

New distribution and host records for *Hectopsylla pulex* Haller (Siphonaptera, Tungidae) with notes on biology and morphology

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Abstract

Hectopsylla pulex Haller is documented for the first time from Cochise County, Arizona on the Lesser Long-nosed bat, *Leptonycteris yerbabuena* Martinez and Villa (Phyllostomidae). This represents the first record of this flea on this Chiropteran Family. The most favorable site of attachment of *H. pulex* appears to be the head, particularly the ears and tragus. The potential interference of echolocation caused by flea attachment at or near the tragus is discussed in addition to host preferences and specialized morphological features. It is demonstrated that expansion of abdominal segments during egg development is a function of mechanical design and not neosomy such as occurs in *Tunga monositus* Barnes and Radovsky, *Neotunga euloidea* Smit and some vermipsyllid fleas.

Keywords

Arizona, bats, fleas, *Leptonycteris*, neosomy, Phyllostomidae

Introduction

Members of the flea genus *Hectopsylla* Barrera parasitize birds, small non-volant mammals and bats. A comprehensive review of the genus *Hectopsylla* was provided by Hastriter and Méndez (2000) to include 12 species and a key to the genus *Hectopsylla*.

Nine species are parasites of non-volant mammals, two species on avian hosts, and one on bats. Details of distribution and host specificity are outlined in Hastriter and Méndez (2000) for *Hectopsylla* species found on non-volant mammals. Blank et al. (2007) subsequently described a third avian species, *Hectopsylla narium* Kutzschen, from the nostrils and below the tongue of the Burrowing Parrot, *Cyanoliseus patagonus patagonus* (Vieillot) (Psittacidae) from Patagonia. *Hectopsylla psittaci* Frauenfeld, another avian parasite, has a broad distribution in Central and South America, southwestern United States (California) (Nelson et al. 1979, Schwan et al. 1983), and several populations were introduced into aviaries in England and the Netherlands (Hopkins and Rothschild 1953). *Hectopsylla knighti* Traub and Gammons, known only from a single female, was collected from the head of a swift (species unknown) in Michoacán, Mexico. *Hectopsylla pulex* (Haller) is the only hectopsyllid that occurs on bats. Subsequent to Hastriter and Méndez (2000), two additional records of *H. pulex* were reported from molossid bats in Brazil (Esbérard 2001, Luz et al. 2009). Three female specimens of *H. pulex* are herein reported and represent new host and distributional records.

Materials and methods

As part of a long-term ecological study of insectivorous bats in the southwestern United States between 23 June and 4 September 2013, 23 Lesser Long nosed bats, *Leptonycteris yerbabuenae* Martínez and Villa (Phyllostomidae), were captured using a mist net placed adjacent to a hummingbird feeder. Bats were weighed, measured, and examined and fleas were removed with forceps and preserved in 70% ethanol pending processing. A total of three female fleas were collected from the ears of a young adult male *Leptonycteris yerbabuenae*. One flea is deposited in the Brigham Young University DNA flea voucher collection and the other two in the collection of Christopher Newport University. Images were prepared using an Olympus BX61 Compound Microscope, Olympus CC12 digital camera accompanied with an Olympus Microsuite™ B3SV program and Adobe Photoshop, CS4.

Results and discussion

A single attached replete female flea was observed anterior to the tragus of *L. yerbabuenae* captured at Paradise, Cochise County, Arizona on 23 June 2013. This specimen was not collected but a cellular phone photo was taken to document what probably represents a replete female *H. pulex*. Although tentative, this identification is supported by the facts that *H. pulex* is: 1) the only representative of the genus that occurs on bats 2) it is the only member of the genus previously reported in the United States, 3) it was present in the same locality, and 4) that it was present in simultaneous collections of *H. pulex* on the same host species (*L. yerbabuenae*). On 27 July 2013, three additional female *H. pulex* specimens were observed and removed from the anterior base

of the tragus of *L. yerbabuena*e captured in White Tail Canyon, Chiracahua Range, Cochise County, Arizona. A photograph was taken of the one flea prior to its removal from the left ear (Fig. 1), while the other two specimens attached at the same site on the right ear were collected but not photographed. No additional fleas were noted on the other 21 *L. yerbabuena*e specimens examined.

Modest swelling of the skin of the bat adjacent to the base of the attached flea (Fig. 1, arrows) possibly indicates residual scarring from previously attached stick-tight fleas. These fleas attach and feed for extended periods. Little is known about their biology; however, other stick-tight fleas, e.g., *Echidnophaga gallinacea* (Westwood), *Juxtapulex echidnophagoides* Wagner and *Tunga penetrans* (Linnaeus), attach to their host with similar lacinae that are serrated along their margin to enable attachment (Fig. 2, arrow). This group of fleas represents two types of stick-tight fleas: 1) those that attach, feed, and drop off, and 2) those that attach, feed to repletion, become gravid, and ultimately die *in situ*. The first type attaches, retain their legs, and eventually detach and fall off of the host. These may feed multiple times. The second type that includes *T. penetrans* and *H. pulex* remain attached and autosever their legs as often noted by black scarring of the apices of each severed leg. Severing usually occurs at the apices of the coxae or femora.

It is unknown whether males of *H. pulex* copulate with females on or off the host. Males of *H. pulex* have never been found attached to a host and males have been collected only from bat guano of molossid bats (Traub and Gammons 1950, Méndez 1977). This would suggest that they copulate prior to the female acquiring a host. Following attachment, females become replete with eggs and the abdomen expands many times its original size (compare Figs 2 and 3). Overall length of abdomen of unfed female (Fig. 2) is 620 μm compared to 2400 μm for the fed replete female (Fig. 3). Comparison of an unfed female from Panama and our fed gravid specimen elucidates that the great expansion is not a feature of neosomic development that is documented in *Tunga monositus* Barnes and Radovsky, *Neotunga euloidea* Smit and some vermip-syllid fleas, but rather a pre-established expansible design. This can clearly be seen in Figs 4 and 5. Arrows, Fig. 4, indicate a hyaline membrane folded under the tergites. In addition, the tergites are compressed under one another in a “shingle” fashion (Fig. 4). The fed and expanded female (Fig. 5) illustrates the fully expanded tergites and the membrane that stretches between the posterior margin of the preceding sclerite and the next sclerite (arrows). After eggs develop, eggs are expelled out onto the host and fall onto the substrate. Only eggs that fall into the guano deposits near host colonies (roosting structures) have any chance of completing the life cycle (egg, larva, pupa and imago). Newly emerged imagines then acquire a new host near the guano deposits.

Hectopsylla pulex was reported by Hastriter and Méndez (2000) on 13 bat species represented by three families and eight genera: Molossidae (4 genera), Vespertilionidae (3 genera), and Noctilionidae (1 genus). Although a relatively common flea, our finding on *L. yerbabuena*e represents the first report on this genus and the family Phyllostomidae. This flea has been documented only once in the United States by Augustson and Ryan (1948) in Medina and Uvalde Counties, Texas on the Mexican Free-tailed

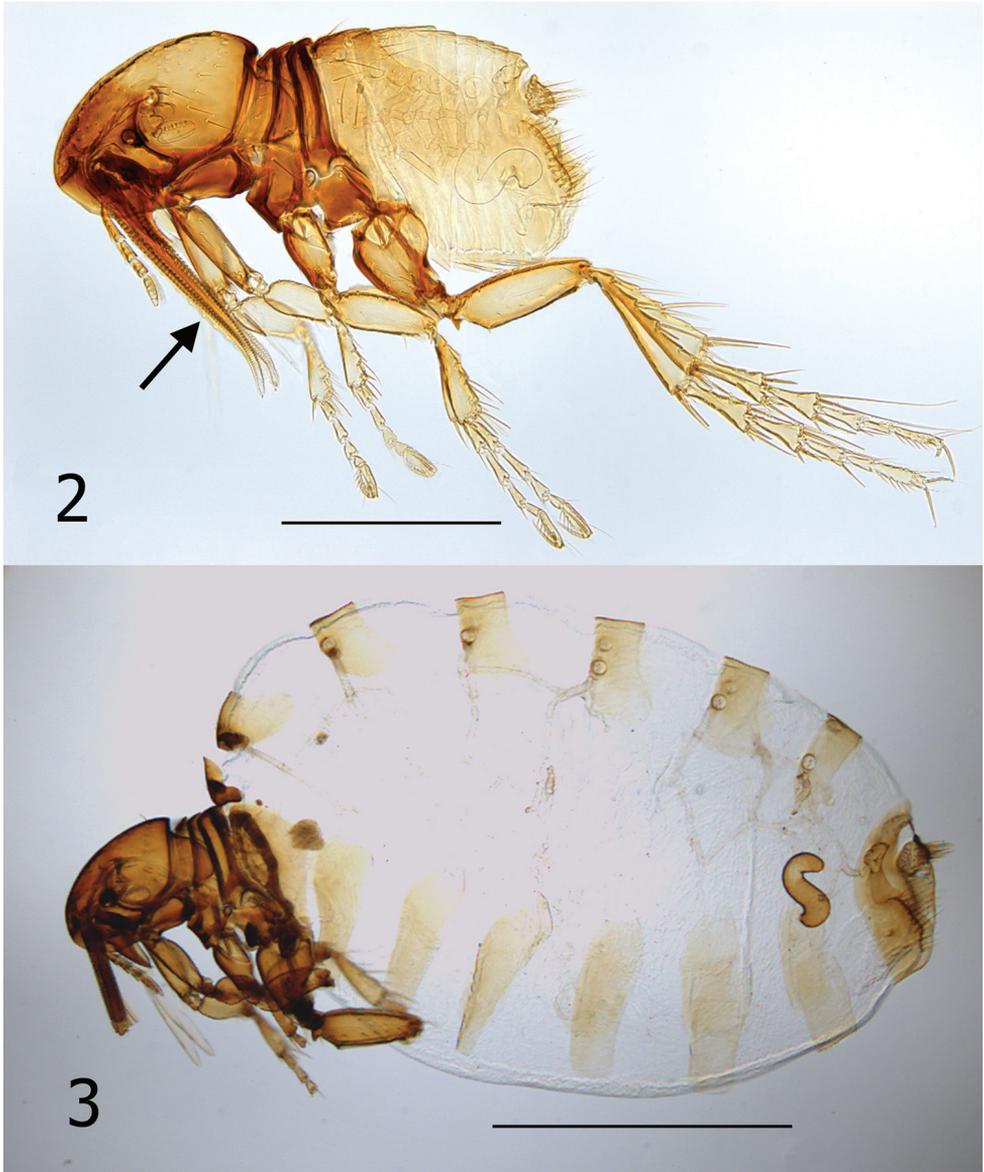


Figure 1. Young male *Leptonycteris yerbabuena* with *Hectopsylla pulex* attached near tragus. Insert is enlargement of attached *H. pulex* (arrows indicate previous flea attachment sites).

bat *Tadarida brasiliensis* (I. Geoffroy). The occurrence of *H. pulex* in Cochise County, Arizona is a new State record and also represents the most northern and western limit for the species.

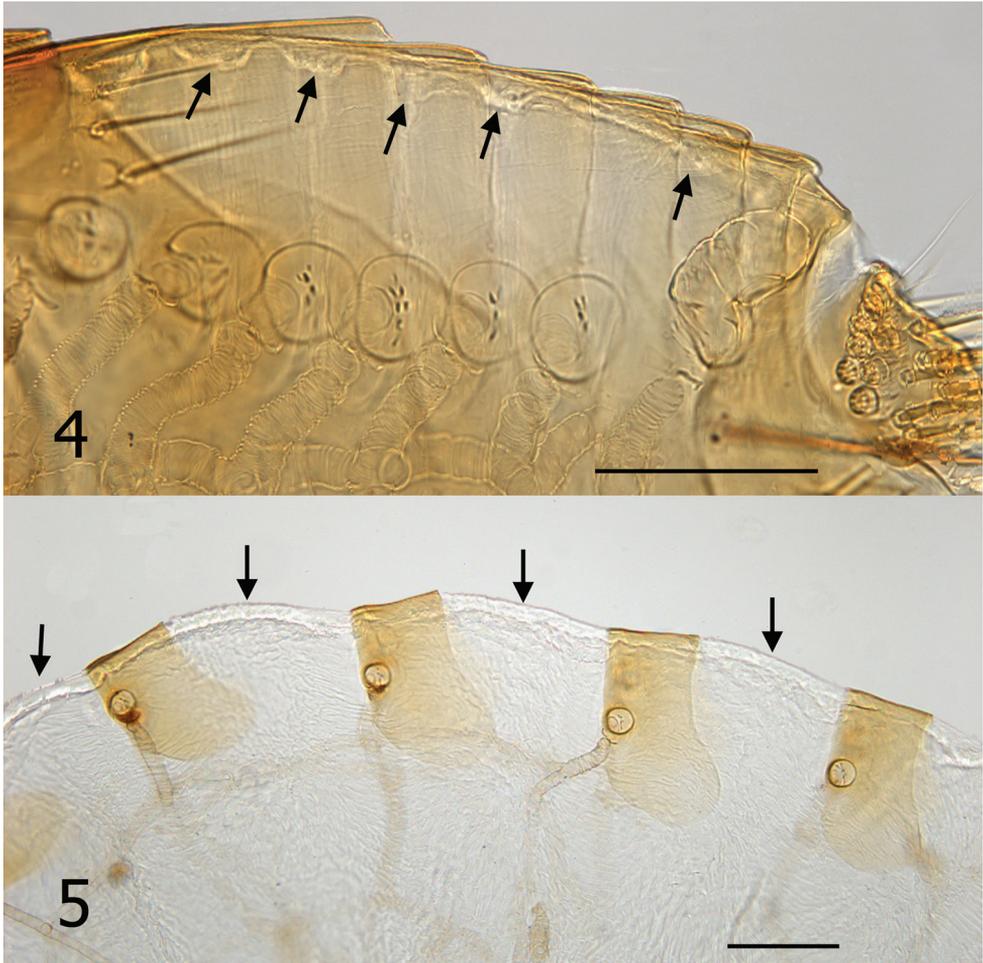
According to Luz et al. (2009), the most common attachment sites for *H. pulex* parasitizing *Molossus rufus* É. Geoffroy and *Molossus molossus* (Pallas) were the ear and tragus. The ear was the site of attachment for 26 of 50 *M. rufus* examined, while 15 were attached to the tragus. Of the 19 specimens of *M. molossus* examined, 12 were attached to the ear and five to the tragus.

Only 11 of the total 69 fleas taken from these two bat species had fleas attached on areas other than the ear and tragus. Esbérard (2001) also reported the head as the most common site of attachment on *M. molossus*. Chen and Moss (2005) determined that the pinna and tragus of *Eptesicus fuscus* Palisot de Beauvois, play important roles in filtering returning echos. They found that any manipulation of the tragus adversely affects the bat's ability to acquire prey and evade obstacles. The large size of the replete *H. pulex* female is nearly as large as the tragus of *L. yerbabuena* (see Fig. 1). The potential adverse effect of this on the bats echolocation ability may be significant. Additional collecting of this flea from *L. yerbabuena* is needed to evaluate if the attachment site immediately at the anterior base of the tragus is a common phenomenon and a potential impairment of the bat's echolocation. *Leptonycteris yerbabuena* are nectivorous and feed primarily on species of *Agave*. Hence, their echolocation ability may be less important than that of insectivorous bat species that require acrobatic agility to capture insects in flight. On the contrary, molossid bats are insectivorous and may be at a disadvantage with fleas attached near the tragus or other parts of the ear pinna. This might be a fascinating area for additional research.



Figures 2–3. *Hectopsylla pulex*. **2** Overview of an unfed female, Pacora, Panama collected from bat guano. Arrow indicates lacinae **3** Overview of a replete gravid female, host: *Leptoncyteris yerbabuena*, White Tail Canyon, Chiracahua Range, Cochise County, Arizona.

Comparison of *H. pulex* from Panama (Tipton and Méndez 1966) and Arizona demonstrate minor differences. The head of Arizona specimens is only slightly convex at posterior occipital area, whereas the occipital area of Panamanian specimens is more convex. There are also minor differences in the metepimeron, tergum I, and tergum II. Arizona specimens have a heavily sclerotized plate on the anterior portion of the



Figures 4–5. Tergites of *Hectopsylla pulex*. **4** Unfed non-gravid female from Pacora, Panama; arrows indicate membrane prior to expansion **5** Replete gravid female, arrows indicate expanded membrane to accommodate expansion from feeding and egg development.

metepimeron bearing six setae and the dorsal portion of the bases of terga I and II are more heavily sclerotized. The overall dimensions of Arizona specimens are slightly larger, resulting in comparably larger measurements of spiracle diameters, head length, and length and width of the vermiform spermatheca.

Acknowledgments

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and collaborative support, and Ambre Delpopolo for providing the original bat image published herein. The senior author acknowledges with gratitude the continued support of Michael F. Whiting, Shawn Clark, and the staff of the Monte L. Bean Life Science Museum, Brigham Young University for providing space, materials and equipment to carry on studies of Siphonaptera.

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The taxonomic accounts of the genus *Symmorphus* Wesmael (Hymenoptera, Vespidae, Eumeninae) from China, with descriptions of three new species

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Abstract

In this study, we recognize and review a total of 19 species of the genus *Symmorphus* Wesmael from China. We also provide a key to these species. Three new species are described and illustrated, namely *Symmorphus* (*Symmorphus*) *tianchiensis* Li & Chen, **sp. n.**, *S. (S.) cavatus* Li & Chen, **sp. n.**, and *S. (S.) nigriclypeus* Li & Chen, **sp. n.** The following four species are newly recorded from China: *Symmorphus* (*S.*) *fuscipes* (Herrich-Schaeffer), *S. (S.) lucens* (Kostylev), *S. (S.) sublaevis* Kostylev, and *S. (S.) violaceipennis* Giordani Soika. In addition, we map the species geographical distributions in China of these 19 species. Type specimens of these three new species are deposited in Chongqing Normal University and Yunnan Agricultural University.

Keywords

Hymenoptera, Vespidae, Eumeninae, *Symmorphus*, new species, China

Introduction

The genus *Symmorphus* Wesmael contains 44 species with two subspecies, and is distributed in the Palearctic, Oriental, Nearctic regions and the northernmost Neotropical region. These species are usually slender and easily recognized by the combination of the following characters: mesoscutum with well-developed notaulices; metasomal tergum 1 distinctly narrower than tergum 2, but not petiolate, with a basal transverse carina and a median longitudinal furrow; and antennal apex in male simple, not forming a recurved hook. The known species of the genus were described or revised in detail by Giordani Soika (1975), Tsuneki (1977), Cumming and van der Vecht (1986), Cumming (1989), Yamane (1990), Gusenleitner (1999, 2000, 2002, 2004, 2010), Kim and Lee (2002, 2006), and so on. However, a systematic research on the Chinese *Symmorphus* is absent. Twelve species were already recorded from China (Giordani Soika 1966, 1986; Li 1981, 1985; Cumming 1989; Gusenleitner 1999, 2000, 2002, 2004). During the study of the Chinese eumenine wasps, 19 species of *Symmorphus* are recognized, including three new species and four new records. In the present paper, a key to all Chinese species of *Symmorphus* is updated and the species geographical distributions in China are mapped (Fig. 22). In addition, we also provide the taxonomic information and global distributions of these species. The key and distributions were produced based on both the examination of specimens and the information extracted from literatures.

Materials and methods

The specimens examined are deposited in the Institute of Entomology and Molecular Biology, Chongqing Normal University, Chongqing, China (CQNU) and Department of Entomology, College of Plant Protection, Yunnan Agricultural University, Kunming (YNAU), respectively. Descriptions and measurements were made under a stereomicroscope (Nikon SMZ1500), and all figures were taken with a stereomicroscope (LEICA EZ4HD) attached to a computer using Leica Application Suite version 2.1.0 software. The ratios used throughout the descriptions were measured in the same amplifying multiple of stereomicroscope. All measurements were taken as the maximal length of body parts measured. Body length was measured from the anterior margin of head to the posterior margin of metasomal tergum 2. For the density description of punctures, the phrase widely spaced means that the intervals between are larger than diameter, moderately spaced means equal to diameter, and whereas closely spaced means less than diameter. The abbreviations used in the text are shown as follows: T1 for metasomal tergum 1, T2 for metasomal tergum 2, S1 for metasomal sternum 1, S2 for metasomal sternum 2, and so on. Terminology principally follows Carpenter (1982) and Cumming and van der Vecht (1986).

Taxonomy

Symmorphus Wesmael, 1836

Symmorphus Wesmael, 1836: 45, subgenus of *Odynerus* Latreille; Li 1985: 115; Cumming 1989: 13–15; Kim and Lee 2006: 27–28.

Type species. *Odynerus elegans* Wesmael, 1833, designated by Richards (1935).

Symmorphus (*Symmorphus*) *tianchiensis* Li & Chen, sp. n.

<http://zoobank.org/FCA23B0A-F2DB-499B-B1B6-15D75C34CBAB>

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

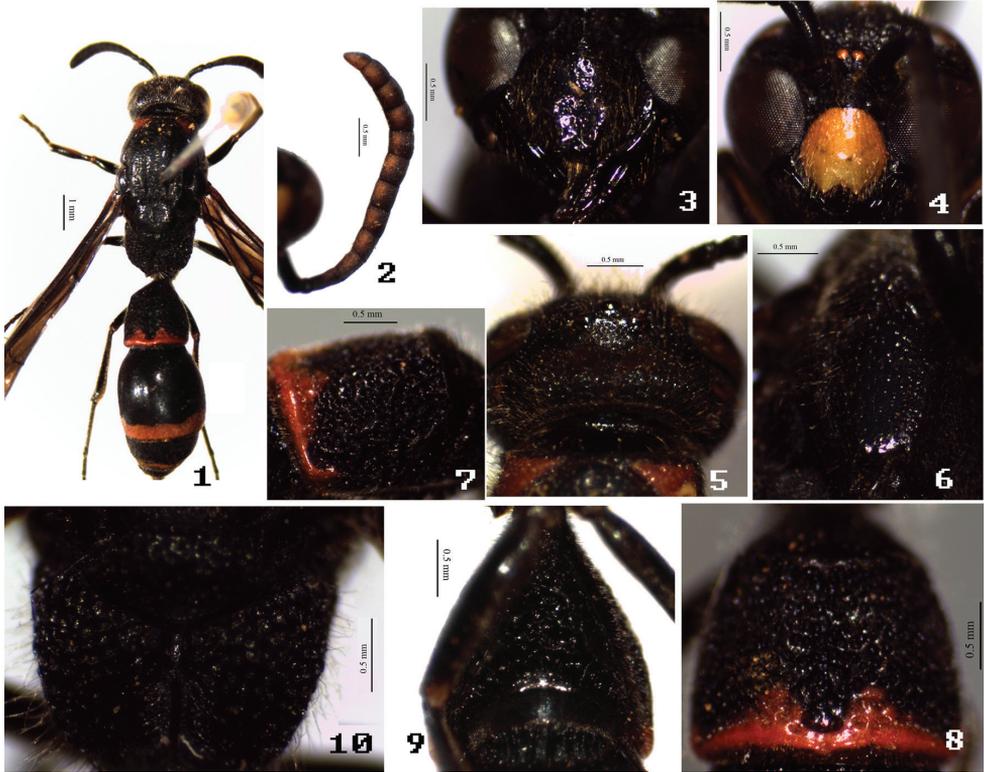
Figs 1–10

Material examined. Holotype. ♀, China, Yunnan Prov., Dali City, Yunlong County, Tianchi National Nature Reserve, 25°52'13.05"N, 99°17'14.33"E, 2579 m, 9.VII.2011, Tingjing Li, No. 1001516 (CQNU); **Paratypes:** 1♀1♂, the same as holotype, Nos. 1001524, 1001517 (CQNU); 1♀, China, Yunnan Prov., Nujiang City, Lanping County, Jinding Town, Xinchengqiao National Forest Park, 26°26'56.36"N, 99°23'04.69"E, 2412 m, 12. VII.2011, Tingjing Li, No. 1004036 (CQNU).

Description. Female (Fig. 1): body length 9.5–10.5 mm, forewing length 10.0–10.5 mm. Black; with the following parts orange-red to red: dorsal pronotal spot, apical border of T1, and subapical border of T2, S2 and T4 (absent in one female paratype); interantennal spot and post-ocular dot orange-yellow; fore tibia inside brown. Wings lightly infuscate. Hairs pale brown; mesosoma with sparse lengthened hairs, in addition to short pubescence.

Head. Clypeus sparsely punctate-puncticulate to foveolate-puncticulate, apex broadly and moderately emarginated, evenly convex, with apical teeth, and slightly reflexed anteriorly (Fig. 3); frons and vertex foveolate-puncticulate, major punctures closely spaced; interantennal carina prominent; cephalic fovea somewhat larger than post ocellus, and foveal interval somewhat less than postocellar distance, cephalic foveal carina indistinct (Fig. 5); occipital carina without submedial incisions.

