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First report on the leafhopper genus *Balera* Young (Hemiptera, Cicadellidae, Typhlocybinae, Alebrini) from Argentina, and description of a new species

María Inés Catalano[1,†], Susana L. Paradell[2,‡], Christopher H. Dietrich[3,§]

1 *Centro de Bioinvestigaciones, Departamento de Ciencias Básicas y Aplicadas, Universidad Nacional del Noroeste de la Provincia de Buenos Aires, Monteagudo 2772, Pergamino, Buenos Aires, 2700, Argentina. CONICET* **2** *División Entomología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Paseo del Bosque s/n, La Plata, Buenos Aires, 1900, Argentina. CIC* **3** *Illinois Natural History Survey, Institute of Natural Resource Sustainability, University of Illinois, 1816 S. Oak Street, Champaign, Illinois, 61820, USA*

† *http://zoobank.org/2A8B11C3-0011-48D0-A642-34778A46AC7D*
‡ *http://zoobank.org/AF8CFD04-0CBE-4014-9A5E-FCE56190B04F*
§ *http://zoobank.org/82FCB86C-54B4-456A-AE5E-D7847D271CB9*

Corresponding author: *María Inés Catalano* (mariainescatalano@unnoba.edu.ar; mariainescatalano@gmail.com)

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Abstract

The genus *Balera* Young is reported for first time to Argentina and a new species is described, *Balera floripara* **sp. n.** Detailed morphological descriptions and illustrations of the new species and a key to males of known species are provided. *Habralebra amoena* is also recorded for the first time from Argentina.

Resumen

El género *Balera* Young es registrado por primera vez para Argentina y una nueva especie es descripta, *Balera floripara* **sp. n.** Se provee de detalladas descripciones morfológicas e ilustraciones de la nueva especie, y una clave de las especies conocidas. Además *Habralebra amoena* se registra por primera vez para Argentina.

Keywords
Auchenorrhyncha, identification, morphology, distribution

Palabras claves
Auchenorrhyncha, identificación, morfología, distribución

Introduction

The tribe Alebrini McAtee, 1926 is represented by 34 genera (Balme 2007), six of which were recorded previously from Argentina: *Habralebra* Young, 1952, *Rhabdotalebra* Young, 1952, *Omegalebra* Young, 1957, *Protalebra* Baker, 1899, *Protalebrella* Young, 1952 and *Relaba* Young, 1957 (Young 1957, Dworakowska 1994, Catalano et al. 2010).

The genus *Balera* Young include twelve species recorded from Bolivia, Brazil, Colombia, Ecuador, Panama, Trinidad and Tobago and Venezuela (Young 1952, 1957; Ruppel 1959; Freytag 1992; Dworakowska 1994 and Coelho et al. 2013).

The genus *Habralebra* Young is represented by twelve species recorded from Argentina, Bolivia, Brazil, Ecuador, Nicaragua, Panama and Puerto Rico. *H. willinki* Young, 1957, *H. trimaculata* (Gillette, 1898) and *H. gillettei* Young, 1957 were known previously from Argentina (Young 1957).

Here, we record *Balera* from Argentina for the first time based on a new species, *Balera floripara*, and record *Habralebra amoena* for the first time from Argentina.

Materials and methods

The specimens were collected with Malaise and mercury vapor lights traps in Misiones and Jujuy provinces. For morphological study of the genital structures, clearing was accomplished by immersion of the entire abdomen in a solution of 10% KOH at room temperature for several hours followed by several rinses with water. For illustration, genital structures were embedded in glycerin. The color pattern here described is the post-mortem coloration. In living or recently collected individuals the coloration may be more vivid relative to that of old preserved specimens. Morphological terminology follows Young (1952) and Dietrich (2005) for habitus and genitalia characters. Digital photographs were taken using a QImaging Micropublisher 3.3 digital camera mounted on an Olympus SZX12 stereomicroscope. The type-series of the new species are deposited in the entomological collections of the Museo de Ciencias Naturales de La Plata, Argentina (MLP) and the Illinois Natural History Survey, USA (INHS).

Taxonomy

Alebrini McAtee

***Balera* Young**
http://species-id.net/wiki/Balera

Balera Young, 1952: 25. Type species: *Dikraneura pellucida* (Osborn), by original designation.

Diagnosis. The genus *Balera* can be distinguished by the following combination of characters: forewing with appendix not extending around wing apex; hindwing with submarginal vein distinct and free from apical wing margin; male sternal abdominal apodemes slender and elongate, usually capitate apically; pygofer produced posteriorly, occasionally forming an apical process; subgenital plates with single or double row of weak macrosetae; style sigmoid in lateral aspect; connective V or Y-shaped or triangular; aedeagus shaft with one or two pairs of apical or anteapical processes.

Key to males of *Balera* (modified from Coelho et al. 2013 to include the new species)

1	Aedeagus without long, paired distal processes, with short lobes or keels, or apex bifurcate **2**
1'	Aedeagus with one or more pairs of slender distal processes longer than shaft width **5**
2(1)	Aedeagus inflated, shaft keeled laterally, with 3 apical lobes (Young 1957, fig. 12D) ..... ***B. pellucida* (Osborn)**
2'	Aedeagus not inflated, shaft with or without keels, without apical lobes..... **3**
3 (2)	Aedeagus bifurcated distally **4**
3'	Aedeagus not bifurcated, with pair of lateral keels on apical half (Young 1957, figs 13C, D) ..... ***B. pusilla* Young**
4 (3)	Pygofer without apical process; aedeagus with long bifurcated apex (Ruppel 1959, figs 2E, F, G) ..... ***B. bracata* Ruppel**
4'	Pygofer with short apical process; aedeagus with short bifurcated apex (Figs 2B, F, G) ..... ***B. floripara* sp. n.**
5 (1')	Aedeagus with one pair of apical processes **6**
5'	Aedeagus with two or more pairs of apical processes **11**
6 (5)	Style with acute apex..... **7**
6'	Style with truncate apex (Freytag 1992, fig. 7) ..... ***B. obtusa* Freytag**
7 (6)	Apices of aedeagal processes convergent, in ventral view, near stem base (Freytag 1992, fig. 17) ..... ***B. napoensis* Freytag**
7'	Apices of aedeagal processes not convergent..... **8**
8 (7')	Apex of aedeagus narrow and pointed in ventral view **9**
8'	Apex of aedeagus not pointed in ventral view..... **10**

9 (8) Style slightly angled at midlength; pygofer long, with posterior margin produced, narrowly rounded (Freytag 1992, fig. 23, 24)..... ***B. plagata*** **Freytag**

9' Style strongly angled at midlength; pygofer broad, with posterior margin weakly produced (Freytag 1992, figs 11, 12)..... ***B. ecuadora*** **Freytag**

10 (8') Posterior margin of pygofer broadly rounded (Young 1957, fig. 12L)..... ..... ***B. caraguatae*** **Young**

10' Posterior margin of pygofer with acuminate process (Dworakowska 1994, fig 219)..... ***B. signata*** **Dworakowska**

11 (5') Aedeagus with two pairs of apical processes..... **12**

11' Aedeagus with three pairs of apical processes (Coelho et al. 2013, figs 14, 15)..... ***B. fiuzai*** **Coelho, Nessimian, Da-Silva**

12 (11) Dorsoapical pair of aedeagal processes longer than ventral pair (Freytag 1992, figs 1, 2)..... ***B. myersi*** **Freytag**

12' Dorsoapical pair of aedeagal processes approximately same length as ventral pair (Young 1957, figs13F, H)..... ***B. emarginata*** **(Osborn)**

Balera floripara **sp. n.**
http://zoobank.org/E1AEF78C-AD35-462C-9CE3-20FA2A0DE2A3
http://species-id.net/wiki/Balera_floripara
Figs 1A, 2 A–G

Description. Length of male 3.7–3.8 mm. Ground color pale-yellow; crown, pronotum and scutellum with yellow markings; forewing with longitudinal yellow stripes on clavus and along CuA in corium, apical tip of clavus dark brown, with brown markings on bases of apical cells and apices of anteapical cells arranged in radial pattern (Fig. 1A).

Male: First sternal apodemes (1S) (Fig. 2A) enlarged with apices overlapping. Second sternal apodemes (2S) (Fig. 2A) slender and elongate, reaching sixth segment, apices capitate. Pygofer (Fig. 2B) with posterior margin produced, with short, acute apical process directed dorsad and row of very long, thin setae on postero-ventral margin. Subgenital plate (Fig. 2C), in lateral view, with basal half strongly tapered, apical half with margin parallel through most of length, apex with a small spine slightly curved; basal half with several long macrosetae irregularly arranged and row of moderately long, slender microsetae on dorsal margin, apical half with medial row of short, stout setae. Style (Fig. 2D), in lateral view, sigmoid with three preapical setae. Connective (Fig. 2E) triangular. Aedeagus (Figs 2F–G) with preatrium nearly as long as shaft, dorsal apodeme compressed, racket-shaped in lateral view, incompletely fused to shaft; shaft short and broad, apex bifurcate, without processes; gonopore apical.

Material examined. Holotype male, ARGENTINA: Jujuy, P.N. Calilegua 1600m 23°41'1"S, 64°54'0"W, 14–16 January 2008 Dietrich et al col. Malaise trap [MLP]. Paratypes: 2 males, same data as holotype [INHS].

Etymology. The specific name refers to the arrangement of the five dark markings on the forewing arranged radially in the form of a flower.

Figure 1. Dorsal habitus. **A** *Balera floripara* sp. n. **B** *Habralebra amoena*. Scale = 1 mm.

Note. This species closely resembles *B. bracata* but has a short process on the pygofer and the aedeagus is wider with the apical bifurcation shorter.

New records

Habralebra Young

Habralebra Young, 1952: 33. Type species: *Protalebra nicaraguensis* (Baker), by original designation.

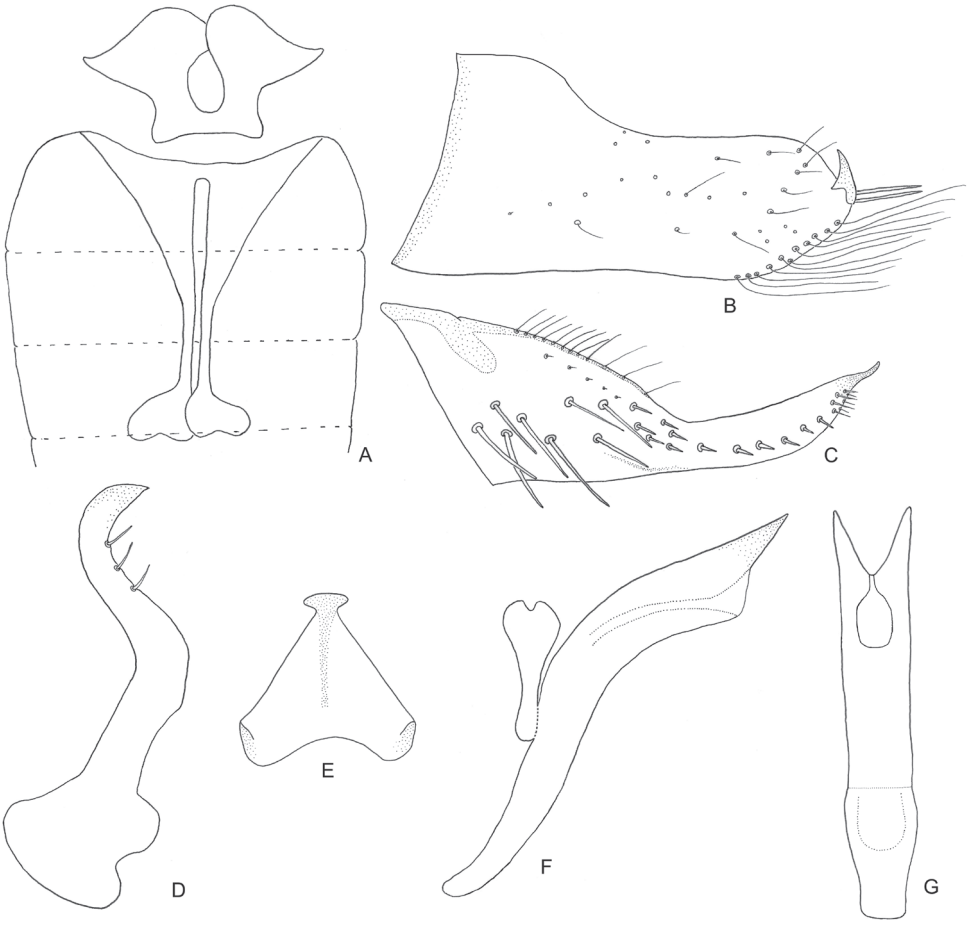

Figure 2. *Balera floripara* sp. n. Male (**A–G**) **A** sternal apodeme 1S and 2S **B** pygofer, lateral view **C** subgenital plate **D** style **E** connective **F** aedeagus in lateral view **G** aedeagus in posterior view.

***Habralebra amoena* Young**
http://species-id.net/wiki/Habralebra_amoena
Fig. 1B

Protalebra amoena Baker, Psyche, vol 8, p. 404, 1899.
Habralebra amoena Young, Univ. Kansas Sci. Bull. 35, p. 34, 1952.

Distribution. Brazil. New record from Argentina, Misiones.

Material examined. 4 males and 1 female, ARGENTINA: Misiones, Puerto Iguazú 200m 25°37'19"S, 54°32'52"W, 7 January 2008 Dietrich col. hand collected at night [2 males and 1 female in MLP, 2 males in the INHS].

Acknowledgements

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RESEARCH ARTICLE

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Deep phylogenetic divergence between *Scolytoplatypus* and *Remansus*, a new genus of Scolytoplatypodini from Madagascar (Coleoptera, Curculionidae, Scolytinae)

Bjarte H. Jordal[1,†]

1 *Natural History Museum, University Museum of Bergen, PB 7800, NO-5020 Bergen, Norway*

† *http://zoobank.org/62B587DB-09CB-450E-B1E1-3708889ECBAE*

Corresponding author: *Bjarte H. Jordal* (bjarte.jordal@um.uib.no)

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Abstract

Scolytoplatypodini Blandford is a monotypic tribe of ambrosia beetles found in Asia, Madagascar and Africa. Only three species are currently known from Madagascar and four additional species are here described as new to science. Phylogenetic analyses of morphological and molecular data revealed that four of the seven endemic species are deeply separated from all other species by genetic and distinct morphological characters and therefore placed in a new genus *Remansus* Jordal. The split between this ancient lineage and *Scolytoplatypus* Schaufuss was estimated to approximate Palaeocene age (63 Ma), extending the minimum age of ambrosia feeding for this tribe to the beginning of the Palaeocene−Eocene thermal maximum (PETM). In addition to the ancient origin of *Remansus* in Madagascar during the Palaeocene, a second origin occurred in *Scolytoplatypus* no more than 13 Ma. A geographical origin of the latter in South-Eastern Africa was unequivocally inferred from the phylogenies.

Keywords

Curculionidae, Scolytinae, Scolytoplatypodini, molecular phylogeny, biogeography, Madagascar, PETM

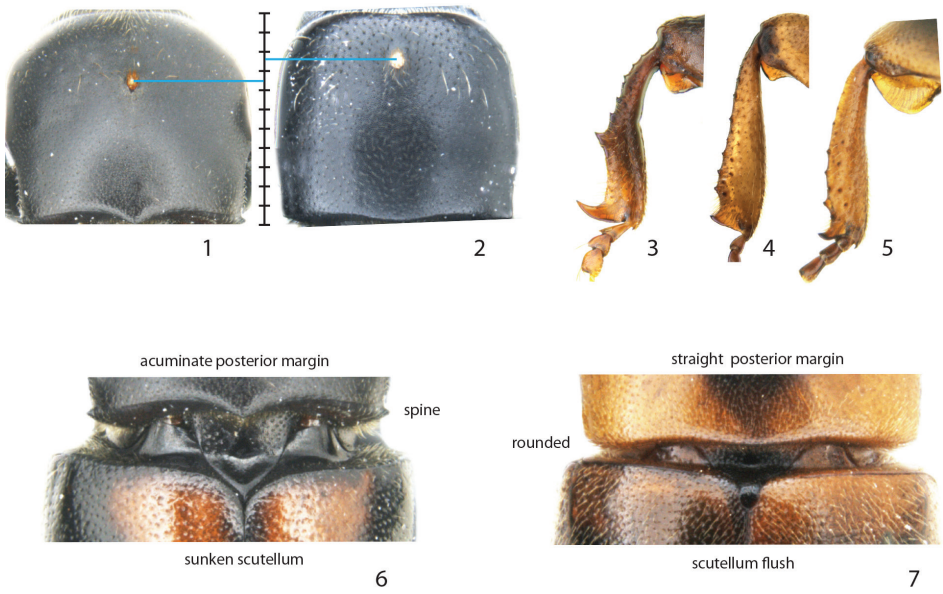
Introduction

Madagascar has one of the highest diversity of plants and animals, a diversity reflected not only by the great number of plant and animal species, but also by a huge number of endemic lineages of higher taxonomic ranks. Forest insects are no exception to this pattern. Woodboring weevils in the subfamily Scolytinae and Platypodinae have dozens of genera and hundreds of species endemic to Madagascar, with several cosmopolitan genera forming particular voluminous species group radiations on this island (Schedl 1977).

Scolytoplatypus is currently the only recognised genus in the tribe Scolytoplatypodini, known from Asia, Madagascar and Africa (Beaver and Gebhardt 2006; Browne 1971; Schedl 1975). These medium to large sized beetles cultivate fungi used as food for their larvae, where females carry spores in a characteristic large dorsal mycangium situated in the anterior third of the pronotum (Figs 1 and 2). Males and females are strongly dimorphic, with the male frons distinctly concave as opposed to the convex female frons. Male protibiae are asymmetric and smooth on its posterior side, with two or more long lateral spines (Fig. 3), whereas the females have much broader protibiae with coarse granules on its posterior face. Browne (1971), and later Beaver and Gebhardt (2006), noted that the Asian species are distinct from the African and Malagasy species by having sexually dimorphic antennae, constricted lateral sides of pronotum in both sexes, and by the acute projections or nodules on the male prosternum. The affiliation of the Malagasy species has not yet been evaluated but no one has so far disputed a close relationship to the African species (see Schedl 1975).

In Madagascar the genus has relatively low diversity with only three species reported, compared to a total of 12 species in Africa (Schedl 1975) and 28 in Asia (Beaver and Gebhardt 2006). Recent field work on the island has revealed four undescribed species collected in very low numbers compared to the other known species in this area. Three of the new species possess morphological features shared with *S. mutabilis* Schedl that deviate from the typical *Scolytoplatypus* species, having a large, flat scutellum that is flush with the elytra, rounded postero-lateral angles of the pronotum (Fig. 7), and nearly parallel-sided male protibiae (Figs 4 and 5). These features are plesiomorphic and indicate a transition from a more typical scolytine bauplan. It is therefore possible that such distinct difference in morphology is reflected in molecular data and that a phylogenetic analysis will enable test of taxon distinctness.

This paper presents a revision of the Malagasy species of Scolytoplatypodini and attempts to relate these species to the African and Asian members of the genus. A phylogenetic analysis of morphological and molecular data is presented to assess the number of independent clades that occur in Madagascar and to document the existence of a new genus *Remansus* for the most ancient clade of Malagasy species. Molecular data are used to place the Malagasy species in an evolutionary time frame, and to explore the geographical origin of the scolytoplatypodine fauna in Madagascar.



Figures 1–7. Diagnostic characters for *Scolytoplatypus* and *Remansus*. **1** Location of mycangia on the pronotum of *S. hova* and **2** *R. pygmaeus* **3** male protibiae of *S. rugosus* **4** *R. serratus* and **5** *R. mutabilis* **6** posterior part of pronotum and scutellum in *S. permirus* and **7** *R. mutabilis*.

Materials and methods

Material of Malagasy Scolytoplatypodini was available from California Academy of Science's biodiversity inventory 2000–2002 and from the author's field collecting in 2012. Additional material collected by the author was available from Africa and Asia (Table 1). The following acronyms are used for the material studied: CAS, California Academy of Science; ZMBN, University Museum in Bergen; NHMW, Naturhistorisches Museum Wien.

Sequences were generated from the mitochondrial cytochrome oxidase 1 (COI) gene (690 bp) and the three nuclear genes CAD (490 bp), EF1*a* (857 bp) and 28S (865 aligned sites). DNA was extracted and amplified using the protocols and primers listed in Jordal et al. 2011. Phylogenies were estimated from a concatenated matrix of all four genes (2894 aligned sites) using the Bayesian criterion in the software MrBayes v. 3.2 (Ronquist and Huelsenbeck 2003), applying a GTR+I+G model. These data were also analysed by maximum parsimony using PAUP (Swofford 2002), with 200 heuristic searches, TBR and random addition of taxa. Bootstrap support was estimated from 200 replicates of 100 random additions for each replicate. The molecular phylogenies were compared to one based on parsimony analysis of 21 morphological characters (Table 2). The morphological analysis included one additional species for which molecular data were not available (*R. serratus* Jordal).

Table 1. Material used for phylogenetic analyses, including their GenBank accession numbers.

Taxon	Country	COI	EF1 *a*	28S	CAD
Polydrusus cervinus (Linnaeus)	Norway	HQ883729	HQ883729	HQ883568	HQ883793
Porthetes hispidus (Boheman)	South Africa	HQ883666	HQ883737	HQ883577	HQ883805
Scolytodes acuminatus Wood	Costa Rica	EU191844	EU191876	EU090351	HQ883790
Remansus mutabilis (Schedl)	Madagascar	KF758328	KF758341	KF758300	KF758316
Remansus pygmaeus Jordal, sp. n.	Madagascar	-	KF758338	KF758294	KF758310
Remansus sahondrae Jordal, sp. n.	Madagascar	KF758331	KF758347	KF758303	KF758319
Remansus serratus Jordal, sp. n.	Madagascar	-	-	-	-
Scolytoplatypus africanus Eggers	Uganda	EU191866	EU191898	AF308391	HQ883822
Scolytoplatypus congonus Schedl	Cameroon	KF758321	KF758334	KF758290	KF758306
	Tanzania	KF758322	KF758335	KF758291	KF758307
Scolytoplatypus eutomoides Blandford	Papua N Guinea	HQ883679	HQ883748	EU090345	HQ883823
Scolytoplatypus fasciatus Hagedorn	South Africa	KF758324	KF758337	KF758293	KF758309
Scolytoplatypus hova Schaufuss	Madagascar	KF758326	KF758340	KF758298	KF758314
	Madagascar	KF758327	KF758344	KF758299	KF758315
Scolytoplatypus javanus Eggers	Sarawak	KF758333	KF758349	KF758305	-
Scolytoplatypus neglectus Schedl	Cameroon	KF758332	KF758348	KF758304	KF758320
Scolytoplatypus permirus Schaufuss	Madagascar	-	KF758339	KF758295	KF758311
	Madagascar	-	KF758342	KF758296	KF758312
	Madagascar	KF758325	KF758343	KF758297	KF758313
Scolytoplatypus rugosus Jordal, sp. n.	Madagascar	KF758329	KF758345	KF758301	KF758317
	Madagascar	KF758330	KF758346	KF758302	KF758318
Scolytoplatypus truncatus Browne	Cameroon	KF758323	KF758336	KF758292	KF758308
Scolytoplatypus tycon Blandford	Japan	JX263861	JX264142	JX263764	-

Table 2. Morphological characters used in the phylogenetic analysis.

1	Male frons convex (0); concave (1)
2	Male antennal club similar to female (0); prolonged (1)
3	Female pronotum with central mycangium absent (0); present (1)
4	Female mycangium placed about one quarter from anterior margin (0); one third or more from anterior margin (1); n/a (-)
5	Males with lateral fovea on pronotum absent (0); present (1)
6	Postero-lateral margin of pronotum straight in both sexes (0); constricted in females only (1); constricted in both male and female (2)
7	Posterior corner of pronotum rounded (0); with spine (1)
8	Posterior margin of pronotum straight (0); acuminate (1)
9	Scutellum is flush with elytra (0); or sunken and near invisible (1)
10	Striae on posterior half of the elytral disk of the male not impressed (0); strongly and broadly impressed (1)
11	Male declivity with interstriae 1, 3 and 5 on male declivity flat (0); convex (1); carinate (2)
12	Female declivity with all striae similarly impressed (0); not impressed or evident (1)
13	Base of declivity smooth (0); with a carinate ring or serration (1)
14	Female apex of the elytra rounded (0); extended into a flange (1)
15	Vestiture scattered and restricted to interstriae (0); uniformly pilose (1)
16	Females with a patch of longer setae close to the elytral apex absent (0); present (1)
17	Procoxae contiguous (0); separated (1)
18	Female protibiae: narrow, parallel-sided and smooth (0); broad, with coarse spines (1)
19	Male protibiae nearly parallel-sided (0); strongly curved and asymmetric (1)
20	Prosternum in males simple, smooth (0); or extended anteriorly into nodules or projections (1)
21	Dorsal side of profemur smooth (0); with spine (1)

The timing of Malagasy origins was estimated in the software Beast (Drummond and Rambaut 2007). Two different analyses were made. In analysis A, a minimum age of 116 Ma was set for the ingroup, defined as Scolytoplatypodini, *Scolytodes acuminatus* Wood and the Molytinae *Porthetes hispidus* (Boheman). In analysis B, a recently published estimate of 36 Ma was used for the most recent common node for three species of *Scolytoplatypus* (see Jordal and Cognato 2012), without constraining these monophyletically. Calibration of nodes was based on a normal distribution with a relatively broad standard deviation of 5 my.

Results and discussion

Taxonomy

Scolytoplatypodini Blandford
http://species-id.net/wiki/Scolytoplatypodini

Revised diagnosis. Female. *Frons* flattened to convex; antennal club flat, pilose, without sutures; *pronotum* with a dorsal mycangium (except seven species), pronotum weakly to strongly constricted laterally in posterior third, hind corners rounded or acute, posterior margin straight to strongly bisinuate; *scutellum* visible, narrow and sunken or broader and flush with elytra; *procoxae* widely separated; *protibiae* broad, on its posterior side with coarse granules and blunt spines, some forming rugae.

Male. Similar to female except *frons* slightly to very strongly concave, *pronotum* without mycangium, some with anterior fovea on lateral sides (Asian species), laterally constricted or not in posterior third; protibiae generally smooth on posterior side, sides straight to strongly curved and asymmetrical, laterally with small or large lateral spines.

Included genera. *Scolytoplatypus* Schaufuss and *Remansus* Jordal, gen. n.

Distribution. Asia, Africa and Madagascar.

***Scolytoplatypus* Schaufuss, 1891**
http://species-id.net/wiki/Scolytoplatypus

Type species. *Scolytoplatypus permirus* Schaufuss.

For a complete diagnosis of the genus and discussions on morphological features, see reviews by Beaver and Gebhardt (2006) and Browne (1971).

Malagasy species of *Scolytoplatypus*

The genus in Madagascar includes three possibly monophyletic species whose ancestor colonized Madagascar rather recently. They have all typical features of the African lineage, including a sharp lateral spine at posterior corners of the pronotum, the female

mycangium about one-third or more from the anterior margin, a strongly bisinuate (acuminate) posterior margin of the pronotum, a narrow and sunken scutellum, and strongly asymmetrical male protibiae with a long and curved lateral distal spine. They lack a dorsal spine on the profemur and therefore key out in couplet 7 in Browne's (1971) key to African species, near *S. fasciatus* Hagedorn.

Scolytoplatypus permirus Schaufuss, 1891

http://species-id.net/wiki/Scolytoplatypus_permirus
Figs 8–13

Scolytoplatypus permirus Schaufuss, 1891: 31.

Diagnosis. Length 2.5–3.1 mm.

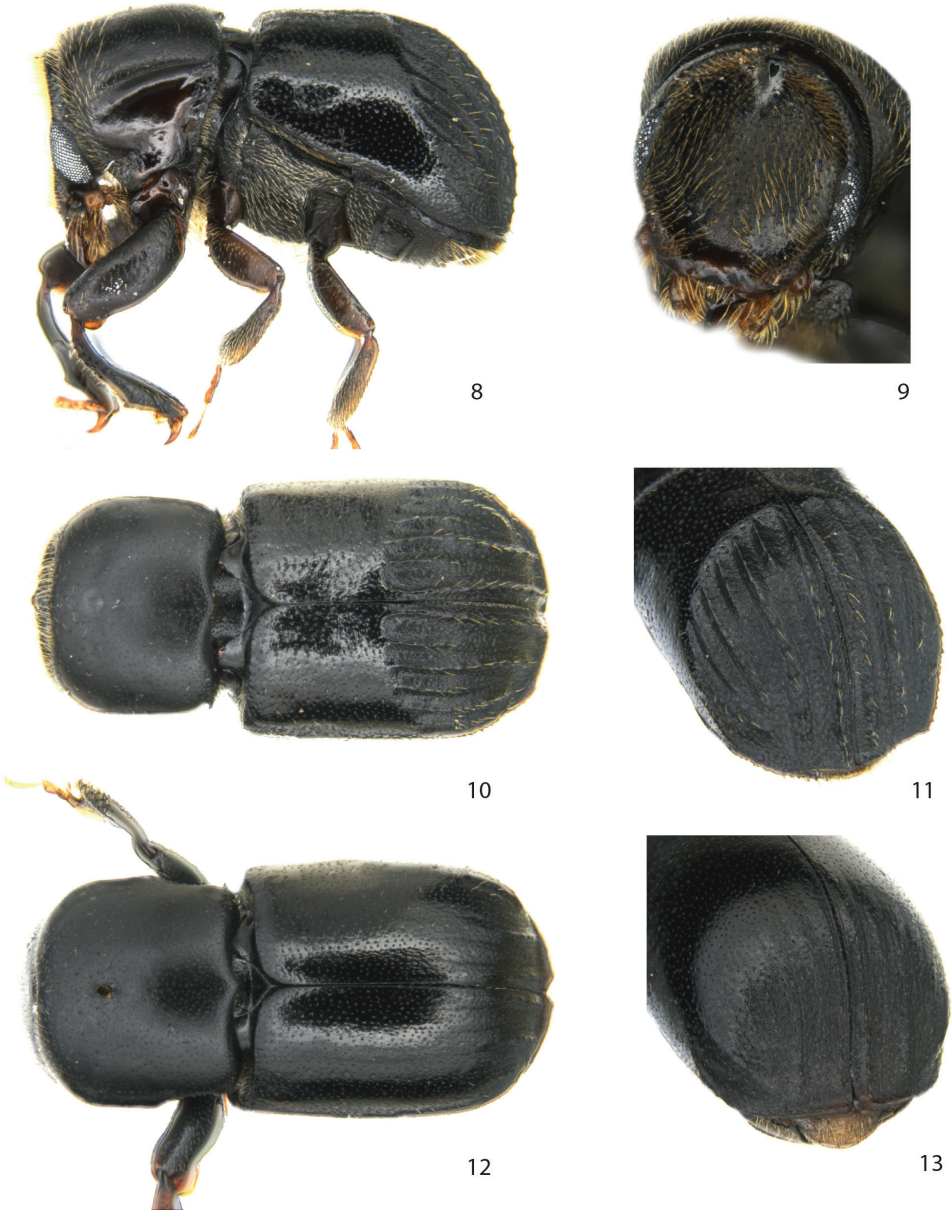
Male. *Frons* concave, marked at its upper margin by a small heart-shaped tubercle. *Pronotum* with a short spine in postero-lateral corners, posterior margin strongly bisinuate. *Scutellum* narrow, sunken between elytra. *Elytral disk* on posterior third and declivity with carinate interstriae and deeply excavated striae; interstriae 2, 4 and 6 not carinate on declivity; declivity in lateral profile gradually rounded.

Female. Similar to male except *frons* convex, *pronotum* with one large mycangial pore, posterior third of pronotum laterally constricted, posterior part of elytral disk smooth, declivity with shallowly impressed striae, interstriae 1, 3 and 5 weakly elevated, *elytral apex* broadly rounded, extended flange less transverse, with broad v-shaped emargination at suture; *protibiae* broad, posterior face tuberculate.

Variability. The amount of interstrial setae and granules on declivity varies considerably between individuals.

Molecular data. DNA barcodes in Table 1.

Distribution and biology. New records: Antsiranana Prov, Parc National Montagne d'Ambre, 12°30'52"S, 049°10'53"E, MA-01-01A-01, 21-26 Jan 2001, Malaise trap. Antsiranana Prov, Sakalava Beach [vegetated beach dunes], 12°15'46"S, 049°23'51"E, MA-01-04B-17, 13-20 Aug 2001, malaise trap. Fianarantsoa Prov, Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20°35'36"S, 046°33'48"E, BLF7155, 22-26 Jan 2003, EB09 sifted litter (leaf mold, rotten wood). Fianarantsoa Prov, Ranomafana National Park, Belle Vue trail, 21°15'59"S, 047°25'13"E, MA-02-09C-23, 31 Mar-7 Apr 2002; MA-02-09C-36, 24 Jul-4 Aug 2002, MA-02-09C-21, 19-26 Mar 2002; MA-02-09C-25, 14-23 Apr 2002, all in Malaise traps; JIRAMA water works, 21°14'55"S, 047°27'08"E, MA-02-09D-08, 21-24 Dec 2001, malaise trap. Toamasina Prov, Andasibe National Park, botanic garden near entrance, 18°55'35"S, 048°24'28"E, MA-01-08B-18, 01-10 Nov 2001, malaise trap [CAS]. Fianarantsoa prov, Ranomafana NP, Centre ValBio [-21.25, 47.42], alt. 950m, ex *Dalbergia* branch, 2012: 1x-7, B.Jordal leg; Vato trail [-21.29, 47.42], alt. 1100m, ex *Xylopia* branch, 2012: 4x-11, B.Jordal leg; Valo area [-21.31, 47.43], alt. 1100m, ex *Albizia* branch, 2012: 6x-9, B.Jordal leg. [ZMBN].



Figures 8–13. *Scolytoplatypus permirus* Schaufuss. **8** male lateral view **9** male frons **10** male dorsal view **11** male declivity **12** female dorsal view **13** female declivity.

A fairly common species throughout the wet forests of Madagascar, where it frequently co-occurs with *S. hova* Schaufuss. It breeds in small diameter branches, typically ranging between 2–5 cm. Previously known from Montagne d'Ambre and Joffreville in the north of the island, from Antananarivo, and in the east from Perinet in

Andasibe national park (Schedl 1977). The many new records from the South-Eastern rain forest in Ranomafana documents its likely presence throughout the moist and wet forests of the island. This is a very polyphagous species, reported previously from 20 host plant species in 14 different plant families (Schedl 1977), adding here another three host genera and one new plant family (Annonaceae).

***Scolytoplatypus hova* Schaufuss, 1905**
http://species-id.net/wiki/Scolytoplatypus_hova
Figs 14–19

Scolytoplatypus hova Schaufuss, 1905: 12.

Diagnosis. Length 3.5–4.5 mm.

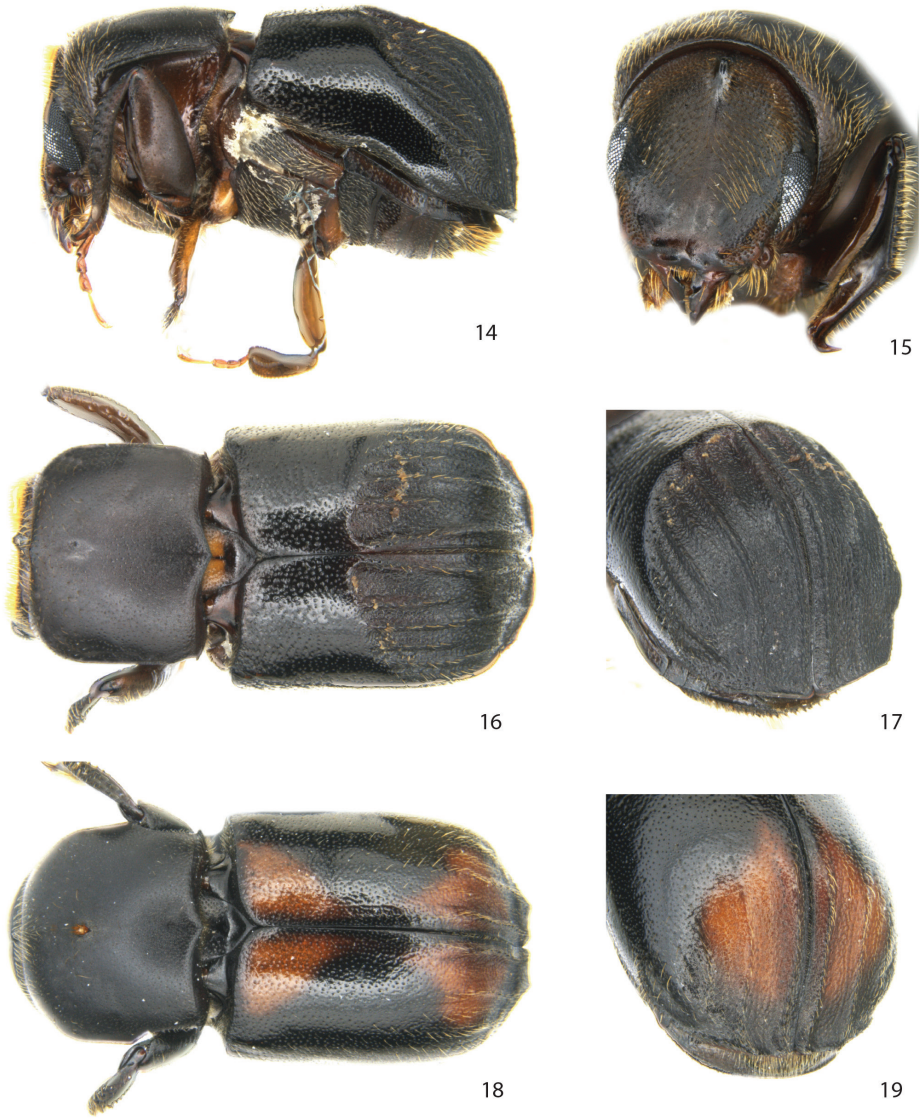
Male. *Frons* concave, marked at its upper margin by a small protruding tubercle. *Pronotum* with a short spine in each postero-lateral corner, posterior margin strongly bisinuate. *Scutellum* narrow, sunken. Posterior half of elytral disk with carinate interstriae and deeply excavated striae; interstriae 2 closer to 3 than to 1 on disk, interstriae 2, 4 and 6 not carinate on declivity; transition from the smooth disk to posterior area with impressed striae angular, appearing hunchbacked, declivity in lateral profile angular.

Female. Similar to male except *frons* convex, *pronotum* with one large mycangial pore, posterior third of pronotum laterally constricted, striae not impressed, interstriae 1, 3 and 5 on declivity weakly elevated, declivity in lateral profile rounded, *elytral apex* transverse and extended between interstriae 1 and 3, with a narrow v-shaped emargination at suture.

Molecular data. DNA barcodes in Table 1.

Distribution and biology. New records: Antsiranana Prov, 7 km N Joffreville, 12°20'00"S, 049°15'00"E, MA-01-07-12, 13-16 May 2001, Malaise trap; Parc National Montagne d'Ambre [Petit Lac road], 12°31'13"S, 049°10'45"E, MA-01-01D-03, 29 Jan-11 Feb 2001, Malaise trap; Fianarantsoa Prov, Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20°35'36"S, 046°33'48"E, BLF7155, 22-26 Jan 2003, EB09 sifted litter (leaf mold, rotten wood); Fianarantsoa Prov, Ranomafana National Park, JIRAMA water works, 21°14'55"S, 047°27'08"E, MA-02-09D-08, 21-24 Dec 2001, malaise trap [CAS]. Fianarantsoa prov, Ranomafana NP, Vato trail [-21.29, 47.42], alt. 1100m, ex *Xylopia* branch, 2012: 4x-11, B.Jordal leg; Valo area [-21.31, 47.43], alt. 1100m, ex *Albizia* branch, 2012: 6x-9, B.Jordal leg. [ZMBN].

The biology and distribution of this species is similar to *S. permirus* and these two species frequently occur on the same host plant. Previously reported from the Montagne d'Ambre area in the North, from Moramanga and Perinet (Andasibe in Toamasina) east of Antananarivo, from Infanadiana (Fianarantsoa) in the south-east, and Fort Dauphin in the south (Schedl 1977). It has been collected from more than ten different host plant genera in eight plant families, adding another two families here (Fabaceae, Annonaceae).



Figures 14–19. *Scolytoplatypus hova* Schaufuss. **14** male lateral view **15** male frons **16** male dorsal view **17** male declivity **18** female dorsal view **19** female declivity.

***Scolytoplatypus rugosus* Jordal, sp. n.**
http://zoobank.org/823D10DE-FD29-44BD-BC99-F378CD4A6EE9
http://species-id.net/wiki/Scolytoplatypus_rugosus
Figs 20–25

Type material. Holotype, male: "Madagascar: Fianarantsoa, Ranomafana, Centre Val-Bio [-21.25, 47.42], alt. 950m, ex *Harungana madagascariensis*, 2012: 29ix-13, B.

Jordal" / "ZMBN/ENT-Scol-2" Allotype, female: same label as holotype. Paratypes: Madagascar: Fianarantsoa, Ranomafana, Vato trail [-21.29, 47.42] alt. 1100m ex *Ocotea* branch. 2012: 3x-2, B.Jordal leg, 2♀♀; same data but collecting code 5x-7, 1♂, 1♀. Madagascar: Morondava distr, Miandrivazo 246km W Antsirabe, D. Hauck lgt, 5.i.2002, 1♂. The holotype and five paratypes ("ZMBN/ENT-Scol-3 – ZMBN/ENT-Scol-7") are deposited in the University Museum of Bergen (ZMBN), one paratype in Miloš Knížek collection, Prague.

Diagnosis. Male. *Protibiae* strongly curved and asymmetrical, *scutellum* narrowly triangular and sunken between elytra, *pronotum* with a lateral spine in each posterior corner.

Female. With mycangial pore on pronotum; declivity identical to male; *frons* and *protibiae* typical dimorphic as for the genus.

