

# Revision of the genus *Buchneria* (Bryozoa, Cheilostomata) from Japan

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## Abstract

*Buchneria dofleini* (Buchner, 1924), type species of *Buchneria* Harmer, 1957, was first described from material collected in 1904–1905 from Sagami Bay, Japan, but the type specimens had not been reexamined since the original description. In this study, I examined specimens of *Buchneria* from historical collections and material recently collected near Akkeshi, Hokkaido, Japan. Three *Buchneria* species were detected, two from Sagami Bay that Ortmann (1890) had placed in *Escharoides*, and one from Akkeshi that Androsova (1958) had described as *Porella variabilis*. I concluded that *Buchneria dofleini* is a junior synonym of *Escharoides teres* Ortmann, 1890; selected a lectotype for *E. teres* among Ortmann's syntypes; and established the new combination *Buchneria teres* (Ortmann, 1890), which becomes the type species of *Buchneria*. I also established the new combination *Buchneria rhomboidalis* (Ortmann, 1890) and selected a lectotype among Ortmann's syntypes. *Porella variabilis* is transferred to *Buchneria* establishing the new combination *Buchneria variabilis* (Androsova, 1958). Here the three new combinations are redescribed and a key to the Japanese *Buchneria* species is provided. Finally, I transferred *Buchneria* to Bryocryptellidae on the basis of ovicell and orifice morphology. Therefore, *Buchneria* now includes a total of three species; *B. sinuata* Harmer, 1957, a species from Indonesia that has hitherto been placed in this genus, is almost certainly not congeneric with other *Buchneria*. As far as is now known, *Buchneria* is endemic to northern Japan and the northern Sea of Japan.

## Keywords

*Buchneria dofleini*, *Buchneria teres*, *Buchneria rhomboidalis*, *Buchneria variabilis*, new combination, synonymy, distribution, Sagami Bay, Akkeshi

## Introduction

Harmer (1957) introduced the cheilostome bryozoan genus *Buchneria* for species with erect colonies, and chose the deep sea species *Palmicellaria dofleini* as type, which was described by Buchner (1924) from Sagami Bay, Japan. According to Harmer's description, zooids in species of *Buchneria* have the proximal margin of the orifice with a broad sinus or nearly straight, with a small suboral avicularium at the edge of the peristome, and have only a few pores in the frontal shield. These characters, however, also match *Escharoides teres* and *Escharoides rhomboidalis*, both described by Ortmann (1890) from Sagami Bay, although Ortmann's (1890) limited descriptions and simplified illustrations are inadequate for taxonomic assessment.

The status of *Buchneria* has not been evaluated subsequent to Harmer (1957). In this study, I reexamined type specimens established by Buchner (1924) and Ortmann (1890) for species of *Buchneria* and morphologically similar genera. I examined relevant material collected in Japan over the past approximately 130 years, as well as material obtained through my own collecting efforts. I review, describe, and illustrate the known species of *Buchneria*.

## Materials and methods

### Material examined

I examined specimens from Sagami Bay and surrounding areas collected by Ludwig Döderlein (1880–1881), Franz Doflein and Karl Haberer (1904–1905), Emperor Showa (1918–1971), and most recently by the National Museum of Nature and Science Tokyo (2001–2005); see National Museum of Nature and Science (2007), Hirose (2010), and Spencer Jones et al. (2011) for historical overviews. This material is housed in Musée Zoologique Strasbourg (MZS), Zoologische Staatssammlung München (ZSM), Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt, Germany (SMF; material on loan there from ZSM), and the National Museum of Nature and Science Tokyo (NMST), now located in Tsukuba (see Supplementary Table 1).

The author collected additional specimens from Sagami Bay by dredge from RV *Tansei-maru* (Japan Agency for Marine-Earth Science and Technology, JAMSTEC) and research boat *Rinkai-maru* (Misaki Marine Biological Station, The University of Tokyo) in November 2007 and February 2012, and outside Akkeshi Bay, Hokkaido, in July 2010 and 2011, by dredge from research boat *Misago-maru* (Akkeshi Marine Station, Hokkaido University) (Fig. 1).

### Preparation and observation of specimens

Specimens were observed by light microscope and scanning electron microscope (SEM). For SEM observation, part of each specimen was removed, soaked in a sodium



**Figure 1.** Map showing the areas in Japan where species of *Buchneria* were collected.

hypochlorite solution to remove the soft tissue, rinsed in water, air dried, and mounted with double-sided adhesive tape or silver paste on an aluminum SEM stub. At Hokkaido University, mounted specimens were coated with Au in a Hitachi E-1030 sputter-coater and observed with a Hitachi S-3000N SEM at 15 kV accelerating voltage. At the SMF, specimens were coated with Pt-Pd and observed with a CamScan SEM. At ZSM, specimens were coated with Au in a POLARON SEM Coating System and observed with a LEO 1430VP SEM at 15 kV accelerating voltage. Fragments removed from specimens in the various collections, prepared and examined by SEM, and subsequently deposited in NMST are indicated in the text by the designation 'NSMT Te' (see Supplementary Table 1).

Measurements were taken from SEM images with ImageJ 1.37v software (Image Processing and Analysis in Java, Wayne Rasband, National Institutes of Health, USA; <http://rsb.info.nih.gov/ij/>). Measurements in the text are presented in millimeters, as ranges followed in parentheses by the mean and standard deviation. Sample sizes for

measurements were  $n = 4\text{--}82$ , generally from more than one colony. Abbreviations used for measurements are as follows; ZL, zooid length; ZW, zooid width; OrL, orifice length; OrW, orifice width; AvL, suboral avicularium length; AvW, suboral avicularium width; OvL, ovicell length; OvW, ovicell width.

## Taxonomy

### Order Cheilostomata Busk, 1852

### Suborder Neocheilostomina d'Hondt, 1985

### Infraorder Ascophorina Levinsen, 1909

### Superfamily Lepralielloidea Vigneaux, 1949

### Family Bryocryptellidae Vigneaux, 1949

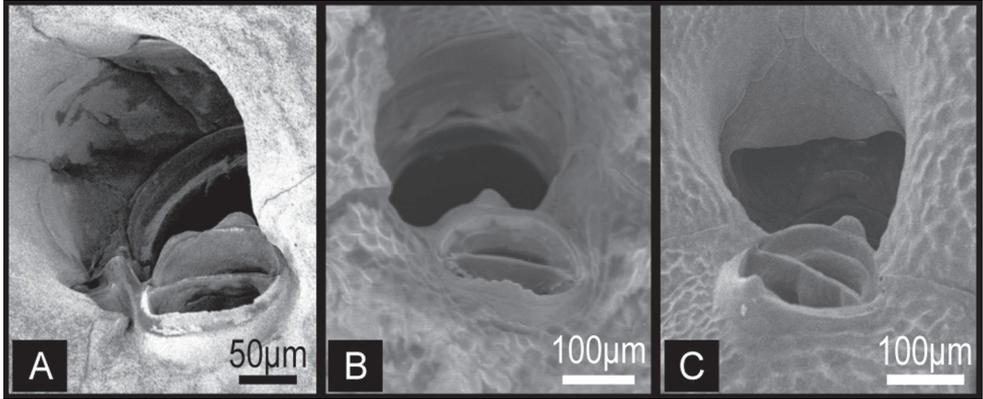
### Genus *Buchneria* Harmer, 1957

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

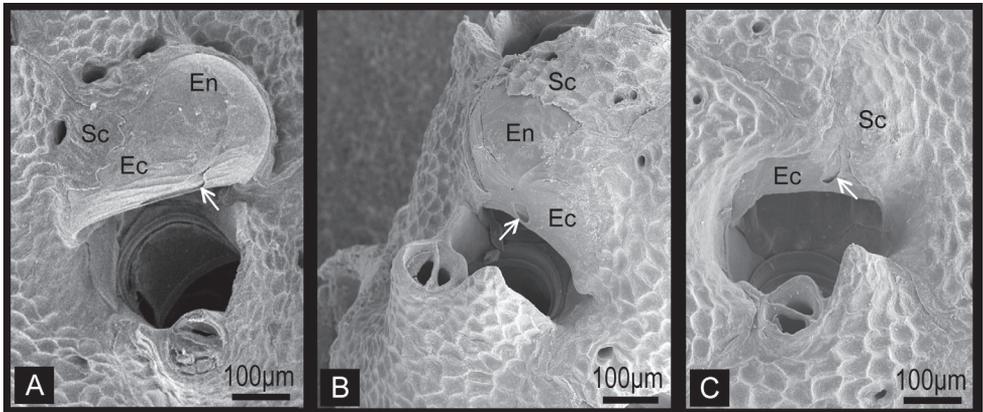
**Type species.** *Palmicellaria dofleini* Buchner, 1924 by original designation by Harmer (1957: 876) (= *Escharoides teres* Ortmann, 1890).

**Diagnosis.** Colony erect, rigid, dichotomously or irregularly branching; branches cylindrical, flattened, or plate-like, fan shaped. Zooidal frontal shield uniformly tessellated, with a few areolar pores near margin or offset centrally in secondarily calcified wall. Orifice deeply immersed, without teeth on distal periphery, without lyrula or condyles, slightly concave or straight proximally; oral spines absent. Secondary orifice at colony surface cormidial, formed by contributions of secondary calcification from distal and lateral zooids. Suboral avicularium lies at proximal margin of secondary orifice, directed proximally or laterally, sometimes enlarged and occupying about half of frontal shield; small, conical tooth associated with avicularium projecting into secondary orifice (Fig. 2). Mandible of the suboral avicularium semicircular or spatulate, but never acute. Vicarious and other frontal avicularia absent. Ovicell globose, acleithral, and is produced by the distal zooid (Fig. 3). Both the endooecium and ectooecium are calcified. Endooecium is completely calcified, whereas ectooecium is not completely covering the endooecium (Fig. 3A, B). Immediately after formation, the ectooecium is then partially covered by the secondary calcification that is coming from the distal and neighbour zooids (Fig. 3B). Finally, the secondary calcification covers most of the ectooecium in the old parts of the colony, but a small area of proximal margin remains uncovered (Fig. 3C). Small basal pore chambers present.

**Remarks.** Harmer (1957) defined *Buchneria* as follows: colony erect, not jointed; large spatulate avicularia present; zooids with a “sinuate” or nearly straight proximal margin of the orifice (the term ‘sinuate’ appears to be misapplied to the evenly concave proximal margin in *Buchneria sinuata*; perhaps Harmer intended the meaning as ‘having a sinus’); small, acute suboral or lateral avicularia on the edge of the secondary orifice; few frontal pores; and a hyperstomial ovicell with an imperforate central tabula.



**Figure 2.** Orifices of three *Buchneria* species showing the small tooth distal to the suboral avicularium. **A** *Buchneria teres* **B** *Buchneria rhomboidalis* **C** *Buchneria variabilis*.



**Figure 3.** Ovicells of *Buchneria teres* showing various stages of development. **A** Younger stage oocidium showing smooth surface of endooecium and ectooecium with less secondary calcification **B** Oocidium started covered by tessellated secondary calcification from neighboring zooids **C** Oocidium almost covered by the secondary calcification with showing endooecium through the small proximal membranous window at ectooecium. Ec, ectooecium; En, endooecium; Sc, secondary calcification. Arrows indicate the proximal membranous window.

His generic diagnosis, however, largely derives from *Buchneria sinuata* Harmer, 1957 from Indonesia. This species is similar to the three *Buchneria* species treated herein in having erect colony form, few frontal or marginal pores, and a deeply immersed primary orifice. However, it differs substantially from them in having large, spatulate frontal avicularia; hyperstomial ovicells with an imperforate central tabula lacking secondary calcification; and a laterally placed, acute oral avicularium (Harmer, 1957: plate LIV, fig. 19). *Buchneria sinuata*, therefore, has currently been thought to belong in another genus, perhaps *Osthimosia* Jullien, 1888 (Gordon, 1984). Gordon (1984) noted several similarities between *Osthimosia virgula* and nominal *B. sinuata* (e.g., broad orificial sinus, a lateral-oral avicularium on peristome, and spatulate frontal avicularia), and

suggested the two species may be congeneric. Subsequently, Gordon (1989) observed and illustrated Japanese material of *Buchneria* present in the Natural History Museum London (NHMUK), and elucidated the umbonuloid frontal shield; he concluded *Buchneria* cannot be grouped together with *Osthimosia* and other lepraliomorphs. Unfortunately, I have never had a chance to check the type material of Harmer's *B. sinuata*, which is not in NHMUK (Mary Spencer Jones, pers. comm. 11 May 2012) and both institutes Zoological Museum Amsterdam (ZMA) and Naturalis Biodiversity Center in Leiden (Elly Beglinger, pers. comm. 19 September 2012). Although I have not checked the type material, I exclude Harmer's *B. sinuata* from the description of the genus in this paper based on the significant differences with the type species of the genus; *B. sinuata* is also different from other *Buchneria* species in mainly imperforate frontal shield, small colony size, and preference of unstable substrate which is unusual for *Buchneria* species. The status of *B. sinuata* is still unclear and should be clarified in future work. With the removal of nominal *B. sinuata* from *Buchneria*, the cormidial orifice and the rounded mandible of suboral avicularia may be considered diagnostic characters for *Buchneria*. Buchner (1924) described large frontal avicularia, but these are enlarged suboral avicularia; therefore, absence of a large frontal avicularium may also be considered diagnostic for *Buchneria*.

Gordon (1989) regarded *Buchneria* close to *Celleporaria* in Lepraliellidae, based on the similarities between the type species of both genera in the umbonuloid and imperforate frontal shield with marginal areolar pores, broad orifice, and suboral avicularium. However, the ovicell of *Buchneria* is different from that of Lepraliellidae in having broader proximal window and deeper oecium, and is more similar to that of *Palmiskeneia* Bishop & Hayward, 1989 in Bryocryptellidae with a few small foramina close to the proximal margin. *Buchneria* also resembles *Palmiskeneia* in the frontal shield having only marginal areolar pores, but differs from the latter in the orifice without condyles and in polymorphic avicularia. *Buchneria* resembles *Marquetta* Jullien, 1903 in having only marginal pores, an ovicell with a few small pores, and oval suboral avicularia, but differs from the latter in lacking frontal avicularia on margin of the frontal shield. *Buchneria* also resembles *Porella* Gray, 1848 and *Porelloides* Hayward, 1979 in having only marginal pores, an ovicell without or with a few small pores, and suboral avicularia, but differs from the latter two genera in lacking lyrula and condyles. Although some species of *Porella* also lack a lyrula, and species of *Porelloides* normally lack condyles, a small tooth on the distal margin of the suboral avicularium is characteristic of *Buchneria*. Considering the similarities of ovicell and orifice morphology between *Buchneria* and the four bryocryptellid genera, *Porella*, *Palmiskeneia*, *Marquetta* and *Porelloides*, I conclude *Buchneria* is much better placed in Bryocryptellidae rather than Lepraliellidae.

Harmer (1957) suggested that *Haswellia auriculata* Busk, 1884 be placed in *Buchneria*, on the basis of orifice morphology and the small lateral avicularia on the edge of the peristome. He also suggested that the species *H. auriculata* and *Myriozoum marionense* Busk, 1884 as described by Calvet (in Jullien and Calvet 1903) represent a single species referable to *Buchneria*, on the basis of very few frontal pores; a large, spatulate frontal avicularium; the form of the peristome with small avicularia; and im-

mersed ovicells (Harmer, 1957). However, *H. auriculata* is currently regarded as a junior synonym of *Galeopsis pentagonus* (d'Orbigny, 1842), and the specimen described as *M. marionense* in Jullien and Calvet (1903) is also considered as a species of *Galeopsis*.

Excluding nominal *B. sinuata*, *Buchneria* presently contains three species, which I redescribe here.

***Buchneria teres* (Ortmann, 1890), comb. n.**

[http://species-id.net/wiki/Buchneria\\_teres](http://species-id.net/wiki/Buchneria_teres)

Figures 4, 5, 6

*Escharoides teres* Ortmann, 1890, 43, pl. 3, fig. 21; type locality, Sagami Bay.

*Palmicellaria ortmanni* Buchner, 1924, 210, fig. V; mentioned only in a caption to a text figure and presumably a *nomen nudum*; see Harmer (1957: 876).

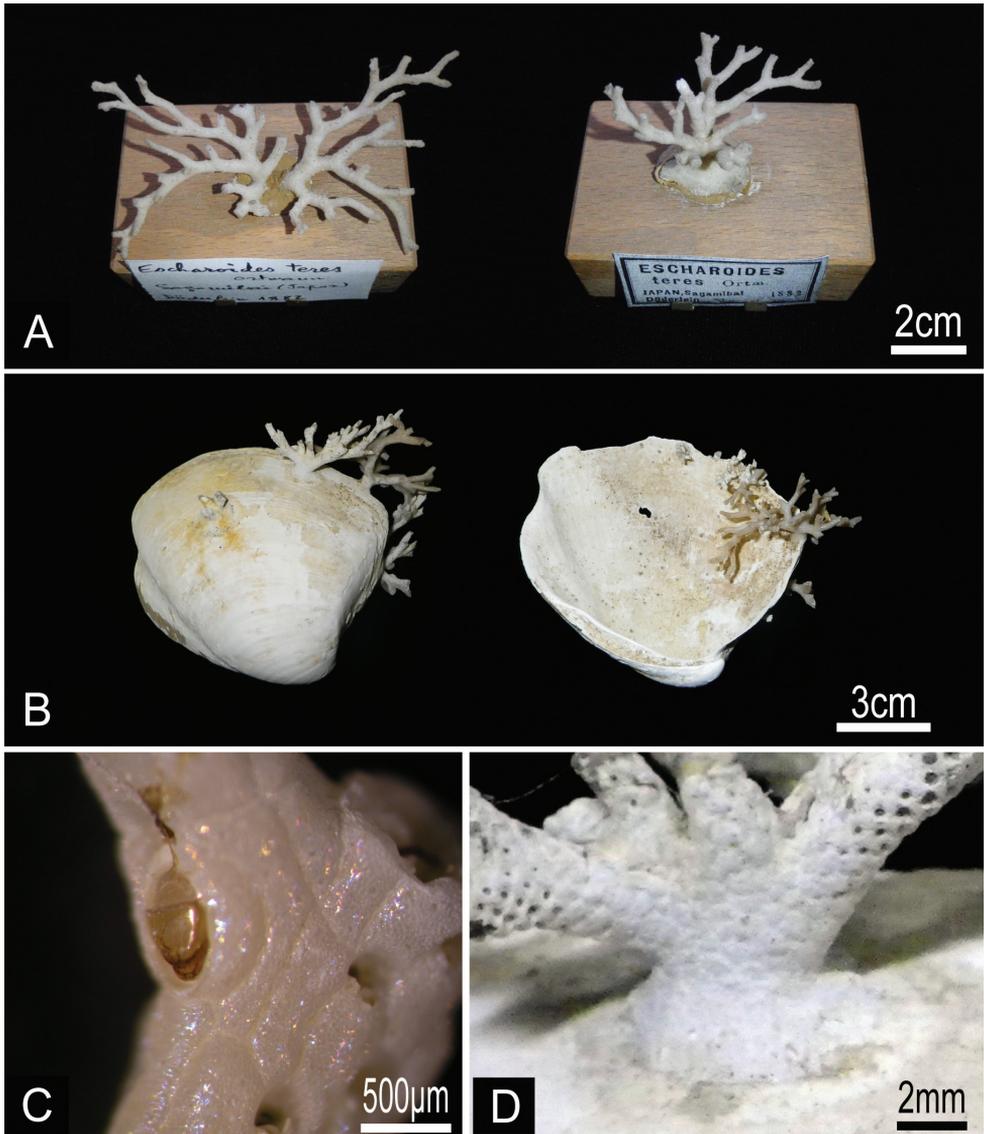
*Palmicellaria dofleini* Buchner, 1924, 210, figs. F, V, pl. 17, figs. 9–12.

*Buchneria dofleini*: Harmer 1957, 876, pl. 17, figs. 9–12; Gordon 1989, 258, figs. 17–20.

**Material examined.** *Lectotype*. Branched colony (MZS 36-2), collected by L. Döderlein, 1882, Sagami Bay. *Paralectotype*. Branched colony (MZS 36-1, 36-3; NSMT Te-738), collected by L. Döderlein, 1882, Sagami Bay. *Other material examined*. Fragment of colony ZSM 20043001, collected by F. Doflein, 17 October 1904, entrance of Tokyo Bay, 600 m depth; fragment of colony ZSM 20100261 collected by F. Doflein, 1904–1905, Sagami Bay; single small living colony on pebble and several fragments of living colonies (NSMT TeS-3, TeS-2), collected by NSMT from RV *Shinyo-maru*, 24 October 2003, Okinose, Sagami Bay (34°58.80'N, 139°31.50'E to 34°59.20'N, 139°31.20'E), 900–950 m depth, by dredge; fragments of colonies (NSMT TeS-4), collected by NSMT from research boat *Rinkai-maru*, 16 March 2001, SW of Hayama, Sagami Bay (35°11.46'N, 139°28.71'E to 35°11.64'N, 139°28.14'E), 432–580 m depth, by dredge; several living and dead colonies (NSMT TeS-5 to TeS-12) on dead *Conchocele bisecta* (Conrad, 1849) shells, collected by NSMT from RV *Tansei-maru*, 24 November 2007, ENE of Hatsushima, Sagami Bay (35°03.41'N, 139°12.55'E to 35°02.73'N, 139°13.73'E), 563–756 m depth, by beam trawl; single small dead colony on pebble (NSMT Te-876), collected by Nagai, 24 April 1997, SW of Shionomizaki, Wakayama Prefecture (33°24.91'N, 135°38.69'E to 33°24.95'N, 135°38.12'E), 500 m depth, by dredge.

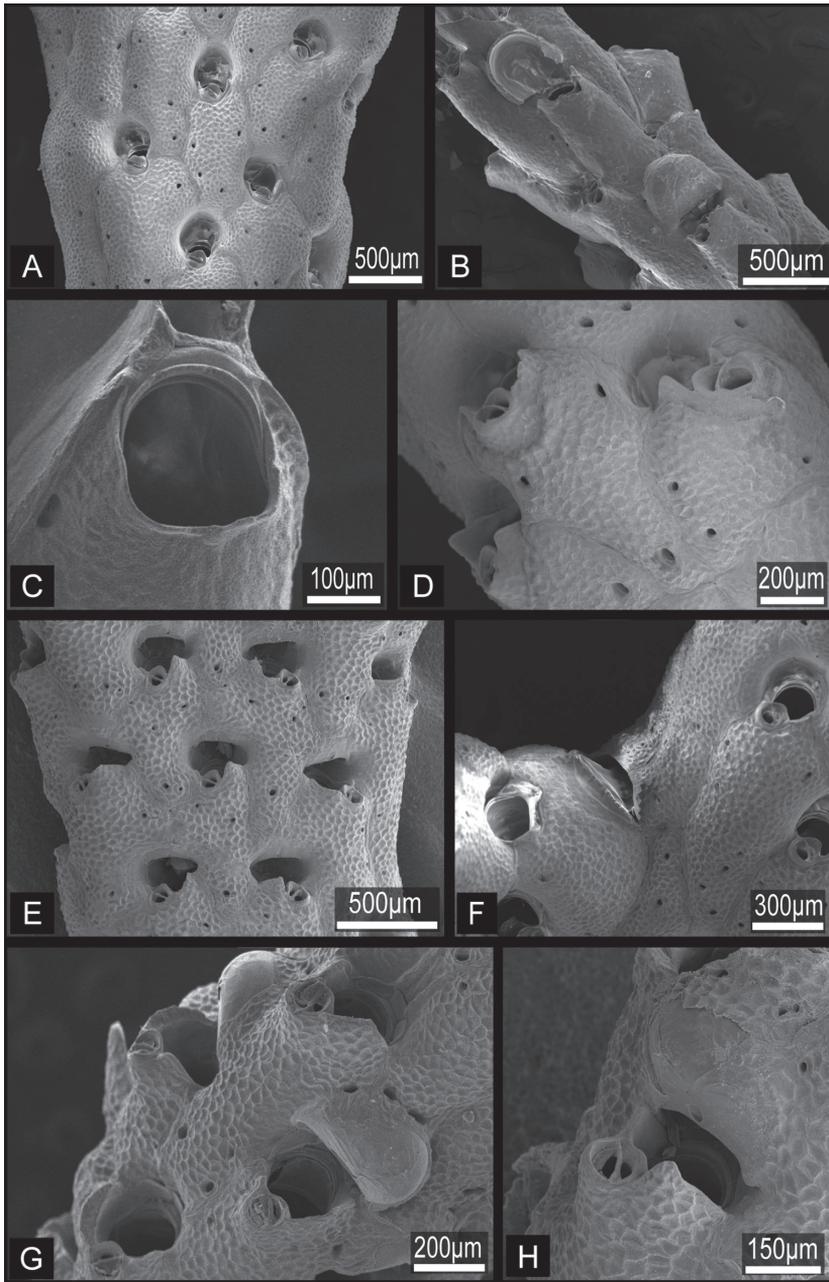
**Measurements.** ZL, 0.595–1.334 (0.978±0.160); ZW, 0.214–0.840 (0.450±0.133); n=65. OrL, 0.131–0.208 (0.171±0.021); OrW, 0.123–0.219 (0.187±0.018); n=32. AvL, 0.078–0.198 (0.110±0.017); AvW, 0.055–0.148 (0.086±0.016); n=82. OvL, 0.205–0.391 (0.311±0.049); OvW, 0.286–0.439 (0.365±0.043); n=29. Additional measurements: large suboral avicularium (LAv) length, 0.619–0.766 (0.682±0.076); LAv width, 0.398–0.453 (0.426±0.027), n=3.

**Description.** Colony erect, rigid, dichotomously branching, widely spreading, antler-like, terminal branches slender. Basal part of colony composed of both autozoo-

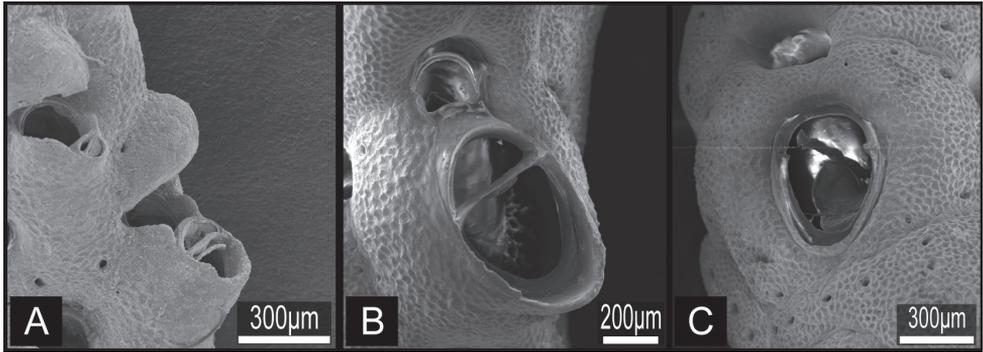


**Figure 4.** *Buchneria teres* comb. n. **A** Lectotype (MZS 36-2) and paralectotype (MZS 36-1) **B** Colonies on dead shells of *Conchocele bisecta*, NSMT TeS-8 and 10 **C** Large suboral avicularium with a semicircular mandible, NSMT TeS-2 **D** Kenozooidal base of the colony, NSMT TeS-8.

ids and kenozooids. Branches cylindrical, 1.39–4.76 mm wide ( $2.77 \pm 0.85$  mm;  $n=25$ ), with zooids opening all around, four or five zooids across in half-view (Fig. 4A, B). Autozooids subrectangular to oval, tapering proximally, cylindrical in younger ends of branches, arranged in quincunx; zooidal borders indistinct. Frontal shield convex, entirely tessellated with minute depressions, with two to six areolar pores offset from margin (Fig. 5A, B). Orifice (Fig. 5C) deeply immersed, elongated semicircular, about as wide as long, slightly concave proximally; lyrula and condyles absent. Oral spines



**Figure 5.** *Buchneria teres* comb. n., scanning electron micrographs. **A** Part of a branch showing autozooids with few frontal pores, NSMT TeS-2 **B** Younger part of a paralectotype branch showing rectangular zooids and semicircular ovicells, NSMT Te-738 (original MZS 36-3) **C** Orifice without lyrula or condyles, NSMT TeS-6 **D** Autozooid (right) with a developing peristomial labium of an intramural bud, NSMT TeS-3 **E** Ovicellate zooids with well-developed peristomial labia, ZSM 20100261 **F** Large avicularium at a branch bifurcation, NSMT TeS-2 **G** Zooids with young ovicells, NSMT TeS-6 **H** Ooecium partly covered by secondary calcification from surrounding zooids, ZSM 20100261.