Mesosoma. Pronotum, except anterior face, foveolate-puncticulate, major punctures closely spaced, more or less costate laterally, anterior face smooth and polish, pronotal carina complete, humeral angle barely projected. Mesoscutum foveolate-puncticulate, major punctures widely spaced medially, moderately spaced anteriorly and posteriorly; notaulus complete; mesepisternum with epicnemial carina dorsally obsolete and ventrally faint (Fig. 6); anterior margin of pseudosternum without high reflexed margin; mesoscutellum foveolate-puncticulate, similar to those on mesoscutum. Dorsal mesepisternum sparsely foveolate-puncticulate, space between punctures smooth and polish, ventral mesepisternum sparsely foveolate-puncticulate, major punctures widely spaced, minor punctures obscure, space between punctures alutaceous; dorsal



Figures 1–10. *Symmorphus (Symmorphus) tianchiensis* Li & Chen, sp. n. **1, 3, 5–10** female, **2, 4** male. **1** general habitus **2** antenna in ventral view **3–4** clypeus **5** vertex in dorsal view **6** mesepisternum in ventral view **7** transverse carina of T1 in lateral view; **8** T1; **9** S1; **10** propodeum.

mesepimeron sparsely foveolate, space between punctures smooth and polish, ventral mesepimeron dull, and coarsely alutaceous. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally, metanotum nearly vertical, dorsal surface narrow. Propodeal dorsum and posterior face coarse, areolate-rugose, propodeal superior shelf moderately long (2.2 times trans-scutal sulcus), lateral face of propodeum striately rugose ventrally, areolate-rugose dorsally, propodeal submedian carina present ventrally, faint and irregular dorsally (Fig. 10), propodeal valvula short posteriorly, fused distally to submarginal carina, propodeal orifice somewhat elliptic dorsally (Fig. 10).

Metasoma. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate (Figs 7–8), postcarinal length of T1/apical width=0.73, carinal width/apical width=0.79, postcarinal sides slightly convergent toward base, transverse carina laterally faint (Fig. 7), longitudinal furrow narrowly and shallowly depressed, with deeper narrow medial sulcus (Fig. 8), apical margin indistinctly depressed; S1 flat and without basal carina anteriorly, areolate-rugose medially and posteriorly, without median longitudinal ridge, and lateral oblique ridges strongly prominent (Fig. 9); segment 2 foveolate-puncticulate basally, major punctures more closely spaced; T3–5

sparsely punctate-puncticulate to foveolate-puncticulate, major punctures subapically; segment 2 except base and S3–6 with evenly minor punctures.

Male. Body length 7.5 mm, forewing length 8.5 mm. Sculpture, punctuation, hairs, and coloration similar to female except as follows: clypeus entirely light yellow to yellow (Fig. 4), except apical margin brown red; antennal segments 3–13 pale brown ventrally (Fig. 2); dorsal pronotal spot, apical border of T1, and subapical border of both T2 and S2 orange-red; mesepisternum dorsally with small yellow spot; fore tibia inside pale brown, fore tarsus brown apically; antennal tyloids absent, segment 13 length/width=1.56 (Fig. 2).

Distribution. China (Yunnan).

Remarks. This species is similar to *S. (S.) sichuanensis* by S1 without basal carina, T1 with transverse carina laterally faint to obsolete, and mesepisternum with epicnemial carina dorsally obsolete; but can be easily distinguished from the similar species and other members of the genus by the combination of the following characters: body moderately long; in both female and male, dorsal pronotal spot orange-red (Figs 1, 5); in female, mesepisternum with epicnemial carina ventrally faint; in male, antenna without tyloids (Fig. 2), and subapical border of both T2 and S2 orange-red.

Etymology. It is named after the type locality of the species, Tianchi National Nature Reserve in Dali city, Yunnan of China.

***Symmorphus (Symmorphus) cavatus* Li & Chen, sp. n.**

<http://zoobank.org/AA3DF78F-D616-4B15-9E0E-8E5FE65CAD35>

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

Figs 11–16

Material examined. Holotype. ♀, China, Yunnan Prov., Xishuangbanna, Jinghong City, Jinuo mountain, 22°02'17.81"N, 101°00'15.36"E, 901 m, 12.IV, 2010, Rui Zhang, No. 1004037 (YNAU).

Description. Female (Fig. 11): body length 6.5 mm, forewing length 7.0 mm. Black; with the following parts pale brown: basal transverse band of clypeus, post-ocular dot, medially uninterrupted dorsal pronotal band, large dorsal mesepisternal spot, tegula, large mesoscutellar spot apically, apex of T1, apical margin of both T2 and S2, apex of fore femur, and fore tibia largely; fore and mid tarsi dark brown. Wings lightly infusate. Hairs pale brown, mesosoma without sparse lengthened hairs, in addition to short pubescence.

Head. Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically, space between punctures smooth and polish; clypeal apex truncated, clypeus evenly convex, without apical teeth (Fig. 12). Frons and vertex foveolate-puncticulate, major punctures closely spaced; interantennal carina prominent; cephalic fovea somewhat smaller than post ocellus, foveal interval subequal to postocellar distance, without cephalic foveal carina; occipital carina with 2 submedial incisions.



Figures 11–16. Female of *Symmorphus* (*Symmorphus*) *cavatus* Li & Chen, sp. n. **11** general habitus **12** clypeus **13** vertex in dorsal view **14** T1–2 **15** mesepisternum; **16** propodeum.

Mesosoma. Pronotum, except anterior face, foveolate-puncticulate, with major punctures closely spaced, more or less costate laterally; anterior face distinctly imbricate; pronotal carina dorsally obsolete; humeral angle slightly projected. Mesoscutum foveolate-puncticulate, major punctures closely spaced anteriorly and posteriorly, widely spaced laterally; notaulus complete; epicnemial carina complete; pseudosternum anterior margin without high reflexed margin. Mesoscutellum foveolate-puncticulate, major punctures closely spaced, with shallowly medial furrow. Mesepisternum with complete epicnemial carina (Fig. 15), dorsally punctate-puncticulate and minor punctures distinct basally, other parts foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron dull and densely striate. Metanotum primarily oblique and not vertical, dorsally dull, coarse and areolate-rugose. Propodeum dull, densely striate laterally, areolate-rugose dorsally, posterior face deeply heart-shaped hollowed, margin reflexed, complete and sharply defined throughout (Fig. 16),

propodeal superior shelf short, 2 times trans-scutal sulcus; propodeal submedian carina entirely absent, propodeal valvula short posteriorly, fused distally to posterior margin; propodeal orifice small and indistinct.

Metasoma. Metasomal tergum 1 with postcarinal area foveolate-puncticulate, major punctures densely spaced, postcarinal length short, postcarinal length/apical width=0.68, carinal width/apical width=0.85, postcarinal sides barely convergent toward base, transverse carina complete, longitudinal furrow narrowly and shallowly depressed, with deeper narrow medial sulcus, apical margin indistinctly depressed (Fig. 14); S1 rugose anteriorly, basal carina inflated and raised posteriorly, fused to lateral oblique ridges, with median longitudinal ridge, lateral oblique ridges slightly prominent, median longitudinal ridge flanked by longitudinal carinate rugae; segment 2 foveolate-puncticulate, major punctures widely spaced from base to apex, minor punctures connected by obscure imbricate subsulpture; T3–T5 and S3 with densely foveolate toward apex; S3–S6 with imbricate subsulpture.

Male. Unknown.

Remarks. This species is easily distinguished at once from all other species of *Symmorphus* by the combination of the following characters: propodeal posterior face deeply hollowed (Fig. 16), and occipital carina with 2 submedial incisions, in other species of the genus propodeal posterior face not hollowed.

Distribution. China (Yunnan).

Etymology. The specific name is the Latin *cavatus* (= hollow), which refers to propodeal posterior face of the species deeply hollowed.

***Symmorphus (Symmorphus) nigriclypeus* Li & Chen, sp. n.**

<http://zoobank.org/C5EFD701-81FE-44EA-B533-E1531BA283FD>

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

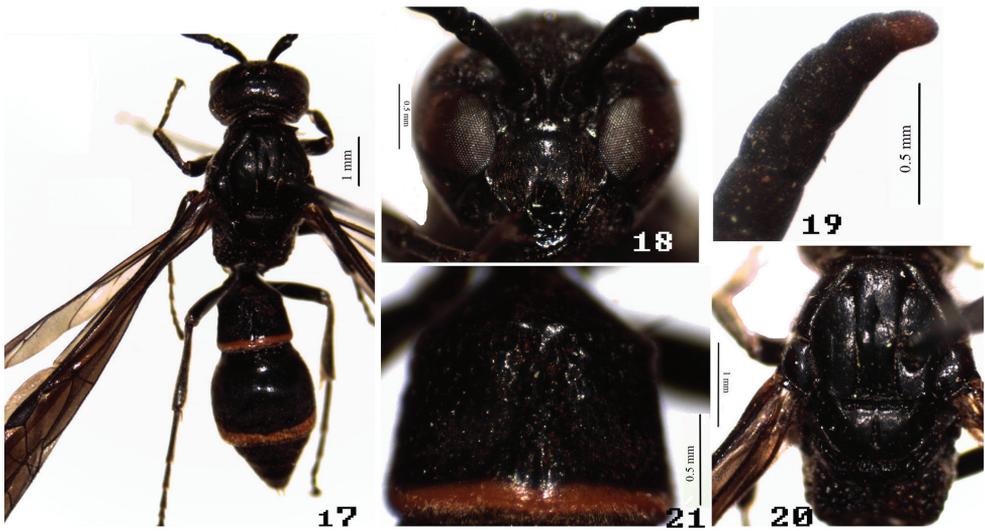
Figs 17–21

Material examined. Holotype. ♂, China, Tibet, Nyingchi, Medog County, 29°71'N, 95°63'E, 3026 m, 13.VII.2013, Yong Zhou, No. 1004038 (CQNU).

Description. Male (Fig. 17): body length 7.0 mm, forewing length 9.0 mm. Black; apical margin of T1 orange-red, subapical margin of both T2 and S2 orange-yellow. Wings lightly infusate. Hairs white, mesosoma with sparse lengthened hairs, in addition to short pubescence.

Head. Clypeus moderately punctate-puncticulate, clypeal apex deeply emarginated and with acute apical toothed laterally (Fig. 18). Frons punctate-puncticulate to foveolate-puncticulate, major punctures closely spaced; vertex punctate-puncticulate and barely foveolate-puncticulate, minor punctures closely spaced; interantennal carina prominent; male antennal segments 10–13 with tyloids, segment 13 length/width=1.43 (Fig. 19).

Mesosoma. Pronotum, except anterior face, punctate-puncticulate to foveolate-puncticulate, major punctures widely spaced, more or less costate laterally, minor



Figures 17–21. Male of *Symmorphus* (*Symmorphus*) *nigriclypeus* Li & Chen, sp. n. **17** general habitus **18** clypeus **19** antennal apex in lateral view **20** mesosoma in dorsal view **21** T1.

punctures evenly and closely spaced; anterior face obscurely imbricate; pronotal carina complete; humeral angle moderately projected. Mesoscutum punctate-punctulate to foveolate-punctulate, primarily punctate-punctulate, minor punctures evenly and densely spaced, major punctures great widely spaced; notaulus complete and distinctly deep (Fig. 20); pseudosternum anterior margin without high reflexed margin. Mesoscutellum similar to mesoscutum. Dorsal mesepisternum sparsely punctate-punctulate to foveolate-punctulate, major punctures very widely spaced, shallow and indistinct, minor punctures obscure; ventral mesepisternum foveolate-punctulate, major punctures widely spaced, minor punctures obscure. Mesepimeron striately rugose. Metanotum nearly vertical, dorsal surface narrow, foveolate-punctulate dorsally, striately rugose ventrally. Propodeum striately rugose laterally, areolate-rugose dorsally; posterior face obscure striately rugose, propodeal superior shelf length 3.1 times trans-scutal sulcus, propodeal orifice broadly and rounded, propodeal submedian carina complete and sharply defined throughout; propodeal valvula short posteriorly, fused distally to submarginal carina.

Metasoma. Metasomal tergum 1 with postcarinal area foveolate-punctulate, postcarinal length/apical width=0.71, carinal width/apical width=0.85, postcarinal sides slightly convergent toward base, transverse carina complete, longitudinal furrow broadly depressed, with deeper narrow medial sulcus; apical margin indistinctly depressed (Fig. 21); S1 rugose anteriorly, basal carina deeply curved posteriorly, fused to lateral oblique ridges, median longitudinal ridge strongly prominent and flanked by longitudinal carinate rugae; segment 2 punctate-punctulate, minor punctures connected by obscure imbricate subsclpture; T3–5 sparsely foveolate-punctulate, major punctures subapically. Segments 3–6 with imbricate subsclpture.

Female. Unknown.

Remarks. This species is easily distinguished from all other species of *Symmorphus* by the combination of the following characters: body black, except apical margin of T1, and subapical margins of both T2 and S2 (Fig. 17); clypeal apex deeply emarginated and with acute apical toothed laterally (Fig. 18).

Distribution. China (Tibet).

Etymology. The specific name *nigrichypeus* is the Latin *nigr* (= black) + *chypeus* (=clypeus), which refers to the clypeus in male of the species black.

***Symmorphus (Symmorphus) ambotretus* Cumming, 1989**

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

Symmorphus ambotretus Cumming 1989: 28; Kim and Lee 2002: 284 (key), 286, figs 1–6; 2006: 28, 29 (key).

Material examined. 1♀, China, Yunnan Prov., Dali, North Gucheng, 9.V.2007, Rui Zhang; 1♀, China, Yunnan Prov., Dali, Yunlong, Luodun Town, 10.VII.2011, Tingjing Li; 1♀, China, Yunnan Prov., Nujiang, Lanping, Yingpan Town, 13.VII.2011, Zhenhu Wu; 1♀, China, Yunnan Prov., Lijiang, Ninglang, Daxing Town, 25.VII.2011, Tingjing Li; 6♂♂, China, Yunnan Prov., Dehong, Yingjiang, Tongbiguan Natural reserve, 3.V.2013; 1♀, China, Chongqing, Wansheng, Heishangu, 4.V.2011, Zhenhu Wu.

Distribution. China (Sichuan, Yunnan, Chongqing); Nepal; Korea.

***Symmorphus (Symmorphus) angustatus* (Zetterstedt, 1838)**

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

Odynerus angustatus Zetterstedt, 1838: 457.

Odynerus suecicus de Saussure, 1855: 187 (key), 190, pl. X fig. 3.

Odynerus laeviventris Thomson, 1874: 86; Gussakovskii 1932: 55.

Symmorphus angustatus (Zetterstedt): van der Vecht 1971: 127; van der Vecht and Fischer 1972: 119 (cat.); Cumming 1989: 3, 5, 23 (key), 44; Kurzenko 1995: 318; Kim and Lee 2002: 285 (key), 290, figs 33–40; 2006: 28 (key), 35–36; Gusenleitner 2003: 864; Castro and Dvořák 2009: 299.

Symmorphus hakutozanus Tsuneki, 1986: 23–24, 26; Cumming 1989: 44.

Symmorphus nansetsurei Tsuneki, 1986: 26, 27; Cumming 1989: 44.

Symmorphus iwatai Yamane, 1990: 115 (key), 127–128, synonymized by Kurzenko 1995.

Material examined. 1♀, China, Jilin Prov., Tonghua, Mehekou, 22.VIII.1993, Zhihong Li.

Distribution. China (Jilin); Norway; Sweden; Finland; Denmark; France; Germany; Austria; Greece; Turkey; Belarus; Russia (to Primorskij Krai); Kazakhstan; Mongolia; the Korean Peninsula; Japan.

Symmorphus (Symmorphus) apiciornatus (Cameron, 1911)

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

Ancistrocerus apiciornatus Cameron, 1911: 288.

Odynerus (Ancistrocerus) apiciornatus (Cameron): von Schulthessi 1934: 74; Giordani Soika 1941: 232.

Symmorphus apiciornatus (Cameron): van der Vecht and Fischer 1972: 119; Giordani Soika 1975: 150, 156, figs 4, 9; Tsuneki 1977: 15; Giordani Soika 1986: 153; Cumming 1989: 3, 5, 24 (key), 79; Kurzenko 1995: 316; Kim and Lee 2002: 286 (key), 295, figs 70-78; 2006: 29 (key), 38-40.

Symmorphus seoulensis Tsuneki, 1986: 22, figs 66-67, female; Cumming 1989: 5, 79.

Material examined. 1♀, China, Beijing, Haidian, 29.IV.1952. Jikun Yang; 1♀, China, Beijing, Gongzhufen, 12.V.1952. Jikun Yang; 1♂, China, Shaanxi Prov., Baoji, Fengxian, Jialing River, 26.V.2007, Xiaoyu, Jiang.

Distribution. China (Beijing, Shaanxi, Fujian, Guangdong, Jiangsu, Sichuan); Russia; South Korea; Japan.

Symmorphus (Symmorphus) aurantiopictus Giordani Soika, 1986

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

Symmorphus aurantiopictus Giordani Soika, 1986: 154, fig. 47; Cumming 1989: 3, 5, 22 (key), 81.

Material examined. No specimens examined.

Distribution. China (Jiangsu).

Symmorphus (Symmorphus) bifasciatus (Linnaeus, 1761)

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

Vespa bifasciata Linnaeus, 1761: 419; Richards 1935: 163.

Symmorphus bifasciatus (Linnaeus): van der Vecht and Fischer 1972: 119 (cat.); Li 1985: 115 (key), 117; Cumming 1989: 3, 5, 24 (key), 57; Kurzenko 1995: 315; Kim and Lee 2002: 285 (key), 292, figs 48–54; 2006: 28 (key), 37-38.

Vespa sinuata Fabricius, 1793: 270; Cumming 1989: 5, 57.

Odynerus sinuatus var. *mutinensis* Baldini, 1894: 78, pl. III fig. 6; Cumming 1989: 5, 57.

Symmorphus sparsus Morawitz, 1895: 490; Cumming 1989: 5, 57.

Symmorphus sinuatissimus Richards, 1935: 162; Giordani Soika 1963: 123; Cumming 1989: 5, 57.

Symmorphus mutinensis Baldamus: van der Vecht and Fischer 1972: 122 (cat.); Cumming 1989: 5, 57.

Symmorphus mutinensis auster Giordani Soika, 1975: 150, 160; Cumming 1989: 5, 57.

Symmorphus mutinensis yezoanus Tsuneki, 1977: 16; Cumming 1989: 5, 57.

Material examined. 1♂, China, Chongqing, Jiangjin, Simianshan National Nature Reserve, 6.V.2012, Ju You.

Distribution. China (Jiangsu, Chongqing); Europe, eastward to northeastern Siberia and Far Eastern Russia; Kyrgyzstan; Kazakhstan; Korea; Japan.

***Symmorphus (Symmorphus) foveolatus* Gussakovskii, 1932**

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

Symmorphus foveolatus Gussakovskii, 1932: 55; van der Vecht and Fischer 1972: 121 (cat.); Tsuneki 1986: 27; Li, 1985: 115–116; Cumming 1989: 3, 5, 23 (key), 35; Kurzenko 1995: 317; Kim and Lee 2002: 285 (key), 289, figs 19–24; 2006: 28 (key), 37–38.

Odynerus captivus Smith: von Schulthessi 1934: 66 (key); Yasumatsu 1938: 111, pl. 3 figs 1–5; Kim 1970: 554; 1980: 116. Misidentification.

Material examined. 6♀♀2♂♂, China, Sichuan Prov., Panzhihua, Renhe Town, 28.VII.2011, Tingjing Li.

Distribution. China (Sichuan); Russia; the Korean Peninsula; Japan.

***Symmorphus (Symmorphus) fuscipes* (Herrich-Schaeffer, 1838), new record**

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

Odynerus fuscipes Herrich-Schaeffer, 1838: 18, pl. 18; Cumming 1989: 77 (designation of neotype).

Symmorphus karelicus Morawitz, 1895: 490.

Symmorphus fuscipes (Herrich-Schaeffer): van der Vecht and Fischer 1972: 121 (cat.); Cumming 1989: 3, 5, 22 (key), 77; Kim and Lee 2006: 28 (key), 31.

Material examined. 2♀♀, China, Liaoning Prov., Liaoyang, Gongchangling, Anping, 7.VII.2012. Ju You; 1♀, China, Jilin Prov., Changchun, Dehui, Xiajiadian, 28.VI.2012, Ju You; 1♀, China, Jilin Prov., Baishan, Linjiang, Naozhi Town, 7.VII.2012, Ju You.

Distribution. China (new record: Liaoning, Jilin); Norway; Sweden; Finland; Netherlands; Germany; Austria; Belarus; Mongolia; Russia.

***Symmorphus (Symmorphus) hoozanensis* (von Schulthess, 1934)**

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

Odynerus hoozanensis von Schulthess, 1934: 67.

Symmorphus hoozanensis (von Schulthess): Cumming, 1989: 3, 5, 21 (key), 26.

Material examined. No specimens examined.

Distribution. China (Taiwan).

***Symmorphus (Symmorphus) lucens* (Kostylev, 1938)**

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

Odynerus lucens Kostylev, 1938: 304; Cumming 1989: 66 (designation of lectotype).

Symmorphus lucens (Kostylev): Gussakovskii 1932: 55; van der Vecht and Fischer 1972: 121 (cat.); Cumming 1989: 3, 5, 24 (key), 66; Kim and Lee 2002: 285 (key), 292, figs 41–47; 2006: 29 (key), 36–37.

Symmorphus ishikawai Giordani Soika, 1975: 151, 159; Cumming 1989: 5, 66.

Material examined. 2♀♀, China, Inner Mongolia, Helan Mountain, Gulamuxiaosong Hill, 30.VII.2010, Jian Li & Junzhe Xue; 1♀, China, Inner Mongolia, Helan Mountain, Halawu Ravine, 20.VII.2006, Ming Luo; 1♀, China, Inner Mongolia, Helan Mountain, Yushuwan, 27.VII.2010, Fangzhou Ma.

Distribution. China (new record: Inner Mongolia), Russia: southern Siberia to Sakhalin; Korea; Japan.

***Symmorphus (Symmorphus) mizuhonis* Tsuneki, 1977**

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

Symmorphus mizuhonis Tsuneki, 1977: 15–20; Cumming 1989: 3, 5, 22 (key), 54; Kurzenko 1995: 316; Kim and Yoon 1996: 205; Kim and Lee 2002: 285 (key), 287, figs 14–18; 2006: 28 (key), 31–32; Castro and Dvořák 2009: 300.

Symmorphus kurentzovi Kurzenko, 1981: 104, figs 111–116; Cumming 1989: 5, 54.

Symmorphus iiyamai Tsuneki, 1986: 26 (key), fig. 70, male; Cumming 1989: 5, 54.

Symmorphus shiroyamai Tsuneki, 1986: 26 (key), 27, fig. 71, male; Cumming 1989: 5, 54.

Symmorphus piceanus Tsuneki, 1986: 26 (key), 27, fig. 72; Cumming 1989: 5, 54.

Symmorphus sassai Tsuneki, 1986: 26 (key), 27, fig. 73; Cumming 1989: 5, 54.

Material examined. 2♀♀4♂♂, China, Yunnan Prov., Diqing, Deqin, Near the county, 19.VII.2011, Tingjing Li; 4♀♀, China, Yunnan Prov., Dali, Yunlong, Tianchi, 9.VII.2011, Tingjing Li.

Distribution. China (Yunnan, Sichuan, Taiwan); Russia: Irkutsk, Primorskij Krai; Kazakhstan; North Korea; Japan.

***Symmorphus (Symmorphus) ornatus* Gusenleitner, 2000**

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

Symmorphus ornatus Gusenleitner, 2000: 939, 945.

Material examined. No specimens examined.

Distribution. China (Taiwan).

***Symmorphus (Symmorphus) sichuanensis* Lee, 1981**

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

Symmorphus sichuanensis Lee, 1981: 423, fig. 1; Li 1985: 115-116; Cumming 1989: 3, 5, 38.

Material examined. 3♀♀: China, Sichuan Prov., Leshan City, Emeishan, Gaoqiao Town, Yanshi Village, 11.VIII.2011, Tingjing Li.

Distribution. China (Sichuan); Thailand.

***Symmorphus (Symmorphus) sublaevis* Kostylev, 1940, new record**

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

Odynerus sublaevis Kostylev, 1940: 40.

Symmorphus sparsus Morawitz: Giordani Soika 1963: 123. Misidentification.

Symmorphus sublaevis (Kostylev): van der Vecht and Fischer 1972: 122 (cat.); Cumming 1989: 3, 5, 24 (key), 68.

Material examined. 5♂♂, China, Ningxia, Jingyuan, Xixia Forest, 15–16.VII.2008, Xiumin Li; 1♂, China, Ningxia, Longde, Sutai Forest, 1–2.VII.2008, Xinpu Wang; 1♂, China, Ningxia, Guyuan, Lvyuan Forest, 9–10.VII.2008, Guodong Ren.

Distribution. China (new record: Ningxia); Kyrgyzstan; Kazakhstan.

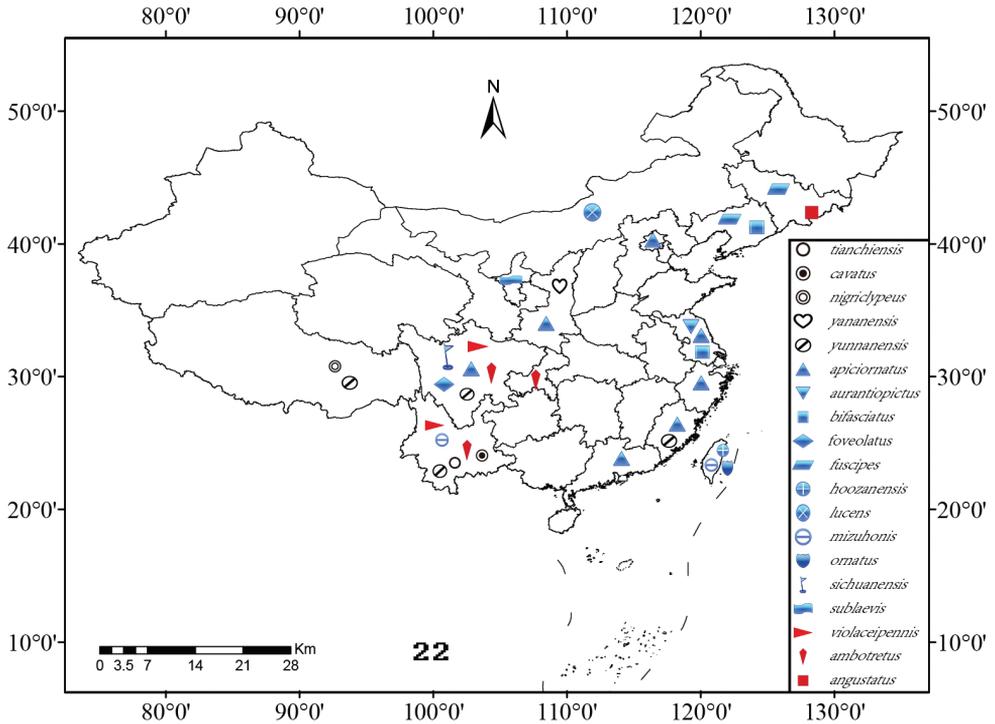
***Symmorphus (Symmorphus) violaceipennis* Giordani Soika, 1966, new record**

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

Symmorphus violaceipennis Giordani Soika, 1966: 102; Cumming 1989: 3, 5, 22 (key), 53.

