A, whereas in other subspecies the tip is narrowly truncated, irregularly semi-rounded or roughly pointed (Fig. 5C-D).

Tab. 1. Biometric data (mean values in mm ± standard error, SE) related to the subspecies of *Abax parallelepipedus* currently accepted with the addition of ssp. *euganensis.*

Subspecies	N.	TL		PL		MPW		PBW		EL		MEW		EBW	
		mm	±SE	mm	±SE	mm	±SE	mm	±SE	mm	±SE	mm	±SE	mm	±SE
							Females								
parallelepipedus	31	18.37	0.14	4.21	0.03	6.40	0.05	5.85	0.05	9.95	0.08	7.40	0.06	6.26	0.05
audouini	25	18.58	0.19	4.21	0.05	6.33	0.07	5.81	0.07	9.95	0.11	7.35	0.07	6.22	0.07
germanus	13	19.14	0.32	4.35	0.09	6.60	0.13	5.98	0.11	10.12	0.14	7.48	0.12	6.41	0.12
inferior	51	18.25	0.12	4.18	0.03	6.36	0.04	5.74	0.04	9.70	0.06	7.19	0.04	6.15	0.04
alpigradus	13	17.23	0.19	3.87	0.07	5.92	0.07	5.28	0.07	9.25	0.12	6.83	0.09	5.78	0.07
lombardus	29	18.63	0.21	4.34	0.06	6.66	0.08	5.98	0.06	9.89	0.12	7.35	0.08	6.19	0.06
euganensis	50	19.22	0.11	4.49	0.03	7.03	0.05	6.35	0.04	10.16	0.07	7.73	0.05	6.70	0.04
contractus	40	18.34	0.10	4.14	0.03	6.16	0.05	5.34	0.04	9.63	0.06	7.10	0.05	5.73	0.04
curtulus	39	17.51	0.19	3.99	0.04	5.91	0.07	5.19	0.05	9.35	0.11	6.92	0.07	5.54	0.06
subpunctatus	42	20.58	0.16	4.74	0.03	7.19	0.05	6.50	0.05	10.87	0.09	8.12	0.06	6.87	0.04
							Males								
parallelepipedus	40	18.39	0.11	4.28	0.03	6.32	0.04	5.76	0.05	9.76	0.06	6.99	0.04	6.17	0.04
audouini	44	18.54	0.12	4.25	0.04	6.33	0.05	5.84	0.04	9.92	0.08	7.07	0.05	6.23	0.04
germanus	26	18.51	0.14	4.29	0.05	6.38	0.06	5.80	0.05	9.78	0.09	7.05	0.07	6.23	0.06
inferior	102	17.97	0.09	4.20	0.02	6.27	0.04	5.71	0.03	9.58	0.05	6.87	0.03	6.08	0.03
alpigradus	24	17.45	0.17	4.04	0.05	5.99	0.07	5.47	0.08	9.44	0.11	6.70	0.06	5.89	0.07
lombardus	52	18.43	0.12	4.35	0.03	6.47	0.05	5.86	0.04	9.75	0.08	6.90	0.05	6.14	0.04
euganensis	38	19.09	0.12	4.56	0.03	6.94	0.05	6.34	0.04	10.13	0.08	7.38	0.05	6.64	0.04
contractus	24	17.90	0.13	4.10	0.04	5.98	0.05	5.23	0.04	9.41	0.08	6.61	0.05	5.52	0.04
curtulus	46	17.31	0.11	4.00	0.03	5.81	0.05	5.18	0.04	9.16	0.07	6.46	0.04	5.49	0.04
subpunctatus	63	20.10	0.11	4.69	0.03	6.98	0.04	6.35	0.04	10.68	0.06	7.66	0.04	6.74	0.04

Internal sac (or endophallus). Membranous sac without sclerites or relevant thickenings. When everted and inflated, it appears composed of a main sac having irregular sub-cylindrical shape, with rounded almost conical ends, which expands distally in a narrower cylindrical lobe, curved to 90°, while two smaller globular expansions of different sizes develop laterally (Fig. 6). The inflated internal sac was

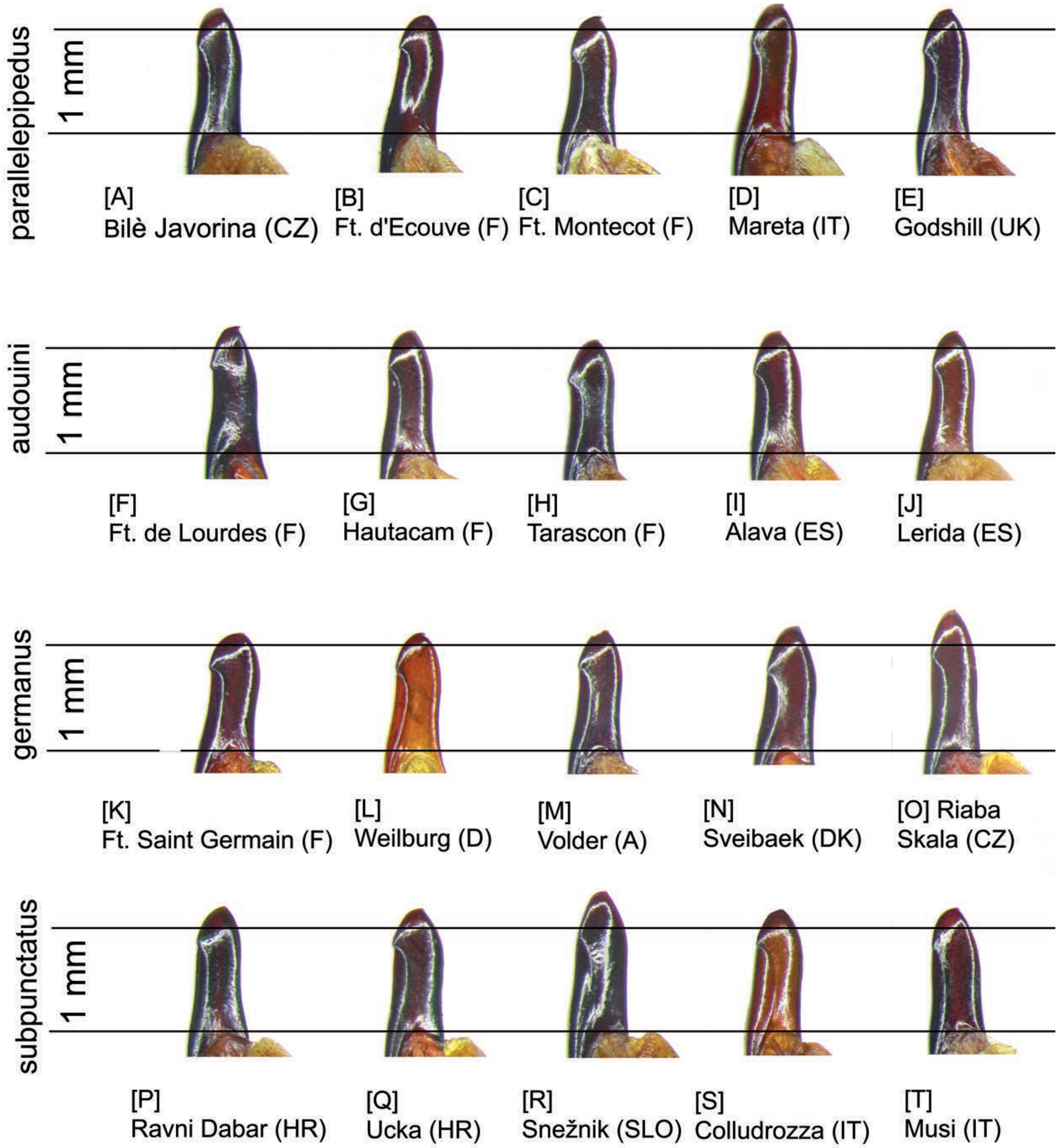

Fig. 2. Apexes of male genitalia in dorsal vision: A-E) *parallelepipedus*; F-J) *audouini*; K-M) *germanus*; N-R) *subpunctatus*.

already used in taxonomy of the genus *Abax* (Brandmayr, 1978), as well as to hypothesize the phylogenetic relationships among some species (Brandmayr & Zetto Brandmayr, 1994). However, in *A. parallelepipedus* it offers scarce characters for diagnoses at subspecific levels, mainly due to the high variation and absence of spines or sclerites. Only the pair *contractus*-*curtulus* frequently showed an additional small

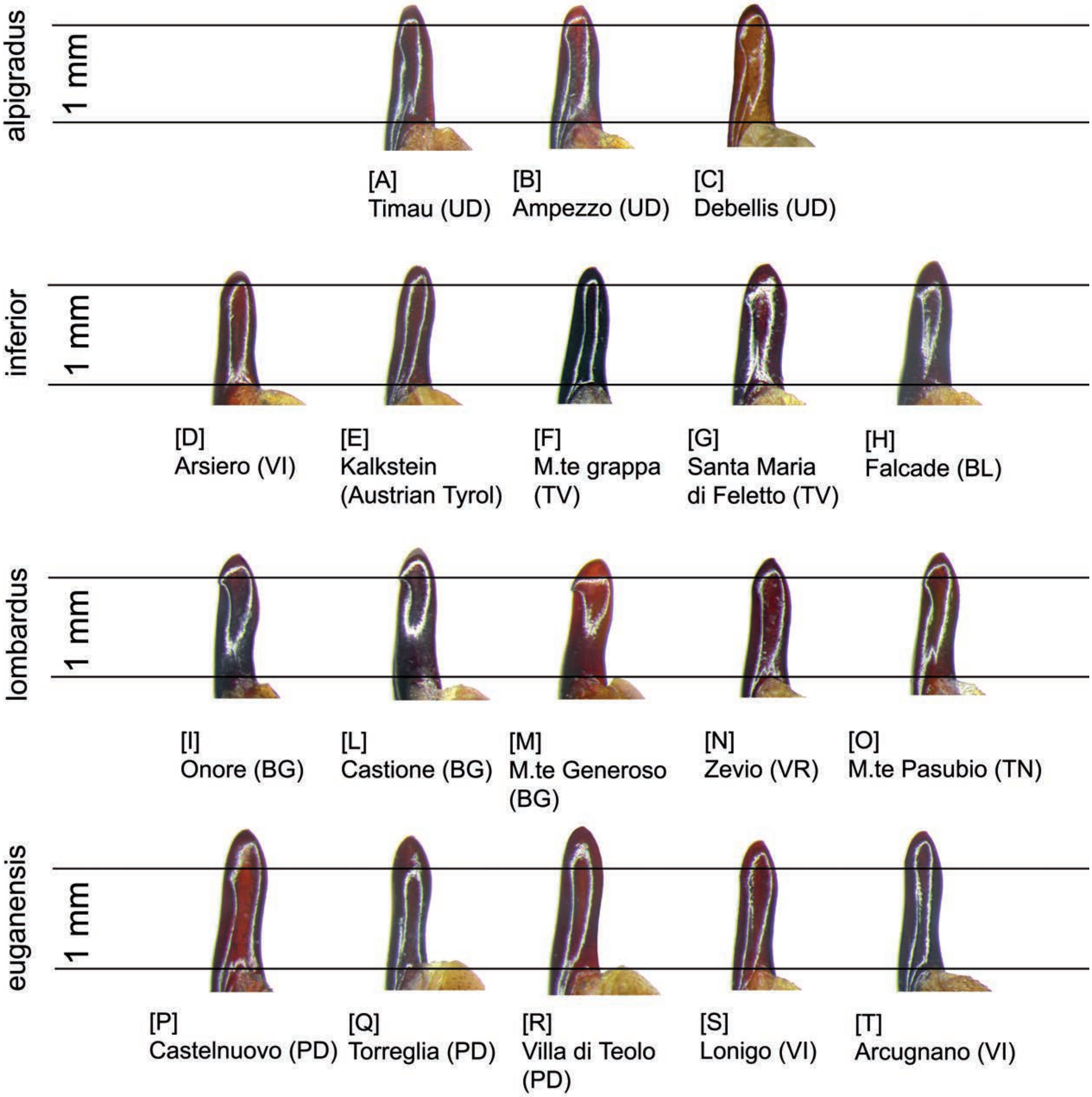

Fig. 3. Apexes of male genitalia in dorsal vision: A-C) *alpigradus*; D-H) *inferior*; I-O) *lombardus*; P-T) *euganensis*.

globular expansion at the left side of the distal lobe base (see arrow in Fig. 6A), highly variable in size and sometimes very small, not observed in the other subspecies. This supernumerary expansion of the internal sac confirms the relevant differentiation of *contractus* and *curtulus* from the typical *parallelepipedus*, as will also be shown by the biometric data. However, abnormal expansions, sometimes similar to those observed in *curtulus-contractus*, were also occasionally observed in other subspecies. These deformities were generally positioned at the base of the cylindrical distal lobe and were sometimes globular in shape, while others took the shape of straight tentacle.