**Figure 6.** *Buchmeria teres* comb. n., suboral avicularia. **A** Two different sizes of suboral avicularia in adjacent zooids, ZSM 20043001 **B** A large, projecting suboral avicularium, NSMT TeS-2 **C** A large suboral avicularium appearing offset to the center of the frontal shield, NSMT TeS-2.

lacking. Secondary orifice cormidial, bounded by contributions of secondary calcification from distal and lateral zooids, with suture lines often evident between the sectors; secondary orifice roughly oval in young zooids, complex in mature zooids, with suboral avicularium offset to one side and a sharp, raised flattened peristomial flange on the other, often with a sinus between the two (Fig. 5D, E). Suboral avicularium lies on peristome periphery; small, circular, with complete pivot; semicircular mandible directed proximolaterally (Fig. 5D, H); orificial side of rostrum with a rounded-triangular tooth or flange (Fig. 5E). Zooids commonly have the small suboral avicularium replaced by a larger (Fig. 6A) or much larger, hypertrophied oval (Fig. 6B) avicularium (Fig. 6A, B), with the latter type sometimes displaced proximally toward the center of the frontal shield (Fig. 4C, 6C). Another type of large avicularium occurs rarely at branch bifurcations (Fig. 5F), appearing almost as a crack in the bifurcation; twice as wide as long, 0.181 mm long by 0.373 mm wide ( $n=1$ ). Interzooidal kenozooids lacking orifice are interspersed with autozooids on branches (Fig. 5A), but are often much more numerous on side of branch facing inward toward the colony axis than on outer side; kenozooids encircle the base of colony (Fig. 4D). Ovicell (Fig. 5B, G, H) globose, recumbent on distal zooid, roughly as wide as long when fully formed; oecium smooth, proximal margin slightly curved, ectoecium is not completely covering the endoecium, leaving a large central membranous foramina and small proximal membranous window (Fig. 3A, B). Ectoecium is partially covered by tessellated secondary calcification from neighboring zooids with age (Fig. 5H). The proximal margin with the central pseudopore remains uncovered in the old parts of the colony (Fig. 3C).

**Distribution.** Sagami Bay, Sagami Sea, Tokyo Bay, and off Kii Peninsula, at depths of 432–950 m. The collecting depth of the specimen (1921.11.7.9.) in NHMUK is 250–330 fathoms, which means 457–603 m; therefore, the depth given in Harmer (1957) is wrong and should be in feet.

**Remarks.** Ortmann (1890) first described *Buchmeria teres* (as *Escharoides teres*) based on Döderlein's specimens from eastern Sagami Bay; these specimens had not been reexamined until this study. Buchner (1924) subsequently described *B. dofleini*

(as *Palmicellaria dofleini*) from Doflein's Sagami Bay specimens. Although Buchner's type specimen of *B. dofleini* was lost during WWII, I found other specimens he identified as this species in the Doflein collection at ZSM. In comparing these specimens with Ortmann's syntypes of *E. teres*, I found no diagnostic differences between the two; Buchner's specimens are simply the distal younger part of branches of *E. teres*. I thus consider *Buchneria dofleini* as a junior synonym of *E. teres*, which accordingly becomes the type species of *Buchneria*. Buchner (1924) reported large frontal avicularia in his species, but these are enlarged suboral avicularia. Although syntypes of *B. teres* in the Döderlein collection lack the colony base, I found an entirely kenozooidal colony base in complete colonies recently collected from Sagami Bay (Fig. 4D).

***Buchneria rhomboidalis* (Ortmann, 1890), comb. n.**

[http://species-id.net/wiki/Buchneria\\_rhomboidalis](http://species-id.net/wiki/Buchneria_rhomboidalis)

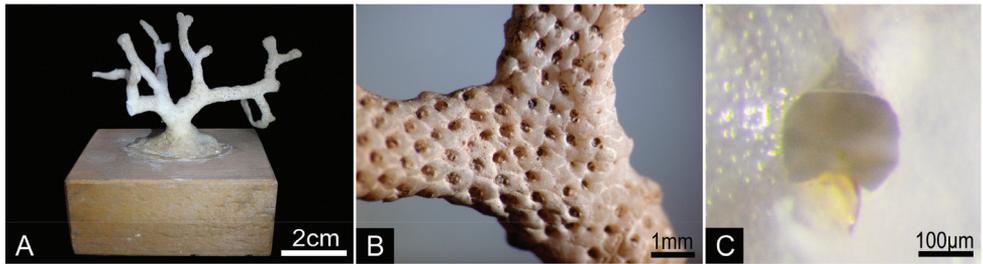
Figures 7, 8

*Escharoides rhomboidalis* Ortmann, 1890, 44, pl. 3, fig. 22; type locality, eastern Sagami Bay.

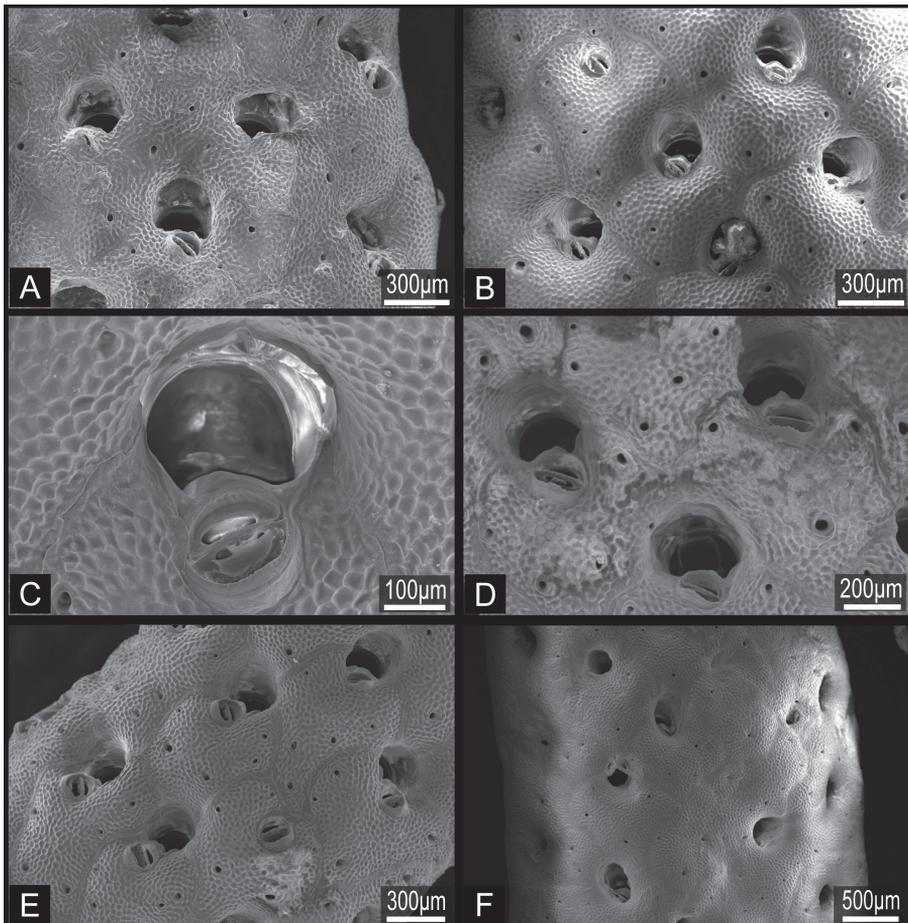
**Material examined.** *Lectotype.* MZS 37-2 (NSMT Te-737), branched colony, collected by L. Döderlein, 1882, Sagami Bay. *Paralectotype.* MZS 37-1, branched colony, collected by L. Döderlein, 1882, Sagami Bay, 370 m depth. *Other material examined.* NSMT-Bry R256, Emperor Showa Collection, collected 8 February 1967, 5 km SW of Jogashima, Sagami Bay, 250–400 m depth; NSMT-Bry R267, Emperor Showa Collection, collected 18 March 1968, 4 km WSW of Jogashima, Sagami Bay, 200–220 m depth; NSMT TeS-1, coll. 14 May 2004, west of Ōshima, Sagami Sea (34°40.95'N, 139°17.92'E to 34°40.68'N, 139°18.22'E), 220–277 m depth, beam trawl, RV *Tansei-maru*; colony (NSMT Te-799), collected by H. Kohtsuka from research boat *Rinkai-maru*, 10 January 2012, SW of Jogashima, Sagami Bay (35°06.101'N, 139°34.284'E to 35°05.684'N, 139°34.061'E), 218–318 m depth; fragments of colonies (NSMT Te-796, Te-797), collected by M. Hirose from research boat *Rinkai-maru*, 24 February 2012, WSW of Jogashima, Sagami Bay (35°07.301'N, 139°33.365'E to 35°07.327'N, 139°32.978'E), 300–493 m depth.

**Measurements.** ZL, 0.767–1.150 (0.948±0.100); ZW, 0.468–1.050 (0.735±0.116); n=32. OrL, 0.152–0.211 (0.177±0.019); OrW, 0.189–0.245 (0.222±0.023); n=14. AvL, 0.106–0.271 (0.171±0.034); AvW, 0.096–0.193 (0.144±0.024); n=28.

**Description.** Colony erect, rigid, dichotomously branching, widely spreading (Fig. 7A). Branches flattened, multiserial, with zooids opening all around; 2.33–6.34 mm wide (3.34±0.88 mm, n=25), five to nine zooids across (Fig. 7B). Autozooids rhomboidal, arranged in quincunx (Fig. 7B), zooidal borders indistinct. Frontal shield convex, entirely tessellated with minute depressions, with two to four small areolar pores (Fig. 8A, B) offset from margin. Orifice subcircular, about as wide as long, smooth distally, proximal margin without sinus; lyrula and condyles absent (Fig. 8C). No oral spines.



**Figure 7.** *Buchneria rhomboidalis* comb. n. **A** Lectotype in the Döderlein collection, MZS 37-2 **B** Enlargement of a branch of the lectotype **C** Enlargement of an orifice showing the proximal margin of the oecium, NSMT Te-796.



**Figure 8.** *Buchneria rhomboidalis* comb. n., scanning electron micrographs. **A** Part of the lectotype, NSMT Te-737 (original MZS 37-2) **B** Specimen NSMT-Bry R256, showing rhomboidal autozooids with few frontal pores **C** Orifice with a round suboral avicularium, NSMT-Bry R267 **D** Suboral avicularia, each with a small, conical distal tooth, NSMT-Bry R267 **E** Autozooids, showing the slightly projecting rostrum of the suboral avicularia, NSMT-Bry R267 **F** Kenozooids interspersed with autozooids at the base of the colony, NSMT TeS-1.

Orifice deeply immersed; aperture at colony surface roughly semicircular in outline, without sinus proximally; cornidial, bounded by contributions of frontal calcification from distal and one or two lateral zooids, with suture lines sometimes evident between the sectors (Fig. 8C, D). Suboral avicularium small, proximal to orifice on the peristome periphery; circular, with complete pivot, rostrum slightly elevated, slightly denticulate, semicircular mandible directed proximolaterally (Fig. 8C, D, E); distal tooth of suboral avicularium small, rounded-conical (Fig. 8D). No other avicularia were observed. On both the edges of branches and in older part of colony, interzooidal kenozooids lacking orifice (Fig. 8F) are interspersed with autozooids; kenozooids especially numerous in the basal part of colony. Ooecium imperforate, smooth, completely immersed, not evident from colony surface; proximal margin almost straight or slightly curved, rarely obscuring the distal edge of primary orifice in ovicellate zooids (Fig. 7C).

**Distribution.** Eastern part of Sagami Bay, and the Sagami Sea southwest of Jogashima and west of Ōshima, at depths of 200–493 m.

**Remarks.** Examination of Ortmann's (1890) type specimens revealed this species belongs not in *Escharoides* but in *Buchneria*, on the basis of the frontal shield with few pores, absence of oral spines, orifice without lyrula, immersed imperforate ooecium, and the suboral avicularia. *Buchneria rhomboidalis* is characterized by having rhomboidal zooids and flat branches. This species resembles *B. teres*, but differs in having flat rather than cylindrical branches, in lacking a peristomial labium and sinus, and in lacking a large avicularium at branch bifurcations. The depth distribution of *Buchneria rhomboidalis* (200–493 m) is shallower than that of *B. teres* (432–3660 m).

***Buchneria variabilis* (Androsova, 1958), comb. n.**

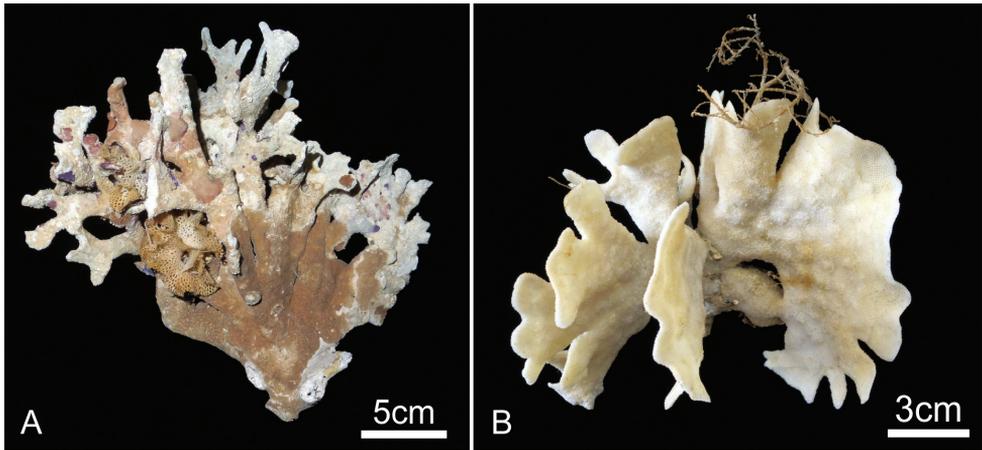
[http://species-id.net/wiki/Buchneria\\_variabilis](http://species-id.net/wiki/Buchneria_variabilis)

Figures 9, 10

*Porella variabilis* Androsova, 1958, 165, fig. 96; type locality, Moneron Island, northern Sea of Japan.

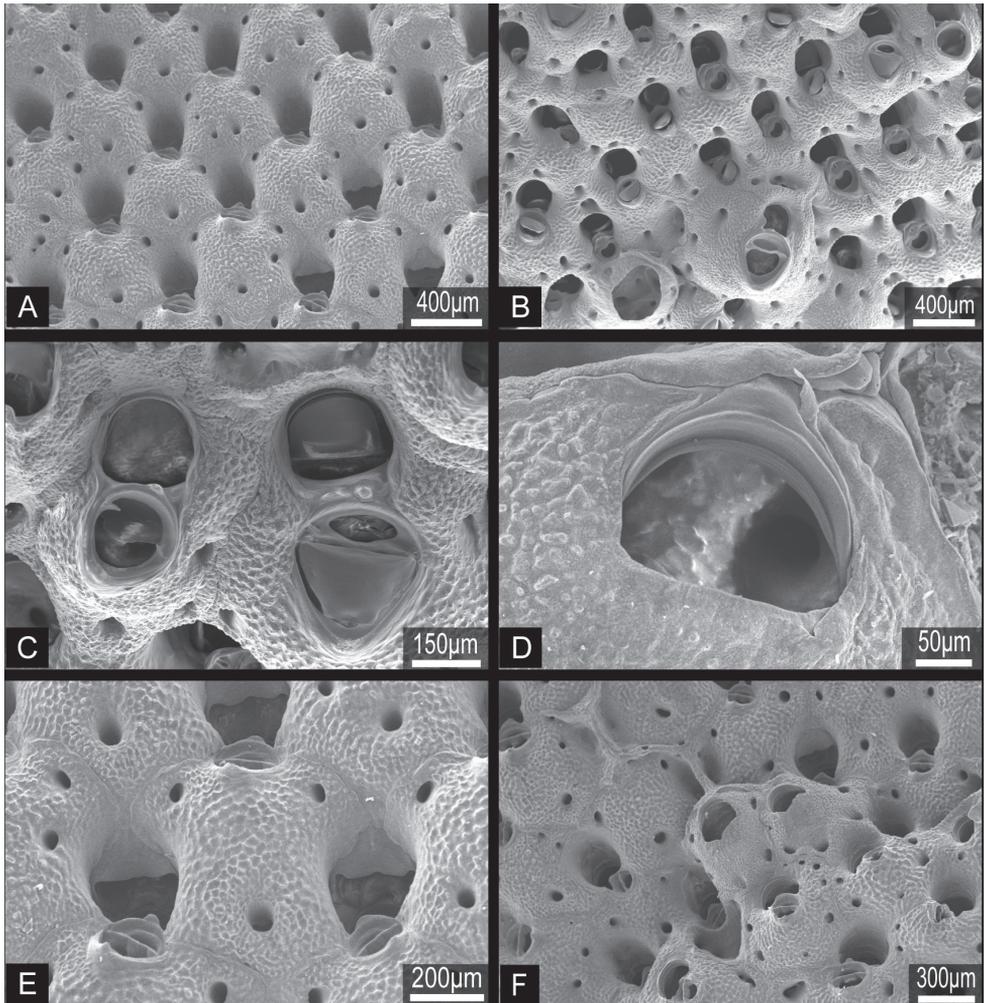
**Material examined.** Androsova's type specimen (ZIN-1/3670) in Zoological Institute of the Russian Academy of Sciences (ZIN RAS), colony collected southwestern region of Sakhalin, Moneron Island (Kaibato), Sea of Japan, 36 m depth, (examined by micrographs); large erect colonies and fragments (NSMT Te-724 to Te-734; ZIHU 4130 and 4131), collected SE of Akkeshi Bay (42°48.37'N, 144°56.22'E) by M. Hirose from research boat *Misago-maru*, 6 July 2010, 116 m depth, by dredge; large erect colony and fragments (NSMT Te-790 to Te-794) collected SE of Akkeshi Bay (42°48.20'N, 144°55.43'E to 42°48.26'N, 144°54.91'E) by M. Hirose from research boat *Misago-maru*, 8 July 2011, 114–116 m depth, by dredge.

**Measurements.** ZL, 0.558–0.921 (0.751±0.101); ZW, 0.408–0.882 (0.611±0.088); n=25. OrL, 0.135–0.223 (0.189±0.019); OrW, 0.130–0.226 (0.192±0.023); n=27. OvL, 0.124–0.444 (0.247±0.072); OvW, 0.104–0.395 (0.214±0.056); n=44.



**Figure 9.** *Buchneria variabilis* comb. n. **A** Large, bushy dead colony with various encrusting epibionts, NSMT Te-726 **B** Large, fan-shaped living colony, NSMT Te-724; note the broad circular monticules at centre right.

**Description.** Colony erect, rigid, robust, with thick, broad, strap-like branches at least 10 zooid widths across, or foliaceous, fan-shaped lobes; lobes or branches 0.86 to 8.04 cm wide ( $2.15 \pm 1.38$  cm,  $n=25$ ), multifurcate or irregularly lobed on distal margin; zooids open on both sides (Fig. 9). Broad lobes of some colonies are covered with conspicuous, closely spaced circular monticules (Fig. 9B). Autozooids oval, rounded hexagonal, or subrectangular in outline; strongly convex frontally, arranged in quincunx, zoecial borders indistinct; frontal shield tessellated, with four to eight areolar pores of irregular size along margin or offset more centrally (Fig. 10A, B). Orifice (Fig. 10C, D) semicircular, broader than long, slightly concave proximally, lyrula and condyles absent (Fig. 10D); deeply immersed with age. Oral spines lacking. Peristome deep, cormidial, formed by contributions of secondary calcification from distal and lateral zooids, with suture lines often evident between the sectors (Fig. 10E). Suboral avicularia approximately same size as orifice, located at margin of peristome; oval, with complete or incomplete pivot, rostrum slightly elevated distally, with a median tooth; mandible semicircular, directed proximally or proximolaterally (Fig. 10B, C). Rounded conical tooth on oral edge of avicularian rostrum conspicuous, projecting into secondary orifice (Fig. 10E). Hypertrophied suboral avicularia are frequent; often larger in area than orifice; distal end of rostrum elevated, pointed; rounded-triangular mandible directed proximally (Fig. 10B, C). I observed no other types of avicularia. Basal part of colony robust, composed of both interzooidal kenozooids and autozooids, borders indistinct. Ooecium imperforate, smooth, completely immersed by secondary calcification from the neighboring zooids, the proximal margin of the ooecium distinctly indented laterally and centrally, obscuring the distal edge of primary orifice in ovicellate zooids (Fig. 10E). Frontal budding frequent (Fig. 10F).



**Figure 10.** *Buchneria variabilis* comb. n., NSMT Te-729, scanning electron micrographs. **A** Autozooids showing the strongly convex frontal wall with few pores **B** Autozooids with various sizes of suboral avicularia **C** Adjacent autozooids showing different sizes of suboral avicularia **D** Orifice without lyrula or condyles **E** Enlargement showing immersed orifices and the narrow, conical tooth distal to suboral avicularia **F** Overgrowth by frontal budding in the central part of the colony.

**Distribution.** Moneron Island, SW Sakhalin, 36 m depth (Androsova 1958); off Akkeshi Bay, Hokkaido, 114–116 m depth (this study).

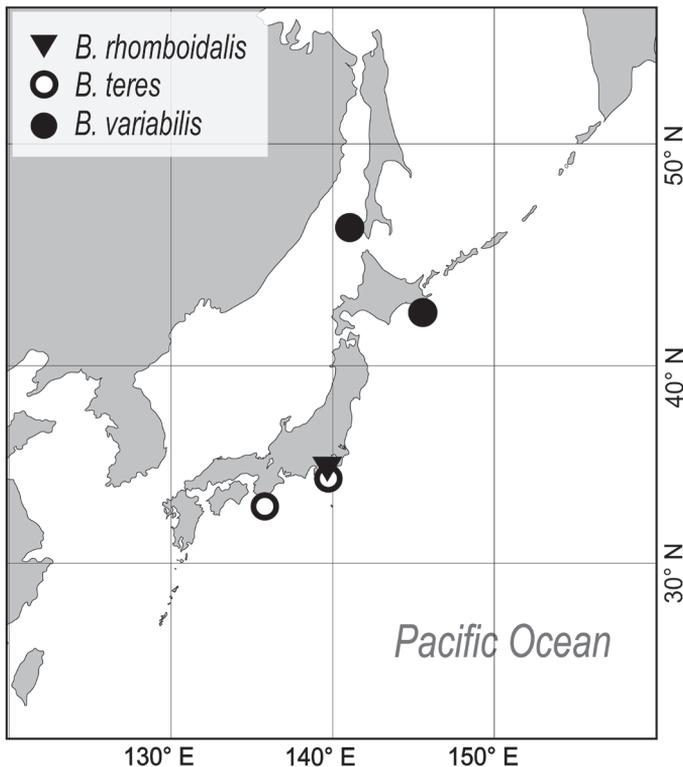
**Remarks.** My material matches Androsova's (1958) description of *Porella variabilis*. She mentioned that the tooth on the proximal margin of the peristome is associated with the suboral avicularium, and that the tooth is present when the avicularium abuts the proximal margin of the peristome, but absent when the avicularium is offset proximally from the peristome. This is the case in all known species of *Buchneria*. An-

drosova (1958) reported *B. variabilis* from 36 m depth, shallower than my specimen from 114–116 m near Akkeshi. This apparent difference in the bathymetric distribution between Sakhalin and Akkeshi may be related to water temperature, as Sakhalin is more northern and colder than Akkeshi.

*Buchneria variabilis* differs from *B. teres* and *B. rhomboidalis* in colony form and in having larger suboral avicularia.

## Discussion

To date, species of *Buchneria* have been only reported from the northwestern Pacific, where they appear to have a cold-temperate distribution (Fig. 11). Most records are from northern Japanese waters; I have not detected *Buchneria* species in field surveys in southern Japan (e.g., near Okinawa). The southernmost record of living *Buchneria* in Japan is *B. rhomboidalis* and *B. teres* from Sagami Bay, of which *B. teres* has been considered as abyssal species (Buchner, 1924; Harmer, 1957) and was collected at depths of more than 400 m in Sagami Bay. Another, more northern *Buchneria* species in Japan showed shallower distribution; *Buchneria variabilis* occurred at 114–116 m depth near Akkeshi and at 36 m depth near Sakhalin (Androsova, 1958).



**Figure 11.** Map showing the known distribution of the three *Buchneria* species in the western Pacific.

While *Buchneria* might be endemic to this region, further sampling around the North Pacific rim, including deep-water sites, may expand the distributions of known species or detect additional species. Furthermore, as *Buchneria* resembles some other North Atlantic genera such as *Porella*, *Palmiskenea*, *Marguetta* and *Porelloides*, taxonomic studies of these other genera may also detect additional *Buchneria* species, and the close relationship may indicate a common history at times when there was a connection between the Pacific and Atlantic.

### Taxonomic key to Japanese *Buchneria* species

- 1a Colony robust; branches thick and broad, fan-shaped distally; hypertrophied suboral avicularia often occur on the frontal shield ..... *Buchneria variabilis* comb. n.
- 1b Colony more delicate, branches cylindrical or flattened, slender distally; hypertrophied suboral avicularia rare or absent ..... 2
- 2a Branches flattened; zooids rhomboidal; hypertrophied suboral avicularia absent ..... *Buchneria rhomboidalis* comb. n.
- 2b Branches cylindrical; zooids rectangular, hypertrophied suboral avicularia present ..... *Buchneria teres* comb. n.

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## Appendix

Specimens examined in this study. (doi: 10.3897/zookeys.241.3175.app) File format: Microsoft Office Excel file (xls).

**Explanation note:** The deposit column indicates the museum where specimens reside: MZS, Musée Zoologique Strasbourg, ZSM, Zoologische Staatssammlung München, NSMT, National Museum of Nature and Science Tokyo (now located in Tsukuba).

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# *Oxydromus* Grube, 1855 reinstated over *Ophiodromus* Sars, 1862 (Polychaeta, Hesionidae)

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## Abstract

The hesionid polychaete genera *Oxydromus* Grube, 1855 and *Ophiodromus* Sars, 1862 have been regarded as synonyms with the former considered as invalid since it was thought to be a junior homonym of *Oxydromus* Schlegel, 1854. However, Schlegel's name is an incorrect subsequent spelling for *Oxydromus* Wagler, 1830 (Aves, Gruiformes, Rallidae) and is not an available name. Consequently, *Oxydromus* Grube, 1855 must be reinstated for this hesionid polychaete genus. A check-list of valid species of *Oxydromus* including 30 new combinations is provided.

## Keywords

Nomenclature, taxonomy, hesionid, Phyllodocida, Annelida

## Introduction

Grube (1855) proposed *Oxydromus* within the polychaete family Phyllodocidae for *O. fasciatus* Grube, 1855, a new species capable of rapid movement from two Mediterranean Sea localities: Trieste (Italy) and Villa Franca (probably Villefranche-sur-Mer, France). Later, Sars (1862) established the genus *Ophiodromus* for a Norwegian species, *O. vittatus* Sars, 1862. He also transferred *Oxydromus* to the family Hesionidae and distinguished it from *Ophiodromus* by the presence of articulated palps and biramous parapodia. Both features were present in *O. fasciatus* but misinterpreted by Grube when he defined them as simple palps and uniramous parapodia (von Marenzeller 1874, Pleijel 2011 pers. comm.).

Pleijel (1998) examined syntypes of *Oxydromus fasciatus* (ZMB 3825), the type species of the genus, and specimens of *Nereis flexuosa* delle Chiaje, 1825 (currently *Ophiodromus flexuosus* fide Pleijel 1998) from near the type locality (type material of this species does not exist). He agreed with McIntosh (1908:116) that the former is a junior synonym of the latter although he didn't go into detail. Nevertheless, regarding the defining generic characters, *Ophiodromus* and *Oxydromus* are synonymous. *Ophiodromus flexuosus* is possibly a senior synonym of the type species *O. vittatus* (fide von Marenzeller 1874, McIntosh 1908, Pleijel 1998, Fauchald 2011). An examination of specimens from the type localities, Gulf of Naples and Norway respectively, is required to resolve their status.

Pleijel (1998) pointed out that *Oxydromus* has seniority over *Ophiodromus* but, as first stated by Hartman (1965), concluded that the former genus name was preoccupied in the class Aves, *Oxydromus* Schlegel, 1854, and for which reason *Ophiodromus* must be used. However, Viéitez et al. (2004) argued that *Oxydromus* is an available genus name and must be considered as valid. Then, following their suggestion, we proposed to reinstate *Oxydromus* over *Ophiodromus* to standardize the worldwide use of both generic names.

## Results

Viéitez et al. (2004:521) realized that *Oxydromus* Schlegel is an incorrect subsequent spelling of *Ocydromus* Wagler, 1830 (Aves, Gruiformes, Rallidae) (itself a junior homonym of the beetle genus *Ocydromus* Clairville, 1806 [Insecta, Carabidae], and replaced by *Gallirallus* Lafresnaye, 1841). Although Schlegel's name was used in later publications (e. g. Reischek 1886, Röse 1890), as an incorrect subsequent spelling it remains unavailable according to Article 33.3 of the International Code of Zoological Nomenclature. This states "Any subsequent spelling of a name different from the correct original spelling, other than a mandatory change or an emendation, is an 'incorrect subsequent spelling'; it is not an available name and, like an incorrect original spelling [Article 32.4], it does not enter in homonymy and cannot be used as a substitute name...". Viéitez et al. erroneously stated that Sars proposed *Ophiodromus* to replace *Oxydromus* Grube due to his mistaken belief that Grube's genus name is a junior homonym of *Oxydromus* Schlegel. Sars actually didn't mention the homonymy; instead he discussed the morphological discrepancy between both genera.

Preservation of the genus-group name *Ophiodromus* as the senior synonym would require a reversal of precedence according to Article 23.9 (ICZN 1999). This states that in order to maintain the prevailing usage the following conditions must be met: 1) the senior synonym (in this case *Oxydromus* Grube, 1855) has not been used as a valid name after 1899 (Article 23.9.1.1), and 2) the junior synonym (namely *Ophiodromus* Sars, 1862) has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years (Article 23.9.1.2). The first condition

is not applicable which negates the need for a reversal of precedence. *Oxydromus* has also been listed as a valid name after 1900 in many publications (e.g. Gravier 1900, McIntosh 1908, Chamberlin 1919, Fauvel 1923, Augener 1927, Uschakov 1955, Hartmann-Schröder 1959, 1965, Hartman 1961, Day 1963, Averincev 1972).