Material examined. 10♀♀, China, Yunnan Prov., Dali, Yunlong, Tianchi, 9.VII.2011, Tingjing Li; 9♀♀, China, Yunnan Prov., Nujiang, Lanping, Yingpan Town, 12.VII.2011, Zhenhu Wu; 1♀, China, Sichuan Prov., Kangding, Paoma Mountain, 7.VII.2005, Hu Zhou.

Distribution. China (new record: Yunnan, Sichuan); India; Nepal.



Figures 22. The species geographical distributions of the genus *Symmorphus* in China.

***Symmorphus (Symmorphus) yananensis* Gusenleitner, 2002**

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

Symmorphus yananensis Gusenleitner, 2002: 345.

Material examined. No specimens examined.

Distribution. China (Shaanxi).

***Symmorphus (Symmorphus) yunnanensis* Gusenleitner, 2002**

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

Symmorphus yunnanensis Gusenleitner, 2002: 345; 2004: 1104.

Material examined. 5♀11♂♂, China, Yunnan Prov., Diqing, Deqin, Near the county, 19.VII.2011, Tingjing Li; 1♂, China, Tibet, Changdu, Mangkang, 3508 m, 5.VII.2013, Yong Zhou.

Distribution. China (Yunnan, Tibet, Fujian).

Key to the Chinese species of the genus *Symmorphus* Wesmael

- 1 Metasomal tergum 2 obtusely angled basally in profile, and S2 abruptly truncate behind basal sulcus **2**
- Metasomal tergum 2 gradually rounded basally in profile, and S2 flat to slightly convex behind basal sulcus..... **3**
- 2 Pronotal carina complete; occipital carina submedially incised.....
..... ***S. (S.) ambotretus* Cumming**
- Pronotal carina obsolete dorsolaterally, only distinct medially; occipital carina submedially at most depressed, but not incised ***S. (S.) hoozanensis* (Schulthess)**
- 3 Mesosoma with sparse lengthened hairs, in addition to dense short hairs **4**
- Mesosoma without sparse lengthened hairs, in addition to dense short hairs... **10**
- 4 Metasomal sternum 1 with basal carina **5**
- Metasomal sternum 1 without basal carina **7**
- 5 Body black, except apical margin of T1 and subapical margin of both T2 and S2 (Fig. 17); clypeal apex deeply emarginated (Fig. 18).... ***S. (S.) nigriclypeus* sp. n.**
- Coloration of body different from the above, or clypeal apex not deeply emarginated..... **6**
- 6 Propodeum with superior shelf moderately long, medial length 2.50–3.11 times length of trans-scutal sulcus; in female, cephalic fovea very small and its maximum diameter 0.25–0.33 times trans-scutal sulcus length, clypeus deeply emarginated apically and with teeth slightly reflexed anteriorly.....
..... ***S. (S.) violaceipennis* Giordani Soika, new record**
- Propodeum with superior shelf shorter, medial length 1.38–2.21 times length of trans-scutal sulcus; in female, cephalic fovea larger and its maximum diameter greater than 0.50 times trans-scutal sulcus length, clypeus moderately emarginated apically and without reflexed teeth ***S. (S.) mizuhonis* Tsuneki**
- 7 Metasomal tergum 1 with complete transverse carina
..... ***S. (S.) angustatus* (Zetterstedt)**
- Metasomal tergum 1 with transverse carina laterally faint to obsolete **8**
- 8 Mesepisternum without epicnemial carina ... ***S. (S.) foveolatus* Gussakovskij**
- Mesepisternum with or at least faint epicnemial carina ventrally **9**
- 9 Mesosoma with orange-red maculation (Figs 1, 5); male antenna without tyloids (Fig. 2) ***S. (S.) tianchiensis* sp. n.**
- Mesosoma black; male antenna with tyloids ***S. (S.) sichuanensis* Lee**
- 10 Pronotal carina obsolete dorsolaterally, only distinct medially; S1 without basal carina ***S. (S.) aurantiopictus* Giordani Soika**
- Pronotal carina complete; S1 with basal carina **11**
- 11 Posterior face of propodeum deeply hollowed (Fig. 16); in female, occipital carina with 2 submedial incisions..... ***S. (S.) cavatus* Li & Chen, sp. n.**
- Posterior face of propodeum not hollowed, at most depressed; occipital carina without submedial incisions **12**

- 12 Submedian carina of propodeum strongly developed as a high and sharp complete carina; T1 in postcarinal area distinctly narrowed toward base.....
..... ***S. (S.) fuscipes (Herrich-Schaeffer), new record***
- Submedian carina of propodeum usually not forming a high and sharp carina; T1 in postcarinal area barely to moderately narrowed toward base..... **13**
- 13 Lateral and posterior faces of propodeum dull and finely striate..... **14**
- Lateral face of propodeum not dull, striately to areolately, posterior face shiny, nearly smooth..... **17**
- 14 Maculation, except male clypeus, red..... ***S. (S.) yunnanensis Gusenleitner***
- Maculation ivory to yellow **15**
- 15 Metasomal sternum 1 without basal carina ***S. (S.) yananensis Gusenleitner***
- Metasomal sternum 1 with basal carina **16**
- 16 Basal band of clypeus wider in female; punctures on mesonotum, mesopleuren and apex of T2 denser than those of the related species
..... ***S. (S.) ornatus Gusenleitner***
- Basal band of clypeus relatively narrower in female; punctures on mesonotum, mesopleuren and apex of T2 sparser ... ***S. (S.) apiciornatus (Cameron)***
- 17 Dorsal mesepisternum foveolate-puncticulate, with major punctures large and densely spaced; in male, antennal segment 13 moderately long to long, length in profile 1.00–1.18 times its maximum width; in female, clypeus moderately emarginated apically ***S. (S.) bifasciatus (Linnaeus)***
- Dorsal mesepisternum punctate-puncticulate to foveolate-puncticulate, with major punctures small to moderate and sparsely spaced; in male, antennal segment 13 short to long, length in profile 0.60–1.15 times its maximum width; in female, clypeus shallowly to moderately emarginated apically **18**
- 18 Metasomal tergum 2 nearly uniformly foveolate-puncticulate, with major punctures slightly larger and more closely spaced toward base; mesosoma at least with yellow dorsal pronotal spot or band ***S. (S.) sublaevis (Kostylev), new record***
- Metasomal tergum 2 foveolate-puncticulate basally to punctuate-puncticulate apically, with major punctures indistinct on apical half; mesosoma black
..... ***S. (S.) lucens (Kostylev), new record***

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Normal University, Hohhot, China) for providing us with the specimens deposited in the insect collections under their care. This research was supported by the National Natural Science Foundation of China (Nos: 31372247, 31000976, 31372265), the Par-Eu Scholars Program, Chongqing Science and Technology Commission (cstc2013j-cyjA80015) and Key Foundation of Chongqing Normal University (12XLZ07).

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A new species of *Grotea* Cresson (Hymenoptera, Ichneumonidae, Labeninae) from Colombia

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Abstract

The genus *Grotea* has 18 described species. A new species, *Grotea villosissima* sp. n., is described here and its host information included. This is the first record of *Grotea* for Colombia.

Keywords

Ichneumonoidea, Groteini, South America, Neotropics, taxonomy, bee parasitoid, *Chilicola*, Labeniformes, host record

Introduction

The Labeninae is a group of parasitoid wasps with a mainly Gondwanan distribution (Townes 1969; Gauld 1983; Wahl 1993, Gauld 2000); although most of its members occur in the Australasian or the Neotropical region, two of its genera, *Labena* and *Grotea*, occur in North America (Townes and Townes 1960; Slobodchikoff 1970, Gauld 2000). According to Gauld and Wahl (2000), those exceptions provide evidence of the spread of some members of this subfamily towards the north after the establishment of the Mesoamerican land bridge (Gauld and Wahl 2000, Gauld 2000).

The described species of *Grotea* can be grouped in 4 species-groups: *Grotea anguina* species-group, *Grotea superba* species-group, *Grotea chiloe* species-group and *Grotea gayi* species-group (Wahl 1993). According to Gauld and Wahl (2000) *Grotea* originated in southern South America, diversified in tropical South America, and colonized North America recently across the Mesoamerican land bridge. Proof of this is that the more basal taxa of *Grotea* are endemic to Chile and that the richness of species and the richness of species groups are highest in South America. *Grotea* comprises 18 species (Yu et al. 2005): 9 occur in South America, 8 in Central America and 3 in North America (Yu et al. 2005). From the 4 species-groups of *Grotea*, the *anguina* species-group is the only one that occurs outside the Gondwanan region (South America, south of equator) (Gauld 2000).

Grotea species parasitize bee hosts of the genera *Ceratina* Latreille, 1802 (Graenicher 1905; Rau 1928; Daly et al. 1967; Slobochikoff 1970), *Chilicola* Spinola, 1851 (Packer 2004; González and Giraldo 2009), *Megachile* Latreille, 1802 and *Manuelia* Vachal, 1905 (Janvier 1967; Gauld 2000; Gauld and Wahl 2000).

The aim of this paper is to describe a new species collected from a nest of *Chilicola* (subgenus *Oroediscelis*) *deborahae* Gonzalez, 2009 (Gonzalez and Giraldo 2009) found in Boyaca, Colombia. This is the first record of *Grotea* for Colombia.

Material and methods

A nest of *Chilicola* (Colletidae) was found by my colleague Victor González in dry branches of *Espeletia argentea*. A *Grotea* specimen emerged from one of the cells. After comparing this specimen with the descriptions made by Cameron (1886), Cresson (1864, 1874, 1879), Gauld (2000), Porter (1989), Schmiedeknecht (1907), Slobodchikoff (1970), Spinola (1851), Thunberg (1822) and Townes and Townes (1960) it was clear that the specimen belongs to a new species. The morphological terminology used in the description of *G. villosissima* sp. n. follows Gauld (1991, 2000).

The holotype is preserved at the Museo de Entomología “Francisco Luis Gallego”, Universidad Nacional, sede Medellín (UNCM).

Systematics

Genus *Grotea* Cresson, 1864

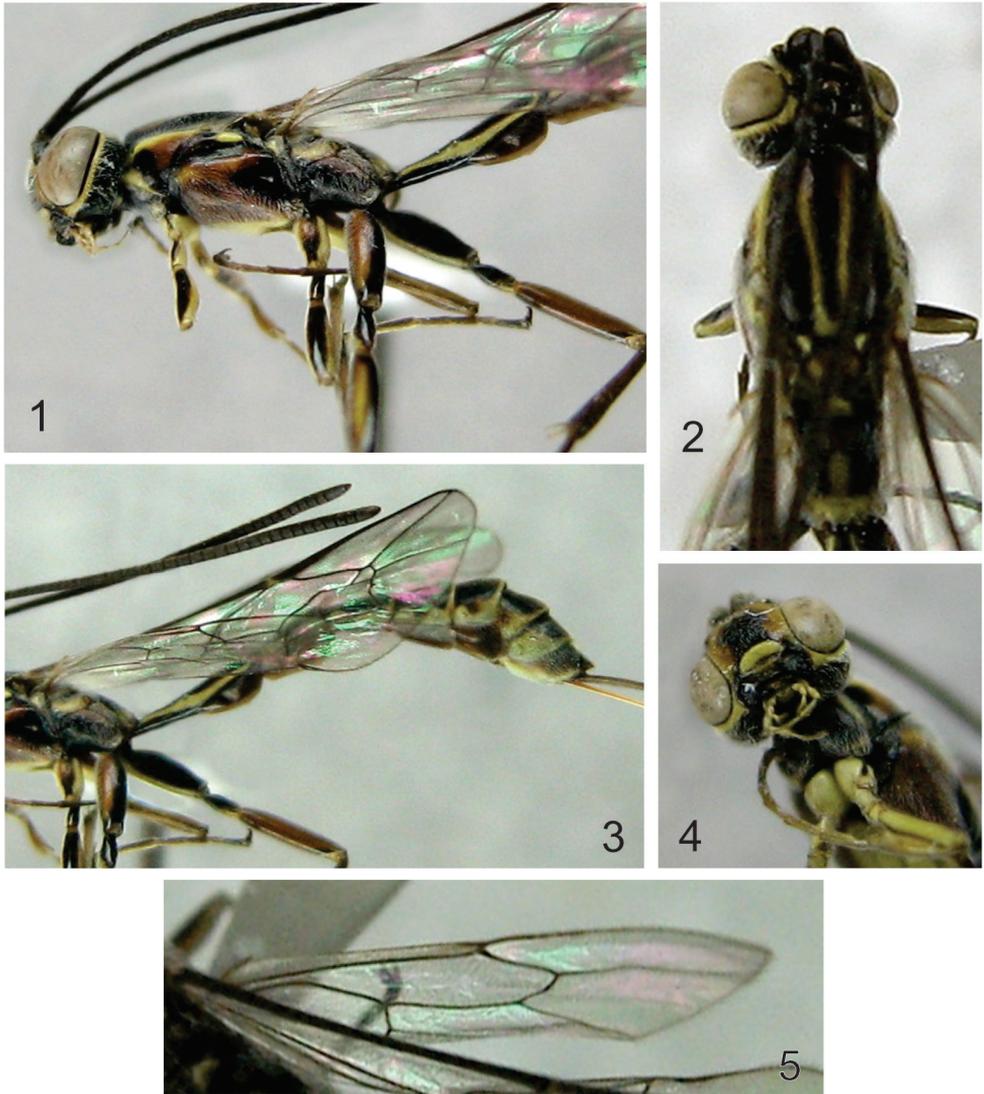
Grotea villosissima Herrera-Flórez, sp. n.

<http://zoobank.org/C7B7AD5D-68C4-49BF-84E1-139B6EA04070>

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

Figures 1–10

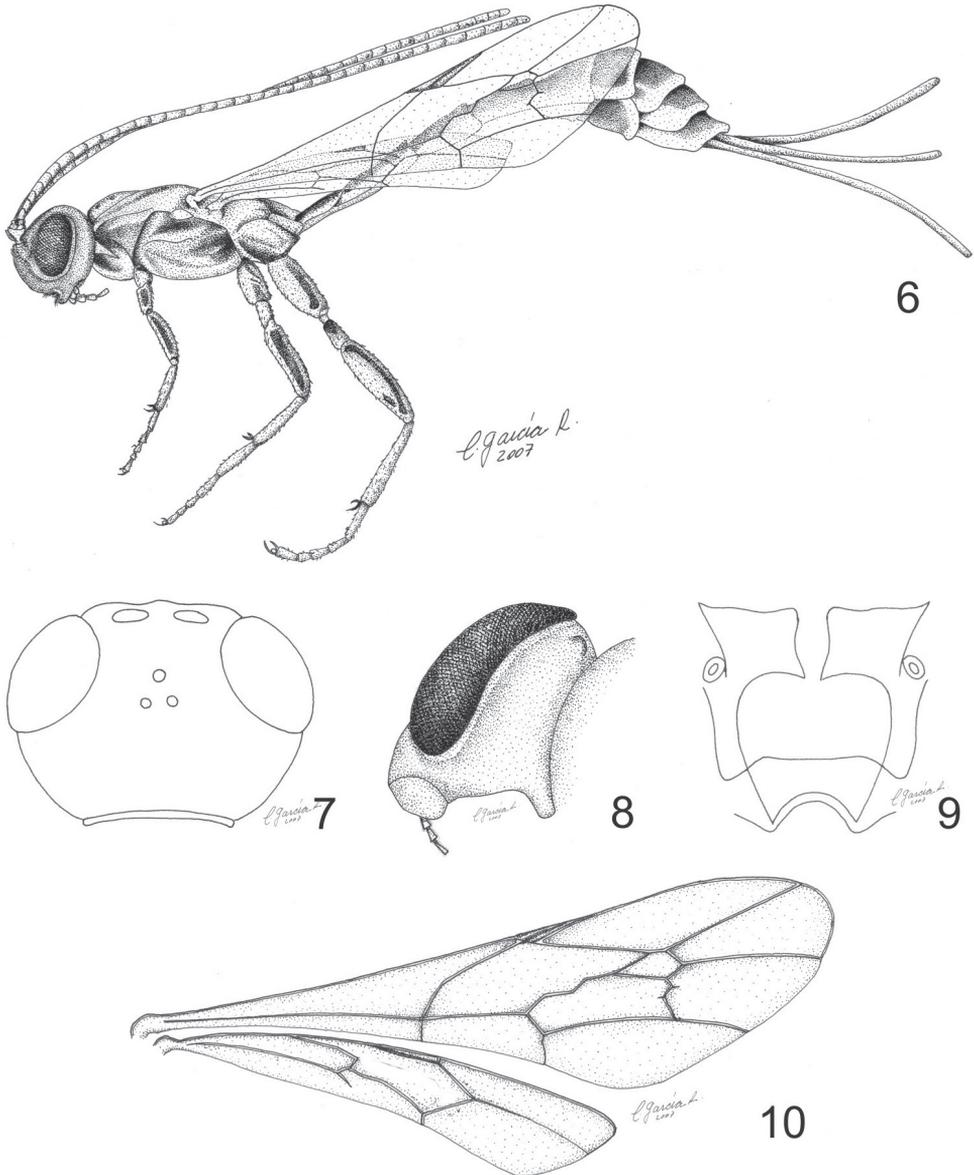
Material examined. *Holotype*: female, “COLOMBIA: Boyacá: Arcabuco. Santuario de Fauna y Flora de Iguaque, Camino de la Laguna, 5°70'N, 73°46'W, 3400–3600m,



Figures 1–5. Photographs of *Grotea villosissima* sp. n. **1** Head, mesosoma and first tergite, lateral view **2** Head, mesosoma, dorsal view **3** Part of mesosoma and metasoma, lateral view **4** Head and part of mesosoma, ventral view **5** Hind wing.

emergió de celda en nido de *Chilicola* (*Oroediscelis*) sp. n. (Apoidea, Colletidae). Ese nido estaba en ramas secas de *Espeletia argentea*, 23 Agosto 2003, leg.V.González (UNCM)”.

Diagnosis. This new species can be recognized from other described species of *Grotea* by the following combination of characters: gena close to the junction of occipital and hypostomal carinae with inwards genal projections (Fig. 8); propodeum with anterior transverse carina centrally weak and indented (Fig. 9); metasoma with



Figures 6–10. Line drawings of *Grotea villosissima* sp. n. **6** Habitus **7** Head, posterodorsal view **8** Head (showing detail of genal projection), posteroventral view **9** Propodeum, dorsal view **10** Wings.

tergite I slender but slightly shorter than mesosoma and rather straight (Figs 1, 3, 6); ovipositor shorter than the fore wing (Fig. 6).

Description. Female. Fore wing 7.4 mm long.

Head in dorsal view with gena behind eyes rounded (Fig. 7); posterior ocellus separated from eye by $1.7 \times$ its own maximum diameter (Fig. 7); genal projection

present, laterally indistinct, ventroposteriorly evident; projection narrowing apically, horizontally oriented to inside of oral cavity; genal projections almost touching each other (Fig. 8); antenna with 35 flagellomeres (Fig. 6); flagellomere I $1.0 \times$ as long as flagellomeres II and III combined. Epomia absent.

Mesosoma. Mesoscutum smooth with isolated inconspicuous punctures; scutellum in profile weakly convex; hind wing with *Cu*1 strongly pigmented, not reaching margin (Figs 5, 10); propodeum (Fig. 9) $2.1\text{--}2.2 \times$ as long as broad; anterior transverse carina complete, centrally weak and indented, thus not forming a smooth arc from side to side (area basalis posteriorly enclosed); pleural carina complete; posterior transverse carina complete, although laterally weak; lateral longitudinal carina complete (area spiracularis enclosed); lateromedian longitudinal carina reaching anterior transverse carina, then absent; area lateralis not enclosed internally, rectangular, about $2.3 \times$ as long as broad, with posterolateral corner at right angle removed from lobe surrounding coxal insertion. Area superomedia not differentiated, basally and distally weak, laterally open.

Metasoma. Tergite I (Figs 1, 3, 6) straight (not bowed upwards) and slender, shorter than mesosoma (mesosoma $1.5 \times$ as long as tergite I); tergite I at least 4 times as long as broad posteriorly; visible part of ovipositor $2.7\text{--}2.9 \times$ as long as hind tibia (Fig. 6).

Color. (Figs 1–5).

A predominantly black species with head with yellow circumocular area and clypeus. Pronotum with two longitudinal yellow spots, along ventral and dorsal margins, and a submedial red spot towards posterior margin. Mesopleuron mostly red with two large black areas, one at epicnemium and other towards posterior margin, and a yellow spot close to tegula. Mesoscutum with yellow longitudinal spots distally. Scutellum mostly brownish anteriorly. Propodeum with brownish area basalis, area superomedia with yellow central spot, yellow areae petiolaris, posteroexterna and spiracularis, dull yellow area lateralis. Metasoma with extensively yellow marked tergites. Dull yellow ovipositor sheath. Fore and mid legs with extensively yellow-marked coxae and femora. Hind leg with extensively red marked coxa and femur. Fore wing hyaline.

Pubescence. Gena, vertex, mesosoma and metasoma with dense, whitish setae, setae longer on propleuron, pronotum, mesopleuron and metapleuron.

Etymology. The name of this new *Grotea* species refers to its uncommon pubescence.

Discussion. The 12 described species of the *Grotea anguina* species-group have backwards-directed genal projections whilst *Grotea villosissima* sp. n. has inwards-projecting genal projections (Fig. 8).

The three described species of the *G. chiloe* species-group have an upwards bowed first tergite, whilst *G. villosissima* sp. n. has a straight first tergite (Figs 1, 3, 6).

The two described species of the *Grotea gayi* species-group lack genal projections, have a strong epomia and have a fully closed area superomedia. *Grotea villosissima* sp. n. has genal projections (Fig. 8), lacks epomia and has an incomplete area superomedia (Fig. 9).

G. superba, the only described species of the *Grotea superba* species-group, is similar to *G. villosissima* sp. n. in having a straight first tergite (Figs 1, 3, 6). However, *G. superba* has sharp downwards-projecting genal projections, 43 flagellomeres, 9.0–12.5 mm fore wing length, hind wing with a strongly pigmented *Cu*1 reaching the margin of the wing,

and ovipositor always longer than the fore wing. *Grotea villosissima* sp. n. has inwards-projecting genal projections, 35 flagellomeres, 7.4 mm fore wing length, hind wing with *Cu*1 not reaching margin of the wing (Fig. 5, 10) and ovipositor shorter than the fore wing (Fig. 6). Finally, there are also clear differences in the color pattern between these two species (e.g. black flagellum with a white ring between flagellomeres 24 to 42 in *G. superba* and a black flagellum (Figs 1, 3) in *G. villosissima* sp. n.). All the differences between *G. villosissima* sp. n. and the described species of *Grotea* make the inclusion of this new species into any of the species-groups proposed by Wahl (1993) uncertain.

G. villosissima sp. n. is the first species of *Grotea* recorded from Colombia, where at least 5 more species of this genus occur (Gonzalez and Giraldo 2009).

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A new interpretation of the bee fossil *Melitta willardi* Cockerell (Hymenoptera, Melittidae) based on geometric morphometrics of the wing

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Abstract

Although bees are one of the major lineages of pollinators and are today quite diverse, few well-preserved fossils are available from which to establish the tempo of their diversification/extinction since the Early Cretaceous. Here we present a reassessment of the taxonomic affinities of *Melitta willardi* Cockerell 1909, preserved as a compression fossil from the Florissant shales of Colorado, USA. Based on geometric morphometric wing shape analyses *M. willardi* cannot be confidently assigned to the genus *Melitta* Kirby (Anthophila, Melittidae). Instead, the species exhibits phenotypic affinity with the subfamily Andreninae (Anthophila, Andrenidae), but does not appear to belong to any of the known genera therein. Accordingly, we describe a new genus, *Andrenopteryx* **gen. n.**, based on wing shape as well as additional morphological features and to accommodate *M. willardi*. The new combination *Andrenopteryx willardi* (Cockerell) is established.