This species is closely related to *S. fasciatus* in south-eastern parts of Africa, but differs from that species by the lack of interstrial granules on declivity, by the more deeply impressed male frons, and by the uniform dark mature body colour. It differs further from all other African and Malagasy species by the transverse crest along the upper margin of the male frons. It is readily distinguished from males of the closely related Malagasy species *S. hova* and *S. permirus* by the much less impressed striae on posterior third of the elytral disk. From the African species *S. opacicollis* Eggers, *S. obtectus* Schedl and *S. fasciatus*, it is distinguished by the extended flange of the female elytral apex, and the stouter body plan (1.7–1.8 *versus* 2.0–2.1 times longer than wide).

Molecular data. DNA barcodes in Table 1.

Description. Male. *Length* 2.3-2.7 mm, 1.7–1.8× longer than wide; *colour* dark reddish brown to black.

Head. Eyes separated above by 4.2× their width. Frons concave from vertex to epistoma between inner eye margins, marked above by a distinct transverse crest at median third; impressed area weakly reticulated, with small shallow punctures separated by 1–2× their diameter, except smooth and shiny on a median triangular area on lower third. Vestiture consisting of short fine setae along the upper rim of concave area, and minute setae in punctures in concave area.

Pronotum 0.75× as long as wide, sides subparallel, surface finely reticulated with shallow punctures spaced by 1–2× their diameter; pronotal vestiture consisting of fine short setae arising from punctures, a few longer setae scattered close to anterior margin.

Elytra 1.0–1.1× longer than wide, 1.5–1.6× longer than pronotum; sides almost straight, broadly rounded behind, with an extended apical flange between suture and interstriae 5; striae impressed only on declivity, strial and interstrial punctures on disk confused, spaced by 1–1.5× their diameter; interstriae on declivity slightly raised, shrivelled, punctures asymmetric and confluent, surface strongly reticulate, mesh-like. Interstriae 10 weakly elevated to level of ventrite I. Vestiture consisting of minute setae in punctures only slightly longer than diameter of a puncture.

*Legs***.** Procoxae separated by 0.6× the width of one coxa. Mesocoxae separated by 0.7× the width of one procoxae. Protibiae strongly asymmetrical, with one large laterally curved distal spine, one medium lateral spine and some 6–7 additional lateral small spiny granules.

Figures 20–25. *Scolytoplatypus rugosus* Jordal, sp. n. **20** male lateral view **21** male frons **22** male dorsal view **23** male declivity **24** female dorsal view **25** female declivity.

Ventral vestiture. Metanepisternum with short, bifid setae.

Female. Similar to male in most respect, including the declivity, but differ by the convex frons and more widely separated eyes (4.5× their width), pronotum laterally

constricted on posterior third, with mycangial pore on anterior third (0.35), by the broad protibiae with spines and granules on its posterior face, and by the broader prosternum being 0.8 as wide as one procoxa.

Etymology. The Latin masculine adjective *rugosus* means 'wrinkled' or 'shrivelled', referring to the surface of declivity with wrinkled interstriae, confluent asymmetrical punctures and strongly reticulate cuticle.

Distribution and biology. Only known from the southern range of the Ranomafana National Park. The collections from *Harungana* (Hypericaceae) and *Ocotea* (Lauraceae) indicate a broad host plant range typical for the genus. Branches between 2–5 cm in diameter were colonized, where male and female joined in monogamous pairs, with the male guarding the entrance when the female excavated the egg tunnels.

Remansus Jordal, gen. n.

http://zoobank.org/6C22EF3E-767C-42A5-A52F-CDAB20678DF8
http://species-id.net/wiki/Remansus

Type species. *Scolytoplatypus mutabilis* Schedl. Gender masculine.

Diagnosis. Male. *Frons* concave, antennal funicle 6-segmented, club flattened and pilose without sutures; *procoxae* widely separated, *protibiae* narrow, nearly parallel-sided; *pronotum* not constricted laterally, posterior corners rounded, posterior margin nearly straight; *scutellum* large, flush with elytra.

Female. Similar to male except *frons* flat to slightly convex; *pronotum* with a median mycangium about one-quarter distance from the anterior margin, posterior lateral margins of pronotum weakly constricted; protibiae very stout, broad, with coarse granules and rugae on its posterior side.

Etymology. Based on the Latin masculine participle meaning 'left behind' or 'having endured', referring to the first branch of Scolytoplatypodini that has remained in Madagascar since the origin of the tribe.

Remansus mutabilis (Schedl, 1965), comb. n.

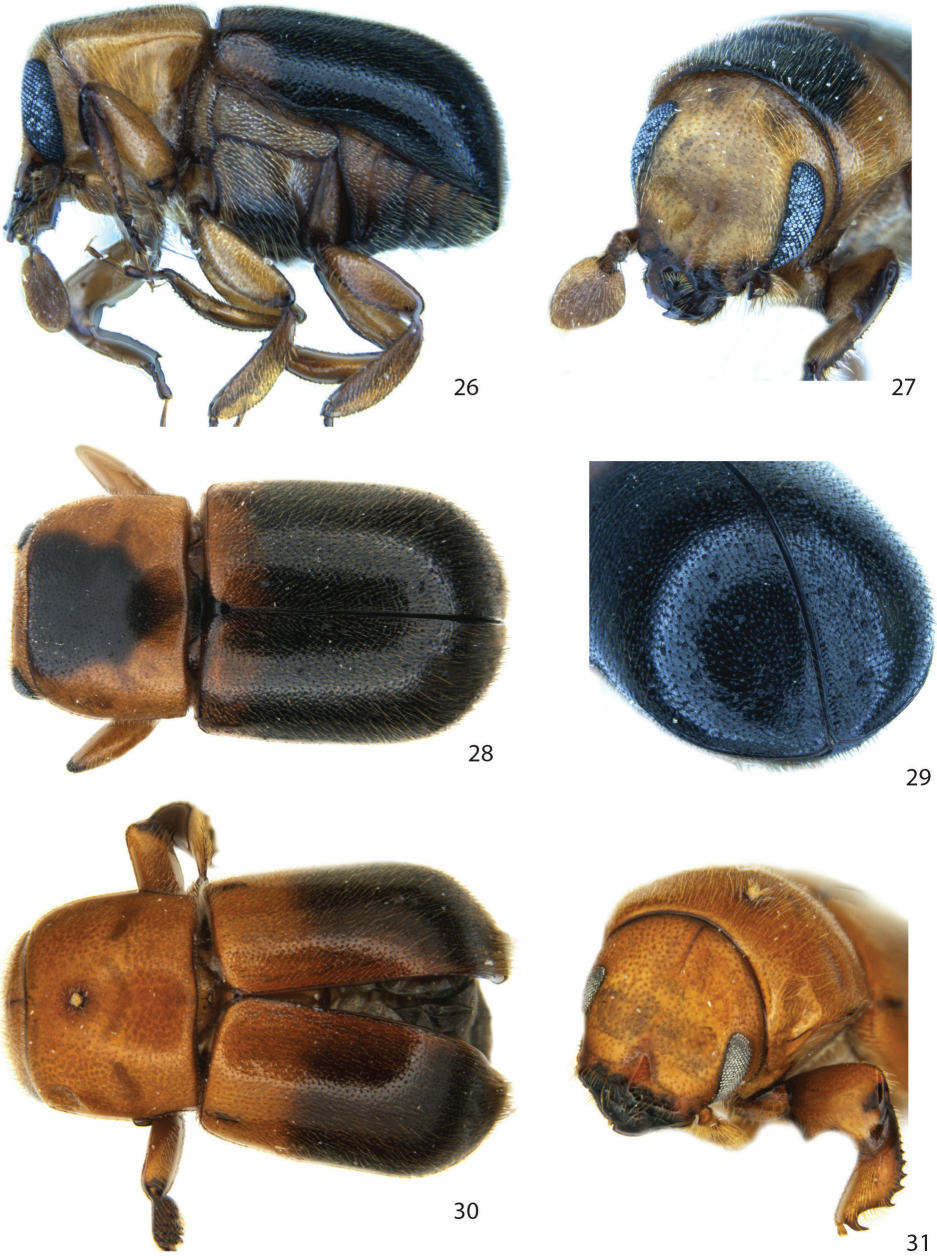
http://species-id.net/wiki/Remansus_mutabilis
Figs 26–31

Scolytoplatypus mutabilis Schedl, 1965: 78.

Type material examined. Holotype, male: Madagascar, Perinet, 16.XI. 1952, K.E. Schedl, leg (NHMW).

Diagnosis. Length 3.0–3.4 mm.

Male. *Frons* weakly concave, with a feeble longitudinal carina from epistoma to vertex. *Elytra* smooth, striae not impressed on disc and declivity, vestiture of dense,



Figures 26–31. *Remansus mutabilis* (Schedl). **26** male lateral view **27** male frons **28** male dorsal view **29** male declivity **30** female dorsal view **31** female declivity.

short, fine setae not in rows. *Protibiae* almost parallel-sided, with a moderately sized, curved lateral spine at distal end, and four additional smaller spines (granules) towards base. *Procoxae* rounded, separated by 0.7× the width of one coxa.

Female. Similar to male except *frons* weakly convex, eyes more widely separated; *declivity* near apex with two patches of longer and more densely placed setae; *protibiae* broad, with granules on posterior side. *Procoxae* very broad, separated by 0.8× the width of one coxa.

The female is here reported and diagnosed for the first time. It differs externally from the male only in those dimorphic features given in the diagnosis. This is the only species in *Remansus* with both male and female known.

Molecular data. DNA barcodes in Table 1.

Distribution and biology. New records: Fianarantsoa Prov, Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20°35'36"S, 046°33'48"E, BLF7155, 22–26 Jan 2003, EB09 sifted litter (leaf mold, rotten wood). Fianarantsoa Prov, Ranomafana National Park, JIRAMA water works, 21°14'55"S, 047°27'08"E, MA-02-09D-13 and MA-02-09D-08, 21-24 Dec 2001, malaise trap. Fianarantsoa Prov, Ranomafana National Park, radio tower, 21°15'03"S, 047°24'26"E, MA-02-09B-05, 28 Nov-6 Dec 2001, malaise trap, all material in CAS. Fianarantsoa prov, Ranomafana NP, Valo area [-21.31, 47.43], alt. 1100 m, ex *Albizia* branch, 6. Oct. 2012, B.Jordal leg. (ZMBN).

Previously reported from Anjanaharibe and Marojejy forest reserves in the Northern part of the island, and in Perinet east of Antananarivo (Schedl 1977). The new collections from the Fianarantsoa district indicate a broad distribution across the forested parts of the country, although it seems less frequently collected, and in fewer numbers, compared to *S. hova* and *S. permirus*. The collection from *Albizia* (Fabaceae) is the first documented host plant for this species, but a much broader range of host plants is expected due to the association with ambrosia fungi.

Remansus sahondrae Jordal, sp. n.

http://zoobank.org/BAA6B09A-B9A3-4664-8A5A-7980711414DA
http://species-id.net/wiki/Remansus_sahondrae
Figs 32–35

Type material. Holotype, female: "Madagascar: Fianarantsoa, Ranomafana, Vato trail [-21.29, 47.42] alt. 1100m ex *Eugenia* branch. 2012: 2x-9, Sahondra Rahanitriniaina" / "ZMBN/ENT-Scol-8" Paratype, female: same data as holotype except museum label "ZMBN/ENT-Scol-9". The holotype and paratype are deposited in the University Museum of Bergen (ZMBN).

Diagnosis. Female. *Pronotum* with mycangium only one-quarter distance from anterior margin, posterior corners rounded, posterior margin straight; *scutellum* flat at the same level as elytra. It is closely related to *S. mutabilis*, but distinguished from that species by the visible striae, larger elytral punctures, the coarse, short setae on the declivity, and by the much smaller body size.

Molecular data. DNA barcodes in Table 1.

Description. Female. *Length* 2.2–2.3 mm, 1.9–2.0× longer than wide; *colour* black.

32

33

34

35

Figures 32–35. *Remansus sahondrae* Jordal, sp. n., female. **32** lateral view **33** frons **34** dorsal view **35** declivity.

Head. Eyes separated above by 4.6× their width. Frons broadly flattened from vertex to epistoma, surface strongly reticulated, with large punctures spaced by their diameter, except smooth and impunctate on a triangular area on central lower third, a short median longitudinal keel dividing triangular area. Vestiture consisting of a few scattered fine setae.

Pronotum 0.8× as long as wide, sides almost straight, barely constricted on posterior third, surface reticulate with minute shallow punctures spaced on average by their diameter; center of median mycangial pore positioned from anterior margin about 0.24× the pronotal length; pronotal vestiture consisting of sparse fine short setae, with somewhat longer setae on anterior half.

Elytra 1.1× longer than wide, 1.6× longer than pronotum; striae not impressed, punctures in irregular rows, spaced within a row on disc by 2–3× their diameter, closer together towards declivital summit, almost subconfluent; interstrial punctures similar to those in striae, irregularly placed, confused. Interstriae 10 elevated to level of ventrite I. Declivity with small granules, strial punctures 2−3× larger than on disk, oblong or asymmetric, subconfluent; vestiture on declivity consisting of stiff, short, curved

setae, with a patch of longer setae on each side of suture close to apex; a subapical rim runs from the suture to about interstria 8.

Legs. Procoxae separated by 0.5× the width of one coxa. Mesocoxae separated by 0.6× the width of one procoxa. Protibiae broad, with one distal laterally curved spine, and many additional small spines or granules on its posterior side.

Ventral vestiture. Metanepisternum with long bifid setae.

Male: unknown.

Etymology. Named after Sahondra Rahanitriniaina, our helpful Malagasy collegue who collected the type specimens and many other scolytine beetles during our joint field trip to Ranamafana National Park.

Distribution and biology. Only known from the type locality in the Ranomafana National Park. Two females were taken from a fallen branch of *Eugenia* (Myrtaceae).

***Remansus pygmaeus* Jordal, sp. n.**
http://zoobank.org/5776128D-753D-4E2C-ABBB-C91FD86E7788
http://species-id.net/wiki/Remansus_pygmaeus
Figs 36–39

Type material. Holotype, female: "Madagascar, Fianarantsoa, Ranomafana National Park, 5 km NE Centre ValBio [-21.24, 47.41]. Ex *Weinmannia* twig, 10. Oct. 2012, B. Jordal leg." / "ZMBN/ENT-Scol-10". The holotype is deposited in University Museum of Bergen (ZMBN).

Diagnosis. Female. Posterior corners of pronotum rounded; scutellum flat at the same level as elytra; declivity characteristically truncated and marked by a circular blunt rim. One of the smallest known species in the tribe and the only species smaller than 2 mm in Africa and Madagascar. Closely related to *R. serratus*, but distinguished by the much smaller size (1.7 vs. 3.7 mm), the nearly glabrous elytral disk and posterior half of pronotum.

Molecular data. DNA barcodes in Table 1.

Description. Female. *Length* 1.7 mm, 1.85× longer than wide; *colour* black.

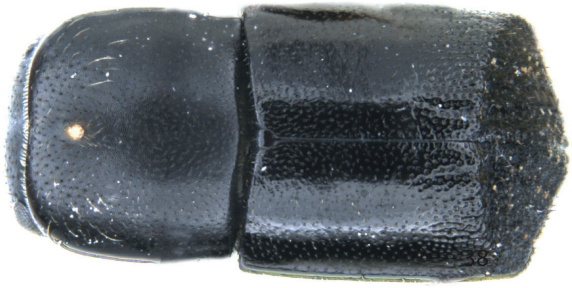
Head. Eyes separated above by 4.0× their width. Frons broadly flattened from vertex to epistoma, surface strongly reticulated, with tiny shallow punctures spaced by 1.5–2× their diameter, except smooth and impunctate on a triangular area on central lower third. Epistoma elevated, shiny, with a short median carina extending from epistoma to impunctate area. Vestiture consisting of a few scattered fine setae.

Pronotum 0.8× as long as wide, sides almost straight, weakly constricted on posterior third, surface reticulate with minute shallow punctures spaced on average by 2× their diameter; median mycangial pore on anterior fifth round with a tuft of setae; pronotal vestiture consisting of sparse fine short setae, and about 20 much longer erect setae on anterior half.

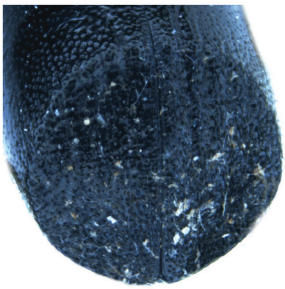
Elytra 1.05× longer than wide, 1.5× longer than pronotum; sides almost straight, slightly constricted just before declivity, broadly triangular at apex; striae not impressed

36

37



38



39

Figures 36–39. *Remansus pygmaeus* Jordal, sp. n. female. **36** lateral view **37** frons **38** dorsal view **39** declivity.

except weakly so at declivital margin; strial and interstrial punctures on disk entirely confused, shallow, with minute setae of variable length. Interstriae 10 elevated to level of ventrite I. Declivity dull, rugose, punctures variable but generally larger than on disk; vestiture on declivity of fine ground setae and fewer but coarser stiff and slightly curved short setae.

Legs. Procoxae separated by 0.5× the width of one coxa. Mesocoxae separated by 0.6× the width of one procoxae. Protibiae broad, with one large laterally curved distal spine, and five additional lateral small spines or granules, with small granules on the posterior face.

Ventral vestiture. Metanepisternum with bifid long setae.

Male: unknown.

Etymology. The Latin masculine adjective *pygmaeus* pertaining to the mythical race of African dwarfs, referring to the relative small size for this species, being the smallest species of Scolytoplatypodini in Africa and Madagascar.

Distribution and biology. Only known from the type locality in the Ranomafana National Park. One female and one pupa were taken from a fallen branch of *Weinmannia* (Cunoniaceae), about 1.5 cm in diameter. The egg tunnel was transversely spiral shaped, with eight pupation chambers directed longitudinally, like bullet chambers in a revolver barrel. Based on empty pupal chambers the brood size in this type of host is 6–10 (n=3).

***Remansus serratus* Jordal, sp. n.**
http://zoobank.org/94073590-56A8-45D0-9EF1-5D38FC16FD19
http://species-id.net/wiki/Remansus_serratus
Figs 40–43

Type material. Holotype, male: "Madagascar, Antsiranana Prov, Parc National Montagne d'Ambre (Petit Lac Road) 12°31'13"S, 49°10'45"E, MA-01-01D-03, 29 Jan – 11 Feb 2001, Malaise trap". The holotype is deposited in California Academy of Science (CAS).

Diagnosis. Male. With a unique *Amasa*-like truncated declivity and rounded posterior angles of the pronotum. Characters suggest a close relationship to *R. pygmaeus* Jordal, but it is distinguished from that species by the much larger size, narrow body shape, the pilose body, and by the slightly elevated scutellum that is not entirely flush-with the elytra. It is further distinguished from males of *R. mutabilis* by the dentate upper declivital margin.

Description. Male. *Length* 3.7 mm, 2.1× longer than wide; *colour* yellowish brown, darker brown on declivity and elytral lateral margins.

Head. Eyes separated above by 4.2× their width. Frons concave from vertex to epistoma via inner eye margins; upper half rugosely, densely punctured, lower half smooth and shiny. Vestiture consisting of fine setae increasing in length towards upper part of concave area, longest and most dense along upper margin from vertex to upper level of eyes.

Pronotum 0.9× as long as wide, sides subparrallel, brodest on anterior half, broadly, transversely rounded in front; surface finely reticulated with minute shallow punctures irregularly spaced by 1–4× their diameter; pronotal vestiture consisting of fine short setae, slightly longer close to anterior margin.

Elytra 1.2× longer than wide, 1.7× longer than pronotum; sides almost straight, broadly triangular at apex; decivital margin marked by a dentate rim, each incision marks the end of diskal stria; striae otherwise not impressed, interstriae on disk only reckognised by the lighter colour, punctures not clearly visible, confused and minute. Interstriae 10 elevated to level of ventrite I. Declivity rugosely granulated, largest granules on interstriae 1 (suture). Vestiture consisting of dense fine setae spaced on disk by less than one-third the length of each seta, on declivity about 2–3× longer than setae on disk.

Legs. Procoxae separated by 0.4× the width of one coxa. Mesocoxae separated by 0.5× the width of one procoxae. Protibiae narrow, with one larger distally lateral curved spine, and 6–7 additional lateral small spines, posterior face mainly smooth, with 4–5 tiny granules close to lateral edge.

Ventral vestiture. Metanepisternum mainly with long simple setae, a few shorter bifid setae anteriorly.

Female: unknown.

Etymology. The Latin masculine adjective *serratus* means 'serrated', referring to the short pointed projections from interstriae at the declivital summit.

Distribution and biology. A single specimen was collected in a Malaise trap just south of Montagne d'Ambre.

Figures 40–43. *Remansus serratus* Jordal, sp. n., male. **40** lateral view **41** frons **42** dorsal view **43** declivity.

Key to the Malagasy genera and species of Scolytoplatypodini

1 Scutellum flat, broad, flush with the elytra and clearly visible; posterior edge of pronotum almost straight; female mycangium closer to anterior margin (0.22–0.28 of pronotum length); male protibiae almost parallel-sided; postero-lateral corners of pronotum without acute spine ..... ***Remansus*** **Jordal, gen. n., 2**

– Scutellum narrowly triangular, obliquely depressed between elytra; posterior edge of pronotum bisinuate; female mycangium closer to centre (0.33–0.36 of pronotum length); male protibiae asymmetric with large incision between lateral spines 1 and 2; postero-lateral corners of pronotum with an acute spine pointing laterad ..... ***Scolytoplatypus*** **Schaufuss, 5**

2 Declivity abrupt, marked by a circum-declivital ring, surface rough, not shining, vestiture evenly distributed in both sexes..... **3**

– Declivity steep, gently rounded, not truncated, surface sub-shining, females with a patch of longer setae close to elytral apex..... **4**

3 Larger, 3.7 mm long, elytra and pronotum densely covered by short fine setae ..... ***R. serratus* Jordal, sp. n.**

– Smaller, 1.7 mm long, elytral disk and posterior half of pronotum almost glabrous ..... ***R. pygmaeus* Jordal, sp. n.**

4 Larger, 3.0–3.4 mm long, striae not impressed, all punctures small .... ***R. mutabilis* (Schedl)**

– Smaller, 2.2–2.3 mm, striae evident from base, slightly impressed on declivital summit, punctures on declivity much larger than on disk .... ***R. sahondrae* Jordal, sp. n.**

5 Male and female declivity similar, without sharp interstrial carinae on posterior part of male elytral disk, interstriae on declivity only slightly raised and shrivelled, granules minute (2.4–2.7 mm) ..... ***S. rugosus* Jordal, sp. n.**

– Males with striae on posterior third of elytral disk deeply excavated between sharply elevated interstriae, male and female declivity with at least interstriae 1 and 3 distinctly raised towards apex, linear, with distinct granules (2.5–4.5 mm) **6**

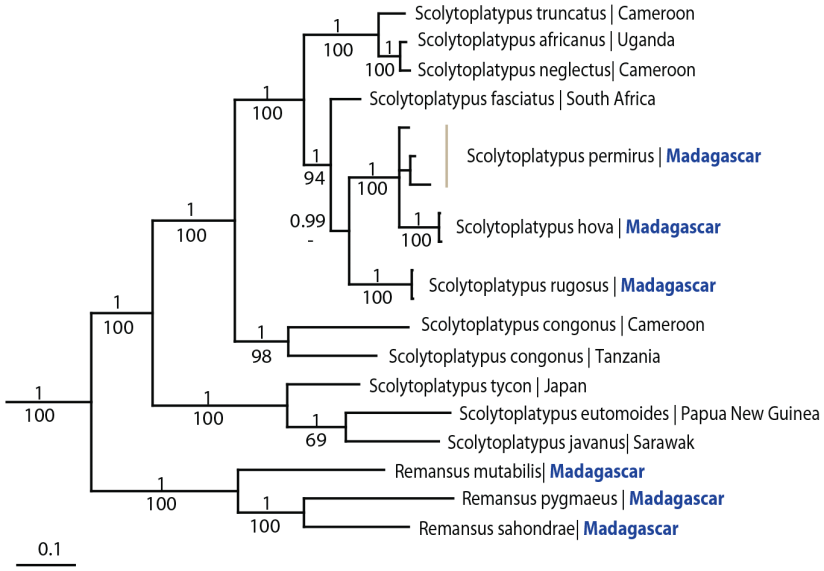
6 Larger, 3.5–4.5 mm; male interstriae 2 closer to 3 than to 1, disk and declivity profile subangular, hunchbacked ..... ***S. hova* Schaufuss**

– Smaller, 2.5–3.0 mm; male interstriae more regularly spaced, declivity profile rounded ..... ***S. permirus* Schaufuss**

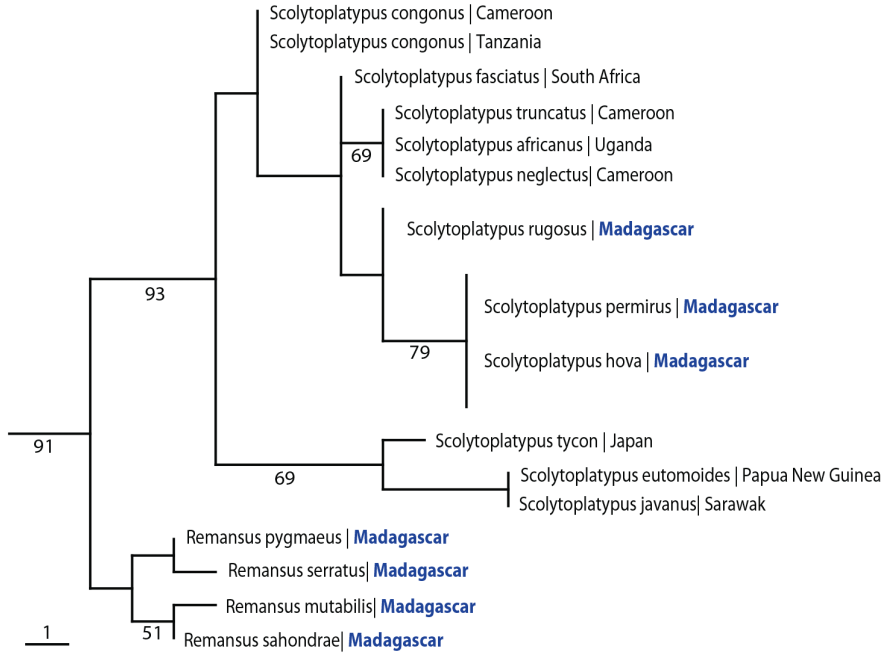
Phylogeny and classification

The tree topology resulting from the Bayesian and parsimony analyses of the combined molecular data were near identical and all nodes except one received high support (Fig. 44). Scolytoplatypodini was monophyletic, with a clade consisting of the Malagasy species *R. mutabilis*, *R. pygmaeus* and *R. sahondrae* as the sister group to all species in *Scolytoplatypus*. The Asian species of *Scolytoplatypus* formed a sister clade to the Malagasy and African species of the genus. The three Malagasy species of *Scolytoplatypus* were nested in a derived monophyletic position in the Bayesian analysis, while *S. rugosus* was sister to the South-East African *S. fasciatus* in the parsimony analysis.

Parsimony analysis of the morphological data resulted in 30 most parsimonious trees. All trees revealed a strongly supported sister relationship between *Remansus* (including also *R. serratus*) and *Scolytoplatypus*. Some of the trees placed *S. congonus* as the sister to the remaining African and Asian species of *Scolytoplatypus*, while in two of the trees the Asian species were sister to all African species (Fig. 45). The ambiguity was likely due to *S. congonus* having two character states shared with *Remansus*, including a broad scutellum that is flush with the elytra and the nearly straight posterior margin of the pronotum (Fig. 7). However, *S. congonus* has spiny hind corners of the pronotum, asymmetrical male protibiae and female mycangium behind anterior third as in other *Scolytoplatypus*. Molecular data unambiguously resolved this issue and strongly supported the Asian-African split in *Scolytoplatypus*, with *S. congonus* as an early diverging lineage in Africa.



44



45

Figures 44–45. Phylogeny of Scolytoplatypodini. **44** Tree topology resulting from Bayesian analysis of 2902 nucleotide sites from one mitochondrial and three nuclear genes. Posterior probabilities are given above, parsimony bootstrap support below **45** Tree topology resulting from parsimony analysis of 21 morphological characters (Table 2, Appendix).

The strongly supported split between the two basal clades justify the designation of a new genus *Remansus*. Although largely defined by plesiomorphic characters such as the 'normal' male protibiae (Figs 4 and 5), rounded posterior corners of pronotum, and a visible large scutellum that is flush with the elytra (Fig. 7), the new genus is also supported by a uniquely derived feature in the female mycangium being displaced anteriorly (Fig. 2 vs. Fig. 1). Taken together with the large genetic divergence in mitochondrial and nuclear loci, the new genus appears to be well supported, and hence constitutes the second genus in the tribe Scolytoplatypodini.

The molecular data also distinguished the Asian species of *Scolytoplatypus* clearly from the African species of that genus. A distinction between these two clades is supported by several morphological characters in the phylogenetic analysis as was noted in two previous publications (Beaver and Gebhardt 2006; Browne 1971). Perhaps the 28 Asian species also deserve a separate genus designation as they are clearly diagnosable. In males, the Asian species are different from the African species by having a strongly modified prosternum with nodules or hooked projections, by the longer and more triangular antennal club, and in all but two species by the large fovea on the antero-lateral angle of the male pronotum. However, this is outside the scope of this paper and more Asian taxa must be included in the molecular analyses before such changes can be made with certainty. The same applies to several African taxa where the phylogenetic data suggest taxonomic revision, including the deep divergence between the *congonus* and *kivuensis* forms of *S. congonus* (see opposing viewpoints by Browne 1971; Schedl 1975), and the near identical sequences obtained from *S. africanus* Eggers and *S. neglectus* Schedl.

In addition to four species of *Remansus*, three additional species are found in Madagascar, in the genus *Scolytoplatypus*. The new species *S. rugosus* was shown to be most closely related to the other two Malagasy species *S. hova* and *S. permirus*, although some analyses placed this species closer to *S. fasciatus* (= *S. obtectus* Schedl?), a species very similar to *S. opacicollis* Eggers. The congruence between the Bayesian analysis of the molecular data and morphology suggests that the most likely scenario is a monophyletic group of Malagasy species, as sister clade to *S. fasciatus*. The three Malagasy species of S*colytoplatypus* share features on the female elytra by having a broad subtransverse apical flange, which, at least in comparison to the African species, seems unique. As typical *Scolytoplatypus* they share with all African species an acute spine at the postero-lateral corner of the pronotum, a bisinuate posterior margin of pronotum, a narrow scutellum that is sunken between the elytra, and similarly shaped antennal clubs in males and females. The three species therefore belong to the African group of *Scolytoplatypus*.

The origin of Malagasy Scolytoplatypodini

With the addition of several new taxa from Madagascar, the age estimated for the tribe Scolytoplatypodini becomes considerably older than previously reported (Jordal and Cognato 2012). Calibration of the node that includes the more advanced weevils (which here also include the molytine genus *Porthetes* and the scolytine *Scolytodes*) to

Table 3. Divergence time estimates for Scolytoplatypodini.

Clade	Analysis A		Analysis B	
	median	95 % CI	median	95 % CI
Scolytoplatypodini: stem age	91.0	71.6–106.4	59.1	45.0–75.6
Scolytoplatypodini: crown age (*Remansus vs. Scolytoplatypus*)	63.1	45.6–80.3	42.3	34.1–53.0
Scolytoplatypus: crown age (Asia split from Africa)	51.6	36.7–67.7	35.2	29.3–40.7
Remansus: crown age	33.2	16.1–50.8	22.0	9.9–33.5
Recent Madagascar clade: stem age	13.1	6.9–21.4	8.8	3.7–13.9
Recent Madagascar clade: crown age	12.5	6.5–18.6	7.3	3.2–12.0

116 Ma, a minimum age for Scolytoplatypodini, and hence the divergence of *Remansus* and *Scolytoplatypus*, was estimated to 63.1 (47–80) Ma (Table 3). Because taxon sampling in this case was somewhat biased as it was designed for a generic revision, it may have produced a slightly inflated time estimate. Hence a second analysis was made based on calibrating the node for the last common ancestor for three taxa included in a previous analysis (Jordal and Cognato 2012: *S. africanus, S. eutomoides*, *S. tycon*). This second analysis produced a minimum estimate of 42.3 (34–53) Ma for the tribe. Irrespective of these discrepancies, the age for the fungus cultivating lineage Scolytoplatypodini is moved further back in time, perhaps as far as the middle or early in the Palaeocene-Eocene period experiencing a thermal maximum (PETM, see Zachos et al. 2001). Thus, these revised estimates provide increased support for the global warming theory in explaining origins of fungus farming (Jordal and Cognato 2012).

The ancient split between *Remansus* in Madagascar and the Asian/African clade of *Scolytoplatypus* is apparently younger than the latest Gondwanan vicariance event involving Madagascar. The separation of India from Madagascar occurred at least 80 Ma (Yoder and Nowak 2006), which is almost certainly older than any of the time scenarios suggested here. Hence, the origin of both *Remansus* and the much later origin of Malagasy *Scolytoplatypus* some 13 Ma (Table 3) were likely due to overseas dispersal. While the geographical distribution of a scolytoplatypodine ancestor cannot be estimated precisely with the data presented here, it seems highly probable that the recent origin of *Scolytoplatypus* in Madagascar was due to dispersal from Africa to the island. The endemic species *S. rugosus, S. hova* and *S. permirus* are all deeply nested within the African clade, being closely related to the South-/South-eastern African species *S. fasciatus*. Due to strong wind and oceanic currents going from Madagascar to Africa, it has been postulated that post-Gondwanan colonisation of Madagascar from Africa is unlikely. However, new models for latitudinal tectonic drift have documented reversed wind and oceanic currents 15–60 Ma (Ali and Huber 2010) and thus help explaining the many origins of plant and animals during the Palaeocene to late Miocene (Samonds et al. 2012; Yoder and Nowak 2006). Even more recent colonisations from Africa have occasionally taken place in various animal groups (Miraldo et al. 2011; Vuataz et al. 2013), which indicate that reaching Madagascar have not at all been impossible during the Pliocene, albeit more difficult than in earlier times.

Acknowledgements

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Appendix

Data matrix for morphological characters (Table 2) used in the phylogenetic analysis.

Polydrusus	0	0	0	-	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Porthetes	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scolytodes	0	0	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
R. mutabilis	1	0	1	1	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0
R. pygmaeus	?	?	1	1	0	?	0	0	0	?	?	1	1	0	0	0	1	1	?	0	0
R. sahondrae	?	?	1	1	0	?	0	0	0	?	?	1	0	0	0	1	1	1	?	0	0
R. serratus	1	0	?	?	0	1	0	0	0	0	0	1	1	?	1	0	1	?	0	0	0
S. africanus	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	1
S. congonus C	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0
S. congonus T	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0
S. eutomoides	1	1	1	0	1	2	1	1	1	0	2	0	0	0	0	0	1	1	1	1	0
S. fasciatus	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0
S. hova	1	0	1	0	0	1	1	1	1	1	2	0	0	1	0	0	1	1	1	0	0
S. javanus	1	1	1	0	1	2	1	1	1	0	2	0	0	0	0	0	1	1	1	1	0
S. neglectus	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	1
S. permirus	1	0	1	0	0	1	1	1	1	1	2	0	0	1	0	0	1	1	1	0	0
S. rugosus	1	0	1	0	0	1	1	1	1	0	1	0	0	1	0	0	1	1	1	0	0
S. truncatus	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	1
S. tycon	1	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0

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RESEARCH ARTICLE

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On five species of the tribes Abacetini and Pterostichini (Coleoptera, Carabidae)

Borislav V. Guéorguiev[1,†]

1 *1 National Museum of Natural History, 1 Blvd. Tzar Osvoboditel, 1000 Sofia, Bulgaria*

† *http://zoobank.org/57F499D1-56FF-4A3D-BA24-7766CE15F42D*

Corresponding author: *Borislav V. Guéorguiev* (gueorguiev@nmnhs.com)

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Abstract

Metabacetus willi **sp. n.** (type locality: Indonesia, Central Java Province, Purworejo Regency, Kaligesing District, cave Seplawan near Donorejo) and *Rhytiferonia beroni* **sp. n.** (type locality: Papua New Guinea, West Sepik Province, Bonforok bil, Tifalmin, 1600 m) are described. Two new combinations: *Poecilus* (*Ancholeus*) *campania* (Andrewes, 1937), **comb. n.** of *Feronia campania* Andrewes, 1937, *Aristochroa poecilma* (Andrewes, 1937), **comb. n.** of *Feronia poecilma* Andrewes, 1937, and a new synonymy: *Pterostichus* (*Oreophilus*) *podgoricensis* B. Guéorguiev, 2013, **syn. n.** of *Pterostichus* (*Oreophilus*) *flavofemoratus pinguis* (Dejean, 1828), are proposed, too.

Keywords

Coleoptera, Carabidae, Abacetini, Pterostichini, taxonomy, new species, new combinations, new synonym, Italy, Pakistan, China, Indonesia, Papua New Guinea

Introduction

This paper announces results achieved by the author during the work with the carabid collection of the National Museum of Natural History, Sofia and in a visit in the Natural History Museum, London in 2009. In the first institution, we found out two

new species among the materials collected by the former director of the museum Petar Beron in Indonesia and Papua New Guinea. In the second institution, we revised the types of two species described in the genus *Feronia* Latreille, 1816 by Herbert Andrewes (Andrewes 1937). These species were described on female specimens and had never been reviewed. In addition, we announce a synonymy of species described recently by ourselves (Guéorguiev 2013).

Material and methods

Except for the above mentioned material, a few other species have been studied. They are listed in the text below.

The measurements and part of drawings were made with an ocular micrometer mounted on a stereoscopic binocular microscope Olympus SZ 60. Another part of the drawings were done with a stereoscopic microscope Carl Zeiss Jena Technival 2.

Measurements: body length from the apex of the longer mandible in closed position to the apex of the longer elytron (BL); body width as maximum distance across body (BW); maximum linear distance across the head, including the eyes (HW); length of pronotum, measured along the midline, from the apical margin to the basal margin (PL); maximum width of pronotum (PW); width of the pronotal apex, between the tips of the fore angles (PaW); width of the pronotal base, between the tips of the hind angles (PbW); length of elytra, from a line connecting the apices of the humeral angles to the apex of the longer elytron (EL); maximum width of elytra (EW).

The examined material is deposited in the following collections

BMNH Natural History Museum, London, United Kingdom (Max Barclay, Beulah Garner)

EMEC Essig Museum of Entomology, University of California, Berkeley, USA (Peter Oboyski)

MCNM Museo Civico di Storia Naturale, Milano (Maurizio Pavesi)

MCSN Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (Maria Tavano)

MNHUB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Manfred Uhlig, Bernd Jaeger)

NHRS Swedish Museum of Natural History, Stockholm, Sweden (Johannes Bergsten)

NMNHS National Museum of Natural History, Sofia (Borislav Guéorguiev)

NMW Naturhistorisches Museum Wien, Vienna, Austria (Harald Schillhammer)

The distribution maps were generated using the online mapping software SimpleMappr (©David P. Shorthouse).

Taxonomic part

ABACETINI

***Metabacetus willi* sp. n.**
http://zoobank.org/0CC6CA65-2C73-4F0D-93E6-42E5A4138BA7
http://species-id.net/wiki/Metabacetus_willi
Figs 1–8, Table 1

Type material. Holotype ♂, "INDONESIA, Java cave Seplawan 2.VI.1994, leg. P. Beron" [typeset], "HOLOTYPE *Metabacetus willi* spec. nov. Guéorguiev des. 2012" [typeset, red label] (NMNHS). Paratypes 4♂♂, 3♀♀, labelled as follow: 3♂♂, 1♀, "INDONESIA, Java cave Seplawan 2.VI.1994, leg. P. Beron" [typeset] (EMEC, BMNH, NMNHS); 1♂, 2♀♀, "INDONESIA, Java v. Kimiri, D.I. Yogyakarta Gua (cave) Nging Rong 29.VIII.1995, P. Beron leg." [typeset] (BMNH, MCNM, NMNHS); all paratypes with subsequently added: "PARATYPE *Metabacetus willi* spec. nov. Guéorguiev des. 2012" [typeset, red label].

Examined type material of other species. *Metabacetus immarginatus* Bates, 1892, syntype ♀, "Carin Ghecù 1300-1400 m L. Fea II-III.88." [typeset], "Typus" [red typeset, white label], "*Metabacetus immarginatus* Bates" [handwritten], "*Metabacetus immarginatus* Bates" [handwritten], "*Metabacetus*, n.g. *immarginatus* (es. typ.) Bates" [handwritten, yellow label, genus name underlined], "Syntypus *Metabacetus immarginatus* Bates, 1892" [handwritten & typeset, red label], "Museo Civico di Genova"[typeset] (MCSN). *Mateuellus troglobioticus* Deuve, 1990, 2♂, 1♀, "Indonesia, Sulawesi Selatan, Bantimurung Gua (Cave) Minpiovo 3.IX.1995, P.Beron leg." (NMNHS).

Diagnosis. A medium-sized, slightly iridescent species of *Metabacetus* (Fig. 1), with elongate and attenuate maxillary palpi, last three segments of antennae surpassing the base of pronotum, pronotum widest just after the middle, with anterior margin much shorter than posterior one, sides much narrower anteriorly (than posteriorly), convex posteriorly, lateral fields broadened and moderately reflexed from the middle to the base and obtuse hind angles, prosternum shallowly sulcate medially near apex, apex of elytra without spines, and specific structure of the median lobe of aedeagus (Figs 2–4).

For detailed information about some measurements and ratios see Table 1.