In accordance with Article 23.9.3 (ICZN 1999), we consider that the *Oxydromus/Ophiidromus* situation does not threaten the stability of nomenclature or the universality of a widespread use, thus no referral to the Commission for a ruling should be required. We propose to reinstate *Oxydromus* over *Ophiidromus* based on the Principle of Priority (Article 23, ICZN 1999).

## Systematics

### Family HESIONIDAE Grube, 1850

### Subfamily OPHIODROMINAE Pleijel, 1998

### Tribe OPHIODROMINI Pleijel, 1998

#### *Oxydromus* Grube, 1855, reinstated

*Oxydromus* Grube, 1855: 98.

*Ophiidromus* Sars, 1862: 87; Pleijel, 1998: 137–143, figs. 31–33 (synonymy).

**Type species.** *Oxydromus fasciatus* Grube, 1855, by monotypy.

*Oxydromus adorsosetosus* (Hartmann-Schröder, 1985), comb. n. (basionym of *Ophiidromus adorsosetosus* Hartmann-Schröder, 1985)

Type locality: Port Lincoln, South Australia.

*Oxydromus adpersus* (Grube, 1874), comb. n. (basionym of *Ophiidromus adpersus* Grube, 1874)

Type locality: Dalmatia, Croatia.

*Oxydromus agilis* (Ehlers, 1864), comb. n. (basionym of *Ophiidromus agilis* Ehlers, 1864)

Type locality: Adriatic Sea.

*Oxydromus angolaensis* (Hartmann-Schröder, 1974), comb. n. (basionym of *Podarke angolaensis* Hartmann-Schröder, 1974)

Type locality: Lobito, Angola.

*Oxydromus angustifrons* (Grube, 1878), comb. n. (basionym of *Irma angustifrons* Grube, 1878)

Type locality: Philippines.

*Oxydromus berrisfordi* (Day, 1967), comb. n. (basionym of *Ophiodromus berrisfordi* Day, 1967)

Type locality: Walvis Bay, Namibia.

*Oxydromus brevipodius* (Uchida, 2004), comb. n. (basionym of *Ophiodromus brevipodius* Uchida, 2004)

Type locality: Wakayama, Japan.

*Oxydromus bunbuku* (Uchida, 2004), comb. n. (basionym of *Ophiodromus bunbuku* Uchida, 2004)

Type locality: Shikoku, Japan.

*Oxydromus constrictus* (Uchida, 2004), comb. n. (basionym of *Ophiodromus constrictus* Uchida, 2004)

Type locality: Wakayama, Japan.

*Oxydromus didymocerus* (Schmarda, 1861), comb. n. (basionym of *Cirrosyllis didymocerus* Schmarda, 1861)

Type locality: New South Wales, Australia.

*Oxydromus fasciatus* Grube, 1855 (possible junior synonym of *O. flexuosus* (delle Chiaje, 1825))

Type locality: Adriatic Sea (Trieste) and Western Mediterranean Sea (Villefranche-sur-Mer, France).

*Oxydromus fauveli* (Uchida, 2004), comb. n. (basionym of *Ophiodromus fauveli* Uchida, 2004)

Type locality: Wakayama, Japan.

*Oxydromus flexuosus* (delle Chiaje, 1825) (basionym of *Nereis flexuosa* delle Chiaje, 1825)

Type locality: Gulf of Naples.

*Oxydromus furcatus* (Hartmann-Schroder, 1962), comb. n. (basionym of *Podarke furcatus* Hartmann-Schroder, 1962)

Type locality: Peru.

*Oxydromus guanicus* (Hoagland, 1919), comb. n. (basionym of *Podarke guanica* Hoagland, 1919)

Type locality: Guanica, Puerto Rico.

*Oxydromus latifrons* (Grube, 1878), comb. n. (basionym of *Irma latifrons* Grube, 1878)

Type locality: Philippines.

*Oxydromus limicolus* (Willey, 1905), comb. n. (basionym of *Irma limicola* Willey, 1905)

Type locality: Sri Lanka.

*Oxydromus longifundus* (Uchida, 2004), comb. n. (basionym of *Ophiodromus longifundus* Uchida, 2004)

Type locality: Okinawa, Japan.

*Oxydromus longicirratu*s (Knox and Cameron, 1971), comb. n. (basionym of *Nereimyra longicirratu*s Knox and Cameron, 1971; not a senior homonym to *O. longicirratu*s (Tenerelli, 1973) as Pleijel (1998) suggested, but this name is considered as nomen dubium)

Type locality: Melbourne, Australia.

*Oxydromus microantennatus* (Hutchings and Murray, 1984), comb. n. (basyonymy of *Podarke microantennata* Hutchings and Murray, 1984)

Type locality: New South Wales, Australia.

*Oxydromus minutus* (Hartmann-Schröder, 1959), comb. n. (basyonymy of *Podarke minuta* Hartmann-Schröder, 1959)

Type locality: San Juan, El Salvador.

*Oxydromus mutilatus* (Treadwell, 1901), comb. n. (basyonymy of *Castalia mutilata* Treadwell, 1901)

Type locality: Puerto Rico.

*Oxydromus notospinosus* (Rosito, 1983), comb. n. (basionym of *Ophiodromus notospinosus* Rosito, 1983)

Type locality: Philippines.

*Oxydromus obscurus* (Verrill, 1873), comb. n. (basyonymy of *Podarke obscura* Verrill, 1873)

Type locality: Massachusetts, United States.

*Oxydromus okudai* (Uchida, 2004), comb. n. (basionym of *Ophiodromus okudai* Uchida, 2004)

Type locality: Nagasaki, Japan.

*Oxydromus pallidus* Claparède, 1864

Type locality: Golfe du Lion, France.

*Oxydromus parapallidus* (Uchida, 2004), comb. n. (basionym of *Ophiodromus parapallidus* Uchida, 2004)

Type locality: Wakayama, Japan.

*Oxydromus pelagicus* (Rioja, 1923), comb. n. (basionym of *Ophiodromus pelagicus* Rioja, 1923)

Type locality: Pontavedra, Spain.

*Oxydromus pugettensis* (Johnson, 1901), comb. n. (basyonymy of *Podarke pugettensis* Johnson, 1901) (Figure 1)

Type locality: Washington, United States.

*Oxydromus spinapandens* (Storch and Niggemann, 1967), comb. n. (basyonymy of *Podarke pugettensis spinapandens* Storch and Niggemann, 1967)

Type locality: Red Sea.

*Oxydromus spinosus* (Ehlers, 1908), comb. n. (basyonymy of *Orthodromus spinosus* Ehlers, 1908)

Type locality: Angola.

*Oxydromus viridescens* (Ehlers, 1864), comb. n. (basyonymy of *Podarke viridescens* Ehlers, 1864)

Type locality: Adriatic Sea.

*Oxydromus vittatus* (Sars, 1862), comb. n. (basionym of *Ophiodromus vittatus* Sars, 1862)

Type locality: Norway.

## Remarks and discussion

Pleijel (1998) revised the phylogeny and classification of the family Hesionidae based on available type and non-type material. He provided descriptions and diagnoses for all supraspecific taxa and world-wide species lists, including 24 nominal taxa in *Ophiodromus*. He newly synonymized *Orseis* Ehlers, 1864 and *Schmardiella* Czerniavsky, 1882, and continued the prior synonymy of *Oxydromus* Grube, 1855, *Podarke* Ehlers, 1864, *Mania* de Quatrefages, 1866 and *Irma* Grube, 1878 with *Ophiodromus* Sars, 1862, whose type species is *O. vittatus* Sars, 1862 (possibly *O. flexuosus* fide Pleijel 1998). However, *Oxydromus* is herein reinstated due to the priority of *Oxydromus* over *Ophiodromus* Sars, with *O. fasciatus* as the type species.

*Oxydromus* (from the Greek *oxys*= fast, quick; *dromus*= runner) (Figure 1) is currently represented by 32 species and is distinguished from other genera by the presence of six pairs of enlarged anterior cirri, prostomium bearing three antennae with the median one sited anteriorly, and biarticulated palps (see Salazar-Vallejo and Orensanz 2006). Uchida (2004) suggested that the species of this genus are among the most difficult groups to identify in the family and considered that the form of parapodia is a more useful character for identification of the species than prostomium and anterior



**Figure 1.** A representative living specimen of *Oxydromus* collected in California. Species: *Oxydromus pugettensis* (Johnson, 1901) (photo: Leslie Harris).

part structures. A detailed revision of the genus *Oxydromus* is required to redefine species, especially those considered to be widely distributed.

### **Acknowledgements**

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# Synopsis of the Argentinian scarab genus *Pseudogeniates* Ohaus (Coleoptera, Scarabaeidae, Rutelinae)

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## Abstract

The scarab beetle genus *Pseudogeniates* Ohaus (Scarabaeidae: Rutelinae: Rutelini) is endemic to Argentina. The genus includes three species: *P. cordobaensis* Soula, *P. intermedius* Ohaus, and *P. richterianus* Ohaus. We characterize the genus, provide a key to species, redescribe and diagnose each species, provide spatial and temporal distributions, and discuss distributions of the species in relation to eco-regions and areas of endemism in Argentina.

## Resumen

El género de escarabajo *Pseudogeniates* Ohaus (Scarabaeidae: Rutelinae: Rutelini) es endémico de Argentina. El género incluye tres especies: *P. cordobaensis* Soula, *P. intermedius* Ohaus, y *P. richterianus* Ohaus. En este trabajo caracterizamos el género, proveemos una clave para las especies, redescibimos y proveemos diagnosis para cada una de ellas y datos de su distribución temporal y espacial y discutimos aspectos de las distribuciones de las especies en relación de las regiones eco-regiones y áreas de endemismo en Argentina.

## Keywords

Endemic, Pampa, Monte, Chaco, intraspecific variation

## Introduction

The leaf chafer genus *Pseudogeniates* Ohaus (Rutelinae: Rutelini) (Figs 1–3) is endemic to Argentina. Species in the genus are associated with arid habitats in the Pampa, Espinal, Monte, and Chaco eco-regions (Fig. 22) (eco-regions as in Ponce et al. 2002).

*Pseudogeniates* species are moderate-sized (12–19 mm), elongate-oval, brown scarabs with striate elytra (Figs 1–3). In many respects, species in the genus are similar in overall gestalt to species in the genus *Geniates* Ohaus (Rutelinae: Geniatiini) or drab-colored species in the genus *Anomala* Samouelle (Rutelinae: Anomalini). Actually, however, form of the labrum, elytra, protibia and tarsomeres, and position of the terminal spiracle, place the genus in the tribe Rutelini (Rutelinae) (see “Classification”). Female gender bias in the most wide-spread species and the fact that specimens are rarely encountered in collections have both contributed to the difficulty in circumscribing species in the genus. Our work revealed a high degree of intraspecific variation that may be due to spatial or temporal isolation of populations. Thus, in addition to rarity and sex bias, circumscription of species is complicated by variation in character states. Heretofore, there has been no comprehensive review of species in the genus. This research provides a synopsis of the three species in the genus and information on the distribution of these poorly studied species.

### Taxonomic history

Ohaus (1910) named the genus *Pseudogeniates* for one species, *P. richterianus* Ohaus, and he based the description on female specimens alone. He puzzled over classification of the genus, discussing its affinities with the ruteline tribes Geniatiini and Anoplognathini. Both of these tribes are orthochilous rutelines, that is, they belong to a broad group of Rutelinae in which the mouthparts (specifically labrum and mentum) project vertically with respect to the head (Ohaus 1918, 1934; Machatschke 1965; Jameson and Hawkins 2005). Based on overall gestalt and proportions of the “hind body”, Ohaus (1910) compared *P. richterianus* with *Geniates barbatus* Kirby and *G. cylindricus* Burmeister (both Geniatiini from South America). He also compared the genus with *Saulostomus weiskei* Ohaus and *S. felschei* Ohaus (both Anoplognathini from Australia) based on the form of the mouthparts. The form of the clypeus and mouthparts were so unusual that when Ohaus first saw specimens, he “believed that the animal was crippled” (Ohaus 1910: 179). After studying two additional female specimens from a different locality, Ohaus realized that these peculiarities were not teratological. Despite lacking male specimens, he described *P. richterianus*, but he declined placing the new genus and species in a ruteline tribe, stating that this would require additional characters from male specimens (Ohaus 1910).

After obtaining additional specimens of *Pseudogeniates* and making comparisons with other Argentinian fauna, Ohaus (1914) placed the genus in the tribe Rutelini (Rutelinae), a tribe of homalochilous rutelines that is characterized by the labrum that is horizontally produced with respect to the clypeus. He discussed affinities of *Pseudogeniates* with *Homonyx* Guerin and *Parhomonyx* Ohaus, both of which are distributed in southern South America and both members of the subtribe Pelidnotina. Based on both male and female specimens, Ohaus (1914) described a new species, *P. intermedius*. Ohaus characterized the two species using differences in the form of the clypeus and antennae:

*P. richterianus* possessed nine-segmented antennae (thus differing from all other Rutelini) and *P. intermedius* possessed ten-segmented antennae (the hypothesized ancestral state within the Rutelini). The antennal character state in *P. richterianus* make this species an exception in the key to tribes of Rutelinae (see Jameson 1990, 2005). However, Ohaus did not have a broad enough sampling of specimens of *P. richterianus* to understand the intraspecific variation of this character: antennae are either 9- or 10-segmented in *P. richterianus*. This variation has confounded identification of *Pseudogeniates* species.

The *Genera Insectorum* on the Rutelini (Ohaus 1934) languished for more than 20 years before publication. Realizing the great delay, Ohaus (1915) published his concepts of higher taxa and descriptions of genera. He formalized use of the subtribe Pelidnotina (as “Pelidnotinorum”) and commented on evolution and affinities of *Pseudogeniates*, *Parhomonyx*, and *Homonyx*. He considered *Parhomonyx* to be an “intermediate stage” that “led *Homonyx* to *Pseudogeniates*” (Ohaus 1915: 258), and that characters of the coloration, clypeus, mouthparts, elytra, hind tibia, and antennae indicated these relationships (or this progression of forms). He thought that these taxa were a good example of how differences in rainfall (dry versus wet; e.g., Ponce et al. 2002) and differences in habitat (forest versus steppe) produced adaptations and changes in morphological characters. He also stated that the Argentinian fauna offered a number of examples of these evolutionary transformations, particularly in scarab beetles.

Nearly 100 years after Ohaus’ work on *Pseudogeniates*, Soula (2009) reviewed the genus based on six specimens in the Ohaus collection (housed at ZMHB), described a new species, *P. cordobaensis*, based on specimens from the type series of *P. intermedius* (which included three males and one female specimen), described the type specimens for each of the species of *Pseudogeniates*, and commented briefly on the unusual character states of the genus. Soula’s species descriptions are not comparative; they do not allow separation and identification of species in the genus; and, because they are based on a limited number of specimens, they do not take into account variation within the species. In addition, Soula (op. cit.) did not provide a key to species and diagnoses. For these reasons, Soula’s work is of little utility for identification and understanding of biodiversity of this group.

### **Definition of taxonomic characters and character examination**

This research is based on 56 specimens from collections including type specimens. About one third of these specimens (19 specimens) were identified in collections; the remaining two thirds were not identified. Out of the 19 specimens that were identified, 9 were incorrectly identified, 4 were correctly identified, and 6 were type specimens. Two specimens were incorrectly identified to genus. Specimens for this research are deposited at the CMNC (Canadian Museum of Nature Collection, Ottawa, Canada), FMNH (Field Museum of Natural History, Chicago, Illinois, USA); IAZA (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina); MACN (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina); MLJC (Mary Liz Jameson collection,

Wichita, Kansas, USA); UCCC (Universidad de Concepción, Concepción, Chile); USNM (United States National Collection, Washington, D.C., USA); and ZMHB (Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany).

Morphological characters formed the basis of this work. The broadest range of potentially phylogenetically informative morphological characters was used for morphological analyses and comparisons. For measurements, we used an ocular micrometer. Body measurements, puncture density, puncture size, and density of setae are based on the following standards. Body length was measured from the apex of the clypeus to the apex of the pygidium. Body width was measured at the widest width of the elytra. Puncture density was considered ‘dense’ if punctures were nearly confluent to less than two puncture diameters apart, ‘moderately dense’ if punctures were from two to six puncture diameters apart, and ‘sparse’ if punctures were separated by more than six puncture diameters. Puncture size was defined as ‘small’ if punctures were 0.02 mm in diameter or smaller; ‘moderate’ if 0.02–0.07 mm, ‘moderately large’ if 0.07–0.12 mm, and ‘large’ if 0.12 mm or larger. Setae density was defined as ‘dense’ if the surface was not visible through the setae, ‘moderately dense’ if the surface was visible but with many setae, and ‘sparse’ if there were few setae. It should be noted that setae are subject to wear and may be abraded away. Elytral discal striae are defined as the striae located between the elytral suture and the elytral humerus. The interocular width measures the number of transverse eye diameters that span the width on the frons between the eyes. This was measured by placing the ocular micrometer in a position such that it intersects the frons and eyes (dorsal view), focusing on the surface of the frons, and then measuring the width of the frons and width of the eyes without adjusting the focus. Mouthparts, wings, and genitalia were examined and card-mounted beneath the specimen. Some specimens were quite fatty, with internal and external greasy build-up. These specimens were cleaned in acetone prior to dissection.

Characters and specimens were observed with 6–48× magnification and fiber-optic illumination. Digital images of specimens and structures were captured using the Leica Application Suite V3.8. Images were edited in Adobe Photoshop CS2 (background removed, contrast manipulated).

Species are characterized by combinations of characters including the form of the mentum and maxilla, form of the metacoxa, and form of the ventral plate of the male parameres. We use the phylogenetic species concept (Wheeler and Platnick 2000) in this work: “A species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states.”

Specimen localities were translated into latitude and longitude using GoogleEarth (<http://www.google.com/earth/index.html>). Maps were generated by entering these data into Microsoft Excel 2008 and uploaded to EarthPoint (<http://www.earthpoint.us/Excel-ToKml.aspx>) and GoogleEarth (Supplementary File: Pseudogeniastes Locality Table.xls). These tools allow for interactive mapping and addition of data by subsequent users. Description of Argentinian eco-regions follows Ponce et al. (2002). Argentinian areas of endemism follow Cabrera and Willink (1973) and Szumik et al. (2012).

***Pseudogeniates* Ohaus, 1910**

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

Figs 1–22

*Pseudogeniates* Ohaus 1910: 179–180

**Type species.** *P. richterianus* Ohaus 1910: 180. By monotypy.

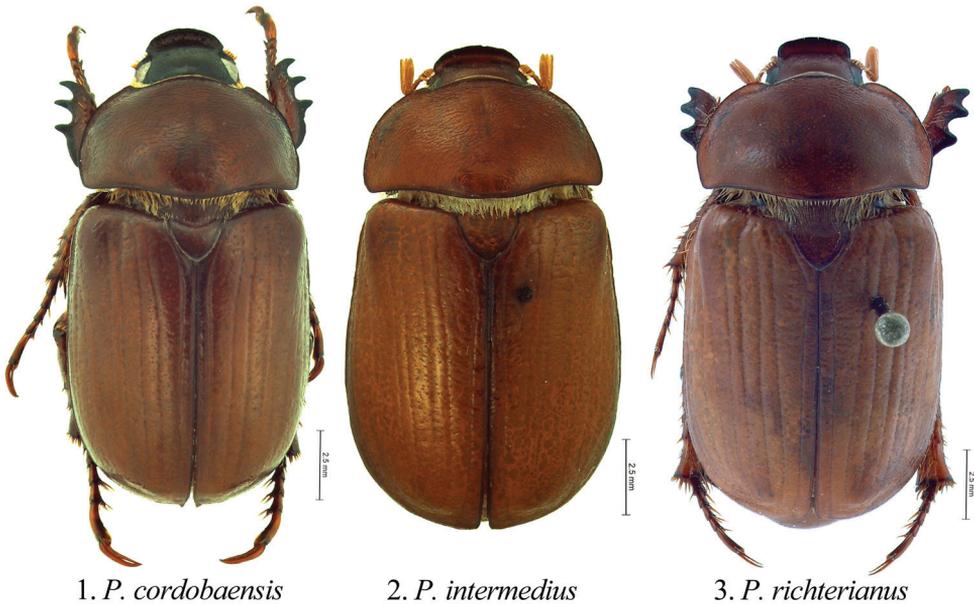
**Tribal classification.** The genus *Pseudogeniates* is a member of the tribe Rutelini. In overall appearance, however, species in the genus *Pseudogeniates* are similar to species in the genera *Geniates* (Geniatini) and *Anomala* (Anomalini). Species in the genus *Pseudogeniates* can be separated from both of these tribes based on the margin of the elytra that lacks an obvious membranous border (membranous border present at the elytral apex in both Geniatini and Anomalini). Additional characters that separate the Rutelini and Geniatini include: the labrum that is horizontally produced with respect to the clypeus in the Rutelini (vertically produced in the Geniatini) and pro-tarsomeres that are subcylindrical and lacking ventral setose pads (dorsoventrally flattened and densely setose ventrally in the Geniatini). Additional characters that separate the Rutelini and Anomalini include: protibia with inner, protibial spur apical in the Rutelini (inner, apical spur subapical in Anomalini) and terminal spiracle positioned in pleural suture in the Rutelini (terminal spiracle not positioned in pleural suture in Anomalini). For a key to tribes of Rutelinae, see Jameson (1990, 2005).

**Subtribal classification.** Ohaus (1915, 1934) placed the genus *Pseudogeniates* in the tribe Rutelini and subtribe Pelidnotina. Based on morphological data, this subtribe was demonstratively paraphyletic and it was eliminated (Jameson 1998). Soula (2009), without justification or discussion, continued use of this higher-level taxon for the genus. We consider the genus *Pseudogeniates* to be a member of the tribe Rutelini (without subtribal designation).

**Phylogeny.** Sister group relationships have not been examined for the genus or for species within the genus.

**Diagnosis of adults.** Members of the genus *Pseudogeniates* differ from other genera in the tribe Rutelini by the following combination of characters: feathery fringe of setae on the ventral edge of the elytra present; elytra obviously striate (Figs 1–3); mesosternal peg lacking; claws simple on all legs (not toothed) (Figs 11–13); frontoclypeal suture incomplete (Figs 16–18); clypeal apex broadly reflexed (Figs 16–18); apex of labrum extending beyond clypeal apex, visible from dorsal view (Fig. 18); apex of mandible with one, apical, recurved tooth (Figs 4, 18); maxillary teeth lacking (Fig. 5).

**Similar taxa.** Species in the genus *Pseudogeniates* share several characters with *Parhomonyx fuscoaeeneus* Ohaus, a monotypic taxon that is also endemic to southern South America. The following characters are shared: fringe of setae at apex of elytra, mesosternal process lacking, mandible with one external tooth, elytra striate, and claws simple. However, *Pseudogeniates* differs from *Parhomonyx* based on the external margin of the mandible that is straight (external margin lobe-like in *Parhomonyx*), maxillary teeth lacking (maxilla with well developed teeth in *Parhomonyx*), maxillary palp rod-shaped

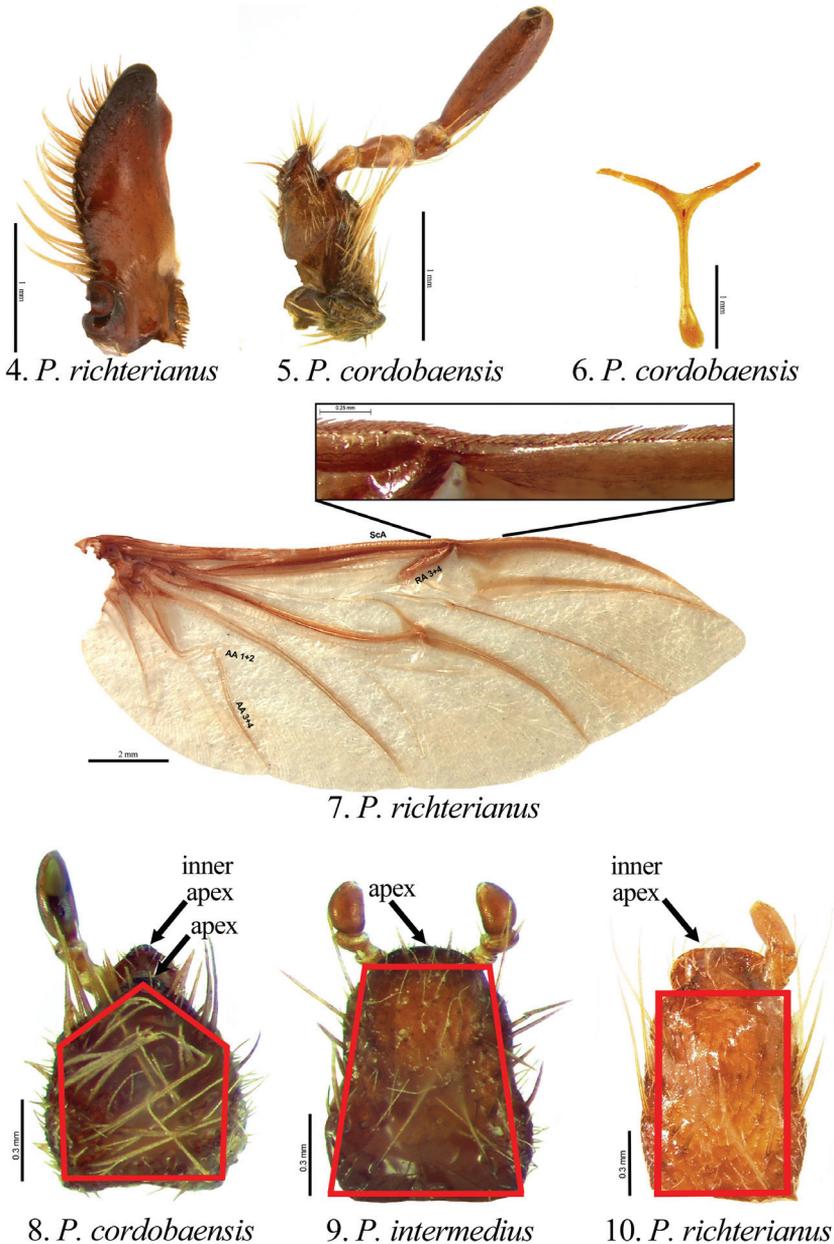
1. *P. cordobaensis*2. *P. intermedius*3. *P. richterianus*

**Figures 1–3.** Dorsal habitus of *Pseudogeniates* species 1 *P. cordobaensis* 2 *P. intermedius* 3 *P. richterianus*

(broadly elliptical in *Parhomonyx*), and fifth tarsomere on all legs of males and females lacking an internal tooth (with two well developed internal teeth on the fifth meso- and metatarsomeres of males and females of *Parhomonyx*).