Remarks on the material examined

Abax parallelepipedus parallelepipedus
(Piller & Mitterpacher, 1783)
Mean TL: 18.4 mm. Pronotum: outer basal foveae generally reach the basal margin, whereas the inner ones almost never. Elytra: elytral striae can be finely punctured or not. Aedeagus: apex with angular expansion always present along the right margin, variably marked. Apex tip sharply truncated, as in Fig. 5A. Distribution: it is the most diffused and occurs in most of the areal, perhaps excepting Spain, Slovenia and the greater part of Croatia. Its presence in Italy is very marginal and often represented by intermediate morphotypes occurring along the borders of the country.
Material examined: 31 ♀ & 40 ♂.
United Kingdom: Godshill (Hampshire) 1 ♂; Solway (Cumbria/Northumberland) 1 ♀ & 1 ♂; France: Brecé (Mayenne) 3 ♂; Colombiers du Plessis (Mayenne) 2 ♀; Ft. Réno-Valdieu (Orne) 13 ♀ & 8 ♂; Ft.d'Ecouve (Orne) 3 ♀ & 7 ♂; Ft. de Montecot (Eur & Loir) 1 ♀ & 1 ♂; Ft. de Saint-Germain-en-Laye (Le Mesnil-le-Roi – Yvelines) 1♂; Ft. de Grésigne (Tarn) 1 ♀ & 1 ♂; Mointagne Noir (Aude) 3 ♀; Italy: Mareta (BZ) 2 ♂; Czech Rep.: Bilé Karpaty 5 ♀ & 7 ♂.
Intermediate form to ssp. *inferior*: Austria: Irschen 1 ♀ & 6 ♂; Italy: Naz-Sciaves (BZ) 1 ♀ & 2 ♂.

Abax parallelepipedus audouini (L. Dufour, 1851)
Mean TL: 18.5 (♂) - 18.6 (♀) mm. Pronotum: scattered fine transversal wrinkles often marked, inner foveae long. Elytra: striae almost constantly unpunctured. Aedeagus: apex with angular expansion very sharp (Fig. 2F-J), tip truncation broad and sharp. Distribution: Val d'Aran (Spain), Pyrenees, mountains of Provence, Bouches-du-Rhone (Sainte-Baume) (Jeannel, 1942: 776). Among the material examined,

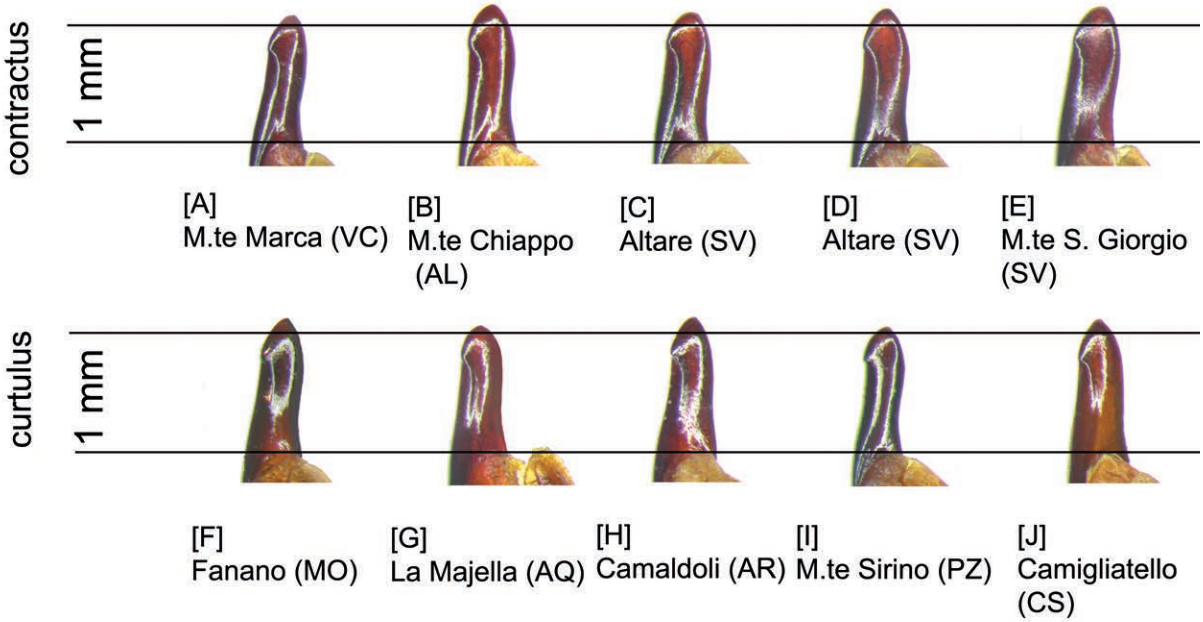

Fig. 4. Apexes of male genitalia in dorsal vision: specimens from the Italian Apennines.

specimens from the Cantabrian Mountains (Espinama, Picos de Europa) also had size and other characters compatible with *audouini*. It therefore seems that *audouini* occurs in the south of France, on the mountains of Provence as well as on the Pyrenees, spreading to Spain across the Cantabrian Cordillera and mountainous areas of Catalonia. However, part of the examined material had a smaller average size than expected (Formigueres, Ordesa, Val de Aran) or the aedeagus apex compatible with the typical form (Peña Cerrada, P.to Velate). My opinion is that the populations occurring in Spain and southern France have developed some peculiar characters but not definitely fixed or substantially different from those of *parallelepipedus*.

REMARKS: Dufour (1851) did not provide any useful information to the diagnosis of this subspecies, however, according to Jeannel (ibidem), it is larger and has wrinkles at basal foveae of pronotum. The characters proposed by Jeannel, as well as others reported here, do not allow a reliable diagnosis. This makes it very problematic to define the distribution of *A. p. audouini*.

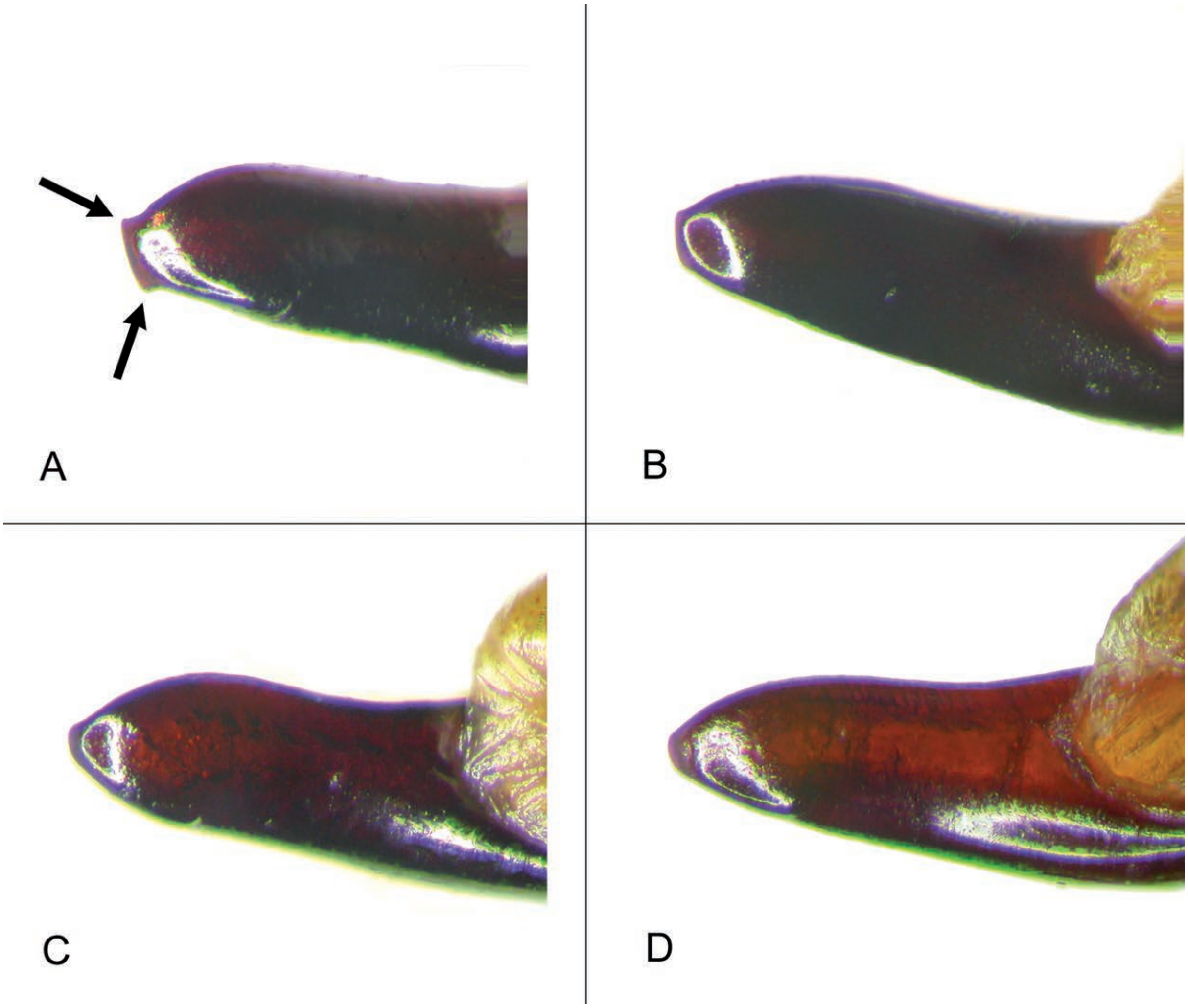

Fig. 5. Median lobe apex of the aedeagus in some subspecies of *Abax parallelepipedus*: A) *parallelepipedus* from Foret de Montecot, France (the arrows mark the angles delimiting the truncation of the tip); B) *inferior* from Falcade (BL), Italy; C) *contractus* from Altare Valbormida (SV) Italy; D) *curtulus* from Sala Berzanga (MO), Italy.