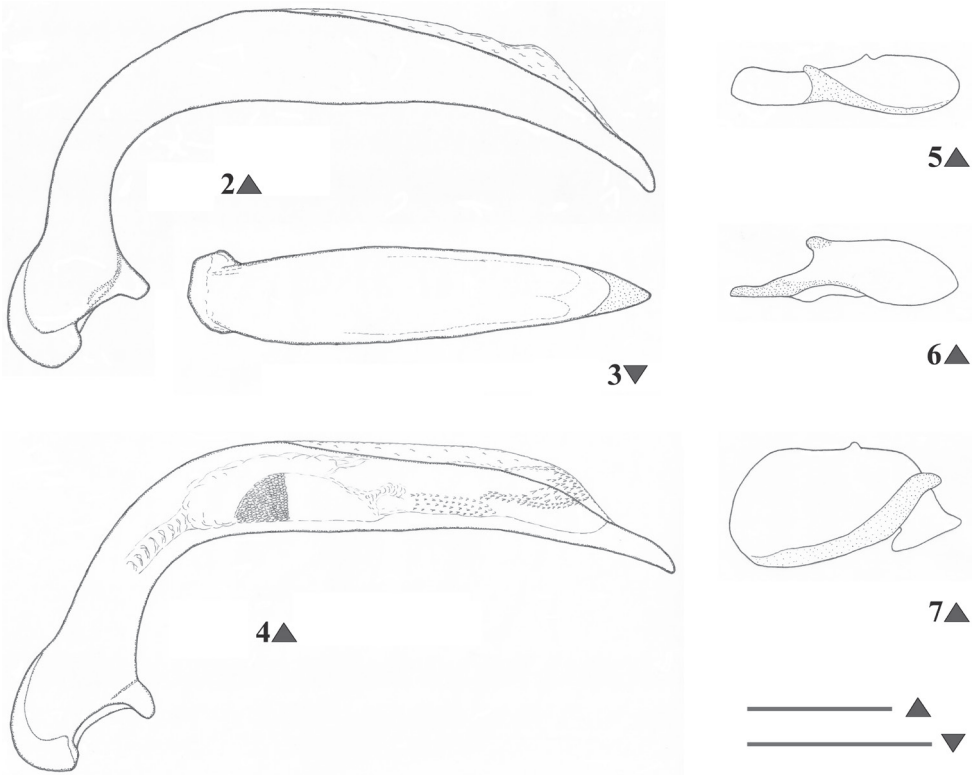
Description. *Habitus*. Moderately-sized species of *Metabacetus* Bates, 1892, with sub-oval and convex body. *Measurements*. BL: 6.1–6.7 mm (mean 6.375 mm); BW = EW, see below; PL: 1.45–1.6 mm (mean 1.53 mm); PW: 1.85–2.1 mm (mean 1.98 mm); EL: 3.45–3.85 mm (mean 3.59 mm); EW: 2.45–2.8 mm (mean 2.61 mm). *Ratios*. PW/HW: 1.71–1.81 (mean 1.748); PW/PL: 1.27–1.31 (mean 1.296); PW/PbW: 1.24–1.28 (mean 1.263); PbW/PaW: 1.31–1.34 (mean 1.326); EW/PW: 1.27–1.35 (mean 1.314); PL/EW: 0.42–0.43 (mean 0.429); EL/EW: 1.33–1.4 (mean 1.374). *Color*. Body dark brown to dark reddish dorsally and ventrally, antennae, legs,

Figure 1. *Metabacetus willi* sp. n., paratype.

Table 1. Data on variation in measurements and ratios among the type series of *Metabacetus willi* sp. n. (mark '*' concerns specimens from cave Ngingrong).

Specimen	BL (mm)	PL (mm)	PW (mm)	EL (mm)	EW (mm)	PW/ HW	PW/ PL	PW/ PbW	PbW/ PaW	EW/ PW	PL/ EL	EL/ EW
HT ♂	6.2	1.5	1.9	3.55	2.6	1.71	1.27	1.27	1.32	1.32	0.43	1.39
PT 1♂*	6.2	1.5	1.95	3.5	2.5	1.71	1.3	1.26	1.31	1.29	0.43	1.4
PT 2♂	6.3	1.55	1.95	3.65	2.6	1.75	1.29	1.26	1.34	1.31	0.43	1.39
PT 3♂	6.4	1.5	2.0	3.6	2.6	1.81	1.29	1.26	1.34	1.35	0.43	1.33
PT 4♂	6.1	1.45	1.85	3.55	2.45	1.71	1.31	1.27	1.32	1.30	0.43	1.38
PT 5♀*	6.7	1.5	2.05	3.85	2.8	1.76	1.31	1.24	1.32	1.35	0.42	1.35
PT 6♀*	6.6	1.6	2.1	3.45	2.75	1.77	1.29	1.26	1.33	1.32	0.43	1.37
PT 7♀	6.5	1.6	2.05	3.6	2.6	1.76	1.31	1.28	1.33	1.27	0.43	1.38
Mean	**6.375**	**1.53**	**1.98**	**3.59**	**2.61**	**1.748**	**1.296**	**1.263**	**1.326**	**1.314**	**0.429**	**1.374**

pronotal margins, and elytral epipleura paler, reddish, palpi yellowish. *Microsculpture and lustre*. Very fine, with transverse microreticulation, distinct on head, pronotum, elytra, and most of ventral surface, visible under magnification > 50×, indistinct on ventral side of head and middle parts of thorax and abdominal sternites; body very shiny throughout, elytra and less ventral surface with slight spectral iridescence. *Head*. Longer than wide, narrow in relation to pronotum; disc smooth, frontal furrows



Figures 2–7. *Metabacetus willi* sp. n., male genitalia (Figs **2–3**, **5–7** holotype, cave Seplawan; Fig. **4** paratype, cave Ngingrong) **2, 4** median lobe of aedeagus, left lateral view **3** median lobe of aedeagus, dorsal view **5** right paramere, internal face **6** right paramere, external face **7** left paramere, internal face. Scale line: 0.3 mm (Figs 2–3; 5–7); 1 mm (Fig. 4).

deeply impressed, oblique, divergent backward, not reach level of anterior supraorbital punctures; eyes projecting laterally, temporae as long as half diameter of eyes; two pairs of supraorbital setae; paraorbital sulci moderately deep, surpassing level of posterior supraorbital pore backward; antennae long, filiform, densely pubescent from second fourth of segment 4, with terminal three articles surpassing base of pronotum and apex of last antennomere surpassing anterior fifth of elytron; mandibles elongate, with apex pointed and slightly hooked; labrum rectangular, with six setigerous punctures on anterior margin; clypeus trapezoid, rectilinear anteriorly, with two setigerous punctures closer to lateral margins than to anterior one; glossal sclerite of ligula with two long setae on anterior margin; mentum shallowly emarginated, with simple, widely round at tip tooth, pair of labial setae, and deep labial pits, epilobes short, sub-triangular distally, slightly exceeding mentum tooth forward, mentum separated by submentum by distinct labial suture; submentum with four setae, two basal setae longer than lateral ones; maxillary palpomeres glabrous, elongate and attenuate, larger in comparison with labial palpomeres, as long as two third of head length, apical three segments

nearly equal in length; labial palpi fusiform, palpomere 2 longer than palpomeres 3, with two long medial setae. *Pronotum*. Disc-shaped, circular, broader than long, widest just after middle; disc smooth, gently convex medially; midline fine, distinct on medial three fourth of pronotum length, obsolescent apically and basally; anterior submarginal sulcus distinct laterally, disappeared medially; anterior and posterior margins of pronotum unbordered, anterior margin scarcely concave, distinctly shorter than posterior one, with fore angles not protruding forward; posterior margin slightly convex backward, hind angles obtuse, incompletely round, not prominent; lateral margins rounded, more anteriorly than posteriorly, without sinuation towards hind angles, lateral fields broadened and moderately reflexed upward towards base, marginal beads continuous, only before hind angles obsolescent; anterolateral seta at anterior second quarter, posterolateral seta at hind angle; posterolateral impressions deep, as long as quarter of pronotum length or so. *Elytra*. Ovoid, wide, rather convex dorsally, slightly narrower basally, with shoulders rounded, widened toward behind as parallel-sided along anterior two thirds, widest along medial third, distinctly sinuate before apex, apices of each elytron rounded at tip; epipleurae with distinct external plicae; striae complete, deeply impressed, internal six striae feebly punctate, striae 7–9 pronouncedly punctate; parascutellar striae present, anastomosing with stria 1; scutellar setigerous pores present, on base of striae 2, slightly removed back from basal margin with distance of diameter of pore or so; basal margin complete; discal setigerous punctures absent; stria 7 with two setigerous punctures near to apex, subapical puncture larger than apical one; intervals moderately convex; umbilicate series of elytra in stria 8, shortly interrupted in middle, consist of 14 setigerous punctures. *Hind wings*. Well-developed. *Ventral surface* (*thorax and abdomen*). Prosternum and proepisterna smooth and glabrous, prosternum only shallowly sulcate medially along apex, prosternal process unbordered; mesosternum smooth, metaepisterna elongate, impunctate, longer than wide, strongly narrowed posteriorly, with wide anterior margins and very short posterior ones; metasternum smooth, only laterally with three-four large punctures from each side, deeply grooved laterally. Abdomen glabrous except one pair paramedial setae on sterna IV–VI, sternum VII with one pair sub-apical setae in males, with two pairs of sub-apical setae in females; sternum II with cluster of deep punctures laterally. *Legs*. Moderately slender and long; protrochanter with one seta; profemur anterior face with a few very short setae, ventral face glabrous, posterior face with three long setae, two medial and one subapical, dorsal face with three-four short setae; mesocoxa with two setae, one medial and one lateral; mesotrochanter with one distal seta; mesofemur anterior face with four long setae, two basal and two medial ones, dorsal face with 7–9 short setae arranged in one-two rows along length, posterior face with several short setae, ventral face glabrous; metacoxa with two lateral setae, one anterior and one posterior, medial transverse sulcus deep and sinuate, not reaching external coxal margin, distant from anterior margin; metatrochanter slightly shorter than half length of metafemur, with one proximal seta, elongate, apex pointed; metafemur anterior face with one basal and one medial (near ventral edge) setae, dorsal face with one rather short seta at distal third, posterior and ventral faces glabrous; structure of pro-, meta-,

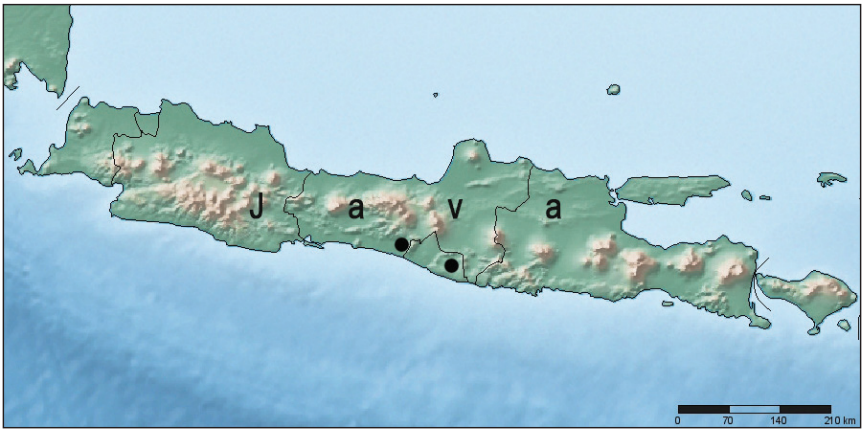


Figure 8. Localities of *Metabacetus willi* sp. n.

and metatibia, as well as of tarsomeres in accordance with that described by Will and Park (2008). *Male genitalia* (Figs 2–7). Median lobe of aedeagus with short and bent basal part and long apical part, apex pointed and curved down in lateral view, internal sac with field of numerous sclerotized scales, situated medially and subapically lengthwise (Figs 2–3), blade long, with margins regularly narrowed towards pointed apex in dorsal view (Fig. 4); right paramere elongate, with short triangular, basal process extended inwardly (Figs 5–6), left paramere conchoid, with massive vermiform, basal process inwardly (Fig. 7).

Etymology. A noun in the genitive case. Honours Kippling Will, a notable American carabidologist, for his studies on the Pterostichitae carabids.

Distribution. So far, this species was only found in two caves in the southern part of Java Island, Indonesia (Fig. 8): cave Seplawan near village Donorejo (Central Java Province, Purworejo Regency, Kaligesing District); cave Ngingrong near village Mulo (Yogiakarta Special Administrative Region, Gunung Kidul Regency).

Affinities. Due to the present knowledge of the taxonomy of the genus and its related taxa, it is difficult to identify the adelphotaxon of the new taxon or to state the most related taxa to it, moreover some unnamed species (see Will and Park 2008: 189–190, Fig. 1) await adequate examination. Based on selected features, namely moderately large size of body, slightly iridescent tegument, sides of pronotum convex posteriorly, with lateral fields broadened and moderately reflexed towards the base, prosternum shallowly sulcate medially near apex, apex of elytra without evident spines, *M. willi* sp. n. seems closer to *M. laotinus* Straneo, 1938 (Laos) and *M. immarginatus* s.l. (India: West Bengal and North Burma) than to the other congeners. However, the species from South Java well differs from the last two species in the presence of more elongate appendages (especially long maxillary palpi), segments IX-XI of antennae reaching beyond the base of pronotum, pronotum widest after the middle, with anterior margin much shorter than posterior one, sides much narrower anteriorly than posteriorly, and obtuse hind angles.

Figure 9. *Mateuellus troglobioticus* Deuve, holotype.

Ecological remarks. *M. willi* sp. n. is the first member of the genus which can be classified as trogloxene (or troglophile). Although slight, it shows several morphological adaptations to cave-dwelling. Compared with the other congeners, its eyes are less protruding, with ommatidia less numerous, its appendages (namely, the maxillary palpi, antennomeres, and legs) a bit longer, and body less robust in sagittal plan and more flattened along the dorsoventral axis. However, the flight wings of the new species are still well-developed and it seems capable of flight. Most probably, this beetle lives not only in caves, but also on the forest floor of woodlands outside the cave systems.

Another related species, *Mateuellus troglobioticus* (Fig. 9), which together with *Metabacetus* belongs to the same clade (Will 2006, Will and Park 2008: 190), displays predominant trilobite mode of life. For the time being, this form has been found three times in caves only (Deuve 1990, present paper).

PTEROSTICHINI

***Poecilus* (*Ancholeus*) *campania* (Andrewes, 1937), comb. n.**
http://species-id.net/wiki/Poecilus_campania

Feronia campania Andrewes, 1937: 3 (type locality: "Punjab : Lyallpur…; Lahore, Shahdara… . India")

Type material. Holotype ♀, "Type" [typeset, round white label with red margin], "Light Collection Lyallpur. 3.IX.29" [typeset], "*Feronia campania* Andr. Type H. E. Andrewes det." [handwritten & typeset] (BMNH, box No 706). Paratype ♀, "India" [typeset], "1765" [typeset], "Bowring. 63**.**47*" [typeset], "Ex. coll. Brit. Mus." [typeset], "Co-type" [typeset, round white label with green margin], "*Feronia campania* Andr. cotype H. E. Andrewes det." [handwritten & typeset], "H. E. Andrewes Coll. B.M.1945-97." [typeset] (BMNH, box No 706).

Other material. 1♀, "Punjab Lyallpur 30.VI.1929 Govt. Entom. Light collection", "*Feronia campania* Andr. H. E. Andrewes det." (BMNH, box No 706).

Remarks. The study of the three females showed that they are conspecific and belong to the genus *Poecilus* Bonelli, 1810. According to several character states: 1/ antennal segment 3 compressed and carinate on internal margin; 2/ onychium without ventral setae; 3/ abdominal sternites 4-6 without distinct transverse furrows along base; 4/ pronotum with two basal impressions at each side, the taxon is best placed in the subgenus *Ancholeus* Dejean, 1828. By the structure of the body, color, and corporal dimensions, *Poecilus campania* seems rather similar to *P. wollastoni* (Wollaston, 1854). However, without a thorough revision of the taxa from *Ancholeus* any opinion for eventual relationship between these species will be tentative. For the time being, the *P. campania* is known only from Pakistan (Faisalabad; Lahore).

***Rhytiferonia beroni* sp. n.**
http://zoobank.org/9DAC8D91-E7AE-4C20-BACB-A703133F19C7
http://species-id.net/wiki/Rhytiferonia_beroni
Figs 10–14

Type material. Holotype ♀, "New Guinea, Bonforok bil, Tifalmin, 1600 m 17.10.75 leg. P. Beron" [typeset], "HOLOTYPE *Rhytiferonia beroni* spec. nov. Guéorguiev des. 2012" [typeset, red label] (NMNHS). Paratypes 2♀♀, labeled as follows: 1♀, "Tifalmin W. Sepic Prov. IX.75" [handwritten], "British Speleological Expedition to Papua New Guinea 1975" [typeset], "*Rhytiferonia* sp. det. B. P. Moore '78" [handwritten & typeset] (NMNHS); 1♀, "Fimin tel 2300 m Western Prov. 30.viii.75 P. Beron" [handwritten], "British Speleological Expedition to Papua New Guinea 1975" [typeset], "*Rhytiferonia* sp. det. B. P. Moore '78" [handwritten & typeset], "UC Berkeley

Figure 10. *Rhytiferonia beroni* sp. n., holotype.

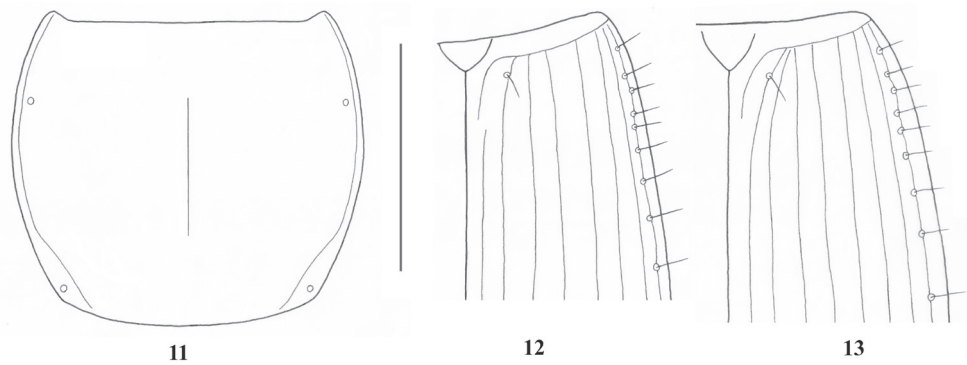
EMEC 345536" [typeset]; paratypes with subsequently added: "PARATYPE *Rhytiferonia beroni* spec. nov. Guéorguiev des. 2012" [typeset, red label] (EMEC).

Examined type material of other species. *Rhytiferonia julianae* Baehr, 2001, paratypes 2♂♂, "IRIAN JAYA: Mt. Juliana Gebiet 16.–17.9.1993 Sab-me Tal" [typeset], "ca. 140°17'E, 04°27'S, 3400–3500m leg. M. Balke (14)" [typeset], "PARATYPE Rhytiferonia julianae, sp.nov. det. M. Baehr 2000" [typeset, red label] (NMW).

Diagnosis. The new species is distinct from all other congeners in the following set of characters: 1) eyes moderately enclosed by temporae laterally; 2) pronotum with obtuse, somewhat perceptible basal angles, side without sinuation in front of angle; 3) posterolateral seta of pronotum slightly removed from angle; 4) elytra with parascutellar setigerous puncture, distinct parascutellar stria in interval 1, and angular base of stria 1 joining stria 2; 5) last three abdominal sterna with transverse sulci superficial, only laterally distinct.

It should be noted that the above diagnosis is based on the descriptions of the known species by Baehr (2001) as specimens of only *Rhytiferonia* species were used for comparison (see chapter "Examined type material of other species").

Description. *Habitus*. Moderately large-sized species of *Rhytiferonia*, with elongate, convex body and basal angles of pronotum rounded off (Fig. 10). *Measurements*. BL: 15.6–17.2 mm (17.1 mm in holotype); BW: 4.9–5.5 mm (5.5 mm in holotype). *Ratios*. PW/HW: 1.38–1.42 (1.42 in holotype); PW/PL: 1.10–1.16 (1.16 in holotype); PW/PbW: 1.35–1.37 (1.37 in holotype); PbW/PaW: 0.98–1.00 (0.98 in holotype); EW/PW: 1.20–1.23 (1.20 in holotype); EL/EW: 1.62–1.68 (1.62 in holotype). *Color*. Deep black on dorsal surface, mouthparts, antennae, legs, and ventral surface black brown to dark reddish. *Microsculpture and lustre*. Very fine, isodiametric, distinct on head and elytra, visible under magnification > 50 x, indistinct on pronotum; dorsal surface shiny. *Head*. Longer than wide, disc smooth, frontal furrows faintly impressed, oblique, divergent backward, hardly reach level of anterior supraorbital punctures; eyes small, modestly projecting laterally, as long as temporae; temporae slightly surpassing eyes laterally; paraorbital sulci moderately deep, reaching level of posterior supraorbital pore backward; labrum rectangular, anterior margin with six setigerous punctures; clypeus trapezoid, slightly emarginated anteriorly and laterally, with two setigerous punctures closer to lateral margins than to anterior one, clypeal suture faint; antennae filiform, pubescent from second fifth of segment 4, with terminal article not reaching base of pronotum; glossal sclerite of ligula with two long setae on anterior margin; maxillary palpomere 1 very massive, twice thicker than following two segments; mentum deeply emarginated, with tooth bifid at tip and pair of labial setae, epilobes large, significantly exceeding mentum tooth forward; submentum with two basal setae, without lateral ones. *Pronotum* (Fig. 11). Large, widest at middle, disc gently convex, smooth; midline very fine, distinct on medial half of pronotum, obsolescent apically and basally; anterior and posterior margins unbordered, almost of equal length, anterior margin slightly concave, fore angles moderately protruding forward; basal margin rather convex backward, hind angles subangular, incompletely round; lateral margins slightly convex to straight, without sinuation towards hind angles, marginal field narrow in apical half, widened and explanate towards base; anterolateral seta at apical third, posterolateral seta slightly in front of hind angles; posterolateral impressions faint. *Elytra* (Figs 12–13). Subelongate, oviform, convex dorsally, coalescent along suture, widest at third fourth; sides narrow basally, gradually widened apically; shoulders angulate, with minute teeth; lateral margins slightly sinuate before rounded apex; striae well impressed, complete, impunctate, parascutellar striae present, not anastomosing with stria 1 back, angular base of stria 1 present, joining stria 2 (in paratype) or reduced (in holotype), scutellar pores present, removed back from basal margin with distance from one to three diameters of pore, situated on angular base of stria 1, stria 7 deepened in apical third, with one setigerous puncture near to apex, discal setigerous punctures absent; intervals gently convex; umbilicate series of elytra entire, not interrupted in middle, consist of 19–21 setigerous punctures. *Hind wings*. Vestigial. *Ventral surface* (*thorax and abdomen*). Prosternum laterally with conspicuous longitudinal sulci; prosternal process unbordered; metaepisterna wider than long, with anterior



Figures 11–13. *Rhytiferonia beroni* sp. n. **11** pronotum, holotype **12–13** base of elytra (**12** holotype **13** paratype). Scale line: 3 mm.

Figure 14. Localities of *Rhytiferonia punctigera* (grey circle) and *R. beroni* sp. n. (black circle).

margins longer than inner ones and as long as outer margins; apical three abdominal sternites with transverse sulci superficial, distinct laterally, indistinct in middle; last visible sternite quadrisetose in female. *Legs*. Fore and middle legs relatively short and massive, hind legs longer; fore and middle trochanteri with one seta, hind trochanteri asetose, with pointed apex, as long as half of hind femora; fore coxae asetose, middle coxae with two setae, hind coxae with three setae, including medial setae after meeting point of coxae; profemur posterior margin with four pores, mesofemur posterior margin with five pores, metafemur anterior margin with three pores; onychium setose ventrally. *Female genitalia*. Not studied.

Etymology. A noun in the genitive case. Honour Dr. Petar Beron, a prominent Bulgarian zoologist, who first collected the new species.

Distribution. Papua New Guinea, Sandaun Province (= West Sepik Province), Telefomin District, Tifalmin env. (Fig. 14). For the time being, it is the first documented representative of *Rhytiferonia* Darlington, 1962 from Papua New Guinea.

Affinities. The new species is provisionally placed in the *nigra*-group, which includes *R. nigra* Darlington, 1962, *R. iebele* Darlington, 1962, and *R. punctigera* Baehr, 2001. Baehr (2001: 43) associated the species from this complex due to the presence of: 1/ markedly enclosed eyes; 2/ basal angles of pronotum rounded off, without sinuation in front of them; 3/ posterolateral seta of pronotum far removed from angle; 4/ complete, deep, sharply impressed transverse sulci on three apical abdominal sterna; 5/ median lobe of aedeagus narrow, elongate, little curved medially, without spiniform sclerites near apex of internal sac. As the male genital characters of the new species are unknown, it possesses only two from the remaining four features: markedly enclosed eyes (i) and basal angles of pronotum rounded off, without sinuation in front of angles (ii). In contrast to that, *R. beroni* sp. n. possesses posterolateral seta of pronotum only slightly removed from basal angle and apical three abdominal sternites with superficial, distinct only laterally transverse sulci.

Except for the characters shared by the new species with the species from the *nigra* group, *R. beroni* sp. n. most resembles *R. punctigera* in: 1) the pronotum with obtuse basal angles; 2) presence of parascutellar pore; 3) presence of parascutellar stria, which not anastomose with stria 1, and angular base of stria 1 joining stria 2. This set of shared traits places the last two species closer to each other than any of them to another species of *Rhytiferonia*. The new species can be distinguished from its closest congener in the following row:

1) temporae ("orbits", after Baehr 2001) laterally slightly surpassing eyes, vs. laterally perceptibly surpassing eyes in *R. punctigera* (Baehr 2001: 45, 55, fig. 16);
2) pronotum widest in the middle, with fore angles moderately protruding (Fig. 11), vs. widest in anterior third, with fore angles little produced in *R. punctigera* (Baehr 2001: 45, 54, fig. 9);
3) anterior and posterior margins of pronotum almost of equal length, PbW/PaW: 0.98, vs. "Base clearly narrower than apex." (Baehr 2001: 45) in *R. punctigera*;
4) posterolateral seta of pronotum slightly removed from hind angle (Fig. 11), vs. far removed from hind angle in *R. punctigera* (Baehr 2001: 45, 54, fig. 9);
5) transverse sulci on three apical abdominal sternites superficially impressed laterally, indistinct in middle, vs. complete and deep, sharply impressed in *R. punctigera* (Baehr 2001: 45);
6) umbilicate series of 19–21 setigerous punctures, vs. umbilicate series of 18 setigerous punctures in *R. punctigera* (Baehr 2001: 45).

In addition, several ratios with different values in the two species (*R. punctigera* in brackets): PW/HW: 1.38–1.42 (vs. 1.27); PW/PL: 1.10–1.16 (vs. 1.07); PW/PbW: 1.35–1.37 (vs. data questionable, 1.24, according to Baehr 2001: 46, but 1.32, according to Baehr 2001: 52); EL/EW: 1.62–1.68 (vs. 1.79).

Key to the species of *nigra*-group

1 Elytra with parascutellar pore; parascutellar stria present, not anastomosing with stria 1; angular base of stria 1 present, joining stria 2 forward or reduced (Baehr 2001: 55, fig. 20; present work, Figs 12–13) **2**

– Elytra without parascutellar pore; parascutellar stria present, anastomosing with stria 1; angular base of stria 1 absent (Baehr 2001: 55, fig. 19)..... **3**

2 Basal angles of pronotum rounded off at tip; abdominal sternites 4–6 with transverse sulci complete and deep, sharply impressed .... ***R. punctigera*** **Baehr, 2001**

– Basal angles of pronotum subangular at tip (Fig. 11); abdominal sterna 4–6 with transverse sulci superficial laterally, indistinct in middle..... ***R. beroni*** **sp. n.**

3 Pronotum base distinctly narrow than apex, widest diameter in front of middle ..... ***R. nigra*** **Darlington, 1962**

– Pronotum base almost as wide as apex, widest diameter in middle..... ..... ***R. iebele*** **Darlington, 1962**

***Pterostichus* (*Oreophilus*) *flavofemoratus pinguis* (Dejean, 1828)**
http://species-id.net/wiki/Pterostichus_flavofemoratus_pinguis

Pterostichus (*Oreophilus*) *podgoricensis* B. Guéorguiev, 2013: 59 (type locality: "Titograd Yugoslavia"), syn. n.

Type material. Holotype ♂, "NHRS-JLKB 000020046" [typeset], "Titograd Yugoslavia" [handwritten], "coll. J. Ferrer" [handwritten], "HOLOTYPE Pterostichus podgoricensis sp. n. Guéorguiev des. 2012" [typeset red label] (NHRS). Paratype ♀, "Teneriffa Coll. O. Thieme" [typeset], "PARATYPE Pterostichus podgoricensis sp. n. Guéorguiev des. 2012" [typeset red label] (MNHUB). For additional data about these specimens see also Guéorguiev (2013: 59).

Other examined material. *Pterostichus flavofemoratus pinguis*, 4♂♂, 5♀♀, Italy, valley de Gressoney (AO), Fontainemore, 1500 m, forest, 10.VIII.2004, leg. & det. G. Allegro (NMNHS).

Remarks. *P. podgoricensis* has been described by the author after two specimens (Guéorguiev 2013). Then I regarded this taxon as most allied to *P. flavofemoratus* (Dejean, 1828) and *P. spinolae* (Dejean, 1828). Following the publication, two colleagues (see Acknowledgements) informed me that my species may be conspecific with *P. flavofemoratus pinguis*, a form that I uncritically considered synonymous with *P. flavofemoratus*. The study of material of *P. flavofemoratus pinguis* from the Pennine Alps sent me by Gianni Allegro and its comparison with *P. podgoricensis* showed that the two taxa are identical.

***Aristochroa poecilma* (Andrewes, 1937), comb. n.**
http://species-id.net/wiki/Aristochroa_poecilma

Feronia poecilma Andrewes, 1937: 5 (type locality: "S.E. Tibet : Tsangpo Valley, Nyima La, 15,000 feet")

Type material. Holotype ♀, "Type" [typeset, white round label with red margin], "Brit. Mus. 1925-189." [typeset], "S.E.Tibet: Tsangpo Valley, Nyima La. 15,000 22.VI.1924. F. Kingdon Ward." [handwritten], "*Feronia poecilma* Andr. Type H. E. Andrewes det." [handwritten & typeset] (BMNH, box No 682).

Examined material of other species. *Aristochroa gratiosa* Tchitcherine, 1898, 1♂, with two labels in Chinese and a third one "Qinhai province China" (BMNH, box No 682); *Aristochroa* sp., 2♀♀, (BMNH, box No 682). The last two specimens with label "E. TIBET: Pochö. 12-16,000 ft. 18-20.vii.1936", and one of them with second label "*Feronia poecilma* Andr. Type H. E. Andrewes det.".

Remarks. The study of the Andrewes's type has proved that it belongs to the subtribe Trigonognathina Tschitschérine, 1898, which includes *Aristochroa* Tschitschérine, 1898, *Myas* Sturm, 1826 (incl. *Trigonognatha* Motschulsky, 1858), *Steropanus* Fairmaire, 1888, and *Xenion* Tschitschérine, 1902. The presence of the following set of characters: 1/ anterior margin of ligula with four or more setae; 2/ elytra with intervals 1, 3, 5, and 7 wider, more or less distinctly raised and differently colored than the other intervals; 3/ terminal segment of both the maxillary and labial palpi not enlarged, revealed that the only specimen of this taxon belongs to *Aristochroa*.

The holotype of *Aristochroa poecilma* was found at Nyima La, a high-mountain passage in the Nyingchi Prefecture, the southeastern part of the Tibet Autonomous Region, China.

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A new genus and eight new species of the subtribe Anillina (Carabidae, Trechinae, Bembidiini) from Mexico, with a cladistic analysis and some notes on the evolution of the genus

Igor M. Sokolov[1,†]

1 *Department of Entomology, California Academy of Sciences, Golden Gate Park, 55 Music Concourse Drive, San Francisco, CA 94118, USA*

† *http://zoobank.org/7381B90A-40F4-455B-8DEA-8E2839A5B725*

Corresponding author: *Igor M. Sokolov* (isokolov@calacademy.org)

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Abstract

One new genus and eight new species of anilline carabids are described from southern Mexico. The new genus, *Zapotecanillus* **gen. n.**, is established for *Z. oaxacanus* (type species) **sp. n.**, *Z. nanus* **sp. n.**, *Z. iviei* **sp. n.**, *Z. ixtlanus* **sp. n.**, *Z. montanus* **sp. n.**, and *Z. kavanaughi* **sp. n.** from the Sierra Madre de Oaxaca, *Z. pecki* **sp. n.** from the Sierra Madre del Sur, and *Z. longinoi* **sp. n.** from the Sierra Madre de Chiapas. A taxonomic key for all described species of *Zapotecanillus* and a cladistic analysis, based on morphological data, are provided. Morphological, behavioral and biogeographical aspects of the speciation in the genus obtained from the resulting cladogram are discussed.

Keywords

Coleoptera, Adephaga, Anillina, *Zapotecanillus*, new genus, new species, southern Mexico, Isthmus of Tehuantepec, forest litter, identification key, cladistic analysis, syntopic speciation, allopatric speciation, biogeography

Introduction

The anilline fauna of Mexico remains extremely inadequately investigated in spite of numerous publications on carabids of the region. Monographs by Jeannel, revising the world fauna of Anillina, contain no information on Mexican representatives (Jeannel 1937, 1963a, b). To date, only two species from two different genera: *Mexanillus sbordonii* Vigna Taglianti and *Geocharidius zullini* Vigna Taglianti, have been recorded from Mexico (Vigna Taglianti 1973). The genus *Mexanillus* Vigna Taglianti (1973) was established for beetles that were collected in caves and closely resembled troglobitic trechines in several specialized features and peculiar habitus. The genus *Geocharidius* Jeannel had been established 10 years earlier by Jeannel (1963a) for a Guatemalan species, *G. integripennis*, described by H. W. Bates (Bates 1882) in his grand "Biologia Centrali-Americana". Because Jeannel's description of *Geocharidius* was insufficient, Vigna Taglianti (1973) re-described the genus on the basis of the two species, *G. integripennis* and *G. zullini*, known to him at that time. At present, *Mexanillus* is a monospecific genus, whereas *Geocharidius* includes 6 species (Lorenz 2005), five of which are limited in their distributions to Guatemala (Erwin 1982).

Preparing a review of the *Geocharidius* species, I determined that anilline specimens from Oaxaca and, in part, from Chiapas, which were identified mostly as *Geocharidius* by different entomologists, actually belong to the undescribed genus. This paper presents the results of a taxonomic study of this genus.

Materials and Methods

Material. This study is based on examination of 150 specimens of a new genus, representing nine species, eight of which are described as new. The material was borrowed from and/or deposited in the following institutions, identified in the text by the following associated codens:

CAS	California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California, U.S.A. 94118 (D. H. Kavanaugh, Curator)
CMNC	Canadian Museum of Nature, Entomology, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4 (R. S. Anderson, Curator)
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A. 15213 (R. L. Davidson, Collections Manager)
KUNHM	University of Kansas Natural History Museum, 1345 Jayhawk Blvd., Lawrence, Kansas, U.S.A. 66045-7593 (Z. H. Falin, Collections Manager)
MTEC	Montana Entomology Collection, Montana State University, Bozeman, Montana, U.S.A. 59717 (M. A. Ivie, Curator)
NMNH	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. 20013-7012 (T. L. Erwin, Curator)

Verbatim label data are given for type specimens of all newly described taxa, with label breaks indicated by a slash ("/"). In a case of series of KUNHM specimens with the same geographical labels but differing in various barcode numbers only, these numbers were replaced in the text by periods of ellipsis.

Measurements. All specimens were measured electronically using a Leica M420 microscope equipped with a Syncroscopy AutoMontage Photomicroscopy system (SYNCROSCOPY, Synoptics Ltd.). Measurements for various body parts are encoded as follows: LH = length of head, measured along midline from anterior margin of labrum to the virtual line, connecting posterior supraorbital setae; WH = width of head, at level of anterior supraorbital setae; WPm = maximal width across pronotum; WPa = width across anterior angles of pronotum; WPp = width across posterior angles of pronotum; LP = length of pronotum from base to apex along midline; WE = width of elytra, at level of 4th umbilicate setae; LE = length of the elytra, from apex of scutellum to apex of left elytron; SBL = standardized body length, a sum of LH, LP and LE. SBL measurements are given in mm; others are presented as nine ratios: mean widths-WH/WPm and WPm/WE and body parts-WPa/WPp, WPm/WPp, WPm/LP, WE/LE, LE/SBL, WE/SBL and LP/LE. All values are given as mean ± standard deviation.

Illustrations. Digital photographs of the dorsal habitus of new species were taken with the AutoMontage system using a Leica M420 microscope. Line drawings of selected body parts were made using a camera lucida on an Olympus BX 50 microscope or grids on a Labomed Lx400 compound microscope. Scanning electron micrographs were made either with coating on a LEO 1450VP SEM or without coating using low vacuum mode on an ESEM FEI Quanta 200.

Dissections. Dissections were made using standard technique. Genitalia were dissected from the abdomens of specimens previously softened in boiling water for 20–30 minutes. Contents of the abdomen were cleared using boiling 10% KOH for 2–3 minutes to remove internal tissues, and then washed in hot water before examination. After examination, genitalia were mounted on plastic transparent boards in dimethylhydantoin formaldehyde resin (DMHF) and pinned beneath the specimen. In some species, investigation of body parts was undertaken in the following way. The whole specimen was cleared, using boiling 10% KOH for ~5 minutes, then washed and dissected in the typical way. Disassembled body parts from one specimen were placed on plastic transparent board, properly oriented, mounted in DMHF and pinned together with the specimen labels.

Type material. I had no opportunity to investigate the type material of the Mexican species of Anillina described by A. Vigna Taglianti, so, *Mexanillus sbordonii* is known to us only by the original description. The concept of *Geocharidius* used here, is based on the investigation of a long series (>20 specimens) of *G. integripennis* (Bates) (Terry Erwin's identification) from the Quiché Department of Guatemala, which is not the type locality of the species (the latter is located within neighboring Totonicapán Dept.); but these specimens exhibit features that closely match diagnostic features of the genus, mentioned in the literature (Jeannel

1963a, Vigna Taglianti 1973). Types of the Guatemalan species of *Geocharidius* described by T. L. Erwin in his revision of Central American Bembidiini (Erwin 1982) were examined.

Terms. Terms used in the paper are largely of general use and follow the literature (Ball and Bousquet 2000; Ball and Shpeley 2005, 2009; Erwin 1974; Jeannel 1963a; Shpeley and Ball 2000), except those for ventral surface structures, terms of which follow the Handbook of Zoology (Lawrence et al. 2010).

Species ranking. Species recognition is in accordance with our previous approach (Sokolov et al. 2004).

Arrangement of taxa in the text. Taxonomic treatments of species in the text follow mostly the geographical basis. The species sequence starts with the type species, and each following species is more distant from the latter geographically, and, presumably, genetically. Within the Sierra Madre de Oaxaca the sequence generally corresponds to the virtual movement along the Tuxtepec – Oaxaca road in SW direction.

Descriptions. The scheme of descriptions follows that of Ball and Shpeley (Ball and Shpeley 2005, 2009).

Maps. Maps were downloaded from the web-site: http://www.maps-for-free.com/ and adjusted with the help of Photoshop software.

Cladistic analysis. Morphological data were used to reconstruct the phylogenetic relationships among species of *Zapotecanillus*. The analysis was based on the assumption that the ancestral lineage of Mesoamerican anillines was represented by a true litter-dwelling, but not endogean, species. Accordingly, as outgroup taxa, two litter species from the anilline genera *Nesamblyops* and *Geocharidius* were chosen for analysis. The geographically proximate *Geocharidius phineus* Erwin from Guatemala represents the globose species of the genus and is confined to the litter of mid-altitudinal forests (Erwin 1982). Geographically distant *Nesamblyops* sp. from New Zealand, because of the presence of rudiment eyes is considered to be close to the ancestral type of normally blind Anillina (Moore 1980). Furthermore, molecular data, although scarce, suggest that this genus forms a branch on the phylogenetic tree of Trechitae basal to the European and American genera of Anillina (Maddison and Ober 2011). A total of 32 binary or multistate characters (29 parsimony informative) were derived from the external morphological features (22), male genitalia (9), and female genitalia (1) (see Tables 1 and 2 in the Appendix). A character matrix was generated using NEXUS Data Editor 0.5.0. for Windows (Page 2001), and the analysis was performed using PAUP* version 4.0 (Swofford 2002), with heuristic tree searches using random addition sequences (100 replicates), holding 10 trees at each step, swapping on all trees, and excluding parsimony-uninformative characters from the data sets. Character states were treated as unordered and unweighted. Bootstrap analyses (Felsenstein 1985) were conducted with resampling at 1,000 replications using the previously mentioned settings. Branch support was also examined using Bremer support indices (Bremer 1994), calculated using the TreeRot.v3 software (Sorenson and Franzosa 2007).

Taxonomic treatment

***Zapotecanillus* gen.n.**
http://zoobank.org/CA8A1E66-49BA-4ADC-9587-E8C210CCA380
http://species-id.net/wiki/Zapotecanillus

Type species. *Zapotecanillus oaxacanus* sp. n., by present designation.

Etymology. The name *Zapotecanillus* derives from the Zapotecs, the name of the indigenous people living in the territory of Oaxaca during historic times, and the generic name *Anillus* Jacquelin du Val, the type genus of the subtribe.

Recognition. The members of this genus are distinguished from the other North and Central American representatives of Anillina by the following combination of characters: frontal area of head flat, without a median tubercle; maxillary palps with palpomere 4 longer than 1/3 of palpomere 3; labium with glossal sclerite with short but distinct paraglossae, and with mentum and submentum fused, without mental-submental suture; pronotum forward of the lateral seta and towards anterior angles with a row of elongate setae; elytra without fixed discal setae and with 8th and 9th pores of umbilicate series much closer to each other than the 7th pore is to the 8th (i.e. the "geminate" condition). The most distinctive features of the representatives of the new genus, easily distinguishing them from the species of *Geocharidius*, are the presence of elongate setae at the anterior angles of pronotum forward of the lateral pronotal setae (cf. Fig. 1 versus Fig. 2), a longer maxillary palpomere 4 (cf. Fig. 5 versus Fig. 6), the absence of suture between the mentum and the submentum (cf. Fig. 7 versus Fig. 8), the "geminate" state of the 8th and 9th pores of umbilicate series (cf. Fig. 3 versus Fig. 4), the cross-shaped metendoventrite and the truncate intercoxal process between the hind legs (cf. Fig. 13 versus Fig. 14).