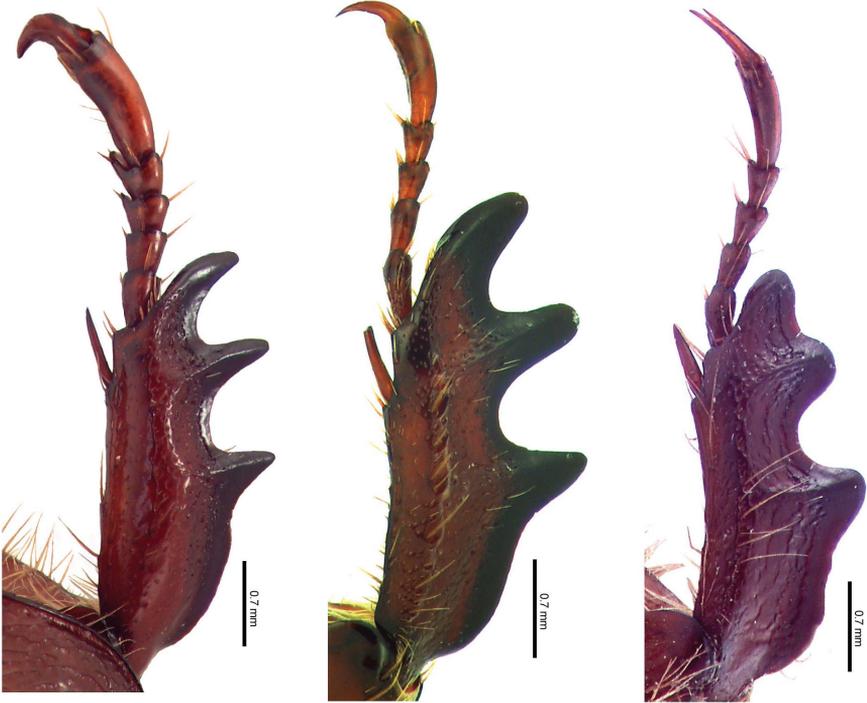
**Description of adults.** Length from apex of clypeus to apex of pygidium 12.0–19.0 mm; width at mid-elytra 6.0–11.0 mm. Color: Dorsal and ventral surfaces testaceous to castaneous. Form (Figs 1–3): Elongate oval, sides subparallel, pygidium exposed beyond apices of elytra, apex of elytra broadly rounded. Head (Figs 16–18): Disc of frons and clypeus in lateral view nearly flat, clypeus with margins and apex reflexed. Frons and clypeus variably sculptured, punctate and/or rugose. Frontoclypeal suture weakly indicated, incomplete at middle. Eye canthus weakly cariniform. Interocular width 2.9–4.8 transverse eye diameters. Clypeal apex rounded or quadrate, with or without basolateral constriction, lacking bead; frontal view flat, length (at middle) about 1/3 length of frons, disc variably punctate and setose. Mandible (Fig. 4) with 1 apical, acute, recurved tooth; scissorial region with 1 poorly developed tooth; molar region narrow. Labrum projecting beyond clypeus, trapezoidal, apex emarginate or quadrate; apex moderately emarginate medially, surface moderately densely punctate, punctures moderate in size, some setose (setae moderately long and short, rufous). Maxilla (Fig. 5) lacking teeth; galea fused or not, with moderately dense, moderately long setae and with 1 to 2 long, bristle-like seta on disc; terminal segment of palpus with dorsal, longitudinal sulcus from based to sub-apex. Mentum (Figs 8–10) rectangular, trapezoidal, or pentagonal, inner apex produced anteriorly or not, with or without inner shelf. Antenna 9 or 10-segmented with 3-segmented club; club subequal in length to segments 1–7 combined or slightly longer than segments 1–7 combined. Pronotum:

Widest at middle, apical angles obtuse, basal angles obtuse. Dorsal surface punctate, rugopunctate, or imbricate, with or without median line. Bead complete anteriorly, laterally, and basally. Margin sparsely setose (setae short, rufous). Scutellum: Parabolic, wider than long; base declivous at elytral base. Wing: Dense, thick setae present anterior to RA3+4 to apex; ScA with dense, thick setae near fold, lacking precostal pegs; AA1+2 shorter than AA3+4 (Fig. 7). Mesepimeron: Apex entirely hidden by base of elytra in dorsal and lateral views. Elytra: Variably sculptured with longitudinal, punctate striae; punctures variable. Sutural stria sulcate, impressed from base of scutellum to apex. Epipleuron from base to mid-metacoxa with shelf and associated setae; epipleuron from mid-metacoxa to apex beaded and with associated setae. Apex of elytra weakly rounded; sutural apex spiniform, rounded, or square. Elytral sutural length about 6.5 times length of scutellum. Propygidium: Hidden beneath elytra. Pygidium: Semitriangular, about twice as wide as long at middle; variably sculptured, punctate, shagreened, or weakly rugose. Margins beaded. Apex rounded. Apical bead with moderately long to long setae; setae tawny to rufous or testaceous. Venter: Prosternal keel triangular; apex projecting anteroventrally at about 35° with respect to ventral plane; apex produced to level of prothorax, blunt; surface flat (lacking protuberance). Mesometasternal keel lacking. Sternites 1–4 subequal in length in male and female, sternites 5–6 about twice length of sternite 4. In lateral view, male sternites flat, female sternites weakly convex. Last sternite with apex quadrate in male, posteriorly rounded in female. Legs: Protibia (male and female) with width at base 1/3<sup>rd</sup> to 1/4<sup>th</sup> greater than width at apex (Figs 11–13), inner base with weak Protibial notch, with 3 external teeth in apical half (2 apical teeth removed from basal tooth external teeth or not); spur present, subapical. Modified foreclaw of male (Fig. 11) about 3 times width of unmodified claw, not toothed, inner apical tooth present at apex, small. Foreclaws of female simple, internal claw slightly wider than outer claw. Unguitractor plate laterally flattened, exposed beyond tarsomere 5; apex with 0–1 moderately long setae. Mesotibia with sides subparallel, apex weakly divergent; external edge with 2 carinae; inner apex with 2 spurs; apex with 10–20 spinulae. Meso- and metatarsomere 4 apicomediaally with 4 medial spinulae (male) or 2 medial spinulae and 1 seta-like long spinule laterad of each medial spinula (female). Meso- and metatarsal claws of male and female simple, internal claw slightly wider than outer claw. Metatarsomere 1 moderately divergent at middle and apex (male and female). Metatrochanter with apex weakly produced beyond posterior border of femur. Metacoxal corner (female) rounded or square. Metatibia (Figs 14–15) with sides subparallel, divergent towards apex; external edge with 1–2 carinae; inner apex with 2 spurs; inner apex with 25–40 short, stout spinulae. Spiculum gastrale: Y-shaped, lacking associated sclerites (Fig. 6). Parameres and phallobase: Plates fused dorsally/ventrally (not laterally). Dorsal plate symmetrical, apex rounded and with or without two apical, rounded teeth (Figs 19–21); not diagnostic for species. Ventral plate elongate (as long as dorsal plate or ½ length of dorsal plate), apex acute, quadrate, or rounded; diagnostic, species specific (Figs 19–21). Parameres slightly longer than phallobase. Female Genitalia: Gonocoxites subquadrate with sparse setae; not diagnostic for species.



**Figures 4–10.** Characters for species of *Pseudogeniates* **4** Left mandible of *P. richterianus*, dorsal view (with one apical, acute, recurved tooth; poorly developed scissorial region, and narrow molar region) **5** Maxilla of *P. cordobaensis*, ventral view (lacking teeth, terminal segment of palpus with dorsal, longitudinal sulcus) **6** Spiculum gastrale of *P. cordobaensis* **7** Wing of *P. richterianus* showing form and inset showing dense, thick setae associated with ScA and region anterior to RA3+4 **8** Mentum, ventral view, of *P. cordobaensis* (shape pentagonal, inner apex projecting anteriorly and with inner shelf) **9** Mentum, ventral view, of *P. intermedius* (shape broadly trapezoidal, apex not projecting anteriorly and without inner shelf) **10** Mentum, ventral view, of *P. richterianus* (shape rectangular, inner apex projecting anteriorly and without inner shelf)

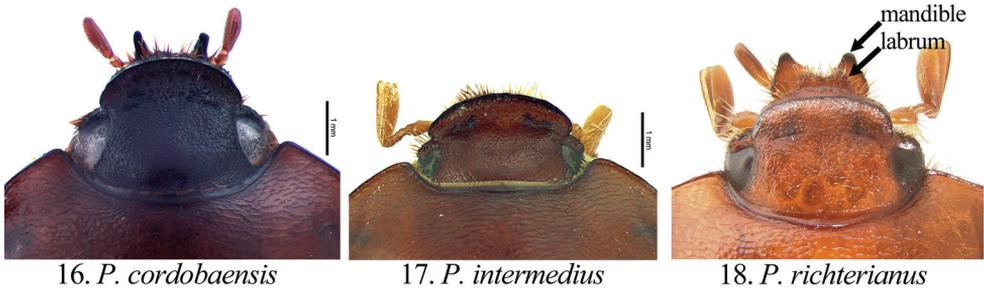


11. *P. cordobaensis*, male12. *P. richterianus*, unworn female13. *P. richterianus*, worn female14. *P. cordobaensis*, male15. *P. richterianus*, female

**Figures 11–15.** Form of protibia (11–13) and metatibia (14–15) in *Pseudogeniates* species **11** Protibia of *P. cordobaensis* (male) **12** Protibia of unworn specimen of *P. richterianus* (female) showing **13** Protibia of worn specimen of *P. richterianus* (female) **14** Metatibia of *P. cordobaensis* (male) **15** Metatibia of *P. richterianus* (female)

Head (Fig. 16): Frons densely punctate to confluent punctate (mid-disc), rugopunctate laterally and apically; punctures small and moderately large, mixed. Clypeus with dorsal surface densely punctate to confluent punctate (mid-disc), rugopunctate laterally and apically, punctures small and large (mixed), some setose; setae short to moderate, rufous, sparse; shape broadly semicircular, apex and sides broadly reflexed, with or without constriction basolaterally; disc (frontal view) densely rugopunctate, punctures small and large, mixed, some setose (setae short to moderately long, rufous, sparse). Labrum setose; setae moderately long and short, rufous. Maxilla (Fig. 5) with galea distinct, with 1 elongate, bristle-like, medial seta. Mentum (Fig. 8) nearly as long as wide or slightly longer than wide, form pentagonal, inner apex projects anteriorly, with inner shelf. Antenna 10-segmented with 3 segmented club; club slightly longer than stem. Pronotum: Medial line obsolete. Surface (disc and mediolaterally) moderately densely imbricate with sparse, short, testaceous setae. Margin with short, rufous setae. Elytra: Sutural stria impressed from base of scutellum to apex. Elytral apex weakly spiniform or quadrate. Discal striae weakly impressed, punctate; 5 on disc mesad of humerus, 5 laterad of humerus; discal stria 1 (adjacent to sutural stria) extending from base to apical umbone; striae 2-3 and 4-5 paired, extending from near base to apical umbone, stria 5 faintly impressed and incomplete; humeral striae 1-4 faintly impressed, incomplete, indicated by shallow punctures, stria 5 moderately impressed, extending from base of metacoxa to subapex; small to moderate in size, some longitudinal (Fig. 5). Intervals with moderately dense, random punctures, punctures minute to moderate in size; interval 1 broader than others. Pygidium: Disc and apex sparsely punctate; base and sides moderately densely imbricate, nearly obsolete; punctures minute to small. Legs: Protarsomere 5 of male subequal to tarsomeres 2-4. Modified proclaw of male subequal in length to tarsomeres 2-4; internoapical tooth present. Protibia (Fig. 11) (male and female) with teeth evenly separated; basal 1/3 weakly dilated (male) or moderately dilated (female). Mesotibia (male) with sides subparallel, weakly divergent towards apex (male) or weakly divergent (female); apex oblique with 10-11 moderately long spinulae; external edge with weak carina in basal 1/3, 1 carina in apical 1/3. Metatrochanter (male) weakly produced beyond posterior border of femur. Metacoxal corner square (female). Metacoxa at middle weakly produced posteriorly. Metatibia of male (Fig. 14) with sides subparallel, weakly divergent towards apex; external edge with 1 carina in basal 1/3 (faint), 1 carina in apical 1/3 (faint); apex without corbel, with 2 inner spurs (spurs equal in width in male, weakly curved at apex), inner apex with 28 short, stout spinulae. Metatibia of female divergent at apical 1/5; external edge with 1 carina in basal 1/3, 1 carina in apical 1/3; apex without corbel, with 2 inner spurs, inner apex with 28 short, stout spinulae. Parameres: Ventral plate nearly as long as dorsal plate with sides converging to a quadrate apex (Fig. 19).

**Diagnosis.** *Pseudogeniates cordobaensis* is separated from other species in the genus by the pentagonal form of the mentum (width subequal to length) that has the inner apex projecting anteriorly and has an inner shelf (Fig. 8). In comparison, the form of mentum is longer than wide in *P. intermedius* and *P. richterianus* (Figs 9-10). In *P. intermedius*, the inner apex of the mentum does not project anteriorly, but does possess



**Figures 16–18.** Form of the head (dorsal view) in *Pseudogeniates* species **16** *P. cordobaensis* showing form of clypeal apex **17** *P. intermedius* showing form of clypeal apex **18** *P. richterianus* showing form of clypeal apex, labrum, and mandible

an inner shelf (Fig. 9); in *P. richterianus*, the inner apex projects anteriorly, but does not possess an inner shelf (Fig. 10). The ventral plate of the male parameres in *P. cordobaensis* is nearly as long as dorsal plate with sides converging to a quadrate apex (Fig. 19). The ventral plate of *P. richterianus* is about half the length of the dorsal plate (Fig. 21), whereas in *P. intermedius* the ventral plate is nearly as long as the dorsal plate, but the sides converge with a weak constriction preapically and a rounded apex (Fig. 20).

**Distribution (Fig. 22).** *Pseudogeniates cordobaensis* is distributed in the Monte de Sierras y Bolsones in the Monte eco-region in Argentina. The distribution of this species coincides with the Montane Forest region (Navarro et al. 2009) and the Yungas Forest area of endemism in Argentina (Szumik et al. 2012).

**Locality data.** 27 specimens from IAZA, WSUC, and ZMHB. **ARGENTINA** (27): CATAMARCA (26): Salar de Pipanaco, Pío Brizuela (37 km S Andalgala, 27°49'34"S, 66°14'47"W, 751 m), Quirós (2 km S on RN 157, 28°48'43.3"S, 65°06'22.6"W), CÓRDOBA (1): Huerta Grande (Sierra de Córdoba).

**Temporal data.** December (9).

**Remarks.** The holotype specimen for this species was part of the type series for *P. intermedius*, a series that included three specimens from Santiago del Estero and one specimen (= *P. cordobaensis*) from Huerta Grande in the Sierra de Córdoba, Córdoba Province (Ohaus 1914).

**Natural history.** This species is attracted to black lights. It was recorded from an elevation of 751 m.

### *Pseudogeniates intermedius* Ohaus, 1914

[http://species-id.net/wiki/Pseudogeniates\\_intermedius](http://species-id.net/wiki/Pseudogeniates_intermedius)

Figs 2, 9, 17, 20

*P. intermedius* Ohaus 1914: 303.

**Material examined.** Type material (3 males, 1 female) at ZMHB. Lectotype male labeled: a) "ARGENTINA Santiago d E. Wagner" (typeset, white label), b) male genitalia

card-mounted, c) mouthparts card-mounted, d) "Typus!" (typeset, red label), e) "*Pseudogeniates intermedius* Ohs." (Ohaus' handwritten, red label), f) "SYNTYPUS *Pseudogeniates intermedius* Ohaus, 1914 labelled by MNHUS 2007" (typeset, red label), g) "Lectotype 2009 *Pseudogeniates intermedius* Oh. Soula" (typeset and handwritten, red label). Paralectotype female labeled: a) "ARGENTINA Santiago del Estero" (typeset, white label), b) female symbol, c) mouthparts card-mounted, d) "*Pseudogeniates intermedius* cotype Ohs." (Ohaus' handwritten, red label), e) "SYNTYPUS *Pseudogeniates intermedius* Ohaus, 1914 labelled by MNHUS 2007" (typeset, red label), f) "Paralectotype 2009 *Pseudogeniates intermedius* Oh. Soula det." (typeset and handwritten, red label), g) "Alloréférent *Pseudogeniates intermedius* M. SOULA det 19" (handwritten and typeset, white label with scribed red boarder), h) "Paralectotype 2009 *Pseudogeniates intermedius* Oh. Soula det." (typeset and handwritten, red label). A second male paralectotype labeled: a) "MUSEUM PARIS PROV. DE SANTIAGO del Estero Barrancas Banados de Rio Dulce, 80 kil. O. d'Icano E.R. WAGNER 1909", b) "*Pseudogeniates intermedius* cotype Ohs." (Ohaus' handwritten, red label), c) "SYNTYPUS *Pseudogeniates intermedius* Ohaus, 1914 labelled by MNHUS 2007" (typeset, red label), d) "Paralectotype 2009 *Pseudogeniates intermedius* Oh. Soula det." (typeset and handwritten, red label). An additional paralectotype from Córdoba is the holotype specimen for *P. cordobaensis* Soula (see treatment for *P. cordobaensis*). Ohaus (1914) stated that he described the species based on four specimens: two males and one female from Santiago del Estero (Wagner collection) and one male from Sierra de Córdoba.

**Description** (based on 2 males and 1 female). Length 14.0–15.7 mm. Widest width 7.5–9.0 mm. Color: Dorsum, venter, and appendages rufotestaceous to castaneous (Fig. 2). Head (Fig. 17): Frons densely, confluent punctate or rugopunctate; punctures small and moderately large, mixed. Clypeus with dorsal surface densely punctate, confluent punctate or rugopunctate, punctures small and large, mixed; clypeal shape broadly semicircular, apex and sides broadly reflexed, with or without constriction basolaterally; disc (frontal view) with surface densely rugopunctate, punctures small and large, mixed, some setose (setae short to moderately long, rufous, sparse). Labrum with setae moderately long and short, rufous. Maxilla with galea fused, with 1 or 2 elongate bristle-like, medial, setae. Mentum (Fig. 9) longer than wide, form subtrapezoidal (base broader than apex), inner apex not projecting anteriorly, with inner shelf. Antenna 10-segmented with 3 segmented club; club subequal to stem. Pronotum: Medial line obsolete (male) or weakly indicated (female). Surface (disc) moderately densely imbricate with sparse, short, testaceous setae; surface (mediolaterally) moderately densely rugopunctate, punctures minute and small. Margin with setae short, testaceous. Elytra: Elytral apex rounded or quadrate (not spiniform). Discal striae punctate; 5 on disc mesad of humerus, 5 laterad of humerus; discal stria 1 (adjacent to sutural stria) extending from base to apical umbone; striae 2-3 and 4-5 paired, extending from near base to apical umbone; humeral stria 1 incomplete (extending from mid-elytron to near apical umbone), stria 2 extending from humerus to near apical umbone, striae 3-4 extending from base of metacoxa to near apical umbone (indicated by punctures, not sulcate), stria 5 poorly indicated, extending from



19. *P. cordobaensis*      20. *P. intermedius*      21. *P. richterianus*

**Figures 19–21.** Form of male parameres (dorsal and ventral views) in *Pseudogeniates* species **19** *P. cordobaensis* (ventral plate nearly as long as dorsal plate, apex quadrate) **20** *P. intermedius* (ventral plate nearly as long as dorsal plate, apex rounded) **21** *P. richterianus* (ventral plate about half length of dorsal plate, apex acute)

base of metacoxa to subapex (indicated by punctures near base, sulcate near apex); punctures small, some longitudinal. Intervals with moderately dense, random punctures, some transversely wrinkled (on disc), punctures small; interval 1 broader than others. Pygidium: Disc and apex moderately densely punctate, some transverse; base and sides closely, weakly rugulose; punctures minute to small. Legs: Protarsomere 5 of male subequal to tarsomeres 2–4. Modified foreclaw of male subequal in length to tarsomeres 2–4; internoapical tooth present. Protibia (male and female) with external teeth evenly separated; basal 1/3 weakly dilated (male) or moderately dilated (female) (e.g., Figs 11–13). Mesotibia (male) with sides subparallel, weakly divergent towards apex; apex oblique with 8–11 moderately long spinulae; external edge with weak carina in basal 1/3, 1 carina in apical 1/3. Metatrochanter (male and female) weakly produced beyond posterior border of femur. Metacoxal corner square (female). Metacoxa at middle weakly produced posteriorly. Metatibia (male) with sides subparallel, apex weakly divergent; external edge with 1 carina in basal 1/3, 1 carina in apical 1/3; apex without corbel, with 2 inner spurs (spurs equal in width in male, with a weak curve at apex), inner apex with 21–25 short, stout spinulae. Metatibia (female) greatly divergent at apical 1/5; external edge with 1 carina in basal 1/3, 1 carina in apical 1/3; apex without corbel, with 2 inner spurs, inner apex with 28 short, stout spinulae. Parameres: Ventral plate nearly as long as dorsal plate but the sides converge with a weak constriction preapically and a rounded apex (Fig. 20).

**Diagnosis.** *Pseudogeniates intermedius* is known from only three specimens. It is separated from other species in the genus by the form of the mentum (Fig. 9) and the form of the male parameres (Fig. 20). It is distinguished from *P. cordobaensis* by the form of the mentum (longer than wide and subtrapezoidal in *P. intermedius* [Fig. 9]; length

subequal to width and pentagonal in *P. cordobaensis* [Fig. 8]) and apex of the ventral plate of the male parameres (with a weak constriction preapically and a rounded apex in *P. intermedius* [Fig. 20]; lacking preapical constriction and with quadrate apex in *P. cordobaensis* [Fig. 19]). It is separated from *P. richterianus* by the apex of the mentum (with an inner shelf in *P. intermedius*; lacking inner shelf in *P. richterianus* [Fig. 9 versus Fig. 10]) and length of the ventral plate of the male parameres (nearly as long as dorsal plate in *P. intermedius* [Fig. 20]; half length of dorsal plate in *P. richterianus* [Fig. 21]).

**Distribution** (Fig. 22). *Pseudogeniates intermedius* is distributed in the Chaco-seco eco-region in Argentina.

**Locality data.** 3 specimens from ZMHB. **ARGENTINA** (3): SANTIAGO DEL ESTERO (3): Barrancas (Bañados de Río Dulce, 80 km W. d'Icaño), No data.

**Temporal data.** December (1).

**Natural history.** This species is known from two male specimens and one female specimen, and the natural history is not known.

**Remarks.** Ohaus (1914) distinguished *P. intermedius* from *P. richterianus* based on the 10-segmented antenna (versus 9-segmented in *P. richterianus*), the “front corners” of the clypeus (rounded in *P. richterianus* versus absent in *P. intermedius*), and elytral coloration (brownish-red color in *P. intermedius* versus reddish-yellow in *P. richterianus*). Based on our examination of specimens, these characters are highly variable and are not reliable for identification. Coloration varies within species (from testaceous to castaneous), form of the clypeus varies, and antennae vary from 9 to 10 segments. However, characters provided in our “Diagnosis” are sufficient to separate *P. intermedius* and *P. richterianus*.

### *Pseudogeniates richterianus* Ohaus, 1910

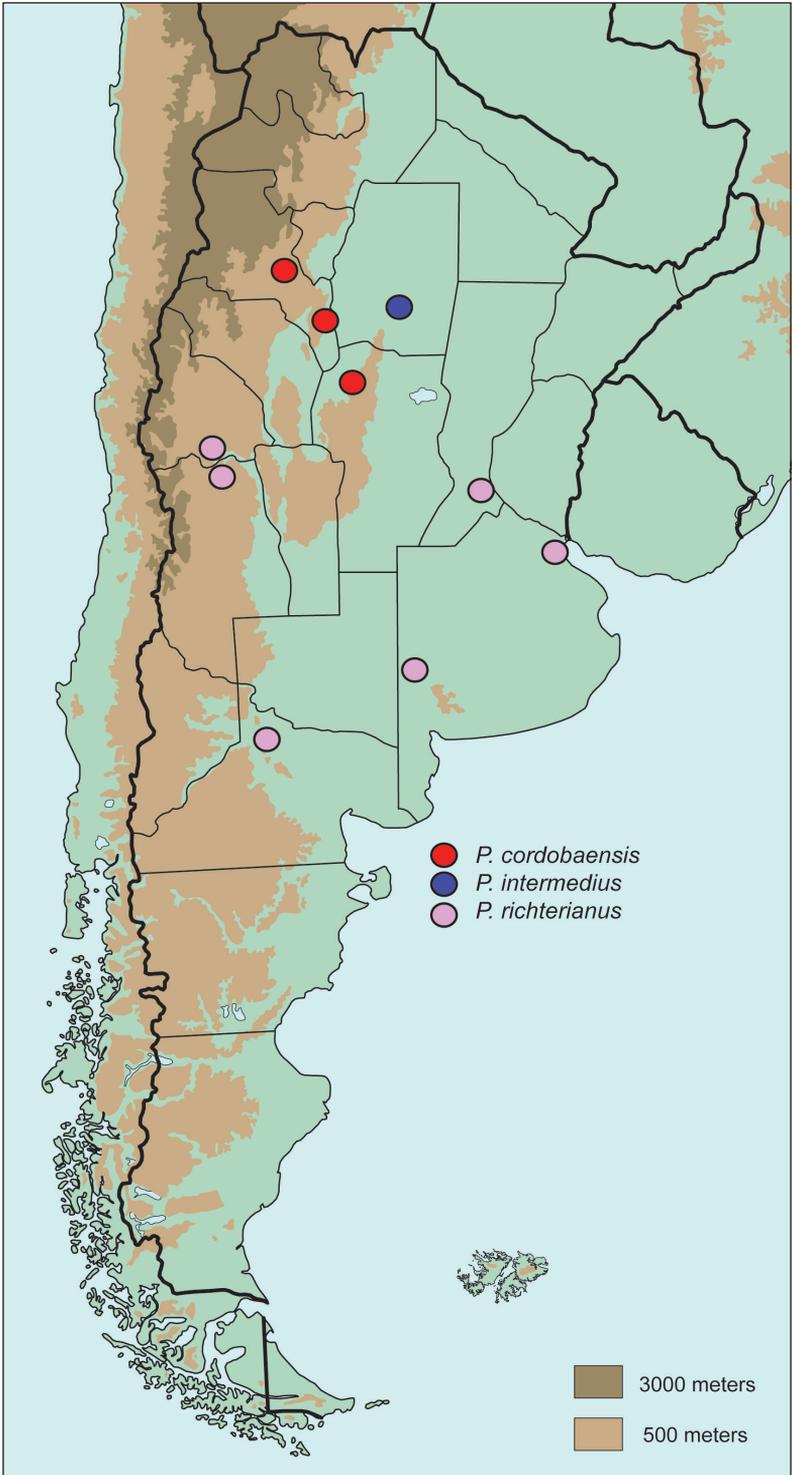
[http://species-id.net/wiki/Pseudogeniates\\_richterianus](http://species-id.net/wiki/Pseudogeniates_richterianus)

Figs 3–4, 7, 10, 12–13, 15, 18, 21–22

*P. richterianus* Ohaus 1910: 180.

*P. richteri* Ohaus (*lapsus* in Ohaus 1934, table 2, figure 6).

**Material examined.** Two female co-types examined at ZMHB. Female lectotype labeled: a) “ARGENTINA Buenos Aires XII.08 H.R.” (typeset and handwritten on upperside and underside of white label), b) “*Pseudogeniates Richteri* cotype Ohs.” (Ohaus’ handwritten, red label), c) “SYNTYPUS *Pseudogeniates richterianus* Ohaus, 1910 labelled by MNHUB 2007” (typeset, red label), d) “Lectotype 2009 *Pseudogeniates Richterianus* Oh. Soula” (typeset and handwritten, red label). Paralectotype female labeled: a) “Rep. Argentina Prov. Santa Fe, R. Richter”, b) female symbol, c) mouthparts card-mounted, d) “Typus!” (typeset, red label), e) “*Pseudogeniates Richterianus* Oh.” (Ohaus’ handwritten, red label), f) “SYNTYPUS *Pseudogeniates richterianus* Ohaus, 1910 labelled by MNHUB 2007” (typeset, red label), d) “Lectotype 2009 *Pseudogeniates Richterianus* Oh. Soula det.” (typeset and handwritten, red label). The



**Figure 22.** Distribution of *Pseudogeniates* species in Argentina

paralectotype has the head, thorax, and abdomen glued together. It is, in fact, a chimaera with the head of *Parhomonyx fuscoaneus* and body of *Pseudogeniates richterianus*. Ohaus (1910) stated that he described the species based on three female specimens from Santa Fé, Argentina (Hans Richter collection) and Buenos Aires. The location of one specimen is not known.

**Description** (based on 4 males and 22 females). Length 12.0–18.4 mm. Widest width 7.8–10.0 mm. Color: Dorsum, venter, and appendages rufotestaceous to castaneous (Fig. 3). Head (Fig. 18): Frons moderately densely punctate or rugopunctate; punctures small and moderately large, mixed. Clypeus with dorsal surface weakly rugopunctate, punctures small and large, mixed; shape broadly rounded apically and laterally or subquadrate, with or without constriction basolaterally, apex and sides broadly reflexed; disc (frontal view) moderately densely punctate or rugopunctate, punctures small and large, mixed, some setose (setae short, testaceous, sparse). Labrum with setae moderately long and short, testaceous. Maxilla with galea not fused, with 1-2 moderately long, bristle-like medial setae. Mentum (Fig. 10) longer than wide, rectangular, inner apex projecting anteriorly, without inner shelf. Antenna 9 or 10-segmented with 3-segmented club; club subequal to or slightly longer than stem. Pronotum: Medial line weakly impressed or obsolete. Surface (disc) moderately densely punctate (mid-disc), rugopunctate, or imbricate; punctures small to moderate. Margin with setae moderately long, testaceous. Elytra: Elytral apex rounded, quadrate, or with obtuse angle. Discal stiae, sulcate-punctate; 5 on disc mesad of humerus, 5 laterad of humerus; discal stria 1 (adjacent to sutural stria) extending from base to apex, stiae 2-6 extending from near base to apical umbone; humeral stria 1 incomplete (extending from mid-elytron to near apical umbone), stria 2 extending from humerus to near apical umbone, striae 3-4 extending from base of metacoxa to near apical umbone (indicated by punctures, not sulcate), stria 5 extending from base of metacoxa to subapex (indicated by punctures near base, sulcate near apex); punctures small to moderate in size, some longitudinal. Intervals with moderately dense, random punctures, some transversely wrinkled (on disc), punctures small to moderate in size; interval 1 subequal in width to other intervals. Pygidium: Disc and apex moderately densely punctate or transversely rugopunctate; base and sides closely, rugopunctate or weakly rugose; punctures small. Legs: Pro-tarsomere 5 of male slightly longer than tarsomeres 2-4. Modified foreclaw of male slightly longer than tarsomeres 2-4; internoapical tooth present. Protibia with external teeth often worn; 2 apical teeth removed from basal tooth; basal 1/3 weakly dilated (male; Fig. 12) or moderately dilated (female; Fig. 13). Mesotibia with sides subparallel, apex weakly divergent and weakly oblique; external edge with weak carina in basal 1/3, 1 carina in apical 1/3; apex with 8-14 short spinulae. Metatrochanter weakly produced beyond posterior border of femur. Metacoxal corner (female) rounded, with or without inner tooth. Metacoxa at middle not produced posteriorly. Metatibia (male) with sides subparallel, apex moderately divergent in apical 1/3; external edge with 1 carina in basal 1/4, 1 carina in apical 1/4; apex without corbel, with 2 inner spurs (spurs equal in width in male), inner apex with 28-35 short, stout spinulae. Metatibia (female; Fig. 15) greatly divergent at apical 1/4; external edge with 1 carina in basal 1/3, 1 carina in apical 1/3;

apex without corbel, with 2 inner spurs, inner apex with 28–35 short, stout spinulae. Parameres: Ventral plate half length of dorsal plate (Fig. 21).