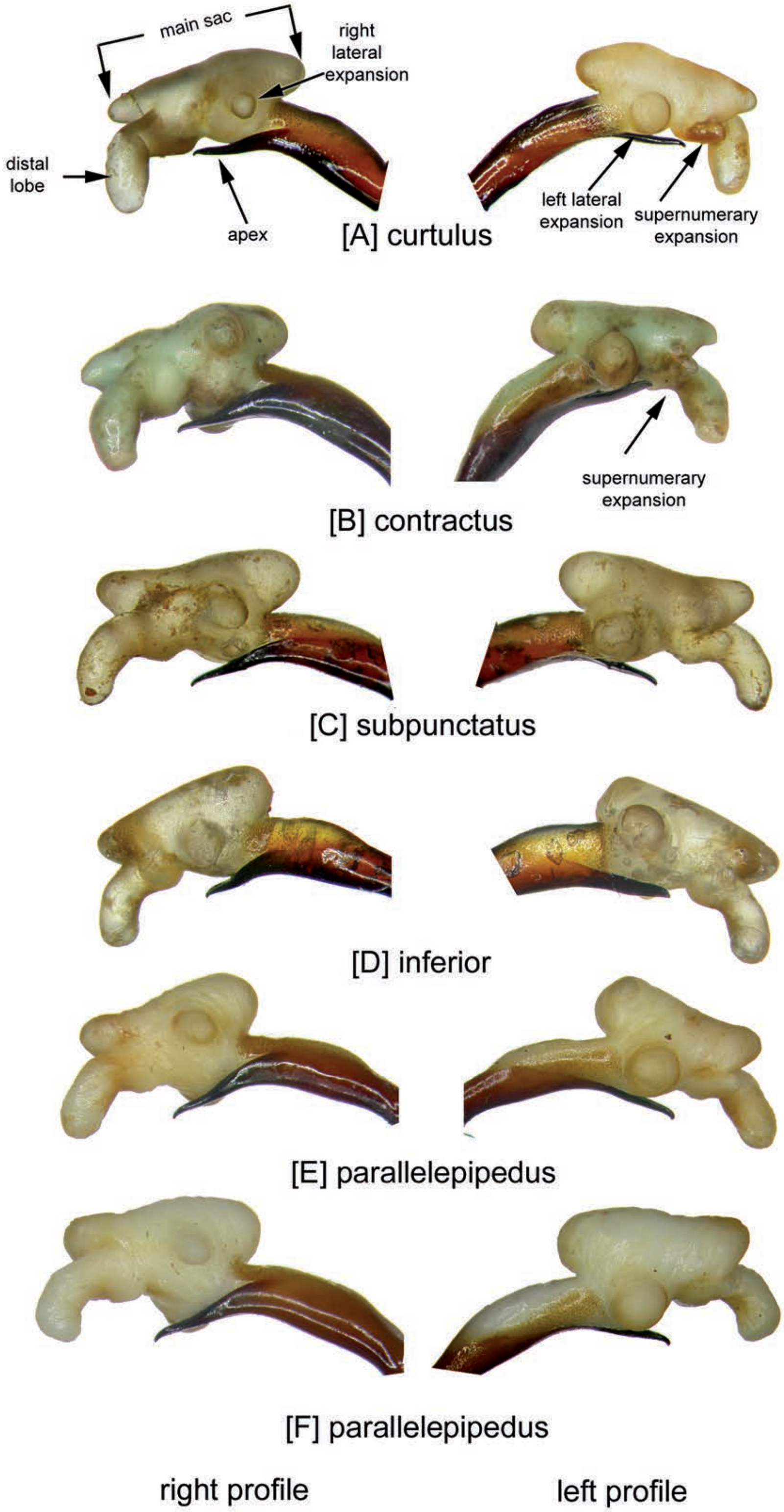

Fig. 6. Male genitalia with everted inner sac sampled from different subspecies of *A. parallelepipedus*: A) *curtulus* from Fanano (MO, Italy); B) *contractus* from Altare Val Bormida (SV, Italy); C) *subpunctatus* from Ravni Dabar (Croatia); D) *inferior* from Falcade (BL, Italy); E) *parallelepipedus* from Bilé Karpaty (Czech Rep.); F) *parallelepipedus* from Ft. d'Ecouve (Orne, France).

Material examined: 25 ♀ & 44 ♂.
France: Hautacam (Hautes Pyrénées) 1 ♂; Bois de Lourdes (Hautes Pyrénées) 4 ♀ & 5 ♂; Macaye (Pyrénées-Atlantiques) 1 ♂; Château-Pignon (Pyrénées-Atlantiques) 1 ♀ & 4 ♂; Tarascon (Ariège) 1 ♂; Formigueres (Pyrénées-Orientales) 2 ♂; Spain: Lérida-Pont Aut (Catalonia) 1 ♀ & 1 ♂; Val de Aran (Catalonia) 3 ♂; Ordesa (Aragón, Spain Pyrenees) 5 ♀ & 1 ♂; P.to Echegarrate (Navarra) 2 ♀ & 2 ♂; Peña Cerrada (Navarra) 1 ♀ & 1 ♂; P.to Velate (Navarra) 1 ♀ & 2 ♂; P.to de Urquiola (Biscay) 4 ♂; P.to de San Glorio 4 ♀ & 4 ♂ (Galicia), Espinama (Cantabria) 6 ♀ & 12 ♂.

Abax parallelepipedus germanus Schauberger, 1927
Mean TL: 18.5 (♂) - 19.1 (♀) mm. Pronotum: Inner basal foveae short and never reaching the thickened basal margin. Elytra: more elliptical than the typical form according to Schauberger (1927). Aedeagus: apex shorter and broader, always with marked angular expansion along the right side according to Schauberger (idem). Distribution: The most constant differential character was the short inner foveae, observed in specimens from Germany, Denmark, France, Switzerland, Austria, Czech Republic and Slovakia.
Remarks: No relevant and constant differential traits were observed on the aedeagus (Fig. 2K-O). This taxon has been considered by some authors (Kofler, 2005) as a junior synonym of the nominotypical form.
Material examined: 13 ♀ & 26 ♂.
Denmark: Svejbaek 3 ♂; Germany: Kassel (Nordhausen) 2 ♂; Weilburg (Hessen) 1 ♂; Kubach (Hessen) 1 ♂; Czech Rep.: Schneekoppe (Trutnov distr.) 1 ♀; Žilina (Kladno distr.) 1 ♀ & 1 ♂; Loučeň (Nymburk distr.) 1 ♀ & 4 ♂; Rozkoš (Znojmo distr.) 1 ♂; Dobrá (Stožec distr.) 1 ♂; Slovakia: Riaba skala (Humenné distr.) 1 ♂; France: ft. Saint-Germain-en-Laye (Yvelines dept.) 1 ♂; Fontainebleau (Seine-et-Marne dept.) 2 ♀ & 2 ♂; Vichy (Auvergne dept.) 1 ♀; Puy de Dôme (Auvergne dept.) 1 ♂; Switzerland: Bottmingen (Arlesheim dist.) 2 ♀ & 1 ♂; Blauen (Laufen distr.) 4 ♀ & 2 ♂; Stockhorn (Niedersimmenthal distr.) 1 ♂; Rolle (Nyon distr.) 1 ♂; Pissevache (Martigny distr.) 1 ♂; Austria: Volders (Tirol) 1 ♀ & 1 ♂.

Abax parallelepipedus subpunctatus (Dejean, 1828)
Mean TL: 20.1 (♂) - 20.6 (♀) mm. Pronotum: inner basal foveae elongated and sometimes reaching the basal margin (Fig. 7B). Elytra: striae almost always unpunctured. Aedeagus: apex not significantly different from the nominotypical form, although with a strong angular expansion (Fig. 2P-T). Apex tip is truncated but sometimes delimited by blunt angles. Distribution: Italian Karst, part of Styria, Slovenia and Croatia. Its distribution remains undefined in the eastern Dinaric Alps and surrounding regions.
Material examined: 42 ♀ & 63 ♂ (some ex-Yugoslavia localities are followed by their Italian name recurring in the literature earlier than 1945)
Austria: Graz 1 ♂; Italy: Piano d'Arta (UD) 1 ♀; Malchina (TS) 1 ♂; Sistiana (TS) 1 ♀ & 2 ♂; Grotta Noè - Aurisina (TS) 1 ♀; Grotta dell'Alce - Gabrovizza (TS) 1 ♀ & 4 ♂; Colludrozza (TS) 2 ♀ & 2 ♂; Basovizza (TS) 1 ♂; Slovenia: Radoha 4 ♂; Mt. Ljubnik-Škofja Loka 1 ♂; Trnovski gozd-Selva di Tarnova 1 ♀ & 10 ♂; Mount Nanos 1 ♂; Slivnika-M.te delle Streghe 1 ♂; Praewold-Prevallo 1 ♀; Veliko Gradišče-M.te Castellaro 3 ♂; Zidovonik Sežana-M.te Murato 2 ♀ & 1 ♂; Monte Hemana 1 ♀ & 1 ♂; Postojna-Postumia 7 ♀ & 1 ♂; Montpreis, Planina pri Sevnici 1 ♀; Divača-Divaccia 1 ♀ & 1 ♂; Vremščica-M.te Auremiano 1 ♀ & 1 ♂; Lipica-Lipizza 1 ♀; Rodik-Roditti 2 ♂; Schneeberg - M. Nevoso 1 ♂; Snežnik-M. Nevoso 2 ♀ & 3 ♂; Croatia: Mount Ucka-Monte Maggiore 3 ♀ & 3 ♂; Stolac (Velebit) 2 ♀; Ravni Dabar (Gospic Velebit) 8 ♀ & 9 ♂; Rijeka-Fiume 3 ♀ & 4 ♂.
Intermediate form to ssp. inferior: Italy: Musi (UD) 2 ♀ & 5 ♂

Abax parallelepipedus alpigradus Schauberger, 1927 (*sensu* Schatzmayr)
Mean TL: 17.5 (♂) – 17.2 (♀) mm. Pronotum: very variable in shape, as also occurs in *inferior*, sides sometimes similar to the typical *parallelepipedus* and other times slightly rounded. Aedeagus: apex lacks the angular expansion along the right side (Fig. 3A-C), resulting as very similar to *inferior* even if the shape is less slender. Distribution: The studied population is distributed along the Italian-Austrian border and is surrounded by *subpunctatus* to the east, *inferior* to the south and southwest, and the nominotypical form to the west and northwest.
Remarks: Schauberger (1927) described this form from some localities of the upper Austria. Unfortunately, it was possible to examine only specimens from Carinthia determined as *alpigradus* by Schatz-

mayr (collection of the Natural History Museum of Milan) and material from the Carnic and Julian Alps (collection of the Natural History Museum of Venice). None of these specimens were from the type localities indicated by Schauberger.

Material examined: 13 ♀ & 24 ♂

Austria: Bad Gastein (Salzburg) 4 ♂; Dobratsch (Carinthia) 1 ♀ & 1 ♂; Graz (Styria) 2 ♂; Italy: Forcella Lavardet (BL) 3 ♀ & 1 ♂; Collina (UD) 1 ♀; Timau (UD) 2 ♀ & 5 ♂; Passo di Pura (UD) 1 ♀ & 2 ♂; Ampezzo (UD) 2 ♂; Musi (UD) 1 ♀ & 2 ♂; Passo Tanamea (UD) 1 ♂; Mount Starmaz (UD) 1 ♂; Debellis (UD) 1 ♀ & 1 ♂; Mount Bernadia (Tarcento, UD) 1 ♀; Mount Peralba (BL) 2 ♀ and 2 ♂.

Abax parallelepipedus inferior (Seidlitz, 1887)

Mean TL: 18.0 (♂) – 18.3 (♀) mm. Head: thin transverse wrinkles are scarce and generally confined between the eye furrows. Pronotum: sides almost straight (most frequent) or slightly rounded between the maximum width and hind angles. Inner basal foveae often reach the basal margin. Elytra: striae variable in depth in males and often very finely punctured. Aedeagus: apex slender, without angular expansion on the right margin (Fig. 3D-H), although this can be faintly present in some local populations (Fig. 3G). Apex tip with narrow truncation delimited by blunt angles (Fig. 5B). Distribution: NE Italy, from Friuli Venezia Giulia to the western borders of Veneto (excepting the province of Verona and part of the province of Vicenza) and Trentino Alto Adige.

Remarks: Since the Seidlitz's description does not provide useful diagnostic characters, this study was based on morphological traits (mainly of the male genitalia) and geographical range reported by later authors (Schauberger, 1927; Schatzmayr, 1944; Magistretti, 1965). Some diagnostic characters suggested by Fiori (1896) and Porta (1903) were not confirmed on the material examined.

Material examined: 51 ♀ & 102 ♂.