Description. *Size.* SBL range 1.01–1.55 mm.

Habitus. Body form weakly to moderately convex, ovoid or subparallel (Figs 24–31).

Color. Body bicolored (Fig. 24) or monocolorous (Figs 25–31), brunneorufous, rufotestaceous or testaceous, appendages testaceous.

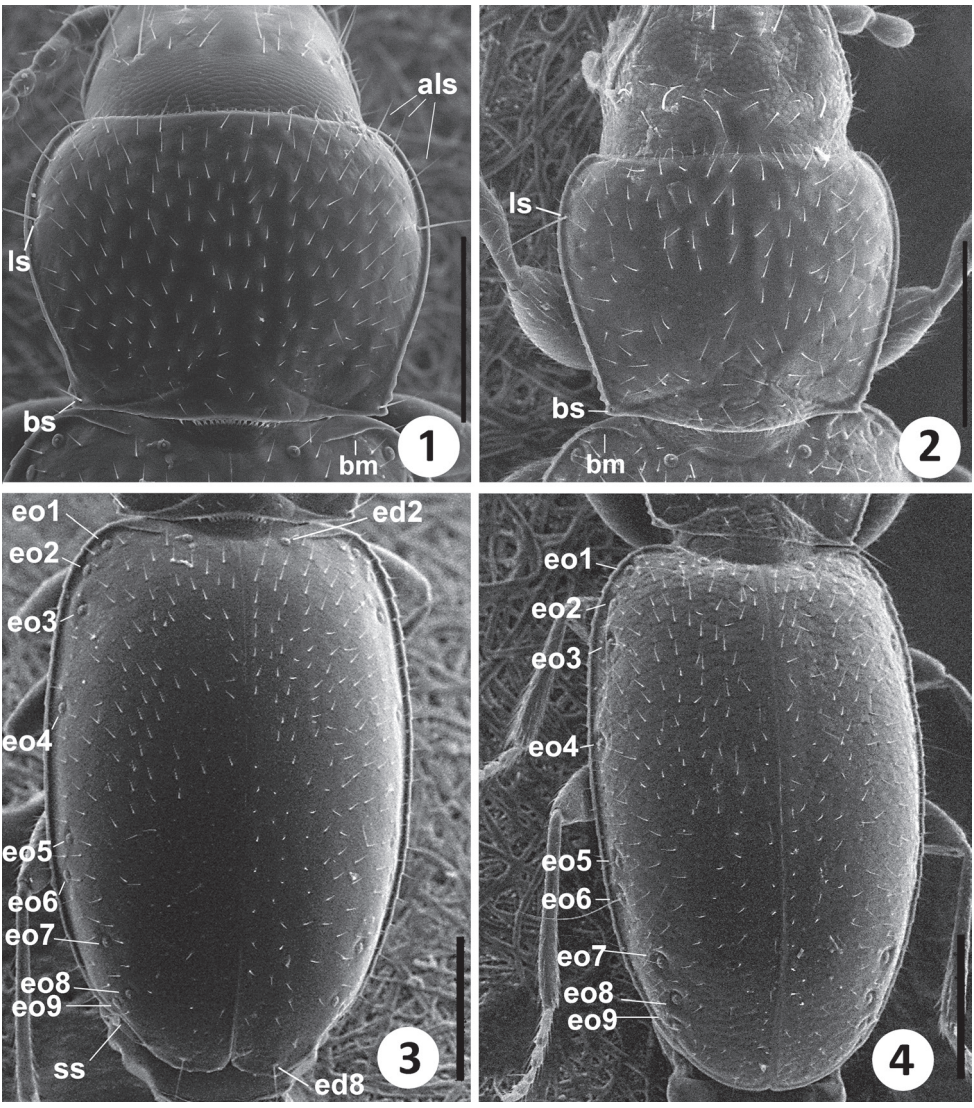
Microsculpture. Dorsal microsculpture of polygonal sculpticells on head, pronotum and elytra. Mesh pattern varies on different body parts. On head, sculpticells transverse, 2-3 times wider than long (Fig. 5). On pronotum, sculpticells longer, 1.5–2 times wider than long. On elytra, sculpticells form mostly isodiametric mesh pattern. Development of microsculpture on pronotum varied among different species.

Luster. Body surface shiny.

Macrosculpture. Body surface sparsely and finely punctate.

Vestiture. Body surface covered with sparse yellow setae of moderate length. Anterior angles of pronotum bear several long setae laterally, which are two times longer than adjacent vestiture (Fig. 1, als).

Fixed setae. Primary head setae include a pair of clypeal (cs), a pair of frontal (fs) and two pairs of supraorbital (ass and pss) setae (Fig. 5). Mentum with three pairs of long primary (medial, paramedial and lateral) setae (Fig. 11, mms, pms, lms). Medial



Figures 1–4. SEM images of body parts of *Zapotecanillus* and *Geocharidius*. Pronotum: **1** *Z. oaxacanus* **2** *G. integripennis*. Elytra: **3** *Z. oaxacanus*; **4** *G. integripennis*. als – anterior lateral pronotal setae; ls – mid-lateral pronotal seta; bm – basal margin; bs – basilateral pronotal seta; ed2 – scutellar seta; ed8 – apical seta; eo1-9 – setae 1–9 from the umbilicate series; ss – subapical sinuation. Scale bar= 0.2mm.

mental setae located on mental tooth, not near its base on mentum (Fig. 7, mms). Submentum with two pairs of long primary setae in two rows (lss1, prss) and 1 additional pair of shorter setae (lss2) located laterally (Fig. 11). Maxilla with long stipetal and palpiferal setae (Fig. 12). Pronotum with two long primary lateral setae (middle, ls, and basal, bs) on each side (Fig. 1). Elytra lack discal setae (Fig. 3), but with scutellar (ed2) and apical (ed8) setae. Last two (8th and 9th) pores (eo8 and eo9) of umbilicate series

much closer to each other than 7th (eo7) pore is to 8th (Fig. 3). Fifth visible sternite of male with two and of female with four setae along the posterior margin.

Head. Anterior margin of clypeus (cl) straight (Fig. 5). Frontal area flat without tubercle (ft) medially near frontoclypeal suture. Fronto-lateral carinae distinct and long.

Eyes. Eyes absent.

Antennae. Submoniliform, 11-segmented, extended to about posterior margin of pronotum. Antennomeres 1 and 2 elongate, of equal length and 1.4–1.5 times longer than antennomere 3, which is only slightly elongate and 1.1–1.2 times longer than antennomere 4. Antennomeres 4 to 10 globose, last antennomere (11) conical and 1.6-1.8 times longer than penultimate antennomere.

Labrum. Labrum (l) transverse with straight, entire anterior margin with six setae apically, increasing in size from the central pair outwards (Fig. 5).

Mandibles. General plan of *Bembidion* type (Maddison 1993). Right mandible with distinct anterior (art) and posterior retinacular (prt), terebral (tt), premolar (pm) and molar (m) teeth (Fig. 10). Left mandible with distinct terebral (tt), posterior retinacular (prt), premolar (pm) and molar (m) teeth only (Fig. 9).

Maxillae. Maxillary palps (Fig. 12) similar to *Bembidion* (Maddison 1993) with basal trianguloid cardo, and stipes with dorsal and ventral lobes (dls, vls), dimerous galea (g1, g2), and standard lacinia (lc), with subulate palpomere 4 (mp4). Palpus (Fig. 5) with long 4th palpomere (mp4), 0.4–0.5 length of palpomere 3 (mp3).

Labium. Labium (Fig. 7) with mental tooth; mentum and submentum fused, without mental-submental suture (ms) and with moderately enlarged lateral mental lobes, which are translucent along the lateral margins (llm). Glossal sclerite (gsc) with short but distinct paraglossae (pg) laterally and with two setae apically. Central area of mental-submental complex with a field of pores and 1-2 pairs of shorter setae additionally (Fig. 11).

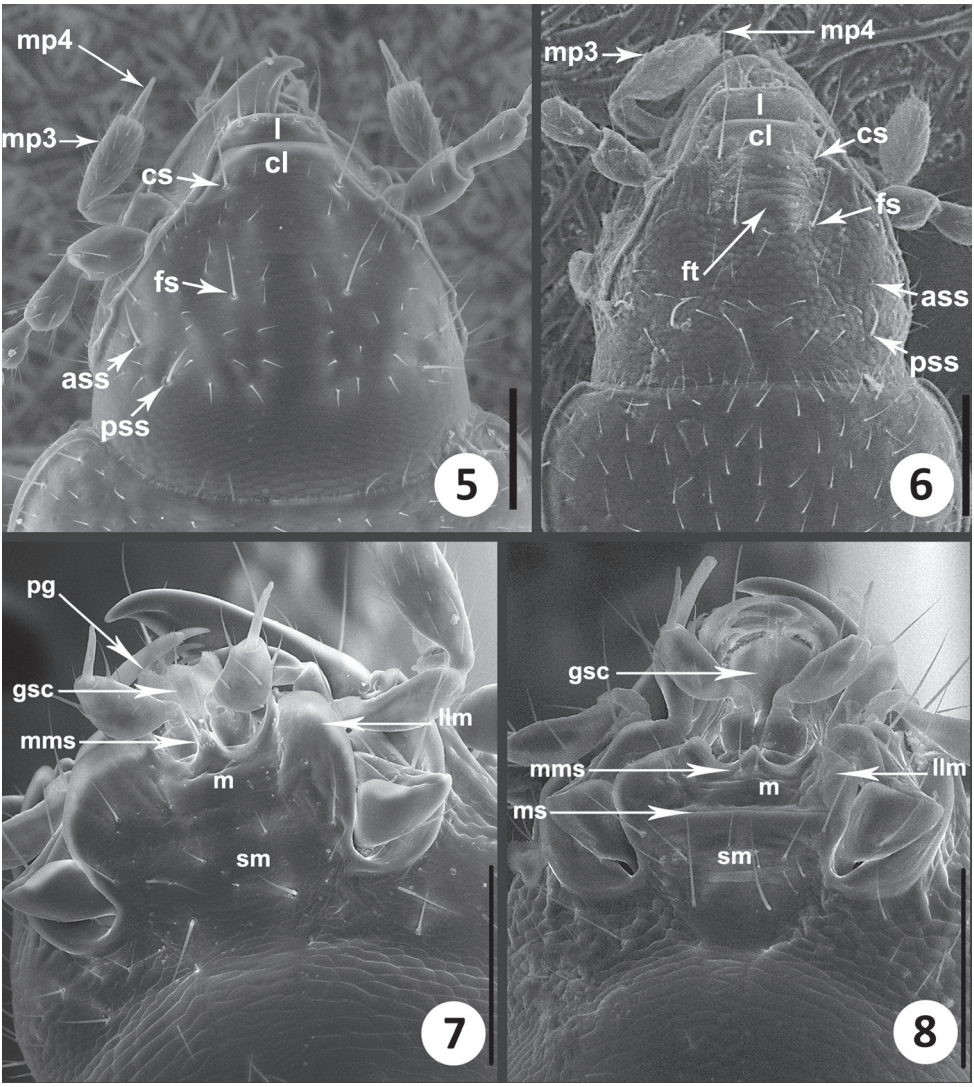
Prothorax. Pronotum cordiform, moderately convex, not sinuate (Figs 32–33) or slightly sinuate posteriorly (Figs 34–35). Basal margin of pronotum either straight (Fig. 32), or oblique laterally (Figs 33–34), in one species bisinuate laterally, at posterior angles (Fig. 35). Anterior angles indistinct, broadly rounded. Posterior angles denticulate, without or with 1-2 small denticles in front of the angles. Widths across anterior margin and between posterior angles of approximately equal length (WPa/WPp varies from 0.96 to 1.04 among species).

Scutellum. Externally visible, triangular, with narrowly rounded apex.

Elytra. Elytra of moderate length (LE/SBL from 0.57 to 0.58 among species) without visible interneurs (Fig. 3). Humeri rounded to form right angle with longitudinal axis of body. Basal margination (bm) distinct and long, reaches half the distance between humeral angle and scutellar pore (Fig. 1). Apical half of elytra with shallow but evident subapical sinuation (ss) (Fig. 3).

Hind wings. Absent.

Pterothorax (Fig. 13). Metaventrite (mtv) short, distance between meso- and metacoxae about of the diameter of mesocoxa. Metanepisternum (mte) short, subquadrate, with anterior and outer margins of equal length. Metendoventrite (mes) cross-shaped with long lateral arms.



Figures 5–8. SEM images of structural features of *Zapotecanillus* and *Geocharidius*. Head, dorsal aspect. **5** *Z. oaxacanus* **6** *G. integripennis*. Labium, ventral aspect **7** *Z. oaxacanus* **8** *G. integripennis*. ass – anterior supraorbital seta; cl – clypeus; cs – clypeal seta; fs – frontal seta; ft – frontal tubercle; gsc – glossal sclerite; l – labrum; llm – lateral lobe of mentum; m – mentum; mms – medial mental setae; mp3 – maxillary palpomere 3; mp4 – maxillary palpomere 4; ms – mental-submental suture; pg – paraglossa; pss – posterior supraorbital seta; sm – submentum. Scale bar = 0.1mm.

Legs. Legs of moderate length, not elongate. Prothoracic legs of males variable in structure of tarsomere 1. Typically, 1st protarsomere markedly dilated apico-laterally with two rows of oval articulo-setae (Stork 1980) on the ventral surface (Figs 20–21). Some species with 1st tarsomere only slightly dilated and with only one (outer) row of oblong articulo-setae (Fig. 22), and other species with 1st tarsomere non-dilated and

without adhesive vestiture (Fig. 23). Protibiae (Figs 15, 17–19) with antenna cleaner of type B (Hlavac 1971), with both anterior (asr) and posterior (psr) apical setal rows and concave apico-lateral notch (Fig. 18, tbn). Profemora moderately swollen. Mesotibiae with two terminal spurs and tibial brush. Metafemora unmodified, metatibiae with two terminal spurs. Tarsi pentamerous, 5th and 1st tarsomeres are the longest, 2-4 tarsomeres of equal length on the tarsi of all legs, 1st tarsomere shorter than combined length of 2–4 tarsomeres (Fig. 15). Tarsal claws simple, untoothed (Fig. 16).

Abdominal ventrites. Five visible abdominal ventrites: 2nd ventrite longest (Fig. 13), more than 3 times longer than 3rd or 4th, 3rd and 4th equal in length; the last, 5th, approximately 1.5 times longer than 4th. Intercoxal process (ipa) of 2nd ventrite broad, truncate anteriorly (Fig. 13).

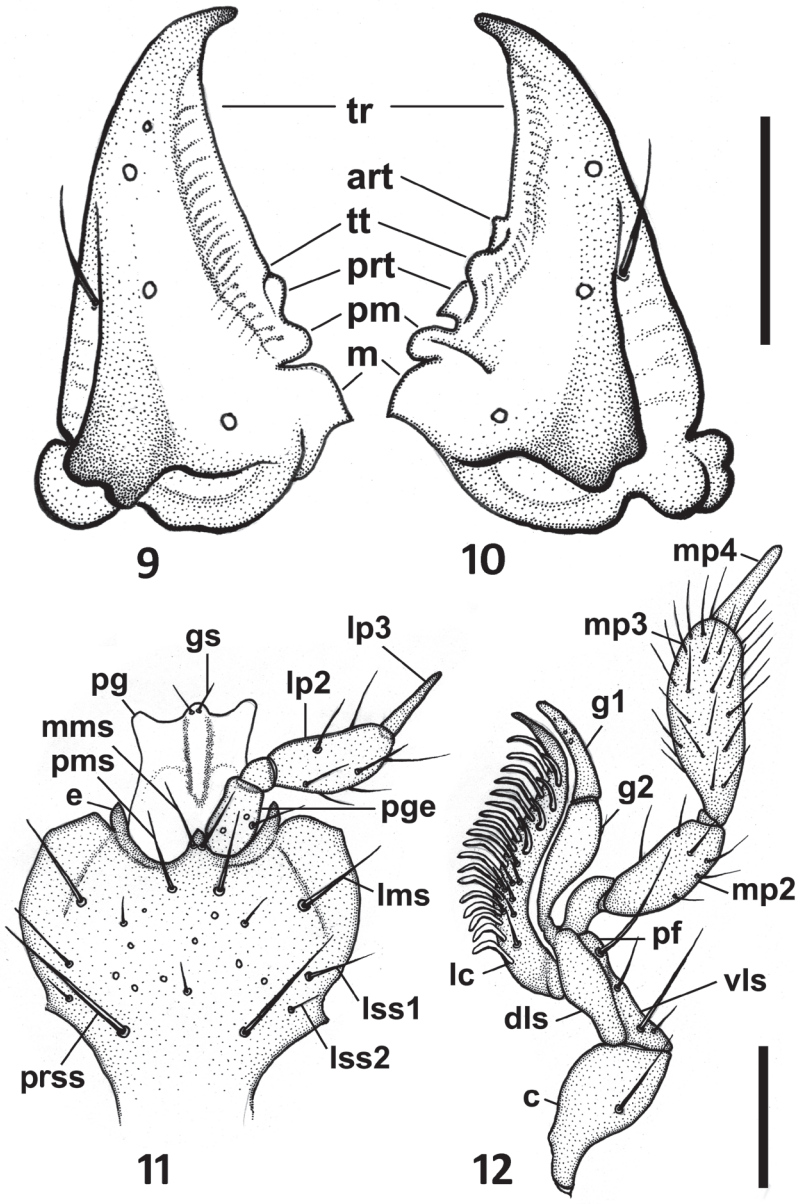
Male genitalia (Figs 36–59). Median lobe of aedeagus anopic, elongate, twisted and slightly arcuate. Internal sac with two groups of copulatory sclerites: dorsal group represented by 2 plates, and ventral group represented by weakly sclerotized fold or folds. Dorsal plate 1 (dp1) in form of an elongate plate, rounded or pointed at basal end, and tapered into a needle-like structure apically. Dorsal plate 2 (dp2) much smaller than plate 1, also needle-attenuated apically, curved and enlarged towards base; coplanarly adjoined to dorsal plate 1 apically in lateral view and divergent from plate 1 basally as a ventrally directed protuberance; can be seen as a separate structure in some species (Figs 54, 57). Ventral sclerites (vsc) of varied shape, dependent on development of sclerotization. Additional spines or scaled membranous fields of internal sac are absent. Parameres typically bisetose, except right paramere of *Z. pecki* 3-setose (Fig. 53). Left paramere large and broad, either evenly tapered to apex (Figs 43, 46) or with short attenuation before setal attachment (Figs 37, 40). Ring sclerite broadly ovate with transverse handle-like extension of varied length and shape (Figs 60–67, hd).

Female genitalia (Figs 68–76). Ovipositor sclerites: Gonocoxite 1 asetose (gc1). Gonocoxite 2 triangular (gc2), 1.6–1.8 times longer than its basal width, slightly to moderately curved, with 2 lateral ensiform (es) and apical nematiform (ns) setae. Laterotergite (lt) with 5–8 setae. Internal genitalia with spermatheca sclerotized, rufous, spherical and ball-shaped in most species, fusiform with a bulb-like enlargement apically in *Z. kavanaughi* (Fig. 75).

Included taxa. The new genus includes eight species: *Z. oaxacanus* sp. n., *Z. nanus* sp. n., *Z. ixtlanus* sp. n., *Z. iviei* sp. n., *Z. montanus* sp. n., *Z. pecki* sp. n., *Z. kavanaughi* sp. n., and *Z. longinoi* sp. n.

Geographical distribution. The species of this genus are known from three mountain ranges of Mexico: the Sierra Madre de Oaxaca, the Sierra Madre del Sur and the Sierra Madre de Chiapas, within the states of Oaxaca and Chiapas (Fig. 77). This type of distribution best fits Halffter's (1987) Meso-American Montane Distribution Pattern.

Way of life. According to the label information, specimens of the new genus were taken from the leaf litter within the 1200–3000m range of altitudes at the Sierra Madre de Oaxaca, and in mesophyll and cloud forests within the 1330–2140m range of altitudes at the Sierra Madre de Chiapas. Collecting dates are May, June, July and August. One specimen from the Sierra Madre de Oaxaca was taken "under bark hardwood".



Figures 9–12. Drawings of the mouthparts of *Zapotecanillus oaxacanus*. **9** left mandible, dorsal aspect **10** right mandible, dorsal aspect **11** labium, ventral aspect **12** right maxilla, ventral aspect. art – anterior retinacular tooth; c – cardo; dls – dorsal lobe of stipes; e – epilobe of mentum; gs – glossal seta; g1 – galeomere 1; g2 – galeomere 2; lc – lacinia; lms – lateral mental seta; lp2 – labial palpomere 2; lp3 – labial palpomere 3; lss1 – lateral submental seta 1; lss2 – lateral submental seta 2; m – molar tooth; mms – medial mental seta; mp2 – maxillary palpomere 2; mp3 – maxillary palpomere 3; mp4 – maxillary palpomere 4; pf – palpifer; pg – paraglossa; pge – palpiger; pm – premolar tooth; pms – paramedial mental seta; prss – primary submental seta; prt – posterior retinacular tooth; tr – terebral ridge; tt – terebral tooth; vls – ventral lobe of stipes. Scale bars = 0.1mm (Figs **9–10**); 0.05mm (Figs **11–12**).

Relationships. The position of *Zapotecanillus* within the North and Central American Anillina is unclear at present, and awaits molecular data analysis or further discoveries and subsequent morphological analyses of the Middle American anilline taxa. Members of this new genus differ principally from those of the southern stock of Middle American anilline genera (*Geocharidius* Jeannel, *Honduranillus* Zaballos, *Mexanillus* Vigna Taglianti) in having a different arrangement of the last three pores of the umbilicate series and the fused labium, and from geographically proximate *Geocharidius* and *Mexanillus* in having distinct paraglossae. They differ from members of the northern stock of North American anilline genera (*Anillaspis* Casey, *Anillinus* Casey, *Anillodes* Jeannel, *Micranillodes* Jeannel, *Serranillus* Barr) in lacking fixed discal pores on the elytra.

The key provided below allows distinguishing members of the new genus from those of the other continental North and Middle American anilline genera:

1 Elytra without fixed discal setae (Figs 3–4). Mexico and Central America... **2**

– Elytra with 3 pairs of fixed discal setae. North of Mexico..... .....**other genera (*Anillaspis* Casey, *Anillinus* Casey, *Anillodes* Jeannel, *Micranillodes* Jeannel, *Serranillus* Barr)**

2 Labium fused, without mental-submental suture (Fig. 7). Pores 8 and 9 of umbilicate series geminate, much closer to each other, than 8th to 7th (Fig. 3).. ..... ***Zapotecanillus*, gen. n.**

– Labium free, with distinct mental-submental suture (Fig. 8). Pores 7, 8 and 9 of umbilicate series equidistant (Fig. 4)..... **3**

3 Pronotum convex. Glossal sclerite without distinct paraglossae (Fig. 8). Size smaller, less than 2.7mm..... **4**

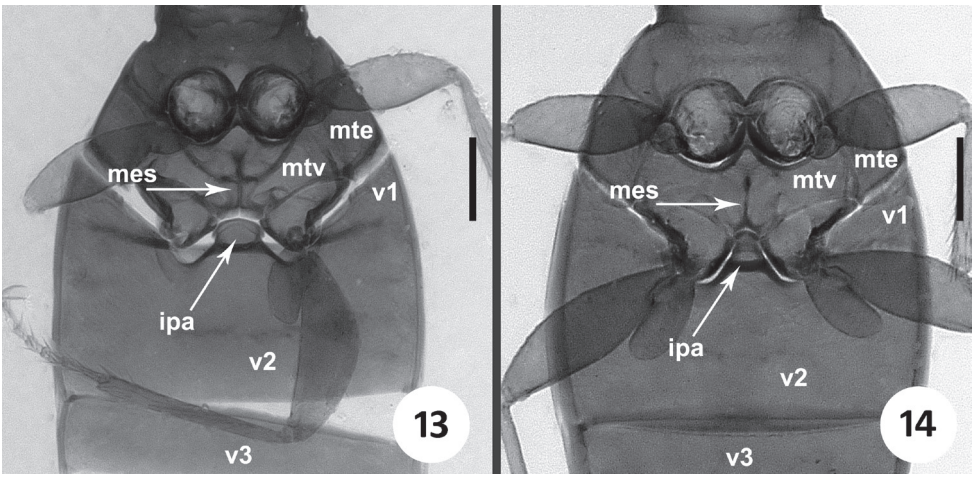
– Pronotum subdepressed. Glossal sclerite with distinct paraglossae (as in Fig. 7). Size larger, 3mm..... ***Honduranillus* Zaballos**

4 Length greater than 2.2 mm. Head with impressed, subparallel frontal furrows and shortened latero-frontal carinae. Appendages, especially tarsi, elongate; 1st tarsomeres of middle and hind legs very long, longer than the length of tarsomeres 2-4 combined. Troglobitic beetles..... ***Mexanillus* Vigna Taglianti**

– Length less than 1.9 mm. Head with faint and divergent frontal furrows and long latero-frontal carinae. Appendages of standard length, 1st tarsomere of middle and hind legs shorter than tarsomeres 2-4 combined. Litter-dwelling beetles..... ***Geocharidius* Jeannel**

***Zapotecanillus oaxacanus* sp. n.**
http://zoobank.org/86234081-8CB0-45D0-861D-721A0C05174A
http://species-id.net/wiki/Zapotecanillus_oaxacanus
Figs 1, 3, 5, 7, 9–13, 15–18, 22, 24, 32, 36–38, 60, 68, 72, 77, 90–92, 94

Type material. HOLOTYPE, male, in NMNH, point-mounted, labeled: \MEXICO. Oaxaca 18.7mi S Valle Nacional 5200' 17 Aug.1973\ A.Newton Collector \ Loan from



Figures 13–14. Images of metaventrite and first abdominal ventrites of *Zapotecanillus* and *Geocharidius*. **13** *Z. oaxacanus* **14** *G. integripennis*. ipa – intercoxal process of abdominal ventrite 2; mes – metendosternite; mte – metanepisternum; mtv – metaventrite; v1-v3 – abdominal ventrites 1–3. Scale bar = 0.1mm.

NMNH 2051867\. PARATYPES (8 ex., 4♂2♀ were dissected), labeled same as a holotype, except two specimens, which have an additional label: *Geocharidius n.sp.* det. T.L.Erwin *76*\ each, where italicized font means handwritten (deposited in CAS, NMNH).

Specific epithet. The specific epithet is a Latinized adjective in the masculine form based on Oaxaca, the state of Mexico from which the new species is described.

Type locality. Mexico, Oaxaca, 18.7mi S from Valle Nacional.

Recognition. Adults of this new species can be distinguished easily from those of other species of the genus by the following combination of external characters: bicolored and robust appearance, comparatively small head and distinctly transverse pronotum.

Description. *Size.* Medium-sized for the genus (SBL range 1.30-1.36 mm, mean 1.33±0.049 mm, n=8).

Habitus. Body form (Fig. 24) moderately convex, slightly elongate (WE/SBL 0.41±0.09), head narrow for genus compared to pronotum (WH/WPm 0.69±0.015), pronotum wide compared to elytra (WPm/WE 0.81±0.017).

Color. Body bicolored: head and pronotum brunneorufous, elytra rufotestaceous, appendages testaceous.

Microsculpture. Disc of pronotum with well-developed microsculpture.

Prothorax. Pronotum (Fig. 32) relatively long (LP/LE 0.44±0.006) and markedly transverse (WPm/LP 1.33±0.022), with lateral margins straight and moderately constricted posteriorly (WPm/WPp 1.32±0.034). Basal margin straight. Contour of posterior angles nearly rectangular (100–110°) with 1–2 small denticles in front of the angles.

Elytra (Fig. 3). Convex, not depressed along suture, comparatively wide (WE/LE 0.73±0.013). Margins rounded, slightly divergent in basal half, evenly rounded to apex in apical half, maximal width of elytra at midpoint.

Legs. 1st male protarsomere only slightly dilated (Fig. 22).

Male genitalia. Median lobe of aedeagus (Fig. 36), with short and transverse apex, broadly rounded at tip. Dorsal plate 1 long, with apical pointed attenuation of moderate length. Dorsal plate 2 joined to plate 1 at its middle ventrally, where it forms a distinct protuberance. Ventral sclerites elongate, with subparallel sides and obliquely stretched from dorsal plates towards ventral margin of median lobe. Right paramere short and moderately wide (Fig. 38). Left paramere with distinct apical constriction (Fig. 37). Ring sclerite with long handle-like extension, widely rounded apically (Fig. 60).

Female genitalia. Gonocoxite 2 rather long, with slightly curved blade and rounded apex (Fig. 68). Laterotergite with 7-8 setae. Spermatheca standard for genus (Fig. 72).

Geographical distribution. This species is known only from the type locality in the Sierra de Juárez Range, a part of the Sierra Madre de Oaxaca, within the high course of the Rio de Valle Nacional (Figs 77 and 94, black quadrangles).

Way of life. Specimens of this species were collected at an altitude of 5200 feet (1600 m).

Relationships. The armature of internal sac of *Z. oaxacanus* males is nearly indistinguishable from that of *Z. nanus* and *Z. ixtlanus* males, described below, clearly suggesting both of them as closest relatives. The former species is sympatric with *Z. oaxacanus* and, based on the same label data, may also be syntopic (i.e., their members may occur together in the same habitat). See also Fig. 90 for cladistic affinities.

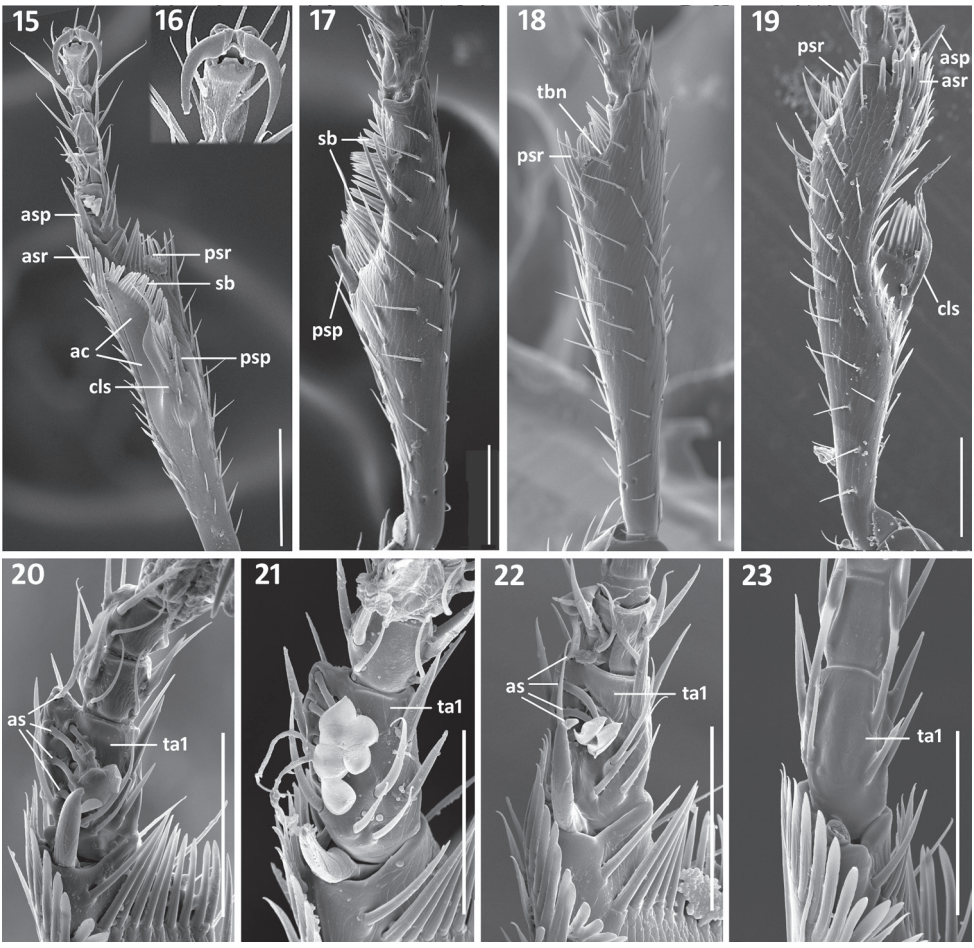
***Zapotecanillus nanus* sp. n.**
http://zoobank.org/E3677571-83C4-4836-9252-BC1B5C11129E
http://species-id.net/wiki/Zapotecanillus_nanus
Figs 19, 20, 25, 39–41, 61, 69, 73, 77, 90–92, 94

Type material. HOLOTYPE, male, in NMNH, point-mounted, labeled: \ MEX. Oax., 15mi. S. Valle Nacional, 4000' 21.V.1971 S.Peck Ber.204, leaf litter \ Borrowed Ex. J.M. Campbell \ USNMNH 2051867\. PARATYPES (27 ex., 4♂4♀ were dissected), 4 ex. labeled same as holotype, except one specimen, which has an additional label: *Geocharidius n.sp.* det. T.L.Erwin *76*\, where italicized font means handwriting.; 12 ex. labeled: MEXICO: Oaxaca, 15mi. S. Valle Nacional, 4000' 21 May 1971, leaf litter, S. Peck \ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\; 1 ex. labeled: \ MEXICO: Oaxaca 15.1mi S Valle Nacional 4300' VIII-11-18-1973 \ under bark hardwood A.Newton \ Borrowed ex. MCZ \ Loan from USNMNH 2051867\; 10 ex. labeled: \ MEXICO. Oaxaca 18.7mi S Valle Nacional 5200' 17 Aug.1973\ A.Newton Collector \ Loan from USNMNH 2051867\ (deposited in CAS, CMNH, NMNH).

Specific epithet. The specific epithet is a Latin adjective, *nanus*, in the masculine form, meaning *dwarf, miniature,* and refers to the small size of the beetles.

Type locality. Mexico, Oaxaca, 15mi S from Valle Nacional.

Recognition. Adults of this new species are distinguished from those of other species of the genus by the combination of small size and brunneorufous color; and males can be further distinguished by the shape of the median lobe (Fig. 39).



Figures 15–23. Structural features of front legs of *Zapotecanillus*. Left protibia of *Z. oaxacanus*: **15** ventral aspect **16** tarsal claws **17** lateral aspect **18** dorso-lateral aspect. Left protibia of *Z. nanus*: **19** dorsal aspect. Male left protarsi, ventral aspect: **20** *Z. nanus* **21** *Z. iviei* **22** *Z. oaxacanus* **23** *Z. kavanaughi*. ac – antenna cleaner; as – articulo-seta, asp – anterior spur; asr – anterior setal row; cls – clip setae; psp – posterior spur; psr – posterior setal row; sb – setal band; ta1 – tarsomere 1; tbn – tibial notch. Scale bars = 0.1mm (Figs **15, 17–19**); 0.05mm (Figs **20–23**).

Description. *Size.* Small for genus (SBL range 1.02–1.16 mm, mean 1.10±0.049 mm, n=12).

Habitus. Body form (Fig. 25) moderately convex, slightly elongate (WE/SBL 0.41±0.09), head of normal proportions for genus (WH/WPm 0.75±0.016), pronotum narrow compared to elytra (WPm/WE 0.75±0.028).

Color. Body monocolorous, brunneorufous, appendages testaceous.

Microsculpture. Microlines partially effaced on disc of pronotum.

Prothorax. Pronotum relatively long (LP/LE 0.43±0.020) and moderately transverse (WPm/LP 1.26±0.030), with margins straight and markedly constricted posteri-

orly (WPm/WPp 1.38±0.044). Basal margin slightly oblique laterally. Posterior angles small, contour of posterior angles obtuse (112–126°) without or with 1 small denticle in front of the angles.

Elytra. Slightly convex, not depressed along suture, comparatively wide (WE/LE 0.72±0.025). Margins rounded, moderately divergent in basal half, evenly rounded to apex in apical third, maximal width of elytra slightly behind the midpoint.

Legs. 1st male protarsomere markedly dilated apico-laterally (Fig. 20).

Male genitalia. Median lobe of aedeagus (Fig. 39), with small, slightly elongated apex, angulately rounded at tip. Dorsal plate 1 long, with apical pointed attenuation of moderate length. Dorsal plate 2 joined to plate 1 at its middle ventrally, where it forms a distinct protuberance. Ventral sclerites with sides divergent ventrally, trianguloid in shape. Right paramere short and moderately narrow (Fig. 41). Left paramere with distinct apical constriction (Fig. 40). Ring sclerite with long handle-like extension, pointed apically (Fig. 61).

Female genitalia. Gonocoxite 2 comparatively short, with slightly curved blade and narrowly rounded apex (Fig. 69). Laterotergite with 5-6 setae. Spermatheca standard for genus (Fig. 73).

Geographical distribution. The species is known from a few localities in the Sierra de Juárez Range, a part of the Sierra Madre de Oaxaca, along the ~5km stretch of the Rio de Valle Nacional (Figs 77 and 94, white triangles).

Way of life. According to the label data, the elevations of localities range from 4000' to 5200' (1200–1600 m).

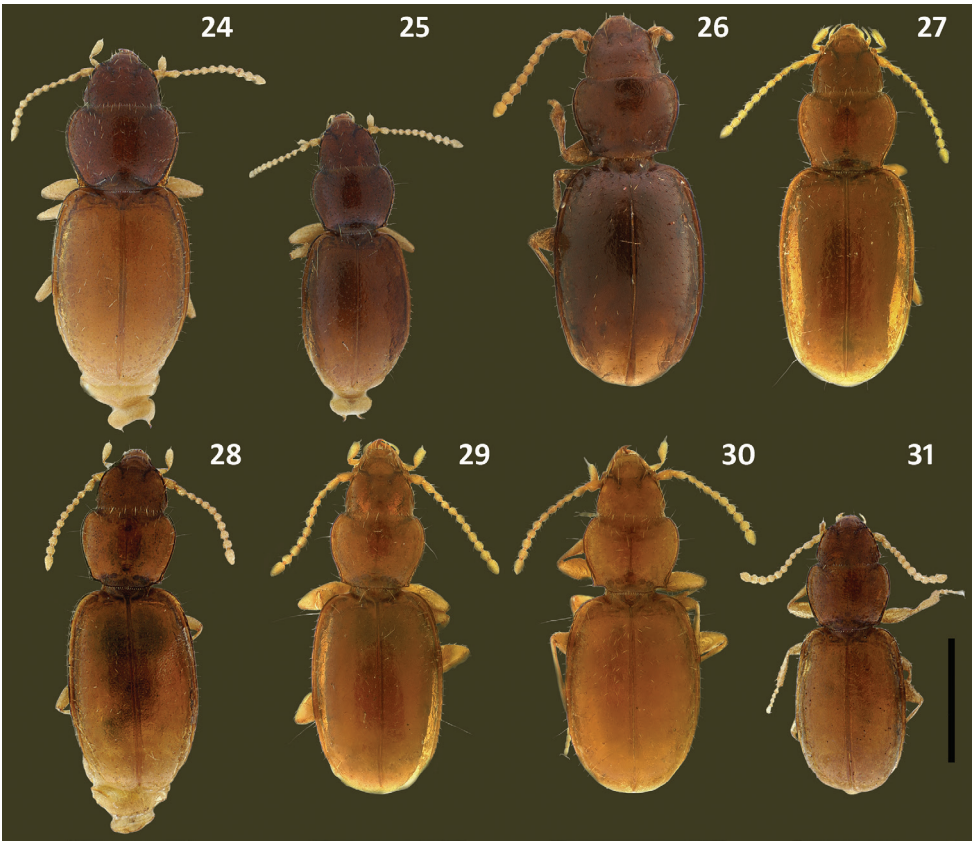
Relationships. Aedeagal characters (shape of dorsal plates and left paramere) suggest that *Z. nanus* is most closely related to the sympatric *Z. oaxacanus*. See also Fig. 90 for cladistic affinities.

Zapotecanillus ixtlanus sp. n.

http://zoobank.org/3349A2CB-9EA6-4F1E-8472-F9C7C4854CDC
http://species-id.net/wiki/Zapotecanillus_ixtlanus
Figs 26, 42–44, 62, 77, 90, 92, 94

Type material. HOLOTYPE, male, in CMNH, point-mounted, labeled: \MEXICO: Oaxaca, 32 miles S Valle Nacional, 7000 ft. 23 May 1971, ex. leaf litter, Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\. PARATYPES (17 ex., 3♂1♀ were dissected), 10 ex. labeled same as a holotype; one male labeled: 8500', 37mi. S. Valle Nacional, Oax. Mex. V.24.1971 H.Howden \ Borrowed Ex. H.F. Howden \ Loan from USNMNH 2051867\; 3 ex. labeled: \MEXICO: Oaxaca, 37 mi. S Valle Nacional, 8500 ft. 23 May 1971, ex. leaf litter, Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\; 3 ex. labeled: \MEXICO: Oaxaca, 37 mi. S Valle Nacional, oak litter, 25 May 1971, S. Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\ (deposited in CAS, CMNH, NMNH).

Specific epithet. The specific epithet is a Latinized adjective in the masculine form based on *Ixtlan*, the district of the state of Oaxaca, Mexico from which the new species is described.



Figures 24–31. Habitus images of *Zapotecanillus* species. **24** *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National), paratype **25** *Z. nanus* (MEXICO, Oaxaca, 18.7mi N Valle National), paratype **26** *Z. ixtlanus* (MEXICO, Oaxaca, 37mi S Valle National), paratype **27** *Z. iviei* (MEXICO, Oaxaca, 2mi S Cerro Pelon), paratype **28** *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan), paratype **29** *Z. montanus* (MEXICO, Oaxaca, 52mi N Oaxaca), paratype **30** *Z. pecki* (MEXICO, Oaxaca, 3.5mi S Suchixtepec), paratype **31** *Z. longinoi* (MEXICO, Chiapas, Sierra Morena), paratype. Scale bar = 0.5mm.

Type locality. Mexico, Oaxaca, 32mi. S. Valle Nacional.

Recognition. Males of this new species can be distinguished from those of other species of the genus by the combination of the large size and shape of the median lobe (Fig. 42).

Description. *Size.* Large for genus (SBL range 1.32–1.53 mm, mean 1.39±0.069 mm, n=12).

