

Gianni ALLEGRO*

**Three new *Pseudaptinus* (subgenus *Thalpius*) from Ecuador,
with notes on *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke
(Coleoptera, Carabidae, Zuphiini)**

Abstract: *Pseudaptinus* (*Thalpius*) *bartolozzii* n. sp., *Pseudaptinus* (*Thalpius*) *moreti* n. sp., and *Pseudaptinus* (*Thalpius*) *gracilis* n. sp., three new flightless species from Ecuador, are described. *P. bartolozzii* n. sp. shows a peculiar ant-like habitus; *P. moreti* n. sp. and *P. gracilis* n. sp. form, together with *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke, a morphologically very homogeneous species group. Moreover, the holotype of *P. aptinoides* is illustrated, and a re-description of this species is given. Finally, a key to all species of *Pseudaptinus* subgenus *Thalpius* so far recorded from South America is provided.

Riassunto: Tre nuovi *Pseudaptinus* (sottogenere *Thalpius*) dell'Ecuador, con note su *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke (Coleoptera, Carabidae, Zuphiini).

Vengono descritti *Pseudaptinus* (*Thalpius*) *bartolozzii* n. sp., *Pseudaptinus* (*Thalpius*) *moreti* n. sp. e *Pseudaptinus* (*Thalpius*) *gracilis* n. sp., tre nuove specie brachittere dell'Ecuador. *P. bartolozzii* n. sp. presenta un peculiare habitus mirmiciforme; *P. moreti* n. sp. e *P. gracilis* n. sp. formano, insieme a *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke, un gruppo di specie morfologicamente molto omogeneo. Inoltre, viene illustrato l'olotipo di *P. aptinoides* e viene data una ridescrizione di questa specie. Infine, viene fornita una chiave per l'identificazione di tutte le specie del sottogenere *Thalpius* di *Pseudaptinus* conosciute fino a oggi in Sudamerica.

Key words: *Pseudaptinus* (*Thalpius*) *bartolozzii* n. sp., *Pseudaptinus* (*Thalpius*) *moreti* n. sp., *Pseudaptinus* (*Thalpius*) *gracilis* n. sp., *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke, South America, taxonomy, identification key.

To meet the requirements by the International Code of Zoological nomenclature (ICZN), this article was registered at ZooBank (12 December 2024) under the ZooBank Life Science Identifier (LSID): urn:lsid:zoobank.org:pub:F67D6215-2EA3-4945-A793-99DE2275AB45
Published: 29 August 2025.

INTRODUCTION

The tropical Andes can be considered one of the most biodiverse ecoregions on Earth, with a high level of insect diversity and endemism (Myers *et al.*, 2000). Nevertheless, the huge diversity of tropical insects is a challenge to entomological research, and very little is known about the invertebrate fauna of some ecosystems, such as the Andean humid forests, as well as the forests of the Amazon basin (AA.VV., 2021).

Thanks to Luca Bartolozzi, I was able to find in the collections of the Zoological Museum 'La Specola' at the University of Florence (MZUF) a single specimen of a flightless *Thalpius* from the Ecuadorian Amazon basin showing a peculiar ant-like habitus, which undoubtedly represents a new species for science. At the same time, Pierre Moret (University of Toulouse) gave me for study four brachypterous specimens of *Thalpius* from the Ecuadorian Andean forest, which

proved to belong to two different new species very similar to each other and forming, together with *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke, 1934, described from Venezuela, a morphologically very homogeneous species group. The comparison of the new species with the latter has been made possible thanks to high-definitions photographs of the holotype of *P. aptinoides* taken by David Schimrosczyk, curator of insect collection at the Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ), where this type is deposited (Mroczkowski, 1960).

The genus *Pseudaptinus* Laporte, 1834 includes, at the present state of knowledge, 54 species (Lorenz, 2024) arranged by most authors into the subgenera *Pseudaptinus* s. str. (18 species), distributed in the Western Hemisphere, and *Thalpius* LeConte, 1851 (36 species), distributed in the Western Hemisphere as well as in Australia (Anichtchenko, 2014). Some au-

*Gianni Allegro, World Biodiversity Association, Strada Patro 11, 14036 Moncalvo (AT), Italy.
E-mail: gianni.allegro54@gmail.com

thors have treated the two subgenera as genera (Reichardt, 1977; Martinez, 2005; Ball & Shpeley, 2013; Lemaire *et al.*, 2023), but the most important feature distinguishing them, that is the presence (*Thalpius*) or the absence (*Pseudaptinus* s. str.) of a spine at posterior angles of pronotum, is in my opinion too feeble to justify a separation at genus level; for this reason, in agreement with Liebke (1934, 1939), Blackwelder (1957), Messer (2011), Bousquet (2012), Anichtchenko (2014) and Lorenz (2005, 2024), *Thalpius* will be treated as a subgenus of *Pseudaptinus* in the present paper.

Only 11 species of *Thalpius* are currently recorded from South America, none of these from Ecuador, despite many specimens waiting for study in museum collections; moreover, the most recent descriptions of South American *Thalpius* date back to 1939 (Liebke, 1939), and the most comprehensive taxonomic revision of the genus *Pseudaptinus*, which is the richest in species among Zuphiini in South America, dates back to exactly 91 years ago (Liebke, 1934). The main reason for this lack of recent studies can probably be found in the difficulty of studying for comparison old type specimens, some of which are damaged or lost.

In this paper, three new species (*Pseudaptinus bartolozzii* n. sp., *Pseudaptinus moreti* n. sp., and *Pseudaptinus gracilis* n. sp.) are described and illustrated. Moreover, a photographic plate of the holotype of *P. aptinoides* is provided, as this species was never previously illustrated in the literature, and a re-description of the type based on high-resolution pictures is given. Finally, a revised key (based on the key published by Liebke, 1934) to all species of South American *Thalpius*, including the newly described ones, is provided. It is noteworthy that Liebke omitted to consider, in his key, *Pseudaptinus (Thalpius) granulosus* (Chaudoir, 1872), which is instead included in the key of this paper based on a detailed digital photograph of the holotype provided by Olivier Montreuil of the Muséum National d'Histoire Naturelle of Paris (MNHN).

MATERIALS AND METHODS

The specimens studied or mentioned in the text are deposited in the following museums and private collections:

CAI: Gianni Allegro Collection (Moncalvo, Asti, Italy).

CMo: Pierre Moret Collection (Toulouse University, France).

MIZ: Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland.

MNHN: Muséum national d'Histoire naturelle, Paris, France.

MZUF: Museo Zoologico 'La Specola', University of Florence, Italy.

The abbreviations used for the type material are:

HT: holotype.

PT: paratype.

The type locality is quoted in the original label form.

Apparent body length (ABL) is measured from the apex of the labrum to the apex of the longer elytron. PL: pronotum length measured from apical to basal margin along midline; PW: pronotum width at the widest point; EL: elytral length from humerus to apex of longer elytron; EW: elytral width at the widest point.

Digital images of *Pseudaptinus bartolozzii* n. sp., *Pseudaptinus moreti* n. sp., and *Pseudaptinus gracilis* n. sp. were taken by a Leica DFC295 camera mounted on a Leica M205 C stereomicroscope, using Leica Application System V4.0 software.

Digital images of the HT of *Pseudaptinus aptinoides* were taken by David Schimrosczyk (MIZ) using a Keyence VHX-7000 Digital Microscope. Before being photographed, genitalia were cleared in 10% cold potassium hydroxide and then stained in chlorazol black.

Pseudaptinus (Thalpius) bartolozzii n. sp.

urn:llsid:zoobank.org:act:

BFC0CA82-82D6-468E-AD60-17726EAE3B4

TYPE LOCALITY. Ecuador: Napo, Rio Hollin, 1200 m.

TYPE SERIES. HT ♂: Ecuador: Napo, Rio Hollin, 1200 m, 9-13.II.1993, L. Bartolozzi legit (Mag. 1406) (MZUF, provisionally at author's address).

DIFFERENTIAL DIAGNOSIS. A small-sized (ABL: 5.82 mm) brachypterous zuphiine species belonging to the genus *Pseudaptinus* (subgenus *Thalpius*), pubescent throughout with striking ant-like external morphology. Fore body (head and pronotum) piceous black and elytra dark brown; pronotum longer than wide, posterior angles provided with a sharp laterally prominent spine; elytral striae deeply impressed, coarsely punctate and rugulose, with intervals punctate and costulated, sutural apex of each elytron prominent. It is easily distinguished from other South American brachypterous *Thalpius* by deeply impressed and coarsely punctate elytral striae, together with costulated intervals.