Austria: Kalkstein (Tirol) 1 ♀ & 2 ♂; Italy: Prato della Drava (BZ) 1 ♀ & 1 ♂; Villabassa (BZ) 16 ♀ & 32 ♂; Sesto (BZ) 1 ♂; Lago di Braies (BZ) 1 ♀; Sarentino (BZ) 1 ♂; Gleno (BZ) 2 ♂; Favogna (BZ) 1 ♀; Val di Genova (TN) 1 ♂; Lavarone (TN) 1 ♀; Asiago (VI) 2 ♂; Val Digon (BL) 1 ♂; Cima Sappada (BL) 1 ♂; Cadore (VI) 1 ♂; Cortina (BL) 1 ♂; P.sso Giau (BL) 1 ♀ & 1 ♂; San Vito in Cadore 1 ♀ & 1 ♂; Auronzo (BL) 3 ♂; Lorenzago (BL) 1 ♀ & 3 ♂; Falcade (BL) 6 ♀ & 8 ♂; Alleghe (BL) 2 ♀ & 4 ♂; Forno di Zoldo (BL) 1 ♂; Rif. Vazzoler (Col Negro di Pelsa, BL) 1 ♂; Longarone (BL) 1 ♂; Pieve d'Alpago (BL) 2 ♀ & 2 ♂; Monte Cavallo (BL) 2 ♀ & 1 ♂; Pian Cansiglio (BL) 1 ♂; Monte Pizzoc (TV) 1 ♂; Valsalega (TV) 1 ♀; San Pietro di Barbozza (Valdobbiadene, TV) 7 ♀ & 10 ♂; Santa Maria di Feletto (TV) 1 ♀ & 1 ♂; San Michele di Feletto (TV) 1 ♂; Seren del Grappa (BL) 2 ♂; Monte Grappa 5 ♀ & 7 ♂; Ciano (TV) 1 ♀; Montello (TV) 2 ♂; Monte Raut (PN) 4 ♂. Intermediate form to ssp. *lombardus*: Passo Xomo (Posina, VI) 1 ♂; Pian delle Fugazze (TN) 1 ♂.

Abax parallelepipedus lombardus A. Fiori, 1896

Mean TL: 18.4 (♂) and 18.6 (♀) mm. Head: frons almost lacking fine transversal wrinkles. Pronotum: broad, disc more convex (Fig. 7C), sides often slightly rounded between the middle and the hind angles, inner basal fovea sharply separated from the outer one. Aedeagus: apex definitely longer than 1 mm and less broad than in the typical form (Fig. 3I-O), moderately sinuous along the left margin, as in the accentuated case shown in Fig. 3I. Apex tip roughly pointed or very narrowly truncated. Angular expansion along the right margin of the apex present in populations occurring to the west of Lake Garda (Fig. 3I-M), sometimes assuming the appearance of a small tooth, whereas it tends to decrease gradually until it disappears in the eastern populations (Fig. 6N-O). Distribution: from Monti Lessini (western Veneto region) to Lake Maggiore and Canton of Ticino.

Remarks: Populations from Monte Baldo, Monte Pasubio and Monti Lessini almost lack the angular expansion at the aedeagus apex and often show a slight reduction in body size. The pronotum is less broad and with sides less rounded. These traits led some authors (*e.g.* Magistretti, 1965) to interpret them as extreme morphotypes of *inferior*. I have interpreted them as *lombardus* because of the following characters that I consider very typical of this subspecies: convex pronotal disc and inner basal foveae well separated from the outer ones; aedeagus apex sinuous along the left side. However, since these mountains are at the eastern limit of its distribution, the presence of *inferior* cannot be excluded in some localities. The simultaneous presence (presumably in different localities) of these two subspecies recorded by Luigioni (1929: 128) at Monti Lessini is therefore plausible.

Interestingly, specimens with external characters typical of *lombardus*, but with aedeagus apex lacking sinuosity along the left margin, were recorded from Valtellina and other localities in the province of Sondrio. It is possible that these specimens are intermediate form to *germanus,* which occurs in Switzerland and perhaps in some Italian border localities.

Material examined: 29 ♀ & 52 ♂.

Italy: Maccagno (VA) 1 ♀; Campo dei Fiori (VA) 2 ♀ & 2 ♂; Gaggiolo (VA) 4 ♂; Monte Generoso (CO) 1 ♂; San Primo (CO) 1 ♀ & 3 ♂; Primaluna Valsassina (LC) 1 ♀; Valsassina (LC) 2 ♀; Pian di Bobbio (LC) 1 ♂; Piani Resinelli (LC) 3 ♂; Bus del Buter (Caprino Bergamasco, BG) 1 ♂; Valmalenco (SO) 1 ♂; Piazzatorre (BG) 1 ♀ & 5 ♂; Pizzo Arera (BG) 1 ♂; Castione della Presolana (BG) 4 ♀ & 4 ♂; Onore (BG) 2 ♀ & 4 ♂; Passo Vivione (BG) 1 ♀ & 1 ♂; San Colombano

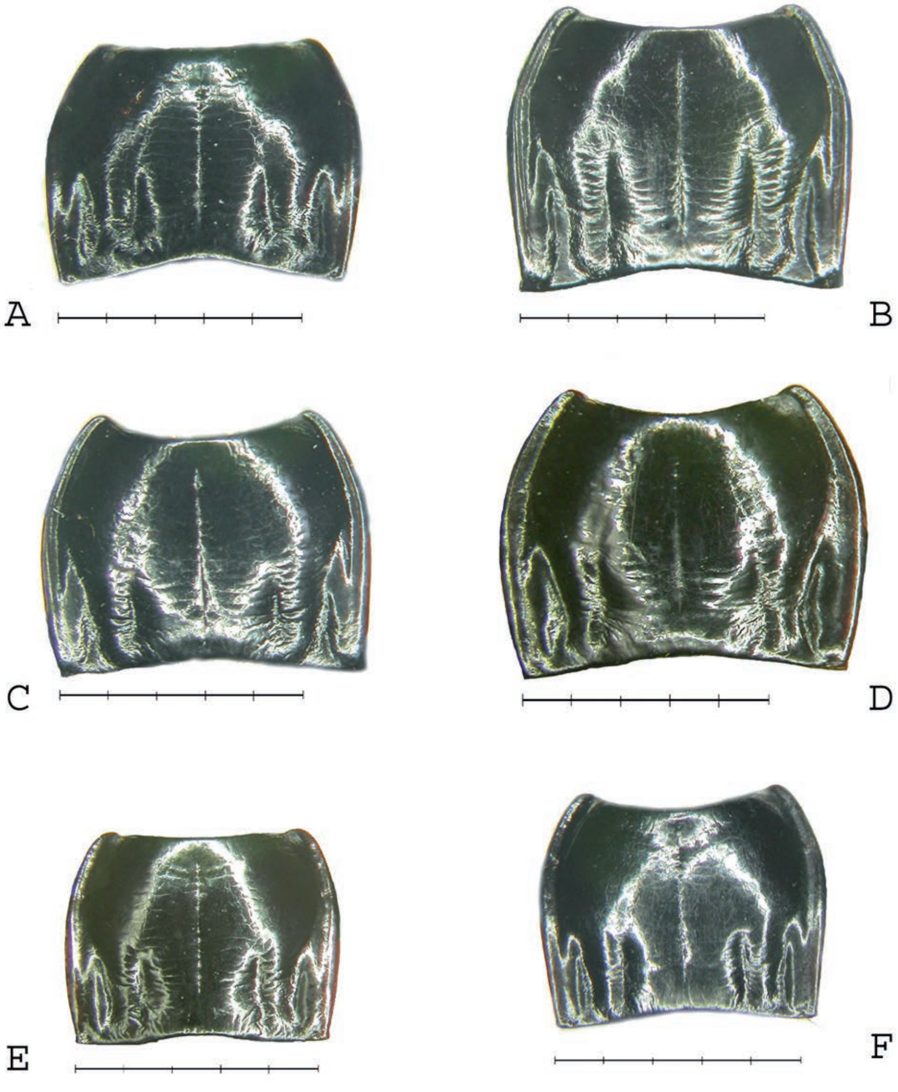

Fig. 7. Pronotum of some subspecies of *Abax parallelepipedus* (males): A) *parallelepipedus* [Montecot (F)]; B) *subpunctatus* [Ravni Dabar (HR)]; C) *lombardus* [Onore, BG (IT)]; D) *euganensis* [Castelnuovo, PD (IT)]; E) *curtulus* [La Trappola, AR (IT)]; F) *contractus* [Altare Valbormida, SV (IT)]. Sample scale: 5 mm.

(MI) 2 ♂; Monte Pizzoccolo (BS) 1 ♀; Fabrezza (BS) 1 ♀; Passo Croce Domini (BS) 2 ♀; Monte Baldo loc. Naole (VR) 1 ♀ & 1 ♂; Monte Baldo loc. Dossioli (VR) 2 ♀ & 5 ♂; Ferrara di Monte Baldo (VR) 1 ♂; Monti Lessini (Spiazzi, VR) 1 ♂; Cavalo di Fumane (Valpolicella, VR) 1 ♂; Pigozzo (Val Squaranto, VR) 1 ♀; Zevio (VR) 1 ♀ & 1 ♂; Monti Lessini – grotta Spluga Carpene (San Mauro di Saline, VR) 2 ♂; Valdagno (VI) 2 ♀ & 4 ♂.
Intermediate form to ssp. *germanus*: Alpe Musella (SO) 1 ♂; Ardenno (SO) 1 ♀; Sondrio 1 ♀ & 1 ♂.
Intermediate form to ssp. *inferior*: Monte Pasubio (Pian delle Fugazze, Vallarsa, TN) 1 ♀ & 1 ♂.

Abax parallelepipedus euganensis Schatzmayr, 1944
Mean TL: 19.1 (♂) - 19.2 (♀) mm. Pronotum: transverse and very stout, sometimes with sides weakly but regularly rounded (Fig. 5D). Disc less convex than in *lombardus* but more than in typical *parallelepipedus*. Elytra: proportionally broader and markedly parallel-side shaped. In males, interstriae almost flat even if this character is quite variable and not completely fixed. Aedeagus: apex slender and definitely longer than 1 mm, apical tip roughly pointed; left side less sinuous than in *lombardus* and angular expansion always lacking along the right side (Fig. 3P-T). In most differentiated specimens, the aedeagus apex is narrow at the basal tract and enlarges at the terminal section (Fig. 3Q). Distribution: endemic to the Euganean Hills (where the most differentiated form is observed) and Berici Hills, volcanic hills that rise to heights of 300 to 600 m from the Veneto plain, in the provinces of Padua and Vicenza respectively.
Remarks: It generally occurs in chestnut woods, in fresh and moist clearings or close to small bodies of stagnant or running water, although some findings were also recorded in meadows and cultivated fields (Ratti *et al.*, 1998).
Material examined: 50 ♀ & 38 ♂.
Italy. Colli Berici (VI): Arcugnano (grotta Spruggia dei Cavani) 11 ♀ & 3 ♂; Lago di Fimon 2 ♂; Lonigo 3 ♀ & 3 ♂; Lugugnano 6 ♂. Colli Euganei (PD): Baone (Val di Spin) 1 ♀; Castelnuovo 1 ♂; Monte Calbarina 1 ♀; Monte Ceva 1 ♀; Monte delle Are 5 ♀; Monte della Madonna 1 ♀ & 1 ♂; Monte Pendice 2 ♀; Monte Rua 12 ♀ & 6 ♂; Rocca Pendente (Teolo) 2 ♀; Schivanoia (Teolo) 1 ♀ & 5 ♂; Teolo 1 ♀; Torreglia 3 ♀ & 4 ♂; Torreglia (Lago) 1 ♀ & 1 ♂; Torreglia (Roccolo) 1 ♀ & 1 ♂; Valnogaredo 1 ♀; Valsanzibio 2 ♂; ;Villa di Teolo 3 ♀ & 3 ♂.