Habitus. Body form (Fig. 26) moderately convex, slightly elongate (WE/SBL 0.41±0.016), head of normal proportions for genus (WH/WPm 0.72±0.013), pronotum narrow compared to elytra (WPm/WE 0.72±0.038).

Color. Body monocolorous, rufobrunneous, appendages testaceous.

Microsculpture. Disc of pronotum with well-developed microsculpture.

Prothorax. Pronotum relatively small (LP/LE 0.39±0.020) and moderately transverse (WPm/LP 1.31±0.039), with margins straight and distinctly constricted posteriorly (WPm/WPp 1.41±0.050). Basal margin oblique laterally. Contour of posterior angles obtuse (111–123°) with a small denticle.

Elytra. Convex, not depressed along suture, of moderate width (WE/LE 0.70±0.023). Margins subparallel at middle, slightly divergent in basal third, evenly rounded to apex in apical third, maximal width of elytra slightly behind midpoint.

Legs. 1st male protarsomere markedly dilated apico-laterally.

Male genitalia. Median lobe of aedeagus (Fig. 42) with short semicircular apex. Dorsal plate 1 long, with short apical attenuation. Dorsal plate 2 joined to plate 1 at its middle ventrally, where it forms a distinct protuberance. Ventral sclerites slightly sclerotized, trianguloid in shape. Right paramere short and moderately wide (Fig. 44). Left paramere without apical constriction (Fig. 43). Ring sclerite with short handle-like extension, pointed apically (Fig. 62).

Female genitalia. Spermatheca standard for genus.

Geographical distribution. The species is known only from the type locality in the Sierra Juárez Range, a part of the Sierra Madre de Oaxaca (Figs 77 and 94, white circle).

Way of life. Specimens were collected at altitudes 7000-8500' (2100–2600 m) in oak litter.

Relationships. Aedeagal characters (shape of the median lobe and dorsal plates) suggest that *Z. ixtlanus* is closely related to *Z. oaxacanus* and *Z. nanus*. See also Fig. 90 for cladistic affinities.

***Zapotecanillus iviei* sp. n.**
http://zoobank.org/7B74C66E-1EEB-4706-8AFE-A7B6D9A056CC
http://species-id.net/wiki/Zapotecanillus_iviei
Figs 21, 27, 34, 45–47, 63, 74, 77, 90, 94

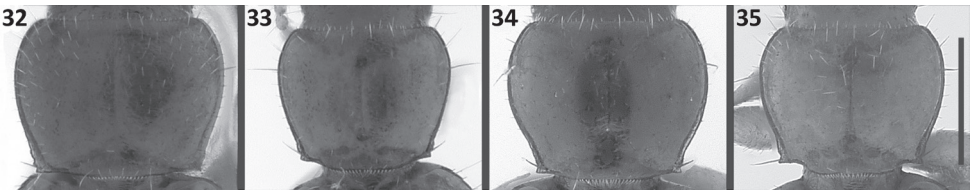
Type material. HOLOTYPE, male, in CAS, point-mounted, labeled: \ MEX: OAXACA, 2 mi S. Cerro Pelon, 8–9000 ft. 03 JUL 1982 M.A. Ivie colr.\ ex rotten pine \ *Geocharidius* n. sp. det. M. A. Ivie 1983 (handwriting)\. PARATYPES (34 ex., 4♂2♀ were dissected), labeled same as a holotype (deposited in CAS, MTEC).

Specific epithet. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of Michael A. Ivie, Associate Professor and Curator of Entomology at the Montana State University, the collector of the type series of the species.

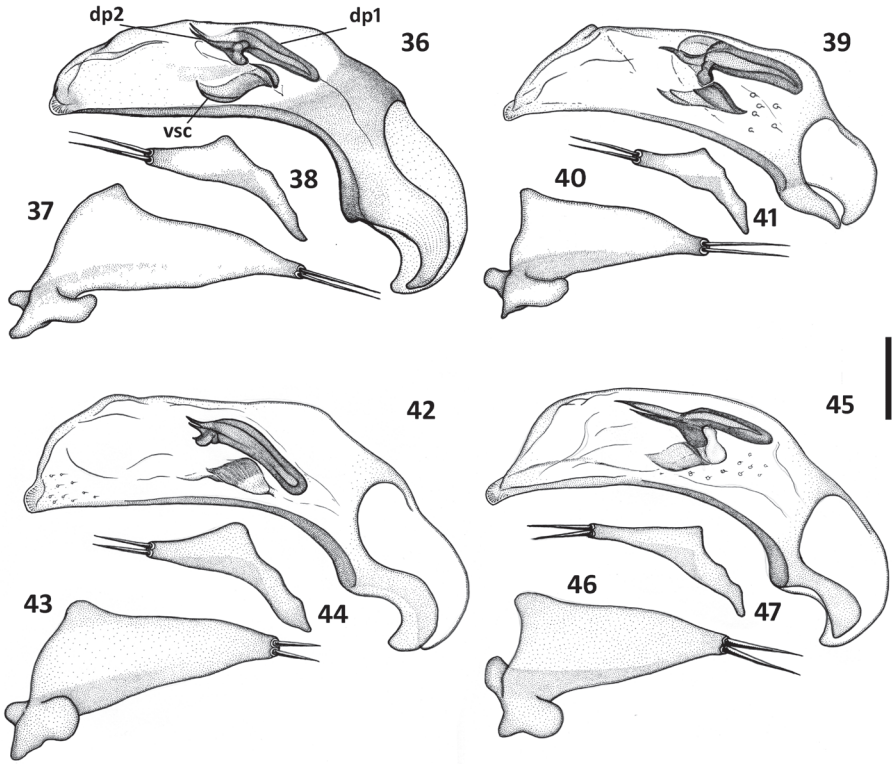
Type locality. Mexico, Oaxaca, 2 miles S Cerro Pelon.

Recognition. Adults of this new species can be distinguished from those of other species of the genus by the combination of elongate habitus and comparatively narrow pronotum; and males can be further distinguished by the shape of the copulatory sclerites of the median lobe (Fig. 45).

Description. *Size.* Large for genus (SBL range 1.34–1.55 mm, mean 1.43 ± 0.066 mm, n=21).



Figures 32–35. Pronotum images of *Zapotecanillus* species. **32** *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **33** *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan) **34** *Z. iviei* (MEXICO, Oaxaca, 2mi S Cerro Pelon) **35** *Z. pecki* (MEXICO, Oaxaca, 3.5mi S Suchixtepec). Scale bar = 0.25mm.



Figures 36–47. Illustrations of male aedeagus of *Zapotecanillus* species. *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **36** median lobe, right lateral aspect **37** left paramere, left lateral aspect **38** right paramere, right lateral aspect. *Z. nanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **39** median lobe, right lateral aspect **40** left paramere, left lateral aspect **41** right paramere, right lateral aspect. *Z. ixtlanus* (MEXICO, Oaxaca, 37mi S Valle National) **42** median lobe, right lateral aspect **43** left paramere, left lateral aspect **44** right paramere, right lateral aspect. *Z. iviei* (MEXICO, Oaxaca, 2mi S Cerro Pelon) **45** median lobe, right lateral aspect **46** left paramere, left lateral aspect **47** right paramere, right lateral aspect. dp1 – dorsal plate 1; dp2 – dorsal plate 2; vsc – ventral sclerite. Scale bar = 0.05mm.

Habitus. Body form (Fig. 27) slightly convex, moderately elongate (WE/SBL 0.39±0.09), head of normal proportions for genus (WH/WPm 0.74±0.013), pronotum narrow compared to elytra (WPm/WE 0.72±0.022).

Color. Body monocolorous, rufotestaceous, appendages testaceous.

Microsculpture. Partially effaced on disc of pronotum.

Prothorax. Pronotum (Fig. 34) relatively short (LP/LE 0.39±0.011) and slightly transverse (WPm/LP 1.22±0.025), with margins slightly sinuate and markedly constricted posteriorly (WPm/WPp 1.42±0.039). Basal margin oblique laterally. Contour of posterior angles obtuse (114–124°) without or with 1 small denticle in front of the angles.

Elytra. Slightly convex, not depressed along suture, rather narrow (WE/LE 0.66±0.019). Margins subparallel at middle, slightly divergent in basal forth, evenly rounded to apex in apical forth, maximal width of elytra at midpoint.

Legs. 1st male protarsomere markedly dilated apico-laterally (Fig. 21).

Male genitalia. Median lobe of aedeagus (Fig. 45), with small, slightly elongated apex, angulately rounded at tip. Dorsal plate 1 long, with long apical attenuation. Dorsal plate 2 joined to plate 1 at its middle ventrally, where it forms a distinct protuberance. Ventral sclerites weakly sclerotized. Right paramere rather long and narrow (Fig. 47). Left paramere without apical constriction (Fig. 46). Ring sclerite with short handle, which is widely rounded apically (Fig. 63).

Female genitalia. Spermatheca (Fig. 74) standard for genus.

Geographical distribution. The species is known only from the type locality in the Sierra Juárez Range, a part of the Sierra Madre de Oaxaca (Figs 77 and 94 black star).

Way of life. According to the label data (elevation ranges 2600–2700m), these beetles inhabit the pine-oak forest zone of the Sierra Madre de Oaxaca.

Relationships. Externally, adults of *Z. iviei* are similar to those of *Z. kavanaughi*, *Z. pecki* and *Z. montanus*, described below, but the armature of the internal sac of the median lobe suggests closer relatedness to *Z. oaxacanus*, *Z. nanus* and *Z. ixtlanus*. See also Fig. 90 for cladistic affinities.

***Zapotecanillus kavanaughi* sp. n.**

http://zoobank.org/129C5EFE-EB44-4528-A228-DF4315902D76

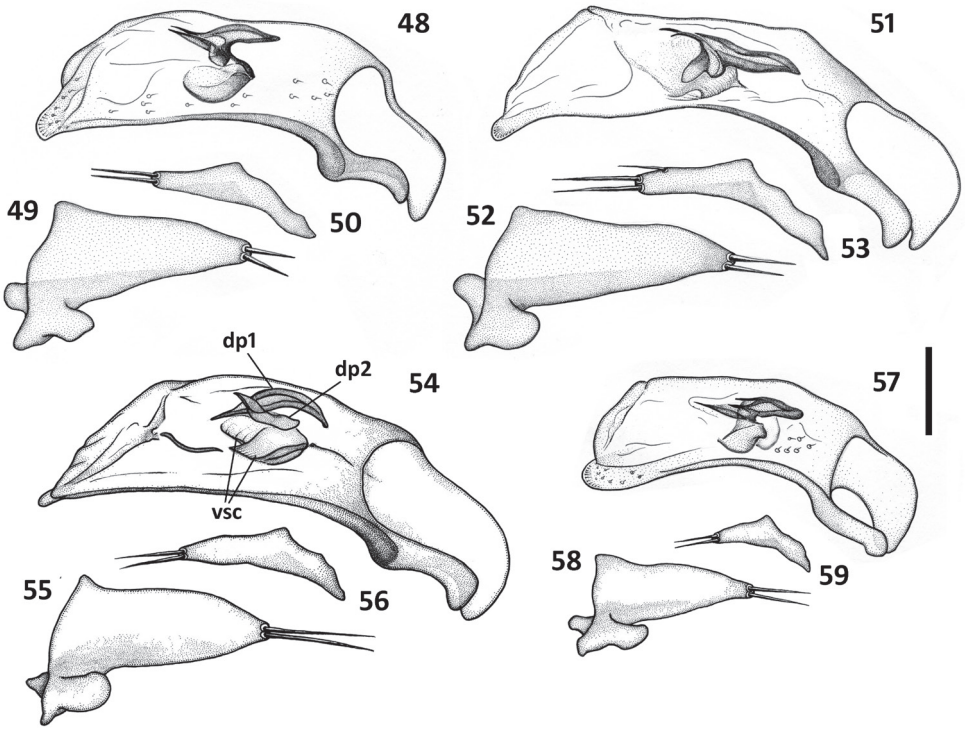
http://species-id.net/wiki/Zapotecanillus_kavanaughi

Figs 23, 28, 33, 54–56, 66, 70, 75, 77, 90, 94

Type material. HOLOTYPE, male, in CMNC, point-mounted, labeled: \MEX. Oax. 14km N SanJuan del Estado 2600m. 4-VIII.1986 H. & A. Howden\ berlese\ CMNC\. PARATYPES (8 ex., 2♂2♀ were dissected), labeled same as a holotype (deposited in CAS, CMNC).

Specific epithet. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of David H. Kavanaugh, Senior Curator of the Entomology Department of the California Academy of Sciences, whose enthusiastic efforts in locating and borrowing the material for the current investigation were so magnanimous and productive.

Type locality. Mexico, Oaxaca, 14 km N San Juan del Estado.



Figures 48–59. Illustrations of male aedeagus of *Zapotecanillus* species. *Z. montanus* (MEXICO, Oaxaca, 52mi N Oaxaca) **48** median lobe, right lateral aspect **49** left paramere, left lateral aspect **50** right paramere, right lateral aspect. *Z. pecki* (MEXICO, Oaxaca, 3.5mi S Suchixtepec) **51** median lobe, right lateral aspect **52** left paramere, left lateral aspect **53** right paramere, right lateral aspect. *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan) **54** median lobe, right lateral aspect **55** left paramere, left lateral aspect **56** right paramere, right lateral aspect. *Z. longinoi* (MEXICO, Chiapas, Sierra Morena) **57** median lobe, right lateral aspect **58** left paramere, left lateral aspect **59** right paramere, right lateral aspect. dp1 – dorsal plate 1; dp2 – dorsal plate 2; vsc – ventral sclerites. Scale bar = 0.05mm.

Recognition. Adults of this new species are distinguished from those of other species of the genus by the combination of elongate habitus and comparatively narrow pronotum; and males can be further distinguished by the shape of median lobe (Fig. 54).

Description. *Size.* Medium-sized for genus (SBL range 1.25–1.42 mm, mean 1.34±0.055 mm, n=9).

Habitus. Body form (Fig. 28) slightly convex, moderately elongate (WE/SBL 0.38±0.13), head of normal proportions for genus (WH/WPm 0.77±0.014), pronotum narrow compared to elytra (WPm/WE 0.74±0.020).

Color. Body monocolorous, rufotestaceous, appendages testaceous.

Microsculpture. Partially effaced on disc of pronotum.

Prothorax. Pronotum (Fig. 33) relatively short (LP/LE 0.40±0.009) and slightly transverse (WPm/LP 1.23±0.031), with margins rectilinear and distinctly constricted

posteriorly (WPm/WPp 1.36±0.039). Basal margin oblique laterally. Contour of posterior angles obtuse (116–122°) with 1–2 small denticles in front of the angles.

Elytra. Slightly convex, not depressed along suture, rather narrow (WE/LE 0.66±0.023). Margins almost subparallel, slightly divergent in basal half, evenly rounded to apex in apical third, maximal width of elytra posterior to midpoint.

Legs. 1st male protarsomere not dilated, without adhesive vestiture (Fig. 23).

Male genitalia. Median lobe of aedeagus (Fig. 54), with very narrow, elongate apex. Dorsal plate 1 short, pointed basally, with apical attenuation of moderate length. Dorsal sclerite 2 in a form of a separate structure, crosses plate 1 at apical third. Ventral sclerites slightly sclerotized. Right paramere rather long and moderately wide (Fig. 56). Left paramere without apical constriction (Fig. 55). Ring sclerite with long handle-like extension, widely rounded apically (Fig. 66).

Female genitalia. Gonocoxite 2 comparatively short, with moderately curved blade and rounded apex (Fig. 70). Laterotergite with 5-6 setae. Spermatheca atypical for genus (Fig. 75).

Geographical distribution. The species is known only from the type locality in the Sierra Aloapaneca Range, a part of the Sierra Madre de Oaxaca (Figs 77 and 94, black circle).

Way of life. All beetles were collected at an elevation of 2600 m.

Relationships. Externally, adults of *Z. kavanaughi* are similar to those of *Z. iviei*, *Z. pecki* and *Z. montanus*, described below, but males and females differ from those of these species in features of the median lobe and shape of the spermatheca, respectively. See also Fig. 90 for cladistic affinities.

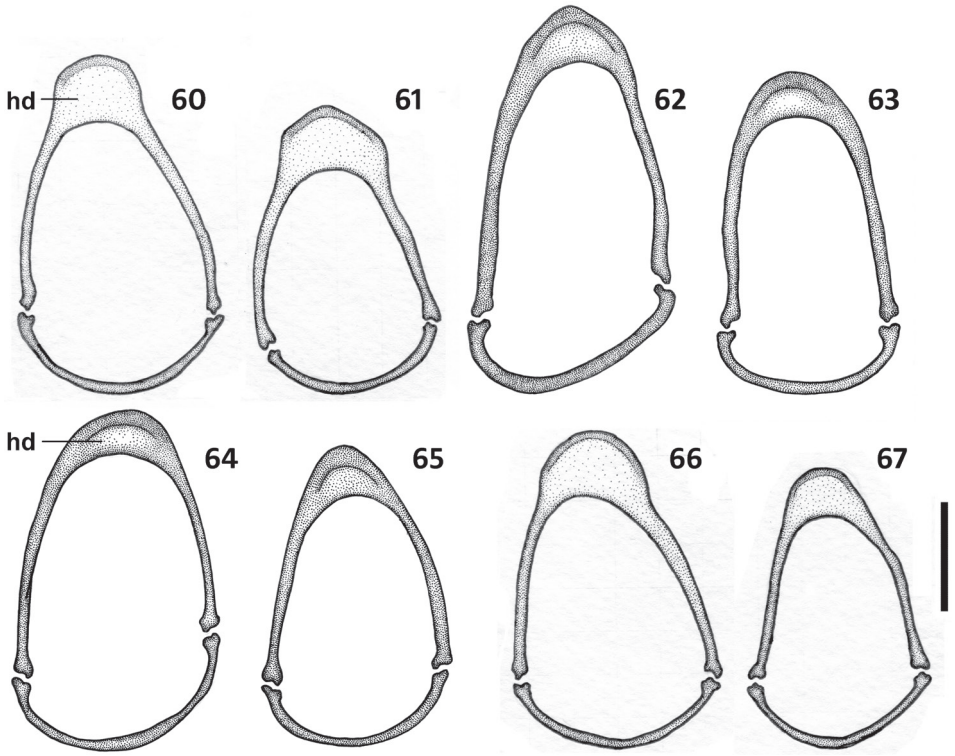
***Zapotecanillus montanus* sp. n.**
http://zoobank.org/805794A0-A363-4C93-9041-C40DDBB9675D
http://species-id.net/wiki/Zapotecanillus_montanus
Figs 29, 48–50, 65, 77, 90, 94

Type material. HOLOTYPE, male, in CMNH, point-mounted, labeled: \ MEXICO, Oaxaca, 52miles N of Oaxaca, Ber.202, sink litter, 17 May 1971 S.B.Peck collector\ CMNH \. PARATYPES (14 ex., 3♂4♀ were dissected), 6 ex. labeled same as a holotype; one female labeled: \ MEX. Oax., 52mi. N Oaxaca, 9500' 17.V.71 S.Peck Ber.202, leaf lit.\ *Anillinus* (handwriting)\; 7 ex. labeled: \MEXICO: Oaxaca, 52miles N Oaxaca, 9500 ft., 25 May 1971, ex. litter in sinkhole, S.Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\ (deposited in CAS, CMNH).

Specific epithet. The specific epithet is a Latin adjective from *mons* (= mountain), in the masculine form, meaning *mountain-dwelling*, and refers to the altitudinal data of the species locality.

Type locality. Mexico, Oaxaca, 52 miles N of Oaxaca.

Recognition. Males of this new species are distinguished from those of other species of the genus by the combination of elongate habitus and shape of the median lobe (Fig. 48).



Figures 60–67. Illustrations of ring sclerite of *Zapotecanillus* species, male genitalia, dorsal aspect. **60** *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **61** *Z. nanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **62** *Z. ixtlanus* (MEXICO, Oaxaca, 37mi S Valle National) **63** *Z. iviei* (MEXICO, Oaxaca, 2mi S Cerro Pelon) **64** *Z. pecki* (MEXICO, Oaxaca, 3.5mi S Suchixtepec) **65** *Z. montanus* (MEXICO, Oaxaca, 52mi N Oaxaca) **66** *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan) **67** *Z. longinoi* (MEXICO, Chiapas, Sierra Morena). hd – handle of ring sclerite. Scale bar = 0.1mm.

Description. *Size.* Medium-sized for genus (SBL range 1.29–1.40 mm, mean 1.35±0.037 mm, n=7).

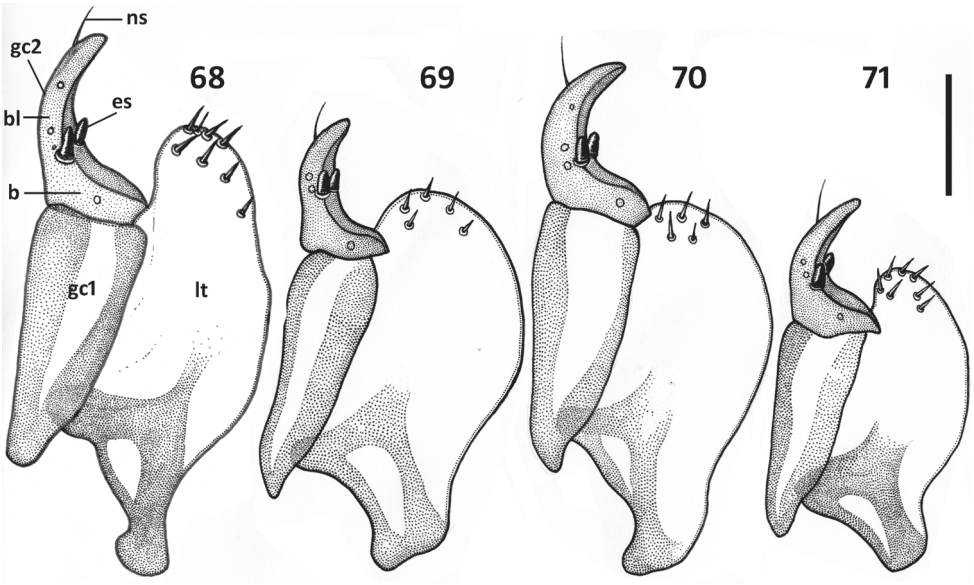
Habitus. Body form (Fig. 29) slightly convex, moderately elongate (WE/SBL 0.40±0.10), head of normal proportions for genus (WH/WPm 0.75±0.041), pronotum narrow compared to elytra (WPm/WE 0.70±0.012).

Color. Body monocolorous, rufotestaceous, appendages testaceous.

Microsculpture. Partially effaced on disc of pronotum.

Prothorax. Pronotum relatively short (LP/LE 0.38±0.009) and moderately transverse (WPm/LP 1.26±0.028), with margins rectilinear and markedly constricted posteriorly (WPm/WPp 1.40±0.028). Basal margin oblique laterally. Contour of posterior angles obtuse (115–125°) with 1–2 small denticles in front of the angles.

Elytra. Convex, not depressed along suture, of moderate width (WE/LE 0.69±0.016). Margins subparallel at middle, slightly divergent in basal third, evenly rounded to apex in apical third, maximal width of elytra at midpoint.



Figures 68–71. Illustrations of ovipositor sclerites of *Zapotecanillus* species. **68** *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **69** *Z. nanus* (MEXICO, Oaxaca, 15.1mi N Valle National) **70** *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan) **71** *Z. longinoi* (MEXICO, Chiapas, Sierra Morena). b – base of gonocoxite 2, bl – blade of gonocoxite 2, es – ensiform seta; gc1 – gonocoxite 1; gc 2 – gonocoxite 2; lt – laterotergite; ns – nematiform seta. Scale bar = 0.05mm.

Legs. 1st male protarsomere markedly dilated apico-laterally.

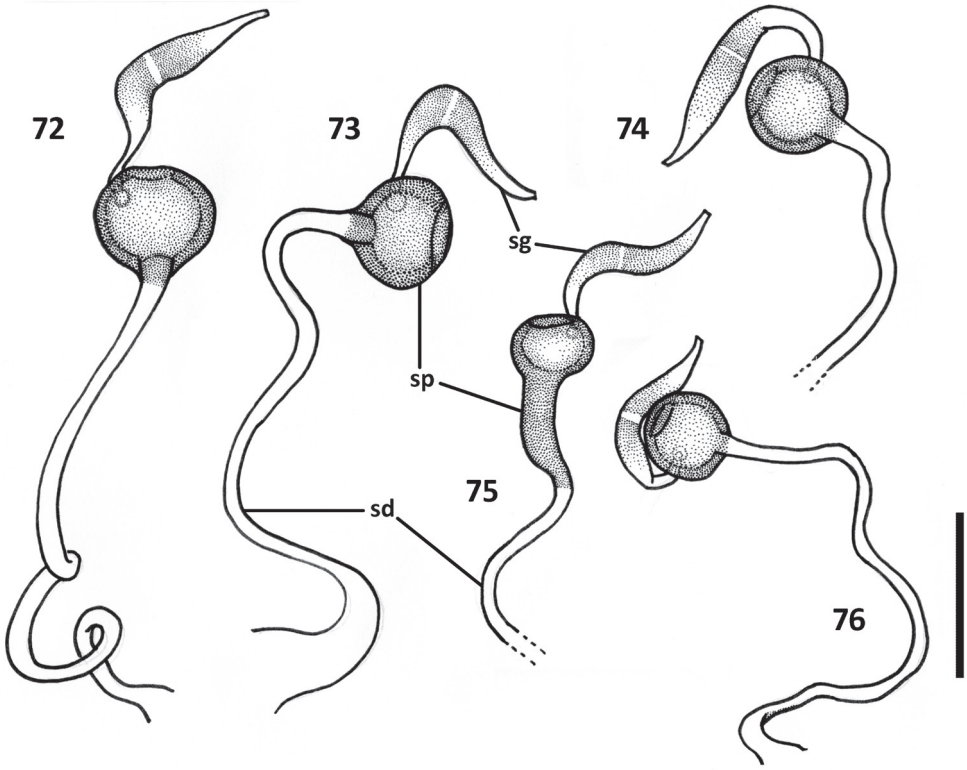
Male genitalia. Median lobe of aedeagus (Fig. 48) with slightly elongate apex, angulately rounded at tip. Dorsal plate 1 short, pointed apically and basally. Dorsal plate 2 joined to plate 1 at its middle ventrally, where it forms a distinct protuberance. Ventral sclerites with pronounced sclerotization ventrally. Right paramere short and moderately wide (Fig. 50). Left paramere without apical constriction (Fig. 49). Ring sclerite with handle conically rounded apically (Fig. 65).

Female genitalia. Spermatheca standard for genus.

Geographical distribution. The species is known only from the type locality in the Sierra Juárez Range, a part of the Sierra Madre de Oaxaca (Figs 77 and 94, white quadrangle).

Way of life. Specimens of this species were collected at 2900–3000m, which is the highest locality known among the *Zapotecanillus* species. The collection site was located in a limestone area with sinkholes and karst topography, covered with a pine-oak forest. Soil temperature at the time of collection was 48°F (S.Peck, pers. comm.).

Relationships. Externally, adults of *Z. montanus* are similar to those of *Z. kavanaughi, Z. iviei* and *Z. pecki*, but males of *Z. montanus* may be distinguished from those of the other species by the shape of the median lobe (Fig. 48). See also Fig. 90 for cladistic affinities.



Figures 72–76. Illustrations of spermatheca, spermathecal duct, and spermathecal gland of *Zapotecanillus* species. **72** *Z. oaxacanus* (MEXICO, Oaxaca, 18.7mi N Valle National) **73** *Z. nanus* (MEXICO, Oaxaca, 15.1mi N Valle National) **74** *Z. iviei* (MEXICO, Oaxaca, 2mi S Cerro Pelon) **75** *Z. kavanaughi* (MEXICO, Oaxaca, 14km N San Juan) **76** *Z. longinoi* (MEXICO, Chiapas, Sierra Morena). sd – spermathecal duct; sg – spermathecal gland; sp – spermatheca. Scale bar = 0.05mm.

Zapotecanillus pecki sp. n.

http://zoobank.org/AFF220F9-B257-44DF-8A08-F07F9E6988F3
http://species-id.net/wiki/Zapotecanillus_pecki
Figs 30, 35, 51–53, 64, 77, 90, 94

Type material. HOLOTYPE, male, in CMNH, point-mounted, labeled: \ MEXICO, Oaxaca, 3.5miles S of Suchixtepec,\ Ber.208, leaf litter, 3 June 1971 S.B. Peck collector\ CMNH\. PARATYPES (16 ex., 4♂2♀ were dissected), 6 ex. labeled same as a holotype; 6 ex. labeled: \ MEXICO, Oaxaca, 13 mi. N of Suchixtepec, 9500ft., ex. leaf litter, 4 June 1971, S. Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\; 4 ex. labeled: MEXICO, Oaxaca, 13.5 mi. S of Suchixtepec, 8000ft., ex. leaf litter, 3 June 1971, S. Peck\ THOMAS C. BARR COLLECTION 2011 Acc. No. 38014\ (deposited in CAS, CMNH).

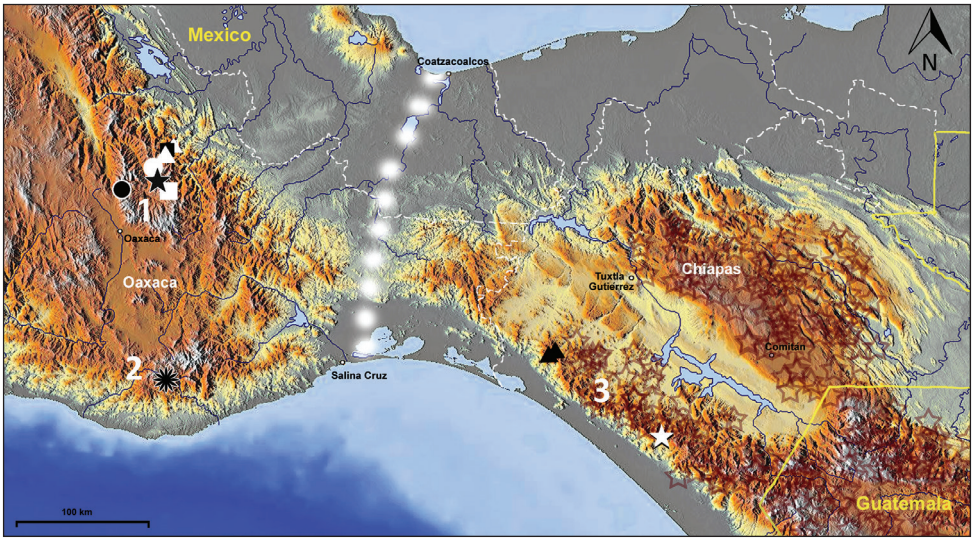


Figure 77. Map of southern Mexico and adjacent part of Guatemala, showing positions of locality records for the species of *Zapotecanillus*. *Z. oaxacanus* – black quadrangle; *Z. nanus* – white triangles; *Z. ixtlanus* – white circle; *Z. iviei* – black star; *Z. kavanaughi* – black circle; *Z. montanus*- white quadrangle; *Z. pecki* – black flower; *Z. longinoi* – black triangles; *Z.* sp. – white star. Brown stars – range of *Geocharidius* species (original data). 1 – Sierra Madre de Oaxaca; 2 – Sierra Madre del Sur; 3 – Sierra Madre de Chiapas. White dots – the Isthmus of Tehuantepec.

Specific epithet. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of Stewart B. Peck, Professor in the Biology Department of Carleton University, Ottawa, Canada, the collector of the type series of this species.

Type locality. Mexico, Oaxaca, 3.5miles S of Suchixtepec.

Recognition. Males of this new species are distinguished from those of other species of the genus by the shape of the median lobe (Fig. 51).

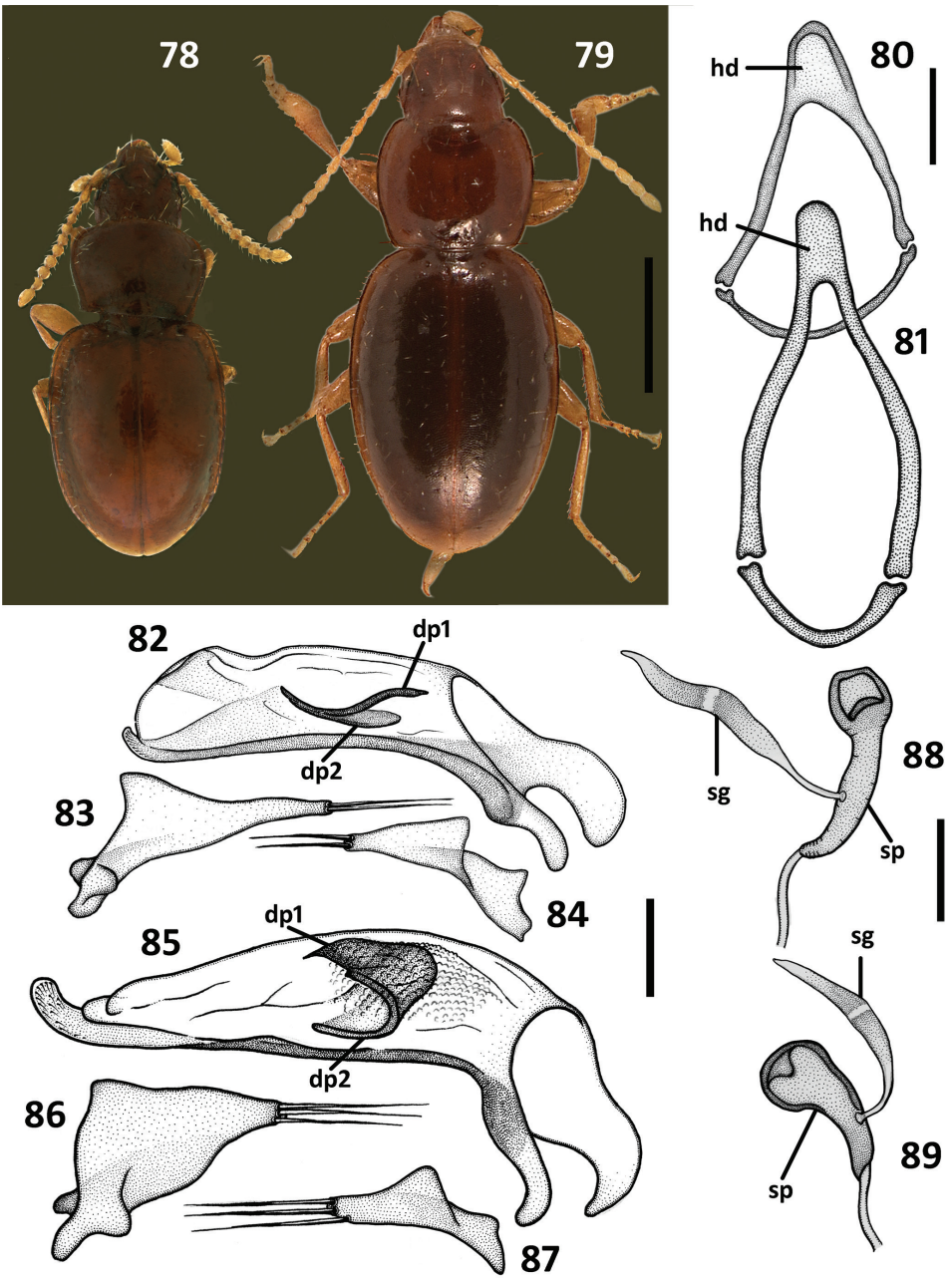
Description. *Size.* Medium-sized for genus (SBL range 1.32-1.38 mm, mean 1.35±0.026 mm, n=5).

Habitus. Body form (Fig. 30) slightly convex, moderately elongate (WE/SBL 0.41±0.08), head of normal proportions for genus (WH/WPm 0.73±0.011), pronotum narrow compared to elytra (WPm/WE 0.72±0.009).

Color. Body monocolorous, rufotestaceous, appendages testaceous.

Microsculpture. Microlines partially effaced on disc of pronotum.

Prothorax. Pronotum (Fig. 35) relatively short (LP/LE 0.41±0.012) and slightly transverse (WPm/LP 1.24±0.030), with margins slightly sinuate and distinctly constricted posteriorly (WPm/WPp 1.36±0.043). Basal margin bisinuate near posterior angles. Contour of posterior angles slightly obtuse (108–118°) with 1-2 small denticles in front of the angles.



Figures 78–89. Structural features of the litter anilline species, chosen as an outgroup for the cladistic analysis of *Zapotecanillus* species. *Geocharidius phineus* Erwin **78** habitus **80** ring sclerite, dorsal aspect **82** median lobe, right lateral aspect **83** left paramere, left lateral aspect **84** right paramere, right lateral aspect **88** spermatheca. *Nesamblyops* sp. **79** habitus **81** ring sclerite, dorsal aspect **85** median lobe, right lateral aspect **86** left paramere, left lateral aspect **87** right paramere, right lateral aspect **89** spermatheca. dp1 – dorsal plate 1; dp2 – dorsal plate 2; hd – handle of round sclerite; sg – spermathecal gland; sp – spermatheca. Scale bars = 0.5mm (Figs **78–79**), 0.1mm (Figs **80–81**), 0.05mm (Figs **82–89**).

Elytra. Slightly convex, not depressed along suture, of moderate width (WE/LE 0.70±0.022). Margins subparallel at middle, slightly divergent in basal half, evenly rounded to apex in apical half, maximal width of elytra at midpoint.

Legs. 1st male protarsomere markedly dilated apico-laterally.

Male genitalia. Median lobe of aedeagus (Fig. 51), with elongate apex, rounded at tip. Dorsal plate 1 long, pointed apically and basally. Dorsal plate 2 joined to plate 1 at its apical third, where it forms a pronounced biapical protuberance. Ventral sclerite faintly sclerotized, barely visible. Right paramere rather long and moderately wide, with additional (3rd) seta dorsally (Fig. 53). Left paramere without apical constriction (Fig. 52). Ring sclerite with short handle, widely rounded apically (Fig. 64).

Female genitalia. Spermatheca standard for genus.

Geographical distribution. The species is known only from the type locality in the Sierra Madre del Sur, in the surroundings of Suchixtepec (Figs 77 and 94, black flower).

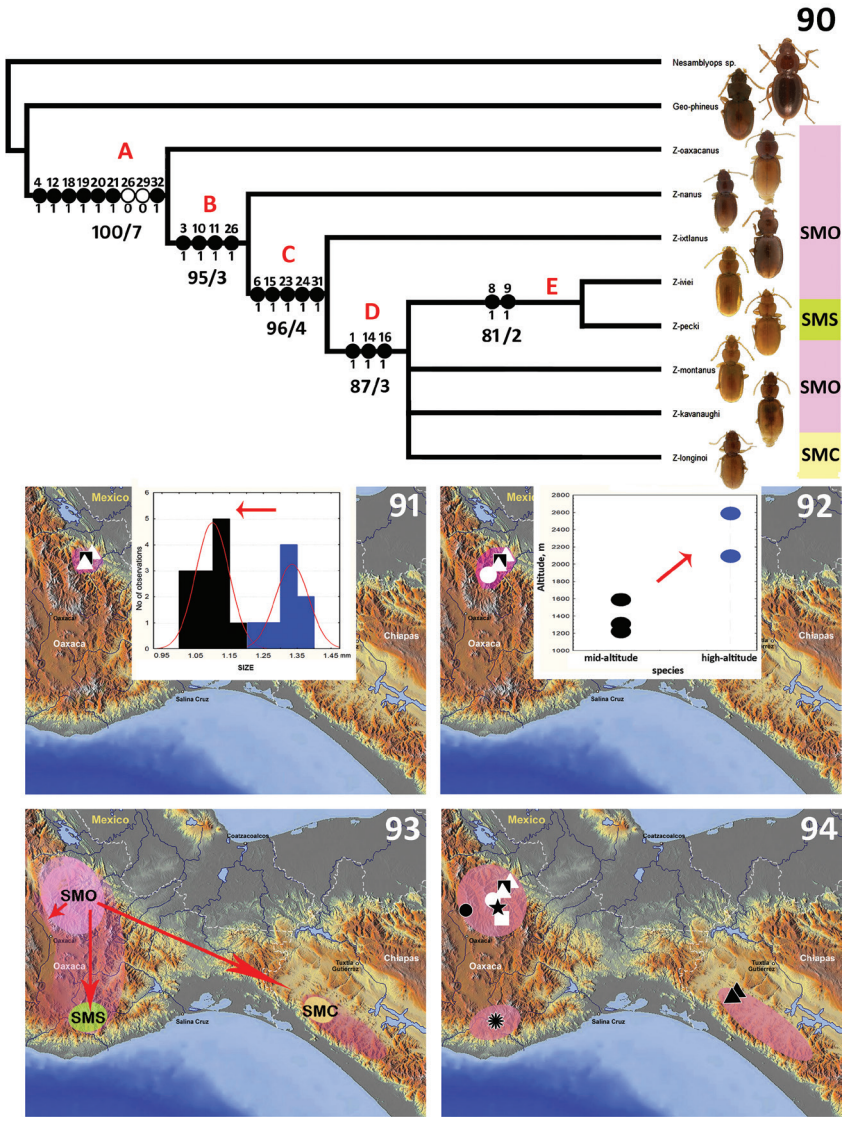
Way of life. Members of this species live at elevations of 8000-9500' (2440-2900 m). At 8000' (= 2440 m), beetles were collected in mixed pine-oak forest with *Alnus*, *Carpinus*, etc, and soil temperature at the time of collection was 56°F (S. B. Peck, pers. comm.).

Relationships. Males of this species are easily distinguished from those of other members of the genus by the structure of the median lobe (Fig. 51) and setation of the right paramere (Fig. 53); and the geographical distribution of this species sets it apart from all its congeners. See also Fig. 90 for cladistic affinities.