DESCRIPTION. A small-sized *Pseudaptinus* (subgenus

Thalpius) species with striking ant-like external morphology. ABL: 5.82 mm (HT ♂).

Habitus and color (Fig. 1): body parallel-sided, pubescent throughout, shiny, with mouth parts reddish-brown, fore body (head and pronotum) piceous black and elytra dark brown; antennae and legs paler. Females unknown.

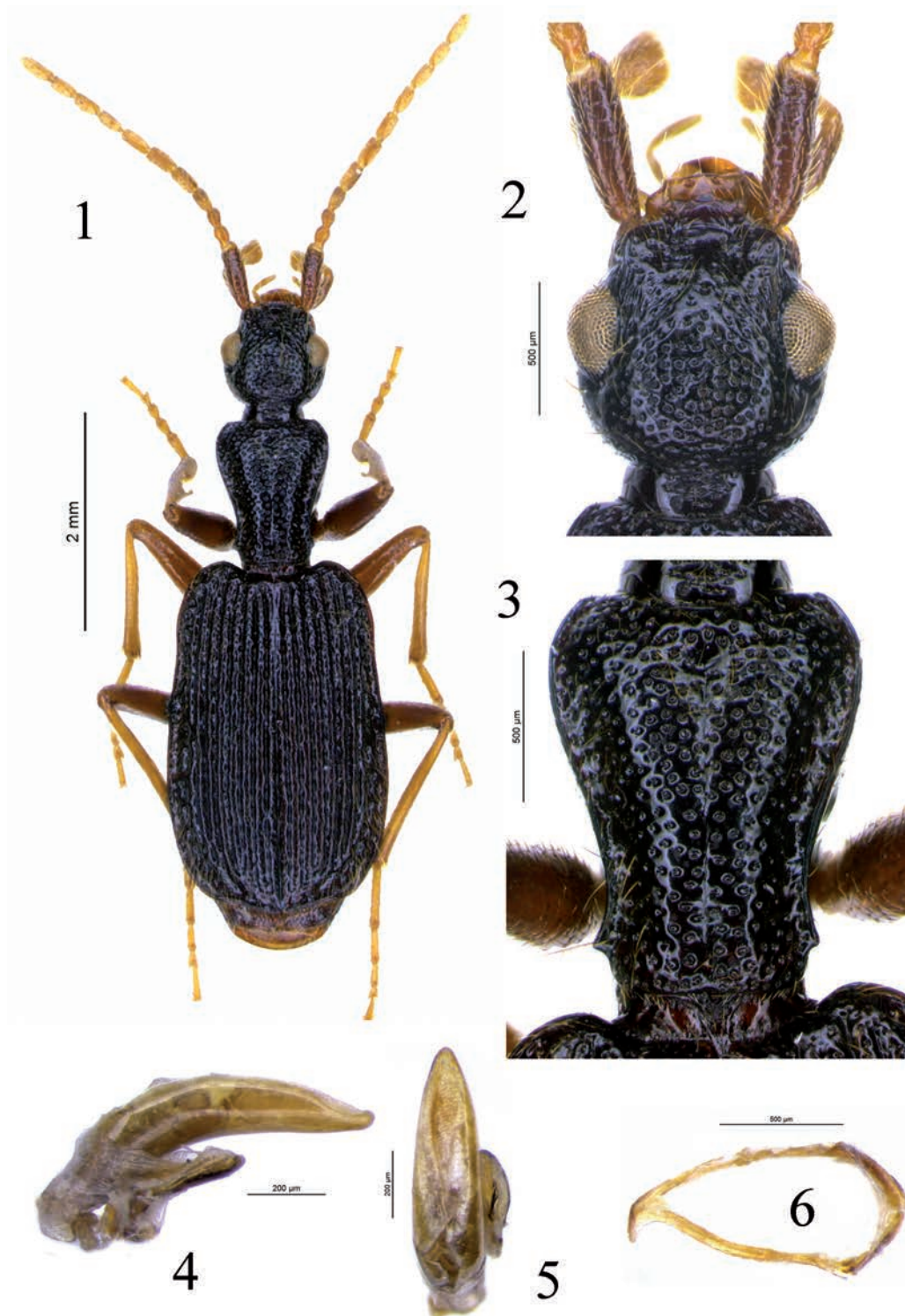
Head (Fig. 2): laterally convex, slightly narrower than pronotum, dorsally coarsely punctate, more densely at vertex, anteriorly rugulose near eyes and posteriorly abruptly constricted in a thick neck punctate at middle, nearly 2/3 as wide as head; collar constriction dorsally distinct; ocular area globose and eyes large, convex, oval but posteriorly obliquely truncate; two supraorbital setae on each side; microsculpture indistinct; frontal impressions deep, broad and very short, ending before the anterior edge of eye; temples convex, densely pubescent with long bristles and nearly as long as diameter of eye; a narrow supraorbital carina distinctly dilated above antennal insertion; labrum rectangular, with six setigerous punctures on anterior margin, which is slightly concave at sides; clypeus transverse trapezoid, rectilinear anteriorly and paler than head; a couple of central setae at anterior margin of clypeus and three further setae at each side. Antennae moderately long and slender, surpassing elytral base when stretched backwards, densely pubescent; the first antennomere darker than followings, which are progressively paler towards apex; the first antennomere nearly as long as antennomeres 2-4 together, the fourth one 1.84 times longer than wide, the followings over 2 times longer than wide. Mandibles moderately long, pointed, and abruptly curved at apex, narrowly darkened at inner side. Mentum distinctly broader than long, sparsely pubescent, anterior margin shallowly emarginate; epilobes rather broad, laterally prominent and anteriorly acutely pointed; mentum tooth acute and not exceeding level of epilobes; suture between mentum and submentum present. Maxillary palpi much larger than labial palpi, with palpomere 4 markedly enlarged; penultimate labial palpomere multisetose with one pair of major erect setae on anterior margin.

Thorax (Fig. 3): PL: 1.30 mm; PW: 1.05 mm; PL/PW: 1.24. Pronotum coarsely punctate throughout, without any distinct microsculpture, pubescent with long yellow erect setae, more dense near anterior margin; form slender, longer than wide, widest at anterior eighth; side margins regularly rounded at anterior fourth and then markedly sinuate backwards up to the basal angles, each provided with a sharp spine laterally prominent

and with an angular seta; posterior margin distinctly pedunculate at middle; basal impressions long and markedly impressed, joining with the lateral border of pronotum at basal half; anterior margin with front angles almost absent; a marginal seta at anterior tenth on each side; lateral marginal bead anteriorly narrow and progressively broader towards base, where it joins with the basal impressions; anterior and posterior margins unbordered; medial longitudinal sulcus deep, ending before apex and base.

Elytra: EL: 3.27 mm; EW: 2.04 mm; EL/EW: 1.60. Subparallel sided, moderately convex but depressed at basal third, slightly narrower at base and widest towards apex, with shoulders rounded and moderately prominent forwards; laterally concave at basal third and delicately sinuate before apex, which is moderately prominent. Surface smooth, without any distinct microsculpture, pubescent with long yellow setae, erect at basal third and reclined at the following 2/3. Epipleura without distinct external plicae ('uncrossed epipleura'). Intervals markedly convex, costulated, deeply punctate; striae deeply impressed for the whole length, distinctly punctate and rugulose. Parascutellar stria absent; scutellar setigerous pore present between striae 1 and 2, adjacent to the first stria. Basal margin nearly indistinct. Each elytron with acute sutural apex; the outer posterior angle rounded. Discal setigerous punctures absent; umbilicate series widely interrupted at middle. Hind wings absent. Ventral surface (thorax and abdomen): prosternum punctate and pubescent with long yellow erect setae; proepisterna anteriorly pubescent and punctate, posteriorly smooth and glabrous. Mesosternum pubescent, densely punctate. Metepisterna moderately short, rugosely punctate, narrowed backwards, and nearly as long as the anterior margin. Prosternal intercoxal process broadly rounded at apex and apically setose. Sterna densely pubescent.