**Diagnosis.** *Pseudogeniates richterianus* is a highly variable species. Variation is observed in the antenna (9- or 10-segmented), labrum (weakly or moderately emarginated), length of antennal club (subequal to slightly longer than the stem), elytral apex (spiniform, quadrate, rounded, or obtusely angled), pronotal medial line (weak or obsolete), and form of the clypeus. However, several characters reliably separate this species from others in the genus. *Pseudogeniates richterianus* is separated from *P. intermedius* and *P. cordobaensis* by the form of the mentum (rectangular and without inner shelf in *P. richterianus* [Fig. 10]; subtrapezoidal and with inner shelf in *P. intermedius* [Fig. 9]; pentagonal and nearly as wide as long in *P. cordobaensis* [Fig. 8]), ventral plate of the parameres (half length of the dorsal plate in *P. richterianus* [Fig. 21]; nearly as long as dorsal plate in *P. intermedius* and *P. cordobaensis* [Figs 20 and 19, respectively]), metacoxal corner in female (rounded in *P. richterianus*; square in *P. intermedius* and in *P. cordobaensis*), and posterior margin of the metacoxa (not produced posteriorly in *P. richterianus*; produced posteriorly in *P. intermedius* and *P. cordobaensis*).

**Distribution** (Fig. 22). *Pseudogeniates richterianus* is the most wide-spread species in the genus. It is distributed in the Pampa, Espinal, and Monte de Llanuras y Mesetas (Monte) eco-regions in Argentina.

**Locality data.** 26 specimens deposited in CMNC, FMNH, IAZA, MACN, MLJC, UCCC, and ZMHB. **ARGENTINA** (26): BUENOS AIRES (16): Caballito, Dept. Puán, No data. MENDOZA (7): Lavalle (Brazo S. Río San Juan Area San Miguel S 32°20'7", W 68°26'57.9", 500 m), San Rafael, No data. NEUQUEN (1): No data. RIO NEGRO (1): Villa Regina. SAN JUAN (1): Los Berros (Dept. Sarmiento). SANTA FE (1): Rosario.

**Temporal data.** November (5), January (3), February (1).

**Natural history.** Based on specimens in collections, there is a female sex bias in this species (24 females: 4 males). Many specimens (male and female) have worn protibiae (Fig. 13), indicating that adults dig in abrasive soil. Label data indicate that this species was collected at mercury vapor light and at 500 m elevation.

**Remarks.** Ohaus (1914) distinguished *P. richterianus* from *P. intermedius* based characters that vary within the species (see “Remarks” for *P. intermedius*), including number of antennal segments, form of the clypeus, and coloration. Although these characters are unreliable for diagnosis of the species, we provide characters that are useful (see “Diagnosis”). Ohaus (1910) named the species in honor of Herr Hans Richter from Buenos Aires.

## Discussion

Species in the genus *Pseudogeniates* exhibit a great deal of character variation, thus causing historical difficulty with circumscription of the species. Variation in the number of antennomeres, length of the antennal club, and form of the clypeal apex,

labrum, elytral apex exhibit intraspecific variability. Variation of this degree is not unprecedented within the Scarabaeoidea. In particular, species associated with high elevations (e.g., *Parabyrsopolis* Ohaus) and species associated with arid habitats (e.g., *Anomiopsoides heteroclyta* (Blanchard), *Eucranium arachnoides* Brullé [both Scarabaeinae], and *Allidiostoma hirtum* Ohaus [Allidiostomatinae]) are known to possess broad intraspecific variation (Jameson 1990, Ocampo 2007). In some populations, individuals of *Parabyrsopolis chihuahuanae* (Bates) exhibit a wide range in clypeal shapes (quadrate or parabolic, reflexed or not) (Jameson 1990). Individuals of *A. heteroclyta* exhibit high variability in clypeal shapes and clypeal processes, as well as variation in pronotal sculpture (puncture shape and density) (Ocampo 2007). Species in the Mexican genus *Parachrysina* Bates are unusual in that some species have 8-segmented antennae and others have 9-segmented antennae (Jameson 1991). Molecular analysis of species of *Pseudogeniates*, as well as other highly variable species, may reveal underlying mechanisms for high intraspecific variation.

High intraspecific variation may have been the product of historical climatic and concomitant habitat fluctuations. During the Pleistocene, climatic fluctuations in northern Argentina may have resulted in broad regions being inhabited by Yungas forests (reaching to Córdoba province in the south) (Navarro et al. 2009). Subsequently, these forests have been replaced with remnant patches of Yungas, Chaco, and Espinal forests (Navarro et al. 2009). Climatic fluctuations and changing habitats, in combination with the latitudinal and altitudinal gradient of the montane region (Barquez and Díaz 2001), may have assisted in isolating populations (such as ancestral populations of *Pseudogeniates*), influencing species diversifications, and leading to high levels of endemism (Navarro et al. 2009, Szumik et al. 2012).

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## Appendix

*Pseudogeniates* locality table. (doi: 10.3897/zookeys.241.3802.app) File format: Microsoft Excel document (xls).

**Explanation note:** Distribution maps were generated by entering latitude and longitude data into Microsoft Excel 2008 and uploaded to EarthPoint (<http://www.earthpoint.us/ExcelToKml.aspx>) and GoogleEarth (<http://www.google.com/earth/index.html>). This supplementary file allows addition of data and interactive mapping or niche modeling.

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# A revision of the *Cautires obsoletus* species group from Java (Coleoptera, Lycidae)

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**Citation:** Bocak L (2012) A revision of the *Cautires obsoletus* species group from Java (Coleoptera, Lycidae). ZooKeys 241: 55–66. doi: 10.3897/zookeys.241.3089

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## Abstract

The Javanese fauna of the species group *Cautires obsoletus* is revised. Altogether, eight Javanese species were classified in the group; five of them are proposed to be junior subjective synonyms: *Cautires fruhstorferi* Dudkova & Bocak, 2010, a replacement name of *Bulenides lineatus* Pic, 1921, *Cautires javanicus* Bourgeois, 1883, *Cautires inhumeralis* (Pic, 1921), *Cautires nigromaculatus* (Pic, 1925), and *C. pudicus* (Kleine, 1931) (all synonymized to *Cautires obsoletus* Waterhouse, 1879). Three Javanese species are redescribed: *C. apicalis* (Pic, 1925), *C. obsoletus* (Waterhouse, 1878), and *C. singularithorax* (Pic, 1925). *C. apicalis* (Pic, 1925) is removed from the synonymy of *C. corporaali* (Pic, 1921) and reinstated as a valid name. Three new species are proposed: *Cautires walteri* **sp. n.**, *C. taoi* **sp. n.**, and *C. sukosarensis* **sp. n.** All species are keyed and principal diagnostic characters are illustrated. The distribution and relationships to *Cautires* fauna of other Great Sundas islands are briefly discussed.

## Keywords

Systematics, Metriorrhynchini, Indonesia, new species, new synonym

## Introduction

The species of the *Cautires obsoletus* group were originally placed in *Bulenides* Waterhouse, 1879 (Kleine 1926, 1933, Bocak 2002, Bocak and Bocakova 2008). Although *Bulenides* was easily recognizable by the presence of a single areola in the pronotum and

nine longitudinal costae in the elytra, a recent study showed that the genus is a polyphyletic assemblage of two independent lineages nested in *Cautires* Waterhouse, 1879 (Dudkova and Bocak 2010). One of these lineages is the *C. obsoletus* group characterized by an almost triangular shape of the pronotum and a long, slender phallus. The classification of Javanese species has, for a long time, been chaotic due to the inadequate work of M. Pic and lack of communication among taxonomists working on the group. The collections of the Natural History Museums in Paris and London, and the Museum and Institute of Zoology in Warsaw house all types of this group and they were studied to present a revision which is intended to provide comprehensive information on Javanese species.

## Material and methods

Species delineation and diagnoses are based on the male adult semaphoronts if a male is available. The unique types represented by females represent a problem, as assignment of conspecific males and females is difficult. Diagnoses of female type specimens are based on the morphology of the ovipositor, as the shape of the antennae and relative size of the eyes are uniform.

Male and female genitalia were studied. Dry mounted specimens were transferred to 50% ethanol and apical parts of abdomens were shortly kept in hot 10% KOH to clean them of muscles and fat bodies. Photographs of diagnostic characters and measurements were taken using an Olympus SZX-16 microscope. The following measurements were taken: BL – body length; HW – width at the humeri; PW – pronotal width, measured at the base; PL – pronotal length at midline; Edist – minimum frontal distance between eyes; Ediam – maximum eye diameter in the lateral view.

*Depositories*: BMNH – Natural History Museum, London; KMCT – Kiyoshi Matsuda Collection, Takarazuka city; LMBC – Dept. of Zoology, Palacky University, Olomouc; MHNP – Museum d'histoire naturelle, Paris; MIZW – Museum and Institute of Zoology PAN, Warszawa.

## Taxonomy

### *Cautires* Waterhouse, 1879

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

**Type species.** *Lycus* (gen. 22) *excellens* Waterhouse, 1878; Bourgeois 1891: 345, by subsequent designation.

**Differential diagnosis of the *C. obsoletus* species group.** *Cautires* belongs to the tribe Metriorrhynchini, which is easily recognizable by well-developed pronotal and elytral costae, a circular phallobase and unpaired gland in the vagina (Bocak 2002). All species classified in the *C. obsoletus* group share principal diagnostic characters with other *Cautires*: a medium sized, flattened, feebly sclerotized body, flabellate antennae

in males which are serrate in females, four primary and five secondary longitudinal costae in the elytra, and a lanceolate phallus with membranous internal sac bearing two sickle-shaped thorns at its base (Figs 1–23). The species group is defined by the presence of a single median areola in the pronotum and it differs from the *C. pauper* species group in the obtuse frontal angles resulting in the triangular shape of the pronotum, and a slender phallus (Figs 7–16). The morphology of *Cautires* was described and illustrated in detail by Dudkova and Bocak (2010).

**Distribution and biology.** The low dispersal propensity of metriorrhynchine net-winged beetles results in small ranges and effectiveness of barriers, which are crossed easily by other beetles (Kubecek et al. 2011). Adults of net-winged beetles usually remain under the canopy of the tropical rain forest and do not fly in open habitat (Bocak 2002). Extensive studies of South East Asian *Cautires* and other Metriorrhynchini revealed that each species is typically restricted to a single island, and that these beetles very seldom have extensive ranges (e.g. Dudkova and Bocak 2010, Weiszenstein and Bocak 2011). Although Kleine (1933) recorded several species of *Cautires* from two or more Great Sunda islands, the study of principal collections and extensive collecting activity in Sumatra and Borneo revealed that all Javanese species treated here are endemic to Java and do not occur in the other Great Sunda islands. So, for example, due to high similarity, *C. apicalis* described from Java has been for long time kept in synonymy of *C. corporaali* from Northern Sumatra and is reinstated as a valid species.

The second potential reason for the high level of endemism in net-winged beetles is the role of aposematic coloration. The majority of Metriorrhynchini in the Oriental Region are aposematically colored and the Javanese *Cautires* species are no exception (Figs 1–6). The similar orange and black pattern is known also from higher mountain regions of Sumatra, e.g. Gunung Kerinci, Gunung Merapi and volcanoes in the vicinity of Brastagi. These aposematic patterns are limited to higher mountain habitats and the lower areas are inhabited by differently colored species. The role of color patterns as a factor limiting dispersal was discussed by Bocak and Yagi (2010).

### Key to the *C. obsoletus* species group of Java

- 1 Pronotum dark brown to black (Figs 6, 8)... *Cautires obsoletus* (Waterhouse)
- Pronotum brightly colored, similarly to basal part of elytra (Figs 1–5, 7, 9–11)..... 2
- 2 Body large, over 10 mm, orange part of elytra reaching over half of elytral length ..... 3
- Body small, less than 9 mm, orange part of elytra reaching less than half of elytral length..... 4
- 3 About apical quarter of elytra dark colored (Fig. 5), female genitalia with valvifers 2.1 times the length of coxites (Fig. 18)..... *C. apicalis* (Pic)
- Almost half of elytra dark colored (Fig. 2), regularly, female genitalia with valvifers 1.75 times the length of coxites (Fig. 17) .... *C. singularithorax* (Pic)

- 4 Male eyes large, their frontal minimum distance 0.87 times maximum diameter in lateral view..... ***C. taoi* Bocak, sp. n.**  
 – Male eyes small, their frontal minimum distance more than 1.20 times maximum diameter in lateral view..... **5**  
 5 Phallus very slender, parallel-sided in most of its length, widened at middle, sclerotized spines of internal sac small, phallus about 8.8 times longer than spines of internal sac (Fig. 16)..... ***C. sukosarensis* Bocak, sp. n.**  
 – Phallus moderately slender, narrower towards base and apex, widest at middle of its length, sclerotized spines of internal sac small, phallus about 6.2 times longer than spines of internal sac (Fig. 14) ..... ***C. walteri* Bocak, sp. n.**

***Cautires apicalis* (Pic, 1925b), stat. n.**

[http://species-id.net/wiki/Cautires\\_apicalis](http://species-id.net/wiki/Cautires_apicalis)

Figs 5, 10, 18

*Bulenides apicalis* Pic 1925b: 9.

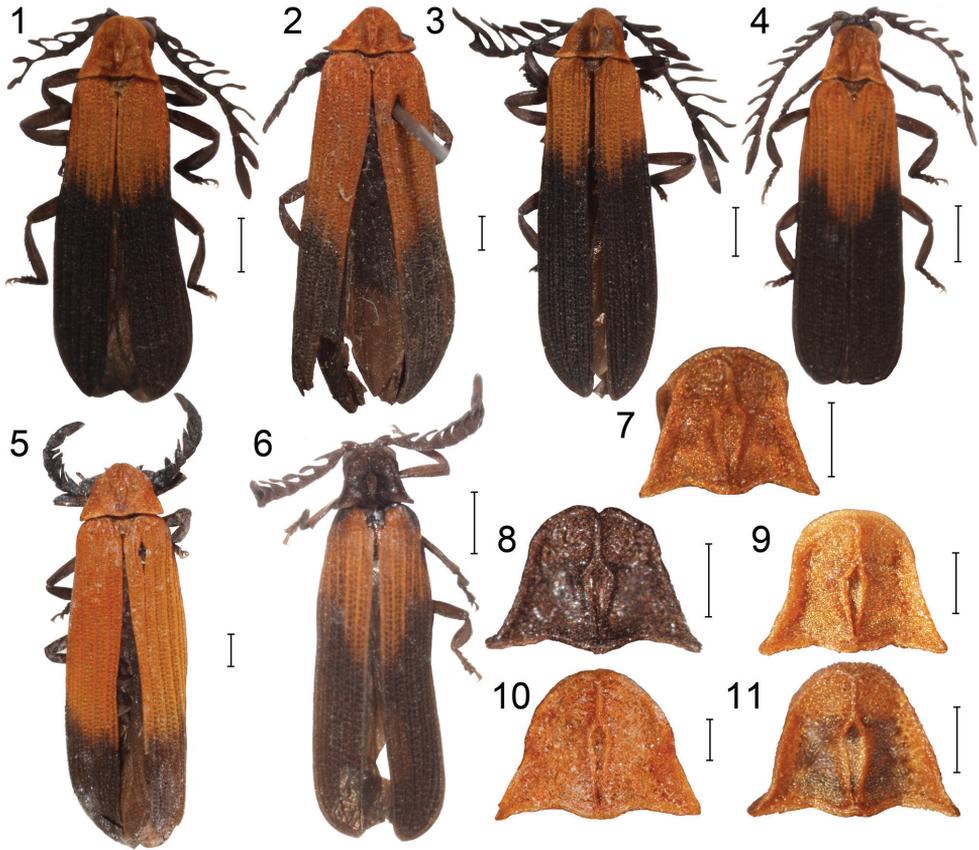
*Cautires apicalis* (Pic 1925b): Dudkova and Bocak 2010: 41.

**Type material.** Female, holotype. [Indonesia] Java occident. Pengalengan, 4000', 1893, H. Fruhstorfer (MHNP).

**Differential diagnosis.** *C. apicalis* differs from the similar Javanese species *C. singularithorax* in the much smaller extent of the dark part of the elytra and in the shape of the ovipositor, which has valvifers more than two times longer than the coxites (Figs 2, 5, 18). Only female specimen is available and we do not have any information on male characters.

**Redescription.** Female. Body medium-sized, dorso-ventrally flattened, slender. Head, body, posterior third of elytra and appendages black, pronotum and basal two thirds of elytra orange, pronotum and elytra covered with dense orange pubescence (Figs 5, 10). Head small, partly hidden in pronotum, clypeus slightly concave, labrum simply rounded, mandibles slender, strongly curved, maxillary palpi slender, apical palpomere pointed, labial palpi similar in shape. Eyes small, hemispherically prominent, their frontal interocular distance 1.50 times eye diameter. Antennae acutely serrate, covered with short, dark colored setae. Pronotum flat, slightly transverse, 1.32 times wider at base than length at midline; frontal margin concave; lateral margins slightly elevated, posterior angles acutely projected, pronotum with slender median areola, attached to middle of basal margin of pronotum, connected to anterior margin by keel occupying one third of midline, lateral keels absent (Fig. 10). Elytra flat, with separately rounded apexes and well developed four primary longitudinal costae; secondary costae very weak, cells irregular, mostly quadrate. Legs laterally flattened, covered with dark colored setae. Ovipositor with valvifers 2.1 times length of coxites (Fig. 18). Male unknown.

**Measurements.** BL 11.9 mm, PL 1.84 mm, PW 2.42 mm, HW 2.72 mm, Edist 0.69 mm, Ediam 0.46 mm.



**Figures 1–11.** General appearance: **1** *Cautires taoi* sp. n. **2** *C. singularithorax* Pic, holotype **3** *C. sukosarensis* sp. n. **4** *C. walteri* sp. n. **5** *C. apicalis* Pic, holotype **6** *C. obsoletus* Waterhouse. Pronotum: **7** *C. walteri* sp. n. **8** *C. obsoletus* Waterhouse **9** *C. taoi* sp. n. **10** *C. apicalis* Pic, holotype sp. **11** *C. sukosarensis* sp. n. Scale bars Figs 1–6 = 1.0 mm, Figs 7–11 = 0.5 mm.

**Distribution.** *C. apicalis* is known only from Western Java.

**Remarks.** Kleine (1933) listed *C. apicalis* as a junior synonym of *C. corporaali* Pic, 1921 from Sumatra, but the study of the holotypes revealed that these species although similar in the color patterns differ in the shape of the pronotum, body size, and female genitalia. Therefore the name *C. apicalis* is removed from synonymy and reinstated as a valid name.

Two large bodied species were described by M. Pic from Western Java, both of them from a single female specimen. Although one male specimen collected in the same region was available for study, it is impossible to assign the name based on female to a male without further information. Therefore, holotypes of *C. apicalis* and *C. singularithorax* are redescribed and illustrated here. More extensive material is necessary for the definitive delineation of these species.

***Cautires obsoletus* (Waterhouse, 1878)**

[http://species-id.net/wiki/Cautires\\_obsoletus](http://species-id.net/wiki/Cautires_obsoletus)

Figs 6, 8, 12–13, 20

*Bulenides obsoletus* Waterhouse 1878: 109.

*Cautires obsoletus* (Waterhouse 1878): Dudkova and Bocak 2010: 43.

*Bulenides lineatus* Pic 1921: 8.

*Cautires lineatus* (Pic 1921): Dudkova and Bocak: 42 (a junior secondary homonym of *Cautires lineatus* (Hope in Gray 1831), syn. n.

*Cautires fruhstorferi* Bocak and Dudkova 2010: 42 (a replacement name for *B. lineatus*), syn. n.

*Bulenides javanicus* Bourgeois 1883: 439.

*Cautires javanicus* (Bourgeois 1883): Dudkova and Bocak 2010: 42, syn. n.

*Bulenides inhumeralis* Pic 1921: 7.

*Cautires inhumeralis* (Pic 1921): Dudkova and Bocak 2010: 42, syn. n.

*Bulenides nigromaculatus* Pic 1925a: 7.

*Cautires nigromaculatus* (Pic 1925a): Dudkova and Bocak 2010: 43, syn. n.

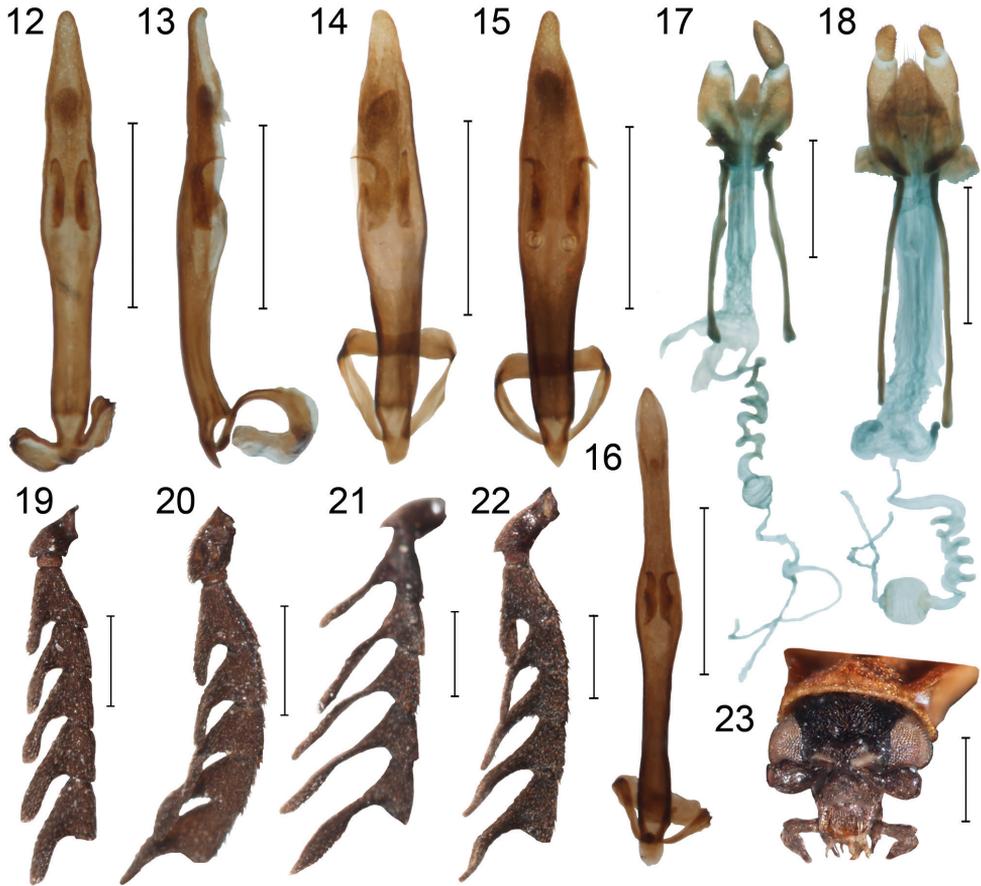
*Bulenides pudicus* Kleine 1931: 257.

*Cautires pudicus* (Kleine 1931): Dudkova and Bocak 2010: 43, syn. n.

**Type material.** Female, holotype of *Bulenides obsoletus*. [Indonesia] Java (without further data, BMNH). Female, holotype of *B. lineatus*. [Indonesia] Java occident., Sukabumi, 2000', 1893, H. Fruhstorfer (MHNP). Male, holotype of *B. javanicus*. [Indonesia, Java] Giava, Tcibodas, Ott. 1874, O. Beccari (MHNP). Male, holotype of *B. inhumeralis*. [Indonesia] Bogor, 1000', v–vi 96, I. Z. Kannegieter (MHNP). Male, holotype of *B. nigromaculatus*. [Indonesia] Java occident., Sukabumi 2000', H. Fruhstorfer (MHNP). Male, holotype of *Bulenides pudicus*. [Indonesia] Toegoe, West-Jawa-Pasteur (without further data, MIZW).

**Differential diagnosis.** *C. obsoletus* differs from the other Javanese species in the black pronotum (Fig. 8) and a very oblique border between the bright and dark parts of elytra (Fig. 6). The basal part of elytra is brown to reddish brown and differs from the brightly orange coloration of the other species in Java.

**Redescription.** Male. Body small to medium-sized, dorso-ventrally flattened, slender; head, body, posterior half of elytra and appendages dark-brown to black; basal half of elytra brown to reddish brown (Fig. 6), body covered with dense pubescence. Head small, partly hidden in pronotum, clypeus slightly concave, labrum simply rounded, mandibles slender, strongly curved, maxillary palpi slender, apical palpomere pointed; labial palpi similar in shape. Eyes small, hemispherically prominent, their frontal interocular distance 1.15 times eye diameter. Antennae shortly flabellate, 11-segmented, covered with short, dark colored setae (Fig. 20). Pronotum flat, only slightly transverse, 1.15 times wider at base than length at midline; frontal margin projected forward; lateral margins slightly elevated, concave, posterior angles acutely projected, pronotum with moderately wide median areola, attached to middle of basal margin of pronotum, connected to anterior



**Figures 12–23.** Male genitalia: **12, 13** *Cautires obsoletus* Waterhouse **14** *C. walteri* sp. n. **15** *C. taoi* sp. n. **16** *C. sukosarensis* sp. n. Female genitalia: **17** *C. singularithorax* Pic, holotype **18** *C. apicalis* Pic, holotype. Male basal antennomeres **19** *C. sukosarensis* sp. n. **20** *C. obsoletus* Waterhouse **21** *C. sukosarensis* sp. n. **22** *C. taoi* sp. n. **23** *C. walteri* sp. n., head frontally. Scale bars = 0.5 mm.

margin by keel occupying one third of midline, lateral keels absent (Fig. 8). Elytra flat, with well developed four primary longitudinal costae; secondary costae considerably weaker, cells regular, mostly slightly longitudinal. Legs laterally flattened, covered with dark colored setae. Male genitalia with phallus widest at midlength and gradually narrowed to apex (Figs 12–13). Female. Body medium-sized, antennae serrate, ovipositor with short valvifers.

**Measurements.** BL 6.45 mm, PL 1.01 mm, PW 1.36 mm, HW 1.47 mm, Edist 0.51 mm, Ediam 0.44 mm.

**Distribution.** *C. obsoletus* is known only from several localities in Western Java.

**Material examined.** 2 males, 1 female, Indonesia, W. Java, Puncak Pass nr Bogor, 23. Mar. 1992, H. Arimoto, lgt.; male, [Indonesia] West Java, Puncak Pass, 22. Mar. 1993, Y. Miyake leg. (KMTC, LMBC).

**Remark.** The holotype of *C. obsoletus* is a strongly damaged female with only a part of one elytron preserved. The basal part of the elytron is testaceous and the loss of reddish coloration may be caused by long-term exposure to light. The holotype of *C. lineatus* is also a female and it differs only in the darker hue of the bright part of the elytra, but it resembles the holotype of *C. obsoletus* in its body shape. The female genitalia of all available specimens are very similar. Holotypes of four other species are males and they do not differ in comparable characters such as body shape and color pattern. Therefore, all these species are considered junior subjective synonyms of *C. obsoletus*.

***Cautires singularithorax* (Pic, 1925a)**

[http://species-id.net/wiki/Cautires\\_singularithorax](http://species-id.net/wiki/Cautires_singularithorax)

Figs 2, 17

*Bulenides singularithorax* Pic 1925a: 7.

*Cautires singularithorax* (Pic 1925a): Dudkova and Bocak 2010: 43.

**Type material.** Female, holotype. [Indonesia] Coll. Dr. H. J. Veth, P. J. Sijthoff, Java, Preanger (MHNP).

**Differential diagnosis.** *C. singularithorax* resemble *C. apicalis* in the body size and color pattern (Figs 2, 5). These species differ in the extent of the bright part of the elytra, which is much smaller in *C. singularithorax* and in V-shaped border between bright and dark part in *C. singularithorax* and almost transverse border in *C. apicalis*. Female genitalia of both species differ in the relative length of valvifers, those of *C. singularithorax* are stout and about 1.8 times longer than coxites (Figs 17, 18). *C. singularithorax* has not been found in the available recently collected material and only unique female specimen is known and we do not have any information on male characters.

**Redescription.** Female. Body medium-sized, dorso-ventrally flattened, slender; head, body, posterior half of elytra and appendages dark-brown to black; pronotum and basal half of elytra orange, pronotum and elytra covered with dense orange pubescence. Head small, partly hidden in pronotum, clypeus slightly concave, labrum simply rounded, mandibles slender, strongly curved apically, maxillary with apical palpomere pointed; labial palpi similar in shape. Eyes small, hemispherically prominent, their frontal interocular distance 1.52 times eye diameter. Antennae acutely serrate, covered with short, dark colored setae. Pronotum flat, transverse, 1.45 times wider at base than length at midline; frontal margin concave; lateral margins slightly elevated, posterior angles very acutely projected, pronotum with median areola, areola widest anteriorly and attached to middle of basal margin, connected to anterior margin by keel occupying one third of midline. Elytra flat, with well developed four primary longitudinal costae; secondary costae considerably weaker, often interrupted, cells irregular, often inconspicuous, mostly quadrate.

Legs laterally flattened, covered with dark colored setae. Ovipositor with valvifers 1.75 times length of coxites (Fig. 25). Male unknown.

**Measurements.** BL 11.8 mm, PL 1.76 mm, PW 2.56 mm, HW 3.04 mm, Edist 0.74 mm, Ediam 0.48 mm, length of valvifer 0.78 mm, length of coxite 0.44 mm.