Keywords

Bees, compression, Oligocene, wing shape, geometric morphometrics, Tertiary

Introduction

Bees (Hymenoptera, Apoidea, Anthophila) are a monophyletic group of largely pollenivorous species derived from among the predatory apoid wasps (Engel 2001a, 2011, Michener 2007). This clade probably appeared in the Early Cretaceous (~120 Myr) (Engel 2001a), and concomitant with the diversification of the Eudicots (Michener 1979, Cardinal and Danforth 2013). While intensive work during the last 20 years has clarified many aspects of bee relationships (e.g., Engel 2011, Danforth et al. 2013), establishing the tempo of this radiation continues to be hampered by significant gaps in their fossil record. Hitherto only 191 fossil species of bees have been described (Michez et al. 2012, Engel et al. 2012, Wappler et al. 2012, Engel and Breitkreuz 2013, Engel and Michener 2013, Engel et al. 2013), but the majority of these come from a relatively restricted number of actual deposits. Four main deposits of bee fossils are known: (i) the Eckfeld/Messel shales (47–44 Myr; Wappler and Engel 2003, Wedmann et al. 2009), (ii) the Baltic amber from the middle Eocene (45 Myr; Engel 2001a, 2008, Gonzalez and Engel 2011), (iii) the Florissant shale from the Eocene-Oligocene boundary (34 Myr; Zeuner and Manning 1976, Engel 2001b, 2002, unpubl. data) and (iv) the Dominican amber from the Miocene (20 Myr; Engel et al. 2012, Engel and Breitkreuz 2013). Specimens in amber are typically preserved with enough fidelity to correctly explore diagnostic morphological characters while compressions generally show a restricted subset of such features (Michener 2000, Engel 2001a). Taxonomic attributions of many compression fossils need objective and robust revision with modern procedures, such as geometric morphometrics (Michez et al. 2012, Wappler et al. 2012), and this is particularly true for the diverse paleofauna from Florissant.

The highly fossiliferous shales of Florissant, Colorado have revealed 34 species and 19 genera belonging to several extant bee families: Apidae, Halictidae, Melittidae, Megachilidae, and Andrenidae (Michez et al. 2012). However, the material is often preserved with little or no relief and specimens typically have only the wing venation or limited structures of the legs and thorax discernible, making comparisons with extant clades difficult. Recently we have had the opportunity to re-examine the putative melittine bee from Florissant, *Melitta willardi* Cockerell 1909 (Figure 1), and to attempt a better understanding of its affinities with extant and other fossil taxa as determined by wing shape analyses.

Material and methods

Sampling

Given that *M. willardi* possesses three submarginal cells we sampled specimens from different extant subfamilies with the same arrangement of cells. All available subfamilies



Figure 1. Photograph of holotype female of *Melitta willardi* Cockerell as preserved (UCM 18737). Specimen is preserved facing toward the viewer, with head missing (note the large opening representing the anterior thoracic fossa).

were included, with a maximum of 20 specimens per subfamily, and with a maximum of five specimens per species. We additionally sampled all species of *Melitta* available with a maximum of five specimens per species. The dataset also included eighteen extinct species [Apidae, Apinae: *Anthophorula persephone* Engel, 2012; *Bombus randeckensis* Wappler & Engel, 2012; *Electrapis meliponoïdes* (Buttel-Reepen, 1906); *E. krishnorum* Engel, 2001; *Electrobombus samlandensis* Engel, 2001; *Eufriesea melissiflora* (Poinar, 1998); *Melikertes stilbonotus* (Engel, 2001); *Melissites trigona* Engel, 2001; *Paleohabropoda oudardi* Michez & Rasmont, 2009; *Protobombus basilaris* Engel, 2001; *Probombus hirsutus* Piton, 1940; *Succinapis goeleti* Engel, 2001; and *Thaumastobombus andreniformis* Engel, 2001; Halictidae, Halictinae: *Cyrtapis anomala* Cockerell, 1908; *Electrolictus antiquus* Engel, 2001; *Halictus petrefactus* Engel & Peñalver, 2006; *Ocymoromelitta sorella* Engel, 2002 and *O. florissantella* (Cockerell, 1906)]. Since the holotype of *M. willardi* is a female, all individuals used in the morphometric analysis are females to avoid potential bias due to any sexual dimorphism. The assembled dataset comprised 360 specimens representing six families of Anthophila, 15 subfamilies, and 109 species (Table 1).

Morphometric and statistical analyses

Taxonomic affinities of the fossil were evaluated based on wing shape. Wing venation is used widely in insect taxonomy and can provide many informative features for phylogenetic analyses and for many Late Paleozoic taxa is sometimes the only form of available data (e.g. Gumiel et al. 2003, Pretorius 2005). Moreover, use of the wings has significant advantages compared to other organs, i.e., they are relatively rigid, articulated, 2D struc-

Table 1. Dataset for the geometric morphometric analysis including 360 specimens from 109 species and 15 subfamilies. N = number of specimens.

FAMILY	SUB-FAMILY	SPECIES	N	
Andrenidae	Andreninae	<i>Andrena bicolor</i> Fabricius, 1775	5	
		<i>Andrena boyerella</i> Dours, 1872	5	
		<i>Andrena flavipes</i> Panzer, 1799	5	
		<i>Andrena fulva</i> (Müller, 1766)	5	
	Oxaeinae	<i>Oxaea flavescens</i> Klug, 1807	1	
		<i>Oxaea fuscescens</i> Sichel, 1865	1	
		<i>Oxaea</i> sp.	1	
		<i>Protoxaea gloriosa</i> (Fox, 1893)	2	
	Panurginae	<i>Borgatomesa brevipennis</i> (Walker, 1871)	1	
		<i>Melitturga clavicornis</i> (Latreille, 1808)	1	
		<i>Melitturga taurica</i> Friese, 1922	5	
		<i>Anthrenoides</i> sp.	2	
		<i>Parapsaenythia puncticutis</i> (Vachal, 1909)	2	
	Apidae	Apinae	<i>Apis florea</i> Fabricius, 1787	5
			<i>Bombus mendax</i> Gerstäcker, 1869	5
<i>Melissodes confusa</i> Cresson, 1878			5	
<i>Anthophora plumipes</i> (Pallas, 1772)			5	
<i>Paleohabropoda oudardi</i> Michez & Rasmont, 2009 †			1	
<i>Anthophorula persephone</i> Engel, 2012 †			1	
<i>Bombus randeckensis</i> Wappler & Engel, 2012 †			1	
<i>Electrapis krishnorum</i> Engel, 2001 †			1	
<i>Electrapis meliponoides</i> (Buttel-Reepen, 1906) †			1	
<i>Electrobombus samlandensis</i> Engel, 2001 †			1	
<i>Eufriesea melissiflora</i> (Poinar, 1998) †			1	
<i>Melikertes stilbonotus</i> (Engel, 2001) †			1	
<i>Melissites trigona</i> Engel, 2001 †			1	
<i>Protobombus basilaris</i> Engel, 2001 †			1	
<i>Probombus hirsutus</i> Piton, 1940 †			1	
<i>Succinapis goeleti</i> Engel, 2001 †		1		
<i>Thaumastobombus andreniformis</i> Engel, 2001 †		2		
Nomadinae		<i>Epeolus cruciger</i> (Panzer, 1799)	5	
		<i>Nomada fabriciana</i> (Linnaeus, 1767)	5	
		<i>Nomada flava</i> Panzer, 1798	5	
		<i>Nomada goodeniana</i> (Kirby, 1802)	5	
Xylocopinae	<i>Ceratina chloris</i> (Illiger, 1806)	5		
	<i>Ceratina dallatorreana</i> Friese, 1896	5		
	<i>Xylocopa olivieri</i> (Lepelletier de Saint Fargeau, 1841)	5		
Colletidae	Colletinae	<i>Xylocopa violacea</i> (Linnaeus, 1758)	5	
		<i>Colletes cunicularius</i> (Linnaeus, 1761)	5	
		<i>Colletes daviesanus</i> Smith, 1846	5	
		<i>Colletes succinctus</i> (Linnaeus, 1758)	5	
		<i>Leioproctus</i> sp.	5	

FAMILY	SUB-FAMILY	SPECIES	N
	Diphaglossinae	<i>Cadeguala occidentalis</i> (Haliday, 1836)	1
		<i>Caupolicana gayi</i> Spinola, 1851	5
		<i>Caupolicana yarrowi</i> (Cresson, 1875)	3
		<i>Crawfordapis luctuosa</i> (Smith, 1861)	2
		<i>Diphaglossa gayi</i> Spinola, 1851	3
		<i>Mydrosoma bobartorum</i> Michener, 1986	1
		<i>Ptiloglossa guinnae</i> Roberts, 1971	1
		<i>Ptiloglossa pretiosa</i> (Friese, 1898)	4
Halictidae	Halictinae	<i>Augochlorella striata</i> (Packer, 1990)	5
		<i>Halictus ligatus</i> Say, 1837	5
		<i>Ruizantheda nigrocaerulea</i> (Spinola, 1871)	5
		<i>Thrinchostoma kandti</i> Blüthgen, 1930	5
		<i>Cyrtapis anomala</i> Cockerell 1908 †	1
		<i>Electrolictus antiquus</i> Engel 2001 †	1
		<i>Halictus petrefactus</i> Engel & Peñalver 2006 †	1
		<i>Ocymoromelitta florissantella</i> Cockerell 1906 †	1
	<i>Ocymoromelitta sorella</i> Engel, 2002 †	1	
	Nomiinae	<i>Dieunomia nevadensis</i> (Cresson, 1874)	1
		<i>Halictonomia decemmaculata</i> (Friese, 1900)	2
		<i>Lipotriches australica</i> (Smith, 1875)	1
		<i>Lipotriches modesta</i> (Smith, 1862)	5
		<i>Nomia melanderi</i> Cockerell, 1906	1
		<i>Nomia diversipes</i> Latreille, 1806	5
	Nomioidinae	<i>Pseudapis diversipes</i> (Latreille, 1806)	5
		<i>Ceylacticus variegatus</i> (Olivier, 1789)	5
		<i>Nomioides facilis</i> (Rossi, 1853)	5
	Rophitinae	<i>Nomioides minutissimus</i> (Rossi, 1790)	1
		<i>Systropha curvicornis</i> (Scopoli, 1770)	2
<i>Systropha maroccana</i> Warncke, 1977		3	
<i>Systropha pici</i> Pérez, 1895		2	
<i>Systropha planidens</i> Giraud, 1861		5	
<i>Systropha</i> sp.	5		
Megachilidae	Fideliinae	<i>Fidelia kobrowi</i> Brauns, 1905	5
		<i>Fidelia paradoxa</i> Friese, 1899	5
		<i>Fidelia villosa</i> Brauns, 1902	1
		<i>Fideliopsis major</i> (Friese, 1911)	2
Melittidae	Meganomiinae	<i>Meganomia andersoni</i> (Meade-Waldo, 1916)	2
		<i>Meganomia binghami</i> (Cockerell, 1909)	5
	Melittinae	<i>Rediviva intermixta</i> (Cockerell, 1934)	5
		<i>Rediviva longimanus</i> Michener, 1981	3
		<i>Melitta americana</i> Smith, 1853	3
		<i>Melitta arrogans</i> Smith, 1879	5
		<i>Melitta bicollaris</i> Warncke, 1973	5
		<i>Melitta californica</i> Viereck, 1909	1
		<i>Melitta cameroni</i> (Cockerell, 1910)	5
		<i>Melitta dimidiata</i> Morawitz, 1876	5

FAMILY	SUB-FAMILY	SPECIES	N
		<i>Melitta eickworti</i> Snelling & Stage, 1995	3
		<i>Melitta ezoana</i> Yasumatsu & Hirashima, 1956	5
		<i>Melitta haemorrhoidalis</i> (Fabricius, 1775)	5
		<i>Melitta hispanica</i> Friese, 1900	5
		<i>Melitta harrietae</i> (Bingham, 1897)	5
		<i>Melitta japonica</i> Yasumatsu & Hirashima, 1956	4
		<i>Melitta magnifica</i> Michez, 2012	3
		<i>Melitta melittoides</i> (Viereck, 1909)	2
		<i>Melitta melanura</i> (Nylander, 1852)	5
		<i>Melitta murciana</i> Warncke, 1973	5
		<i>Melitta seitzi</i> Alfken, 1927	1
		<i>Melitta schultzei</i> Friese, 1909	1
		<i>Melitta sibirica</i> (Morawitz, 1888)	5
		<i>Melitta aegyptiaca</i> (Radoszkowski, 1891)	5
		<i>Melitta leporina</i> (Panzer, 1799)	5
		<i>Melitta maura</i> (Pérez, 1896)	5
		<i>Melitta nigricans</i> Alfken, 1905	5
		<i>Melitta schmiedeknechti</i> Friese, 1898	5
		<i>Melitta tricincta</i> Kirby, 1802	5
		<i>Melitta avontuurensis</i> Michez & Kuhlmann, 2014	1
		<i>Melitta richtersveldensis</i> Michez & Kuhlmann, 2014	5
Total = 360			

tures that present a large number of useful landmarks formed by the homologous intersections of veins. Geometric morphometrics is a procedure which aims at quantifying and analyzing the overall shape of a structure (Bookstein 1991, Rohlf and Marcus 1993, Adams et al. 2004), and can provide a powerful tool in paleontology for discriminating taxa at different levels as well as for discussing taxonomic affinities between extinct and extant taxa (Roberts 2008, Michez et al. 2009, De Meulemeester et al. 2012, Wappler et al. 2012). The holotype of *M. willardi* does not exhibit any signs of post-mortem tectonic deformation, meaning that the venation observed is reflective of as it was in life and did not require any compensation to adjust for taphonomic or diagenetic alteration.

The right forewings of 360 female specimens were initially photographed using an Olympus SZ010 binocular coupled with a Nikon D70 camera. Photographs were gathered in one TPS file using tps-UTIL 1.56 (Rohlf 2013a). To capture the shape, two dimensional Cartesian coordinates of 18 landmarks (Figure 2) were digitized by tps-DIG 2.17 (Rohlf 2013b). Both right and symmetrized-left wings of *M. willardi* were digitized by four experimenters (AD, MD, TD, DM) to obtain an objective and robust identification. All landmark configurations were scaled, translated, and rotated against the consensus configuration by the generalized least square Procrustes superimposition method (Bookstein 1991). The superimposition was performed using R functions of the package “geomorph” (Adams and Otárola-Castillo 2013). The aligned landmark configurations were projected into the Euclidean space tangent to the curved

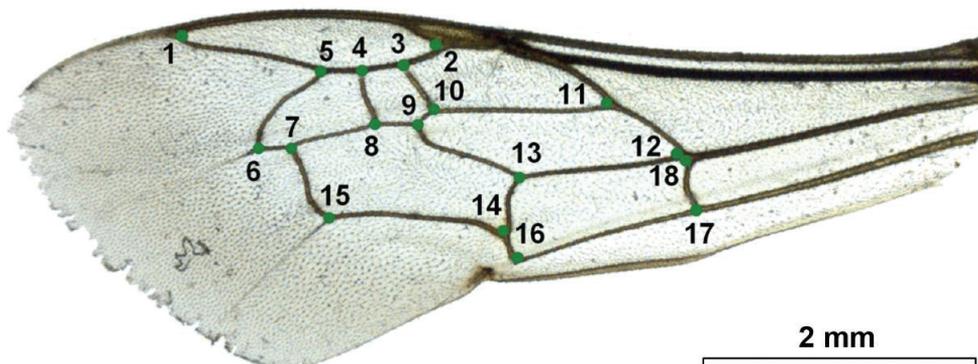


Figure 2. Right forewing of a female of *Melitta leporina* (Panzer) with the 18 landmarks indicated to describe the shape.

Kendall's shape space to aid further statistical analyses. The closeness of the tangent space to the curved shape space was tested by calculating the least-squares regression slope and the correlation coefficient between the Procrustes distances in the shape space with the Euclidean distances in the tangent space (Rohlf 1999). This variation amplitude of our dataset was calculated with tps-SMALL 1.25 (Rohlf 2013c).

Prior to the assignment of the fossil, shape variation within the reference dataset and discrimination of the different taxa was assessed by Linear Discriminant Analyses (LDA) of the projected aligned configurations of landmarks, with subfamily levels as *a priori* grouping by using the software R version 3.0.2 (2013, <http://www.R-project.org/>). The effectiveness of the LDA for discriminating subfamilies was assessed by the percentages of individuals correctly classified to their original taxon (hit-ratio, HR) in a leave-one-out cross-validation procedure based on the posterior probabilities of assignment. Given the observed scores of an "unknown", the posterior probability (PP) equals the probability of the unit to belong to one group compared to all others. The unit is consequently assigned to the group for which the posterior probability is the highest (Huberty and Olejnik 2006).

Taxonomic affinities of the fossil were assessed based on their score in the predictive discriminant space of shapes. After superimposition of the 368 landmark configurations (i.e. corresponding to the reference dataset and the fossil), aligned coordinates of the 360 specimens from the reference dataset were used to calculate the LDA. We included *a posteriori* the eight aligned landmark configurations of *M. willardi* in the computed LDA space as "unknown" specimens and calculated their score. Assignments of the fossil configurations were estimated by calculating the Mahalanobis Distance (MD) between "unknowns" and group mean of each subfamily. We also calculated posterior probabilities of assignment to confirm the assignment to one taxon.

In order to assess the taxonomic affinities of *M. willardi* with the family Andrenidae, PCA was computed to visualize shape affinities between the fossil and andrenid subfamilies.

Results

Morphometric analysis

The regression coefficient between the Procrustes distances and the Euclidean distances is close to 1 (0.9999). This means that the linear tangent space closely approximates the shape space, thereby permitting us to be confident in the variation amplitude of our dataset.

In LDA space with subfamily *a priori* grouping, discrimination of the 15 groups are effective, with a cross-validated HR of 98.61% (e.g., 5 misclassified specimens), and 10 of the 15 subfamilies that account for a HR of 100% (Table 2). Other subfamilies have a HR between 90% and 99%. Due to sampling size within groups, the HR drastically drop down when a single specimen is misclassified. This is the case for the five groups with HR lower than 100%. Cross-validation assignment (Table 2) allows us to be confident in the group discrimination at subfamily level.

All of the 109 specimens of *Melitta* were correctly classified to their original taxon (Melittinae) in the leave-one-out cross-validation procedure. However, the eight landmark configurations of *M. willardi* are assigned to Andreninae (MDs = 2.72 – 4.84; PPs = 0.9999 – 1). Taxonomic affinities of the fossil were also assessed based on non-supervised analyses within Andrenidae. In the morphometric space defined by the PCA, the fossil is undoubtedly clustered with the subfamily Andreninae (Figure 3).

Systematic palaeontology

Family: Andrenidae Latreille, 1802

Subfamily: Andreninae Latreille, 1802

Genus *Andrenopteryx* Dewulf & Engel, gen. n.

<http://zoobank.org/2A2AF004-6EEB-47DE-B13F-B91378CF3557>

<http://species-id.net/wiki/Andrenopteryx>

Type species. *Melitta willardi* Cockerell, 1909.

Included species. The genus presently includes only the type species, *Andrenopteryx willardi* (Cockerell, 1909), comb. n.

Diagnosis. ♀: Forewing with three submarginal cells, first submarginal cell largest, second smallest; r-rs long, about as long as anterior border of second submarginal cell; anterior border of second submarginal cell not dramatically shorter than that of third submarginal cell; 1rs-m relatively straight; 2rs-m greatly arched apical in posterior half; 1m-cu entering second submarginal cell near midpoint; 2m-cu entering third marginal cell at apical third of cell length, 2m-cu relatively straight; pterostigma linear, much longer than wide, border inside marginal cell relatively straight; marginal cell with acutely rounded apex, not truncate or appendiculate, apex on costal margin, apical most abscissa Rs relatively straight such that marginal cell apex tapers gradually

Table 2. Cross-validation assignment in LDA space with subfamily *a priori* grouping (original groups are along the rows, predicted groups are along the columns). HR = Hit ratio.

	Andreninae	Apinae	Colletinae	Diphaglossinae	Fideliinae	Halictinae	Meganomiinae	Melittinae	Nomadinae	Nomiinae	Nomioidinae	Oxaeinae	Panurginae	Rophitinae	Xylocopinae	HR (%)
Andreninae	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
Apinae	-	33	-	1	-	-	-	-	-	-	-	-	-	-	-	97
Colletinae	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	100
Diphaglossinae	-	1	-	19	-	-	-	-	-	-	-	-	-	-	-	95
Fideliinae	-	-	-	-	13	-	-	-	-	-	-	-	-	-	-	100
Halictinae	-	1	-	-	-	24	-	-	-	-	-	-	-	-	-	96
Meganomiinae	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	100
Melittinae	-	-	-	-	-	-	-	117	-	-	-	-	-	-	-	100
Nomadinae	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	100
Nomiinae	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	100
Nomioidinae	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	100
Oxaeinae	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	100
Panurginae	1	-	-	-	-	-	-	-	-	-	-	-	10	-	-	91
Rophitinae	-	-	-	-	-	1	-	-	-	-	-	-	-	16	-	94
Xylocopinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	100

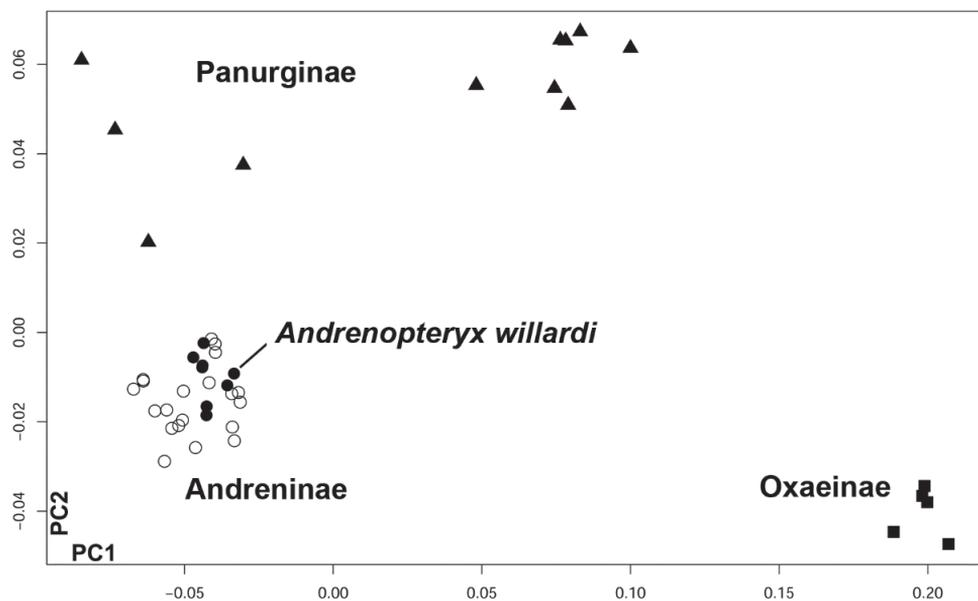


Figure 3. Distribution of extant examined andrenid (36 specimens) and the eight landmark configurations of *Andrenopteryx willardi* (*), along the first two PC axis (PC1= 72%, PC2= 11%).

in width from 2rs-m to apex. Pilosity well developed; flocculus absent; scopa present on metafemur and metabasitarsus; metabasitarsus more than half as long as metatibia; pretarsal claws with minute inner tooth. ♂: Unknown.

Etymology. The new genus-group name is a combination of *Andrena*, type genus of the subfamily Andreninae, and *-pteryx*, meaning “wing”. The name is feminine and refers to the “*Andrena*-like” venation of the wings.

Discussion

Position of *Andrenopteryx* gen. n. in Anthophila

The wings of *Andrenopteryx* gen. n. have three submarginal cells, suggesting that the genus does not probably belong to subfamilies such as Xeromelissinae, Hylaeinae, Euryglossinae (all Colletidae), Dasypodainae (Melittidae), Megachilinae (Megachilidae), or various tribes among the Apidae (i.e., Allodapini, Ammobatini, Ammobatoidini, Biasini, Boreallodapini, Caenoprosopidini, Ctenoplectrini, Neolarrini, and Townsendiellini). Furthermore, *Andrenopteryx* gen. n. clearly possesses pollen-collecting structures, suggesting that the fossil was probably not cleptoparasitic and accordingly those genera may also be excluded (cleptoparasitic genera occur in various families, see Michener 2007). The GM analysis of the wing shape of *Andrenopteryx* gen. n. suggests that this fossil belongs to the Andrenidae (see previous results, vide supra). Nevertheless, diagnostic features of Andrenidae such as the two subantennal sulci and the short to long pointed glossa are not preserved in the only available specimen of the species.

Assuming that its clustering among Andrenidae is an accurate reflection of its relationships, among andrenids the three submarginals cells excludes placement among most of the Panurginae. The species has a long marginal cell with an acutely curved apex that lies along the costal margin as in Andreninae, while the other subfamilies have a marginal cell with a truncate apex (Michener 2007). The holotype clearly possesses a scopa which is limited to the metafemur and metabasitarsus and without a flocculus, unlike the diverse extant genus *Andrena* Fabricius. The metabasitarsus is more than half as long as the metatibia, in stark contrast to the form present in *Megandrena* Cockerell. Lastly, *Andrenopteryx* gen. n. does not have an enlarged inner tooth on the pretarsal claws, and therefore is distinct from the southern South American genus *Orphana* Vachal. Thus, while Cockerell’s species certainly is best placed in the Andreninae it seems generically distinct and this has served as the basis for our decision to describe a new genus.

Geometric morphometrics of wing shape and *Andrenopteryx willardi*

Wing shape analyses were successfully employed in previous studies to discriminate extant bee taxa at various classificatory levels, from subspecies to tribes (e.g., Kandemir et al. 2011, De Meulemeester et al. 2012). In addition, these analyses are sufficient

to confidently associate bee fossils with extant groups (e.g., Michez et al. 2009, De Meulemeester et al. 2012, Wappler et al. 2012), and this lends increased confidence to the affinities of *A. willardi* as outlined above.

Cockerell (1909) mentioned some features that for him indicated that his fossil species was referable to *Melitta*. He noted the three submarginal cells, the particular form of the pterostigma, the scopa confined to the metafemur and metabasitarsus, and the absence of a flocculus. However, a majority of these similarities are unfounded and not indicative of *Melitta*, and in fact some are more suggestive of Andreninae. First, the proportions of the submarginal cells are more similar to Andrenidae than any melittid. Second, the second submarginal cell does not receive the 1m-cu well before its midpoint, and this is true for both the left and right forewings. Thus, even based on the evidence available to Cockerell and from his description the fossil should not be placed within *Melitta*, and it is peculiar to us why he made such a taxonomic decision.