Legs: moderately long and pubescent throughout, light brown with femora a little darker. Metatrochanters very short, as long as 1/4 of metafemora. Protibial antennal cleaning organ well developed, with two clip setae. Protibiae moderately short, robust; mesotibiae and metatibiae slender, about as long as tarsi, without spines except the apical ones, with an apical crown of brush-like setae. Tarsomeres dorsally convex; protarsomeres moderately long, moderately and symmetrically dilated, the first one 1.5 times longer than the 2nd and 3rd, the 4th concave at apex; metatarsomeres slender, the first one 2 times longer than the 2nd; onychium with a double row of adhesive setae; claws smooth.



Figs. 1-6. *Pseudaptinus (Thalpius) bartolozzii* n. sp.: Holotype habitus (1); Head in dorsal view (2); Pronotum (3); Median lobe of aedeagus in lateral view (4); Median lobe of aedeagus in dorsal view (5); Male gonosomite (IX invaginated abdominal segment) (6).

Male genitalia (Figs. 4-6): median lobe of aedeagus in lateral view moderately and regularly curved for most length, rectilinear only near apex, with small basal bulb (Fig. 4); in dorsal view symmetrical and more or less regularly narrowed from base to apex; apical blade short and sub-triangular, blunt at apex (Fig. 5). Ostium moderately long, placed in dorsal position, as long as 2/3 of median lobe, not reaching basal bulb. Right paramere small and narrow, elongate. Male gonosomite (IX invaginated abdominal segment) sub-triangular with proximal apophysis small, right angled and apically acute (Fig. 6).

REMARKS. It is not possible, at the present state of knowledge, to make significant phylogenetic assumptions con-

cerning the closest relatives of *Pseudaptinus* (*Thalpius*) *bartolozzii* n. sp. Maybe these could be found among some other brachypterous South American *Thalpius* living in forest litter (see the '*Pseudaptinus aptinoides* species group'), which, anyway, show evident morphological differences. Due to its peculiar features and its striking ant-like external morphology, *P. bartolozzii* n. sp. can be considered a rather isolated species.

DISTRIBUTION AND ECOLOGY. Geographical distribution: *Pseudaptinus* (*Thalpius*) *bartolozzii* n. sp. is currently recorded only from the Napo province of Ecuador, along the Hollin stream (Fig. 7). This province is part of the Amazon basin, hosting important rainforest areas.



Fig. 7. Distribution map of the new *Pseudaptinus* (*Thalpius*) species in Ecuador (from Google Maps).

Life habits: the unique specimen forming the typical series of *P. bartolozzii* n. sp. was collected at 1200 meters of altitude a.s.l. in forest, along the Hollin stream, by actively searching on the ground and under logs. The striking ant-like external morphology of its body could suggest a behavior involving some degree of myrmecophily, as it was already hypothesized for the zuphiine species *Peruzuphium giachinoi* Allegro, 2024 from Peru (Allegro, 2024).

ETYMOLOGY. I am pleased to dedicate this interesting species to Luca Bartolozzi, former curator at the Entomology Department of the MZUF and specialist in the taxonomy of Coleoptera Lucanidae and Brentidae, who collected the unique specimen recorded so far.

***Pseudaptinus (Thalpius) moreti* n. sp.**

urn:lsid:zoobank.org:act:

4A115AE1-947A-4519-B77F-329C6BFABF08

TYPE LOCALITY. Ecuador, Sucumbíos, Km 9 Sta Bárbara – La Bonita, 2450 m.

TYPE SERIES. HT ♂: Ecuador, Sucumbíos, Km 9 Sta Bárbara – La Bonita, 25.VII.1998, 2450 m, I. Tapia / Nocte ambulans, 20 h – 22 h (CMo). PT ♀: Ecuador, Pichincha, Pataquí dint., m 2575, 14.VIII.2008, legg. Baviera, Bellò, Osella & Pogliano (CAI).

DIFFERENTIAL DIAGNOSIS. A small-sized (ABL: 6.74–6.85 mm) brachypterous zuphiine species belonging to the genus *Pseudaptinus* (subgenus *Thalpius*), pubescent throughout, with *Aptinus*-like elytra. Fore body (head and pronotum) piceous brown and elytra dark brown; mouth parts, antennae and legs paler; pronotum longer than wide, with posterior angles right or moderately acute, not or scarcely laterally prominent; elytra narrow at base and widest towards apex, striae distinctly impressed, irregularly punctate, and intervals delicately convex and densely punctate; elytral apex linearly truncate and sutural angle of each elytron rounded. It is easily distinguished from the South American brachypterous *Thalpius* with *Aptinus*-like elytra by the following set of characters: from *Pseudaptinus gracilis* n. sp. by larger size (6.7–6.9 vs. 5.6–5.7 mm), head dorsally coarsely (vs. delicately) punctate and shape of aedeagus; from *Pseudaptinus aptinoides* Liebke by larger size (6.7–6.9 vs. 5.6 mm), more slender pronotum (PL/PW: 1.24–1.33 vs. 1.15), more slender elytra (EL/EW: 1.58 vs. 1.50) and shape of aedeagus.

DESCRIPTION. A small-sized *Pseudaptinus* (subgenus *Thalpius*) species with *Aptinus*-like elytra. ABL: 6.85 mm (HT ♂), 6.74 mm (PT ♀).

Habitus and color (Fig. 8): body dark brown to piceous brown, slender, shiny, pubescent throughout, with mouth parts, antennae and legs paler.

Head (Fig. 9): laterally convex, slightly narrower than pronotum, dorsally coarsely punctate even at vertex, posteriorly abruptly constricted in a thick neck, punctate at middle, nearly 2/3 as wide as head; collar constriction dorsally distinct; eyes relatively small, scarcely convex, oval but posteriorly obliquely truncate; two supraorbital setae on each side; microsculpture indistinct; frontal impressions moderately deep, broad and short, ending at level of the anterior edge of eye; temples long and convex, densely pubescent with long bristles and about 1.8 times longer than diameter of eye; a narrow supraorbital carina moderately dilated above antennal insertion; labrum rectangular, with six setigerous punctures on anterior margin, which is slightly concave; clypeus transverse trapezoid, rectilinear anteriorly and paler than head; a couple of central setae at anterior margin of clypeus and three further setae at each side. Antennae moderately long and slender, surpassing elytral base when stretched backwards, densely pubescent; the first antennomere longer than antennomeres 2–4 together, the fourth one 1.75 times longer than wide, the following about 2 times longer than wide. Mandibles moderately long, pointed, and abruptly curved at apex, narrowly darkened at inner side. Mentum distinctly broader than long, anterior margin shallowly emarginate; epilobes rather broad, laterally prominent and anteriorly acutely pointed; mentum tooth very short; suture between mentum and submentum present. Maxillary palpi much larger than labial palpi, with palpomere 4 markedly enlarged; penultimate labial palpomere multisetose with one pair of major erect setae on anterior margin.

Thorax (Fig. 10): PL: 1.59 mm, PW: 1.28 (HT ♂); PL: 1.63, PW: 1.23 mm (PT ♀); PL/PW: 1.24–1.33.

Pronotum coarsely punctate throughout, without any distinct microsculpture, pubescent with long yellow semi-adjacent setae, more dense and erect near anterior margin; form slender, longer than wide, widest at anterior fourth; side margins regularly rounded at anterior 2/3 and then markedly sinuate backwards up to the right or moderately acute basal angles, not or scarcely prominent outside and with an angular seta;

posterior margin distinctly pedunculate at middle; basal impressions long and markedly impressed, joining with the lateral border of pronotum at basal third; anterior margin concave with front angles scarcely protruding; a marginal seta at anterior sixth on each side; lateral marginal bead anteriorly narrow and progressively broader towards base, where it joins with the basal impressions; anterior and posterior margins unborded; medial longitudinal sulcus deep, ending before apex and base.

Elytra: EL: 3.74 mm, EW: 2.37 mm (HT ♂); EL: 3.63 mm, EW: 2.31 mm (PT ♀); EL/EW: 1.58 (HT ♂ and PT ♀). Ovoid, moderately convex, narrow at base and progressively widest towards apex, with shoulders markedly prominent forwards; sides sub-rectilinear at basal 2/3, then moderately arcuate towards apex, which is linearly truncate. Apical sutural angle of each elytron rounded; the outer posterior angle widely rounded. Surface smooth, without any distinct microsculpture, pubescent throughout with yellow semi-adjacent setae. Epipleura without distinct external plicae ('uncrossed epipleura'). Intervals delicately convex and densely punctate; striae distinctly impressed for nearly the whole length, more shallowly impressed towards apex, irregularly punctate. Parascutellar stria absent; scutellar setigerous pore present between striae 1 and 2, adjacent to the first stria. Basal margin nearly indistinct. Discal setigerous punctures absent; punctures of the umbilicate series in a continuous row, not interrupted at middle. Hind wings absent.