**Distribution.** The species is known only in the type specimen from Java.

***Cautires taoi* Bocak, sp. n.**

urn:lsid:zoobank.org:act:3B3082A2-0C0E-42C8-BFE9-66B92DF0D789

[http://species-id.net/wiki/Cautires\\_taoi](http://species-id.net/wiki/Cautires_taoi)

Figs 1, 9, 15, 22

**Type material.** Male, holotype. Java, 13–14 km from Sukosari, 25. May 1982, M. Tao (KMTC). Paratypes. 2 males, data same as for holotype, 26. May 1982; 2 males, Java, Mt. Idjen, 15.–16. May 1982; female, E Java, Ijen, Jamba, 18. Apr. 1981, H. Detani leg.; female, E Jawa, Jambu Lijen, Banyuwangi, 12. Aug. 1986, T. Ito leg. (KMTC, LMBC).

**Etymology.** The specific epithet is a patronym in honour of Mr M. Tao (Japan), the collector of the species.

**Differential diagnosis.** *C. taoi* belongs along with *C. sukosarensis* and *C. walteri* to a group of the small-bodied, aposematically colored species with brightly colored pronotum and basal half of elytra (Figs 1, 3–4). This species differs in the large eyes, which are the largest within Javanese species, and the shape of male genitalia (Fig. 15).

**Description.** Male. Body small-sized, dorso-ventrally flattened, slender, body, posterior half of elytra and appendages dark-brown to black (Fig. 1); pronotum and basal half of elytra bright orange red, pronotum and elytra covered with dense orange pubescence (Fig. 1). Head small, partly hidden in pronotum, clypeus slightly concave, labrum simply rounded, mandibles strongly curved apically, maxillary palpi with apical palpomere pointed; labial palpi similar in shape. Eyes large, hemispherically prominent, their frontal interocular distance 0.87 times eye diameter. Antennae shortly flabellate, covered with short, dark colored setae (Fig. 22). Pronotum flat, slightly transverse, 1.35 times wider at base than length at midline; frontal margin projected forward; lateral margins slightly elevated, convex, posterior angles acutely projected, pronotum with moderately robust median areola, attached to middle of basal margin of pronotum, connected to anterior margin by keel occupying one third of midline, lateral keels absent, anterior and lateral part of pronotum with fine, inconspicuous punctures (Fig. 9). Elytra flat, with well developed four primary longitudinal costae; secondary costae weaker, cells regular, tiny, mostly longitudinal. Legs laterally flattened, covered with dark colored setae. Phallus moderately robust, simple, almost parallel-sided (Fig. 15). Female slightly larger, similar in body coloration, antennae serrate. Valvifers 1.3 times length of coxites.

**Measurements.** BL 7.15 mm, PL 1.17 mm, PW 1.54 mm, HW 1.69 mm, Edist 0.50 mm, Ediam 0.57 mm.

**Distribution.** *C. taoi* is known at present only in the type series from Java.

***Cautires sukosarensis* Bocak, sp. n.**

urn:lsid:zoobank.org:act:2E02589C-484A-4078-98BD-8B52CFB151FD

[http://species-id.net/wiki/Cautires\\_sukosarensis](http://species-id.net/wiki/Cautires_sukosarensis)

Figs 3, 11, 16, 21

**Type material.** Male, holotype. Java, 14–16 km from Sukosari, 22. May 1982, M. Tao (KMTC). Paratypes, male, female. Java, 14 km from Sukosari, 23. May 1982, 25. May 1982, M. Tao (KMTC, LMBC).

**Etymology.** The specific epithet refers to the type locality.

**Differential diagnosis.** *C. sukosarensis* belongs along with *C. walteri* and *C. taoi* to a group of the small bodied aposematically colored species with brightly colored pronotum and basal half of elytra (Figs 1, 3, 4). This species resembles *C. walteri* in relatively small eyes and differs from other species in the extremely slender and long phallus and long antennal lamellae (Figs 16, 21). Male genitalia are similar to those of *C. bolavensis* Dudkova & Bocak, 2010 from Laos, but these species differ in the coloration and the size of eyes. Similarity of genitalia may indicate the close relationships of vicariant species from Laos and Java as reported by Bocak and Yagi (2010).

**Description.** Male. Body small-sized, dorso-ventrally flattened, moderately slender; body, posterior half of elytra and appendages dark-brown to black; pronotum and basal half of elytra bright orange red, pronotum and elytra covered with dense orange pubescence (Fig. 3). Head small, clypeus slightly concave, labrum simply rounded, mandibles strongly curved apically, palpi with apical palpomeres pointed. Eyes small, hemispherically prominent, their frontal interocular distance 1.28 times eye diameter. Antennae shortly flabellate, 11-segmented, covered with short, dark colored setae (Fig. 21). Pronotum flat, transverse, 1.39 times wider at base than length at midline; frontal margin projected forward; lateral margins slightly elevated, convex, posterior angles acutely projected, pronotum with moderately robust median areola, attached to middle of basal margin of pronotum, connected to anterior margin by keel occupying one third of midline, lateral keels absent (Fig. 11). Elytra flat, with separately rounded apices and well developed four primary longitudinal costae; secondary costae weak, cells regular, tiny, mostly quadrate. Legs laterally flattened, covered with dark colored setae. Phallus very slender, long, widest at midlength (Fig. 19). Female slightly larger, similar in body coloration, antennae serrate. Valvifers 1.55 times length of coxites.

**Measurements.** BL 8.05 mm, PL 1.18 mm, PW 1.64 mm, HW 1.89 mm, Edist 0.55 mm, Ediam 0.43 mm.

**Distribution.** *C. sukosarensis* is known at present only in the type series from Eastern Java.

***Cautires walteri* Bocak, sp. n.**

urn:lsid:zoobank.org:act:F2656D4E-5E00-463E-9193-9C10BBF546AB

[http://species-id.net/wiki/Cautires\\_walteri](http://species-id.net/wiki/Cautires_walteri)

Figs 4, 7, 14, 19, 23

**Type material.** Holotype. Male, Java, Rancabali, 45 km S of Bandung, 1700 m, 12. Oct. 2002, Bolm lgt. (LMBC). Paratypes. 2 males, data same as for holotype (KMTC, LMBC).

**Etymology.** The specific epithet is a patronym in honour of the late Dr Walter Wittmer (Basel).

**Differential diagnosis.** *C. walteri* resemble *C. sukosarensis* in the relatively small eyes and these species differ in the shape of body and male genitalia. *C. walteri* is characterized by the slender, small body and moderately robust phallus (Figs 1, 14).

**Description.** Male. Body small-sized, dorso-ventrally flattened, slender; body, posterior half of elytra and appendages dark-brown to black; pronotum and basal half of elytra bright orange red, pronotum and elytra covered with dense orange pubescence (Fig. 4). Head small, clypeus slightly concave, labrum simply rounded, mandibles slender, strongly curved, apical palpomeres pointed (Fig. 23). Eyes small, hemispherically prominent, their frontal interocular distance 1.25 times eye diameter. Antennae shortly flabellate, 11-segmented, covered with short, dark colored setae (Fig. 19). Pronotum flat, transverse, 1.19 times wider at base than length at midline; frontal margin projected forward; lateral margins slightly elevated, convex, posterior angles acutely projected, pronotum with moderately robust median areola, attached to middle of basal margin of pronotum, connected to anterior margin by keel occupying one third of midline, lateral keels absent. Elytra flat, with well developed four primary longitudinal costae; secondary costae considerably weaker, cells regular, tiny, mostly quadrate. Legs laterally flattened, covered with dark colored setae. Phallus moderately robust, widest at midlength (Fig. 14). Female unknown.

**Measurements.** BL 6.65 mm, PL 1.01 mm, PW 1.20 mm, HW 1.50 mm, Edist 0.50 mm, Ediam 0.40 mm.

**Distribution.** *C. walteri* is known only in the type series from Western Java.

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# A new, well-preserved genus and species of fossil Glaphyridae (Coleoptera, Scarabaeoidea) from the Mesozoic Yixian Formation of Inner Mongolia, China

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§ [urn:lsid:zoobank.org:author:D507ABBD-6BA6-43C8-A1D5-377409BD3049](https://doi.org/urn:lsid:zoobank.org:author:D507ABBD-6BA6-43C8-A1D5-377409BD3049)

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## Abstract

A new genus and species of fossil Glaphyridae, *Cretohypna cristata* **gen. et sp. n.**, is described and illustrated from the Mesozoic Yixian Formation. This new genus is characterized by the large body; large and strong mandibles; short labrum; elytra without longitudinal carina; and male meso- and possible metatibia apically modified. A list of described fossil glaphyrids of the world is provided. This significant finding broadens the known diversity of Glaphyridae in the Mesozoic China.

## Keywords

Scarabaeoidea, Glaphyridae, new genus, new species, fossil, Early Cretaceous, Yixian Formation, Inner Mongolia, China

## Introduction

The family Glaphyridae MacLeay, 1819, is a relatively small group of Scarabaeoidea, currently comprising about 200 species and subspecies in four extant, two extant and fossil, and two fossil genera (Nikolajev et al. 2011). The fossil species of the Glaphyridae are placed into four genera. Two species of the extant genus *Glaphyrus* Latreille, 1807, have been found in the Miocene (Heer 1862; Krell 2007) and Early Cretaceous (Nikolajev and Ren 2011). One species of the extant genus *Lichnanthe* Burmeister, 1844 has been found in the Late Eocene (Carlson 2002). Two Mesozoic genera *Cretoglaphyrus* Nikolajev, 2005 and *Lithohypna* Nikolajev, Wang & Zhang, 2011 have been described from the Early Cretaceous (Nikolajev 2005; Nikolajev et al. 2011; Nikolajev and Ren 2012). A list of described fossil Glaphyridae of the world is summarized in the Table 1.

Recently, we collected an almost complete and well-preserved fossil specimen (Fig. 1) from the Yixian Formation near Liutiaogou Village, Ningcheng County, Chifeng City, Inner Mongolia, China. Based on a combination of its unique morphological characters (labrum 1.5 times shorter than in all described Glaphyridae, first segment of metatarsus 2.5 times longer than in all described fossil Glaphyridae, and lamellate apex of mesotibia), we erect a new genus and species, *Cretohypna cristata* Yan, Nikolajev & Ren gen. et sp. n. This species is placed in the family Glaphyridae based on the following characters: mandibles produced beyond apex of clypeus, eyes partially divided by canthus, abdomen with six visible sternites, pygidium visible beyond elytra, protibia with three large teeth on outer margin, and mesocoxae moderately separated. This significant finding, the first glaphyrid fossil species with preserved hind wings, broadens the known diversity of Glaphyridae in the Mesozoic China.

**Table 1.** Described fossil Glaphyridae (Coleoptera: Scarabaeoidea) of the world.

number	Species	Age	Locality
1	<i>Glaphyrus ancestralis</i> Nikolajev & Ren, 2011	Early Cretaceous	China
2	<i>Glaphyrus antiquus</i> Heer, 1862	Miocene	Germany
3	<i>Cretoglaphyrus calvescens</i> Nikolajev, 2005	Early Cretaceous	Russia
4	<i>Cretoglaphyrus leptopterus</i> Nikolajev, 2005	Early Cretaceous	Russia
5	<i>Cretoglaphyrus olenguicus</i> Nikolajev, 2005	Early Cretaceous	Russia
6	<i>Cretoglaphyrus rohdendorfi</i> Nikolajev, 2005	Early Cretaceous	Russia
7	<i>Cretoglaphyrus transbaikalicus</i> Nikolajev, 2005	Early Cretaceous	Russia
8	<i>Cretoglaphyrus zherikhini</i> Nikolajev, 2005	Early Cretaceous	Russia
9	<i>Lithohypna chifengensis</i> Nikolajev, Wang & Zhang, 2011	Early Cretaceous	China
10	<i>Lithohypna lepticephala</i> Nikolajev & Ren, 2012	Early Cretaceous	China
11	<i>Lithohypna longula</i> Nikolajev & Ren, 2012	Early Cretaceous	China
12	<i>Lithohypna tuberculata</i> Nikolajev & Ren, 2012	Early Cretaceous	China
13	<i>Lithohypna yuxiana</i> Nikolajev & Ren, 2012	Early Cretaceous	China
14	<i>Lichnanthe defuncta</i> (Wickham, 1910)	Late Eocene	America

## Material and methods

The study is based on one specimen collected near Liutiaogou Village, Ningcheng County, Chifeng City, from Yixian Formation of Inner Mongolia, China. The holotype is deposited in the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China.

The specimen was examined with a Leica MZ12.5 stereomicroscope and illustrated with the aid of a drawing tube attached to the microscope. Line drawings were made using CorelDRAW X4 and Adobe Photoshop CS 5 graphic software.

Body length was measured along the midline from the mandibular apex to the apex of the pygidium and width was measured across the broadest part of abdomen. The length of pronotum was measured along the midline and the width was measured across the broadest part at its posterior angles. Abdomen length was measured along the midline and the width was measured across the broadest part.

The age of the Yixian Formation is debated. Three opinions have been proposed: Late Jurassic, Late Jurassic-Early Cretaceous and Early Cretaceous (Ren et al. 1997; Zheng et al. 2003; Cao 1999; Jin 1999; Chen et al. 2004; Wang et al. 2004; Wang et al. 2005; Swisher et al. 1999; Li et al. 2001; Zhou et al. 2003). Recent studies have confirmed that the Yixian Formation is the Early Cretaceous in age. The precise age is most likely restricted to 129.7-122.1 Ma (Barremian to early Aptian) (Chang et al. 2009; Yang et al. 2007; Zhou and Wang 2010; Zhu et al. 2007). The strata of Yixian Formation are mainly of lacustrine sediments intercalated with volcanoclastics (Ren et al. 1995). The stratigraphy and depositional environments of this area have been discussed in detail by Jiang and Sha (2007) and Jiang et al. (2011). The palaeoclimate of this area was recently interpreted as cool temperate with mean air temperatures of  $10 \pm 4$  °C. (Amiot et al. 2011). The Yixian Formation has provided abundant fossil insects (Bai et al. 2010; Bai et al. 2011; Bai et al. 2012a; Bai et al. 2012b; Chang and Ren 2008; Liu et al. 2008; Yan et al. 2012a; Yan et al. 2012b; Yao et al. 2008; Zhang et al. 2010).

## Systematic paleontology

**Order Coleoptera Linnaeus, 1758**

**Superfamily Scarabaeoidea Latreille, 1802**

**Family Glaphyridae Macleay, 1819**

**Genus *Cretohypna* Yan, Nikolajev & Ren, gen. n.**

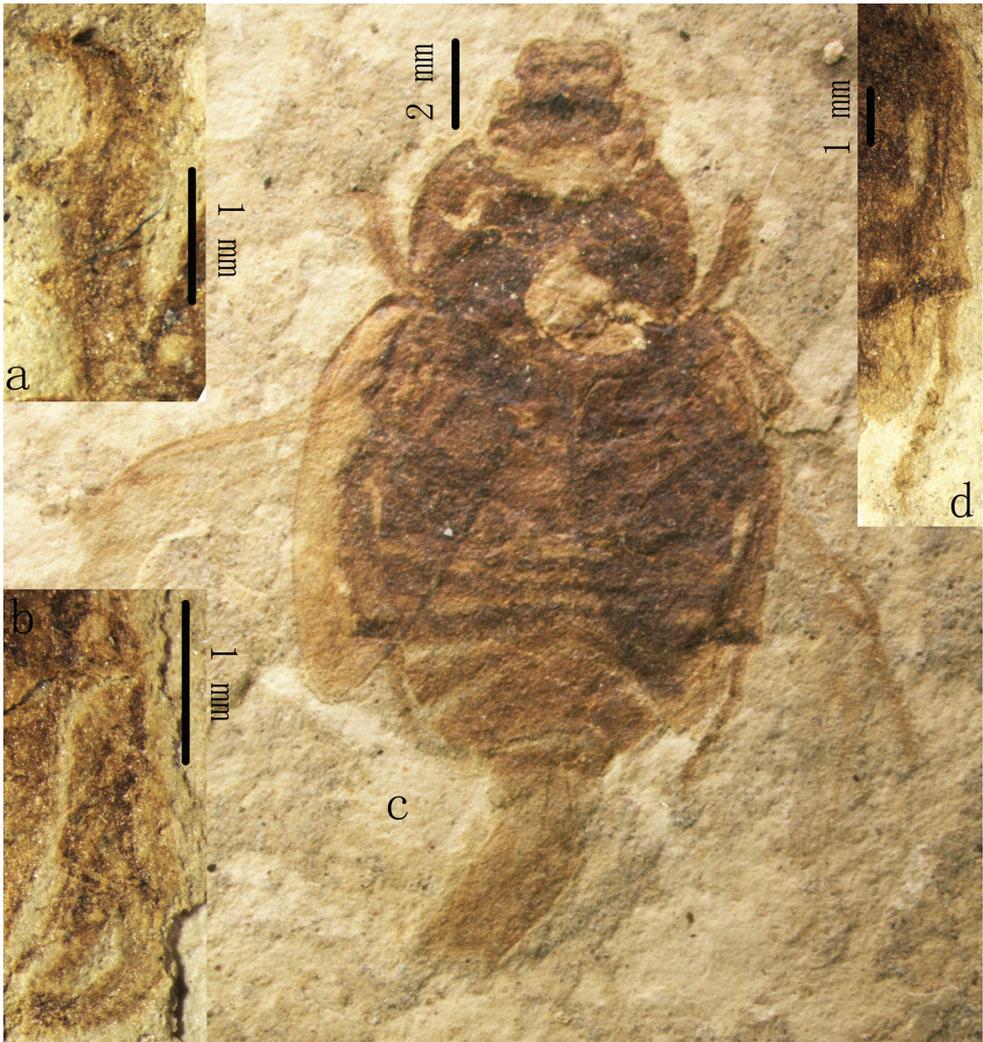
urn:lsid:zoobank.org:act:687EC908-F0F6-425A-9604-72A9298F9C3F

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

Figs 1, 2

**Type species.** *Cretohypna cristata* sp. n.

**Etymology.** The generic name refers to the Cretaceous Period of its origin, and the generic name *Anthypna* Eschscholtz, 1818. Gender: feminine.



**Figure 1.** *Cretohypna cristata* Yan, Nikolajev & Ren gen. et sp. n., holotype, registration No. CNU-COL-NN2011003, **a** protibia **b** mesotibia **c** body in dorsal view **d** metatibia and metatarsus.

**Diagnosis.** Large elongate oval and compact (head, pronotum and mesothorax are very close to each other) scarab beetle (Fig. 1c). Mandibles and labrum exposed beyond apex of clypeus and clearly visible in dorsal view of head, labrum approximately five times as wide as long. Pronotum subquadrate shaped with concave anterior margin and slightly convex lateral and posterior margins. Scutellum triangular. Mesoepimeron clearly visible from above between pronotum and elytron. Elytra convex and thin, without longitudinal carina; hind wings well-developed. Legs short and strong, mesocoxae moderately separated, protibia with three large teeth on outer margin (Fig. 1a), apex of male mesotibia lamellate (Fig. 1b, arrow); mesotibia and metatibia with 2 apical spurs; male metatarsus shorter than corresponding tibia (Fig. 1d). Abdomen

with six visible sternites, first sternites not obscured by hind coxae. Pygidium exposed beyond apices of elytra.

**Species composition.** Only the type species is known.

**Distribution.** The genus is only known from the Early Cretaceous Yixian Formation, Liutiaogou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

**Comparison.** According to the fossil record in the family Glaphyridae, there are three genera described from the Mesozoic Era: *Glaphyrus* (Nikolajev & Ren 2011); *Cretoglaphyrus* (Nikolajev 2005) and *Lithohypna* (Nikolajev et al. 2011).

The new genus is readily distinguished from all Mesozoic Glaphyridae genera by very long first segment of male metatarsus. The new genus is distinguished from the genus *Glaphyrus* by lamellate apex of mesotibia and slender metafemur; from the genus *Cretoglaphyrus* by moderately separated mesocoxae and elytra without longitudinal carina; from the genus *Lithohypna* by short labrum and triangular scutellum.

***Cretohypna cristata* Yan, Nikolajev & Ren, sp. n.**

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[http://species-id.net/wiki/Cretohypna\\_cristata](http://species-id.net/wiki/Cretohypna_cristata)

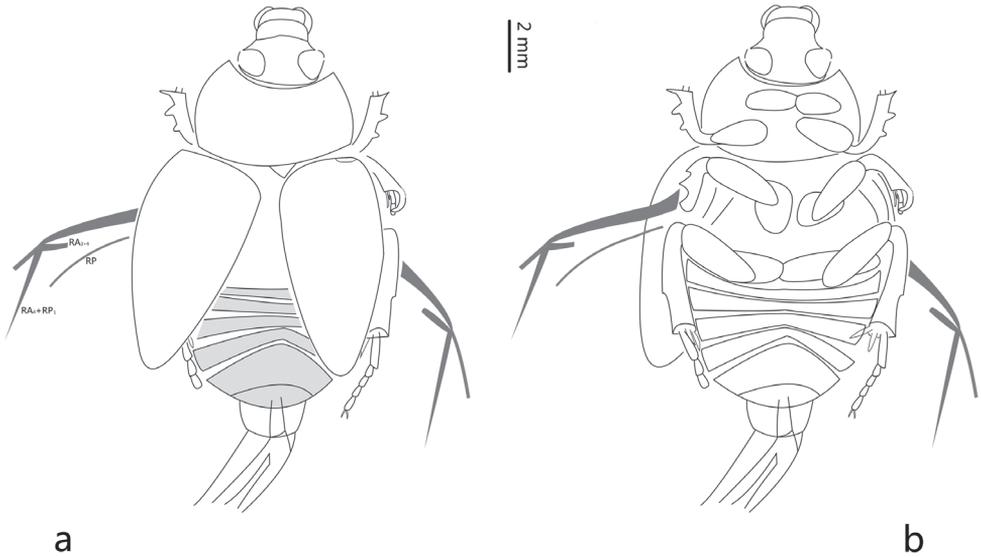
Figs 1, 2

**Etymology.** The specific name is derived from Latin word ‘*crista-*’, which means ‘comb’ or ‘crest’, refers to the presence of a transverse carina on the head.

**Material.** Holotype, a well-preserved male specimen in dorsal view, registration No. CNU-COL-NN2011003. Housed in the Key Lab of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China.

**Diagnosis.** Same as the genus.

**Description.** Body large, elongate oval and compact (Fig. 1c). Head nearly as wide as long, the widest part of head at its middle part, obviously narrower than pronotum, with transverse carina; mandibles strong, labrum and mandibles prominent, labrum exposed beyond apex of clypeus, labrum approximately five times as wide as long; mandibles exposed beyond apex of clypeus; eyes large and developed; anterior margin of clypeus moderately rounded, the presence of a transverse carina on the head. Pronotum transverse, nearly subquadrate; the widest part of pronotum at its base; anterior margin of pronotum concave; with lateral margins slightly convex, posterior margin slightly protruding. Scutellum small, triangular, about 2.2 times wider than long. Elytra long and narrow, slightly constricted to the basis, with lateral margins slightly convex, without longitudinal carina, with weak striae on lateral part, convexly constricted to the apex in the apical quarter, dehiscent. Hind wing: both hind wings preserved, well-developed, the RP, RA<sub>3+4</sub>, RA<sub>4</sub>+RP<sub>1</sub> veins preserved on the fossil. Abdomen with six visible sternites, the first sternites not obscured by hind coxae, pygidium exposed beyond apices of elytra. Genitalia preserved and curved. Procoxa about 2.3 times wider than long, mesocoxae moderately separated. Meso- and metafemur slender. Protibia with three large teeth on



**Figure 2.** *Cretohypna cristata* Yan, Nikolajev & Ren gen. et sp. n., line drawings of holotype **a** dorsal view **b** ventral view.

outer margin (Fig. 1a); mesotibia possibly with two transverse carinae on outer margin (Fig. 1b); two spurs at the end of meso- and metatibia; spurs of mesotibia differing distinctly in length; spurs of metatibia subequal in length. Only two mesotarsomeres are preserved in this specimen, relative length of each segment (base to apex) 59: 49; metatarsus with five segments, relative length of each segment (base to apex) 120: 45: 45: 45: 68 (Fig. 1d).

**Measurements.** Body length 16.1 mm, greatest body width 8.4 mm, head length 3.0 mm, head width 3.4 mm, pronotum length 3.1 mm, pronotum width 6.0 mm, elytron length 8.7 mm, elytron width 4.2 mm, length of abdominal segments: 1–0.4 mm, 2–0.3 mm, 3–0.5 mm, 4–0.4 mm, 5–1.5 mm, 6–0.9 mm.

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# A redescription of the leggiest animal, the millipede *Illacme plenipes*, with notes on its natural history and biogeography (Diplopoda, Siphonophorida, Siphonorhinidae)

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## Abstract

With up to 750 legs, the millipede *Illacme plenipes* Cook and Loomis, 1928 is the leggiest animal known on Earth. It is endemic to the northwestern foothills of the Gabilan Range in San Benito County, California, where it is the only known species of the family Siphonorhinidae in the Western Hemisphere. *Illacme plenipes* is only known from 3 localities in a 4.5 km<sup>2</sup> area; the 1926 holotype locality is uncertain. Individuals of the species are strictly associated with large arkose sandstone boulders, and are extremely rare, with only 17 specimens known to exist in natural history collections. In contrast with its small size and unassuming outward appearance, the microanatomy of the species is strikingly complex. Here we provide a detailed redescription of the species, natural history notes, DNA barcodes for *I. plenipes* and similar-looking species, and a predictive occurrence map of the species inferred using niche based distribution modeling. Based on functional morphology of related species, the extreme number of legs is hypothesized to be associated with a life spent burrowing deep underground, and clinging to the surface of sandstone boulders.

## Keywords

California Floristic Province, paleoendemic, endemic, silk, San Benito County, Silicon Valley, Salinas Valley, sandstone, burrowing, conservation, Gabilan Range

## Introduction

The millipede *Illacme plenipes* has more legs than any other known organism, with one female individual possessing 750 legs on 192 body segments. The Siphonophorida, the order in which *I. plenipes* is placed, comprises a diversity of taxa that have fascinating anatomical features, biogeographical patterns, and very intriguing biology. Siphonophoridan species are mainly Pantropical in distribution with a few outlying taxa in the Himalayas, New Zealand, South Africa and California (Shelley and Golovatch 2011). Despite their interesting biological and life history characteristics and a relictual distribution pattern, the group has been deemed a “taxonomist’s nightmare” and is among the least popular taxa in Diplopoda (Hoffman 1980; Jeekel 2001; Read and Enghoff 2009). At present, two families are recognized in the order: Siphonophoridae and Siphonorhinidae. Among these families, there are three genera of Siphonophorida in the United States: *Siphonophora*, *Siphonacme* and *Illacme*. The first two are classified as Siphonophoridae, while *Illacme* is the only known Western Hemisphere representative of Siphonorhinidae.

Like many other colobognath millipedes, the Siphonophorida often occur in cryptic subterranean habitats, shun light, are infrequently encountered, and therefore are rare in natural history collections. All known taxa are eyeless and have relatively large antennae. Species of the family Siphonophoridae have the front of the head drawn out into a long, narrow extension that is paralleled by a similar extension of the gnathochilarium, forming a tube that encloses reduced, stylet-like mandibles. Fungivory, the consumption of soft fungal tissues and spores, may be linked to this suite of adaptations. Siphonorhinids, in contrast, do not have this “beak” and the head is not strongly modified. The siphonorhinid gnathochilarium has all of its elements indistinguishably fused and is tightly appressed to the ventral surface of the head, leaving only a small opening anteriorly, which may be homologous to the labral indentation in eugnathan millipedes.

The cuticle of *I. plenipes* is adorned with a surprising diversity of peculiarly shaped spines, teeth, setae, sensilla, and other phaneres. Numerous setae clothing the dorsum of the millipede appear to secrete a viscous silk-like substance. The posterior one-third of its gut (the metenteron) is spiraled and visible through its translucent exoskeleton.

*Illacme plenipes* was described by O.F. Cook and H.F. Loomis in 1928 from seven individuals collected from a site located “a short distance after crossing the divide between Salinas and San Juan Bautista...in a small valley of a northern slope wooded with oaks, under a rather large stone” (Cook and Loomis 1928: 12). Cook and Loomis described the species (and genus) without an illustration or image and provided a short differential diagnosis distinguishing it from the other U.S. Siphonophorida species, *Siphonophora* and *Siphonacme*. Based on specimens examined from the type series, Shelley (1996b) provided the first illustrations of the genus and species, and reviewed the current knowledge of the order Siphonophorida in North America some seventy years later. To our knowledge, the species was not seen again in the wild for almost 80 years.

In 2005 and 2007, new specimens were collected from near the type locality (Marek and Bond 2006), as described below. The rediscovery of the species was detailed by

Marek and Bond (2006) and included first-ever live video of the species, natural history observations and scanning electron micrographs of the external anatomy. These recent specimens, and previously collected material conserved in various museums, form the basis of the detailed redescription provided here.