Based on the discovery that Cockerell's fossil *Melitta* is more likely an andrenine, some previous hypotheses regarding the biogeography of North American bees require reconsideration. Michez and Eardley (2007) speculated the presence of *Melitta* in North America during the Oligocene based on Cockerell's (1909) assertion of the taxonomic identity of *A. willardi*, and Dellicour et al. (2014) demonstrated that North American species of *Melitta* form a derived clade within the genus. There is now no evidence for Michez and Eardley's scenario. The origin of *Melitta* could be more recent than previously hypothesized and Dellicour et al.'s North American clade could have entered and diversified on the continent during the Neogene. In contrast, the record of Andreninae in North America during the Oligocene is now corroborated by the present fossil. There are additional records of putative andrenines from Florissant, such as *Lithandrena saxorum* Cockerell, 1906, *Pelandrena reducta* Cockerell 1909, and five additional species Cockerell placed in *Andrena* (Michez et al. 2012), but these are in need of re-evaluation. It is hoped that these species may also be subjected to morphometric analyses and their relationships clarified.

The importance of the Florissant shales

The bees of the Florissant shale have been ignored for a long time (Engel 2002). It was Cockerell's intention to document the whole fossil fauna and flora from Colorado and this partly drove his efforts to document the known bee remains from these deposits (Cockerell 1927, Engel 2002). Cockerell, who largely relied on a hand lens to study specimens, often based his hypotheses regarding the placement of particular fossils on the their general habitus, or relied on a suite of traits recognized nowadays as not indicative of those same families, subfamilies, and even genera. For example, many of the traits concerning wing shape such as the relative positions of the rs-m or m-cu crossveins are quite variable within individual families. Subsequent to Cockerell, Zeuner and Manning (1976) tried to evaluate the Florissant fossil bees, but they based their work solely from Cockerell's original descriptions and did not examine type material. Zeuner and Manning's monograph is further compromised

by the fact that both authors died before the work was completed, leaving behind only notes that were subsequently cobbled together to form the publication, and this explains its poor quality and limited utility (Engel 2002). The only other works were brief accounts by Engel (2001b, 2002), who attempted to re-evaluate Cockerell's Florissant halictines as well as newly discovered material, and to describe a new large carpenter bee. Outside of this, the Florissant fossil bee fauna has remained dormant and given that it is one of the most diverse and specimen-rich deposits for the Anthophila, it is all the more imperative that its species be properly evaluated in a modern context. We hope that this brief treatment of one such species will inspire more investigations into the fossil bees from Colorado.

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Life history and description of larva and pupa of *Platyphileurus felscheanus* Ohaus, 1910, a scarabaeid feeding on bromeliad tissues in Brazil, to be excluded from Phileurini (Coleoptera, Scarabaeidae, Dynastinae)

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Abstract

The third instar larvae and the pupae of *Platyphileurus felscheanus* Ohaus, 1910 (Phileurini), recently synonymized with *Surutu jelineki* Endrödi, 1975 (Cyclocephalini), are described and illustrated, and some life history information is given. The larvae were collected and reared in bromeliads in rain forests of Santa Catarina state in southern Brazil. The systematic position of this monotypic genus is reassessed at the tribe level by considering larval and adult morphological characters. Both character sets, being described and illustrated, suggest the placement of *Platyphileurus* in the tribe Oryctini.

Keywords

Surutu jelineki, Cyclocephalini, Bromeliaceae, beetle, third instar, dynastine tribe, classification

Introduction

The enigmatic *Platyphileurus felscheanus* / *Surutu jelineki*

The rhinoceros beetle *Platyphileurus felscheanus* Ohaus, 1910 (Scarabaeidae: Dynastinae) was described twice as a new species, first under this name in the tribe Phileurini and 65 years later as *Surutu jelineki* by Endrödi (1975) in the tribe Cyclocephalini. Grossi et al. (2010) recently synonymized those two names.

The monotypic genus *Platyphileurus* Ohaus, 1910 is known only from Brazil (Grossi et al. 2010) with one erroneous record from the Ilha do Principe (West Africa) (Endrödi 1977). Grossi et al. (2010) extended the known distribution of the species from Santa Catarina (Ohaus 1910) and Rio de Janeiro (Endrödi 1985) to the states of Bahia, Espírito Santo, Minas Gerais and Paraná.

Platyphileurus felscheanus can be recognized by its flat body, especially anteriorly, by the elytra being laterally dilated posteriorly, by lacking horns or tubercles on the head and pronotum, and by lacking a longitudinal furrow on the pronotum (Figs 26–28). With the anterior half of the body flatter than the posterior half and the flattened pronotum lacking a longitudinal furrow, *Platyphileurus* has an unusual appearance for a phileurine species. Its systematic position needs to be re-examined.

Here we describe the larva and pupa of *P. felscheanus* repeatedly collected in bromeliad rosettes and reared to imagines, present data on their life history, and give new records on the occurrence of this bromelicolous species. We also explore whether characters of the immatures provide indications of the tribal placement of the genus.

Beetles and bromeliads

Among the numerous insects recorded in bromeliad phytotelmata, beetles are typically represented by taxa with aquatic and semiaquatic habits. Larvae of Scirtidae are commonly found in bromeliad tanks (Picado 1913; Kitching 2000; Frank and Lounibos 2008; authors' pers. obs.). Both, larvae and imagines of dytiscids in the genera *Desmopachria* Babington, 1841 and *Copelatus* Erichson, 1832 (formerly *Aglymbus* Sharp, 1880) occur in the water-filled leaf axils and prey on other insects there (Kitching 2000; Frank and Lounibos 2008; authors' pers. obs.). In addition, species of *Phaenonotum* Sharp, 1882, *Lachnodacnum* Orchymont, 1937 and *Omicrus* Sharp, 1879 (Hydrophilidae) live in bromeliad phytotelms (Hansen and Richardson 1998; Kitching 2000; Frank and Lounibos 2008; authors' pers. obs.).

Some few bromeliad associated species are Scarabaeidae (Champion 1913; Lüderwaldt 1915; Pereira et al. 1960; Huijbregts 1984; Costa et al. 1988; Cook 1998; Krell et al. 2002; Cave 2005; Howden 2010; F.Z. Vaz-de-Mello pers. comm. 2010; authors' pers. obs.). Imagines of *Genuchinus* Westwood, 1874 (Cetoniinae) are frequently caught in bromeliads in Guatemala and Brazil (Howden 2010; Vaz-de-Mello pers. comm. 2010), but their life history is unknown. Imagines of a few species of *Bdebyrus* Harold,

1869 (Scarabaeinae) have been collected in bromeliads and seem to be closely associated with the plants (Pereira et al. 1960; Huijbregts 1984; Cook 1998; F.F. Albertoni pers. obs.). Larvae of *Desicasta laevicostata* (van de Poll, 1886) (= *Desicasta reichei* (Thomson, 1860); Cetoniinae) were found in living stalks of the epiphytic bromeliad *Vriesea sanguinolenta* Gogn. and Marchal in Panama and were reported eating the stalk tissue (Krell et al. 2002). One larva of *Trigonopeltastes delta* Forster, 1771 was collected two meters above the ground in the terrarium of *Tillandsia utriculata* L. in Florida. Even though, the larvae of *T. delta* are known to develop in wood and other plant debris (Cave 2005).

Material and methods

Study areas

Bromeliads were collected from five rain forest areas in Santa Catarina state, southern Brazil, specifically on Santa Catarina Island (municipality of Florianópolis). Two sites are secondary forest areas: 1) Unidade de Conservação Ambiental Desterro (UCAD) (27°31'52"S, 48°30'45"W), a 491 ha forest reserve of the Universidade Federal de Santa Catarina (Zillikens and Steiner 2004), and 2) Santo Antônio de Lisboa (27°30'S, 48°31'W) about 2 km away from the former site (Zillikens et al. 2001). Three sites are sand dune habitats ("restinga") with shrubby vegetation at 3) Campeche beach (27°40'38"S, 48°28'48"W), or with trees ("restinga arbórea") at 4) Santinho-Moçambique beach (27°28'5"S, 48°23'13"W, 20 m a.s.l.) and 5) Pantano do Sul beach (27°46'52"S, 48°31'11"W, 7 m a.s.l.).

Collection and rearing of beetles

To sample the associated animals we collected 412 bromeliads of six species from March 2002 to March 2006: *Nidularium innocentii* Lem. (n=99), *Aechmea lindenii* (E. Morren) Baker (n=141), *A. nudicaulis* Griseb. (n=61), *Canistrum lindenii* (Regel) Mez. (n=60), *Vriesea vagans* (L. B. Sm.) L. B. Sm. (n=39), and *Hohenbergia augusta* Mez. (n=12). Whole plants were cut off at the base and examined leaf by leaf in the laboratory (Zillikens et al. 2005). The immature beetles were fixed in 70% ethanol, in Kahle's solution, or in boiling water, and in the last case preserved in 80% ethanol; some larvae were kept alive to be reared.

All large beetle larvae and pupae found in the bromeliads were identified as scarabaeids. We prepared small rosettes of *N. innocentii* from the innermost part of the plant (about 8–10 young leaves), washed with tap water to remove spiders and other predatory arthropods, or arranged freshly cut, clean bromeliad leaves to an artificial rosette in a funnel. Larvae and pupae were placed in the middle of the rosette and covered with 1–2 table spoons of humic leaf litter. The arrangement was covered with gauze and kept moist in the laboratory. Larvae were inspected about every second week

to check their vitality and to replace the eaten up rosettes or leaves with new ones. The identification of *P. felscheanus* was based on imagines obtained from these rearings.

In order to collect more specimens of *P. felscheanus* and to learn about its life history, five additional bromeliads of the genera *Aechmea* Ruiz & Pav., *Nidularium* Lem. and *Vriesea* Beer. were collected between 2008 and 2012 in Florianópolis. In the field, we searched bromeliads for scarabaeid larvae. When a larva was present (n=6), the bromeliad was taken to the laboratory where it was kept upright in a plastic bucket. During the first days or weeks after collection the larvae were left in the bromeliads to observe their behavior. Thereafter, some bromeliad leaves were tied together in small rosettes and each larva was placed in the middle of this artificial rosette which were maintained in plastic pots (n=5). One larva was maintained in the original bromeliad until pupation. They were checked one to three times per week.

Phylogenetic reasoning

A cladistics analysis at tribal or generic level is beyond the scope of this paper. In full consideration that the current tribal classification rests on entirely typological foundations, we apply consistently phylogenetic reasoning sensu Hennig (1982) and Watrous and Wheeler (1981) to interpret character states and their distribution to determine a possible placement of *Platyphileurus* in a current tribe.

Material examined

Platyphileurus felscheanus Ohaus, 1910

The larval description is based on four third instar larvae with the following data:

BRAZIL, Santa Catarina: UCAD, Florianópolis city, in *Canistrum lindenii*, 18.ii.2002, J. Steiner leg. (DMNS ZE.15759); dto., in *Hohenbergia augusta* (plant no. 17), 15.iv.2002, A. Zillikens leg. (DMNS ZE.15761); dto., in *Aechmea lindenii* (plant no. 329), 27.iv.2004, A. Zillikens leg. (DMNS ZE.15760); Santo Antônio de Lisboa, Florianópolis, in *Aechmea nudicaulis* (plant no. 318), 24.iii.2004, A. Zillikens leg. (DMNS ZE.15758).

Further larval material from which additional measurements were taken: BRAZIL: São Paulo: 1 third instar (MZSP 010.247): Salesópolis, Estação Biológica de Boracéia, Atlantic rain forest, 23°32'S, 45°51'W, 4–12.ix.2008, S.A. Casari and M. Duarte (MZC-016-Entomologia de Campo) leg. [NEW STATE RECORD]. **Santa Catarina:** 1 larva fixed (MZSP 010.246): Florianópolis city, Santinho, restinga, in *Vriesea* cf. *friburgensis*, 27°28'42.4"S, 48°23'6.8"W, 2.iii.2008, A.G. Martins and F.F. Albertoni leg. (Fig. 1); 1 larva fixed (MZSP 010.245): Florianópolis city, Santo Antônio de Lisboa, in *Aechmea lindenii* (plant NA20), 4.ii.2004, A.F. Cordeiro and M. Manfredini leg.; 3 larvae (MZSP 010.248): same locality and plant species (plant NA19), 2.iii.2004, A.F.

Cordeiro and M. Manfredini leg.; 1 larva (MZSP 010.249): same locality and plant species (plant NA44), 5.iv.2004, A.F. Cordeiro and M. Manfredini leg.; 1 larva (MZSP 010.250): same locality and plant species (plant no. 362), 15.ix.2004, A. Zillikens and J. Steiner leg.; 1 larva (MZSP 010.251): Florianópolis city, UCAD, Atlantic rain forest, in *Canistrum lindenii* (plant no. 74), 16.v.2003, A. Zillikens and J. Steiner leg.

The pupal description is based on two pupae with the following data: BRAZIL: Santa Catarina: 1 female pupa (reared from larva) (MZSP 010.252) Florianópolis city, Pantano do Sul, “restinga arbórea” in *Vriesea friburgensis* Mez., 06.ii.2008, A.G. Martins and F.F. Albertoni leg. (illustrated and photographed); 1 male pupa (reared from larva) (MZSP 010.253): Florianópolis, Santo Antônio de Lisboa, in *Aechmea* sp., 23.iii.2011, A.G. Martins and F.F. Albertoni leg. (photographed).

Imagines of *P. felscheanus* preserved: BRAZIL: Santa Catarina: 1 male and 1 female (reared from larvae) (LANUFSC): Campeche, Florianópolis, restinga, *Aechmea nudicaulis* (plant no. 235 and 236), 28.xi.2003, A.F. Cordeiro leg.; 1 female (reared from larva) (DMNS ZE.20187): UCAD, Florianópolis, in *Aechmea lindenii* on rock (plant no. 63), 14.x.2002 (emergence: 29.x.2002), A. Zillikens leg.; 1 male (reared from larva) (MZSP): Florianópolis, Santo Antônio de Lisboa, in *Aechmea caudata* Lindm., 26.iv.2008, A.G. Martins and F.F. Albertoni leg.; 1 female (reared from larva) (DMNS ZE.20188), same locality, in *Aechmea lindenii*, 5.vii.2004 (emergence: 8.x.2004), J. Steiner and A. Zillikens leg.; 1 female (reared from larva) (LANUFSC): same locality, in *Aechmea* sp., 23.iii.2011 (emerged: 09.xi.2011), A.G. Martins and F.F. Albertoni leg.; 1 male (LANUFSC): same locality, among the litter of *Hohenbergia augusta*, 27.xi.2012, F.F. Albertoni and J. Linemburg Jr. leg.

Additional material: Two last larval instar exuvia and one pupal exuvia (MZSP) of the reared *P. felscheanus* larvae.

To assess the differences of apical setal patterns of pupae between different species of Dynastinae, pupae of the following species of Phileurini and Oryctini from the immature collection of MZSP were studied (for descriptions see Vanin et al. (1983), Costa et al. (1988)):

***Homophileurus luederwaldti* (Ohaus, 1910)**

BRAZIL: São Paulo: One pupa reared from larva (genital ampulla damaged, sex not determined) (MZSP) Itanhaém, 12.i.1978, L.R. Fontes leg. in nest of *Microceroterme* sp. (Isoptera).

***Trioplus cylindricus* (Mannerheim, 1829)**

BRAZIL: São Paulo: One male pupa reared from larva (MZSP), São Paulo city, Cidade Universitária (USP), 09.i.1979, S.A. Vanin & C. Costa leg. in decaying tree trunk.

***Strategus validus* Fabricius, 1775**

BRAZIL: São Paulo: One male pupa reared from larva (MZSP), Peruíbe city, 25–27.v.1982, exp. MZUSP leg.

***Mystacella* sp. (Diptera: Tachinidae: Exoristinae: Goniini).**

BRAZIL, Santa Catarina: 2 imagines (reared from pupae), 2 puparia and 1 puparial exuvia of *Mystacella* sp. (MZSP) from 1 *P. felscheanus* larva reared to pupa (MZSP): Florianópolis city, Pantano do Sul, “restinga arbórea”, in *Vriesea friburgensis*, 02.ii.2008, A.G. Martins and F.F. Albertoni leg.

Repositories

DMNS: Denver Museum of Nature & Science (Denver, CO, U.S.A.); MZSP: Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); LANUFSC: Laboratório de Abelhas Nativas da Universidade Federal de Santa Catarina (Florianópolis, SC, Brazil).

Results**Description of the third instar larva of *Platyphileurus felscheanus* Ohaus, 1910**

Figs 1–13

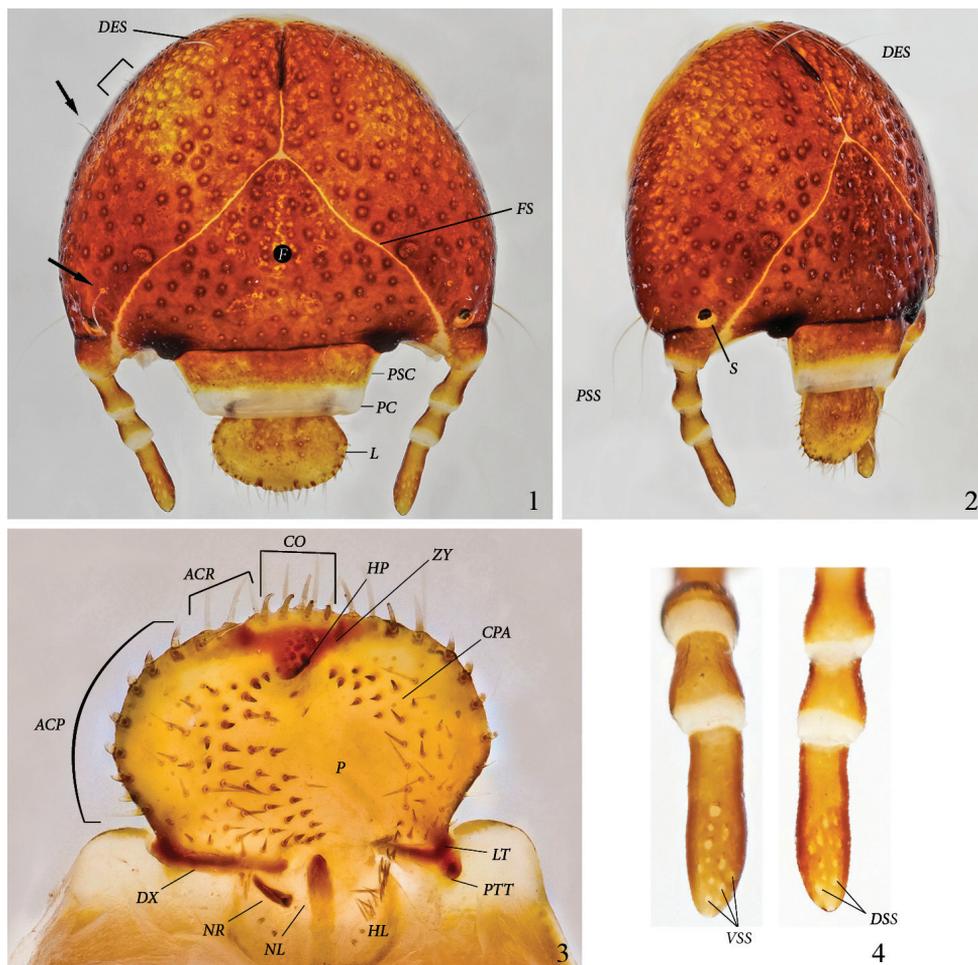
Terminology after Böving (1936), Morón (1986) and Ratcliffe and Skelley (2011).

Body length: 34–62 mm (\bar{x} =46 mm; SD=12.5 mm; n=7 preserved specimens); dehydrated or otherwise contracted specimens measured as low as 26 mm.

Cranium (Figs 1–2): Width of head capsule: 4.9–5.5 mm (\bar{x} =5.2 mm; SD=0.2 mm; n=12). Reddish brown, strongly and moderately densely punctate. Light yellow sharp frontal suture (*FS*) reaches antennal base. Stemma (*S*) present at antennal base, close to frontal suture. Anterior angles of epicranium with 2 long, thin setae behind distal side of antennal base (*PSS*) (1 on dorsal, 1 on ventral side of epicranium). Up to 4 microscopic setae basoventrally of *DES* (often missing). A long, thin seta behind stemma close to frontal suture (arrow); 1 lateral, long, thin seta just behind middle of epicranium, and 1 lateral seta close to epicranial suture (arrow). Frons without setae.

Clypeus (Figs 1–2): Trapezoidal with straight sides. Postclypeus (*PSC*) orange brown, with punctures smaller and sparser than on cranium. One external seta on each side. Preclypeus (*PC*) white, without punctures.

Labrum (*L*) (Figs 1–2): Orange brown with lighter anterior margin. Broadly oval, with rounded, not angulate, lateral margins; with several discal points similar to those



Figures 1–4. *Platyphileurus felscheanus* Ohaus, 1910, third instar DMNS ZE.15758: **1** head capsule frontal, arrows indicate setae, half rectangle indicates three minute setae, *DES* – dorsal epicranial setae, *F* – frons, *FS* – frontal suture, *L* – labrum, *PC* – preclypeus, *PSC* – postclypeus **2** head capsule fronto-lateral view, *DES* – dorsal epicranial setae, *PSS* – post stemmatal setae, *S* – stemmata **3** epipharynx, *ACP* – acanthoparia, *ACR* – acroparia, *CO* – corypha, *CPA* – chaetoparia, *DX* – dextotorma, *HL* – haptolochus, *HP* – haptomerall process, *LT* – laeotorma, *NL* – left nesium, *NR* – right nesium, *P* – pedium, *PTT* – pternotorma, *ZY* – zygum **4** antennae, ventral and dorsal view, respectively, *VSS* – ventral sensory spot, *DSS* – dorsal sensory spot. Photos: C Grinter.

of postclypeus (*PSC*); without posterior labral setae, but with 1 or 2 lateral setae on each side, 1 in front of labral base and 1 close to anterior margin. Anterior margin slightly trilobate, with one seta each on shallow outer lobes and 2 setae on the stronger middle lobe.

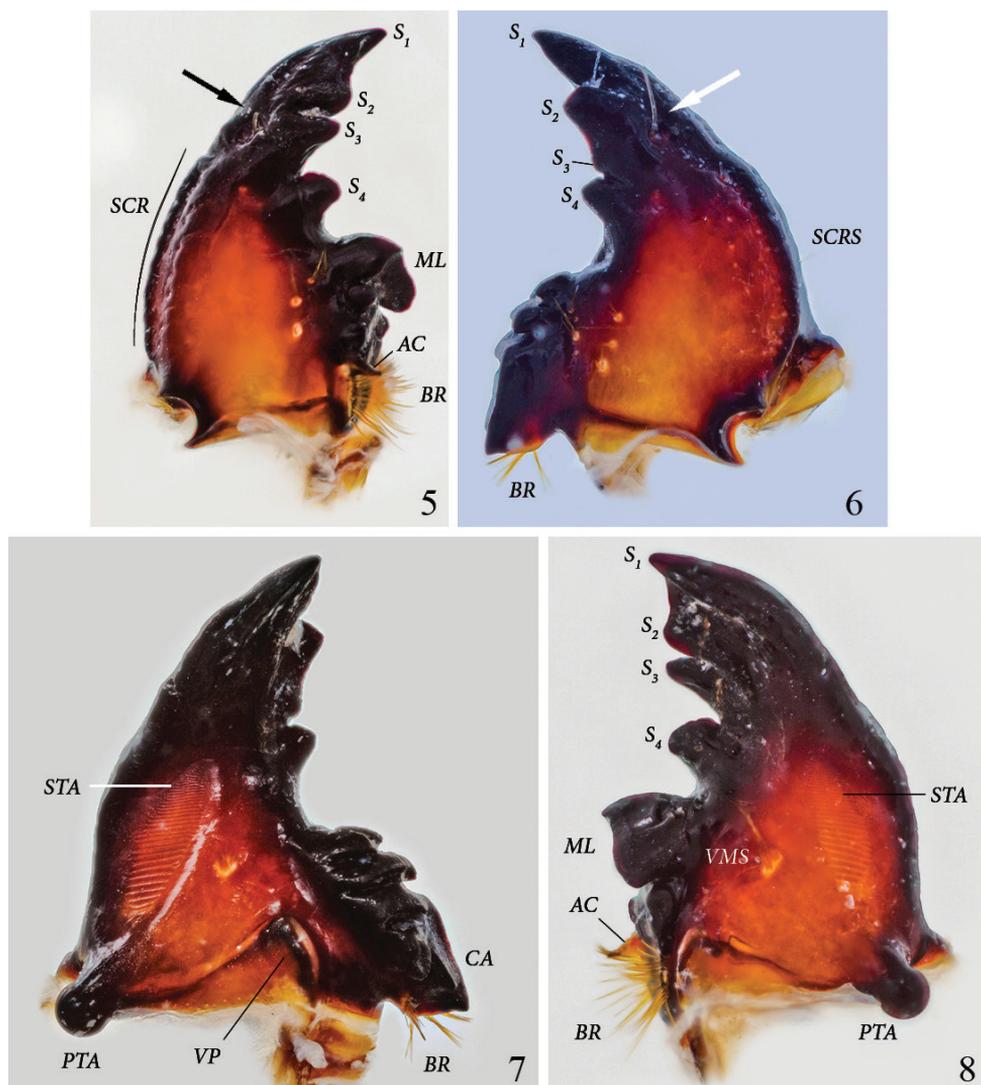
Epipharynx (Fig. 3): Form transversely suboval, asymmetrical, with left lateral margin obtusely angulate in the middle. Right and left chaetoparia (*CPA*) with 53–60 and 33–48 setae, respectively; up to 10 sensilla among setae on each side. Acroparia

(*ACR*) with 3 to 4 thick setae each. Left Acanthoparia (*ACP*) with 5 to 9 thick setae, anterior ones thicker and longer. Right acanthoparia with 6 to 9 thick setae, anterior ones thicker and longer. Pedium (*P*) extended to the left. Corypha (*CO*) with 10 thick setae. Zygum (*ZY*) brown, triangular, with ventral angle forming a blunt haptomeral process (*HP*). Laeotorma (*LT*) shorter than dextortorma (*DX*). Pternotorma (*PTT*) blunt, rounded. Right nesium (*NR*) caudolaterally shifted and enlarged, forming a sharp, ventrally extending tooth. Left nesium (*NL*) caudally elongated with sense cone on anterior tip. Haptolachus (*HL*) without setae except left margin bearing about 20 thin, long setae. Crepis missing.