Ventral surface (thorax and abdomen): prosternum and propisterna punctate and pubescent with long erect yellow setae; mesosternum punctate and sparsely pubescent. Metepisterna moderately short, rugosely punctate, sub-rectangular and nearly as long as anterior margin. Prosternal intercoxal process broadly rounded at apex and apically setose. Sterna densely pubescent.

Legs: moderately long and pubescent throughout, light brown with femora slightly darker. Metatrochanters very short, as long as 1/4 of metafemora. Protibial antennal cleaning organ well developed, with two clip setae. Protibiae moderately short, robust; mesotibiae and metatibiae slender, about as long as tarsi, without spines except the apical ones, with an apical crown of brush-like setae. Tarsomeres dorsally convex; protarsomeres moderately long, moderately and symmetrically dilated, the first one nearly 2 times longer than the 2nd and 3rd, the 4th concave at

apex; metatarsomeres slender, the first one 1.8 times longer than the 2nd; onychium with a double row of adhesive setae; claws smooth.

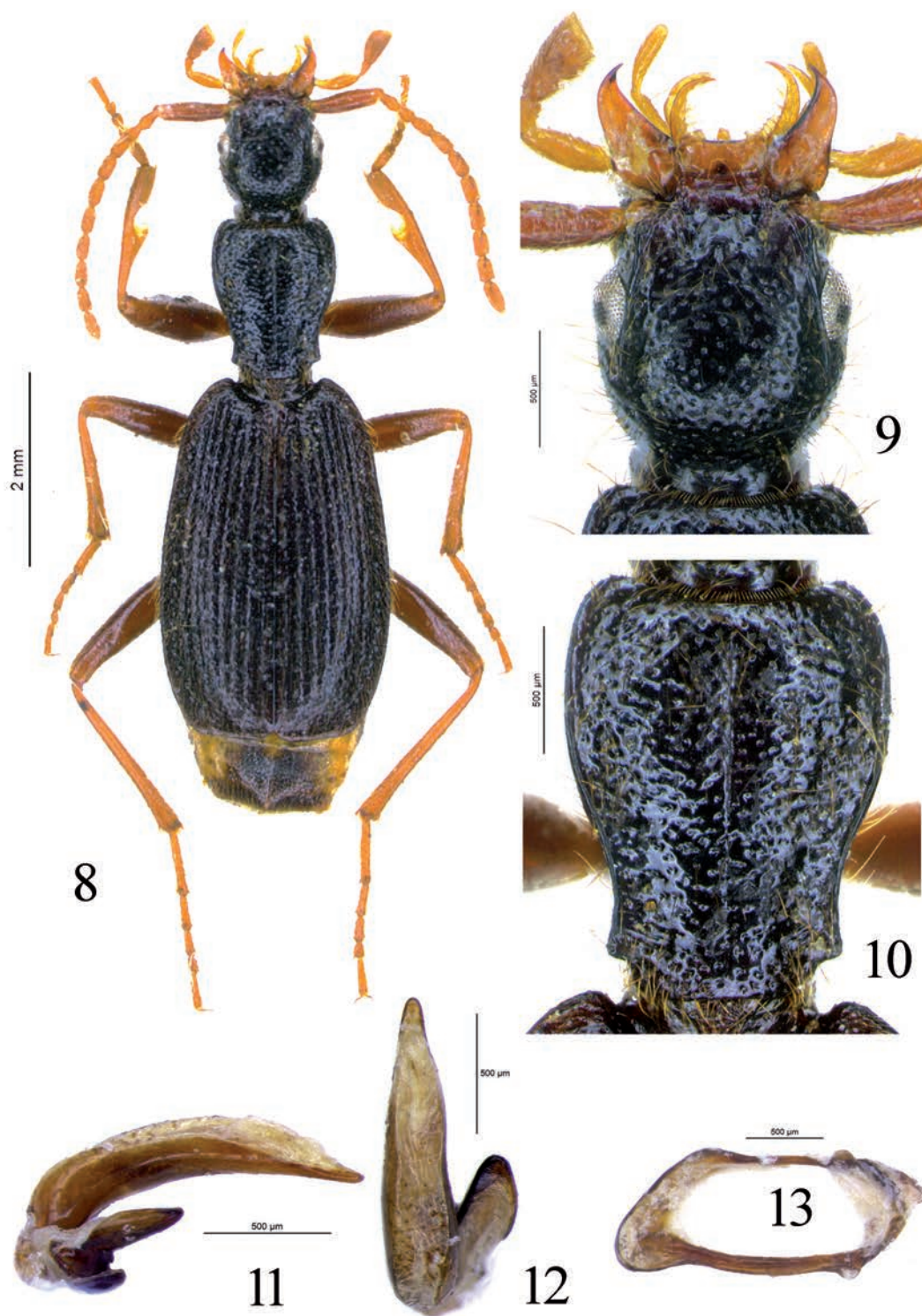
Male genitalia (Figs. 11-13): median lobe of aedeagus in lateral view abruptly curved at 45° just over the small basal bulb, then sub-cylindrical and delicately curved until apex (Fig. 11); in dorsal view more or less symmetrical and regularly narrowed from basal third to apex; apical blade moderately long and slender, sub-triangular and blunt at apex (Fig. 12). Ostium long, placed in dorsal position, as long as the whole dorsal part of median lobe, nearly reaching basal bulb. Right paramere moderately small and narrow, elongate. Male gonosomite (IX invaginated abdominal segment) ovoid with proximal apophysis large, sub-triangular and apically broadly rounded (Fig. 13).

REMARKS. *Pseudaptinus* (*Thalpius*) *moreti* n. sp. shows evident morphological similarities with *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke and with *Pseudaptinus* (*Thalpius*) *gracilis* n. sp., which can be considered, at the present state of knowledge, its closest relatives. Their striking similarities as well as their likely similar way of life indicate the presence of a homogeneous group of species (which is named '*P. aptinoides* species group' after the oldest recognized species), phylogenetically strictly related and recently originated by allopatry due to geographic barriers caused by climatic fluctuations during the Pleistocene. The flightless condition of these species and their consequent reduced dispersal ability may have favoured the specific diversification.

DISTRIBUTION AND ECOLOGY. Geographical distribution: *Pseudaptinus* (*Thalpius*) *moreti* n. sp. is currently recorded only from the provinces of Sucumbios and Pichincha, in northern Ecuador, on both sides of the Andean Cordillera (Fig. 7).

Life habits: the specimens forming the typical series of *P. moreti* n. sp. were collected at 2450-2575 meters of altitude a.s.l. in densely forested areas. On a separate label of the HT, the specimen is reported as 'walking on the ground between 8 pm and 10 pm'. Due to the flightless condition of this species, a forest litter habitat can be hypothesized. Some degree of myrmecophily in its behaviour should not be excluded.

ETYMOLOGY. I am pleased to dedicate this rare and interesting species to Pierre Moret (University of Toulouse), a world-renowned specialist in the taxonomy of Ecuadorian Carabidae, who gave me, in study, the specimens of the type series.



Figs. 8-13. *Pseudaptinus (Thalpius) moreti* n. sp.: Holotype habitus (8); Head in dorsal view (9); Pronotum (10); Median lobe of aedeagus in lateral view (11); Median lobe of aedeagus in dorsal view (12); Male gonosomite (IX invaginated abdominal segment) (13).

***Pseudaptinus* (*Thalpius*) *gracilis* n. sp.**

urn:lsid:zoobank.org:act:

400640D2-9734-4586-84FE-4C56738C15FB

TYPE LOCALITY. Ecuador, Pichincha, Lloa, Rio Blanco, m 2540, S 00°12'95.6" W 78°39'12.3".

TYPE SERIES. HT ♂: Ecuador, Pichincha, Lloa, Rio Blanco, m 2540, 27.VII.2008, S 00°12'95.6" W 78°39'12.3", legg. Baviera, Bellò, Osella & Pogliano (CMo). PT ♀: same data as HT (CAI).