## **Fieldwork**

Following the locality description of Cook and Loomis (1928), oak valleys in San Benito and Monterey counties were searched for populations of *I. plenipes* by P.E.M. and J.E.B in 2005. We focused collecting beside roads connecting the cities of Salinas and San Juan Bautista in the northwestern half of the Gabilan Range, from Fremont Peak northwest to Pinocate Peak and U.S. Highway 101. We thoroughly covered areas on the north slopes of the Gabilan Range closer to San Juan Bautista because the type locality specifically mentions the city, and moister conditions exist on the north-facing slopes. We also (in 2006) searched nine localities in a 67.5 km radius around the site where we rediscovered populations of *I. plenipes* in 2005. We visited the following localities: Frank Raines Park, Henry Coe State Park, Fremont Peak State Park, Pinnacles National Monument, Mount Madonna County Park, Alum Rock, Joseph D. Grant County Park, El Rancho Cienega del Gabilan and a private ranch near San Juan Bautista. Google Maps (Mountainview, CA), USGS geological maps, and topomaps in ACME Mapper 2.0 (Acme Labs, Berkeley, CA) were examined for suitable localities to search for populations of *I. plenipes*. These localities were chosen prior to estimating *I. plenipes*' ecological niche (see methods below). We focused on valleys and oak woodlands because they too are moister. The underside of decaying oak logs and stones were examined for millipedes. When an individual was encountered, featherweight forceps were used to gently lift the millipede and place it into a collecting vial. Geographical coordinates were recorded, and significant biotic and abiotic features were documented. Specimens were each given unique numbers and maintained alive in collecting vials for between 2 – 10 days to photograph, record video footage and observe behavior and locomotion.

## **Ecological niche modeling**

As an approach to understanding species ecology and geography, a niche-based distribution model (DM) was constructed for *I. plenipes*. Niche-based DMs provide estimates for the probability of finding a species at a particular location and general area on a landscape given a known set of coincident ecological and climatic parameters for the species. Locality coordinates for each species were imported into ArcMap (ESRI, Redlands, CA) and converted into shape files. Following the procedure outlined in Bond and Stockman (2008) and Walker et al. (2009), DMs were constructed using environmental layers thought to “likely influence the suitability of the environment” (Phillips et al. 2006) based on previous analyses of other California-distributed taxa (see Stockman and Bond 2007, for further

justification of layer choice). Seven climatic layers were obtained from the WORLDCLIM data set (Hijmans et al. 2005): annual precipitation, precipitation seasonality, annual maximum temperature, annual minimum temperature, temperature seasonality, and mean precipitation during the driest and wettest quarters. A seventh layer, elevation, was constructed from a mosaic of Digital Elevation Models (DEMs) derived from the National Elevation Dataset (USGS). DEMs were converted to raster format in ArcMap and resampled from 30-m resolution to 1-km resolution using bilinear interpolation. All seven layers were clipped to the same extent, cell size, and projection. Niche-based DMs were created using the computer program Maxent (Phillips et al. 2006). Maxent employs a maximum likelihood method that estimates a species' distribution with maximum entropy subject to the constraint that the environmental variables for the predicted distribution must match the empirical average (Elith et al. 2006; Phillips et al. 2006). Parameters for all Maxent analyses used the default values: convergence threshold = 10<sup>-5</sup>, maximum iterations = 500, regularization multiplier = 1, and auto features selected. Additional larger values of the regularization multiplier were used to ensure that models were not overfitting the data.

### Specimen preservation

Specimens from which DNA was not extracted (typically longer females possessing more than 170 segments) were directly preserved in 80% ethanol. The posterior seven segments of two specimens (# SPC000924 and SPC001187) were dissected from live individuals with flame-sterilized forceps and stored in RNAlater (Qiagen Inc., Valencia, CA) at 10°C for 24h, and subsequently at -80°C for long-term preservation and archival storage of DNA and RNA. The enteron was removed from the segments to prevent contamination due to the DNA or RNA of the millipede's gut contents. Specimens from which DNA was extracted were subsequently preserved in 70% isopropanol.

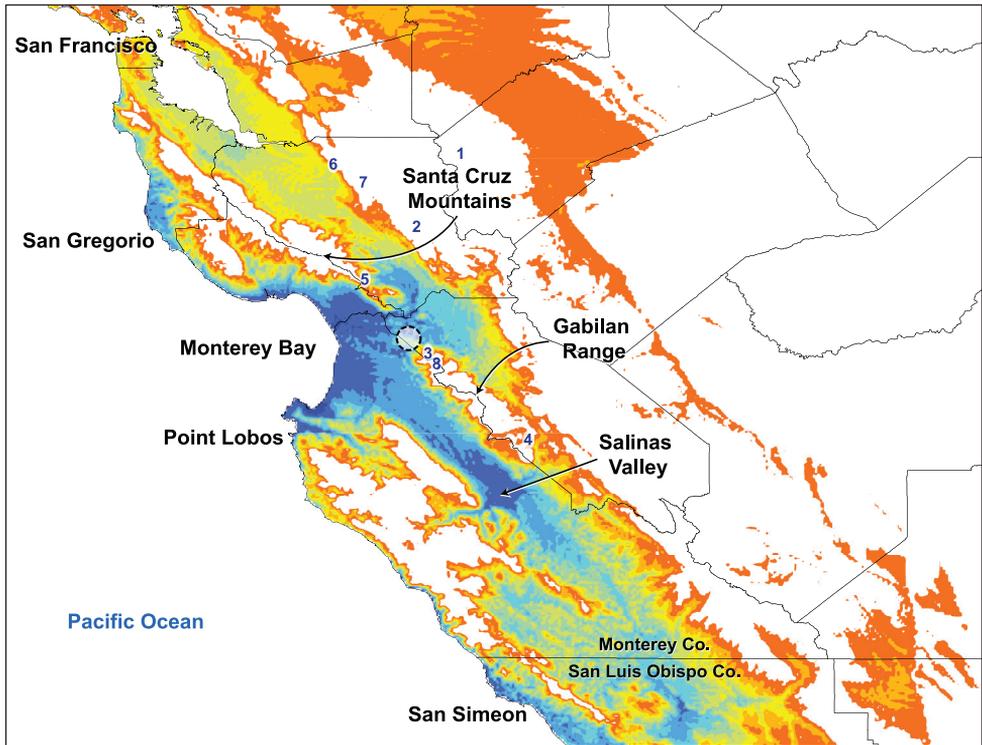
### DNA barcoding

Genomic DNA was extracted from frozen tissue preserved in RNAlater using standard DNeasy tissue extraction protocol (Qiagen Inc., California). Extracted DNA was purified from a fragment of the millipede (specimen #SPC001187) approximately four segments in length, with remaining tissue archived at -80°C in RNAlater. Genomic DNA is archived in Qiagen AE buffer at -20°C and stored in the cryo-collections at the University of Arizona and Auburn University. A region of DNA from the cytochrome c oxidase I gene (COI), was amplified using polymerase chain reaction (PCR) with the universal DNA barcoding primers of Folmer et al. (1994): LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTGG-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'). This region corresponds to the *Drosophila* COI region: 1057 – 1500. PCR amplifications were cleaned, quantified and sequenced at Auburn University (AU Genomics and Sequencing Laboratory, Auburn, AL) on an ABI 3100 capillary DNA

sequencer. For diagnostic identification purposes, COI barcoding DNA from commonly encountered colobognathan millipedes that co-occur with *I. plenipes* in the western U.S. (*Gosodesmus claremontus*, *Brachycybe producta*, *Brachycybe rosea*, and *Siphonacme lyttoni*) and may be confused with the species, was extracted, amplified and sequenced in an identical manner to provide a database of sequences against which unknown query sequences can be compared. Sense and antisense COI sequence chromatograms were processed using Phred and Phrap in the Mesquite ver. 2.75 module Chromaseq (ver. 1.0), which includes matching contiguous regions and base call quality scoring (Ewing and Green 1998; Maddison and Maddison 2011a; Maddison and Maddison 2011b). Sequences were aligned, inspected for length variation, and percent sequence difference among taxa calculated in PAUP ver. 4.0b10 (Swofford 2002). Finally, sequences were annotated and uploaded to GenBank at the NCBI website ([www.ncbi.nih.gov](http://www.ncbi.nih.gov)).

### Descriptive taxonomy

*Illacme plenipes* is represented in natural history museum collections by 17 known specimens, which includes type and non-type material. These specimens were borrowed from the following repositories: Florida State Collection of Arthropods (FSCA), Smithsonian Institution (USNM), and Virginia Museum of Natural History (VMNH). Newly collected material, compared with historical type specimens to confirm species identity, was subsequently georeferenced and databased. The precise locations of recently collected specimens are not plotted on the distribution map; instead, a circle around the coordinates is shown to preserve the confidentiality of sensitive habitat (Fig. 1). Type specimens collected by Cook in 1926 are from an imprecise location on “San Juan grade above Salinas, San Juan Bautista, Calif. Nov. 27, 1926”. However, based on the description, it probably lies on the north side of the Gabilan Range on San Juan Grade Road or Old Stage Road in a radius of 4 km around the coordinates 36.831371°N, -121.562808°W. Due to sensitivity of the habitat and extreme rarity of individuals, locality coordinates from georeferenced material is available upon request from the corresponding author. All of the material (including types and non-type material) was measured, examined in detail and is listed in the “Material examined” section. Specimens were measured at 18 locations on the exoskeleton to summarize continuous morphological variation: (1) body length from anterior margin of labrum to posterior margin of paraprocts, **BL**; (2) head width, **HW**; (3) head length, **HL**; (4) interantennal socket width, **ISW**; (5) antennomere 6 width, **AW**; (6) collum width, **CW**; (7) metazonite width at 1/4 length of body, **W1**; (8) metazonite width at mid-length of body, **W2**; (9) metazonite width at 3/4 length of body, **W3**; (10) metazonite length at 1/4 length of body, **L1**; (11) metazonite length at mid-length of body, **L2**; (12) metazonite length at 3/4 length of body, **L3**; (13) metazonite height at 1/4 length of body, **H1**; (14) metazonite height at mid-length of body, **H2**; (15) metazonite height at 3/4 length of body, **H3**; (16) first apodous metazonite width, **AS1**; (17) anterior gonopod article 5 width, **A5W**; and (18) posterior gonopod article 5 width, **P5W**. Body length was measured from digital photographs of specimens captured through the eyepieces of



**Figure 1.** Niche-based distribution model inferred in Maxent. The model indicates predicted habitat suitability for *Illacme plenipes* based on climatic variables extracted from known geographical coordinates of the species. High levels of habitat suitability are denoted in blue and low levels in red (reverse heat map). Coordinates of recently collected specimens are indicated by a circle around the locations (northwest of the Gabilan Range) to preserve the confidentiality of sensitive habitat. Localities surveyed for additional populations of *I. plenipes*: **1** Frank Raines Park **2** Henry Coe State Park **3** Fremont Peak State Park **4** Pinnacles National Monument **5** Mount Madonna County Park **6** Alum Rock **7** Joseph D. Grant County Park **8** El Rancho Cienega del Gabilan.

a Leica M125 stereomicroscope (Wetzlar, Germany) with an iPhone 4 (Apple, Cupertino, CA) using the segmented line measurement tool in ImageJ64 (Rasband 2011). All measurements are recorded in millimeters and these units are omitted throughout the paper. Anatomical measurements in the variation section are given with the following four summary statistics in the following order and format: maximum–minimum (mean/standard deviation). The mean of measurements 7–9 (average body width across three metazonites) is given as “**WM**”; mean of 10–12 is “**LM**” (average metazonite length); and mean of 13–15 is “**HM**” (average body height). The number of segments were counted and number of legs ( $l$ ) then calculated according to the following formula:  $l = ((p + a) \times 4) - (a \times 4) - (10)$ , where  $p$  is the number of podous tergites (each with four legs),  $a$  is the number of apodous tergites (each without legs), and 10 is the number to be subtracted because the first tergite (or the collum) is legless and the second through fourth tergites (the millipede “thorax”) have only two legs apiece. The gonopods, modified leg pairs 9 and 10

are included in the leg count, albeit non-ambulatory. The telson, which is not a segment and does not bear legs (posterior to the proliferation zone), is not included in the formula (Enghoff et al. 1993). Segment architecture for the specimens is denoted by the shorthand  $p + a + T$ , where  $T$  is the telson and always 1, however always included in the notation (following Enghoff et al. 1993) to indicate that it is never incorporated in the segment tally. Live material was observed through the eyepieces of a Leica 12.5 stereomicroscope to document *I. plenipes* motion, silk production and live habit. Videos were recorded with a Nikon Coolpix 995 digital camera through a C-mounted phototube according to methods described by Marek and Bond (2006). The antennal sensilla nomenclature follows that of Nguyen Duy-Jacquemin (1974) and Chung and Moon (2006). All of the measured material is composed of adult males and females. Because of their rarity, and presumed sensitivity of the species to over-collection, juvenile specimens were not targeted for collection, and are therefore not included in the measurements (one juvenile specimen, listed in the materials examined, was inadvertently collected). Juveniles were identified in the field by a lack of gonopods, small length ( $\leq 10$  mm) and weakly calcified cuticle. Adult males were easily identified by the presence of gonopods, and adult females tentatively by the combination of a lack of gonopods and lengths  $\geq 30$  mm.

## Data resources

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at <http://dx.doi.org/10.5061/dryad.3b3h8> and in the National Center for Biotechnology Information's genetic sequence database GenBank under the accession numbers: JX962721 – JX962725 (<http://www.ncbi.nlm.nih.gov>).

## Results

### Fieldwork

Individuals of *I. plenipes* were found at three localities, geographically separated by a maximum of 4.5 aerial km. The first collecting event was on 29 November 2005, the second on 8 December 2005, and the third 16 December 2007. One survey, at which time specimens were found but not collected, occurred 27 January 2006. Each locality is in the northwestern Gabilan foothills no more than 4.5 aerial km from the mission at San Juan Bautista and 3.2 aerial km southwest of the San Andreas Fault. *Illacme plenipes* were not found in any of the other sites investigated. Individuals were found in moist oak-wooded valleys beneath large arkose sandstone boulders (approximate mean mass = 40 kg), clinging to the surface usually about 10 – 15 cm below the top of the soil. *Illacme plenipes* specimens were always found on these boulders and underground, either on the stone surface, in the lacuna between the stone and the soil, or partially imbedded in the soil horizon. Specimens were never found directly on the normally

dry bottom of the stones, or on fallen logs or any other decaying organic matter or detritus. *Illacme plenipes* were consistently discovered by closely examining the stone surface (approximately 10–15 cm below soil) and the edge of the crater after removing the stone. Nine additional specimens, comprising 4 males, 4 females, and a juvenile were found throughout 2005–2007 in three localities (increasing the total number of specimens for *I. plenipes*, which includes the type series, to 17 total: 6 males, 10 females, and a juvenile). *Illacme plenipes* were uncommon at every locality and individuals were only found after one hour of two persons surveying a suitable-appearing site. Individuals were typically encountered beneath the stones singularly; no more than two individuals were ever found simultaneously.

### Ecological niche modeling

The niche-based distribution model for *I. plenipes* indicates the highest probability of occurrence, representing ecological suitability for the species, in the terrestrial areas on the periphery of Monterey Bay extending just past the gap between the Santa Cruz Mountains and Gabilan Range and throughout the Salinas Valley (Fig. 1). Areas of medium to high probability extend from Monterey Bay along a thin region on the coast northward to San Gregorio and southward to Point Lobos. There are other areas of medium to high probability, also restricted to the coast, between San Simeon in the north and the western boundary between Monterey and San Luis Obispo counties.

### DNA barcoding

Polymerase chain reaction of the COI barcoding region, when electrophoresed and visualized on a 12% agarose gel, recovered single bands of uniform lengths in all species. Sanger sequencing resulted in sense/antisense chromatograms reads of ~600 bp in length when contiguous fragments were assembled in Mesquite. Mean Phred quality scores of individual contigs are between 73–80. When aligned and ragged ends trimmed, sequence length is invariant between species. Mean nucleotide percent sequence difference between species is 25% and between amino acid sequences (total difference), 17%. The NCBI GenBank accession numbers are as follows: *I. plenipes* (JX962724), *G. claremontus* (JX962723), *B. producta* (JX962721), *B. rosea* (JX962722), and *S. lyttoni* (JX962725). The COI barcodes of the Siphonophorida species (*I. plenipes* and *S. lyttoni*) and the Platydesmida species (*G. claremontus*, *B. producta*, and *B. rosea*) are hitherto the only that exist for these two orders; there is only one other DNA barcode for the entire subterclass Colobognatha. The following species are listed in order of increasing percent nucleotide difference from *I. plenipes*, indicated in parentheses (mean percent difference of amino acids proceeds after the “/”): *G. claremontus* (28.7% / 23.8%), *B. producta* (29.7% / 24.4%), *S. lyttoni* (29.9% / 22.3%), and *B. rosea* (30.6% / 24.4%).

## Taxonomy

**Class Diplopoda de Blainville in Gervais, 1844**

**Subclass Chilognatha Latreille, 1802/1803**

**Infraclass Helminthomorpha Pocock, 1887**

**Subterclass Colobognatha Brandt, 1834**

**Order Siphonophorida Hoffman, 1980**

**Family Siphonorhinidae Cook, 1895**

**Genus *Illacme* Cook & Loomis, 1928**

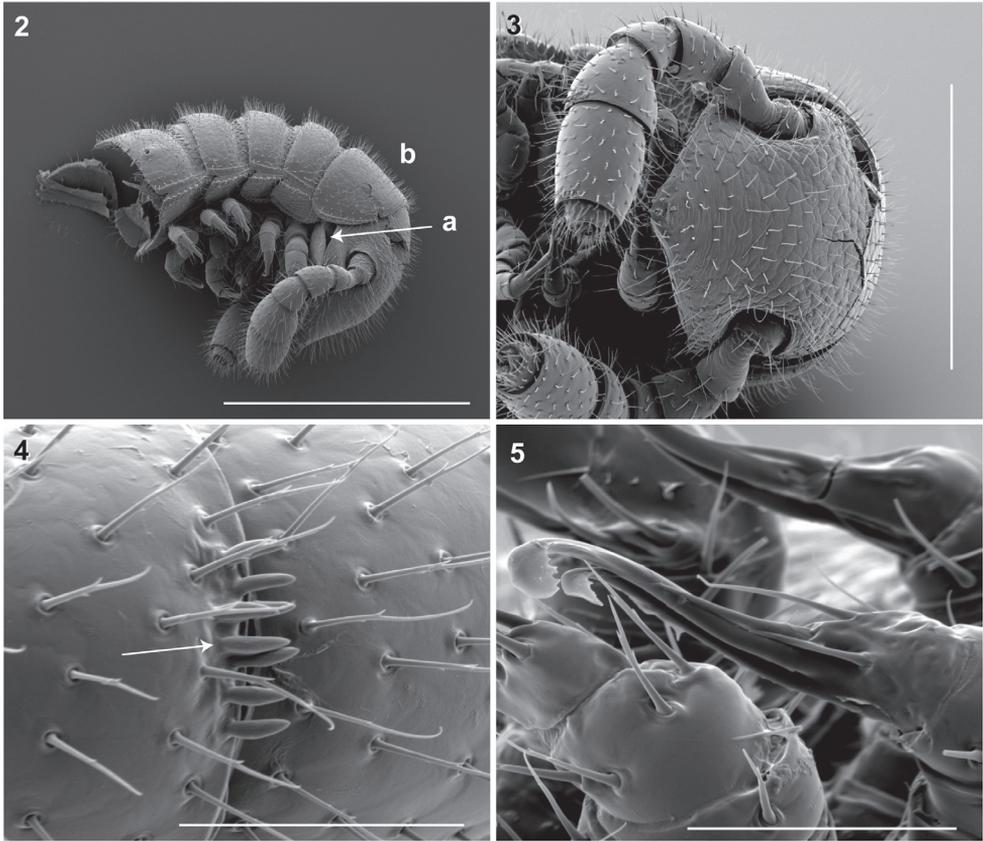
<http://species-id.net/wiki/Illacme>

Cook and Loomis 1928: 12; Chamberlin and Hoffman 1958: 189; Buckett 1964: 29; Jeekel 1971: 39; Hoffman 1980: 116; Shelley 1996b: 23; Shelley 1996a: 1808; Hoffman 1999: 195; Jeekel 2001: 46; Marek and Bond 2006: 707; Shelley 2010: 45.

**Type species.** *I. plenipes* Cook and Loomis 1928: 12; by original designation.

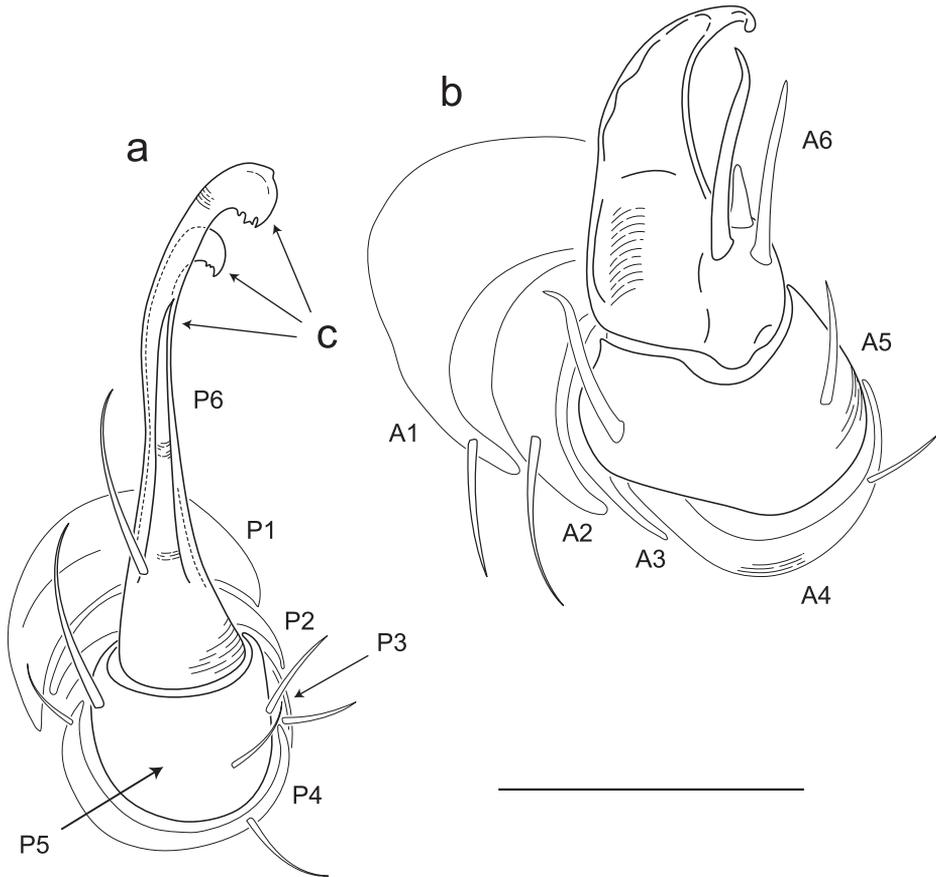
**Family placement.** *Illacme* is placed with other taxa in the family Siphonorhinidae based on the following characters: Head pear-shaped (♂) or triangular (♀), not elongate or bird beak-shaped, as in the Siphonophoridae (Fig. 2, Morphbank 805574, Appendix I). Antennae elbowed between antennomeres 3, 4 (Fig. 3, Mb-805578). Antennomeres 5, 6 with apical dorsal cluster of 7 or 8 basiconic sensilla (Bs<sub>2</sub>) in slight depression, not deep-set into circular pits, as in the Siphonophoridae (Fig. 4, Mb-805575). Posterior gonopods with distal podomere divided into 2 or 3 branches (Fig. 5, Mb-805576, Fig. 6c). See also diagnoses of *Illacme* in Shelley (1996b, p. 23) and of Siphonorhinidae in Shelley and Hoffman (2004, p. 218).

**Diagnosis.** Adults of *Illacme* are distinct from other siphonorhinid genera (and commonly-encountered millipedes co-occurring with *I. plenipes*) based on the combination of – *Exoskeleton*: Body light cream-colored, thread-like, extremely narrow and long (max. width: ♂ 0.55, ♀ 0.64; max. length: ♂ 28.16, ♀ 40.40). Adult individuals with 84 – 192 segments, and with 318 – 750 legs (VMNH paratype ♀ with 192 segments and 750 legs, more than any other organism known on Earth). Body with hirsute vestiture, appearing velvety (Fig. 2, Mb-805577). Antennae elbowed between antennomeres 3, 4 (Figs 2, 3, Mb-805578). Antennomeres 5, 6 enlarged, appearing oversized relative to other millipedes (Figs 2, 3, Mb-805579). Head pear-shaped (♂) or triangular/chevron-shaped (♀), eyeless (Figs 2, 3, Mb-805574, Appendix I). Mouthparts (gnathochilarium, mandibles) and labrum tightly appressed, tapered anteriorly to rounded apex, not bird beak-shaped, as in the Siphonophoridae (Fig. 3, Mb-805586). Labrum with triangular tooth-lined orifice (Fig. 7a, b; Mb-805580). Denticulate shelf-like carina, projecting dorsally from labrum-epistome margin (Fig. 8a, b; Mb-805588). *Internal anatomy*. Posterior one-quarter length of enteron loosely spiraled; when alive, visible through translucent cuticle (Fig. 9, Mb-805582). *Male gonopods*. 9<sup>th</sup> and 10<sup>th</sup> leg pairs modified into gonopods, each comprising 6 podomeres



**Figure 2–5.** **2** Lateral (right) view of head and segments 1–5 (♂). **a** Lateral opening apparent between gnathochilarium and head capsule; gnathochilarium, mandible and head capsule noticeably separate at base, 1/3 head length distally from mandibular joint **b** Collum not covering head, with straight cephalic edge, gradually tapering laterally. Scale bar 0.5 mm. **3** Ventral view of head, antennae and segments 1 – 5 (♂). Scale bar 0.3 mm. **4** Lateral (right) view of antennomeres 5, 6 (♂). Arrow, small basiconic sensilla ( $Bs_2$ ) in cluster of 7 or 8 oriented apical dorsally (retrolaterally) in slight depression on antennomeres 5, 6. Scale bar 0.05 mm. **5** Oblique (right) view of right posterior gonopod (♂). Posterior gonopodal podomere 6 divided, comprising a bundle of 3 stylus-shaped articles. Scale bar 0.05 mm.

(Fig. 6a, b). Anterior gonopod thick, more robust than posterior gonopod (Fig. 10, Mb-805583, Fig. 6b). Anterior gonopodal apex (podomere 6, Fig. 6a, *A6*) shovel-shaped; in repose, cupped sheath-like around flagelliform posterior gonopodal apex (podomere 6, Fig. 11, Mb-805584, Fig. 6b, *P6*). Posterior gonopodal podomere 6 divided, comprising a bundle of 3 stylus-shaped articles (Fig. 5, Mb-805627, Fig. 6a, *P6*); remaining siphonorhinid taxa have 2 stylus-shaped articles with a small spine (*Nematozonium filum*) or 2 articles without a spine (*Siphonorhinus* Pocock, 1894 species and *Kleruchus olivaceus* Attems, 1938). 2 dorsal-most, longest articles of *P6* laminate distally and recurved laterally, with denticulate posterior margins appearing claw-like (Fig. 12, Mb-805585, Fig. 6a, *P6*). Ventral-most, shortest article of *P6*



**Figure 6.** Illustration of anterior and posterior gonopods (♂). **a** Posterior gonopod with podomeres labeled P1-6 **b** Anterior gonopod with podomeres labeled A1-6 **c** 3 stylus-shaped articles. Scale bar 0.05 mm.

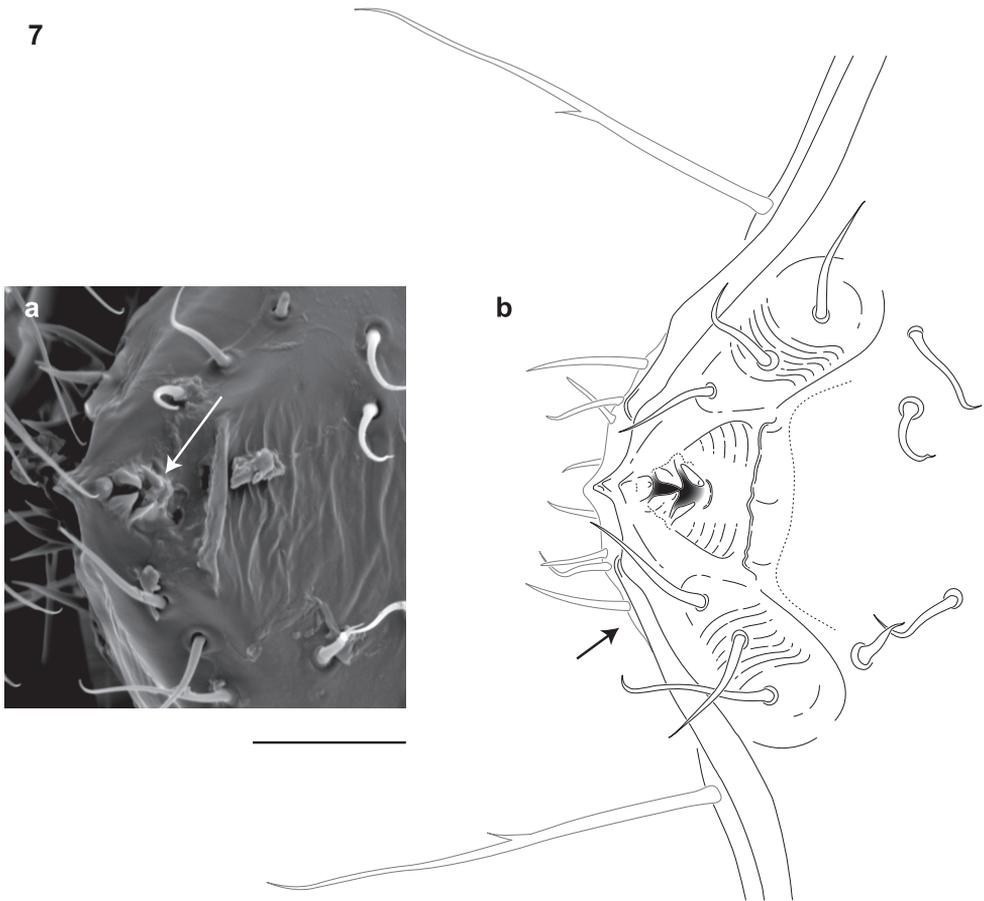
acuminate distally, spike-like. *Habit in life.* Movement very slow, nearly imperceptible (Appendix II, III). Antennae movement rapid, independent. Terminal antennomeres held flat and rapidly tap substrate and surroundings (Appendix IV).