Abax parallelepipedus contractus (Heer, 1841)
Mean TL: 17.9 (♂) - 18.3 (♀) mm. Head: fine transversal wrinkles almost completely lacking. Pronotum: smaller than the nominotypical form. Fine transversal wrinkles on the disc almost completely lacking. Base narrow (Fig. 7F). Elytra: more oval than the nominotypical form, base narrower. Aedeagus: apex less robust, weak angular expansion along the right side (Fig. 4A-E), tip narrowly truncated or roughly pointed (Fig. 5C). Inner sac generally with a small supernumerary expansion at the base of the distal lobe (Fig. 6B). Distribution: from southern France to Italy across the Maritime Alps, spreading on the northern Apennines. The distribution of *contractus* remains not fully known; in addition to the localities listed for the material examined, the following are reported in the literature: France – Hautes-Alpes (Forest of Boscodon, near Embrun), French Maritime Alps at Saint-Martin-Vésubie and l'Authion (Jeannel, 1942: 777). Italy – Italian Maritime Alps: Valle Pesio, S. Bartolomeo, Certosa di Pesio, Pian delle Gorre, Monte Besimauda (Bisio *et al.*, 2013); Monte Fronté (Schatzmayr, 1944); Cottian Alps: Colle delle Finestre (TO) (Magrini & Degiovanni, 2013); Northern Apennines until the Apuan Alps, including the reliefs on the southern borders of Piedmont and Lombardy: Voltaggio (AL), Montecapraro (AL), Monte Lesima (PC/PV), Rivazzano (PV), Colle di Nava (IM), Genova, Monte Antola (GE/AL), Monte Penna (GE/PR), Recco (GE), Fontanigorda (GE), Romito (SP) (Magistretti, 1965).
Remarks: Interestingly, few findings are recorded across the Italian western Alps, so that *contractus* has no or very limited contacts with *lombardus*, which occurs in the Italian central Alps. Among the examined material, Monte Marca (Bielmonte, BI) was the locality closest to the range of *lombardus.* Here, the aedeagus was morphologically different (Fig. 4A) from the typical *contractus* sampled from the Ligurian Apennines (Fig. 4C-E), consistently with the hypothesis of an expansion from the Maritime Alps accompanied by a gradual, though modest, morphological differentiation.
Material examined: 40 ♀ & 24 ♂
Italy: Diano Marina (IM) 2 ♀; Altare Val Bormida (SV) 7 ♀ & 3 ♂; Cadibona (SV) 1 ♀; Monte Marca

(VC) 1 ♀ & 1 ♂; Monte San Giorgio (SV) 19 ♀ & 12 ♂; Montenotte (SV) 1 ♂; Molessana (GE) 1 ♀; Monte Chiappo (Cabella Ligure, AL) 4 ♀ & 4 ♂; Monte Colletta (Brallo di Pregola, PV) 1 ♀ & 1 ♂; Passo di Brallo (PV-PC) 3 ♀ & 2 ♂; Levanto (SP) 1 ♀.

Abax parallelepipedus curtulus (Fairmaire, 1856)
MEAN TL: 17.3 (♂) - 17.5 (♀) mm. HEAD: fine transversal wrinkles almost completely lacking. PRONOTUM: smaller than the nominotypical form. Base narrow, but proportionally less than in *contractus*. Fine transversal wrinkles on the disc almost completely lacking. ELYTRA: more oval as a consequence of their narrower basal margin. AEDEAGUS: apex less robust than in other subspecies; quite variable in shape (Fig. 4F-J), generally weakly restricted from base to tip. Tip roughly pointed (Fig. 5D). In southern populations the apex can be more slender and sinuous as shown in Fig. 4I. Angular expansion generally present along the right side. Inner sac of aedeagus generally with a small supernumerary expansion at the base of the distal lobe (Fig. 6A). DISTRIBUTION: along the Apennines from Emilia Romagna to Calabria, including the reliefs on Gargano (Puglia region).
MATERIAL EXAMINED: 39 ♀ & 46 ♂.
Italy: Ponte Samone-Guiglia (MO) 1 ♂; Zocca (MO) 2 ♀; Montese (MO) 2 ♀; Fanano (MO) 2 ♀ & 1 ♂; Capanno Tassoni (Fanano, MO) 1 ♂; Boschi di Carrega (Sala Baganza, PR) 1 ♀ & 1 ♂; Campigna (FC) 2 ♀ & 3 ♂; Taviano (PT) 1 ♂; Passo della Futa (FI) 1 ♂; Popolano (FI) 2 ♀; Sesto Fiorentino (FI) 2 ♂; Borselli (FI) 2 ♀ & 2 ♂; Vallombrosa (FI) 1 ♀ & 2 ♂; Camaldoli (AR) 3 ♀ & 4 ♂; La Trappola (AR) 1 ♂; Monti Sibillini - Sorgenti Fargno (MC) 1 ♀; M. dei Fiori? (AP/TE) 1 ♂; La Majella – Scanno (AQ) 1 ♂; loc. Prato Rosso (Pescasseroli, AQ) 2 ♀; Monte Marsicano (AQ) 1 ♀ & 1 ♂; Forca d'Acero (Opi, AQ) 2 ♀ & 1 ♂; Parco d'Abruzzo – M.te Difesa 1 ♀; Riofreddo (RM) 1 ♀ & 4 ♂; Monte Gargano (FG) 3 ♀; Monte Vulture (PZ) 1 ♀ & 1 ♂; Monte Viggiano (PZ) 2 ♂; Monte della Madonna (Viggiano, PZ) 2 ♀; Monte Sirino (PZ) 1 ♀ & 2 ♂; Lago della Duglia (Parco del Pollino, PZ) 5 ♀ & 10 ♂; Camigliatello Silano (CS) 2 ♀ & 3 ♂.

MORPHOMETRICS

A synthesis of the mean biometric data is shown in Fig. 8. The TL resulted as very variable and the subspecific subsets are shown in Fig. 8A,B in order of increasing size. As predictable, other biometric variables ranged consistently with the TL, leading to similar size ranking (Fig. 8C-L). Interestingly, *parallelepipedus* occupies a quite central position in the biometric ranges of all the considered variables. Besides, despite some exceptions, the ssp. *inferior*, *germanus, lombardus* and *audouini* resulted as statistically homogeneous with the nominotypical taxon. Considering this "central" group, therefore, the biometric variability does not seem to reveal any oriented differentiating process among the sampled populations, but rather a random morphological variation. This would be consistent with the predictions of the IBD model proposed by Wright (1943), according to which a random selection of traits occurs among semi-isolated subpopulations with short dispersal capacity inhabiting a large territory. However, considering the groups at the extremes of biometric ranges, it is possible to spot some well-oriented diverging trends.

Among the largest subspecies, the statistical analysis attests that *euganensis* and *subpunctatus* constantly show higher biometric values than the group homogeneous with *parallelepipedus*. Interestingly, the body width variables are very similar in *euganensis* and *subpunctatus* (Fig. 8C-L), despite this latter having a significantly higher TL (Fig. 8A,B). This suggests that *euganensis* tends to increase the body width more than its length, especially enhancing the transversal shape of the pronotum (Fig. 8C,D).

Analogously, among the small subspecies, *contractus* and *curtulus* show a remarkable reduction in width of the elytral base, as well of the pronotum base (Fig. 8E-H). The same trend is observed for the maximum width of both these body regions (Fig. 8C,D,I,L), but in less relevant measure. This means that, in *contractus-curtulus*, the shape of the pronotum and elytra tend to become proportionally narrower at their bases, besides being definitely smaller.

A. p. alpigradus shows biometric values similar to *contractus-curtulus*, but has pronotal and elytral bases wider, especially in males.

The morphometric indexes, which are affected by the variations of proportional ratios among the biometric variables rather than by their change in absolute value, confirmed the changes in body shape above described. These indexes (Fig. 9) show a much broader statistical homogeneity among groups than the biometric variables, attesting that change in size often does not correspond to substantial modifications of the

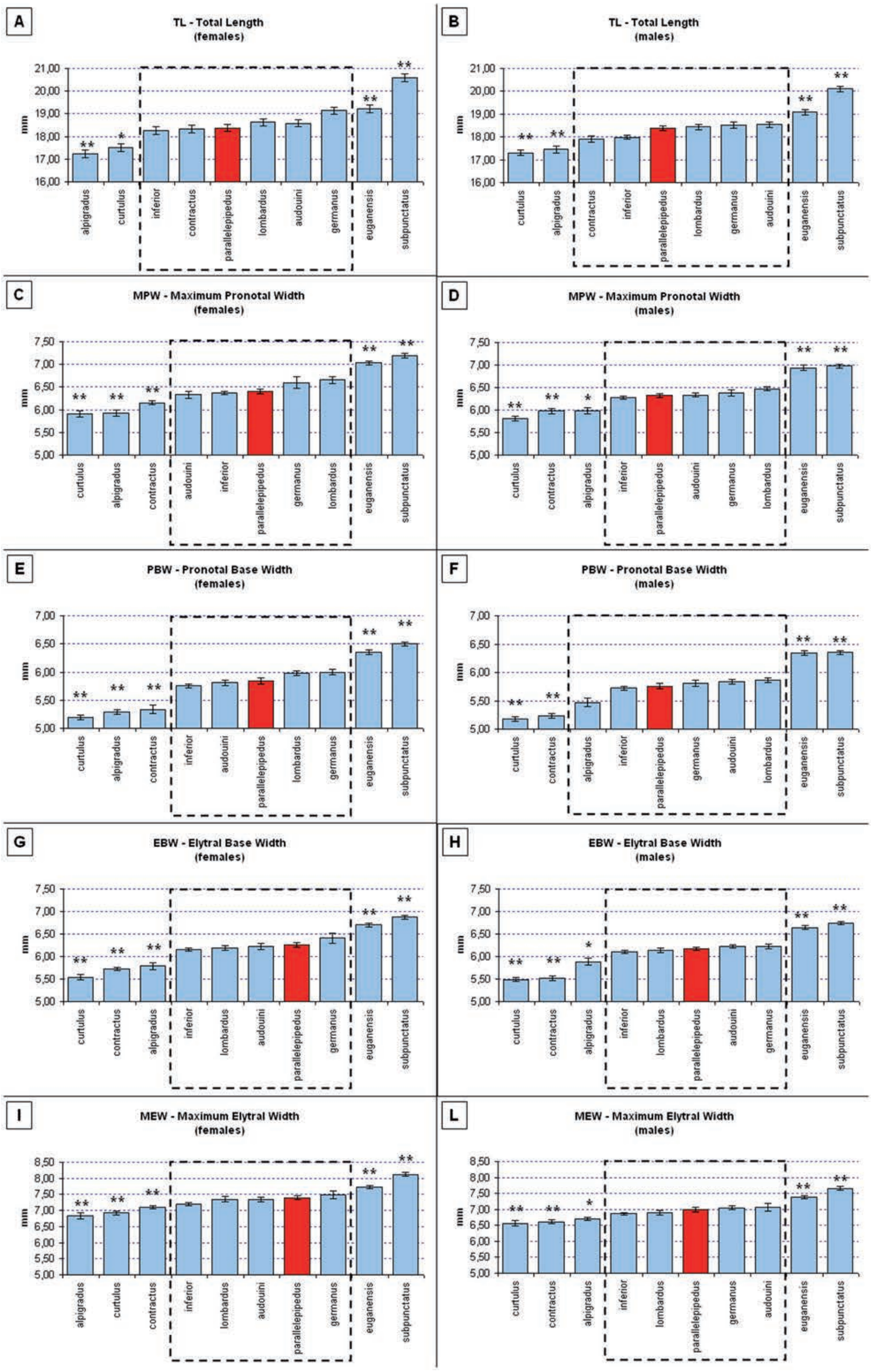

Fig. 8. Mean values (with standard error bars) of biometric variables detected in the subspecies of *A. parallelepipedus*. The histograms grouped by the dashed line are statistically homogenous with the nominotypical subspecies according to the Games-Howell test, while the asterisks mark the histograms statistically different (*P<0.05; **P<0.01).

body shape. For instance, *alpigradus* and *subpunctatus*, despite being placed at the opposite extremes in several variable ranges, are both constantly homogenous with the nominotypical subspecies when analysed by means of the indexes. However, consistently with the interpretations proposed for the biometric data, the morphometric indexes attest that *euganensis* and the pair *curtulus-contractus* are the subspecies most differentiated from the typical *parallelepipedus*.