DIFFERENTIAL DIAGNOSIS. A small-sized (ABL: 5.55–5.74 mm) brachypterous zuphiine species belonging to the genus *Pseudaptinus* (subgenus *Thalpius*), pubescent throughout, with *Aptinus*-like elytra. Body brownish with mouth parts, antennae and legs paler; pronotum longer than wide, with posterior angles right or moderately acute, not or scarcely laterally prominent; elytra narrow at base and widest towards apex, striae distinctly impressed, irregularly punctate, and intervals delicately convex and densely punctate; elytral apex linearly truncate and sutural angle of each elytron rounded. It is easily distinguished from the South American brachypterous *Thalpius* with *Aptinus*-like elytra by the following set of characters: from *Pseudaptinus moreti* n. sp. by smaller size (5.6–5.7 vs. 6.7–6.9 mm), head dorsally delicately (vs. coarsely) punctate and shape of aedeagus; from *Pseudaptinus aptinoides* Liebke by more slender pronotum (PL/PW: 1.22–1.25 vs. 1.15), more slender elytra (EL/EW: 1.59–1.61 vs. 1.50) and shape of aedeagus.

DESCRIPTION. A small-sized *Pseudaptinus* (subgenus *Thalpius*) species with *Aptinus*-like elytra. ABL: 5.74 mm (HT ♂), 5.55 mm (PT ♀).

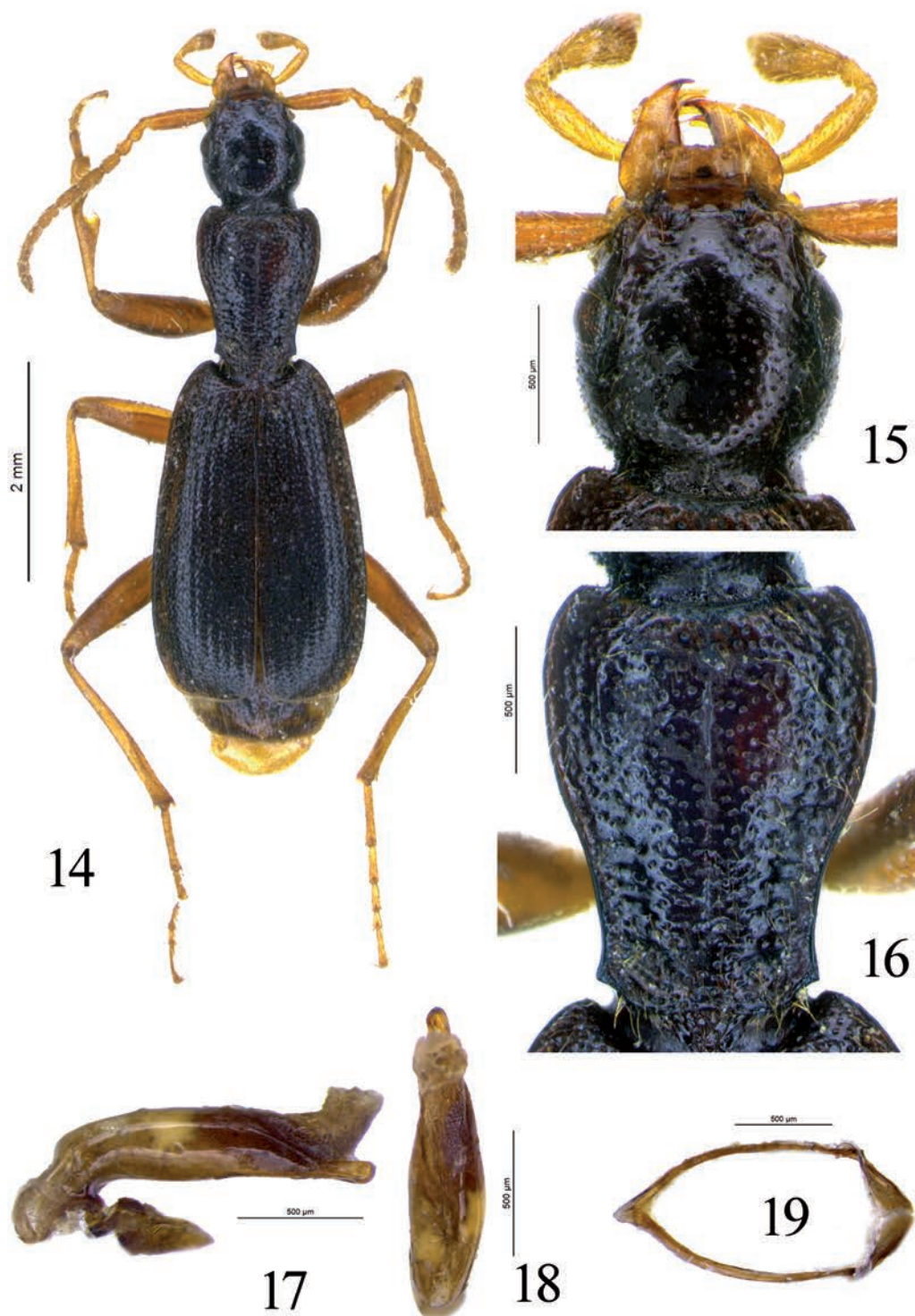
Habitus and color (Fig. 14): body brown, slender, shiny, pubescent throughout, with mouth parts, antennae and legs paler.

Head (Fig. 15): laterally convex, slightly narrower than pronotum, dorsally delicately punctate and nearly smooth at middle, posteriorly abruptly constricted in a thick neck, smooth at middle, nearly 2/3 as wide as head; collar constriction dorsally distinct; eyes relatively small, scarcely convex, oval but posteriorly obliquely truncate; two supraorbital setae on each side; microsculpture indistinct; frontal impressions superficial, broad and short, ending at level of the anterior edge of eye; temples long and convex, densely pubescent with long bristles and about 1.8 times longer than diameter of eye; a narrow supraorbital carina moderately dilated above antennal insertion; labrum rectangular, with six setigerous punctures on anterior margin, which is slightly concave; clypeus transverse trapezoid, recti-

linear anteriorly and paler than head; a couple of central setae at anterior margin of clypeus and three further setae at each side. Antennae moderately long and slender, surpassing elytral base when stretched backwards, densely pubescent; the first antennomere as long as antennomeres 2–4 together, the fourth one 1.75 times longer than wide, the following about 2 times longer than wide. Mandibles moderately long, pointed, and abruptly curved at apex, narrowly darkened at inner side. Mentum distinctly broader than long, anterior margin shallowly emarginate; epilobes rather broad, laterally prominent and anteriorly acutely pointed; mentum tooth nearly indistinct; suture between mentum and submentum present. Maxillary palpi much larger than labial palpi, with palpomere 4 markedly enlarged; penultimate labial palpomere multisetose with one pair of major erect setae on anterior margin.

Thorax (Fig. 16): PL: 1.40 mm; PW: 1.12–1.15 mm; PL/PW: 1.22–1.25. Pronotum coarsely punctate throughout, without any distinct microsculpture, pubescent with long yellow reclined setae, more dense and erect near anterior margin; form slender, longer than wide, widest at anterior fifth; side margins regularly rounded at anterior 2/3 and then markedly sinuate backwards up to the right or moderately acute basal angles, not or scarcely prominent outside and with an angular seta; posterior margin distinctly pedunculate at middle; basal impressions long and markedly impressed, joining with the lateral border of pronotum at basal third; anterior margin concave with front angles scarcely protruding; a marginal seta at anterior fifth on each side; lateral marginal bead anteriorly narrow and progressively broader towards base, where it joins with the basal impressions; anterior and posterior margins unbordered; medial longitudinal sulcus deep, ending before apex and base.

Elytra: EL: 3.14 mm, EW: 1.97 mm (HT ♂); EL: 2.99 mm, EW: 1.86 mm (PT ♀); EL/EW: 1.59 (HT ♂)–1.61 (PT ♀). Ovoid, moderately convex but flattened on disk, narrow at base and progressively widest towards apex, with shoulders markedly prominent forwards; sides sub-rectilinear at basal 2/3, then moderately arcuate towards apex, which is linearly truncate. Apical sutural angle of each elytron rounded; the outer posterior angle widely rounded. Surface smooth, without any distinct microsculpture, pubescent throughout with yellow semi-adjacent setae. Epipleura without distinct external plicae ('uncrossed epipleura'). Intervals delicately convex and densely punctate; striae distinctly impressed for nearly the whole length, more shallowly towards apex, irregularly punctate. Parascutellar stria absent;



Figs. 14-19. *Pseudaptinus (Thalpius) gracilis* n. sp.: Holotype habitus (14); Head in dorsal view (15); Pronotum (16); Median lobe of aedeagus in lateral view (17); Median lobe of aedeagus in dorsal view (18); Male gonosomite (IX invaginated abdominal segment) (19).

scutellar setigerous pore present between striae 1 and 2, adjacent to the first stria. Basal margin nearly indistinct. Discal setigerous punctures absent; punctures of the umbilicate series only a little more spaced at middle. Hind wings absent.