Left mandible (Figs 5, 8): Form falcate. Scissorial area with S_1 and S_2 distant but bridged by flat area forming broad apical blade, separated from S_3 by acute scissorial notch. S_4 of similar size as S_3 , blunt, of cylindrical appearance in ventral view, separated from S_3 by acute and deep notch. Mandible dorsally with 1 long discal seta in front of labium at level of S_3 (arrow). Outer margin convex. Scrobis (*SCR*) with 1 short, thin seta. Dorsal area adjacent to scrobis with 2 rows of 7 sensorial pits. Dorsal area adjacent to molar crown with 3 setae. Acia (*AC*) well developed, with brush of apical setae. Brustia (*BR*) with 12 long setae. Ventral surface with elongate-oval stridulatory area (*STA*) with about 30 narrowly separated, subparallel ridges. Molar area with a tuft of 8 ventral molar setae (*VMS*) (setae very close together and difficult to count). Molar lobe (*ML*) large, forming a dorsoventral ridge, not subdivided. Molar crown with 2 lobes. Postartis (*PTA*) large, spherical. Ventral process triangular with rounded tip.

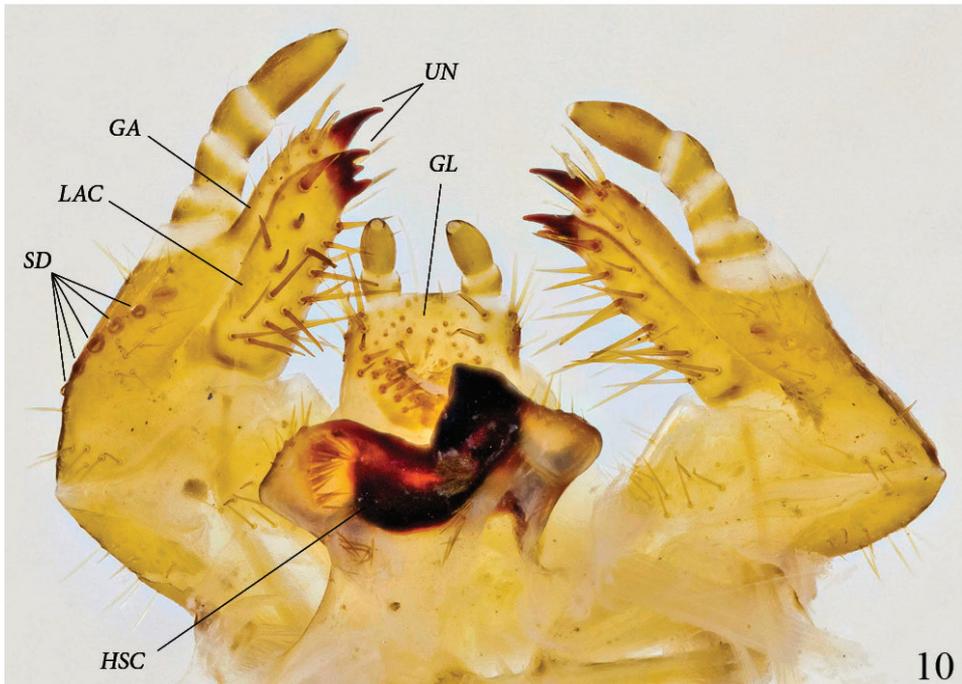
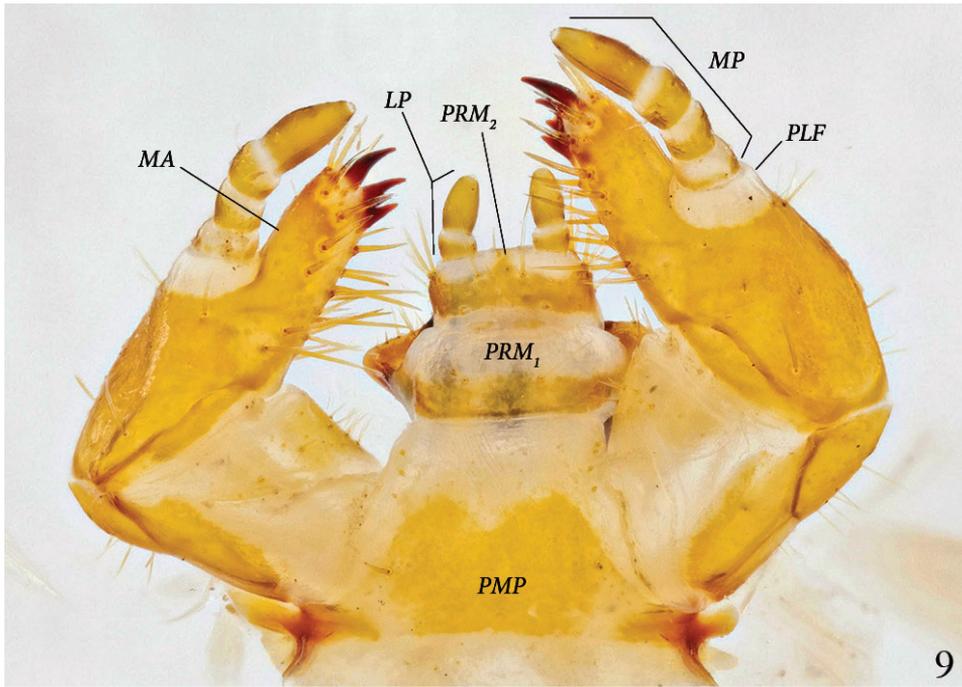
Right mandible (Figs 6–7): Form falcate. Scissorial area with S_2 separated from S_1 by obtusely angled notch. S_2 and S_3 distant but bridged by flat area, S_3 hardly developed as a denticle but with deep, acute notch separating it from S_4 . S_4 triangular, as elevated as S_2 . Mandible with 1 long discal seta in front of labium at level of S_3 (might be lacking or broken off) (Fig. 6, arrow). Outer margin convex. Scrobis with 1 short, thin seta (*SCRS*). Dorsal area of scrobis with an inner row of 5 and an outer row of 9 sensorial pits. Dorsal area adjacent to molar crown with a row of 4 white pits with 0, 4, 1, and 2 setae, respectively; discally with longitudinal row of 3 distinct, white pits with 3, 1, and 2 setae, respectively. Ventral surface with elongate oval, anteriorly tapering, stridulatory area (*STA*) with about 30, narrowly separated, subparallel ridges. Molar area with 5 ventral molar setae. Molar crown with 3 blunt ridges. Calx (*CA*) ventrally and dorsally ending in slightly blunt denticle. Brustia (*BR*) with about 15 setae. Postartis (*PTA*) large, spherical. Ventral process (*VP*) suboval, elongated laterally.

Maxilla and labium, ventral view (Fig. 9): Galea and lacinia fused, forming mala (*MA*). Ventral inner margin and apical area of mala with 7–8 strong, long setae, and another 5 or more on inner side of mala. Maxillary palpus (*MP*) 4-segmented; palpifer (*PLF*) white, membranous; spindle-shaped apical segment about twice as long as each preceding segment. Third segment with 2 strong, ventral setae. Mentum subdivided into 3 segments: yellow post-mentum (*PMP*) with one basolateral and one apicolateral seta on each side, white prementum 1 (*PRM₁*) with orange base and 2 discal setae, orange prementum 2 (*PRM₂*) with 2 setae on white base of each palpus. Labial palpus (*LP*) 2-segmented, spindle-shaped apical segment twice as long as basal segment.

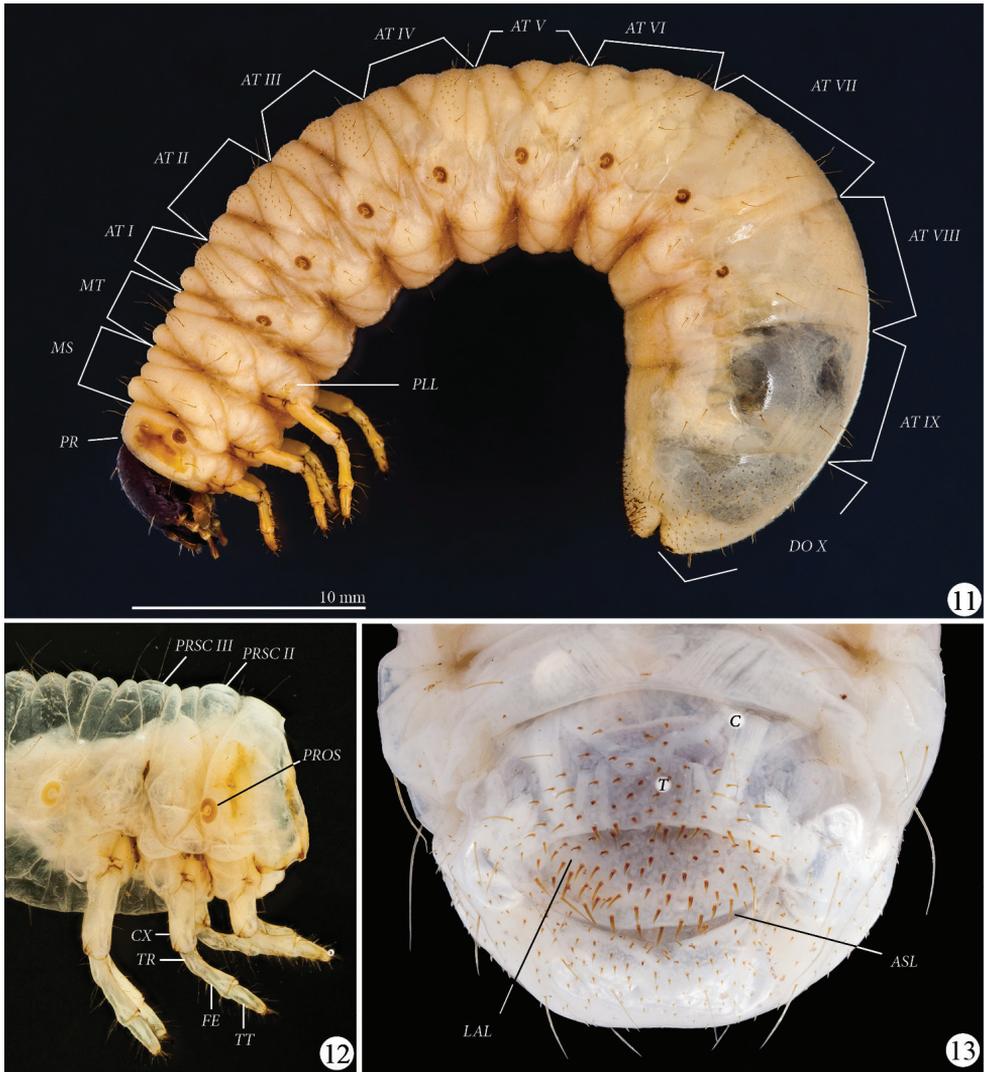


Figures 5–8. *Platyphileurus felscheanus* Ohaus, 1910, third instar mouth parts DMNS ZE.15758: **5** left mandible dorsal view, arrow indicates setae, AC – acia, BR – brustia, ML – molar lobe, S_{1-4} – scissorial teeth, SCR – scrobis **6** right mandible dorsal view, arrow indicates setae, BR – brustia, S_{1-4} – scissorial teeth, SCRS – scrobis seta **7** right mandible ventral view, BR – brustia, CA – calx, PTA – postartis, STA – stridulatory area, VP – ventral process **8** left mandible ventral view, AC – acia, BR – brustia, ML – molar lobe, PTA – postartis, S_{1-4} – scissorial teeth, STA – stridulatory area, VMS – ventral molar setae. Photos: C Grinter.

Maxilla and labium, dorsal view (Fig. 10): Galea and lacinia not fused. Galea (GA) with one apical uncus (UN); apicodorsal margin of galea with 3–4 setae. Lacinia (LAC) with 3 touching subterminal unci; dorsal surface of lacinia with 17–19 long, strong setae. Stridulatory area with 1 large, darker stridulatory tooth and a row of 4 to 6 smaller, rounded, sometimes more lightly colored teeth (SD), reaching longitudi-



Figures 9–10. *Platyphileurus felscheanus* Ohaus, 1910, third instar mouth parts DMNS ZE.15758: **9** maxilla and labium ventral view, LP – labial palpus, MA – mala, MP – maxillary palpus, PLF – palpifer, PMP – postmentum, PRM_{1,2} – Prementum 1 and 2 **10** maxilla and labium dorsal view, GA – galea, GL – glossa, LAC – lacinia, HSC – hypopharyngeal sclerome, SD – stridulatory teeth, UN – uncus. Photos: C Grinter.



Figures 11–13. *Platyphileurus felscheanus* Ohaus, 1910, third instar. **11** lateral view MZSP 010.245, AT I–IX – abdominal tergites I to IX, DO X – dorsum X, MS – mesothorax, MT – metathorax, PLL – pleural lobes, PR – prothorax **12** thorax and legs lateral view DMNS ZE.15758, CX – coxa, FE – femur, PROS – prothoracic spiracle, PRSC II – prescutum II, PRSC III – prescutum III, TR – trochanter, TT – tibiotarsus **13** larval raster DMNS ZE.15760, ASL – anal slit, C – campus, LAL – lower anal lip, T – teges. Photos: FF Albertoni (**11**), C Grinter (**12–13**).

nally towards base of stipes. Glossa (*GL*) with 23–31 long and 12–13 very short setae. Hypopharyngeal sclerome (*HSC*) asymmetrical, with median rectangular incision, right side with one triangular, tooth-like process produced dorsally; left side neither elevated nor protruded. Left lateral lobe with 7 setae on margin, in middle with dense, longitudinal row of about 15 broad setae directed mesally and a few more basally;

right lateral lobe with 8 setae on anterior margin and an oblique row of 6 setae basally at caudomedian border of hypopharyngeal sclerome.

Antenna (Fig. 4): Four-segmented with fourth antennomere the longest, about 1.7 times as long as third, second antennomere slightly shorter than fourth, first antennomere slightly shorter than third but thicker than others. Terminal antennomere with 12–13 ventral sensory spots (*VSS*) and 13–15 dorsal sensory spots (*DSS*); apex with 1 sensory spot.

Thorax (Figs 11–12): Prothoracic spiracle (*PROS*) 0.48–0.54 mm wide, 0.76–0.80 mm long. Respiratory plate light brown, ovals C-shaped, with ends touching. Bulla barely prominent. Respiratory plate with about 35 holes across diameter at middle. Dorsum of pronotum (*PR*) and prescutum II (*PRSC II*) and III (*PRSC III*) each with 2 lateral, long, slender setae, otherwise glabrous.

Legs (Figs 11–12): Tarsal claws falcate, all similarly curved and similar in size, with 1 basal seta and 1 seta in the middle of inner side. Tibiotarsus (*TT*) with 4 apical setae on outer side of the base of claw, and with 2 circular rows of 6 long setae. Femur (*FE*) with 2 circular rows of 4–5 long setae and accessory setae. Trochanter (*TR*) with 5–6 ventral setae. Coxae (*CX*) with 4 setae. Setae of legs light brown to transparent, thin.

Abdomen (Fig. 11): Spiracles of similar size as prothoracic spiracle; last one smaller; rounder than prothoracic spiracle. One long seta on stigma area behind each abdominal spiracle II to VII, no seta behind spiracles I and VIII. Pleural lobes (*PLL*) with 2 long setae. Pedal area with 1 central and 2 lateral long setae per segment. Abdominal tergites (*AT*) I–VII with many tiny, short, dark, spike-like setae, not arranged in rows. Abdominal tergite IX laterally with dark, sparse minute, spike-like setae. Dorsum X (*DO X*) completely covered with such setae.

Raster (Fig. 13): Surface without palidia. Campus (*C*) with 6 slender, moderately long setae. Teges (*T*) with about 110–115 shorter, thorn-like setae (some longer) anterior of transverse anal slit (*ASL*), slightly bent toward anal slit. Lower anal lip (*LAL*) with about 80–100 thinner, shorter, minute, thorn-like setae, some thin and long. Setae not arranged in any pattern.

Description of the pupa of *Platyphileurus felscheanus* Ohaus, 1910

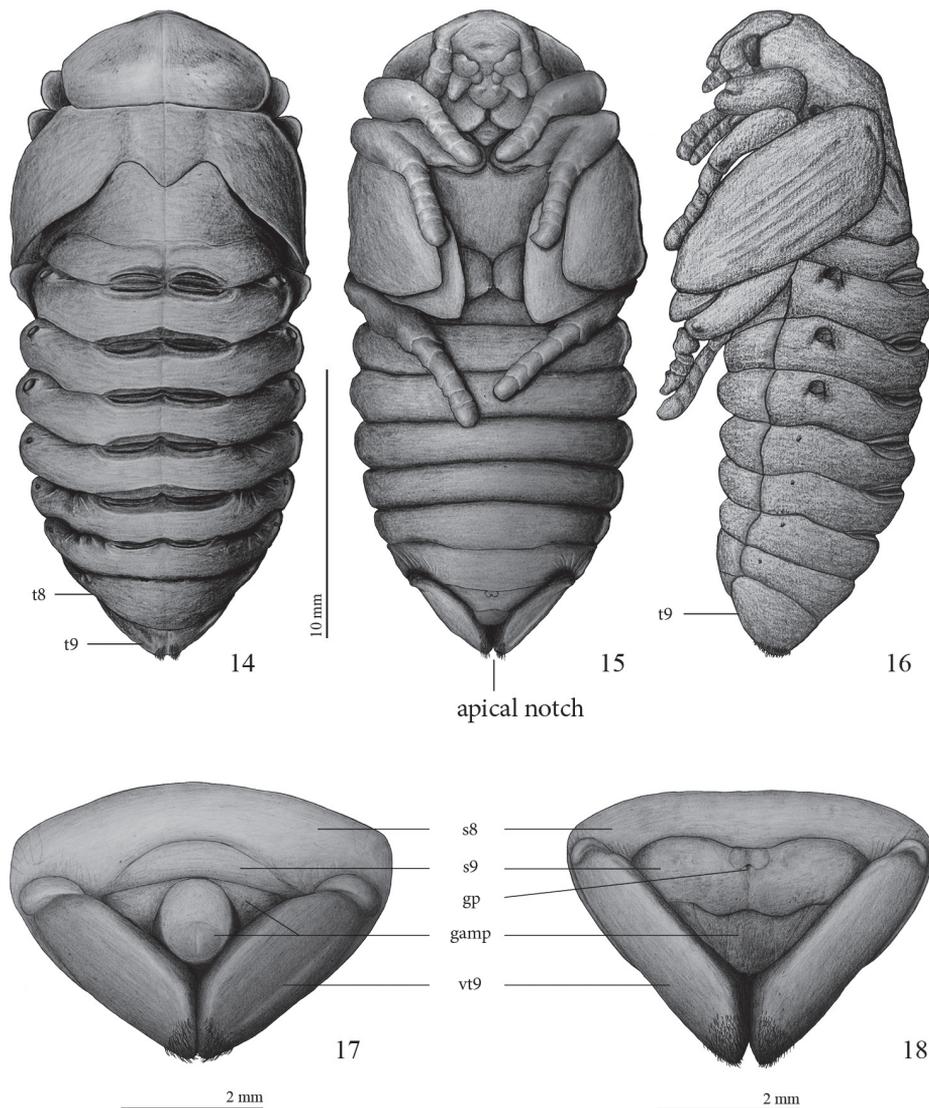
Figs 14–25, 34

Female pupa (Figs 14–16, 18, 20, 22, 24–25, 34):

Length 23.9 mm; largest width 10.4 mm.

Adecticous; exarate; body oblong, smooth, apparently glabrous but with microsetae covering whole body (best seen at magnification > 50 ×), apex of tergite IX with dense tuft of setae seen in dorsal and ventral views; abdominal segments constitute almost two thirds of whole body; yellowish-brown before and after fixation, gin-traps and spiracular rings darker and more strongly sclerotized.

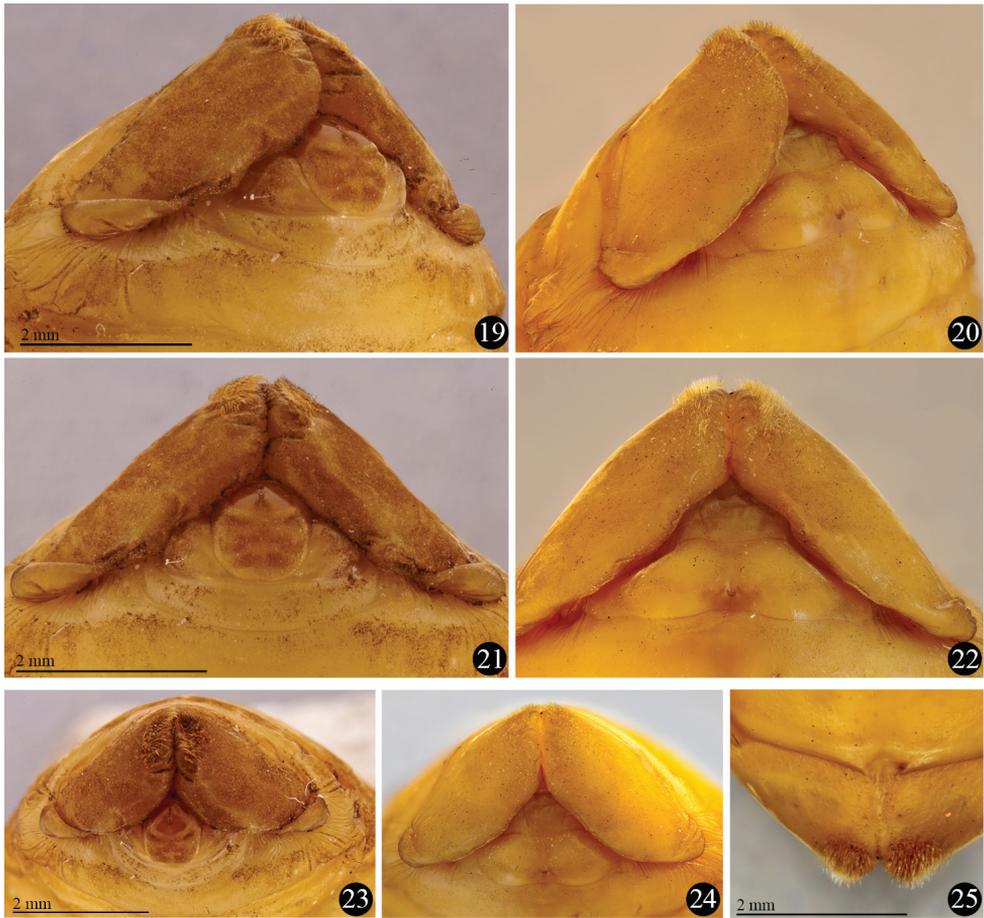
Head: epistomal suture incomplete at middle, clypeus with shallow depression, clypeolabral suture slightly marked.



Figures 14–18. *Platyphileurus felscheanus* Ohaus, 1910, pupa: **14** female pupa dorsal view, *t8*, *t9* – tergite 8 and 9, respectively **15** female pupa ventral view **16** female pupa lateral view **17** male pupa, ventral view of apex with genital ampulla **18** female pupa, ventral view of apex with genital ampulla. Legends: *s8*, *s9* – sternite 8 and 9, respectively; *gamp* – genital ampulla; *gp* – genital pore, *vt9* – ventralized tergite 9. Drawings: FF Albertoni.

Pronotum (Fig. 14): almost twice as wide as long; pentagonal, widest at middle, narrowed anteriorly, lateral margins rounded, medially with slightly transversal groove. Scutellum pentagonal, 1.2 times longer than wide.

Pterotheca (Figs 15–16): close to body, curved ventrally, extending posteriorly to second abdominal segment.



Figures 19–25. *Platyphileurus felscheanus* Ohaus, 1910, pupal apex showing genital ampulla, setose apex of ninth tergite and base of ventralized tergite 9: **19** male, ventro-lateral view **20** female, ventro-lateral view **21** male, ventral view **22** female, ventral view **23** male, frontal view **24** female, frontal view **25** female, dorsal view. Photos: FF Albertoni.

Abdomen: segments 1–7 widened transversally, about 6 times wider than long; segments 3, 4 and 5 widest; segment 8 longer on dorsal view than ventrally, about 4.5 times wider than long (Fig. 14); tergite 9 (*t*9) triangular, laterally extended to ventral side (see Figs 17–18) and with apical notch in ventral view; each side of apical notch covered with a tuft of yellowish, short, thin setae that do not extend ventrally, laterally, or dorsally (Figs 14–16, 18, 20, 22, 24–25); sternite 9 with genital pore; 4 pairs of functional spiracles, first pair almost completely concealed by pterothecae, other 3 pairs protruding about 0.2 mm (Figs 14, 16), 4 pairs of vestigial spiracles on laterotergites 5–8 (Fig. 16). Six pairs of gin-traps mid-dorsally in intersegmental region, the largest and most sclerotized between segments 1 and 2, those between segments 2 and 3, 3 and 4, 4 and 5, and 5 and 6 of same size, those between segments 6 and 7 smallest.