***Zapotecanillus longinoi* sp. n.**
http://zoobank.org/778A7293-CE0E-4EBB-B2E2-AEE3CB9857B2
http://species-id.net/wiki/Zapotecanillus_longinoi
Figs 31, 57–59, 67, 71, 76, 77, 90, 94

Type material. HOLOTYPE, male, in KUNHM, point-mounted, labeled: \ MEXICO: Chiapas: Sierra Morena 16.16001°N, 93.60519°W, 1360m, 12-V-2008, ex. sifted leaf litter, 2° mesophil forest LLAMA08 Wa-A-01-1-all \ SM0833744 KUNHM-ENT \. PARATYPES (16 ex., 2♂3♀ were dissected), 9 ex. labeled same as a holotype, except barcode SM... numbers; 1 ex. labeled: \ MEXICO: Chiapas: Sierra Morena 16.15950°N, 93.60530°W, 1360m, 12-V-2008 sifted leaf litter, 2° mesophil forest LLAMA08 Wm-A-01-1 \ SM0839196 KUNHM-ENT \; 4 ex. labeled: \ MEXICO: Chiapas: Sierra Morena 16.15342°N, 93.60078°W, 1330m, 12-V-2008 ex. sifted leaf litter, 2° mesophil forest LLAMA08 Wa-A-01-2-all \ SM… KUNHM-ENT \; 2 ex. labeled: \ MEXICO: Chiapas, Mpio: Villa Corso, Ejido Sierra Morena, R. Biosfera La Sepultura, 16°09'10.6N, 93°35'25.1W, 1550m, 17–18.VII.2003, R. Anderson, mixed oak/pine forest litter, MEX1A03 110 \ SM… KUNHM-ENT \ (deposited in CAS, KUNHM).

Specific epithet. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of John T. (Jack) Longino, Professor of the Biology Department of the University of Utah, and one of Co-PI's of the LLAMA project, which provided the material on which the description of this species is based.



Figures 90–94. Cladistic relationships and main events of the natural history of *Zapotecanillus* species, inferred from the cladogram. **90** 75%-majority rule cladogram from the parsimony analysis: character states are shown only for nodes, forward changes as filled circles, and reversals as open circles; numbers under internal branches – indicate bootstrap/Bremer support indices; the letters B, C, and D above the nodes correspond to the maps **91, 92** and **93** below, illustrating evolutionary trends at the appropriate node; bar abbreviations, SMO – Sierra Madre de Oaxaca, SMS – Sierra Madre del Sur, SMC – Sierra Madre de Chiapas **91** syntopic miniaturization, blue bars – *Z. oaxacanus*, black bars – *Z. nanus* **92** altitudinal expansion, blue dots – *Z. ixtlanus*, black dots – *Z. oaxacanus* + *Z. nanus* **93** regional dispersal, SMO – Sierra Madre de Oaxaca, SMS – Sierra Madre del Sur, SMC – Sierra Madre de Chiapas **94** modern distribution of species, *Z. oaxacanus* – black quadrangle; *Z. nanus* – white triangles; *Z. ixtlanus* – white circle; *Z. iviei* – black star; *Z. kavanaughi* – black circle; *Z. montanus*- white quadrangle; *Z. pecki* – black flower; *Z. longinoi* – black triangles.

Type locality. Mexico, Chiapas, Sierra Morena, 16.16001°N, 93.60519°W.

Recognition. Adults of this new species can be distinguished from those of other species of the genus by the combination of small size and rufotestaceous color; and males can be further distinguished by the shape of the median lobe (Fig. 57).

Description. *Size.* Small sized for genus (SBL range 1.01-1.12 mm, mean 1.08±0.038 mm, n=12).

Habitus. Body form (Fig. 31) slightly convex, slightly elongate (WE/SBL 0.40±0.10), head of normal proportions for genus (WH/WPm 0.76±0.021), pronotum moderately wide compared to elytra (WPm/WE 0.76±0.014).

Color. Body monocolorous, rufotestaceous, appendages testaceous.

Microsculpture. Partially effaced on disc of pronotum.

Prothorax. Pronotum relatively short (LP/LE 0.41±0.010) and moderately transverse (WPm/LP 1.28±0.035), with margins rectilinear and moderately constricted posteriorly (WPm/WPp 1.35±0.037). Basal margin oblique laterally. Contour of posterior angles obtuse (114–125°) with 0-1 small denticles in front of the angles.

Elytra. Slightly convex, not depressed along suture, of moderate width (WE/LE 0.69±0.015). Margins nearly subparallel, slightly divergent in basal forth, evenly rounded to apex in apical third, maximal width of elytra near midpoint.

Legs. 1st male protarsomere markedly dilated apico-laterally.

Male genitalia. Median lobe of aedeagus (Fig. 57), with enlarged apex and neighboring part of ventral margin. Dorsal plate 1 small, pointed apically and narrowly rounded basally. Dorsal plate 2 located close to plate 1, in form of narrow stylet and shifted slightly apically. Ventral sclerites faintly sclerotized. Right paramere short and moderately wide (Fig. 59). Left paramere as in Fig. 58. Ring sclerite with short handle widely rounded apically (Fig. 67).

Female genitalia. Gonocoxite 2 comparatively short, with moderately curved blade and narrowly rounded apex (Fig. 71). Laterotergite with 7-8 setae. Spermatheca standard for genus (Fig. 76).

Geographical distribution. The species is known only from the type locality in the Sierra Madre de Chiapas (Figs 77 and 94, black triangles).

Way of life. According to the label data, these beetles inhabit mesophyll and mixed oak/pine forests at low elevations.

Relationships. In the structure of median lobe of males and geographical distribution, this species is only remotely related to its congeners. See also Fig. 90 for cladistic affinities.

***Zapotecanillus* sp.**
Fig. 77

Material. MEXICO: Chiapas: 4km SE Custepec 15.71018°N 92.92887°W, 2140m, 20-V-2008 ex. sifted leaf litter, cloud forest LLAMA08 Wa-A-03-1-all \ SM0832667 KUNHM-ENT \ (1♂); MEXICO: Chiapas: 4km SE Custepec 15.70673°N

92.93127°W, 2125m, 20-V-2008 ex: sifted leaf litter, cloud forest LLAMA08 Wa-A-03-2-all \ SM0821667 KUNHM-ENT \ (1♀), both in CAS.

Among the materials at hands, these two teneral specimens remain unidentified because of insufficient material for investigation. They were collected in the cloud forest near Custepec in the Sierra Madre de Chiapas (Fig. 77, white star). Both specimens resemble *Z. longinoi* adults externally but are larger in size, and cannot be identified unambiguously. This locality represents the most southern point of the known range of *Zapotecanillus*.

Adults of the eight described species of this new genus are distinguished using the following key:

Key for identification of the Mexican species of Zapotecanillus

1 Small (1.00–1.20 mm in length). Sierra Madre de Chiapas and Sierra Madre de Oaxaca within Sierra de Juárez **2**

– Large (greater than 1.25 mm in length). Sierra Madre de Oaxaca and Sierra Madre del Sur 3

2 Darker, brunneorufous (Fig. 25). Apex of median lobe unmodified (Fig. 39). Dorsal plate 1 larger (Fig. 39). Sierra Madre de Oaxaca ..... ***Z. nanus,*** p. **63**

– Lighter, rufotestaceous (Fig. 31). Apex of median lobe enlarged (Fig. 57). Dorsal plate 1 smaller (Fig. 57). Sierra Madre de Chiapas ..... ***Z. longinoi,*** p. **77**

3 Less robust and more elongate, body monocolorous, either brunneorufous (Fig. 26) or rufotestaceous (Figs 27–30). Pronotum narrower (WPm/LP < 1.30). Pronotal basal margin oblique (Figs 33–34) or sinuous laterally (Fig. 35)..... **4**

– More convex and robust, body with brunneorufous pronotum and rufotestaceous elytra (Fig. 24). Pronotum wider, distinctly transverse (WPm/LP 1.33±0.022). Pronotal basal margin straight (Fig. 32). Sierra de Juárez..... ..... ***Z. oaxacanus,*** p. **61**

4 Rufotestaceous beetles. Apex of median lobe elongate and narrow (Figs 45; 48, 51, 54). Dorsal plate 1 with long apical attenuation (Fig. 45), OR pointed basally (Figs 48, 51, 54). Sierra Madre del Sur and Sierra Madre de Oaxaca within Sierra de Juárez and Sierra Aloapaneca 5

– Brunneorufous beetles. Apex of median lobe short and broadly rounded (Fig. 42). Dorsal plate 1 long, rounded basally and with short apical attenuation (Fig. 42). Sierra de Juárez..... ***Z. ixtlanus,*** p. **65**

5 Pronotal basal margin bisinuate laterally (Fig. 35). Dorsal plate 2 enlarged basally in form of biapical protuberance (Fig. 51). Sierra Madre del Sur .... ***Z. pecki,*** p. **74**

– Pronotal basal margin oblique laterally (Figs 33–34). Dorsal plate 2 of another shape. Sierra Madre de Oaxaca **6**

6 Median lobe with elongate apex of normal size (Figs 45; 48). Spermatheca ball-shaped (Fig. 74). Sierra de Juárez **7**

– Median lobe with small and narrow apex (Fig. 54). Spermatheca fusiform with apical bulb enlargement (Fig. 75). Sierra Aloapaneca..... ..... ***Z. kavanaughi,*** p. **69**

7 Pronotal baso-lateral margin with weak sinuation before posterior angles (Fig. 34). Dorsal plate 1 greater, rounded basally and with long apical attenuation (Fig. 45). Cerro Pelon, Sierra de Juárez..... ***Z. iviei,*** p. **67**

– Pronotal baso-lateral margin rectilinear constricted towards posterior angles (as on Fig. 33). Dorsal plate 1 small, pointed basally and with rather short apical attenuation (Fig. 48). Sierra de Juárez to the South from Cerro Pelon ..... ***Z. montanus,*** p. **71**

Results of cladistic analysis

The parsimony analysis resulted in two most parsimonious trees (L=53; CI=0.74; RI=0.76); the 75% majority-rule consensus cladogram of these trees is presented in Fig. 90, with the characters and support values mapped on the corresponding internal branches. The main basal nodes of the cladogram are highly supported by Bootstrap and Bremer indices, whereas a part of the terminal nodes is inadequately supported, which results in collapsed branches. The *Zapotecanillus* species form a well-supported monophyletic group (clade A, bootstrap value=100). Their monophyly is supported by the derived states for characters 4 (labial mental suture), 12 (additional apicolateral pronotal setae), 18 (positions of 7, 8, and 9 pores of umbilicate series), 19 (elytral subapical sinuation), 20 (shape of the intercoxal process of the abdomen), 21(shape of the metendoventrite) and 32 (shape of the spermatheca). Within the genus, a basal clade is presented by *Z. oaxacanus*, which is morphologically the closest species to the outgroup taxa (the latter selected from the litter species of anilline genera *Geocharidius* and *Nesamblyops*, Figs 78 and 79, respectively). Clade B is characterized by few traits, highlighting changes in the species' appearance– notably the proportional reduction in the size of pronotum (character 3) and the shifting of the pronotal hind angles in a forward direction (characters 10 and 11); also the apex of median lobe is getting smaller (character 26). Clade C includes species with derived shared characters, which intensify the habitual dissimilarity with outgroup taxa. The pronotum in members of these species is proportionally shorter (character 6) and the elytra are narrower (character 15); also, internal parts of the male genitalia, namely the ring sclerite (characters 23 and 24), and parameres (character 31), are reduced. Clade D includes the species that are most unlike the basal taxa externally. Members of species in this clade have slightly convex bodies (character 1) and are completely yellow in color (characters 14 and 16). Members of Clade E species share a narrow pronotum with a shallow sinuation of the lateral margins anterior to the hind angles (characters 8 and 9). Thus, the cladogram of species' relationships primarily reflects the gradual changes in external characteristics from basal to terminal clades, incorporating some changes in genitalic

structures. The trend in changes in external form on the cladogram (from ovoid and pigmented towards elongate and depigmented beetles) reflects evolutionary adaptations for a more endogean way of life.

Taxonomic and evolutionary issues

New data enable us to discuss several taxonomical and evolutionary issues, despite the limited material available for *Zapotecanillus*.

Taxonomical notes

Remarks on Geocharidius larva. Ten years ago, a description of the first-instar larva of *Geocharidius* was published (Grebennikov 2002), and since then, it has remained the only larva of Anillina known from the New World. Material from the locality where the larva was collected also contained adults of Anillina and was labeled: "MEX: Oaxaca, 17.6mi S Ixtlán de Juárez…" (l.c.). The larva was identified as *Geocharidius* larva by association with adults, first by Vasily Grebennikov (Ottawa Plant Laboratory, Canadian Food Inspection Agency), and later by Terry Erwin (Smithsonian Institute), who approved the identification (l.c.). Based on data available now, *Geocharidius* species do not occur in the state of Oaxaca, whereas *Zapotecanillus* species do occur there. Thus, it is likely that the larva described in 2002 is of a *Zapotecanillus* species, rather than a *Geocharidius* species. Erwin did not distinguish the two genera, so his labeling the representatives of *Zapotecanillus* as *Geocharidius* sp. is understandable.

Notes about Zapotecanillus. As previously mentioned, it is difficult to assess relationships of the new genus to the other North and Central American Anillina without a modern revision of the latter. Therefore, the conclusions drawn below should be treated as preliminary and speculative.

Externally, the absence of discal setae is a feature that members of this new genus share with those of the southern stock of genera, like *Geocharidius*, *Mexanillus* and *Honduranillus* Zaballos (Zaballos 1997). The enigmatic *Honduranillus*, described from one female, is the only genus of Anillina in North and Central America whose members lack elytral discal pores but have distinct paraglossae, traits shared with *Zapotecanillus* members. However, the differences in arrangement of the last umbilicate pores and the length of the apical palpomere of the maxillae suggest that these similarities may be convergent. Historically, great importance has been given to the arrangement of setae in the apical portion of the umbilicate series. The above-mentioned southern stock of anilline genera belongs to the "scotodipnienne" evolutionary lineage, members of which have pores 7 and 8, and 8 and 9 separated from each other by equal distances ("Type B" of Jeannel's classification), whereas *Zapotecanillus* is formally a representative of another evolutionary lineage of Anillina, the "anillienne" lineage, in which pores 8 and 9 are distinctly closer to each other than pore 7 is to pore 8 (the

so-called" geminate" arrangement, "Type A" of Jeannel (1963a)). Recently, Giachino and Vailati (Giachino and Vailati 2011), treating the anilline fauna of Greece, discovered that representatives of the "anillienne" genus *Prioniomus* Jeannel demonstrate great variation in the positions of pores 8 and 9. This discovery led the authors to propose a scheme of positional rearrangements of the setae of umbilicate series, leading from the "scotodipnienne" to the "anillienne" arrangement of pores. Similar rearrangements in the position of the 7th through 9th pores of the umbilicate series may well have occurred with the evolution of *Zapotecanillus* species. If so, *Zapotecanillus* may be the sister-taxon of *Geocharidius*; and the diversification of each genus may then be associated with one of two mountainous regions– namely, Oaxaca and Nuclear Middle America– which are separated by the Isthmus of Tehuantepec (Fig. 77), an important biogeographical barrier in the region under question (Ball 1968; Halffter 1987; Marshall and Liebherr 2000). In this case, the common ancestor of both genera would have been characterized as an anilline beetle with the "scotodipnienne" type of umbilicate series, as well as it would also lack discal pores on the elytra, and would have long last maxillary palpomeres, distinct paraglossae, free labial complex (i.e., mentum and submentum not fused), and simple metendoventrite. Subsequent evolution led to independent modifications of these traits and resulted in the origin of these two genera, members of which are morphologically very dissimilar. Presumably, we can tie the divergence of the two genera to the middle Pliocene, c. 3.1–3.5 Ma, when the Isthmus was replaced by a marine embayment (Barrier et al. 1998). Molecular analyses of many taxa among reptiles (Castoe et al. 2009; Daza et al. 2010), birds (Barber and Klicka 2010), and rodents (Hardy et al. 2013; Ornelas et al. 2013) provide evidence that this time is a historic milestone for Mesoamerican faunal diversification.

To confirm or reject the proposed phylogenetic relationship of *Zapotecanillus* within the North and Central American Anillina, the regional fauna requires further investigation, including analyses of additional morphological and, hopefully, molecular data.

Evolutionary notes

Although cladistic analysis does not allow us to fully resolve phylogenetic relationships, some evolutional trends of *Zapotecanillus*, evident from the resulting cladogram, are worth examining.

Deviations from the form of the pronotum of litter species, such as the reduction in the overall size of the pronotum and forward shift of the hind angles (Fig. 90, clade B), reflect an increase in flexibility of the pronotal-elytral joint. A more flexible joint can potentially expand the number of accessible niches, enabling their bearers to live in a greater number of structurally different litter or soil interspace habitats. It seems that, among the litter-dwelling ancestors of *Zapotecanillus*, adaptations for living in a new environment were restricted by two major directions of species evolution.

The first direction, a syntopic habitat expansion, can be characterized as the intensification of local litter resource exploitation, presumably by means of niche differentiation.

The structural complexity of the litter, undergoing decomposition, produces a graded series of overlapping planes interspersed with intertwined gaps, both of which tend to become smaller as one travels downwards toward the soil (Kaspari and Weiser 2007). In this case, new pronotal features enabling the species to move deeper, downwards through the intertwining environment, resulted in the differentiation of a miniature species *Z. nanus* (Fig. 91), which co-occurred with its relatively larger and morphologically closest relative, *Z. oaxacanus*. Syntopic miniaturization, producing a certain number of related species differing in size can be considered a common evolutionary trend within the anilline world. Pairs of syntopic small/large species pairs are known among the Central American *Geocharidius* (*G. phineus-G. romeoi* Erwin) (Erwin 1982), the North American *Anillodes* (*A. walkeri* Jeannel-*A. minutus* Jeannel) (Jeannel 1963a, 1963b), *Anillinus* (*A. lescheni* Sokolov and Carlton-*A. stephani* Sokolov and Carlton) (Sokolov et al. 2004), and the European *Typhlocharis* Dieck (Pérez-Gonzáles and Zaballos 2013a). In some cases, even more than two species of anillines may be syntopic, as it was shown for the Pyrenean *Typhlocharis* Dieck, among which three species, well-differentiated in size, co-occur (Pérez-Gonzáles and Zaballos 2013b). The evolution of *Z. longinoi*, another miniature species of *Zapotecanillus*, also matches the proposed scheme of evolution, except that, in this case, the role of the large species is played by a representative of another genus, *Geocharidius*.

The second direction of evolution among *Zapotecanillus* species was connected with the altitudinal expansion of the genus and subsequent adaptations to the endogean way of life. In Clade C (Fig. 90), pronotal and elytral morphology have undergone additional modifications. Most of the species of this clade live at elevations above 2400m, as exemplified by *Z. ixtlanus* (Fig. 92). The ability to live at high elevation implies adaptations to withstand daily and seasonal variations in temperature and humidity. One solution to this challenge is the acquisition of adaptations that facilitate vertical migrations, from the litter down into the soil and back to the litter again to track favorable and escape from unacceptable microclimatic shifts (e.g., regular frosts at high elevations of the Sierra de Juárez). Also, changes in forest communities along the elevation gradient can play an additional role in the evolution of species adaptations. In the Sierra Madre de Oaxaca, the humid montane cloud forests at elevations of 1200–1600m are characterized by the dominance of broadleaf tree species, such as *Quercus*, *Liquidambar*, *Carpinus*, and *Fagus* (Flores and Manzanero 1999), while in the temperate high-elevation forests at altitudes of 2200m to 2800m, the dominant tree species are various species of *Pinus* (Peterson et al. 2004, Saynes et al. 2012), presumably with corresponding changes in the forest litter composition and structure. Such features of high-altitude anillines as elongate habitus together with small pronotum with an oblique basal margin, may represent adaptations to differences in the important climatic and vegetation parameters along the altitudinal gradient such as those mentioned above. Changes in the states of characters in Clade D (Fig. 90), including depigmentation and flattening of the body, may reflect and support the transition from the litter to the endogean way of life among the high-altitude *Zapotecanillus*. The same situation was recorded for the high-altitude Appalachian *Anillinus moseleyae*-group of species, Sokolov 2011). All terminals of clade D on the cladogram (Fig. 90)

are represented by species (Figs 27–31) whose morphology suggests an endogean way of life (at least temporarily); and in one case (*Z. montanus*) we have a straight reference to habitat ("sink litter"), which can be treated as support for the proposed speculations.

Distributional notes

A review of the overall distribution of genus *Zapotecanillus* shows that species with endogean lifestyles are distributed across the whole range of the genus (Fig. 90, SMS, SMO, SMC), while litter-dwelling species are restricted to only the eastern slopes of the Sierra Madre de Oaxaca (Fig. 90, SMO). *A priori*, one might expect that litter-dwelling forms would be more broadly distributed than endogean forms, but within *Zapotecanillus*, this does not appear to be so. Perhaps additional litter-dwelling species of the genus remain undiscovered or have gone extinct in this region, but the extensive overall distribution of endogean species clearly suggests a role for them in the expansion and the shape of the modern geographical range of the genus. For instance, in the Sierra Madre de Chiapas, adults of *Z. longinoi* and *Z. sp*., both of the endogean morphological type, were collected at altitudes of 1330m to 2140m, which are approximately the same elevations at which low-altitude *Z. oaxacanus* and *Z. nanus* were collected in the Sierra de Juárez (Sierra Madre de Oaxaca). If a litter-dwelling ancestral *Zapotecanillus* species had dispersed from the Sierra Madre de Oaxaca to the Sierra Madre de Chiapas, one would expect members of the Chiapan descendant species to be similar in life-style and appearance to those of the Oaxacan ancestral form because low elevations are primarily occupied by litter species. However, adults of *Z. longinoi* and *Z. sp*., are flattened and depigmented, and quite different from the convex and pigmented litter-dwelling *Zapotecanillus* forms, as well as from litter-dwelling *Geocharidius* species. It is perhaps significant that *Z. longinoi* and *Z. sp.* members are syntopic with litter-dwelling species of *Geocharidius* in the Sierra Madre de Chiapas. It may be that the presence of two species of *Zapotecanillus* with endogean morphology at low elevations in the Sierra Madre de Chiapas represents a secondary occupation of the region by endogean forms, thus, supporting the idea that at least some endogean *Zapotecanillus* forms are capable of significant dispersal.

If we consider that the endogean way of life of the *Zapotecanillus* species was triggered by changes in microclimate parameters, then regional dispersal of the depigmented and only slightly convex *Zapotecanillus* species also could have been connected with certain climate changes. Such dispersal likely occurred during one or more of the Pleistocene glacial cycles, which enabled species with endogean life-styles to cross the Isthmus of Tehuantepec, and, perhaps, the Central Valleys of Oaxaca, and to establish populations in the Sierra Madre de Chiapas and the Sierra Madre del Sur, respectively (Fig. 93). Evidence that the Isthmus served as a corridor connecting Oaxaca and Chiapas Sierras during Pleistocene glaciations has been shown for some bird species (García-Moreno et al. 2004; Barber and Klicka 2010) as well as cloud forest communities (Ornelas et al. 2013). Regional dispersal of the ancestral *Zapotecanillus* stock even-

tually resulted in allopatric, presumably Quaternary, speciation in the genus, thereby shaping the modern distribution of the genus (Fig. 94).

The described sequence of events and exact mountain regions where the evolution and differentiation of *Zapotecanillus* took place are still debatable, given the paucity of data about the distribution and diversity of the genus and, thus, should be the subject of further investigations. For instance, the fauna of anillines is still unknown for such biogeographically important mountain ranges in Oaxaca as the Sierra de Zempoaltepec and the Sierra de Mijes. It is also still unknown how far to the north and west across the Oaxacan highlands *Zapotecanillus* species are distributed. These and many other questions await further investigation and discoveries.

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Appendix

Table 1. Morphological characters and states used for cladistic analysis.

External characters	
1.	Body shape. 0, moderately convex (Figs 24–26, 78–79); 1, slightly convex (Figs 27–31).
2.	Standardized body length. 0, larger, > 1.20mm; 1, smaller, <1.20mm.
3.	Relative head width, ratio WH/WPm. 0, head narrower, with ratio <0.70; 1, head wider, with ratio > 0.71.
4.	Labial mental suture. 0, present (Fig. 8); 1, absent (Fig. 7).
5.	Paraglossae of ligula. 0, present (Fig. 7); 1, absent (Fig. 8).
6.	Relative pronotal length, ratio LP/LE. 0, pronotum longer, ratio > 0.42; 1, pronotum shorter, ratio < 0.42.
7.	Relative pronotal width, ratio WPm/WE. 0, pronotum wider, ratio > 0.80; 1, pronotum narrower, ratio < 0.78.
8.	Pronotal width, ratio WPm/LP. 0, more transverse, ratio > 1.25; 1, less transverse, ratio < 1.25.
9.	Pronotal basolateral sinuation. 0, absent (Figs 32–33); 1, shallow (Figs 34–35).
10.	Pronotal basal margin. 0, straight (Fig. 32); 1, laterally oblique (Figs 33–34); 2, laterally sinuous (Fig. 35).
11.	Pronotal hind angles. 0, nearly rectangular, <110^0 (Figs 32, 35); 1, slightly obtuse, >115^0 (Figs 33–34).
12.	Additional apicolateral pronotal setae. 0, absent (Fig. 2); 1, present (Fig. 1).
13.	Pronotal discal microsculpture. 0, with distinct mesh microsculpture; 1, with obsolete microsculpture, at most represented by fine parallel lines without mesh formation.
14.	Pronotal coloration. 0, brown; 1, yellowish.
15.	Elytral width, ratio WE/LE. 0, wider, ratio >0.71; 1, narrower, ratio <0.71.
16.	Elytral coloration. 0, brown; 1, yellowish.
17.	Discal pores on elytra. 0, present; 1, absent.
18.	Position of 7, 8, and 9 pores of umbilicate series. 0, equidistant (Fig. 4); 1, 8 and 9 pores close to each other than to 7 (Fig. 3).
19.	Elytral preapical sinuation. 0, elytra evenly tapered (Fig. 4); 1, elytra slightly sinuate subapically (Fig. 3).
20.	Intercoxal process of 2nd ventrite. 0, triangular (Fig. 14); 1, apically truncated (Fig. 13).
21.	Shape of metendosternite. 0, simple, without "arms" (Fig. 14); 1, cross-shaped, with long lateral "arms" (Fig. 13).
22.	Male protarsomere. 0, noticeably expanded, with modified setae (Figs 20–21); 1, barely expanded, with modified setae (Fig. 22); 2, not expanded, without modified setae (Fig. 23).
Male genitalic characters	
23.	Length of a handle of ring sclerite. 0, long (Figs 60–61, 66, 80–81), 1, short (Figs 62–65, 67).
24.	Shape of a handle of ring sclerite. 0, subparallel (Figs 60–61, 66, 80–81); 1, conical (Figs 62–65, 67).
25.	Median lobe shape. 0, bent dorsad from basal opening (Figs 36, 39, 42, 45, 48, 51, 85); 1, bent at basal opening (Figs 54, 57, 82).
26.	Contour of the apex of median lobe, a lateral view. 0, straight, short, of moderate width (Figs 36, 42, 57); 1, straight, slightly elongated, of moderate width (Figs 39, 45, 48, 51); 2, straight, elongated and very narrow (Fig. 54); 3, upcurved, elongated and narrow (Figs 82, 85).
27.	Modification of neighboring parts of apex of median lobe. 0, absent (Figs 36, 39, 42, 45, 48, 51, 54, 82, 85); 1, enlarged ventrally (Fig. 57).
28.	State of dorsal plate 1, a lateral view. 0, long plate with rounded basal part (Figs 36, 39, 42, 45); 1, short plate with rounded basal part (Fig. 57); 2, long plate with pointed basal part (Fig. 51); 3, short plate with pointed basal part (Figs 48, 54); 4, long and curved stylet-shaped plate (Fig. 82); 5, triangular plate (Fig. 85).
29.	State of dorsal plate 2, a lateral view. 0, adjoined to dorsal plate 1, like a small knob-like protuberance (Figs 36, 39, 42, 45, 48); 1, adjoined to dorsal plate 1, like a large biapical protuberance (Fig. 51); 2, like a separate structure either crossing or parallel to dorsal plate 1 (Figs 54, 57); 3, attached to dorsal sclerite 1 in form of a long appendix (Figs 82, 85).
30.	Right paramere, seta number. 0, 3 setae (Figs 53, 87); 1, 2 setae (Figs 38, 41, 44, 47, 50, 56, 59, 84).
31.	Left paramere, shape of apical third. 0, with attenuated apex (Figs 37, 40, 83, 86); 1, with evenly tapering sides to the tip (Figs 43, 46, 49, 52, 55, 58).
Female genitalic characters	
32.	Spermatheca, shape. 0, elongated with apical bulb enlargement (Figs 75, 88–89); 1, spherical, ball-like (Figs 72–74, 76).

Table 2. Data matrix used for cladistic analysis.

										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Nesamblyops sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	5	3	0	0	0
Geocharidius phineus	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	1	3	0	4	3	1	0	0
Zapotecanillus oaxacanus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1
Z. nanus	0	1	1	1	0	0	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1
Z. ixtlanus	0	0	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	0	0	0	0	0	1	1	1
Z. iviei	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	1
Z. montanus	1	0	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	3	0	1	1	1
Z. kavanaughi	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	2	0	0	1	2	0	3	2	1	1	0
Z. pecki	1	0	1	1	0	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	2	1	0	1	1
Z. longinoi	1	1	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	2	1	1	1

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Three new species of *Fufius* Simon, 1888 (Araneae, Cyrtaucheniidae) from Brazil with the redescription of *Fufius funebris* Vellard, 1924 and description of the female of *Fufius lucasae* Guadanucci & Indicatti, 2004

Diego Ribeiro Migueis Ortega[1,†], Roberto Hiroaki Nagahama[1,‡], Paulo Cesar Motta[2,§], Rogério Bertani[1,|]

1 *Instituto Butantan, Laboratório Especial de Ecologia e Evolução, Av. Vital Brazil, 1500, 05503-900, São Paulo – SP, Brazil* **2** *Universidade de Brasília, Departamento de Zoologia, 70910-900, Brasília – DF, Brazil*

† *http://zoobank.org/7A903E78-1805-4A22-B214-2A7CA59A0061*
‡ *http://zoobank.org/A953444F-CDB2-443D-A20E-CB2BD309B9EB*
§ *http://zoobank.org/AC64BE27-5C7A-46BF-B54C-67AEE0D5A763*
| *http://zoobank.org/06059613-6DBE-400C-A68C-BDF43F6D642C*

Corresponding author: *Rogério Bertani* (rogerio.bertani@butantan.gov.br; rogerio.bertani@uol.com.br)

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Abstract

The mygalomorph neotropical genus *Fufius* Simon, 1888 comprises ten species, distributed from Guatemala in Central America to southeastern Brazil, in South America. Most of the species were described from northern South America, in the Amazonian region. Only *F. funebris* Vellard, 1924 and *F. lucasae* Guadanucci & Indicatti, 2004 are known from regions more to the south of the continent. Herein we describe three new Brazilian species, *Fufius minusculus* **sp. n.** and *F. jalapensis* **sp. n.** from the state of Tocantins, and *F. candango* **sp. n.** from Distrito Federal. The female of *F. lucasae* is described for first time and the male and female of *F. funebris* are redescribed based on specimens collected at the type locality.

Keywords

Brazilian Atlantic rainforest, cerrado, mygalomorph, new species, taxonomy

Introduction

The genus *Fufius* comprises ten species distributed from Guatemala (*Fufius atramentarius* Simon, 1888 – type species) southwards to South America: Colombia – *Fufius annulipes* (Mello-Leitão, 1941), Ecuador – *Fufius ecuadorensis* (Simon, 1892), Bolivia – *Fufius lanicius* (Simon, 1892), Trinidad – *Fufius antillensis* (F.O.P-Cambridge, 1898), and Brazil – *F. albovittatus* (Simon, 1891), *F. auricomus* (Simon, 1891), *F. funebris* Vellard, 1924, *F. lucasae* Guadanucci & Indicatti, 2004, and *F. striatipes* (Drolshagen & Bäckstam, 2009). Except for *F. funebris* and *F. lucasae*, all other Brazilian species were described from specimens collected in the Amazon. *Fufius funebris* was described by Vellard (1924) from Catalão, state of Goiás, Brazil. These types are supposed to be lost (Guadanucci and Indicatti 2004), which led these authors to redescribe the species with a female collected at the type locality and a male from the Distrito Federal (ca. 260 km northwards). In the same paper, Guadanucci and Indicatti (2004) describe *F. lucasae*, based only in males, from the state of São Paulo.

Fufius has a very controversial taxonomic position. This originally monotypic genus was formerly included by Simon (1888, 1891) in his Ctenizinae and, subsequently, transferred to his Diplurinae (Simon 1892a, b). Other species, e. g., *F. ecuadorensis*, was described in the genus *Phrissaecia* Simon, 1892 (Aporoptycheae, Ctenizinae), and posteriorly this genus was synonymized with *Fufius* by the same author (Simon 1903). In his revision and cladistics of mygalomorph genera, Raven (1985) considered *Fufius* unequivocally to belong in the Cyrtaucheniidae, where it is presently included. However, posterior morphological cladistic analyses performed by Goloboff (1993; 1995) suggest that the Cyrtaucheniidae is paraphyletic. More recent analysis carried out using morphological and molecular data (Bond et al. 2012) suggests a polyphyly of Cyrtaucheniidae. The same analysis show that *Fufius* is undoubtedly more related to the Nemesiidae. Besides the difficulty in stablishing the taxonomic position of *Fufius*, most species in the genus were described either with a single female or male specimen, limiting the information on the intra and interespecific morphological variability of the genus.

Herein we collaborate to a better knowledge of this little known genus, describing three new *Fufius* species from non-amazonian Brazil, two from the state of Tocantins, and one from the Distrito Federal. The female of *F. lucasae* is described for first time and the male and female of *F. funebris* are redescribed based on specimens collected at the type locality. The male of *F. funebris* redescribed by Guadanucci and Indicatti (2004) was misidentified by those authors, and corresponds to the new species herein described from Distrito Federal.

Methods

All measurements are in millimeters. Total length does not include chelicerae or spinnerets. Leg and palp measurements were taken from the dorsal aspect of the left side (unless appendages were lost or obviously regenerated) with a Mitutoyo digital caliper,

which had an error of 0.005 mm, rounded up to two significant decimals. A Leica LAS Montage and LAS 3D module mounted on a Leica M205C dissecting microscope were used for image capture and measurements of other spider structures. Spermathecae were cleared by means of immersion in clove oil. Abbreviations: ALE = anterior lateral eyes, AME = anterior median eyes, ap = apical, d = dorsal, ITC = inferior tarsal claw, p = prolateral, PLE = posterior lateral eyes, PLS = posterior lateral spinnerets, PME = posterior median eyes, PMS = posterior median spinnerets, r = retrolateral, SB = spermatheca bulb, spnf = spiniform, STC = superior tarsal claws, SS = spermatheca stalk, and v = ventral. Terminology for spermatheca follows Coyle (1995), for spination follows Petrunkevitch (1925).

Specimens are deposited in the following institutions: DZUB, Departamento de Zoologia, Universidade de Brasília, Brasília (Paulo C. Motta); IBSP, Instituto Butantan, São Paulo (Yara Cury); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (Ana L. Tourinho); MNHN, Muséum national d'Histoire naturelle, Paris (Christine Rollard); MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo (Ricardo Pinto-da-Rocha).

Geographical coordinates: primary sources are between round brackets and secondary sources (Google Earth©) are between square brackets. The coordinates from the secondary source were obtained from the center of the municipality cited in the specimens labels and are in DMS (Degrees, Minutes and Seconds) format rounded off to minutes.

Additional type material examined: *Fufius albovittatus* (Simon, 1891), holotype male, MNHN 9666, from Brazil, Manaus, Haunwell leg.; *Fufius atramentarius* Simon, 1888, holotype female, MNHN 4945, from Guatemala, Perrot leg.; *Fufius ecuadorensis* (Simon, 1892), holotype female, Ecuador, Loja; *Fufius striatipes* (Drolshagen & Bäckstam, 2009) holotype male, Brazil, state of Amazonas, Manaus, Tarumã Mirim, 03°06'00"S, 60°01'48"W, J. Adis leg., February 1982 (INPA 3507), examined by photographs.

Taxonomy

Cyrtaucheniidae Simon, 1889

Fufius Simon, 1888

Fufius Simon, 1888:213 (type species by monotypy *Fufius atramentarius* Simon, 1888).
Hapalothele (in part: *H. albovittata* Simon, 1891:306; *H. auricomus* Simon, 1891:305; *H. lanicia* Simon, 1892:283).
Brachythele (in part: *B. antillensis* F.O.P.-Cambridge, 1898:899).
Phrissaecia Simon, 1892:274 (type species by monotypy *Phrissaecia ecuadoriensis* Simon, 1892). First synonymized by Simon 1903:967.
Hermorhachias Mello-Leitão, 1941:234 (type species by original designation *Hermorhachias annulipes* Mello-Leitão, 1941). First synonymized by Raven 1985:134.

Metriura Drolshagen & Bäckstam, 2009:365 (type species by monotypy *Metriura striatipes* Drolshagen & Bäckstam, 2009). First synonymized by Bertani et al. 2012.

Fufius funebris Vellard, 1924

http://species-id.net/wiki/Fufius_funebris
Figs 1–11, 45

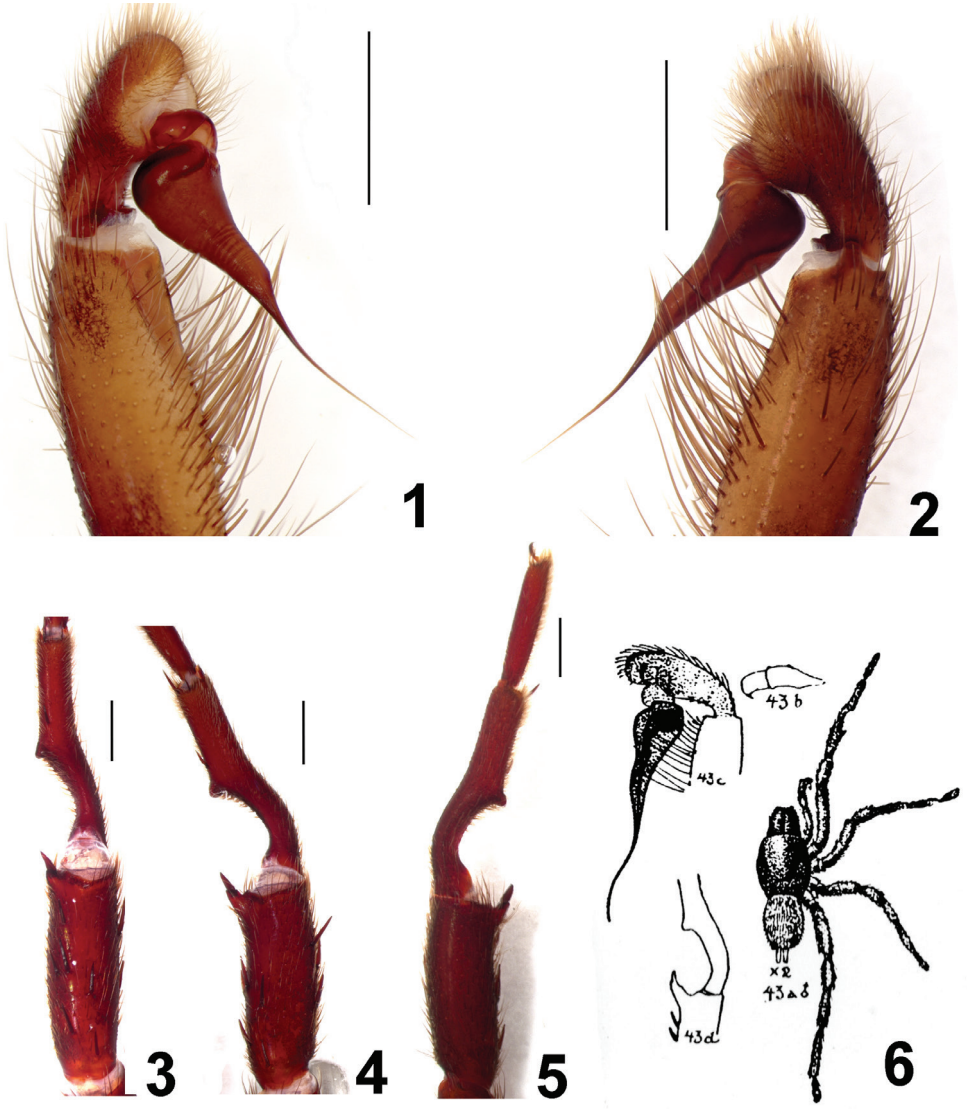
Fufius funebris Vellard, 1924:153; Guadanucci and Indicatti 2004:256, fig. 7 (redescribed male and female, male misidentified).

Diagnosis. The male differs from those of all other species in the genus by the characteristic very long embolus having a subtle constriction on its middle (Figs 1–2). The female differs from those of all other species by the spermathecae having spiraled stalks (Fig. 9).

Types. Syntypes, 3 males and 8 females, should be deposited in Instituto Vital Brazil, Niterói; 1 female, 1 male in the personal collection of Jean Vellard. Types lost (Guadanucci and Indicatti 2004).