Ventral surface (thorax and abdomen): prosternum punctate and pubescent with long erect yellow setae; proepisterna sparsely pubescent. Mesosternum sparsely pubescent and punctate. Metepisterna moderately short, rugosely punctate, sub-rectangular and nearly as long as anterior margin. Prosternal intercoxal process broadly rounded at apex and apically setose. Sterna densely pubescent.

Legs: moderately long and pubescent throughout, uniformly light brown. Metatrochanters very short, as long as 1/4 of metafemora. Protibial antennal cleaning organ well developed, with two clip setae. Protibiae moderately short, robust; mesotibiae and metatibiae slender, about as long as tarsi, without spines except the apical ones, with an apical crown of brush-like setae; all tibiae longitudinally moderately flattened. Tarsomeres dorsally convex; protarsomeres moderately long, moderately and symmetrically dilated, the first one 1.5 times longer than 2nd and 3rd, the 4th concave at apex; metatarsomeres slender, the first one 1.8 times longer than 2nd; onychium with a double row of adhesive setae; claws smooth.

Male genitalia (Figs. 17-19): median lobe of aedeagus in lateral view abruptly curved at 45° just over the small basal bulb, then rectilinear until apex, moderately swollen at mid length (Fig. 17); in dorsal view more or less symmetrical and regularly narrowed from basal third to apex; apical blade long and stout, thick and rounded at apex (Fig. 18). Ostium moderately long, placed in dorsal position, as long as 2/3 of median lobe, not reaching basal bulb. Right paramere moderately small and narrow, elongate. Male gonosomite (IX invaginated abdominal segment) ovoid with proximal apophysis small, sub-triangular and apically pointed (Fig. 19).

REMARKS. *Pseudaptinus* (*Thalpius*) *gracilis* n. sp. shows evident morphological similarities with *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke as well as with *Pseudaptinus* (*Thalpius*) *moreti* n. sp., which can be considered, at the present state of knowledge, its closest relatives. They probably form, on account of their striking similarities as well as their likely similar way of life, a homogeneous group of species phylogenetically strictly related (see also remarks concerning *P. moreti* n. sp.).

DISTRIBUTION AND ECOLOGY. Geographical distribution:

Pseudaptinus (*Thalpius*) *gracilis* n. sp. is currently recorded only from the Pichincha province of Ecuador, near Lloa, along the Río Blanco stream (Fig. 7).

Life habits: the two specimens forming the typical series of *P. gracilis* n. sp. were collected at 2540 meters of altitude a.s.l., along the Río Blanco stream. This area is densely forested, and therefore, due to the flightless condition of this species, it is very likely a way of life in the forest litter. Some degree of myrmecophily in its behaviour should not be excluded.

ETYMOLOGY. The specific epithet refers to the tiny and slender habitus of this species, in comparison with the other members of the '*Pseudaptinus aptinoides* species group'.

***Pseudaptinus* (*Thalpius*) *aptinoides* Liebke, 1934**
(Redescription based on high-resolution photographs of HT)

Pseudaptinus (*Thalpius*) *aptinoides* Liebke, 1934: 381.

Pseudaptinus (*Thalpius*) *aptinoides* Liebke, 1934:
Lorenz, 2005: 505.

Pseudaptinus (*Thalpius*) *aptinoides* Liebke, 1934:
Blackwelder, 1957: 69.

TYPE LOCALITY. Caràcas, Venezuela.

TYPE SERIES. HT ♂: Caràcas, Venezuela / *Pseudaptinus aptinoides* Lbk. Type. M. Liebke determ. / Sammlung M. Liebke / Type (red label) / Inst. Zool. P.A.N. Warszawa Holotypus n. 1648 (red label) / Mus. Zool. Polonicum Warszawa 31/54.

RE-DESCRIPTION. A small-sized *Pseudaptinus* (subgenus *Thalpius*) species with *Aptinus*-like elytra. ABL: 5.57 mm (HT ♂).

Habitus and color (Fig. 20): body solid reddish-brown, slender, shiny, pubescent throughout, with mouth parts, antennae, and legs paler.

Head (Fig. 21): laterally convex, distinctly narrower than pronotum, dorsally coarsely punctate, more sparsely at vertex, posteriorly abruptly constricted in a thick neck, nearly 2/3 as wide as head; collar constriction dorsally distinct; eyes moderately small, scarcely convex, oval but posteriorly obliquely truncate; two supraorbital setae on each side; microsculpture indistinct; frontal impressions moderately deep, broad and short, ending at level of the anterior edge of eye; temples long and convex, densely pubescent with long bristles and about 1.5 times longer than diameter of eye; a narrow supraorbital carina moderately dilated above antennal insertion. Antennae moderately

short, slightly surpassing elytral base when stretched backwards, densely pubescent; the first antennomere longer than antennomeres 2-4 together, the 4th to 10th about 1.3-1.4 times longer than wide, the terminal one about 1.8 times longer than wide. Mentum distinctly broader than long, anterior margin shallowly emarginate; epilobes rather broad, laterally prominent and anteriorly acutely pointed; mentum tooth nearly indistinct; suture between mentum and submentum present. Maxillary palpi much larger than labial palpi, with palpomere 4 markedly enlarged; penultimate labial palpomere multisetose with one pair of major erect setae on anterior margin.

Thorax (Fig. 22): PL: 1.32 mm, PW: 1.15; PL/PW: 1.15. Pronotum distinctly wider than head, coarsely punctate (much more densely than on head) and rugose throughout, without any distinct microsculpture, pubescent with long yellow semi-adjacent setae; form moderately slender, only slightly longer than wide, widest at anterior third; side margins nearly rectilinear at apical third, then regularly arcuate and finally markedly sinuate at basal third, up to the sharply acute basal angles, scarcely prominent outside and with an angular seta; posterior margin distinctly pedunculate at middle; basal impressions long and markedly impressed, joining with the lateral border of pronotum at mid length; anterior margin concave with front angles scarcely protruding; a marginal seta at anterior fifth on each side; lateral marginal bead anteriorly narrow and progressively broader towards base, where it joins with basal impressions; anterior and posterior margins unbordered; medial longitudinal sulcus deep, ending before apex and base.

Elytra: EL: 3.02 mm, EW: 2.01 mm; EL/EW: 1.50. Ovoid, moderately convex and slightly depressed on disk, narrow at base and progressively widest towards apex, with shoulders markedly prominent forwards; sides scarcely arcuate at basal 2/3, then decidedly arcuate towards apex, which is linearly truncate. Apical sutural angle of each elytron rounded; the outer posterior angle widely rounded. Surface smooth, without any distinct microsculpture, pubescent throughout with yellow semi-adjacent setae. Epipleura without distinct external plicae ('uncrossed epipleura'). Intervals convex and densely punctate; striae distinctly impressed for nearly the whole length, nearly indistinctly punctate. Parascutellar stria absent; scutellar setigerous pore present between striae 1 and 2, adjacent to the first stria. Basal margin nearly indistinct. Discal setigerous punctures absent; punctures of the umbilicate series in a continuous row, not interrupted at middle. Hind wings absent.