Figures 26–30. Imago of *Platyphileurus felscheanus* Ohaus, 1910. **26, 27 and 28** male habitus, dorsal, ventral and lateral, respectively **29** mentum DMNS ZE.20187 **30** hind leg ventral and dorsal view respectively DMNS ZE.20188. Photos: FF Albertoni (26–28), C Grinter (29–30).

Female genital ampulla (*gamp*) (Figs 18, 20, 22, 24): at middle with 2 almost parallel lines slightly convergent anteriorly and 2 diagonal lines, 1 per side.

Male pupa (Figs 17, 19, 21, 23):

Length: 19.0 mm; largest width 10.1 mm.

Most characteristics as in female but basal part of ventral side of ninth tergite (*vt9*) with much stronger constrictions than in female (Figs 17–25). In males, they resemble 2 lateral lobes, whereas in females they are less folded (Figs 19–24). Sternite 9 (*s9*) anteriorly convex in males, in females with different form (see Figs 17–22).

Male genital ampulla (*gamp*) (Figs 17, 19, 21, 23) divided into 2 parts: a rounded structure and a narrow, trapezoidal band strongly emarginated at middle, surrounding partially the rounded structure; rounded structure with circular, glabrous area at apex, glabrous area with longitudinal, dark line impressed at apex.

Life history

In 14 ground-growing bromeliads, we collected 19 larvae of *P. felscheanus*, 13 of them in *Aechmea lindenii*, three in *A. nudicaulis*, one in *Canistrum lindenii*, one in *Hohenbergia augusta*, and one in *Nidularium innocentii*. The highest number of larvae in one bromeliad was four in a single *A. lindenii*, but the majority of bromeliads had only one larva.

Second instars were found at the base of more external leaves of the rosette among leaf litter. No damage to bromeliad leaves near the larvae was observed. Third instars were always found in the center of the rosette with the surrounding leaves strongly damaged (Figs 32–33).

Coincidentally, when the bromeliad leaves started to dry and consequently to decompose, the larvae stopped feeding and started pupation. They built their pupal chamber in the center of the leaf rosettes or among leaves near the center, using leaf litter, twigs, and humus that had accumulated there. The larval exuvia was pushed to the rear of the pupal chamber (Fig. 34). Observations of the second phase are summarized in Table 1.

Parasitism by Tachinidae flies was observed in one pupa (Fig. 35). As the bromeliad with the larva was kept open in the laboratory, we do not know whether parasitism occurred in the laboratory or in the field. The chamber of the affected pupa seemed crudely done, mainly built with plant fiber and missing a more consistent humus wall.

Discussion

Pupal morphology

Generally, pupae of Scarabaeidae are of uniform appearance, mainly differing by adult characters such as horns. Usually they do not have pupa-specific ornamentations or setae for chaetotaxy analysis unlike pupae of other beetle families which might be the



Figures 31–35. *Platyphileurus felscheanus* Ohaus, 1910, natural habitat: **31** bromeliad *Vriesea friburgensis* with leaf litter in open area of Atlantic Forest, Santa Catarina, Florianópolis **32** *Aechmea* sp., cylinder of the central leaves eaten by *P. felscheanus* larva **33** larva on bromeliad leaf from the very center rosette **34** pupa in its pupal chamber built with pieces of leaves, twigs and humus **35** puparia of *Mystacella* sp. (Diptera: Tachinidae) and pupal exuvia of *P. felscheanus* (arrow). Photo: A Zillikens (31), FF Albertoni (32–35).

reason for the poor attention that scarabaeoid pupae have gained in the past (see Costa et al. 1988; Costa and Ide 2008).

Several descriptions of pupae from Dynastinae tribes, such as Cyclocephalini, Philaurini, Oryctini point out the thin golden setae present at the apex of 9th abdominal segment but rarely mention the shape of the 9th tergite and the genital ampulla (Philaurini: Vanin et al. 1983; Morelli [1991]; Neita-Moreno and Ratcliffe 2010, 2011; Cyclocephalini: Neita-Moreno et al. 2007; Neita-Moreno and Morón 2008; Oryctini:

Table 1. Results of second phase of study on *P. felscheanus* life history.

	Pantano do Sul, restinga arborea	Santinho/Mocambique, restinga arborea	Sto Antonio
Bromeliad searched/ collected	6 <i>Vriesea fibroargensis</i> (Fig. 31) No damage to plant	3 <i>Aechmea</i> sp. Plant senescent	5 <i>Aechmea</i> sp. and 3 <i>Nidularium</i> sp. Plant apparently not injured.
Larvae found	1 second instar larva (n° 1); 2.iv.2008. In outer leaf axils with much litter, but moved into the centre of rosette. Smaller than specimens n° 2 and 3.	1 second instar larva (n° 3); 2.iii.2008. Between dry external leaves; later moved slowly into the central rosette. Moulted on 7.iii.2008.	1 third instar larva (n° 5) in <i>Aechmea</i> sp. 23.iii.2011. Down in center of rosette. 1 third instar larva (n° 6) in <i>Aechmea</i> sp. Just next to the bromeliad of n° 5; Down in center of rosette.
Ate what?	Ate basal parts of leaves.	Ate the basal parts of leaves.	Ate the basal (and green) parts of leaves.
Pupa	6.ii.2009 starts pupal chamber, 10.ii pre-pupa, 15.ii. pupa, (fixed).	22.ix.2008 larva fixed.	On 08.x.2011.
Remarks	9.i.2009 emergence of 2 flies, fixed together with puparia.	Larva fixed with boiling water, preserved in ethanol 90%.	Male pupa. It seemed to pupate before final growing time and turns to smaller pupa than n° 1. pupa smaller than n°. 1 and 5 Female imago emerged on 10.xi.2011. Are banana. Stayed most part of the time buried. Died on 9.xii.2011.

Ratcliffe and Chalumeau 1980; Costa et al. 1988; Morelli 1997; Alvarez Castillo et al. 1998; Neita-Moreno and Orozco 2009; Pardo-Locarno et al. 2009), characters which seem to vary within Scarabaeidae. Our examination of pupae from Phileurini and Oryctini revealed that they can be distinguished from that of *P. felscheanus* based on the form of the 9th tergite and genital ampulla and the distribution and size composition of those apical setae.

Comparison with other scarabaeid pupae

In a pupa of *Homophileurus luederwaldti* examined (length: 25.3 mm, largest width: 13.0 mm; Phileurini) the setation on the apex differs from that of *P. felscheanus* by covering a much wider area, until the middle of the ventral part of *t*₉, and the setae also extend slightly towards the dorsal side. The apical notch is more open than it is in *P. felscheanus*. The genital ampulla region was damaged, and could not be analysed. In a male pupa of *Trioplus cylindricus* (length: 22.0 mm, largest width: 9.3 mm; Phileurini), the setae on the apical tergite are similar to the pupa of *H. luederwaldti*. They cover a larger area, spreading laterally towards the dorsal region, but almost do not change in density and sizes as in *H. luederwaldti*. The rounded structure of the genital ampulla is wider posteriorly and narrowed from middle to base, thus not rounded or elliptical. There are two longitudinal marks, one smaller anteriorly and the longer posteriorly. In a male pupa of *Strategus validus* (length: 60 mm, largest width: 27 mm; Oryctini), the rounded structure of the genital ampulla is elliptical with one longitudinal mark at the apex and thus, similar to that of *P. felscheanus*. Tergite 9 has a transversal depression laterally (not present in *P. felscheanus*); pubescence of uniform, small setae covering a wide area throughout the segment, ventrally covering almost the whole area extending laterally unto the edge of the lateral depression; and an apical notch connected mesally by V-shaped fold (absent in *P. felscheanus*).

Furthermore, in *Hemiphileurus elbitae* Neita-Moreno and Ratcliffe 2010 (Phileurini), the apex of *t*₉ appears to be more densely setose over a larger area, and with longer setae (Neita-Moreno and Ratcliffe 2010) than in *P. felscheanus*. The apices of male and female pupa of *Homophileurus tricuspis* Prell, 1914 (Phileurini) have setae that extend significantly more sideways (Neita-Moreno and Ratcliffe 2011) than in *P. felscheanus*. The pupa of *Phileurus affinis* Burmeister, 1847 (Phileurini) has *t*₉ covered with small and abundant setae on the apex, but there is no detailed illustration to compare (Morelli [1991]). The female pupa of *Aspidolea singularis* Bates, 1888 (Cyclocephalini) has the setae on *t*₉ similarly distributed as those of *P. felscheanus*, but dorsally and laterally the shape of *t*₉ is different. In the former, it is almost as long as wide, and in the latter it is two times wider than long. In addition *t*₈ is more sharpened medially and projected towards the apex, whereas it is rounded in *P. felscheanus*. The pupa of *Ancognatha ustulata* Burmeister, 1847 (Cyclocephalini) has setae widely distributed ventrally on *t*₉ (Neita-Moreno and Morón 2008).

Even though the knowledge of pupae is much more limited than that of larvae, pupae do have some exclusive characters such as setae, spurs, tubercles and modified

spiracles (Costa and Ide 2008). As demonstrated here, the apex of the abdomen, namely the shape of t_9 , genital ampulla, and setal pattern could be a source of important characters for distinguishing between subfamilies, tribes, and genera of Scarabaeidae and perhaps could even be used in systematic and phylogenetic analyses, but need to be much more comprehensively studied. Altogether, we consider the data from pupal morphology presented here to be too limited to contribute to the discussion of the systematic placement of *P. felscheanus*.

Life history

Dynastinae larvae frequently feed on decaying plant matter, especially wood (Ritcher 1958; Carlson 1991; Ratcliffe et al. 2002), although food sources vary between species and include roots of living plants, especially monocots, and general organic matter (Ritcher 1958; Gassen 1989). Lourenção et al. (1999) reported larvae of *Strategus* Hope, 1837 (Oryctini) as a pest of Arecaceae feeding on live plant tissue. Larvae of Oryctini and Cyclocephalini are often associated with feeding on live plant tissue, unlike those in the tribes Phileurini and Dynastini that are known to feed on decaying wood or humus associated with decaying vegetable matter. Thus *P. felscheanus* would be the first known exception in the Phileurini tribe.

Krell et al. (2002) reported larvae of a species of Cetoniinae feeding on living bromeliad tissue and already referred to an unidentified large dynastine larva collected by Lüderwaldt (1915) in bromeliads at Colonia Hansa, Blumenau, in Santa Catarina state, Brazil. Nevertheless, this is the first report of identified larvae of Dynastinae feeding on living leaf tissue (Fig. 32) and the only species of Dynastinae known so far whose larvae develop in bromeliad rosettes.

Considering the place where we found the younger larvae, females most likely lay eggs into the external leaf axils that are rich in decaying plant matter and humus, and usually dryer than the water-filled central rosette. Our observations suggest that the larvae initially feed on dead decaying vegetal matter and then migrate into the center of the rosette to feed on the white basal part of living leaves. It is during this second phase that the larvae gain most weight.

The construction of pupal chambers in Dynastinae species is poorly documented. Larvae of *Phileurus hospes* Burmeister, 1847 built their pupal chamber only with humus from the decaying tree trunk in which the larvae were found (F. F. Albertoni pers. obs.). The termitophilous species *Homophileurus luederwaldti*, *Actinobolus tribolus* Luederwaldt, 1910 and *Actinobolus radians* Westwood, 1841 used their own faeces and soil from the termite nest to build their pupal chambers (Luederwaldt 1911). *Homophileurus tricuspis* Prell, 1914 seemed to make a hole in the termite nest wall where the larvae delimited their pupal chamber (Neita-Moreno and Ratcliffe 2011). *Trioplus cylindricus* larvae built their pupal chamber excavating the wood or using fragments of wood (Vanin et al. 1983). As is the case with *P. felscheanus*, these larvae seem to have opportunist behaviour by using the substrate next to them. The



Figure 36–37. Imago of *Mystacella* sp., parasite of *P. felscheanus*. **36** dorsal view **37** lateral view. Photos: FF Albertoni.

location, size, and the material used by *P. felscheanus* for building its pupal chamber (Fig. 34) resembles those of another bromeliad associated insect, the lepidopteran *Geyeria decussata* (Castniidae) (Albertoni et al. 2012) except for the fact that the beetle larva does not use silk.

According to Ritcher (1958), most Scarabaeidae push the last larval exuvia to the rear of pupal chamber during pupation, but in Rutelinae and most Dynastinae the last larval exuvia splits longitudinally along the middorsal line and the pupa stays inside the larval exuvia. However, in a few genera such as *Oryctes* Hellwig, 1798 and *Strategus* Hope, 1837 (both Oryctini) the larval exuvia is pushed to the rear of the pupal chamber as was observed with *Platyphileurus* (Fig. 34).

Among the South American Coleoptera that are hosts of Tachinidae, Chrysomelidae and Scarabaeidae are the families with the highest numbers of parasitized species (Guimarães 1977), but none of the 7 genera of Goniini listed in Guimarães's catalogue parasitized Coleoptera. Neither was the monotypic genus *Platyphileurus* Ohaus, 1910 registered as a host, nor was *Mystacella* van der Wulp, 1890 (Figs 36–37) registered as parasite for any beetle species. In North America, *Mystacella* spp. was recorded as parasitizing Lepidoptera of the families Arctiidae and Noctuidae and *M. chrysoprocta* (Weidemann, 1830) parasitizing Scarabaeidae of the genus *Xyloryctes* Hope, 1837 (Arnaud 1978). Thus, our observations constitute a new host-parasitoid association.

Transfer of *Platyphileurus* from Phileurini to Oryctini on the basis of larval and adult characters

Since the species studied here was not only described as two species, *P. felscheanus* and *S. jelineki*, but also as belonging to different tribes, namely Phileurini and Cyclocephalini, it is appropriate to explore whether larval characters can contribute to resolving its tribal classification.

Antennal sensory spots: Larvae of Cyclocephalini are characterized by 2, 3, or 4 sensory spots on the last antennomere plus an apical one (Ritcher 1944; Remède de Gavotto 1964; Morelli and Alzugaray 1994; Ramírez-Salinas et al. 2004; Neita-Moreno et al. 2007; Bezerra de Souza et al. 2014). With 12 to 13 dorsal and 13 to 15 ventral sensorial spots on the apical antennomere, *P. felscheanus* would be the only known exception in this tribe.

Likewise, the species would have the highest number of antennal sensilla ever recorded in Phileurini larvae. So far, *Homophileurus integer* (Burmeister, 1847) had the highest number with 5 dorsal and 8 ventral sensory spots (Ratcliffe and Skelley 2011); most Phileurini have a lower number. In Dynastinae, a similarly high number of antennal sensilla was only found in the Dynastini species *Xylotrupes gideon* s.l. (Linnaeus, 1767) (Bedford 1974) and *Chalcosoma atlas* (Linnaeus, 1758) (Bedford 1976), in *Oryctoderus* (Oryctoderini; Bedford 1974), and in several species of the tribe Oryctini, namely a few *Strategus* species (Ritcher 1944; Ratcliffe and Chalumeau 1980; Costa et al. 1988; Morón and Ratcliffe 1990), *Heterogomphus chevrolati* Burmeister, 1847 and *Enema endymion* (Chevrolat, 1843) (Ratcliffe 2003), *Coelosis biloba* (Linnaeus, 1767) (Pardo-Locarno et al. 2006), *Oryctes monoceros* (Olivier, 1789) (Marcuzzi et al. 1977), *Oryctes boas* Fabricius, 1775 (Oberholzer 1959), *Trichogomphus fairmairei* Arrow, 1919, *Scapanes australis* (Boisduval, 1835) (Bedford 1974), and *Podischnus agenor* (Olivier, 1789) (Pardo-Locarno et al. 2009). With outgroup taxa (Rutelinae, Melolonthinae) having only 1 to 4 antennal sensilla (Ritcher 1966), and a high number of sensilla as in *Platyphileurus* not occurring in other Dynastinae tribes, this character is likely to be an apomorphy of Dynastini, Oryctoderini, and Oryctini.

Larval mandibles: The shape of the larval left mandible of *Platyphileurus* resembles most the larval mandibles of some Oryctini species. Particularly the large, blunt scissorial denticle S_4 is most commonly found in Oryctini, namely in *Strategus splendens* (Palisot de Beauvois, 1809) (Ritcher 1944); *Strategus jugurtha* (Burmeister, 1847) (smaller, but blunt; Morón and Ratcliffe 1990); *Podischnus agenor* (slightly incised; Pardo-Locarno et al. 2009; Neita-Moreno and Orozco 2009), *Heterogomphus chevrolati* and *Enema pan* Fabricius, 1775 (Ratcliffe 2003), *Heterogomphus dilaticollis* Burmeister, 1847 (Neita-Moreno and Orozco 2009), *Trichogomphus fairmairei*, *Scapanes australis* (Bedford 1974), and thinner, but still blunt in *Heterogomphus pauson* Perty, 1830 (Alvarez-Castillo et al. 1998). It is also found in Dynastini, namely in *Megasoma elephas* Fabricius, 1775 (Morón 1977). In Cyclocephalini, S_4 is mostly missing, only being present in *Ancognatha* Erichson, 1847 as a blunt or acute denticle (see Ramírez-Salinas et al. 2004; Neita-Moreno and Morón 2008). In Phileurini S_4 is, if present, always smaller and triangular (Vanin et al. 1983; Dechambre and Lumaret 1986; Morelli [1991]; Ocampo and Morón 2004; Ratcliffe and Skelley 2011).

Other larval characters: According to Neita-Moreno and Orozco (2009), Oryctini larvae can be diagnosed by the combination of the following characters: cranium densely punctate, dark reddish brown; maxillary stridulatory teeth truncate; antennomere 4 with 2–15 dorsal sensory spots; tarsal claws with 2–4 long, stout setae; raster without palidia or septula. *Platyphileurus* larvae show all those characters. According

to the larval characters this genus could belong to Oryctini, or possibly Dynastini (but these having rather rounded stridulatory teeth), but it is unlikely to belong to Cyclocephalini, Phileurini, or Pentodontini.

Adult characters: To exclude the possibility of *Platypheleurus* belonging to Oryctini, the adult mouthparts were examined. The mentum (labium) of *Platypheleurus* is triangular, basally broad, tightly tapered to a blunt, rounded, thin and slightly protruding tip (Fig. 29). The basis of the labial palps is almost visible, being slightly covered by the margin of the mentum only. This is different from the form of the mentum diagnostic for Phileurini, being broad and covering the basis of the labial palps completely. In fact, the mentum of *Platypheleurus* resembles broad menta of Oryctini or Pentodontini.

Problems with the current tribal classification: In the current, typological classification, Oryctini are separated from Pentodontini by one variable adult character, the apex of the hind tibia, of which Ratcliffe and Cave (2006: 189) noted: "We remain concerned that this single, sometimes variable (or transitional) character used to separate taxa at the tribal level is not reliable." Likewise, Dynastini are separated from Oryctini by only two adult characters: a cylindrical first tarsomere of the hind legs (triangularly dilated in Oryctini and other tribes) and anterior legs in males more or less prolonged (no such dimorphism in Oryctini and other tribes) (Endrődi 1985; Ratcliffe and Cave 2006). Although Dynastini could well be monophyletic characterized by those two potential autapomorphies, it would leave the Oryctini without an autapomorphy in the current classification since the character separating it from Pentodontini, the crenulated or denticulate metatibial apex, is also present in Dynastini and possibly a synapomorphy of Oryctini and Dynastini. Without an autapomorphy, Oryctini cannot be diagnosed as a monophylum (cf. Hennig 1982: 93; Wheeler 2012: 41). Being entirely typological, the current tribal classification is likely to contain paraphyletic or even polyphyletic tribes.

In a caryological study Dutrillaux et al. (2013) found that *Augosoma* Burmeister, 1847, currently in Dynastini, might be closer to *Oryctes* Hellwig, 1798 (Oryctini) than to other Dynastini. The recent cladistic analysis of Dynastini by Rowland and Miller (2012) proposes *Augosoma* to be sister to the remaining analysed genera of the subtribe Dynastina, indicating its early branching within the Dynastini. This analysis cannot help clarifying the relationship between Dynastini and Oryctini (or Oryctini+Pentodontini) since representatives of the latter were not included. The relationship between Oryctini and Dynastini remains unresolved, but the recent studies indicate that Oryctini could be paraphyletic in respect to a - possibly polyphyletic - Dynastini.

Tribal placement of *Platypheleurus*: The apex of the hind tibia in *Platypheleurus* (Fig. 30), being (weakly) dentate and not truncate, would place this genus in Oryctini or Dynastini, not in Pentodontini in the current sense. This is supported by the number of sensilla on the larval antenna and the shape of the left larval mandible. The slightly broader first tarsomere of the hind legs, together with the small body size being unusual for Dynastini, indicates that it rather belongs to Oryctini than to Dynastini in the current sense. The shape of the adult mentum, the large number of sensilla on the larval antenna, and the strong S4 of the left larval mandible are not found in Phi-

leurini. We accordingly propose the transfer of *Platyphileurus* from Phileurini to Oryctini. We consider the flat body of *Platyphileurus* a convergence with the body shape of Phileurini, likely related to the unique habitat among the tight bromeliad leaves, where the larva pupates and that enable adults hiding between their leaves.

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A new troglomorphic species of *Harmonicon* (Araneae, Mygalomorphae, Dipluridae) from Pará, Brazil, with notes on the genus

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Abstract

A new species of *Harmonicon* F. O. Pickard-Cambridge, 1896 (Araneae, Dipluridae) is described, from a medium-sized lateritic cave in Parauapebas, Pará, Brazil. The male holotype and only specimen known of *H. cerberus* **sp. n.** was found near the entrance of Pequiá cave. This taxon is the fourth species described and the southernmost record for the genus. The new species displays some troglomorphic characteristics, such as reduction and merging of the posterior median and both pairs of lateral eyes and pale yellow to light brown coloration. Both characters are diagnostic when compared to the normal separated eyes and reddish to dark brown of other *Harmonicon* species. Other diagnostic characteristics are isolated, long, rigid setae distal to the lyra and the shape of the copulatory bulb. This is the second troglomorphic mygalomorph species from Brazil and the first from the Amazonian region.

Keywords

Amazonia, biodiversity, cave, Diplurinae, Neotropics, taxonomy

Introduction

Harmonicon F. O. Pickard-Cambridge, 1896 is a Neotropical genus of Mygalomorphae, belonging to the family Dipluridae. There are three described species from the Amazon region (Platnick 2014): *H. audeae* Maréchal & Marty, 1998 (males and females, from Sinnamary, French Guiana), *H. oiapoqueae* Drolshagen & Bäckstam, 2011 (males and females, from Saint Georges, French Guiana), and *H. rufescens* F. O. P.-Cambridge, 1896 (immature, from Santarém, Pará state, Brazil). This genus was removed from former synonymy with *Diplura* C. L. Koch, 1850 by Maréchal and Marty (1998), and it was recently placed in Diplurinae by Drolshagen and Bäckstam (2011), due to the presence of a lyra. In the family Dipluridae, this structure is known only in two other genera of that subfamily, *Diplura* and *Trechona* C. L. Koch, 1850.

The new species was found in the entrance of Pequiá cave, a medium-sized lateritic cave in the Floresta Nacional de Carajás, Parauapebas, Pará, Brazil. One of approximately 1,100 caves in iron ore deposits found in Carajás, Pequiá cave is situated at 06°05'15" S; 50°07'13" W (DMS), circa 427 m above sea level (IBAMA 2003, Piló and Auler 2009, IPHAN 2013). This cave has a projection of approximately 72 m, an L-shaped form, and contains a permanent water pool covered with guano (IBAMA 2003, Magalhães 2012, IPHAN 2013). Pequiá cave harbors important remains of earlier indigenous occupation in the Amazon region (IBAMA 2003, Magalhães 2012, IPHAN 2013).

There are several studies on the cave fauna of the iron ore cave region of Carajás (ex. Cunha et al. 2007, Pellegrini and Ferreira 2011, Prous et al. 2011). Several troglobitic species have been found in these iron ore caves, including a beetle and a centipede (Trajano and Bichuette 2010; Pellegrini and Ferreira 2011). There is a high potential of iron caves as habitat of troglobitic invertebrates in Brazil (Trajano and Bichuette 2010). As determined by Prous et al. (2011), there are an average of 2.5 troglobitic species in each cave with permanent water bodies in the Carajás region.

This is the second troglomorphic mygalomorph species from Brazil, but the first species from the Amazonian region. Recently, a troglobitic Theraphosidae was described from Bahia state (Bertani et al. 2013). Troglobitic or troglomorphic Dipluridae are common in subfamilies other than Diplurinae (ex. Euagriinae, see Coyle 1988), but the only other diplurine described solely from caves is *Linothele cavicola* Goloboff, 1994. This species lacks most of the modifications commonly associated with cave life, such as pigmentation and eye reduction, but displays elongated appendages, a reduced number of teeth on tarsal claw, and does not spin webs (Goloboff 1994).

Methods

The color pattern was based on a specimen preserved in 75% ethanol. Observations, photographs and measurements were made with an Olympus stereoscopic microscope. Measurements are given in millimeters, unless otherwise noted. Cephalothorax length was measured from the posterior border to the anterior margin of the clypeus. Total

length was measured from the posterior border of the anal tubercle to the anterior margin of the clypeus, not including the spinnerets. Each article of the pedipalp and legs was measured in retrolateral view, from the basal condylus to the distal one. Photographs were taken with a Sony Cybershot DSC-V1 camera attached to the stereomicroscope. The software package COMBINEZ, version COMBINEZP (Hadley 2013), was used to create composite images with extended depth of field. Geographical coordinates for localities were obtained from GEONAMES (2013). The distribution map was elaborated using ESRI ARCGIS 10 software.