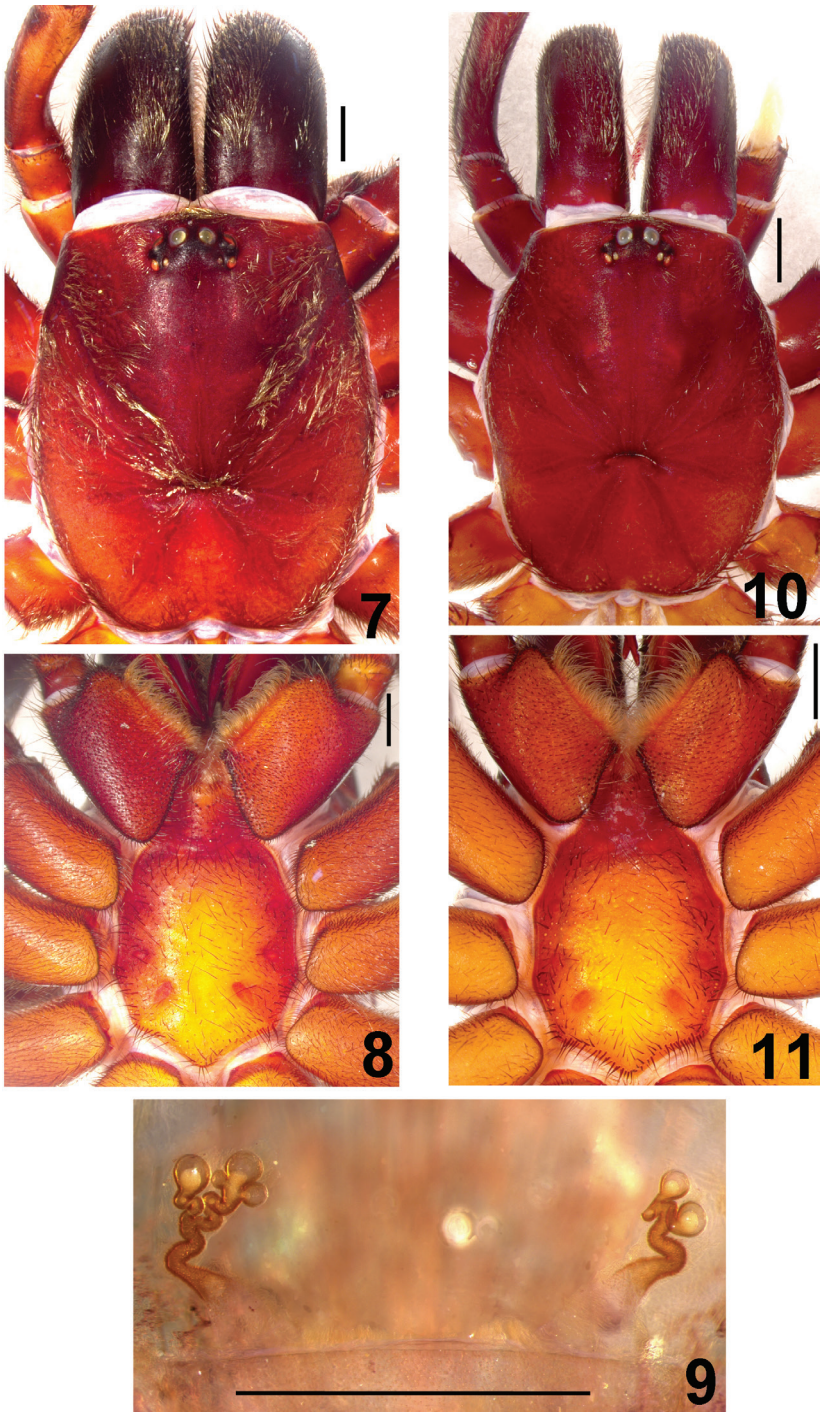
Additional material examined. BRAZIL: *Goiás*: Catalão [18°09'S, 47°56'W], 2 males, 1 female, 20 October 2001, P.C. Motta, with pitfall trap (DZUB 2531); 1 female, 22 October 2001, P.C. Motta, on termite mound (DZUB 435); *Minas Gerais*: Uberlândia [18°54'S, 48°15'W], Fazenda do Glória, 1 female, P. C. Motta (IBSP 11102); 3 females, 1 immature, 14 November 1990, P.C. Motta (DZUB 4470); Fazenda São José, 1 female, 15 July 1992, P.C. Motta (DZUB 318).

Male redescription (DZUB 2531–1). Total length: 9.70. Carapace 5.89 long, 4.63 wide, chelicerae 2.87 long, 1.48 wide. Palp: femur 2.92, patella 1.65, tibia 2.25, tarsus 0.95, total 7.77. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 4.18, 2.65, 3.10, 3.55, 2.28, 15.76. II: 4.07, 2.31, 2.70, 2.97, 2.08, 14.13. III: 3.31, 2.01, 2.17, 2.96, 1.77, 12.22. IV: 3.87, 2.27, 3.25, 4.09, 1.79, 15.27. Mid-widths (lateral): femora I–IV = 1.01, 0.92, 1.10, 1.13, palp = 0.90; patellae I–IV = 1.11, 0.94, 1.02, 1.07, palp = 0.83; tibiae I–IV = 1.31, 0.86, 0.68, 0.84, palp = 0.83; metatarsi I–IV = 0.78, 0.54, 0.63, 0.52; tarsi = 0.52, 0.38, 0.45, 0.48, palp = 0.75. Abdomen 5.90 long, 4.10 wide. Spinnerets: PMS, 0.8 long, 0.31 wide, 0.46 apart; PLS, 1.25 basal, 0.96 middle, 0.96 distal; mid-widths (lateral), 0.61, 0.57, 0.4 respectively. Carapace (Fig. 10): length to width 1.27. Fovea strongly recurved, 0.93 wide. Eyes: tubercle 0.38 high, length 0.71, width 1.17. Clypeus 0.14. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.30, ALE 0.30, PME 0.15, PLE 0.22, AME–AME 0.21, AME–ALE 0.09, PME–PME 0.61, PME–PLE 0.02, ALE–PLE 0.10, AME–PME 0.14, ALE–ALE 0.77, PLE–PLE 0.82. Eye group width 1.16, length 0.59. Maxillae (Fig. 11) 2.04 long, 1.34 wide. Cuspules: 61 spread over ventral inner heel. Labium: 0.95 long, 1.02 wide, with 4 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 3.16 long, 2.56 wide. Three pairs of sigillae, first, second rounded, posterior ovals, all one diameter from margin. Cheli-



Figures 1–6. *Fufius funebris*. Male (DZUB 2531-1) **1–2** right palpal bulb **1** retrolateral view **2** prolateral view **3–5** right leg I tibial spur **3** ventral view **4** prolateral view **5** retrolateral view **6** reproduction of Vellard's 1924 *F. funebris* plate. Scale bar = 1mm.

cerae: basal segment with 9 teeth. Legs: leg formula: I IV II III. Scopula: tarsi I–IV scopulate. Metatarsi I–II 1/3 scopulate. Spines: palp: femur p0-0-1ap, patella p1-0-1; leg I: femur d1-1-2(spnf), patella v1, p2, tibia v2-2-1, p1-5-0, metatarsus v0-1-1ap; leg II: femur d1-2-1(spnf), patella v1, p2, tibia v4-3-2(2ap), metatarsus v5-3-2ap, p0-1-0; leg III: femur d1-2-1(spnf), patella p3, r1, tibia d1-0-0, v2-4-2ap, p0-0-1, r0-0-1, metatarsus d3-2-2, v3-2-2ap, p0-2-0, r0-0-1ap; leg IV: femur d2-1-1(spnf), tibia



Figures 7–11. *Fufius funebris* **7–9** female (DZUB 2531-2) **7** carapace **8** sternum, labium and maxillae **9** spermathecae, dorsal view **10–11** male (DZUB 2531-1) **10** carapace **11** sternum, labium, and maxillae. Scale bar = 1mm.

v2-2-2ap, r1-0-1, metatarsus d0-1-2ap, v2-3-3(2ap), r0-0-1ap, p1-1-1ap. Preening-comb: absent on retrolateral tip of metatarsus IV. ITC smooth, STC with two rows of 5–8 teeth on both margins on all legs. Palp: embolus 1.76 in length. Embolus (Figs 1–2) basal, middle and distal width of 0.34, 0.03, 0.01, respectively. Tegulum 0.49 long. Tibial spur (Figs 3–5) formed by single branch 0.63 long, 0.42 wide, on retrolateral margin, with apical spine. Color pattern: carapace black with some long golden setae. Sternum brown, labium, maxillae dark brown. Abdomen dorsally black with rounded whitish spot on anterior central region, brown punctuations on remaining areas, ventrally with two large whitish areas on lateral regions. Spinnerets light brown with brown setae. Leg I black with some golden setae. Legs II–IV dark brown with brown spots, femur darker, with several golden setae, coxae brown with some brown setae.

Female redescription (DZUB 2531-2). Total length: 17.46. Carapace 7.24 long, 6.13 wide, chelicerae 3.31 long, 2.34 wide. Palp: femur 3.54, patella 1.94, tibia 2.00, tarsus 2.32, total 9.80. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 4.65, 3.34, 3.31, 3.56, 2.36, 17.22. II: 4.40, 3.14, 2.95, 3.21, 2.17, 15.87. III: 4.06, 2.66, 1.86, 2.95, 2.06, 13.59. IV: 5.35, 2.93, 3.66, 4.12, 2.14, 18.20. Mid-widths (lateral): femora I–IV = 1.28, 1.15, 1.43, 1.33, palp = 0.80; patellae I–IV = 1.40, 1.29, 1.31, 1.31, palp = 1.14; tibiae I–IV = 1.28, 0.98, 1.13, 1.05, palp = 1.16; metatarsi I–IV = 0.72, 0.72, 0.52, 0.66; tarsi = 0.49, 0.49, 0.47, 0.57, palp = 0.84. Abdomen (damaged) ca. 9.84 long, 6.74 wide. Spinnerets: PMS, 1.03 long, 0.48 wide; PLS, 1.82 basal, 1.07 middle, 1.71 distal; mid-widths (lateral), 0.96, 0.87, 0.72 respectively. Carapace (Fig. 7): length to width 1.18. Fovea recurved, 1.77 wide. Eyes: tubercle 0.44 high, length 1.16, width 1.59. Clypeus 0.03. Anterior and posterior eye row recurved. Eyes sizes and interdistances: AME 0.42, ALE 0.34, PME 0.17, PLE 0.26, AME–AME 0.18, AME–ALE 0.14, PME–PME 0.85, PME–PLE 0.06, ALE–PLE 0.21, AME–PME 0.25, ALE–ALE 1.02, PLE–PLE 1.22. Eye group width 1.58, length 0.74. Maxillae (Fig. 8) 2.71 long 2.77 wide. Cuspules: ca. 57 spread over ventral inner heel. Labium: 1.28 long, 1.46 wide, with 3 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 4.29 long, 3.35 wide. Three pairs of sigillae, first rounded, second, third ovals, all one diameter from margin. Chelicerae: basal segment with 9 teeth. Legs: leg formula: IV I II III. Scopula: tarsi I–II scopulate. Metatarsi I 2/3, II 1/2 scopulate. Spines: palp: femur, patella 0, tibia v2-2(spnf)-2ap, p1-0-1ap(spnf), tarsus v2-0-0; leg I: femur, patella 0, tibia v0-0-2ap(spnf), metatarsus v0-1-2ap; leg II: femur, patella 0, tibia v0-1-2ap(spnf), metatarsus v2-2-2ap, p0-0-1ap; leg III: femur 0, patella p4, r1, tibia v2-2-2(spnf), p0-0-1ap, metatarsus d1-1-1ap, p0-2-1, v2-2-2ap; leg IV: femur, patella 0, tibia v3-2-1ap(spnf), r0-0-1(spnf), metatarsus d0-0-1ap, r0-1-1ap, v2-1-2(1ap), r0-1-1. Preening-comb: absent on retrolateral tip of metatarsus IV. Palp with a single claw having 6 small teeth on internal margin. ITC smooth, STC with two rows of 5–8 teeth on both margins on all legs. Spermathecae: two spermathecae having a narrow, spiraled stalk, giving origin to two spiraled branches with 1–3 bulbs. Color pattern: as in male, except legs black with two (femur, patella, tibia) or one (metatarsus, tarsus) brown stripes (lacking setae) on dorsal area. Abdomen ventrally without two large whitish areas on lateral regions.

Remarks. Vellard (1924) described *Fufius funebris* based on 3 males and 8 females from Catalão, Goiás, Brazil. The types should be deposited in the collection of Instituto Vital Brazil, Niterói, but were not found and considered lost (Guadanucci and Indicatti 2004). These authors redescribed this species based on a female from the type locality and a male from Brasilia, Distrito Federal, ca. 260 km northwards. However, additional specimens we obtained from type locality, both male and female, and show that the female was correctly identified by Guadanucci and Indicatti (2004), but not the male. Vellard (1924) published a figure showing in detail the *Fufius funebris* embolus morphology (Fig. 6), which is very long and has a median constriction. An embolus tapering to its tip can be easily distinguished from the Guadanucci and Indicatti (2004) drawings, as shown in their figs 1–3. Conversely,the bulbs of the specimen we obtained from type locality (Figs 1–2) fits very well with the figure of Vellard (1924) (Fig. 6) and can be assigned without doubts to *F. funebris*. The male of the species Guadanucci and Indicatti (2004) attributed to *F. funebris* belongs to a new species, described below as *Fufius candango* sp. n.

Distribution. Brazil: states of Goiás (Catalão) and Minas Gerais (Uberlândia) (Fig. 45).

Fufius lucasae Guadanucci & Indicatti, 2004

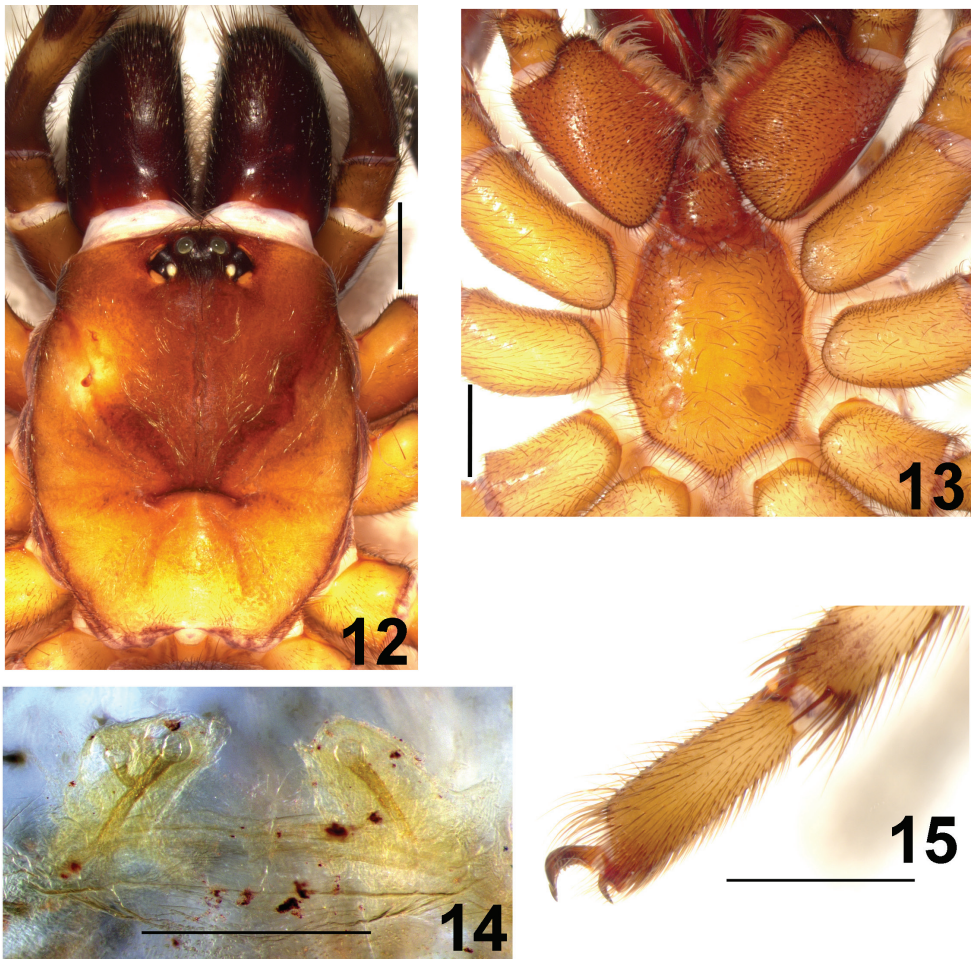
http://species-id.net/wiki/Fufius_lucasae
Figs 12–15, 44, 45

Fufius lucasae Guadanucci & Indicatti, 2004:257, figs 8–13.
Fufius lucasi: Platnick 2013. (N.B. matronym for Sylvia Lucas).

Diagnosis. The male differs from those of *F. funebris* by the shorter and tapering embolus (see figs 8–10 in Guadanucci and Indicatti 2004), from *F. jalapensis* sp. n. by having spines on tibia I, from *F. minusculus* sp. n. by having a carapace less than 1.5 times longer than the width, from *F. albovittatus* by metatarsus I being very curved at the basis and having only 2 spines on tibia I, from *F. candango* sp. n. by the preening comb on metatarsus IV formed by macrosetae instead of small spines, and from *F. striatipes* by having only 2 spines on tibia I instead of 11. The female differs by the spermatheca stalk being straight and narrow, and giving origin to 1–2 lobes (Fig. 14).

Types. Holotype male from Brazil, *São Paulo*, São Paulo, Parque Estadual da Serra da Cantareira, Núcleo da Pedra Grande [23°26'S, 46°38'W], December 2000, C. C. Aires et al., with pitfall trap (MZSP 23231), examined; paratypes: 2 males, same collector and date (MZSP 23226, IBSP 10993), examined; male from Brazil, *São Paulo*, São Paulo, Parque Estadual do Jaraguá [23°27'S, 46°46'W], 17 January 2004, R. P. Indicatti (IBSP 10952), not examined; 2 males from Brazil, *São Paulo*, Cotia, Caucaia do Alto, Reserva Florestal do Morro Grande [23°39'S, 46°57'W], December 2002, J. M. B. Ghelleri (MZSP 22017), examined.

Additional material examined. BRAZIL: *São Paulo*: São Paulo, Parque Estadual da Serra da Cantareira, Núcleo da Pedra Grande [23°26'S, 46°38'W], 1 male, December 2000, C. C. Aires et al., with pitfall trap (MZSP 23225); 1 male, same collector and



Figures 12–15. *Fufius lucasae*, female (DZUB 8021) **12** carapace **13** sternum, labium and maxillae **14** spermathecae, dorsal view **15** left metatarsus IV, retrolateral, showing preening-comb. Scale bar = 1mm.

date (MZSP 23227); 1 male, same collector and date (MZSP 23229); 1 male, same collector and date (MZSP 23230); 2 males, same collector and date (MZSP 23232); 1 male, same collector and date (MZSP 23233); 1 male, same collector and date (MZSP 23234); 1 male, same collector and date (MZSP 23235); 1 male, same collector and date (MZSP 23236); 1 male, same collector and date (MZSP 23237); Itapecerica da Serra [23°46'S, 46°50'W], 1 male, 16 May 2004, D.R.M. Ortega (DZUB 8018); 1 female, 1 immature, 2004, same collector, on a web on the trunk of a "Quaresmeira" tree (*Tibouchina* sp., Melastomatacea) (DZUB 8019); 1 female, 2005, same collector and date (DZUB 8020); 1 female, June 2006, same collector (DZUB 8021).

Female description (DZUB 8021): Total length: 15.61. Carapace 6.49 long, 5.26 wide, chelicerae 3.40 long, 2.11 wide. Palp: femur 3.45, patella 1.84, tibia 2.00, tarsus 2.25, total 9.54. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 4.61, 2.70, 3.49,

3.69, 2.23, 16.72. II: 3.96, 2.66, 2.95, 2.83, 2.17, 14.57. III: 3.02, 2.33, 1.93, 2.48, 1.90, 11.66. IV: 4.25, 2.51, 3.69, 3.20, 1.91, 15.56. Mid-widths (lateral): femora I–IV = 1.04, 1.06, 1.29, 1.29, palp = 0.93; patellae I–IV = 1.05, 1.07, 1.16, 1.10, palp = 1.06; tibiae I–IV = 0.96, 1.04, 0.98, 1.02, palp = 0.97; metatarsi I–IV = 0.69, 0.62, 0.68, 0.63; tarsi = 0.62, 0.51, 0.47, 0.53, palp = 0.89. Abdomen 9.24 long, 5.87 wide. Spinnerets: PMS, 0.96 long, 0.48 wide, 0.63 apart; PLS, 1.43 basal, 0.94 middle, 1.08 distal; mid-widths (lateral), 0.86, 0.73, 0.48 respectively. Carapace (Fig. 12): length to width 1.23. Fovea recurved, 1.57 wide. Eyes: tubercle 0.58 high, length 0.88, width 1.75. Clypeus 0.05. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.27, ALE 0.34, PME 0.18, PLE 0.30, AME–AME 0.28, AME–ALE 0.251, PME–PME 0.78, PME–PLE 0.10, ALE–PLE 0.14, AME–PME 0.20, ALE–ALE 1.22, PLE–PLE 1.12. Eye group width 1.7, length 0.72. Maxillae (Fig. 13) 1.71 long, 2.42 wide. Cuspules: ca. 62 spread over ventral inner heel. Labium: 1.15 long, 1.21 wide, with 18 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 3.56 long, 2.67 wide. Three pairs of sigillae, first rounded, second, third ovals, all one diameter from margin. Chelicerae: basal segment with 8 teeth. Legs: leg formula: I IV II III. Scopula: tarsi I–II scopulate. Metatarsi I 2/3, II 1/3 scopulate. Spines: palp: femur, patella 0, tibia v2-4-3ap(spnf), tarsus v2-0-0; leg I: femur 0, patella p1, tibia v1-1-2ap(spnf), metatarsus v2-1-2ap; leg II: femur, patella 0, tibia v1-1-1ap(spnf), metatarsus v1-2-2ap, r0-0-1ap; leg III: femur 0, patella p2, tibia p1-1-0, v2-2-1ap(spnf), metatarsus d3-2-0, p0-2-1ap, v2-2-2ap, r0-1-0; leg IV: femur, patella 0, tibia v0-1-1(spnf), metatarsus d0-1-0, v2-3-2ap, p0-0-1ap. Preening-comb (Fig. 15): formed by 4 spiniform setae between two spines on retrolateral tip of metatarsus IV. Palp with single claw having 6 small teeth on internal margin. ITC smooth, STC with two rows of 4–6 teeth on both margins on all legs. Spermathecae (Fig. 14): two spermathecae having narrow, straight stalk, giving origin to one or two straigth branches ending in 1–2 bulbs. Color pattern (Fig. 42): carapace light brown with some long golden setae, sternum and coxae light brown, labium and maxillae dark brown. Abdomen dorsally black with rounded whitish spot on anterior central region, brown punctuations on remaining areas. Spinnerets light brown with dark brown setae. Legs yellow with brown spots on basal and apical region of femur, patella, tibiae, and metatarsus, in addition, a central spot on metatarsus.

Distribution. Brazil: state of São Paulo (São Paulo, Cotia and Itapecerica da Serra) in the Brazilian Atlantic Forest (Fig. 45).

***Fufius candango* sp. n.**
http://zoobank.org/EAB79FAB-20C4-4F6F-A4A4-73AF5FE4E052
http://species-id.net/wiki/Fufius_candango
Figs 16–26, 45

Fufius funebris: Guadanucci and Indicatti 2004:256, figs 1–6 (male, misidentified).

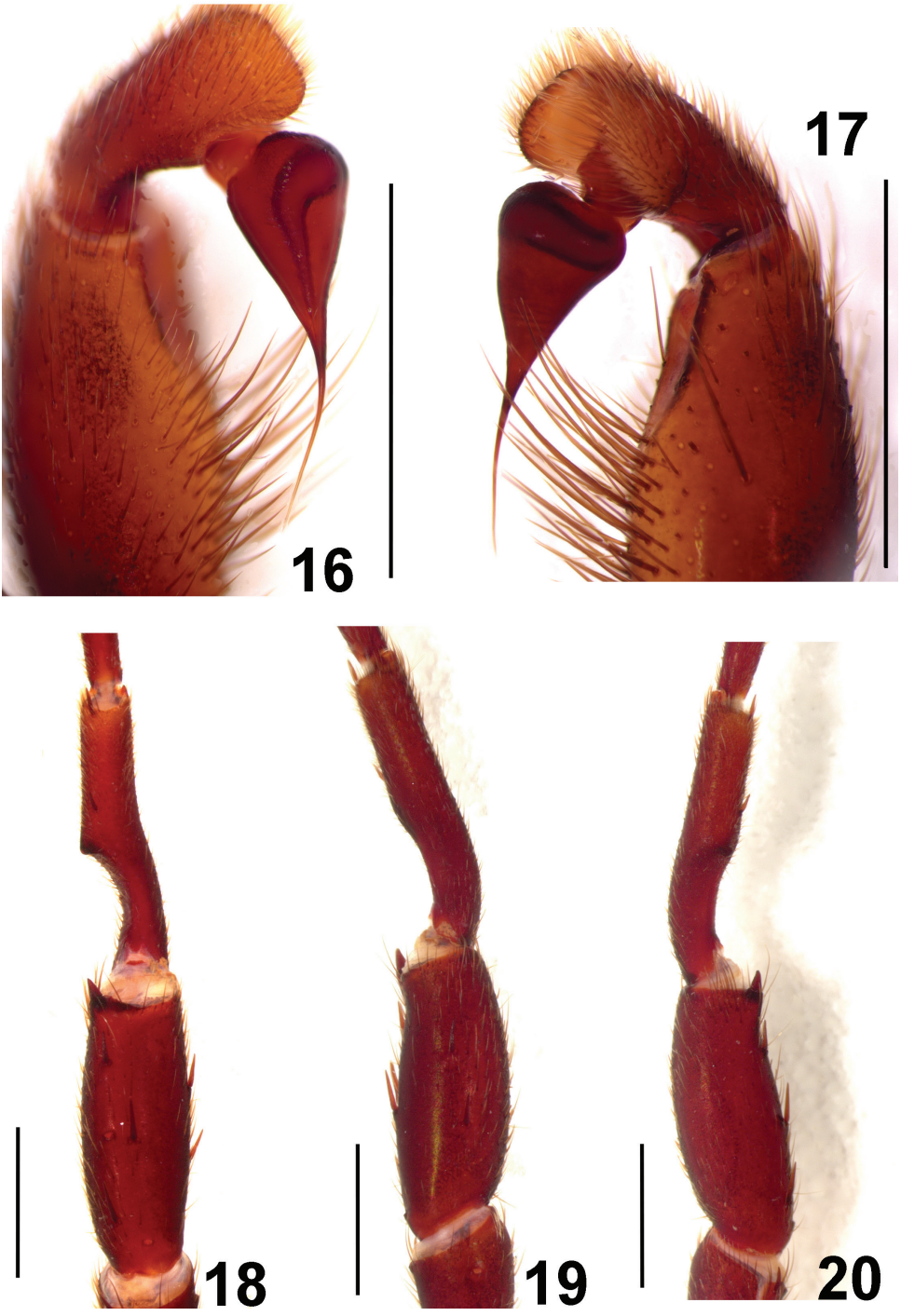
Diagnosis. Male and female differ from those of all other species by presence of preening comb on retrolateral tip of metatarsus IV formed by small spines (Fig. 24).

Etymology. The specific name, candango, refers to the workers who were largely responsible for building Brazil's capital, Brasilia, where the type specimens of the new species were collected.

Types. Holotype male from Brazil, *Distrito Federal*, Brasília, campus da Universidade de Brasília [15°45'S, 47°52'W], 26 November 1996, E. Mamede, with pitfall trap (DZUB 709). Paratypes: male from Brazil, *Distrito Federal*, Brasília, Reserva do IBGE [15°56'S, 47°53'W], 06 December 1996, E. Mamede, with pitfall trap (DZUB 714); 2 females, junction of railway DF 140 with BR 251 [15°56S, 47°49'W], inside a burrow covered with silk strands in an embankment, 7 October 2006, P.C. Motta (DZUB 4492).

Additional material examined. BRAZIL: *Distrito Federal*: Brasília, Reserva da Marinha [16°00'S, 47°57'W], 3 males, 29–31 October 1999, G.G. Montingelli, with pitfall trap (IBSP 8015).

Male description (DZUB 709). Total length: 9.74. Carapace 4.77 long, 3.85 wide, chelicerae 3.70 long, 1.16 wide. Palp: femur 2.41, patella 1.24, tibia 1.49, tarsus 1.01, total 5.88. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 3.31, 2.01, 2.21, 2.84, 2.68, 13.05. II: 2.99, 1.68, 2.02, 2.35, 1.57, 10.61. III: 2.70, 1.40, 1.83, 2.27, 1.48, 9.68. IV: 3.51, 1.80, 2.82, 3.12, 1.54, 12.79. Mid-widths (lateral): femora I–IV = 0.80, 0.85, 0.95, 0.91, palp = 0.51; patellae I–IV = 0.79, 0.84, 0.84, 0.87, palp = 0.65; tibiae I–IV = 1.04, 0.65, 0.58, 0.77, palp = 0.78; metatarsi I–IV = 0.56, 0.38, 0.26, 0.39; tarsi = 0.38, 0.37, 0.29, 0.29, palp = 0.61. Abdomen 3.96 long, 2.61 wide. Spinnerets: PMS, 0.61 long, 0.26 wide, 0.23 apart; PLS, 0.75 basal, 0.52 middle, 0.69 distal; mid-widths (lateral), 0.39, 0.34, 0.26, respectively. Carapace (Fig. 25): length to width 1.24. Fovea strongly recurved, 0.74 wide. Eyes: tubercle 0.29 high, length 0.69, width 1.07. Clypeus 0.04. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.25, ALE 0.27, PME 0.09, PLE 0.15, AME–AME 0.11, AME–ALE 0.07, PME–PME 0.50, PME–PLE 0.02, ALE–PLE 0.07, AME–PME 0.09, ALE–ALE 0.69, PLE–PLE 0.73. Eye group width 1.06, length 0.53. Maxillae (Fig. 26) 1.06 long, 1.79 wide. Cuspules: 39 spread over ventral inner heel. Labium: 0.73 long, 0.80 wide, with 3 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 2.61 long, 2.13 wide. Three pairs of sigillae, first, second rounded, posterior ovals, all one diameter from margin. Chelicerae: basal segment with 7 teeth. Legs: leg formula: I IV II III. Scopula: tarsi I–II scopulate. Metatarsus I 1/2, II 1/3 scopulate. Spines: palp: femur p0-0-1ap, patella p1, tibia 0; leg I: femur d1-1-2, p0-0-1ap, patella v2, p0-1-0, tibia v2-2-0, p0-0-1, metatarsus v0-1-1; leg II: femur d1-1-2; patella v0-0-2ap, p0-1-1ap; tibia: v2-5-2ap, p0-1-1ap, r0-0-1ap; metatarsus v2-5-2ap, p0-1-0; leg III: femur d1-2-2(1ap), patella p4, r1, tibia v2-3-2ap, d0-1-0, r1-1-0, p1-1-0, metatarsus v2-4-2ap, d3-2-2ap, r0-1-1ap, p1-2-1ap; leg IV: femur d2-1-1, patella 0, tibia v2-2-2ap, r1-0-1, metatarsus: v0-5-2ap, d0-0-1ap, r0-1-1ap, p0-1-1(1ap). Preening-comb: formed by 4–5 small spines between 2 larger spines on ventral-retrolateral tip of metatarsus IV. ITC smooth, STC with two rows of 5–6 teeth on both margins on all legs. Palp (Figs 16–17): embolus 0.77 in length. Embolus basal, middle, distal width of 0.14, 0.03, 0.01, respectively. Tegulum 0.55 long. Tibial spur (Figs 18–20)



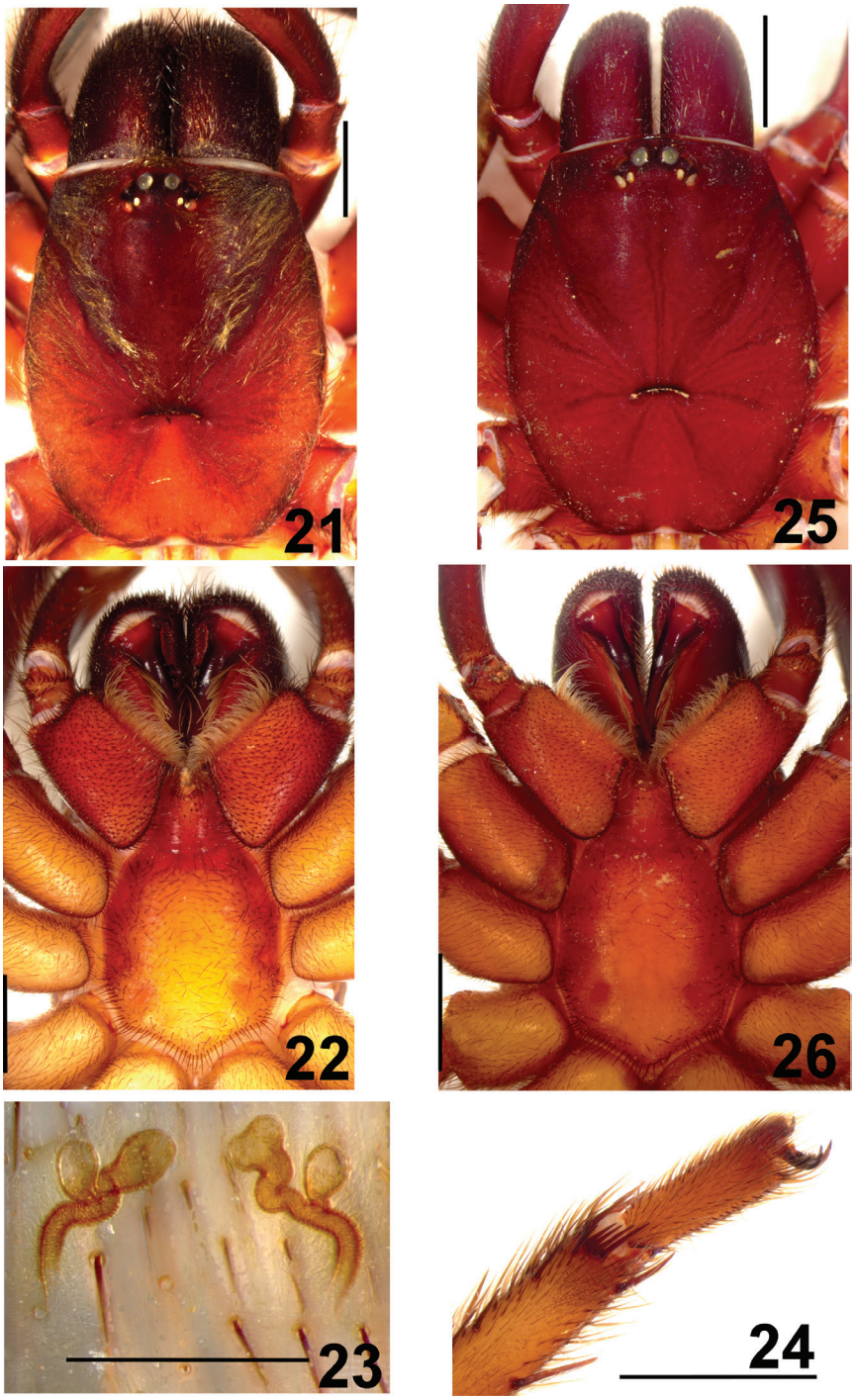
Figures 16–20. *Fufius candango* sp. n., holotype male **16–17** right palpal bulb **16** prolateral view **17** retrolateral view **18–20** right leg I tibial spur **18** ventral view **19** prolateral view **20** retrolateral view. Scale bar = 1mm.

formed by single branch 0.2 long, 0.2 wide, on retrolateral margin, with apical spine. Color pattern: carapace dark brown with some long golden setae. Sternum, labium, maxillae, coxae orange brown. Abdomen black with rounded whitish spot on dorsal anterior region, brown punctuations on remaining areas. Spinnerets light brown with brown setae. All legs uniform brown.

Female description (DZUB 4492-1). Total length: 12.71. Carapace 5.58 long, 4.40 wide, chelicerae 1.71 long, 1.45 wide. Palp: femur 2.19, patella 1.47, tibia 1.29, tarsus 1.49, total 6.44. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 3.84, 2.35, 2.11, 2.29, 1.67, 12.26. II: 2.98, 2.16, 1.65, 2.12, 1.56, 10.47. III: 2.56, 1.83, 1.28, 1.93, 1.48, 9.08. IV: 3.88, 2.01, 2.80, 2.64, 1.30, 12.63. Mid-widths (lateral): femora I–IV = 0.94, 0.96, 1.06, 1.11, palp = 0.60; patellae I–IV = 0.90, 0.96, 0.88, 0.93, palp = 0.77; tibiae I–IV = 0.84, 0.55, 0.73, 0.75, palp = 0.61; metatarsi I–IV = 0.52, 0.48, 0.48, 0.42; tarsi = 0.52, 0.46, 0.40, 0.38, palp = 0.62. Abdomen 6.34 long, 3.56 wide. Spinnerets: PMS, 0.81 long, 0.31 wide, 0.44 apart; PLS, 1.15 basal, 0.84 middle, 0.91 distal; mid-widths (lateral), 0.62, 0.60, 0.43 respectively. Carapace (Fig. 21): length to width 1.27. Fovea recurved, 1.11 wide. Eyes: tubercle 0.41 high, length 0.80, width 1.16. Clypeus 0.16. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.30, ALE 0.26, PME 0.09, PLE 0.21, AME-AME 0.14, AME–ALE 0.10, PME–PME 0.53, PME–PLE 0.06, ALE–PLE 0.08, AME–PME 0.11, ALE–ALE 0.75, PLE–PLE 0.73. Eye group width 1.16, length 0.56. Maxillae (Fig. 22) 1.63 long, 1.91 wide. Cuspules: ca. 39 spread over ventral inner heel. Labium: 0.84 long, 1.01 wide, with 4 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 2.85 long, 2.56 wide. Three pairs of sigillae, first rounded, second, third ovals, all one diameter from margin and hardly visible. Chelicerae: basal segment with 7 teeth. Legs: leg formula: IV I II III. Scopula: tarsi I–II scopulate. Metatarsus I 1/4, II 1/3 scopulate. Spines: palp: femur p-0-0-1, patella 0, tibia v2-2-3(2ap), p0-1-0, tarsus v2-0-0; leg I: femur p0-0-1, patella p1; tibia v0-1-2ap, metatarsus v1-2-2ap; leg II: femur p-0-0-1, d1-0-1, patella p0-1-0, tibia v1-1-2ap, p0-0-1, metatarsus v1-3-2ap, p0-1-0, r0-0-1ap; leg III: femur d1-0-0; patella p7; tibia: v2-2-2ap, p1-1-1ap, r0-1-1, metatarsus d3-3-2ap, p0-0-1ap, v2-4-2(2ap), r1-1-1ap; leg IV: femur: d1-0-0, patella 0, tibia v2-2-2ap, r0-2-1(1ap), metatarsus: d0-0-1(1ap), p0-2-3(2ap), v2-2-2ap, r0-0-1ap. Preening-comb (Fig. 24): formed by 4–5 small spines between two bigger spines on ventro-retrolateral tip of metatarsus IV. Palp with single claw having 6 small teeth on internal margin. ITC smooth, STC with two rows of 8 teeth on both margins on all legs. Spermathecae (Fig. 23): two spermathecae having narrow and inward curved stalk, giving origin to two spiraled branches ending in single bulb. Color pattern: as in male, except carapace brown, cephalic area darker; ventral abdominal area with lighter portion close to spinnerets; legs black with two (femur, patella, tibia) or one (metatarsus, tarsus) brown stripes (lacking setae) on dorsal area.

Remarks. The male of this species was erroneously attributed to *Fufius funebris* Vellard (1924) by Guadanucci and Indicatti (2004). See discussion for *Fufius funebris* above.

Distribution. Known only from type locality: Brazil, Distrito Federal (Brasília) (Fig. 45).



Figures 21–26. *Fufius candango* sp. n. **21–24** Paratype female **21** carapace **22** sternum, labium and maxillae **23** spermathecae, dorsal view **24** right metatarsus IV, retrolateral, showing spiniform preening-comb **25–26** holotype male **25** carapace **26** sternum, labium and maxillae. Scale bar = 1mm.

***Fufius minusculus* sp. n.**
http://zoobank.org/F1E97285-664F-45E8-8E2B-D793F0CBE42A
http://species-id.net/wiki/Fufius_minusculus
Figs 27–36, 45

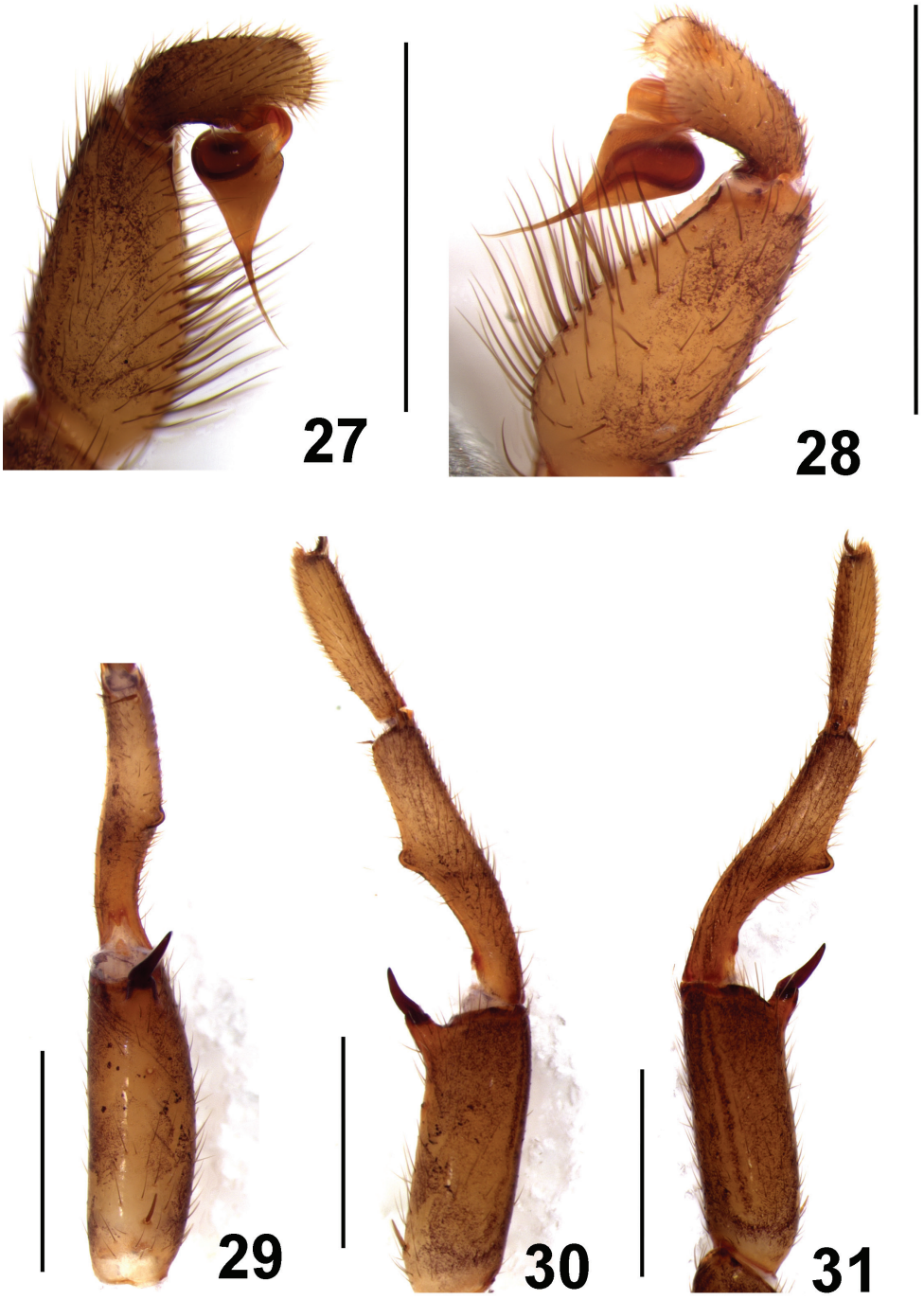
Diagnosis. Male and female differ from those of all other species by carapace at least 1.5 times longer than wide and small sternal sigillae (Figs 32–36).