In *euganensis*, pronotum becomes more transverse (Fig. 9A,B) and elytra tend to enlarge in respect to their length, especially in females (Fig. 9E,F). The elytral ratio between maximum width and base (ERI) is also reduced (Fig. 9G,H), enhancing the parallel-sided shape of the body. As a result, *euganensis* has a decidedly broader shape than *parallelepipedus*, enlarging the pronotum more than the elytra.

On the contrary, *curtulus* and *contractus* show a pronotum that not only becomes proportionally smaller, but also less transverse, assuming an appearance that is reminiscent of the genus *Pterostichus*. This trend is shared between these two subspecies as highlighted by the decrease of their PWI in comparison to *parallelepipedus* (Fig. 9A,B), although this morphological differentiation does not assume statistical significance according to the Games-Howell test, which is very conservative. Furthermore, especially in *contractus*, pronotum base narrows more than the maximum width, so increasing the PRI (Fig. 9C,D). Analogously, both *contractus* and *curtulus* show an increased ERI, attesting to the trend of elytra to develop more oval sides (Fig. 9G,H).

Therefore, interestingly, the pair *contractus-curtulus* share similar changes of both size and body shape, evolving in a direction diametrically opposed to that observed in *euganensis*.

The other subspecies, despite the variation in size pointed out by the biometric variables, maintain a body shape substantially similar to the typical *parallelepipedus,* according to the data provided by the morphometric indexes.

CONCLUSIONS

Abax parallelepipedus is a brachypterous species with limited or absent gene flow between geographically distant populations. It is not surprising, therefore, that morphologically differentiated populations are observed in the presence of a very broad distribution. However, the subspecific taxa described in the literature attest to the difficulty experienced by entomologists in distinguishing between geographical variations and subspecies, defined as evolving populations that represent partially isolated lineages of species (Braby *et al.*, 2012). These latter have the potential to split into new species and, from a systematic point of view, fall within the “grey zone” described by De Queiroz (2007) as a transition phase that a lineage crosses during the process of separation and divergence (speciation). Unfortunately, a lack of standardized criteria for the diagnosis of subspecies makes it very difficult to recognize them within geographical variations and delimit their boundaries (Thorpe, 1987; Braby *et al.*, 2012).

Abax parallelepipedus shows a very complex pattern of morphotypes and subspecies that have probably originated both from ecological factors and historical processes. In this study, the geographical variation was evaluated by means of a morphometric approach, adopting statistical methods in order to establish which populations had biometric traits distinct from the nominotypical subspecies. Furthermore, the morphometric results were confirmed and supplemented by studying the morphology of the male genitalia, according to the approach proposed by Ortuño & Arribas (1992) for distinguishing the subspecies of *Abax pyrenaeus* (Dejean, 1828). The data reported here suggest that some populations are actually differentiating from the nominotypical subspecies.

One of the main interferences encountered performing the morphological analyses was due to the relevant variation in size observed. Extreme values of TL were detected in populations having broad distribution, as in the case of *subpunctatus* and *curtulus*, respectively the largest and smallest, but also in small and local populations, as in the case of *alpigradus* (*sensu* Schatzmayr). This latter was clearly differentiated from the surrounding populations on the basis of its small size, but showed somatic proportions consistent with other groups and was substantially assimilated to *inferior* on the basis of the male genitalia morphology. A significant change of TL can actually reveal an adaptive trend, especially when constantly expressed in widespread populations (as in the case of *subpunctatus* and *curtulus*). Nevertheless, given the complex pattern of variation observed for this variable among the sampled populations, it is preferable to leave aside the TL as diagnostic character, focusing on

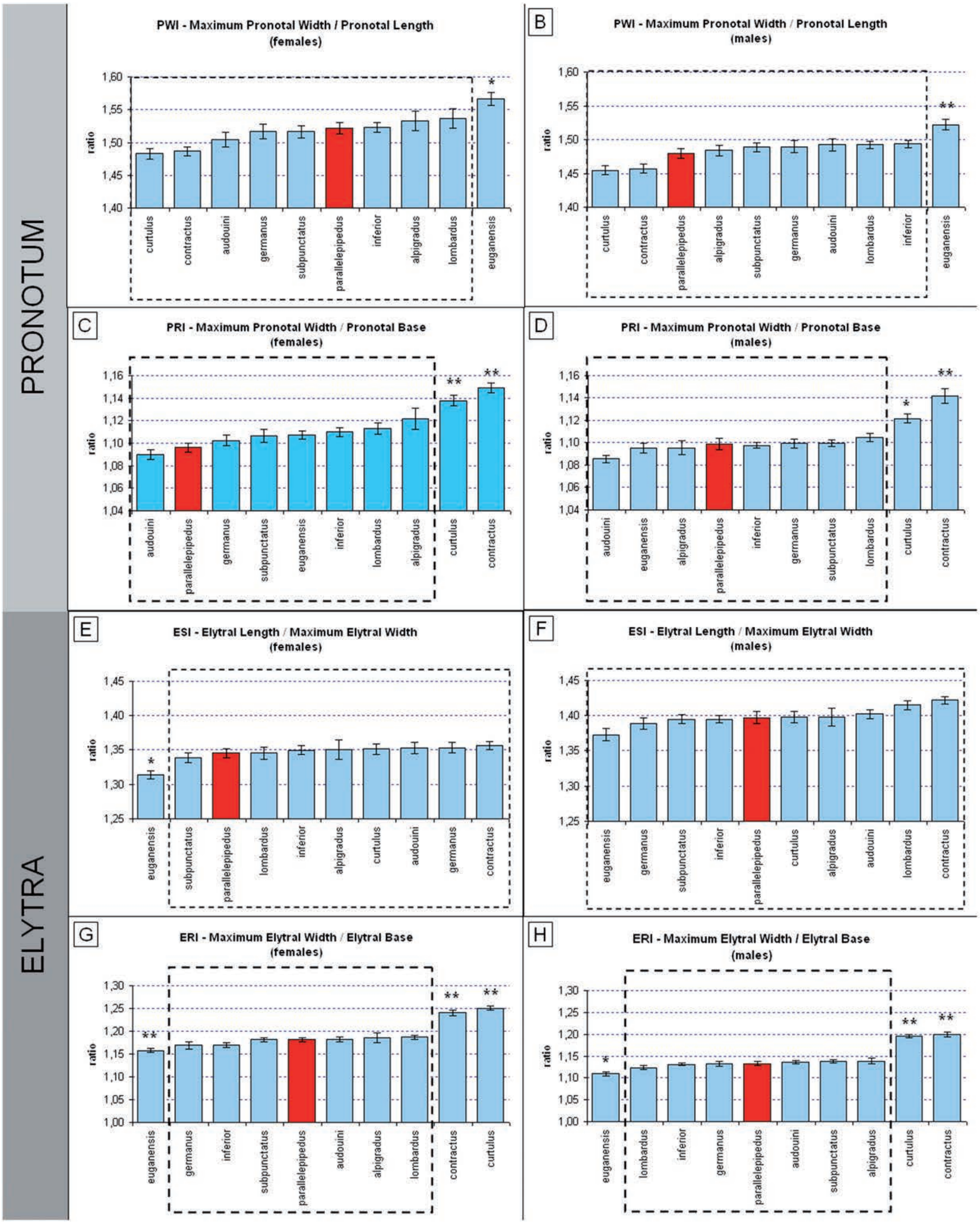

Fig. 9. Mean values (with standard error bars) of the morphometric indexes calculated for the subspecies of *A. parallelepipedus*. The histograms grouped by the dashed line are statistically homogenous with the nominotypical subspecies according to the Games-Howell test, while the asterisks mark the histograms statistically different (*P<0.05; **P<0.01).

other biometric variables and above all on the morphometric indexes, which better reveal changes in body shape.

The combined analysis of morphometric data and male genitalia suggest that the populations occurring in central and western Europe (*i.e. subpunctatus*, *germanus* and *audouini*), with the exception of the Italian territory (*i.e. inferior*, *alpigradus sensu* Schatzmayr, *euganensis*, *lombardus*, *contractus* and *curtulus*), can be synonymized to the nominotypical subspecies.

The ssp. *germanus* and *audouini* showed a slightly stouter size than the typical *parallelepipedus* (Fig. 8), as indicated by Schauberger (1927) and Jeannel (1942) respectively, but this character does not induce any relevant variation of the somatic proportions (Fig. 9). According to the observations made in this study, other secondary differential characters of these two taxa, as well as the shape of their aedeagus apex (Fig. 2), also do not support a subspecific status.

An analogous situation was detected for *subpunctatus*, which did not show significantly differentiated traits apart from the large size. Nevertheless, the strong and constant difference in size occurring between *subpunctatus* and the neighbouring Austrian and Italian populations marks a relevant discontinuity. This suggests that this morphotype, although not separable at subspecific level, might be the extreme branch related to the expansion of populations differentiated in eastern Europe and later moving westward along the southern corridor across the Dinaric Alps. However, these hypotheses would require an extensive investigation of eastern populations of *Abax parallelepipedus*, which has not so far been undertaken.

With regard to the aedeagus morphology, a general comment can be proposed for the extra-Italian populations. The apex shape shows a substantial homogeneity, especially in the angular expansion on the right margin (Fig. 2) and truncated tip (Fig. 5A). The stouter morphotypes, *i.e. germanus*, *audouini* and *subpunctatus*, generally have an aedeagus apex with more pronounced angular expansion. Furthermore, the aedeagus of *audouini* generally shows a particularly marked truncation of the apex tip, delimited by sharp angles. Although all these morphological details do allow recognition of local populations, they do not substantially change the aedeagus shape, which falls within the variation of the typical *parallelepipedus*.

All these results make it reasonable to propose the synonymization of *germanus*, *audouini* and *subpunctatus* with the nominotypical *parallelepipedus*.

Instead, the high morphological variation observed among European populations suggests some interesting biogeographical cues. Among the studied specimens, particular attention should be paid to those from the Czech Republic and Slovakia. Interestingly, specimens from these regions can be externally interpreted as *germanus* or *parallelepipedus* depending on the catch locality and, above all, show a relevant variation of their aedeaga (Fig. 10). As can be observed, the specimen from Žilina (Fig. 10A) has some traits typical of *inferior*, the one from Dobrà (Fig. 10B) has a very robust shape, whereas the one from Rozkos (Fig. 10C) is slender and elongated in a manner similar to specimens of *lombardus* from the province of Sondrio (Italy). However, despite this variation, all these aedeaga have the same tip truncation observed in the nominotypical form.

These external and aedeagic traits, observed in contiguous (parapatric) populations inhabiting the territories indicatively coinciding with Bohemia and Moravia, are separately fixed in some of the main morphotypes classified as nominotypical *parallelepipedus*, *germanus*, *inferior* etc. Considering the geographical distribution of the discussed morphotypes, the most parsimonious hypothesis is that Bohemia and Moravia might be the area of origin from which *A. parallelepipedus* started its geographical diffusion throughout the rest of Europe, where a complex combination of genetic drift, local selective factors and historical events favoured the selection of different morphotypes. The Pleistocene glaciations are probably the driving factor that pushed part of the species towards southern glacial refugia (Iberian Peninsula, Italian Peninsula and Balkans), while some populations survived in central European refugia located in the Carpathians and north of the Alps. The existence of multiple glacial refugia in the north of the Alps has also recently been hypothesized by Homburg *et al.* (2013) to explain the origin of allopatric subspecies of *Carabus irregularis*. Interestingly, the existence of glacial refugia in the Carpathians (Provan & Bennett, 2008; Schmitt, 2009), as well as the role of cryptic northern refugia (Habel *et al.,* 2010; Stewarth *et al.*, 2010), have recently assumed increasing importance for explaining the biodiversity distribution in Europe.

The alternative hypothesis compatible with the described scenario instead appears hardly acceptable, as it would require a centripetal migration of differentiated populations from the periphery towards the centre of Europe, with progressive loss of their characteristic traits.