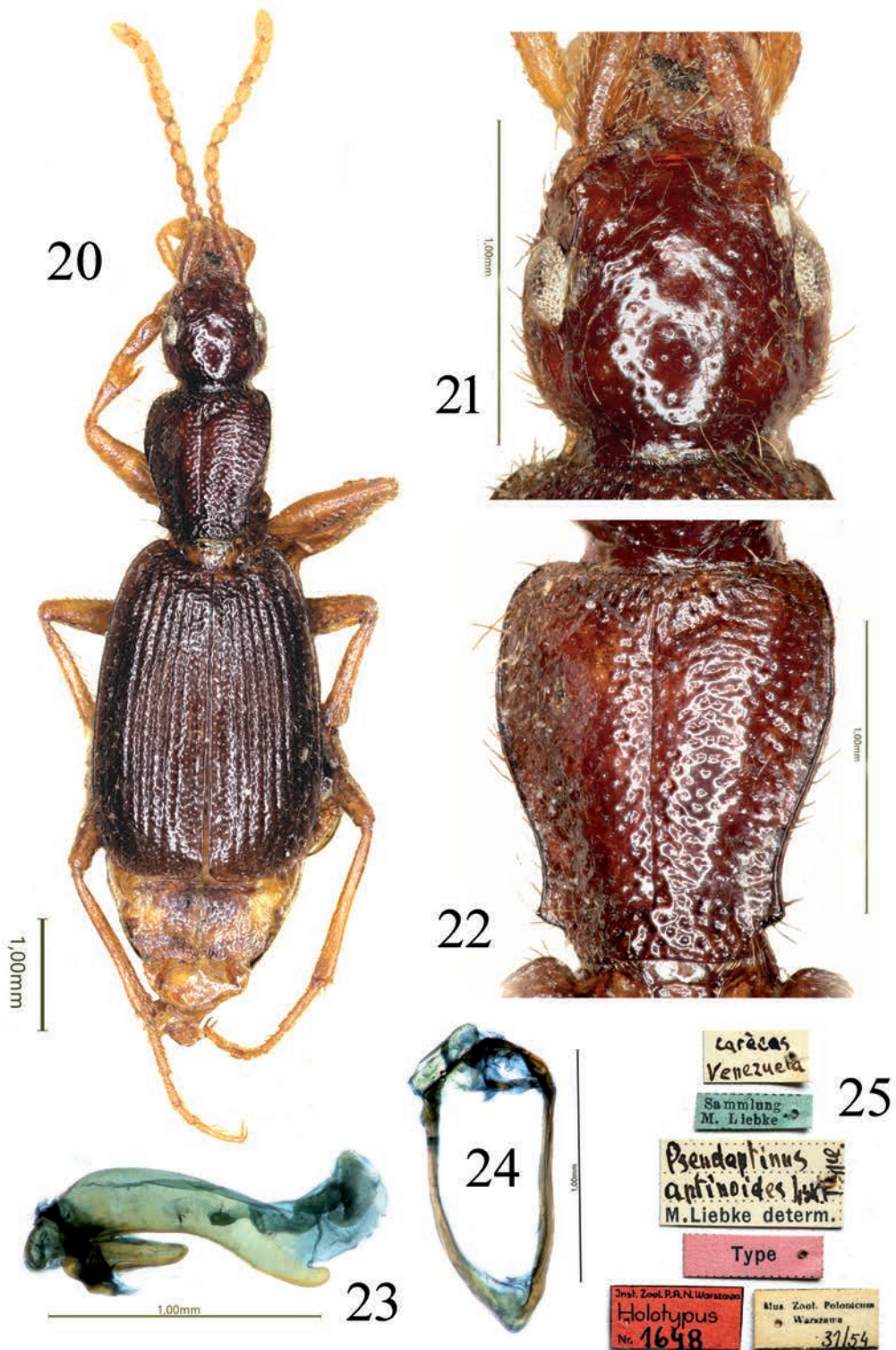
Ventral surface (thorax and abdomen): prosternum densely punctate and pubescent with long erect yellow setae; proepisterna densely punctate only anteriorly; mesosternum punctate and sparsely pubescent. Metepisterna moderately short, rugosely punctate, sub-rectangular, and nearly as long as anterior margin. Prosternal intercoxal process broadly rounded at apex and apically setose. Sterna densely pubescent.

Legs: moderately long and pubescent throughout, light brown with femora slightly darker. Metatrochanters moderately short, as long as 1/3 of metafemora. Protibial antennal cleaning organ well developed, with two clip setae. Protibiae moderately short, robust; mesotibiae and metatibiae slender, about as long as tarsi, without spines except the apical ones, with an apical crown of brush-like setae. Tarsomeres dorsally convex; protarsomeres moderately long, moderately and symmetrically dilated, the first one nearly 2 times longer than the 2nd and 3rd, the 4th concave at apex; metatarsomeres slender, the first one 1.8 times longer than the 2nd; claws smooth.

Male genitalia (Figs. 23 and 24): median lobe of aedeagus in lateral view sub-cylindrical and regularly curved at basal 2/3, then counter wise curved upwards until apex, which is short and blunt (Fig. 23). Male gonosomite (IX invaginated abdominal segment) sub-rectangular with proximal apophysis short, sub-triangular and apically blunt (Fig. 24).

REMARKS. *Pseudaptinus (Thalpius) aptinoides* Liebke shows evident morphological similarities with *Pseudaptinus (Thalpius) moreti* n. sp. and with *Pseudaptinus (Thalpius) gracilis* n. sp., which can be considered, at the present status of knowledge, its closest relatives. Their striking similarities as well as their likely similar way of life indicate the presence of a homogeneous group of species phylogenetically strictly related and recently originated by allopatry due to geographic barriers caused by climatic fluctuations during the Pleistocene. The flightless condition of these species and their consequent reduced dispersal ability may have favored the specific diversification.

DISTRIBUTION AND ECOLOGY. Geographical distribution: *Pseudaptinus (Thalpius) aptinoides* Liebke is currently recorded, according to label data (Fig. 25), only from Caracas, Venezuela. It is the most geographically isolated species within the species group. Life habits: no information is available on the preferred habitat of this species. Due to its flightless condition, it can be hypothesized a way of life in the forest litter, similarly to the newly described species of the same group.



Figs. 20-25. *Pseudaptinus* (*Thalpius*) *aptinoides* Liebke (photos by David Schimrosczyk - MIZ): Holotype habitus (20); Head in dorsal view (21); Pronotum (22); Median lobe of aedeagus in lateral view (23); Male gonosomite (IX invaginated abdominal segment) (24); Labels (25).

DISCUSSION

The four species of *Pseudaptinus* (subgenus *Thalpius*) concerned in this paper are, as far as I know, the only *Thalpius* species so far recorded showing a flightless condition. This condition is fairly common among the high-Andean Carabid species inhabiting paramo (Moret, 2005), but it becomes less common, at least at lower elevations, among the tropical forest species, most of which live in canopies and show good flight dispersal abilities (Basset *et al.*, 2015; Moret, 2024). In forest ecosystems, flightless condition is mainly found among litter inhabitants (Richardson & Richardson, 2013), which sometimes exhibit more or less close relationships with ants (Parker, 2016).

Wing reduction implies reduced dispersal ability, which is one of the causes, together with isolation due to geographic barriers and climatic fluctuations, of the interruption of gene flow and therefore of high levels of species differentiation in geographically restricted areas (Muñoz-Tobar & Caterino, 2019). This seems to be the case of the three new species here described, which are currently recorded only from restricted forest areas of Ecuador.

As the tropical Andean area can be regarded as a set of fragmented alpine islands (Anthelme *et al.*, 2014) and the insect fauna of the Amazon basin is still little known, it is likely that further future research in these Ecuadorian environments will lead to the discovery of other new microendemic species belonging to the genus *Pseudaptinus*, or even to the '*P. aptinoides* species group', although new records of these species, due to their high rarity, will take time and patience.