The following abbreviations are used: ALE = anterior lateral eyes; AME = anterior median eyes; ITC = inferior (or unpaired) tarsal claws; PLE = posterior lateral eyes; PLS = posterior lateral spinnerets; PME = posterior median eyes; PMS = posterior median spinnerets; STC = superior (or paired) tarsal claws. Spines (or macroseta): ap = apical; p = prolateral; pld = prolaterodorsal; plv = prolateroventral; r = retrolateral; rld = retrolaterodorsal; rlv = retrolateroventral; v = ventral; MNRJ = Museu Nacional, Universidade do Brasil/Universidade Federal do Rio de Janeiro, Brazil.

Taxonomy

Harmonicon F. O. P. Cambridge, 1896

Harmonicon F. O. P.-Cambridge, 1896: 755; Maréchal and Marty 1998: 500; Drolshagen and Bäckstam 2011: 91; Platnick 2014.

Harmonicon cerberus sp. n.

<http://zoobank.org/9AE08814-D3FA-4DCC-9F8E-1493D6CE7E13>

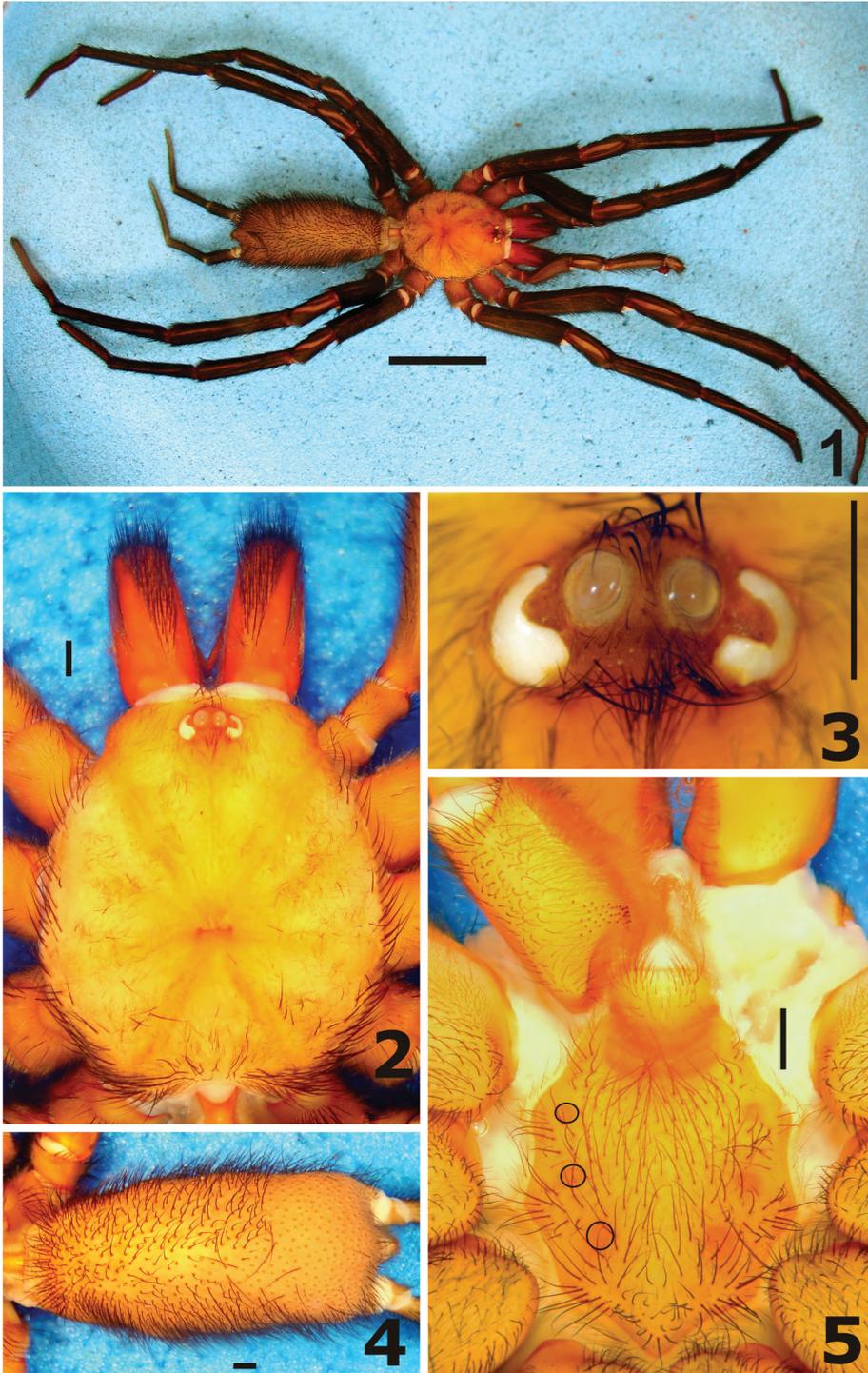
http://species-id.net/wiki/Harmonicon_cerberus

Figs 1–11, Map 1, Table 1

Diagnosis. This species may be easily recognized by the fusion of the PME and all lateral eyes (Figs 1–3), elongated chelicerae, and pale coloration (Figs 1–2). Another diagnostic trait is the strongly thickened setae near the lyra (Fig. 6). In other *Harmonicon*, similar setae are found, but they are never so thickened. In prolateral view, the globose bulb, with a strong constriction around the basis of the embolus, resembles *H. oiapoqueae*, in contrast to the piriform bulb, regularly tapering toward the embolus, in *H. audeae*. The embolus is slightly longer than the bulb itself (ratio 1.3), similar to *H. audeae* (1.2), but shorter than in *H. oiapoqueae* (1.6).

Type material. Male holotype from Brazil: *Pará*: Parauapebas, Floresta Nacional de Carajás, Pequiá Cave, near entrance, September 2003, Bittencourt, R. (MNRJ 04319).

Etymology. The specific epithet “*cerberus*” is an apposition noun and a reference to the three-headed watchdog that guards the entrance to the underworld, the Hades, in Greek mythology.



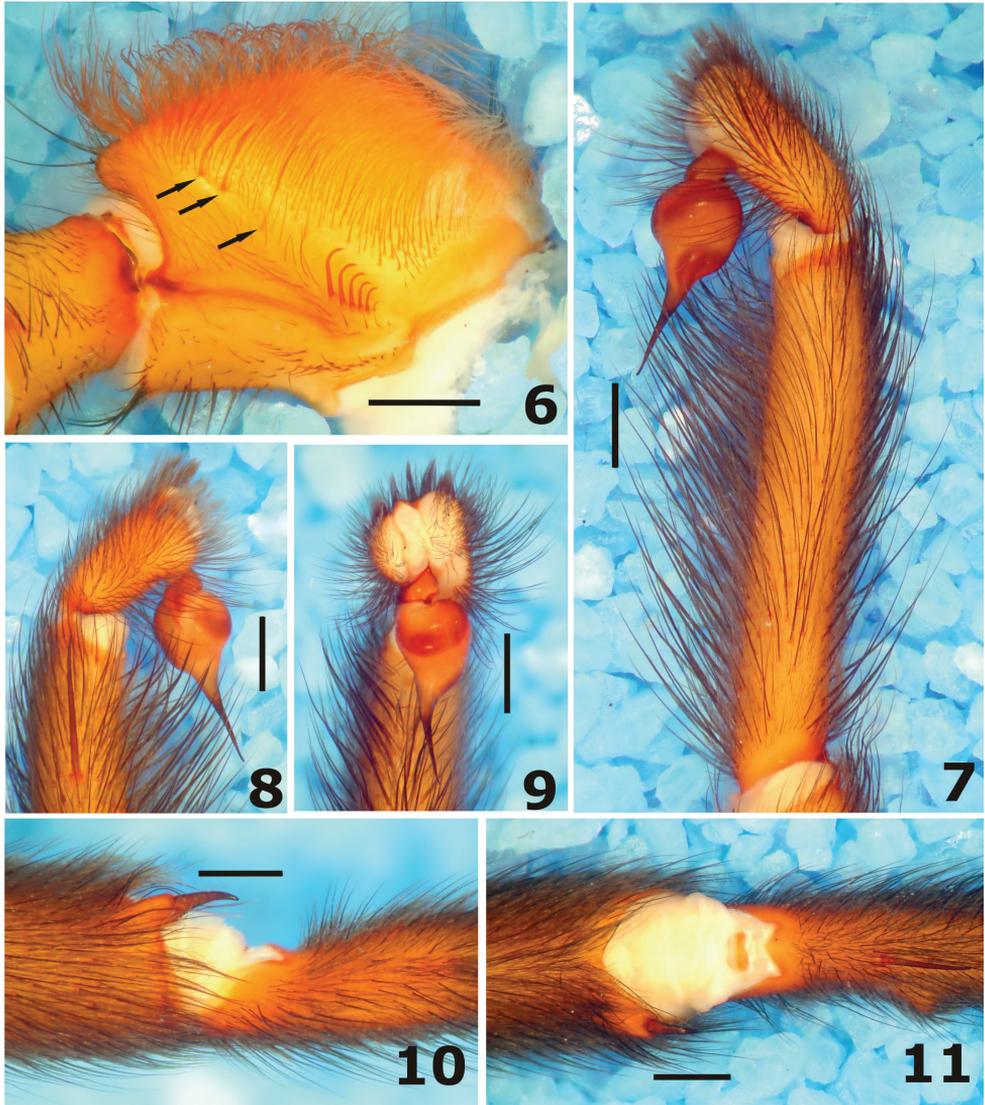
Figures 1–5. *Harmonicon cerberus* sp. n. Male holotype: **1** habitus **2** carapace, dorsal view **3** eyes, dorsal view **4** abdomen, dorsal view **5** sternum, ventral view.

Table 1. *Harmonicon cerberus* sp. n. male holotype. Length of leg articles.

	Leg I	Leg II	Leg III	Leg IV
Fe	13.2	12.1	11.2	13.6
Pa	5.7	4.9	4.7	5.0
Ti	10.2	9.9	9.4	11.9
Mt	13.8	11.9	13.1	17.2
Ta	9.3	8.8	8.0	10.0
Total	52.2	47.6	46.4	57.7

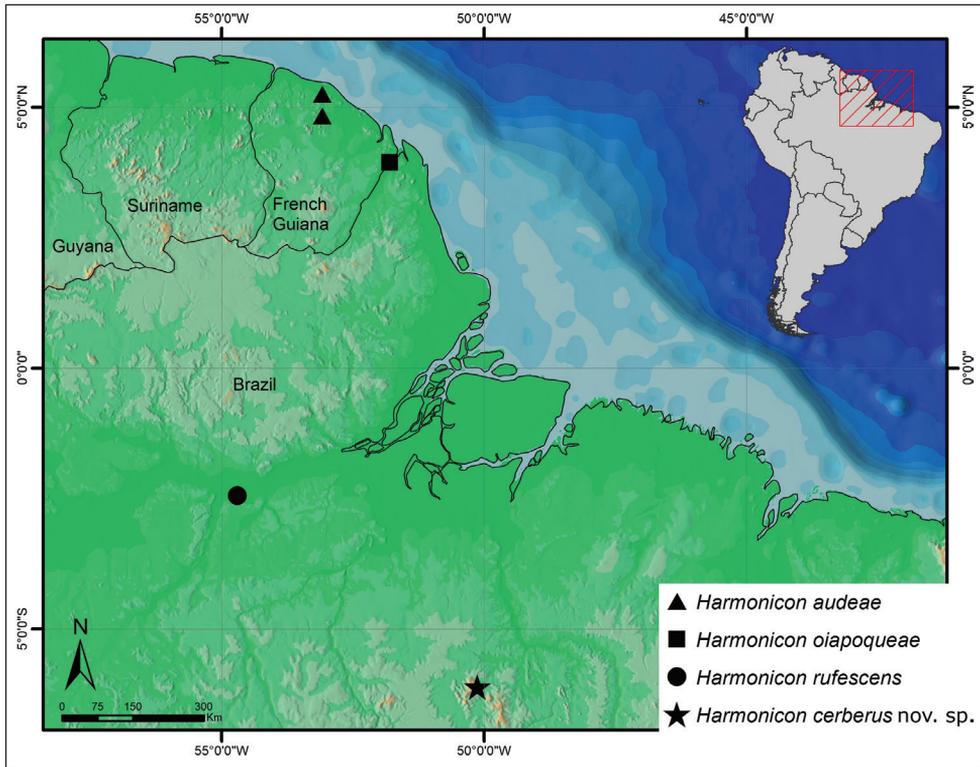
Description. Male (holotype, Figs 1–11). Measurements: carapace 10.7 long, 9.3 wide, chelicerae 4.4. Abdomen 14.5 long, 6.6 wide. Spinnerets: PMS 2.1 long, 2.0 apart; PLS, total length 18.1, basal article 4.9, middle 6.2, distal 7.0, 2.0. apart; respectively. Legs: see Table 1.

Carapace (Figs 1, 2) length/width 1.15; flat, cephalic area slightly raised, thoracic furrows shallow and wide. Fovea: 1.0 wide; deep, straight. Carapace with many short, thin setae, interspersed with some longer and thicker setae; border with abundant long and thick setae pointing out, increasing in number towards posterior angles. Clypeus 0.3, frontal margin bearing 9 thick, long, erect setae (Fig. 3). **Eye tubercle** (Fig. 3) length 0.9, width 1.9, with sparse thin setae separating eyes of both sides and thicker, longer setae at the anterior and posterior borders. AME elliptical, with a milky lens, yellowish brown background, no retina or eye pigments visible. Left AME larger than right one. All other eyes (ALE, PME and PLE) fused in an asymmetrical, crescent shaped, lateral eye mass, with irregular borders, covered by a thin lens, with uniform white background. Right lateral eye mass thinner, shorter and with a more pronounced notch than the left one. Eye row curvature not definable, but AME anterior border a little advanced in relation to anterior border of lateral eye mass (Fig 3). Right AME 0.3, AME–AME 0.3, right lateral eye mass 0.6 long. **Chelicerae** (Fig. 2) length/carapace length 0.41, 11 and 12 teeth on promargin, on the left and right chelicera, respectively. **Maxillae** (Figs 5, 6) length\width: 2.1. Cuspules: 36 spread over ventral inner heel. Lyra at the ventral side of the maxilla, asymmetrical, formed by 4–5 modified thick, long setae, increasing in size from basal to distal one, strongly curved at apical portion, apex just tapering to a point. Right lyra with just 4 setae, left lyra with 5 large setae and a very small, thinner basal one. Thick, erect, regularly curved setae (Fig. 6, arrow) placed distally and a bit internally in relation to lyra, in number of 4 at the right maxilla and 3 at the left one. Labium: length/width 0.8, no cuspules. Labio-sternal groove deep, with elongated sigilla. **Sternum** (Fig. 5) length (up to labium border) 5.3, width 4.7. Posterior angle in a blunt point, not separating coxae IV. Sigilla: three pairs, elliptical, increasing in size backwards, all far from margin by its own size. **Palp** long, without spines at retrolateral side, one prolateral spine at distal third of femur, 2 prolateral spines at tibia, distal one longer and thicker. Tibia: length 6.3, thin and long, with similar diameter throughout, length/width 9.1. **Leg** formula 4123. Legs covered with more abundant short, thin, horizontal black setae and with



Figures 6–11. *Harmonicon cerberus* sp. n. Male holotype: **6** maxillae and lyra, ventral view **7** palp and bulb, retrolateral view; copulatory bulb **8** prolateral view **9** frontal view; tibia and metatarsus of leg I **10** retrolateral view **11** ventral view.

many longer, thicker, erect black setae. Leg I with modified tibia and metatarsus, forming a retrolateral clasping mechanism (Figs 10–11). Tibia I with a retrolateral distal spur (or apophysis) relatively long, somewhat curved, blunt, bearing a curved, pointed spine at tip. Metatarsus I with small retrolateral tubercle, situated distally to basis of first ventral spine. Tarsal trichobothria much longer than covering setae, placed in a row along the midline of dorsal face. Scopula undivided, covering distal half of metatarsus I and distal third of metatarsi II–III; all tarsi covered with scopula throughout



Map I. Distribution map with published records for *Harmonicon* species.

length. All tarsi flexible, with abundant cracks. Spines: leg I: femur d2-2-0 left, d2-1-0 right, pld0-2-1 left, pld1-1-1 right, rld1-2-1 left, rld1-1-2 right; patella 0; tibia p1-0-1, r1-0-1 left, r1-0-0 right, v1-1-1ap (apophysis) left, v2-1-1ap (apophysis) right; metatarsus p0-1-0, v1-2-0 left, v1-2-1ap right; leg II: femur d2-2-0 left, d3-1-0 right, pld1-3-1 left, pld1-2-1 right; patella 0; tibia p1-1-1 left, p1-0-1 right, v2-1-1ap left, v1-1-1ap right; metatarsus pld0-1-0, v1-2-2ap; leg III: femur d2-1-0 left, d3-1-0 right, pld0-2-1, rld1-1-1 left, rld1-2-1 right; patella 0, tibia plv0-1-0 right, pld1-0-1 right, rld1-2-1, v2-2-2ap; metatarsus d2-1-1 left, d1-1-1 right, pld2-2-1 left, pld1-2-0 right, rld1-3-0 left, rld1-3-1 right, v2-1-3ap left, v1-1-2ap right; leg IV: femur d2-1-0, pld1-2-1 left, pld0-2-1 right, rld2-3-1 left, rld2-1-2 right; patella 0, tibia pld1-1-0 left, pld1-2-0 right, rld1-2-2(1ap) left, rld1-2-1 right, v2-2-2ap; metatarsus d1-1-1 left, d2-1-0 right, pld2-1-1 left, pld2-2-1 right, rld2-3-2 left, rld1-2-1 right, v2-1-2ap. Claws: ITC without teeth. Teeth at STC: leg I inner row 4–5, outer row 10–13; leg II inner row 4–5, outer row 10–12; leg III inner row 3, outer row 9–11; leg IV inner row 2–3, outer row 7–10. **Bulb** (Figs 7–9) globose, with moderately long embolus, a little longer than basis (ratio 1,3). Bulb with prolateral face convex, gently and uniformly curved, retrolateral face convex at basis and concave at end portion, due to an abrupt curve, forming a strong constriction of bulb near basis of embolus. Embolus with a broad

basis, regularly tapering to tip, both in prolateral and retrolateral views. In frontal view, embolus placed at prolateral margin of bulb, slightly curved initially, straight through most of its length, with apex bent retrolaterally (Fig. 9). Also, there is a strong bulge of bulb near embolus basis at same view.

Color pattern (in 75% ethanol). Carapace pale yellow, with thoracic furrows and cephalic area just a little darker, with orange hue, chelicerae light reddish brown, labium, sternum and leg coxae grayish yellow, sigillae darker, with orange hue, other leg articles brownish yellow. Abdomen grayish yellow, with abundant long, thick black hairs.

Distribution (Map 1). known only from type locality, in southern Pará state, Brazil.

Remarks

Troglophism. The pale body, fused and reduced eyes and the elongated chelicerae (Figs 1–3) observed in *H. cerberus* sp. n. seem to be troglomorphic. *Harmonicon* species display usually a highly contrasting color pattern, with a reddish carapace, a black, dark brown or reddish brown abdomen and dark brown legs. Eyes of *Harmonicon* typically are without modification, with two large AME, surrounded by distinct ALE, PME and PLE. The retina and pigmentation of the AME are easily seen through the clear crystalline lens. In contrast, the AME of the new species bears a milky crystalline and no trace of a retina or pigmentation are visible behind it. The ALE and AME of the other *Harmonicon* bear distinct crystalline and spherical lenses. However, ALE, PME and PLE of *H. cerberus* sp. n. are fused, forming an irregular and asymmetrical white macula, covered by a shallow and irregular lens (Fig. 3). To the best of our knowledge, the crescent shaped lateral eye mass is a rare character in spiders. The elongated chelicera (more than 40 % of the length of carapace) is longer than in other species of the genus. The legs and spinnerets are also elongated, but males of *H. audeae* and *H. oiapoqueae* also have similar long legs. An additional possible troglomorphic character is the elongated trichobothria at the leg tarsus. In comparison to other *Harmonicon* species, the trichobothria of the new species are approximately twice as longer than the covering hairs and clearly visible in lateral view. Furthermore, *H. cerberus* sp. n. seems to bear more unequivocal troglomorphic characteristics compared to *Linothele cavicola*, the only other cave inhabiting Diplurinae (Goloboff 1994).

This spider may be a troglobitic species, despite the small dimensions of Pequiá cave. Several other troglobitic species have been collected in some of the more than a thousand iron ore caves in Carajás (Piló and Auler 2009, Trajano and Bichuette 2010, Pellegrini and Ferreira 2011). Most of those caves are reduced in size (horizontal projection 20–30 m), but they may be connected by small conduits, due to the porosity and spongiform nature of the iron ore deposits of the area (Piló and Auler 2009).

Pequiá cave and its surroundings have been thoroughly investigated recently (Pederroso, pers. obs.). However, no additional specimens of *Harmonicon* have been found. On the other hand, only the entrance and the beginning of the lateral tube were investigated (around 1/3 of the cave), as there is a large water pool mixed with abundant

guano. Unfortunately, the exploration of the terminal portion of the lateral tube of Pequiá cave needs special equipment, such as floaters. This portion appears to be the best candidate for new attempts to find additional specimens of *H. cerberus* sp. n., as it is farthest away from the mouth and the darkest area of the cave. Other possible areas for exploration are the numerous caves near Pequiá cave, specially Gavião cave, a larger cave situated *circa* 4 km from Pequiá cave (Magalhães 2012).

Notes on *Harmonicon*. In their paper on the revalidation of *Harmonicon*, Maréchal and Marty (1998) proposed a series of diagnostic characters for the genus: leg I longer than IV (leg formula 1423), contrasting with formula 4123 found in *Diplura* and other Diplurinae; legs longer and thinner than in *Diplura*; metatarsus I of males without the prolateral knob found in other Diplurinae; lyra formed by only 5 setae, with a flattened and curved tip, compared to *Diplura*, where it presents more setae, with a different tip.

The diagnosis of *Harmonicon* is not so clear-cut. Regarding the leg formula, the female of *H. audeae* itself, the species described by Maréchal and Marty (1998), has leg formula 4123, as does the female of *H. oiapoqueae* (Drolshagen and Bäckstam 2011). The males of *H. audeae* and *H. oiapoqueae* do have a leg formula of 1423. On the other hand, the legs of the male holotype of *H. cerberus* sp. n. follow the formula 4123. Furthermore, most Diplurinae males have longer anterior legs, following the formula 1423 (and even 1243), so this character is not reliable for diagnosing *Harmonicon*.

Another inconsistent character is the absence of the prolateral knob of male metatarsus I. Both *H. oiapoqueae* and *H. cerberus* sp. n. present the cited knob, so its absence may be an autapomorphy of *H. audeae*.

Considering the lyra, the number and shape of the setae are not consistent throughout Diplurinae. Some *Diplura* species we have examined have lyra with just a few setae (down to 2), sometimes with tip curved and somewhat flattened. The setae tip though is not as curved and flattened as in *Harmonicon*. Again the number of setae is not a reliable character for *Harmonicon*, as already suggested by Drolshagen and Bäckstam (2011).

Additional diagnostic characters for *Harmonicon* were proposed by Drolshagen and Bäckstam (2011): presence of dense scopula in more than the apical third of pedipalpal tarsus, presence of scopula in the apical third of most leg metatarsi, and leg tarsi “pseudosegmented” (instead of showing only a few cracks). The dense scopula in legs is similar to that found in *Trechona*, where it is very dense. In *Diplura*, the scopula is thin, sometimes not conspicuous at all.

The presence of additional, rigid, and somewhat thickened, setae situated distally to the lyra (Fig. 6) may be diagnostic for *Harmonicon* or at least most of its species. Besides *H. cerberus* sp. n., these setae are found in specimens of *H. rufescens* from Altamira (unpublished data), *H. oiapoqueae* (see a picture on the website of Drolshagen 2013) and several undescribed species from Brazil. However, an undescribed *Harmonicon* from Mato Grosso lacks these setae altogether. No such setae were found in all other species of Diplurinae genera we examined.

Some additional characters may prove to be diagnostic, at least in relation to *Diplura*. The longer tibia of the male pedipalp may distinguish *Harmonicon* from

Diplura species, in which tibia are usually short and stout. Long and relatively thin tibia are found also in the diplurines *Trechona* (ex. Pedroso and Baptista 2004, Pedroso et al. 2008) and *Linothele* Karsch, 1879 (ex. Paz and Raven 1990). The copulatory bulb of males of most *Harmonicon* is also remarkably similar to *Trechona* species (ex. Pedroso and Baptista 2004, Pedroso et al. 2008), with an enlarged basal portion and an elongated embolus.

The legs and palp with denser and longer scopula, the longer tibia of the male palp and the flexible, highly cracked tarsi may indicate a closer relationship between *Harmonicon*, *Trechona*, and perhaps *Linothele*. Another common trait of these genera is the increased body size, compared to *Diplura*. Compared to *Trechona*, some easily seen diagnostic characters of *Harmonicon* are the lyra composed by less than ten setae (vs. complex lyra, with more than 50 setae in several layers) and the absence of the chevron pattern on the abdomen (vs. presence).

All the published records for described *Harmonicon* species are located in the northeastern Amazon region, from northern French Guiana to central Pará state, Brazil (Map 1). The type locality of *H. cerberus* sp. n. is the southernmost record for the genus, located in southern Pará state. However, we examined specimens of several *Harmonicon* species covering a much larger area, ranging from Peru in the west, to states in northeastern (Bahia, Ceará) and central (Mato Grosso, Goiás) regions in Brazil.

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