In this context, particular attention should be paid to the populations inhabiting the mountainous territories of Austria. It seems that the expansion of the primitive population with high genetic variability over this mountainous region had produced a mosaic of localized morphotypes, which does not find correspondence in the other mountain systems farther from the potential point of origin of the species diffusion (*e.g.* Swiss Alps, Dinaric Alps, Pyrenees, etc.). Although few specimens were examined, the detected data and information reported in the literature attest to the occurrence of the following subspecies/morphotypes in Austria: *germanus* (Volders, Nordtirol; Fig. 2M) and *inferior* (Kalkstein, Osttirol) in Tyrol; typical *parallelepipedus* (Irschen) and *alpigradus* (Dobratsch) in Carinthia; again *alpigradus* in Salzburg (Bad Gastein), Styria (Graz) and Upper Austria (Schauberger, 1927); finally, *subpunctatus* in Styria (Graz).

Of course these data are inadequate to represent the complicated geonemy of the morphotypes occurring in Austria, nevertheless they point out the relevant effects produced by a limited gene-flow on the high morphological plasticity of *A. parallelepipedus*. It is generally accepted that organisms with low dispersal capacity would be more sensitive to IBD and show stronger effects of geographical barriers on their morphologies (Monsen & Blouin, 2004). The strong impact of physical barriers on the genetics of *A. parallelepipedus* was also detected for modest interruptions of the environmental continuity (Keller *et al.*, 2003a, 2004). Therefore, the discontinuous contiguity of differentiated populations in the Austrian Alps, and the development of subspecies with the increasing distance from the origin of the migration, as recorded in the Italian Alps, are consistent with the selection or genetic drift caused by widespread mountainous barriers.

The map in Fig. 11 gives a concise summary of the comments and ideas proposed so far: it shows the hypothetical routes followed by *Abax parallelepipedus* during its geographical spread throughout Europe (both subspecies and morphotypes are represented).

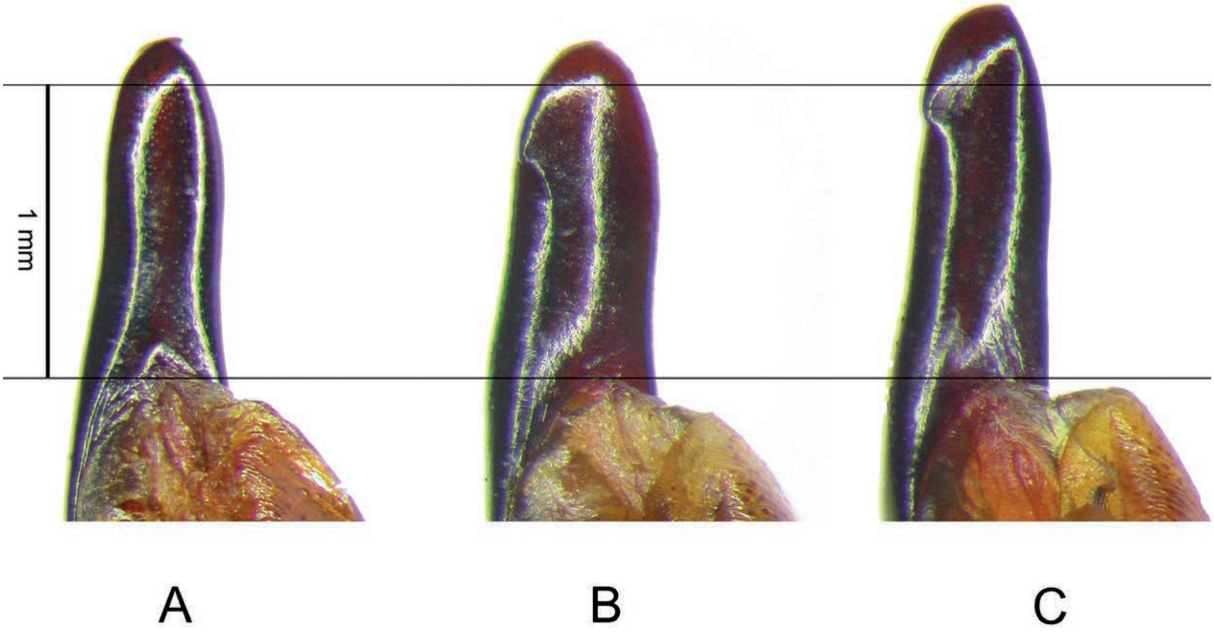

Fig. 10. Three morphological examples of aedeagus apex in specimens from the Czech Republic: A) Žilina (central Bohemia); B) Dobrà (Stozek distr.; southern Bohemia); C) Rozkoš (Moravia).

Biogeographic remarks on the Italian subspecies

It is known that Italy was one of the main refugia for European biota during the Quaternary glaciations (Hewitt, 1996, 2004; Tribsch & Schönswetter, 2003; Schönswetter *et al.*, 2005; Habel *et al.*, 2010) and that the Alps interfered with the northward post-glacial expansions of these peripheral populations (Schmitt, 2009). Taberlet *et al.* (1998) studied the phylogenies of 10 European taxa (plants, mammals, amphibians and arthropods), disclosing that the Italian lineages were often isolated due to the presence of the Alpine barrier, favouring intraspecific polymorphism and the development of endemic lineages. Conclusions consistent with this hypothesis were also reached to explain the morphological and genetic differences observed in subspecific populations of *Carabus solieri* with transalpine distribution (Garnier *et al.*, 2004). The morphological data discussed in this study seem to confirm the biogeographic role of the Alpine barrier, which would have promoted the independent evolution of the populations of *A. parallelepipedus* migrated over the Alps before and/or between the glaciations.

The main subspecific taxa occurring in the Italian Alps are represented by *inferior* and *lombardus*, while the most eastern morphotype, *A. p. subpunctatus*, remains local to the karst area of Venezia Giulia, only marginally involving the Italian territory. The presence of intermediate forms along the Italian border allow these two subspecies to be put in connection

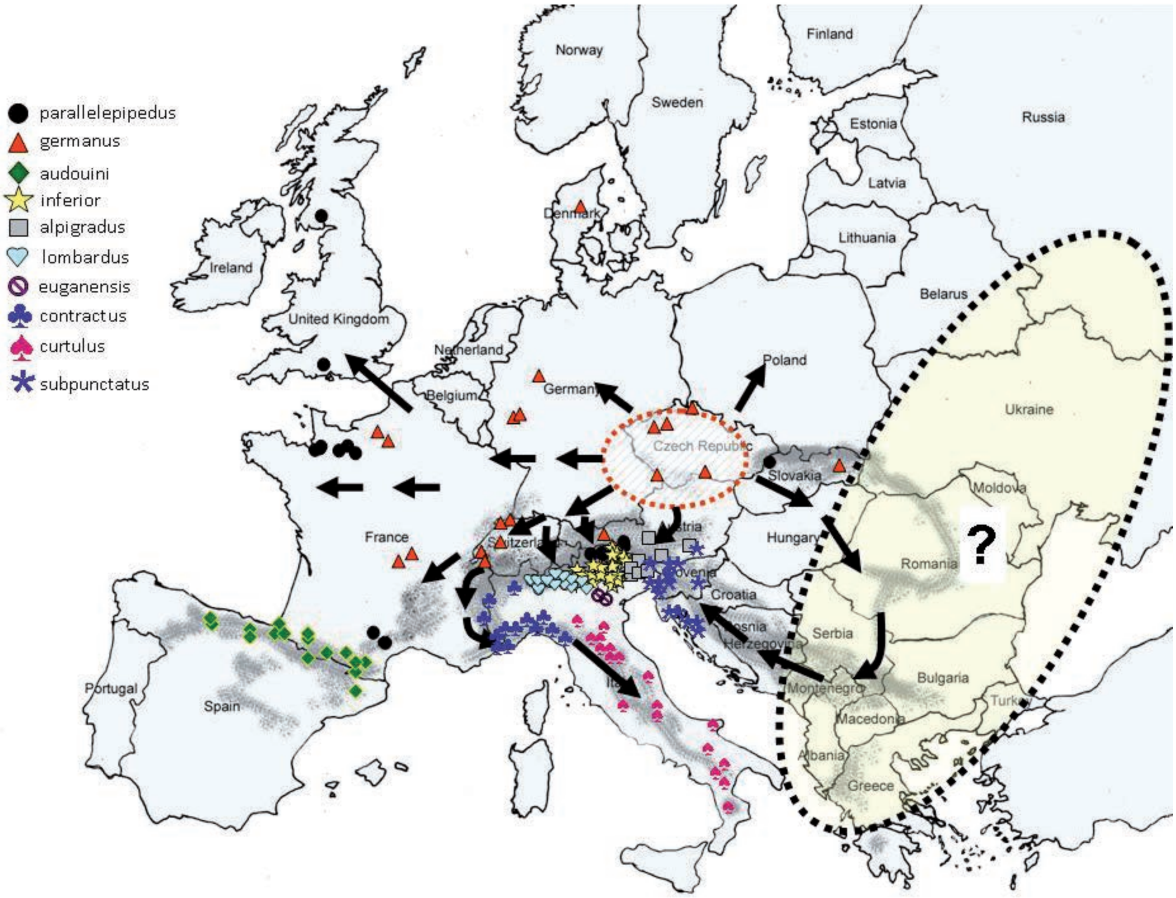

Fig. 11. Localities of provenience (circle marks) of the studied specimens and hypothetical routes followed by the different morphotypes and subspecies of *Abax parallelepipedus* throughout their geographical dispersal. The gray areas indicate the main mountain systems.

with different populations of *parallelepipedus* occurring in the northern side of the Alps. The high variation of *inferior*, especially with regard to pronotum shape, is probably due to genetic contributions of *alpigradus* from Carinthia, which is an extreme form of *inferior*, and also of nominotypical *parallelepipedus* and *germanus* from Tyrol. The ssp. *inferior* is therefore a polymorphic group, probably at the early phase of its differentiation process. Its distinctive trait is the slender shape of the aedeagus, lacking the angular expansion on the right side (Fig. 3D-H) but preserving a recognisable truncation of the aedeagic apex, even if narrow and delimited by blunt angles (Fig. 5B). Populations with differentiated morphologies are often localized in Alpine valleys, where they probably remained quite genetically isolated.

The second Alpine taxon, *A. p. lombardus*, occurs in the central Alps and probably differentiated from populations of *germanus* coming from Switzerland, since intermediate specimens were collected on the mountains in the border province of Sondrio. Its distribution is centred on the biogeographic region of "Insubria" connecting the southern side of the European Alps with the Po Plain, which is known for its mild-humid climate, very atypical for an Alpine environment (Pautasso, 2013). It is externally distinguishable from *inferior* and *parallelepipedus* by the more convex pronotum disc. The aedeagus apex is markedly sinuous along the left side (Fig. 3I-O) and ends with a narrowly truncated or almost pointed tip. The aedeagus apex has a marked angular expansion in specimens occurring on the west of Lake Garda, whereas it is almost smooth in specimens from the east of the lake (Monte Baldo, Monti Lessini). This latter form was interpreted as *inferior* by Magistretti (1965), whereas Depoli (1939) proposed the variety *A. p. lombardus lessinicus*.

The relevant morphological variation reported for *inferior* and *lombardus* is consistent with an initial genetic contribution coming from different European populations that crossed the Alpine barrier through spaced points of entrance. However, this scenario also supports the possible genetic isolation experienced by populations survived in restricted Pleistocene refugia during the last glaciations (1.6-0.01 Myr BP). In fact, studies on plant phylogeography hypothesized distinct glacial refugia scattered along the southern margin of the Italian Alps (Tribsch & Schönswetter, 2003; Schönswetter *et al.*, 2005). Interestingly, the Alpine sectors referable to some of these refugia fit quite well with the distributive pattern reported here for the morphotypes of *inferior* and *lombardus*.