Key to the species of *Pseudaptinus* (subgenus *Thalpius*) from South America
(modified from Liebke, 1934)

1. Longitudinal diameter of eye longer than temple (interval between posterior eye border and constricted neck) > **2**
 - Longitudinal diameter of eye equal to or shorter than temple > **8**
2. Eye diameter double the temple length > **3**
 - Eye diameter triple the temple length > **4**
3. Pronotum longer than wide (L/W=1.13). Bolivia > ***lugubris*** Liebke, 1934
 - Pronotum nearly as long as wide (L/W=1.02). Brazil (Santa Catharina) > ***granulosus*** (Chaudoir, 1872)
4. Antennae very short, segments 5 – 6 as long as wide. Brazil (Santa Catharina) > ***plaumanni*** Liebke, 1939
 - Antennae short, segments 5 – 6 1.25-1.33 times longer than wide > **5**
 - Antennae longer, segments 5 – 6 1.5 times longer than wide > **6**
5. Antennal segments 5 – 6 1.25 times longer than wide. Dorsum uniformly colored dark red-brown. Argentina > ***brunneus*** Liebke, 1934
 - Antennal segments 5 – 6 1.33 times longer than wide. Elytra yellow-brown, head and elytra darkened. Brazil (La Plata river basin) > ***fluvialis*** Liebke, 1934
6. Pronotum short and wide. Dorsum uniformly black. Length 9 mm. Brazil (Amazon) > ***batesi*** Chaudoir, 1862
 - Pronotum somewhat longer than wide. Smaller species > **7**
7. Larger, 6-7 mm long. Body wide, robust. Pronotum with hind angles strongly protruding. Brazil (Amazon) > ***polystichoides*** Chaudoir, 1862
 - Smaller, 5.5 mm long. Body more slender. Pronotum with hind angles less protruding. Colombia (Amazon) > ***intermedius*** Chaudoir, 1872
8. Eye diameter equal to temple length. Elytra more or less parallel-sided > **9**
 - Eye diameter shorter than temple length. Elytra *Aptinus*-like shaped with marked narrowing of shoulders > **11**
9. Pronotum narrower, only slightly wider than head, with hind angles laterally projected as short thorn. Body size smaller (6 mm) > **10**
 - Pronotum much wider than head, with hind angles laterally projected as long thorn. Body size larger (8 mm). Dorsum reddish-brown. Argentina, Uruguay > ***argentinicus*** Liebke, 1929
10. Dorsum uniformly light yellow-brown, dull. Elytral intervals moderately convex. Argentina > ***bruchi*** Liebke, 1934

- Dorsum dark brown to piceous black, shiny. Elytral intervals costulated. Ecuador > *bartolozzii* n. sp.
- 11. Antennae relatively short, segments 5 – 6 at most 1.4 times longer than wide. Pronotum more transverse (PL/PW 1.15); elytra stocky (EL/EW 1.50). Venezuela > *aptinoides* Liebke, 1934
- Antennae longer, segments 5 – 6 at least 1.7 times longer than wide. Pronotum more slender (PL/PW >1.20); elytra more slender (EL/EW about 1.60). Species from Ecuador > **12**
- 12. Larger, about 7 mm long. Head dorsally coarsely punctate (Fig. 9). Median lobe of aedeagus evenly curved throughout its length, with thin, pointed apex (Fig. 11). Ecuador > *moreti* n. sp.
- Smaller, 5.7 mm long. Head dorsally finely punctate (Fig. 15). Median lobe of aedeagus nearly rectilinear throughout its length, with thick, blunt apex (Fig. 17). Ecuador > *gracilis* n. sp.

ACKNOWLEDGEMENTS

I would like to express my heartfelt thanks to the colleagues and friends (in alphabetical order) who made this research possible: Luca Bartolozzi (MZUF), for the loan of the material collected by himself in Ecuador and deposited in MZUF; Thierry Deuve, for his kind assistance; Pier Mauro Giachino, for the helpful suggestions and the check of the manuscript; Paolo Magrini, for facilitating contacts with MZUF; Dominika Mierzwa, for facilitating contacts with MIZ; Olivier Montreuil (MNHN) for the photograph of the HT of *Pseudaptinus granulosus*; Pierre Moret, for the loan of material from his collection, the check of the manuscript and the gift of PTs to the author; David Schimroszyk (MIZ), for the research in the MIZ collections and the photographs of the HT of *Pseudaptinus aptinoides*; Elena Vergnasco for linguistic revision.

REFERENCES

- AA.VV., 2021 - Biodiversity hotspot of the tropical Andes. Ecosystem profile. 2021 Update. Critical Ecosystem Partnership Fund, 571 pp.
- ALLEGRO G., 2024 - *Peruzuphium* n. gen. *giachinoi* new species of the tribe Zuphiini from Peru, with notes on *Metaxidius brunnipennis* Chaudoir (Coleoptera, Carabidae, Dryptinae). Bollettino della Società Entomologica Italiana, 156(1): 21-28.
- ANICHTCHENKO A., 2014 - Subgenus *Thalpius* LeConte, 1851. Available from <https://carabidae.org/taxa/thalpius-leconte-1851>.
- ANTHELME F., JACOBSEN D., MACEK P., MENESES R.I., MORET P., BECK S., DANGLES O., 2014 - Biodiversity patterns and continental insularity in the tropical High Andes. Arctic, Antarctic, and Alpine Research, 46(4): 811-828.
- BALL G.E., SHPELEY D., 2013 - Western Hemisphere Zuphiini: descriptions of *Coarazuphium whiteheadi*, new species, and *Zuphioides*, new genus, and classification of the genera (Coleoptera, Carabidae). Zookeys, 315: 17-54.
- BASSET Y., CIZEK L., CUÉNOUD P., DIDHAM R.K., NOVOTNY V., ØDEGAARD F., *et al.*, 2015 - Arthropod Distribution in a Tropical Rainforest: Tackling a Four Dimensional Puzzle. PLoS One, 10(12): e0144110.
- BLACKWELDER R.E., 1957 - Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. United States National Museum Bulletin, 188 pp.
- BOUSQUET Y., 2012 - Catalogue of Geadephaga (Coleoptera, Adephaga) of America, north of Mexico. ZooKeys, 245: 1-1722.
- LEMAIRE J.M., JOURDAN T., TOUROULT J., 2023 - Les Zuphiini des Antilles françaises II. Les genres *Pseudaptinus* et *Thalpius* (Coleoptera, Carabidae, Harpalinae). Le Coléoptériste, 26(3): 144-150.
- LIEBKE M., 1934 - Die Arten der Gattung *Pseudaptinus* Cast. (Col. Carabidae). Revista de Entomologia, 4(3): 372-388.
- LIEBKE M., 1939 - Neue Laufkäfer. Festschrift zum 60. Geburtstag von Prof. Dr. Embrik Strand, 5: 91-130.
- LORENZ W., 2005 - Systematic list of extant Ground Beetles of the World (Insecta Coleoptera Geadephaga: Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). Tutzing, 530 pp.
- LORENZ W., 2024 - Carabcat database (version 03 (08/2021)). In Bánki O., Roskov Y., Döring M., Ower G., Hernández Robles D.R., Plata Corredor C.A., Stjernegaard Jeppesen T., Örn A., Vandepitte L., Pape T., Hobern D., Garnett S., Little H., DeWalt R.E., Ma K., Miller J., Orrell T., Aalbu R., Abbott J. (eds.), Catalogue of life (Version 2024-09-25). Available from: <https://www.checklistbank.org/dataset/309120/source/1146>.
- MARTINEZ C., 2005 - Introducción a los escarabajos Carabidae (Coleoptera) de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, 546 pp.
- MESSER P.W., 2011 - *Pseudaptinus* (*Thalpius*) *nobilis* Liebke, new to the United States, and a key to the species of subgenus *Thalpius* LeConte in North America, including Mexico (Coleoptera: Carabidae: Zuphiini). Zookeys, 147: 419-424.
- MORET P., 2005 - Los coleópteros Carabidae del páramo en los Andes del Ecuador. Sistemática, ecología y biogeografía. Quito,

- Pontificia Universidad Católica del Ecuador, Centro de Biodiversidad y Ambiente, Monografía 2, Gruppo Editoriale il Capitello, Torino, 306 pp.
- MORET P., 2024 - Description of new Platynini from the montane cloud forest of Ecuador, with a redefinition of the genera *Glyptolenus* Bates and *Glyptolenoides* Perrault (Coleoptera, Carabidae). *Faunitaxys*, 12(63): 1-23.
- MROCKOWSKI M., 1960 - List of type specimens in the collection of the Institute of Zoology of the Polish Academy of Sciences in Warszawa III. Carabidae (Coleoptera). *Annales Zoologici*, 18(21): 365-409.
- MUÑOZ-TOBAR S.I., CATERINO M.S., 2019 - The role of dispersal for shaping phylogeographical structure of flightless beetles from the Andes. *PeerJ*, 7: e7226.
- MYERS N., MITTERMEIER R. A., MITTERMEIER C. G., FONSECA G. A., KENT J., 2000 - Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.
- PARKER J., 2016 - Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News*, 22: 65-108.
- REICHARDT H., 1977 - A synopsis of the genera of Neotropical Carabidae (Insecta (Coleoptera). *Quaestiones Entomologicae*, 13: 346-493.
- RICHARDSON B.A., RICHARDSON M.J., 2013 - Litter-based invertebrate communities in forest floor and bromeliad microcosms along an elevational gradient in Puerto Rico. *Ecological Bulletins*, 54: 101-115.