Etymology. The specific name refers to the tiny size of the species.

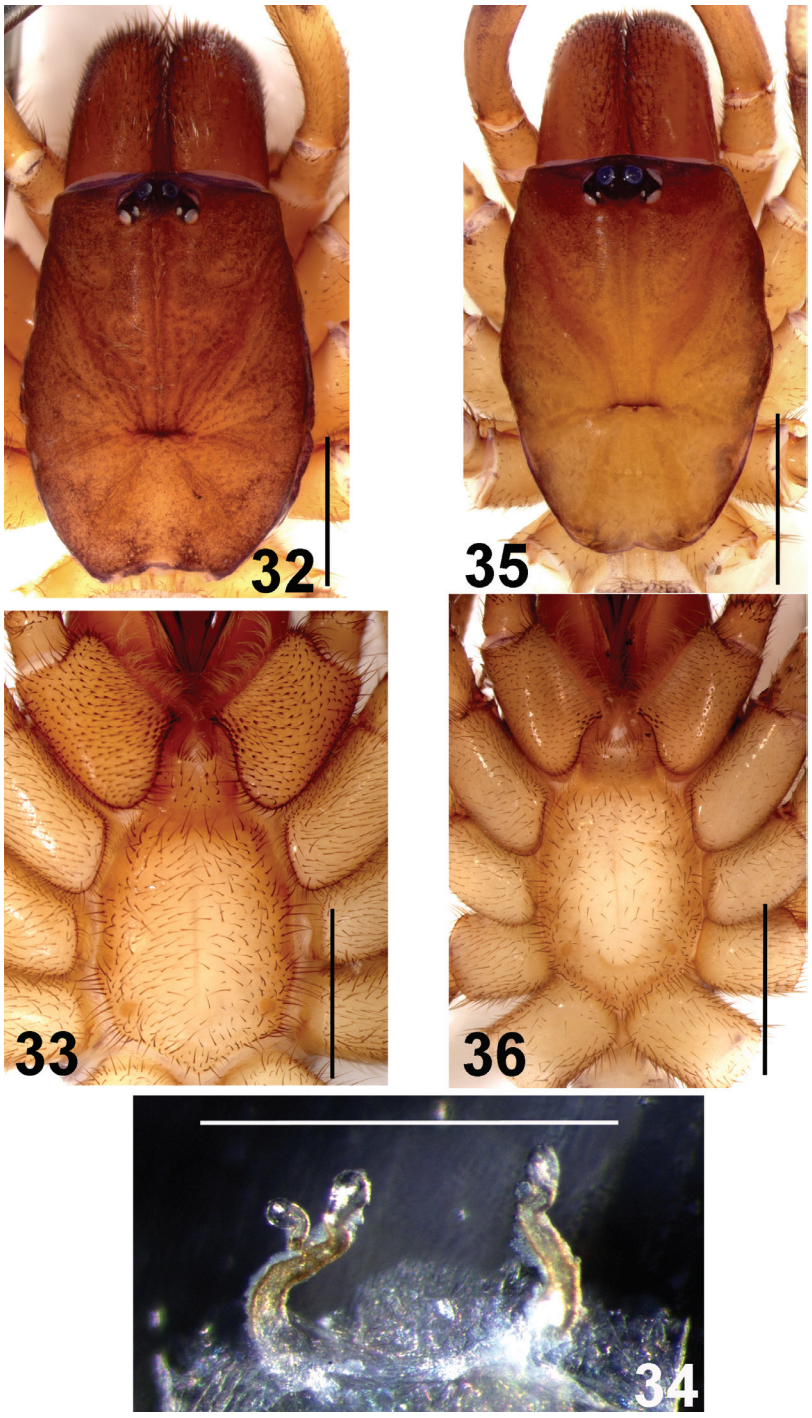
Types. Holotype male from Brazil, *Tocantins*, Mateiros, Jalapão [10°32'S, 46°24'W], 01 November 2004, S. Balbino, with pitfall trap (DZUB 3416). Paratype: female from Brazil, *Tocantins*, Palmas, km 1.5 on the railway TO-010 (Palmas-Lajeado) [10°09'S, 48°18'W], 3 November 2001, I. Knysak & R. Martins (IBSP 9695).

Additional material examined. BRAZIL: *Tocantins*: Palmas [10°10'S, 48°19'W], 2 immatures, 30 September 2001, I. Knysak & R. Martins (IBSP 9689).

Male description (DZUB 3416). Total length: 5.11. Carapace 2.42 long, 1.60 wide, chelicerae 1.09 long, 0.60 wide. Palp: femur 1.24/ patella 0.66/ tibia 0.86/ tarsus 0.46/ total 3.22. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 1.88, 1.07, 1.39, 1.41, 0.95, 6.70. II: 1.61, 0.93, 1.31, 1.30, 0.97, 6.12. III: 1.14, 0.78, 0.70, 0.98, 0.35, 3.95. Leg IV missing. Mid-widths (lateral): femora I–III = 0.40, 0.38, 0.51, palp = 0.31; patellae I–III = 0.38, 0.32, 0.38, palp = 0.34; tibiae I–III = 0.49, 0.23, 0.30, palp = 0.44; metatarsi I–III = 0.27, 0.19, 0.18; tarsi I–III = 0.21, 0.13, 0.18, palp = 0.26. Abdomen 2.41 long, 1.29 wide. Spinnerets: PMS, 0.25 long, 0.15 wide, 0.13 apart; PLS, 0.34 basal, 0.22 middle, 0.28 distal; mid-widths (lateral), 0.26, 0.20, 0.15, respectively. Carapace (Fig. 35): length to width 1.51. Fovea slightly recurved, 0.37 wide. Eyes: tubercle 0.19 high, length 0.32, width 0.50. Clypeus 0.02. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.14, ALE 0.14, PME 0.05, PLE 0.11, AME–AME 0.05, AME–ALE 0.04, PME–PME 0.23, PME–PLE 0.02, ALE–PLE 0.03, AME–PME 0.05, ALE–ALE 0.34, PLE–PLE 0.31. Eye group width 0.54, length 0.26. Maxillae (Fig. 36) 0.59 long, 0.80 wide. Cuspules: 12 spread over ventral inner heel. Labium: 0.31 long, 0.52 wide, with 2 cuspules. Labio-sternal groove shallow, flat, sigillae not evident. Sternum: 1.44 long, 1.13 wide. Sigillae: first, second pairs small, rounded, less than one diameter from margin. Third small, oval, one diameter from margin. Chelicerae: basal segment with 6 teeth. Legs: leg formula: I II III (legs IV missing). Scopula: tarsi I–II scopulate. Metatarsi III ascopulate (leg IV missing). Spines: palp: femur p-0-0-1, patella 0, tibia 0; leg I: femur d1-0-0, patella 0, tibia v1-1-0, metatarsus v0-0-ap1, p0-0-ap1; leg II: femur d 1-0-0, patella 0, tibia v 1-1-1ap, metatarsus v1-1-1ap; leg III: femur v1-0-0, patella p4, tibia d1-0-1, r0-0-1ap, v0-1-2ap, p0-0-1ap, metatarsus d1-3-2(1ap), r0-0-1ap, v1-2-2ap, p0-1-1. Leg IV missing. ITC smooth, STC with two rows of 5–8 teeth on both margins on all legs. Palp (Figs 27–28): embolus 0.46 in length. Embolus basal, middle, distal width of 0.22, 0.02, 0.01, respectively. Tegulum 0.24 long. Tibial spur (29–31) formed by single branch 0.28 long, 0.22 wide, on retrolateral margin, with apical spine. Color pattern: carapace, chelicerae reddish brown, darker on cephalic area, carapace margin, chelicerae; sternum, labium, maxillae, coxae of legs and palp light brown; abdomen



Figures 27–31. *Fufius minusculus* sp. n., holotype male **27–28** left palpal bulb **27** prolateral view **28** retrolateral view **29–31** right leg I tibial spur **29** ventral view **30** prolateral view **31** retrolateral view. Scale bar = 1mm.



Figures 32–36. *Fufius minusculus* sp. n. **32–34** paratype female **32** carapace **33** sternum, labium and maxillae **34** spermathecae, dorsal view **35–36** holotype male **35** carapace **36** sternum, labium, and maxillae. Scale bar = 1mm.

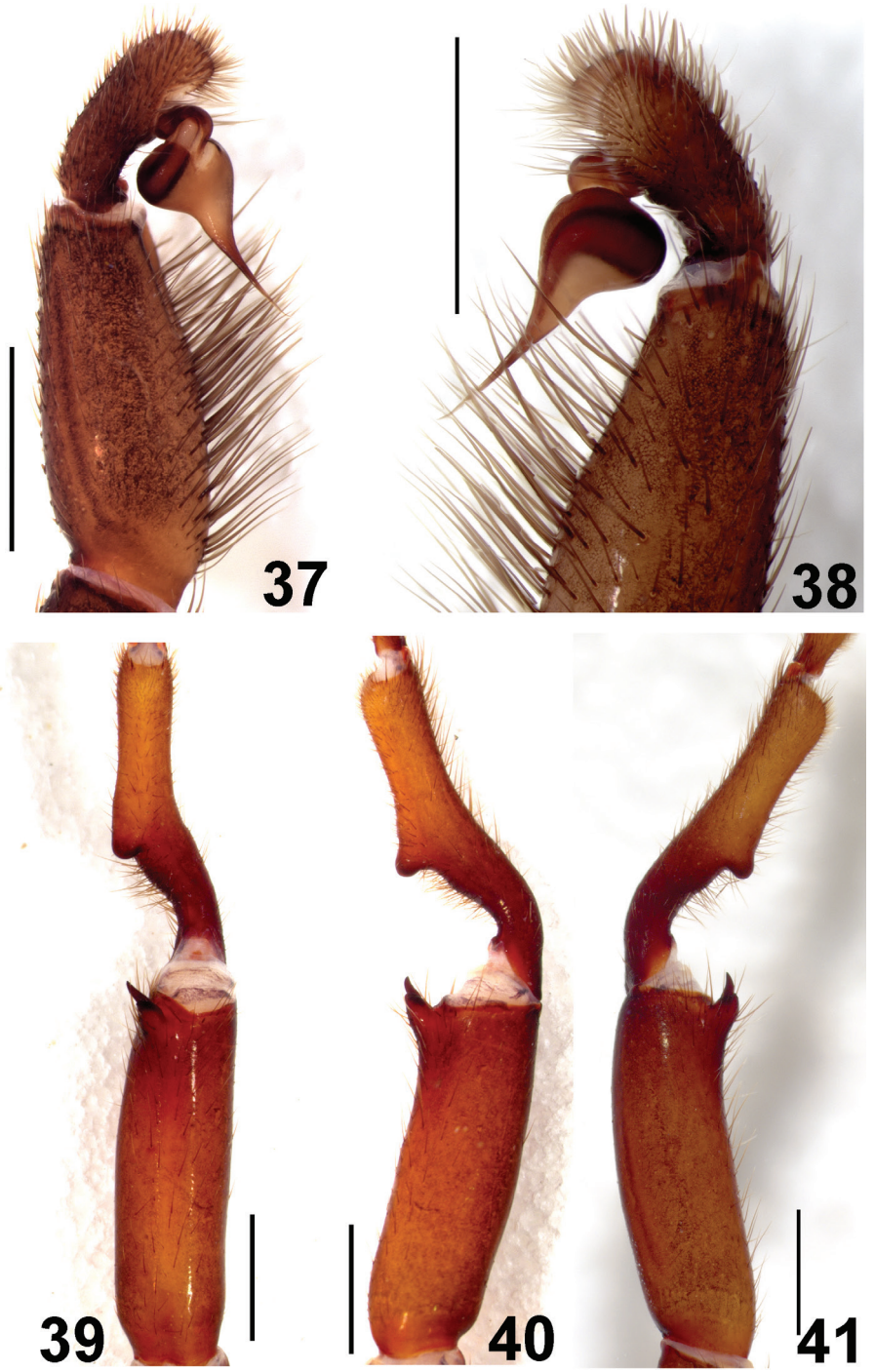
dark with light brown punctuations on dorsum, larger white spot on central anterior area. Ventrally dark with central area whitish. Spinnerets light brown with dark brown setae. Legs yellowish with black areas on distal femora, most of patellae, tibiae, metatarsi.

Female description (IBSP 9695). Total length: 5.19. Carapace 3.16 long, 2.18 wide, chelicerae 0.93 long, 0.75 wide. Palp: femur 1.58, patella 0.98, tibia 0.68, tarsus 0.93, total 4.17. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 1.79, 1.15, 1.20, 1.06, 0.77, 5.97. II: 1.32, 0.88, 0.85, 0.98, 0.98, 5.01. III: 1.35, 0.92, 0.64, 0.89, 0.88, 4.68. IV: 1.69, 1.09, 1.56, 1.41, 0.76, 6.51. Mid-widths (lateral): femora I–IV = 0.48, 0.51, 0.56, 0.51, palp = 0.40; patellae I–IV = 0.46, 0.46, 0.45, 0.43, palp = 0.38; tibiae I–IV = 0.44, 0.33, 0.37, 0.38, palp = 0.38; metatarsi I–IV = 0.27, 0.21, 0.23, 0.24; tarsi I–IV = 0.26, 0.22, 0.17, 0.22, palp = 0.29. Abdomen 3.36 long, 2.40 wide. Spinnerets: PMS, 0.40 long, 0.23 wide, 0.35 apart; PLS, 0.65 basal, 0.51 middle, 0.49 distal; mid-widths (lateral), 0.34, 0.28, 0.26, respectively. Carapace (Fig. 32): length to width 1.45. Fovea slightly recurved, 0.45 wide. Eyes: tubercle 0.15 high, length 0.46, width 0.62. Clypeus 0.07. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.17, ALE 0.18, PME 0.08, PLE 0.11, AME 0.05, AME–ALE 0.04, PME–PME 0.27, PME–PLE 0.03, ALE–PLE 0.03, AME–PME 0.07, ALE–ALE 0.45, PLE–PLE 0.40. Eye group width 0.63, length 0.29. Maxillae (Fig. 33) 0.72 long, 0.93 wide. Cuspules: ca. 30 spread over ventral inner heel. Labium: 0.45 long, 0.55 wide, with 2 cuspules. Labio-sternal groove shallow, flat, sigillae not evident. Sternum: 1.60 long, 1.23 wide. Sigillae: first, second pairs small, rounded, less than one diameter from margin. Third small, oval, one diameter from margin. Chelicerae: basal segment with 7 teeth. Legs: leg formula: IV I II III. Scopula: tarsi I–II scopulate. Metatarsi I 1/3 scopulate. Spines: palp: femur 0, patellae r1-1-0, tibia v2-2-3ap, r1-1-1ap, p0-0-1, tarsus v2-0-0; leg I: femur p0-0-1ap, patellae p0-0-1ap, tibia v1-1-1ap, metatarsus v1-1-2ap; leg II: femur 0, patellae r1-1-0, tibia v1-1-2, metatarsus v0-3-3(2ap), p0-1-0, r0-0-1; leg III: femur 0, patellae p4, r1, tibia d1-0-0, r0-1-0, v0-2-2ap, p1-1-0, metatarsus d1-3-2ap, r0-0-1, v0-4-2ap, p0-1-0; leg IV: femur 0, patella 0, tibia v0-1-2, r0-1-1, metatarsus d0-0-1ap, r0-1-0, v0-2-1ap, p1-1-1ap. Preening-comb: absent on retro-lateral tip of metatarsus IV. Palp with single claw having 8 small teeth on internal margin. ITC smooth, STC with two rows of 5–9 teeth on both margins on all legs. Spermathecae (Fig. 34): two spermathecae having narrow and inward curved stalk, giving origin to two sinuous branches ending in single bulb each. Color pattern: as in male.

Distribution. Brazil, state of Tocantins (Palmas and Mateiros) (Fig. 45).

***Fufius jalapensis* sp. n.**
http://zoobank.org/8D27137C-9415-45B0-A01A-5B79248E1C4C
http://species-id.net/wiki/Fufius_jalapensis
Figs 37–43, 45

Diagnosis. Male differs from those of all other species by tibia I lacking spines (Figs 39–41) and the presence of several spines (ca. 11) on the prolateral patella III. The female is unknown.



Figures 37–41. *Fufius jalapensis* sp. n., holotype male **37–38** left palpal bulb (mirrored) **37** retrolateral view **38** prolateral view **39–41** right leg I tibial spur **39** ventral view **40** prolateral view **41** retrolateral view. Scale bar = 1mm.

Figures 42–43. *Fufius jalapensis* sp. n., holotype male. **42** carapace **43** sternum, labium, and maxillae. Scale bar = 1 mm.

Etymology. The specific name, jalapensis, refers to the type locality, "Jalapão", a state park in the eastern state of Tocantins, Brazil.

Types. Holotype male from BRAZIL, *Tocantins*: Mateiros, Jalapão [10°32'S, 46°24'W], 01 November 2004, S. Balbino (DZUB 3370). Paratype male, same collector and date (DZUB 4469).

Male description (DZUB 3370). Total length: 11.72. Carapace 5.92 long, 4.61 wide, chelicerae 1.89 long, 1.39 wide. Palp: femur 2.88, patella 1.46, tibia 2.09, tarsus 0.83, total 7.26. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 4.47, 3.15, 3.86, 3.71, 2.35, 17.54. II: 3.44, 2.63, 3.33, 3.29, 2.03, 14.72. III: 2.95, 1.91, 2.14, 3.08, 1.84, 11.92. IV: 4.33, 2.47, 4.55, 4.24, 1.83, 17.42. Mid-widths (lateral): femora I–IV = 0.89, 0.80, 1.14, 1.21, palp = 0.47; patellae I–IV = 0.80, 0.70, 0.86, 0.87, palp = 0.78; tibiae I–IV = 0.89, 0.57, 0.64, 0.79, palp = 0.87; metatarsi I–IV = 0.61, 0.44, 0.38, 0.45; tarsi = 0.49, 0.45, 0.40, 0.33, palp = 0.55. Abdomen 5.51 long, 3.27 wide. Spinnerets: PMS, 0.60 long, 0.28 wide, 0.15 apart; PLS, 0.88 basal, 0.49 middle, 0.81 distal; mid-widths (lateral), 0.52, 0.44, 0.33 respectively. Carapace (Fig. 42): length to width 1.28. Fovea strongly recurved, 1.29 wide. Eyes: tubercle 0.24 high, length 0.64, width 1.14. Clypeus 0.07. Anterior and posterior eye row recurved. Eyes sizes and inter-distances: AME 0.30, ALE 0.28, PME 0.10, PLE 0.22, AME–AME 0.06, AME–ALE 0.10, PME–PME 0.60, PME–PLE 0.04, ALE–PLE 0.14, AME–PME 0.13, ALE–ALE 0.73, PLE–PLE 0.80. Eye

Figure 44. *Fufius lucasae*, female from Itapecerica da Serra, state of São Paulo. Photo: R. Bertani.

group width 1.11, length 0.54. Maxillae (Fig. 43) 2.06 long, 1.32 wide. Cuspules: 31 spread over ventral inner heel. Labium: 0.73 long, 1.0 wide, with 3 cuspules. Labio-sternal groove shallow, flat with two large sigillae. Sternum: 3.04 long, 2.54 wide. Sigillae: first pair rounded, second, third ovals, all less than one diameter from margin. Third pair large, twice the diameter of second. Chelicerae: basal segment with 7 teeth. Legs: leg formula: I IV II III. Scopula: tarsi I–III scopulate. Metatarsi I 1/5, II 1/3 scopulate. Spines: palp 0; Leg I 0; Leg II: femur, patella 0, tibia v1-1-2ap, p0-0-1ap, metatarsus v0-2-1ap, r0-0-1ap; Leg III: femur 0, patella p11, tibia d0-1-0, v0-1-1ap, p0-1-2(1ap), metatarsus d1-3-1ap, r0-0-1ap, v2-3-2ap, p2-1-3(2ap); Leg IV: femur, patellae 0, tibia r0-0-1, v0-1-0, metatarsus r0-1-1ap, v1-3-1ap, p1-0-2ap. Preening-comb: formed by 6 spiniform setae between two spines on ventro-retrolateral tip of metatarsus IV. ITC smooth, STC with two rows of 3–9 teeth on both margins on all legs. Palp: embolus 0.82 in length. Embolus basal, middle, distal width of 0.28, 0.05, 0.02, respectively. Tegulum 0.36 long. Tibial spur formed by

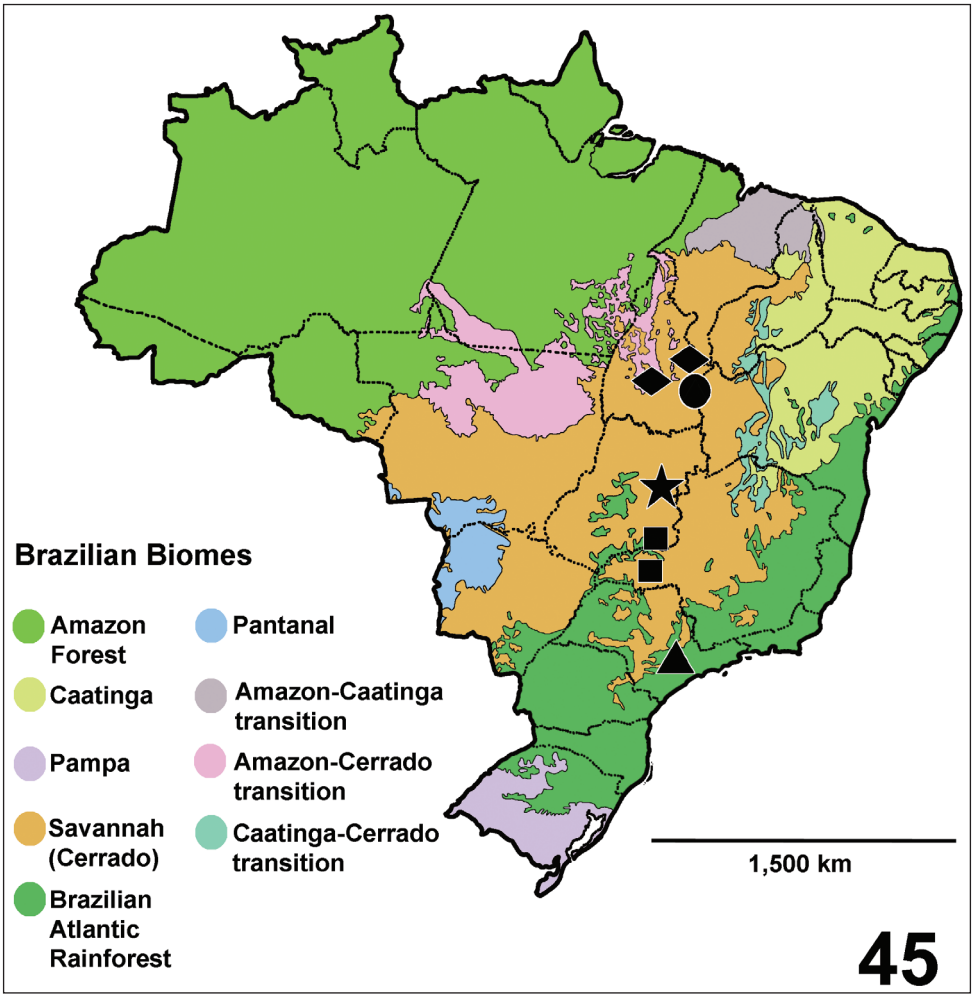


Figure 45. Map showing records of *Fufius funebris* (square), *F. lucasae* (triangle), *F. candango* sp. n. (star), *F. minusculus* sp. n. (diamond) and *F. jalapensis* sp. n. (circle) in different Brazilian Biomes.

single branch 0.54 long, 0.36 wide, on retrolateral margin, with apical spine. Color pattern: carapace, chelicerae brown, darker on cephalic area, carapace margin, chelicerae; sternum, labium, maxillae, coxae of legs and palp light brown; abdomen dark with light brown punctuations on dorsum, a larger white spot on central anterior area, ventrally dark with book-lung area whitish. Spinnerets light brown with dark brown setae. Legs an almost homogeneous brown.

Female. Unknown.

Distribution. Known only from the type locality, Brazil, state of Tocantins (Jalapão region) (Fig. 45).

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RESEARCH ARTICLE

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First description of the male of *Thaida chepu* Platnick, 1987 (Araneae, Austrochilidae) with micro-computed tomography of the palpal organ

Peter Michalik[1,2], Martin J. Ramírez[3]

1 *Allgemeine und Systematische Zoologie, Zoologisches Institut und Museum, Ernst-Moritz-Arndt-Universität, J.-S.-Bach-Str. 11/12, D-17489 Greifswald, Germany* **2** *Research Associate, Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA* **3** *Museo Argentino de Ciencias Naturales - CONICET, Buenos Aires, Argentina*

Corresponding author: *Peter Michalik* (michalik@uni-greifswald.de)

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Abstract

The male of the austrochilid spider *Thaida chepu* Platnick, 1987 is described for the first time. We analyzed the internal anatomy of the palpal organ by using micro-computed tomography to investigate the spermophor as well as the muscles and tendons in the cymbium and tibia in detail. As shown by our data, muscles 29 and 30 originate in the tibia and continue with tendons to the base of the bulb, which resembles the ancestral organization for the male palp of spiders; this condition has not been described for Araneomorphae until now. The 3D reconstruction of the spermophor confirms recent interpretations of the male palp sclerites within Austrochilidae.

Keywords

Taxonomy, micro-CT, spermophor, palp

Introduction

The family Austrochilidae consists of three genera with a very peculiar distribution. Whereas the genera *Austrochilus* Gertsch & Zapfe, 1955 (6 species) and *Thaida* Karsch, 1880 (2 species) are endemic to the forests of Central and Southern Chile and adjacent Argentina, the monotypic genus *Hickmania* Gertsch, 1958 is endemic to Tasmania (Forster et al. 1987). The Austrochilidae, which together with the family Gradungulidae comprise the superfamily Austrochiloidea, are of high interest for spider systematics since it is ambiguously placed among the early derivative taxa of Araneomorphae (e.g., Griswold et al. 2005). Thus, detailed knowledge of taxon-specific structures such as the genitalia is highly valuable not only for species determination but also for a better understanding of interrelationships among the Araneomorphae. In the present study, we describe the male of *Thaida chepu* Platnick, 1987 for the first time. Furthermore, we studied the internal anatomy of the male palpal organ using X-ray microtomography (micro-CT) in order to reconstruct the spermophore (sperm duct) and position of the embolus, which was debated in former studies (see Griswold et al. 2005: 17).

Material and methods

We collected a male of *T. chepu* close to the type locality in a wet lowland mixed forest at Lago Huillinco (Chiloé, Chile) (Fig. 1). The material was examined and documented (extended focal range images) in 80% ethanol using a Zeiss Discovery V20 stereo microscope with a Zeiss MCr camera. Editing of images to adjust brightness, contrast and color was performed using Adobe Photoshop CS4. Measurements (given in millimeters) were obtained from digital images using the IntMess module in the program Zeiss AxioVision 4.8 (Carl Zeiss MicroImaging GmbH, Göttingen, Germany). The style of the description is based on Forster et al. (1987) and Grismado et al. (2003).

For the micro-CT analyses of the male palp, the sample was dehydrated in graded ethanol and stained with a 1% iodine solution for 12 hours. After washing in pure ethanol, the sample was scanned in ethanol with an Xradia MicroXCT-200 X-ray imaging system (Carl Zeiss X-ray Microscopy Inc., Pleasanton, USA) at 40 kV and 8 W using phase contrast (4.0 scintillator-objective lens unit, 15 s exposure time, 4.15 µm pixel size). The obtained data were processed using the 3D analysis software AMIRA v. 5.4.2 (Visage Imaging, Berlin, Germany). Virtual reconstruction of the spermophore was performed by delineation in each section (segmentation) and a smooth surface was computed using the surface editor. The image stack is stored in MorphDBase under creative commons attribution (CC-BY; ID: P_Michalik_20130729-M-4.1; https://www.morphdbase.de?P_Michalik_20130729-M-4.1).

Abbreviations

ALE	anterior lateral eye
AME	anterior median eye
bH	basal hematodocha
Cb	cymbium
Ch	chelicera
E	embolus
HSt	hook of subtegulum
m29	muscle 29
m30	muscle 30
mA	median apophysis
mH	median hematodocha
MOQ	median ocular quadrangle
PLE	posterior lateral eye
PME	posterior median eye
PSt	process of subtegulum
S	spermophor
St	subtegulum
Te	tegulum
tm29	tendon of muscle 29
tm30	tendon of muscle 30
ZIMG	Zoologisches Institut und Museum Greifswald (Germany)

Taxonomy

Family Austrochilidae Zapfe 1955
Subfamily Austrochilinae Zapfe 1955
Genus *Thaida* Karsch 1880

***Thaida chepu* Platnick, 1987**
http://species-id.net/wiki/Thaida_chepu

Material examined. CHILE: Region de Los Lagos (X), Chiloé province, Isla de Chiloé, Lago Huillinco, N margin, 4.6 km (air) ESE Cucao, S42.64117°, W74.04763° (GPS, ±100m), elev. 12 m (MJR-loc-86), 16 February 2012, 1 male, coll. K. Huckstorf, M. Izquierdo, P. Michalik, M. J. Ramirez, C. S. Wirkner (ZIMG II/28126).

Diagnosis. Similar to *T. peculiaris* by the clypeus about three times the diameter of the anterior median eyes (Fig. 3); males distinguished from *T. peculiaris* by the copulatory bulb, which has the median apophysis longer than the embolus (Figs 5–10; about half the length of the embolus in *T. peculiaris*, Forster et al. 1987, figs 155–157), a stout and curved

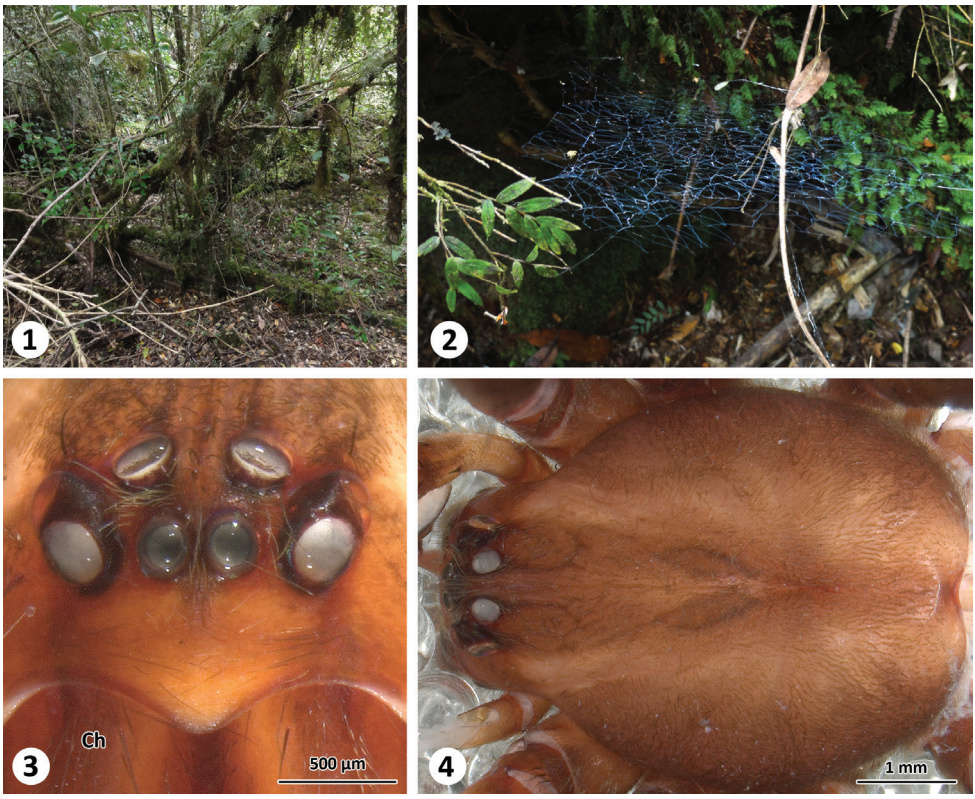

Figure 1–4. Habitat (**1**), web (**2**) and somatic characters (frontal (**3**) and dorsal (**4**) view of prosoma) of *Thaida chepu*.

process of the subtegulum (slender and straight in *T. peculiaris*, Forster et al. 1987, figs 155–157), and the bent embolus with a curved tip (embolus of *T. peculiaris* without distinct tip, Forster et al. 1987, figs 155–157). Diagnosis of the female in Forster et al. (1987).

Description. Male (ZIMG II/28126). Carapace 5.59 long and 4.38 wide; clypeal height 0.68 (in the middle about three times AME diameter in height; Fig. 3); coloration as depicted in Fig. 4. Eye sizes and interdistances: AME 0.24, ALE 0.31, PME 0.25, PLE 0.30; AME-AME 0.05, AME-ALE 0.15, PME-PME 0.26, PME-PLE 0.22, ALE-PLE 0.06; MOQ length 0.77, median ocular quadrangle width 0.78. Spination: femora: I d 1-0-1, p 2-3-3, r 2-3-3; II d 1-2-1, p 2-2-2, r 2-2-2; III d 1-2-1, p 1-2-2, r 2-2-2; IV d 2-2-1, p 0-1-2, r 0-1-3; tibiae: I p 2-3-2, v 3-3-4, r 2-2-2; II p 2-2-2, v 3-4-3, r 1-1-2; III d 1-0-1, p 0-2-2, v 1-1-4, r 0-2-1; IV missing; metatarsus: I p 3-1-2, v 1-1-1, r 2-2-2; II d 0-1-2, p 1-2-2, v 0-1-2, r 1-1-0; III p 1-1-2, v 2-3-2, r 2-2-1; IV missing. Palp (Figs 5-10): cymbium slender, median apophysis slender and spine-shaped with serrated tip, embolus broad with twisted, membranous flange and slit-like opening, membranous spermophor as depicted in Figs 8–10, m29 and m30 originating in tibia. The 3D reconstruction revealed that the spermophor fills most of the subtegulum and is flattened and thin within the embolus (Video 1). Abdomen missing.

Figure 5–10. Left male palp of *Thaida chepu*. **5–7** extended focal plane images of male palp in prolateral (**5**), ventral (**6**) and retrolateral (**7**) view **8–10** surface model of the spermophor superimposed on the volume rendering of the male palp to illustrate dimension and shape of the spermophor. The views correspond to Figs **5–7**. The cymbium, subtegulum and tegulum are (partly) removed in Fig. 8 to show tendons and muscles. The arrows point to the opening of the embolus.

Appendages measurements:

	I	II	III	IV	Palp
Femur	8.82	7.67	5.95	7.3	2.99
Patella	2.02	1.83	1.54	1.69	0.92
Tibia	9.91	7.55	4.63	missing	1.43
Metatarsus	9.40	7.60	5.39	missing	-
Tarsus	3.68	3.04	2.17	missing	3.27
Total	33.84	27.71	19.69		8.62

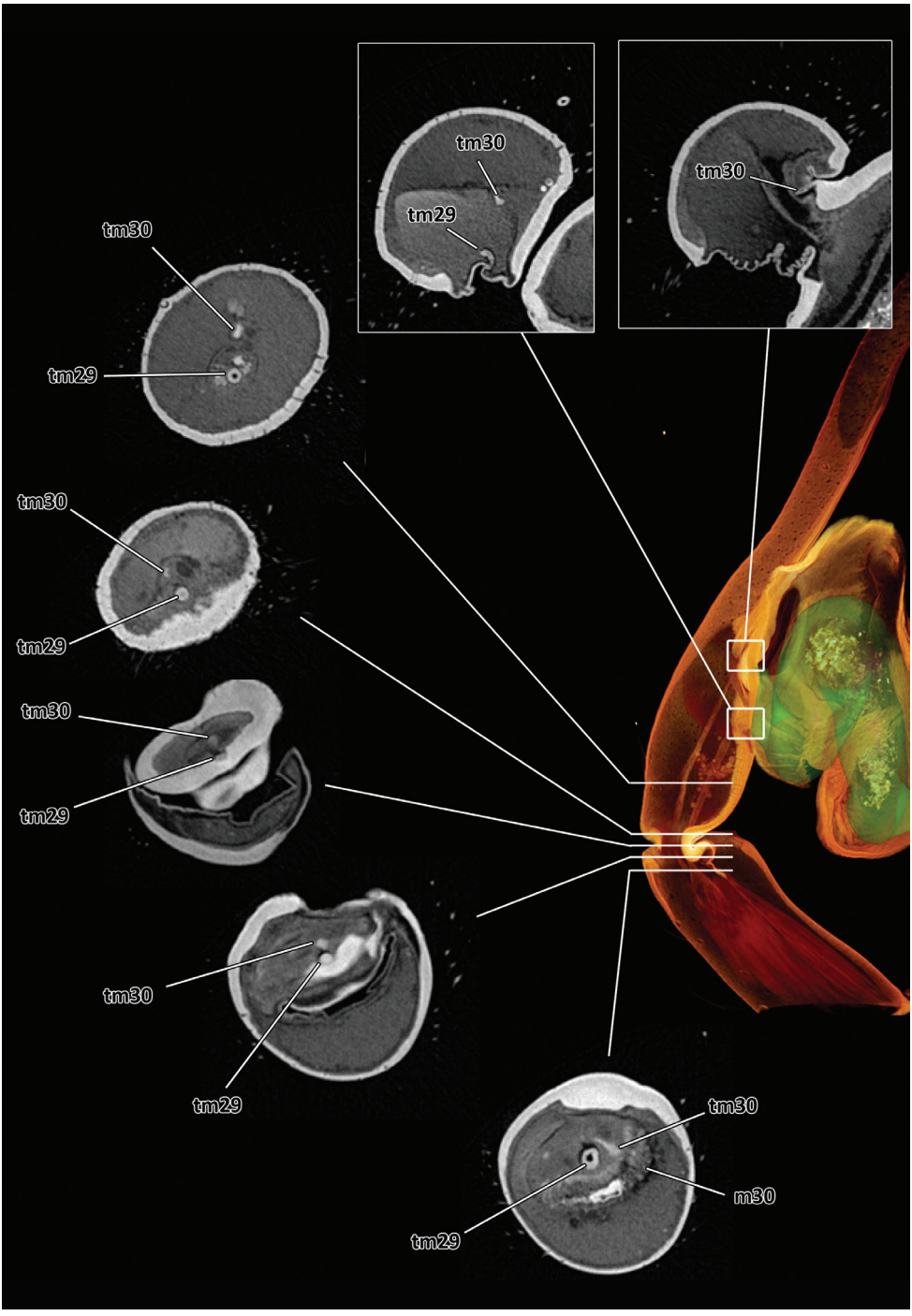

Figure 11. Series of virtual cross sections through the left male palp of *Thaida chepu* showing the course of the two tendons.

Video 1. Surface model of the spermophor superimposed on the volume rendering of the male palp. Video available for download in full resolution from http://www.pensoft.net/J_FILES/1/articles/6021/export.php_files/Michalik_Ramirez_Video_1.avi.

Natural history. The webs of *T. chepu* are very similar to those described for *Thaida peculiaris* Karsch 1880 and *Austrochilus forsteri* Grismado, Lopardo & Platnick, 2003 by Lopardo et al. (2004) (Fig. 2).

Discussion

Based on the micro-CT data and manual segmentation of the spermophor we confirm the interpretation of the male palp sclerites especially with regard to the position of the embolus given by Griswold et al. (2005). The spermophor of austrochilines is membranous, with thin cuticle, not evident without preparation (e.g., micro-CT or clearing by clove oil; see also Huber 2004). Moreover and in contrast to the findings of Huber (2004) on *T. peculiaris*, our micro-CT analysis revealed that no muscles originate in the cymbium (tarsus) of *T. chepu*. Instead, the muscles 29 and 30 originate in the tibia and are connected by tendons with the bulbal sclerites (Figs 8, 11) - an organization only known from the basal spider genera *Liphistius* Schiödte, 1849 and *Atypus* Latreille, 1804 (Huber 2004). Preliminary micro-CT analyses of the palp

of the sister group Hickmaniinae (*H. troglodytes*) (Lipke, personal communication), histological sections as well as micro-CT analyses of representatives of Gradungulidae (Huber 1994; Michalik et al. 2013) and *Hypochilus* (Hypochilidae) (Huber 1994) revealed that the muscle 30 originates in the cymbium as typical for araneomorph spiders (Huber 2004). This is especially important since austrochilids are key taxa that might reveal important information to interpret the transition from muscular to hydraulically-controlled copulatory organs (Huber 2004), and towards the evolution of higher Araneomorphae (i.e. Haplogynae and Entelgynae).

As shown here micro-CT data can be used for precise and transparent descriptions (for details on the method and data handling see Faulwetter et al. 2013) as well as revealing internal anatomical characters useful for spider taxonomy, systematics and evolutionary/functional morphology.

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