In this context, a special place is occupied by *euganensis*, consisting of populations isolated in the Po Plain. This taxon increased the body width, especially at the pronotum, and developed flattened elytral interstriae in males. The elongated aedeagus apex, with narrow basal tract and absence of angular expansion on the right side, further supports the subspecific status. This subspecies probably split from the population at Monti Lessini, as a consequence of the migrations induced by the glaciations. During the Late Glacial, *i.e.* the interval following the Last Glacial Maximum between 19,000 and 11,500 cal yr BP, the extension of the ice sheet across the southern Alps determined the lowering of the vegetation line. The forests occupied the external belt of the Pre-Alps and adjoining plain (Ravazzi *et al.*, 2007). It can be assumed that *Abax parallelepipedus* spread towards the Po Plain, where there was a predominance of cold-steppe vegetation (Kaltenrieder *et al.*, 2010). At the onset of the Holocene (11,600-11,500 cal yr BP), the rapid climate warming induced a substantial change of the environments on the south of the Alps: thermophilous trees expanded in the lowlands and reached sites below ca 1500 m a.s.l. within a few centuries at most (Vescovi *et al.*, 2007). Furthermore, throughout the postglacial, the forest cover diminished in the lowlands, probably as a consequence of river disturbance on the Po Plain (Kaltenrieder *et al.*, 2010). It may be assumed that this environmental context favoured the isolation of residual populations of *lombardus* in enclaves entrenched on the Berici and Euganean Hills, while the main population progressively moved to the Alps following the retreat of the conifer belt. These isolated hills have maintained peculiar climatic conditions during the last 10,000 years. The Euganean Hills are now considered a xero-thermal oasis that permits the survival of many thermophilous Coleoptera typical of southern Italy (Ratti *et al.*, 1998). It is not surprising, therefore, that these environmental conditions, very different from the cool European forests, have led to the differentiation of *euganensis*.

A completely different history has to be proposed for *contractus*, which cannot be properly considered an Alpine subspecies. This taxon is connected to the European populations through the Maritime and Ligurian Alps, whereas it remains substantially separated from the other populations inhabiting the central-eastern Italian Alps. The Maritime and Ligurian Alps are considered zones of high biogeographic interest for their role as glacial refugia, biodiversity hotspots and "areas of endemism" (Casazza *et al.* 2008; Szövényi *et al.*, 2009).

A. p. contractus might therefore have found here the environmental conditions to differentiate from the nominotypical form. It then spread throughout the northern Apennines, whereas just sparse populations expanded over the western Italian Alps. Starting from the Tuscan-Emilian Apennines, it is substituted by *curtulus*. The phylogenetic relationship between *curtulus* and *contractus* is not disputable, since *curtulus* has no geographical contacts with other populations of *A. parallelepipedus*.

The peculiar differentiation expressed by *contractus-curtulus* substantially diverges from the trends observed in any other population of *A. parallelepipedus*: decrease in size, proportional reduction of pronotum and ovalization of elytra. This is consistent with the hypothesis that glacial refugia located in the Maritime Alps and Apennines led to genetic isolation from conspecific populations inhabiting the Alps, as shown by Labra *et al.* (2006) studying *Pinus sylvestris*. Interestingly, Grassi *et al.* (2009) demonstrated that *Saxifraga callosa*, a plant growing in the same regions as *contractus-curtulus*, shows diverging genetic structure in three major clades, consistent with distinct glacial refugia located in the Maritime Alps, Apuan Alps and Apennines. Furthermore, a study on the genetic clades of the Apennine endemic stream frog *Rana italica* showed that spaced glacial refugia can be hypothesized along the Apennines (Canestrelli *et al.*, 2008). It can therefore be assumed that *contractus* and *curtulus* derived from a common primitive population expanded along the Maritime Alps - Apennines route, then differentiated in distinct refugia during the Quaternary glaciations.

NOMENCLATORIAL PROPOSALS

It can be concluded that *Abax parallelepipedus* shows typical European chorology (Vigna Taglianti *et al.*, 1999) and high morphological variation that has led to the development of some populations with traits significantly differentiated from the nominotypical form. These differential characters are generally not distinct enough to justify the status of subspecies, but there are some exceptions among the populations occurring in the Alps and Italian Apennines.

The following new synonymies are proposed:

Abax parallelepipedus parallelepipedus (Piller & Mitterpacher, 1783)
= *A. p. subpunctatus* (Dejean, 1828) **syn. nov.**
= *A. p. audouini* (L. Dufour, 1851) **syn. nov.**
= *A. p. germanus* Schauberger, 1927 **syn. nov.**

Abax parallelepipedus inferior (Seidlitz, 1887)
= *A. p. alpigradus* Schauberger, 1927 (*sensu* Schatzmayr) **syn. nov.**

The resurrection of *A. p. euganensis* Schatzmayr, 1944 from synonymy of *inferior* is also proposed.

These microsystematic arrangements are summed up in the dichotomous key reported below, which should be read bearing in mind that the diagnostic characters are detected statistically and their presence is not constant.

KEY TO SUBSPECIES OF *ABAX PARALLELEPIPEDUS*

1. Median lobe of the aedeagus with wider apex (Fig. 2), angular expansion on the right side always present, tip sharply truncated (Fig. 12A). Mean size between 17 and 22 mm. All European countries, only marginally occurring in northern Italy ....*parallelepipedus* (Piller & Mitterpacher, 1783)

\- Median lobe of the aedeagus with narrower and variously shaped apex, angular expansion along the right side sometimes lacking (Fig. 12B), tip narrowly truncated or roughly pointed (Fig. 12C,D). Mean size between 17 and 20 mm. Populations occurring in Italy **2**

2. Median lobe of the aedeagus with slender apex and lacking the angular expansion on the right margin (Fig. 12B), this latter can rarely be faintly hinted **3**

\- Median lobe of the aedeagus with variously shaped apex but with angular expansion along the right side, sometimes very small.........................**4**

3. Pronotum with more convex disc, median lobe of aedeagus with left side sinuate at apex and tip pointed or very narrowly truncated (Fig. 3N-T). Populations occurring between the east side of Lake Garda and Euganean Hills **4**

- Convexity of pronotum disc as in typical *parallelepipedus*, variably shaped pronotal margins, inner basal foveae often reaching the basal margin. External morphology similar to *parallelepipedus*. Fine transversal wrinkles less dense on head and pronotum. Eastern Alps: Italy (Trentino Alto Adige, Veneto and Friuli Venezia Giulia) and Austria (Ost-Tirol, Carinthia). Populations along the Italian-Austrian border, Carnia and Carinthia, generally smaller in size (morphotype *alpigradus sensu* Schatzmayr)..........***inferior*** (Seidlitz, 1887)

4. Larger size. Pronotum wider, mean maximum width >6.3 mm (min. 5.9 mm; max 7.8 mm) in ♀♀ and >6.2 (min. 5.8 mm; max 7.6 mm) in ♂♂. Elytra more parallel-sided. Populations occurring between the central Alps and Berici and Euganean Hills ...**5**

- Smaller size. Pronotum narrower, mean maximum width <6.3 mm (min. 5.6 mm; max 6.7 mm) in ♀♀ and <6.2 (min. 5.5 mm; max 6.6 mm) in ♂♂. Elytra more oval. Populations occurring in the Apennines, martime and ligurian Alps, and marginally in the western Alps...**6**

5. Pronotum disc more convex, the relief interposed be-

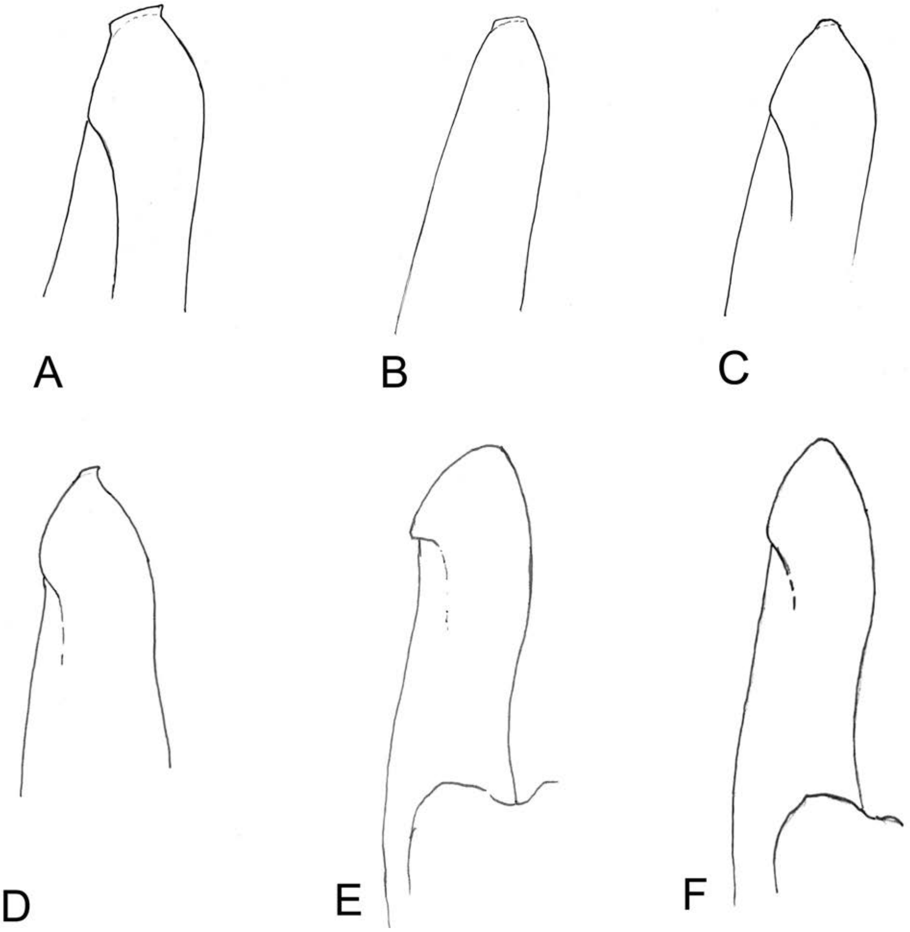

Fig. 12. Aedeagus apex of some subspecies of *Abax parallelepipedus* (aedeaga in figs 12A-D tilted 45° upward): A) typical *parallelepipedus*; B) *inferior*; C) *contractus*; D) *curtulus*; E) *lombardus* (from the west of Lake Garda) F) *lombardus* (from the east of Lake Garda).

tween inner and outer foveae is pronounced along all its length. Median lobe of aedeagus with apex slender and a little more elongated than in *parallelepipedus*, left side moderately sinuous (Fig. 12E; this character often lacking in specimens from the province of Sondrio). Apical tip with narrow truncation delimited by blunt angles or roughly pointed. Apex of median lobe of aedeagus with sharp angular expansion along the right side in specimens from the west of Lake Garda (Fig. 12E), whereas it is almost lacking in those occurring to the east of the lake (Fig. 12F). Canton Ticino, Lombardy, western Veneto (Monte Baldo, Monte Pasubio, Monti Lessini) ....***lombardus*** A. Fiori, 1896

\- Pronotum more transverse and stouter than *parallelepipedus*, elytral base broad, median lobe of aedeagus with apex slender and definitely exceeding 1 mm in length, almost symmetrical and lacking the angular expansion on the right side. Endemic to Berici and Euganean Hills (Veneto, Italy)............. ....***euganensis*** Schatzmayr, 1944

6\. Larger size (mean TL 18.3 ♀♀ - 17.9 ♂♂). Pronotum less transverse than *parallelepipedus* and pronotum base proportionally narrower in comparison to its maximum width. Elytra more oval. Median lobe of aedeagus with apex less broad than the typical form, scarcely exceeding 1 mm in length, right side with small angular expansion. Apical tip roughly pointed or with narrow truncation delimited by blunt angles, almost pointed (Fig. 12C). France (Haute-Alpes, Maritime Alps) and Italy (Liguria, Piedmont, Lombard Apennines).... ....***contractus*** (Heer, 1841)

\- Smaller size (average TL 17.5 ♀♀ - 17.3 ♂♂). Similar to *contractus* but with pronotal base proportionally less narrow. Median lobe of aedeagus with apex less broad than *contractus*, with pointed tip or very narrowly truncated (Fig. 12D). Endemic to Italian Apennines from the south of the Apuan Alps......... ....***curtulus*** (Fairmaire, 1856)

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