***Illacme plenipes* Cook & Loomis, 1928**

[http://species-id.net/wiki/Illacme\\_plenipes](http://species-id.net/wiki/Illacme_plenipes)

Cook and Loomis 1928: 12. Chamberlin and Hoffman 1958: 189; Buckett 1964: 29; Shelley 1996b: 23; Shelley 1996a: 1808; Hoffman 1999: 195; Jeekel 2001: 46; Shelley and Hoffman 2004: 221; Marek and Bond 2006: 707; Read and Enghoff 2009: 554; Shelley 2010: 45; Shelley and Golovatch 2011: 26.

**Material examined.** *Type specimens:* ♂ holotype (USNM), 1♂, 3♀ paratypes (FSCA) and 3♀ paratypes (VMNH)—from United States, California, San Benito County,



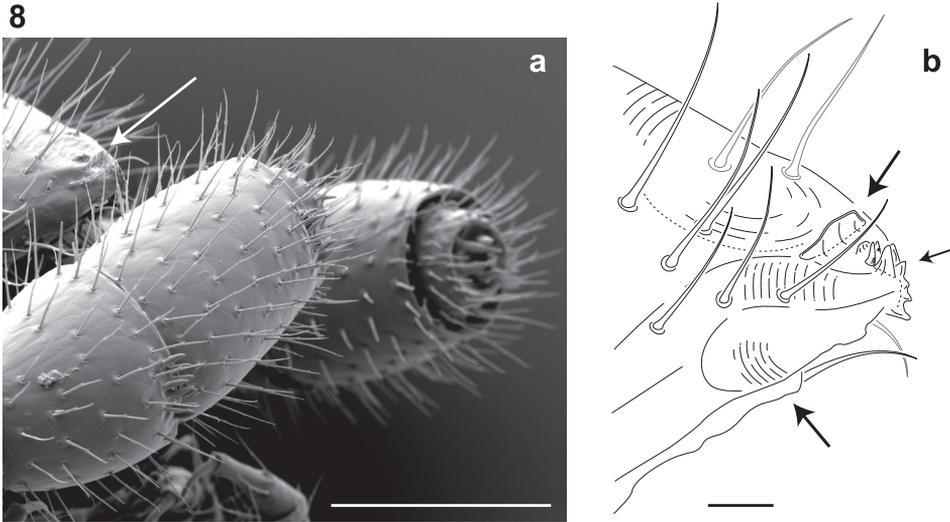
**Figure 7.** Dorsal view of anterior region of head and labrum ( $\sigma$ ). **a** Scanning electron micrograph: arrow, labrum with triangular tooth-lined orifice **b** Line drawing: shaded area, triangular tooth-line orifice; arrow, gnathochilarium. Scale bar 0.02 mm.

from “near divide between Salinas and San Juan Bautista” [an imprecise location probably on the north side of the Gabilan Range on San Juan Grade Road or Old Stage Road in a radius of 4 km around the coordinates 36.831371°N, -121.562808°W], 27.xi.1926 (Coll. O.F. Cook). *Non-type specimens*: California, San Benito County: 1 $\sigma$  (SPC000924), 2 $\text{f}$  (SPC000930, -931), Gabilan Range, San Juan Bautista, 29.xi.2005 (Colls: P. and R. Marek); 3 $\sigma$  (SPC000932, -933, -934), 1 juvenile (SPC000935), *loc. ibid.*, 8.xii.2005, (Coll: J. Bond). 2 $\text{f}$  (SPC001187, MIL0020), Gabilan Range, San Juan Bautista, 16.xii.2007, 13:00 (Colls: P. and R. Marek).

**Diagnosis.** (See generic diagnosis.)

**Description of holotype** ( $\sigma$ ) USNM TYPE NO. 976 – *Counts and measurements*:  $p = 143$ .  $a = 2$ .  $l = 562$ . ( $143 + 2 + T$ ).  $HW = 0.30$ .  $HL = 0.34$ .  $ISW = 0.20$ .  $AW =$  [antennae missing].  $CW = 0.42$ .  $W1 = 0.53$ .  $W2 = 0.55$ .  $W3 = 0.55$ .  $L1 = 0.20$ .  $L2 = 0.20$ .  $L3 = 0.18$ .  $H1 = 0.31$ .  $H2 = 0.30$ .  $H3 = 0.33$ .  $AS1 = 0.45$ .  $A5W = 0.05$ .  $P5W$

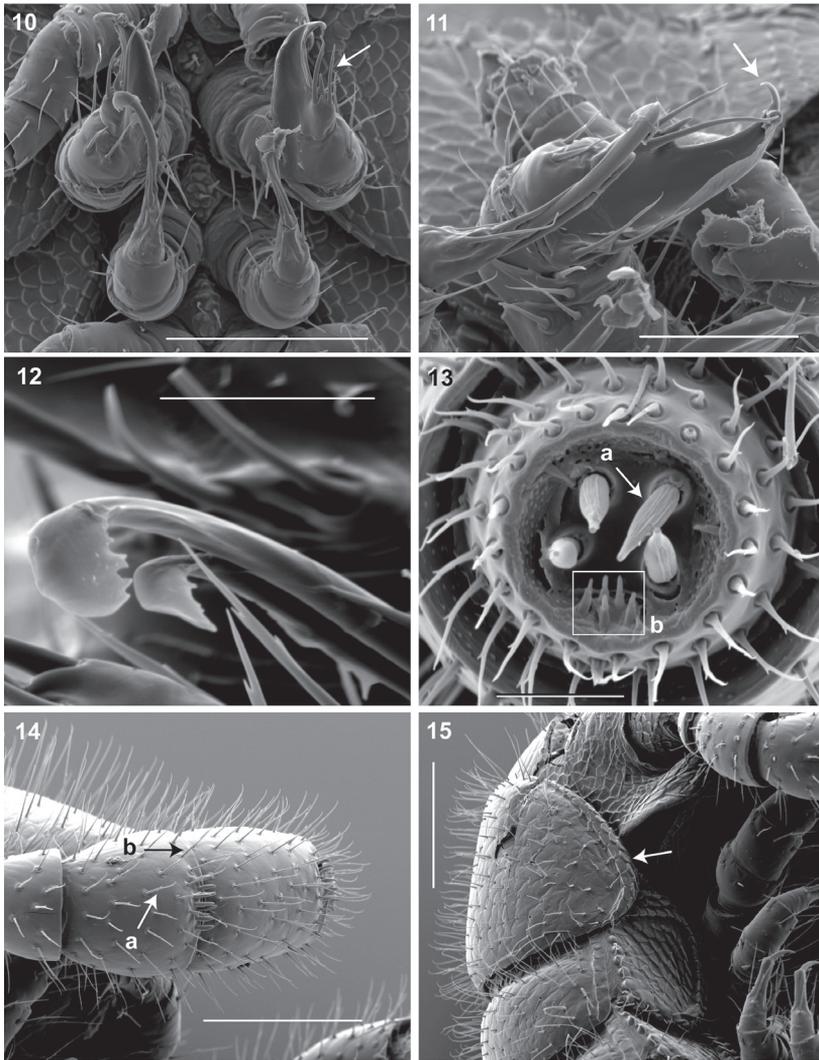
= 0.04. **BL** = 28.16. *Head* pear-shaped, tapered anteriorly to round point at a 160° angle anterior from antennal sockets; occipital area posterior from antennal sockets gradually curved medially towards neck (Figs 2, 3, Mb-805574—note: all SEMs herein are images of specimen #SPC000932, not the holotype). Head pilose, covered with long, slender setae (Fig. 2, Mb-805577). *Mouthparts* (gnathochilarium, mandibles) and labrum tightly appressed, tapered anteriorly to round point (Fig. 3, Mb-805586). Gnathochilarium elements (stipes, promentum, etc.) indistinguishably fused, tightly appressed to the ventral surface of the head, leaving a small opening anteriorly. Lateral opening apparent between gnathochilarium and head capsule (Fig. 2a, Mb-805587). Mandibles thin, stylet-like, with heavily calcified apices (viewed dorsally through translucent head capsule at 400× with a compound microscope). Labrum with triangular tooth-lined orifice (Fig. 7a, b; Mb-805580). Denticulate shelf-like carina, projecting dorsally from labrum-epistome margin (Fig. 8a, b; Mb-805588). Gnathochilarium, mandible and head capsule noticeably separate at base, 1/3 head length distally from mandibular joint (Fig. 2a, Mb-805589). *Antennae* sub-geniculate, elbowed between antennomeres 3, 4, comprising 7 antennomeres (Fig. 3, Mb-805578). Antennae massive distally; antennomeres 5, 6 enlarged (Fig. 3, Mb-805579). Five sensillum types: 4 apical cones (AS) oriented in a trapezoidal cluster on 7th antennomere, with longitudinally grooved outer surface and apical circular invagination (Fig. 13, Mb-805590). Chaetiform sensilla (CS) widely spaced on antennomeres 1–7, each sensillum with 2 or 3 barbules (Fig. 14a, Mb-805591). Trichoid sensilla (TS) oriented apically encircling antennomeres 1–7, lacking barbules (Fig. 14b, Mb-805592). Small basiconic sensilla (Bs<sub>2</sub>) in clusters of 7 or 8; in slight depressions oriented apical dorsally (retrolaterally) on antennomeres 5 and 6; smooth, finger-shaped, 1/2 length of chaetiform sensillum (Fig. 4, Mb-805593). Spiniform basiconic sensilla (Bs<sub>3</sub>) in cluster of 5, oriented apical dorsally on 7th antennomere; tips facing apical cones (on longitudinal axis with Bs<sub>2</sub> on antennomeres 5, 6); each sensillum with 2 barbules (Fig. 13b, Mb-805594). Antennae extend posteriorly to middle of 3rd tergite. Relative antennomere lengths 6>2>5>3>4>1>7. *Segments*: Collum not covering head, with straight cephalic edge, gradually tapering laterally (Fig. 2b, Mb-805595). Collum with carina present on anterolateral margin, appearing scaly (Fig. 15, Mb-805596). Carina repeated serially on lateral tergal and pleural margins (absent from telson). Lateral tergal and pleural carinae jagged, pronounced on midbody segments (Fig. 16a, Mb-805597). Lateral margin of collum round. *Tergites*: Metazonites rectangular, 3× wider than long, slightly convex (Fig. 17, Mb-805598). Paranota absent. Metazonite dorsal surface pilose, covered with long, slender setae (Fig. 2, Mb-805599). Tergal setae hollow, cavity diameter 1/8 that of setae diameter; tipped with silk-like exudate, tangled, appearing adhered to neighboring setae (Fig. 18, Mb-805600). (NB: Tergal silk-like exudate observed in scanning electron micrographs, and by the observation of fine strands issuing from the metaterga of live individuals, viewed while magnified at 80× with a stereomicroscope. Silk stickiness was indicated by increased adherence of soil particles after handling and live observation of the millipede's coiled body becoming stuck together.) Metazonite posterior margin (limbus) lined with posteriorly projecting anchor-shaped spikes and a row of conical spikes



**Figure 8.** Lateral (right) view of antennal and cephalic apices (♂). **a** Scanning electron micrograph: arrow, denticulate shelf-like carina, projecting dorsally from labrum-epistome margin. Scale bar 0.1 mm **b** Line drawing: top arrow, shelf-like carina; middle arrow, triangular tooth-lined orifice; bottom arrow, gnathochilarium. Scale bar 0.01 mm.

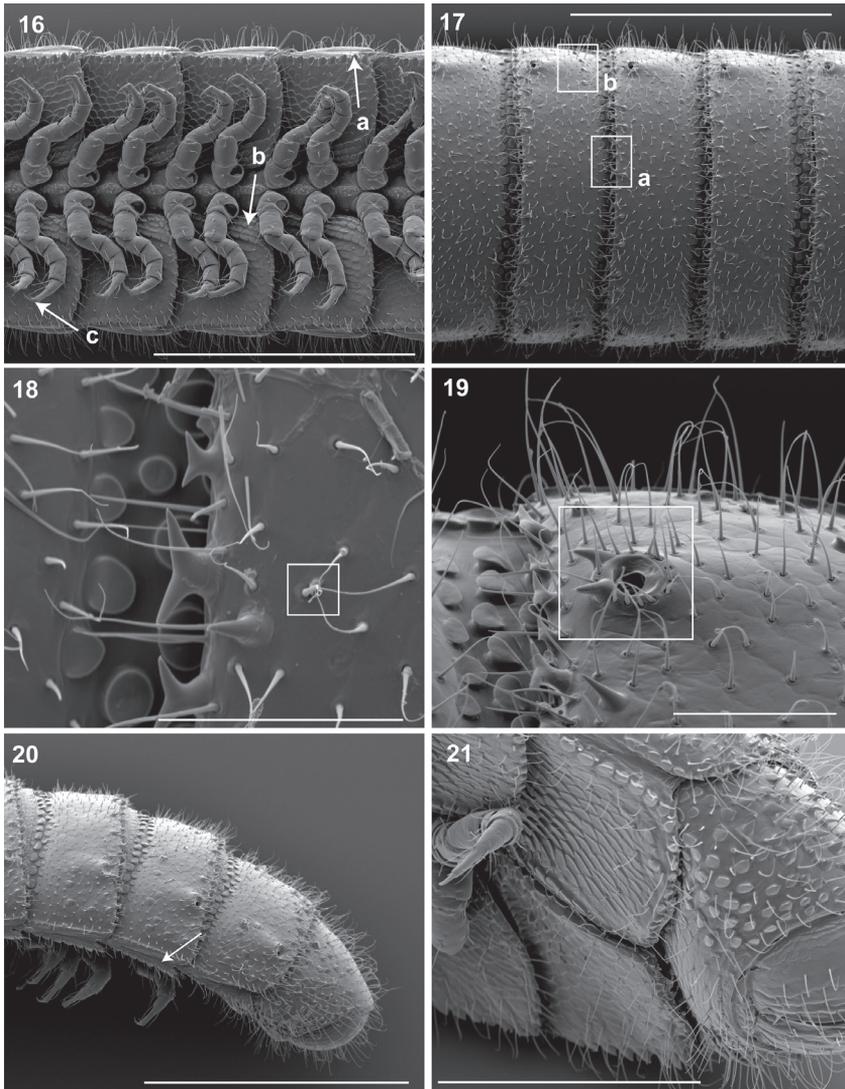


**Figure 9.** *Illacme plenipes* ♀ with 170 segments and 662 legs (specimen # SPC000931). Top inset, 2× magnified view of posterior segments with corkscrew-shaped metenteron visible through cuticle; bottom inset, 3× magnified illustration of corkscrew-shaped metenteron. Scale bar 1 mm.

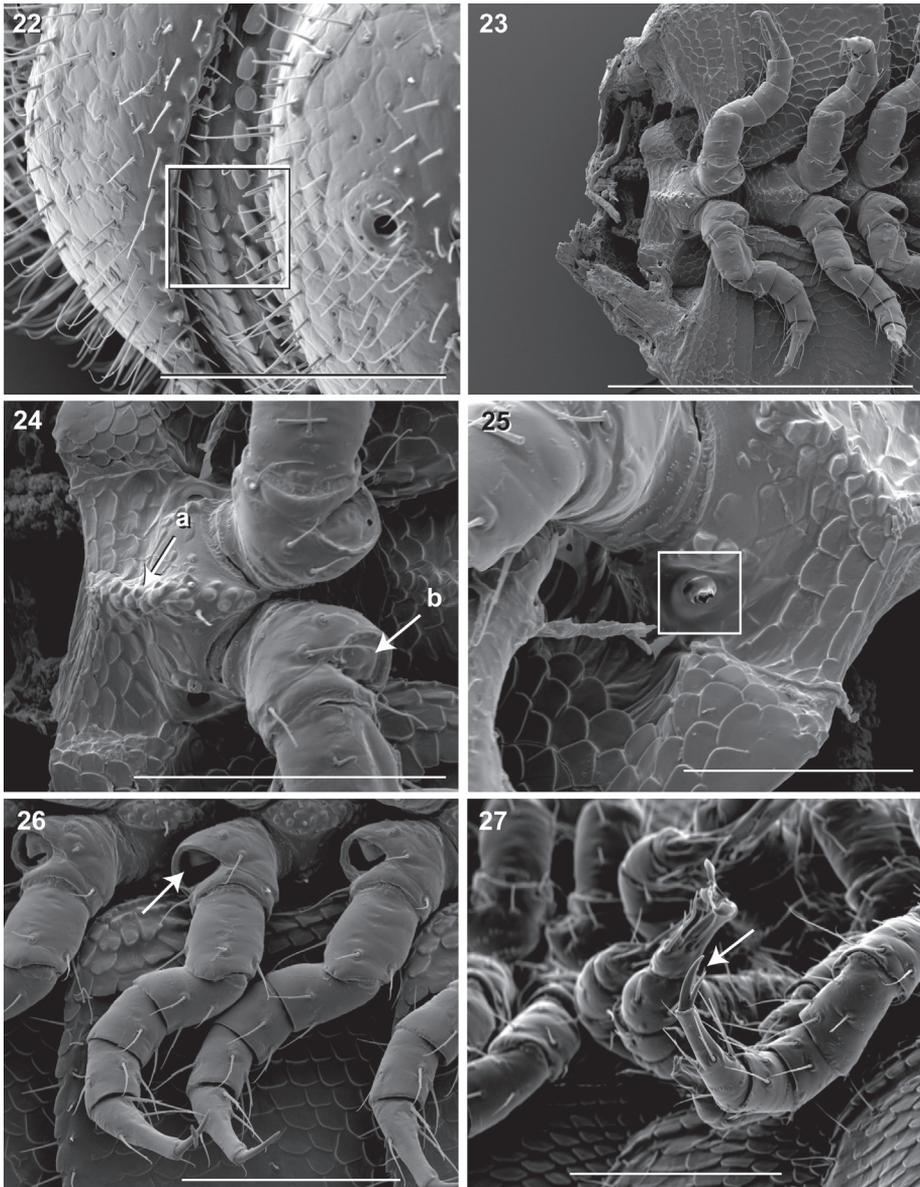


**Figures 10–15.** **10** Ventral *in situ* view of gonopods (♂). Arrow, anterior gonopod thick, more robust than posterior gonopod. Scale bar 0.1 mm **11** Medial view of right gonopods (♂). Arrow, Anterior gonopodal apex (podomere 6) shovel-shaped; in repose cupped sheath-like around flagelliform posterior gonopodal apex (podomere 6). Scale bar 0.05 mm **12** Oblique (right) view of right posterior gonopodal apex (♂). 2 dorsal-most, longest articles laminate distally and recurved laterally, with denticulate posterior margins appearing claw-like. Scale bar 0.02 mm. **13** Antennomere 7 apex (♂). **a** Four apical cones (AS) oriented in a trapezoidal cluster on 7th antennomere, with longitudinally grooved outer surface and apical circular invagination **b** Spiniform basiconic sensilla (Bs<sub>1</sub>) in cluster of 5, oriented apical dorsally on 7th antennomere; tips facing apical cones (on longitudinal axis with Bs<sub>2</sub> on antennomeres 5, 6); each sensillum with 2 barbules. Scale bar 0.02 mm. **14** Lateral (right) view of right antenna (♂). **a** Chaetiform sensilla (CS) widely spaced on antennomeres 1–7, each sensillum with 2 or 3 barbules **b** Trichoid sensilla (TS) oriented apically encircling antennomeres 1–7, lacking barbules. Scale bar 0.1 mm. **15** Lateral (right) view of head, collum and segments 2, 3 (♂). Arrow, collum with carina present on anterolateral margin, appearing scaly. Carina repeated serially on lateral tergal and pleural margins (absent from telson). Scale bar 0.1 mm.

just dorsal to anchor-shaped spikes (Fig. 17a, Mb-805601). Anchor-shaped spikes alternating in size (large, small) along row. Ozopores oriented dorsally, located near limbus, absent from tergites 1 – 3 and telson. Ozopores elevated slightly (porosteles absent), with 2 stout posteriorly projecting spines and encircled by 13 – 15 robust setae (Fig. 19, Mb-805602). 3 or 4 stout flat tubercles opposite ozopore near anterior margin, lunate arrangement encircling ozopore (Fig. 17b, Mb-805603). Posterior tergites more convex, covered with a greater density of long, slender “silk”-exuding setae (Fig. 20, Mb-805604). Lunate-arranged tubercles opposite ozopores on posterior metazonites: conical and spiked, not flat. Apodous segments lacking sterna, pleurites contiguous in midline. Apodous tergites densely setose, covered with unevenly distributed spikes (Fig. 21, Mb-805605). Telson densely covered with irregularly oriented and unevenly distributed stout spines; posterior margin lined with variably-shaped posterodorsally oriented anchor-shaped spikes. Tergal tubercles and spikes: consistently projecting posteriorly, occasionally posterodorsally. Prozonite highly sculptured, with 5 rows of discoidal flat tubercles; anterior 3 rows staggered and posterior 2 rows aligned (Fig. 22, Mb-805606). *Pleurites* quadrate, flat, with jagged scaly lateral, posterior and medial margins (Fig. 16, Mb-805609). Pleurite medial margin broad, with scaly carina (Fig. 16b, Mb-805610). Left and right pleurites plate-like, comprising 4/5's of ventral segment space. Left and right pleurites broadly overlapping sternite, covering spiracles (Fig. 23, Mb-805612). *Sternites* free, separate from pleurites; heart-shaped, wider anteriorly. Sternal surface with broad, jagged scales. Medial sternal ridge projecting ventrally, with spiracles and legs oriented ventrally (Fig. 24, Mb-805614). Spiracles circular, orifice open; oriented dorsally above legs (Fig. 25, Mb-805615). Anterior and posterior sternites separate. Tergites, pleurites and sternites separated by arthrodial membrane (Fig. 20, Mb-805616). Arthrodial membrane between tergites and pleurites wider posteriorly. *Telson* pilose, covered with long, slender posteriorly recurved setae (Fig. 20, Mb-805628). Paraprocts semihemispherical, anterior margins slightly scaly. Epiproct absent. Hypoproct small, one-eighth area of paraproct, with row of posterior projecting setae. *Legs*: six subequally shaped podomeres, with coxa slightly shorter and tarsus slightly longer. Legs with sparse setae, appearing similar to trichoid sensilla, with 2 or 3 barbules. Coxae nearly contiguous medially, separated by thin sternal ridge. Large posteroventral D-shaped opening for eversible sac (Fig. 26, Mb-805618). Eversible sacs membranous, bulging slightly from opening (Fig. 24b, Mb-805620). Pregonopodal tarsus with stout bifurcate claw; dorsal subdivision thicker, more arcuate (Fig. 27, Mb-805621). Postgonopodal tarsus with two separate claws, co-terminal on tarsal apex; dorsal claw thick and arcuate, ventral claw thin and setiform (Fig. 16c, Mb-805623). 2nd leg pair with posteriorly oriented coxal gonapophyses; rounded, protuberant, one-third length of prefemur. *Gonopods*: 9<sup>th</sup>, 10<sup>th</sup> leg pairs modified into gonopods, each comprising 6 podomeres (Fig 6a,b). Anterior gonopod thick, more robust than posterior gonopod (Fig. 10, Mb-805583, Fig. 6b). Anterior gonopodal apex (podomere 6) shovel-shaped; in repose cupped sheath-like around flagelliform posterior gonopodal apex (podomere 6, Fig. 11, Mb-805584). Posterior gonopodal podomere 6 divided, comprising a bundle of 3 stylus-shaped articles (Fig. 5, Mb-805627, Fig 6a). 2 dorsal-most, longest articles



**Figure 16–21.** **16** Ventral view of segments ( $\sigma$ ). **a** Lateral tergal and pleural carinae jagged, pronounced on midbody segments **b** Pleurite medial margin broad, with scaly carina **c** Postgonopodal tarsus with thinner claw and without bifurcation, but with stout seta. Scale bar 0.4 mm. **17** Dorsal view of segments ( $\sigma$ ). **a** Metazonite posterior margin (limbus) lined with posteriorly projecting anchor-shaped spikes and a row of conical spikes just dorsal to anchor-shaped spikes **b** 3 or 4 stout flat tubercles opposite ozopore near anterior margin, lunate arrangement encircling ozopore. Scale bar 0.4 mm. **18** Dorsal view of tergites ( $\sigma$ ). Square, tergal setae tipped with silk-like exudate, tangled, appearing adhered to neighboring setae. Scale bar 0.05 mm. **19** Dorsal view of left ozopore ( $\sigma$ ). Square, ozopores elevated slightly, with 2 stout posteriorly projecting spines and encircled by 13 – 15 robust setae. Scale bar 0.05 mm. **20** Right lateral view of posterior segments and telson ( $\sigma$ ). Arrow, tergites, pleurites and sternites separated by arthrodial membrane. Scale bar 0.4 mm. **21** Oblique (right) ventrolateral view of 2 apodous segments, telson, hypoproct and paraproct ( $\sigma$ ). Apodous segments lacking sterna, pleurites contiguous in midline. Apodous tergites densely setose, covered with unevenly distributed spikes. Scale bar 0.2 mm.



**Figure 22–27.** **22** Lateral view of fifth metatergite and prozonite (♂). Square, prozonite highly sculptured, with 5 rows of discoidal flat tubercles; anterior 3 rows staggered and posterior 2 rows aligned. Scale bar 0.1 mm. **23** Ventral view of mid-length sternites, pleurites and legs (♂). Left and right pleurites broadly overlapping sternite, covering spiracles. Scale bar 0.3 mm. **24** Ventral view of mid-length sternites and leg bases (♂). **a** Medial sternal ridge projecting ventrally, with spiracles and legs oriented ventrally **b** Eversible sacs membranous, bulging slightly from opening. Scale bar 0.1 mm. **25** Oblique (right) lateral view of sterna and spiracle (♂). Square, spiracles circular, orifice open; oriented dorsally above legs. Scale bar 0.05 mm. **26** Ventral (right) view of legs, with posteroventral eversible sac opening (♂). Arrow, large posteroventral D-shaped opening for eversible sac. Scale bar 0.1 mm. **27** Oblique (right) lateral view of pregonopodal legs (♂). Arrow, pregonopodal tarsus with stout bifurcate claw. Scale bar 0.1 mm.

of P6 laminate distally, recurved laterally, denticulate posterior margins, appearance similar to a chicken foot in *rigor mortis* (Fig. 12, Mb-805585, Fig 6a). Ventral-most, shortest article of P6 acuminate distally, spike-like. Thin ridge-shaped sterna present between left and right gonopods, thicker between anterior gonopods.

**Description of largest paratype** (♀) VMNH – *Counts and measurements*: **p** = 190. **a** = 2. **l** = 750. (**190 + 2 + T**). **HW** = 0.37. **HL** = 0.44. **ISW** = 0.30. **AW** = antennae missing. **CW** = 0.44. **W1** = 0.58. **W2** = 0.58. **W3** = 0.57. **L1** = 0.23. **L2** = 0.21. **L3** = 0.23. **H1** = 0.46. **H2** = 0.44. **H3** = 0.48. **AS1** = 0.44. **BL** = 40.40. Anatomical description similar to male holotype. In combination with its measurements, the following structures *differ* from male holotype. *Head* triangular, chevron-shaped, tapered anteriorly to round point at a 135° angle anterior from antennal sockets; occipital area posterior from antennal sockets straight, not curved medially towards neck. *Cyphopods* large, area 1/6 the segmental area in widest cross-section; almond-shaped, bivalvular, narrow apex oriented ventrolaterally. Valves transparent, glassy. Ventral valve thickened and clam-like, with 4 or 5 thick setae; dorsolateral valve thin and flat, with 2 or 3 spines. Oviduct connected posteriorly to cyphopod, opening oriented ventromedially and located between valves. Oviduct tube wrinkled, appearing highly expandable in width, cross-section 1/8 area of cyphopod. Receptacle, suture and operculum absent.

**Etymology.** Cook and Loomis (1928) named this species “in highest fulfillment of feet”. *Il* = “in” (Latin); *acme*, ἀκμή (Greek) = “the highest point, or culmination”; *pleni* = “full” (Latin); *pes* = “foot” (Latin).

**Variation.** There is negligible variation in coloration among live specimens. (FSCA paratype specimens that have been stored in alcohol for 86 years are dark mahogany brown, which is likely an unnatural color and a result of alcohol preservative, vial stopper and age.) The predominant source of variation between specimens is segment and leg counts (Tables 1 – 3). Females have between 486–750 legs with a standard deviation of 78, and males between 318–562 legs with a standard deviation of 107. The segments of *I. plenipes* (males and females) are uniform in length, width and height along

**Table 1.** Segment and leg count, head measurements.

	<b>p</b>	<b>l</b>	<b>HW</b>	<b>HL</b>	<b>ISW</b>	<b>AW</b>	<b>CW</b>
♂	<b>84–145</b> (107/27)	<b>318–562</b> (410/107)	<b>0.295–0.308</b> (0.301/0.006)	<b>0.344–0.406</b> (0.382/0.024)	<b>0.172–0.202</b> (0.189/0.011)	<b>0.098–0.103</b> (0.101/0.002)	<b>0.374–0.422</b> (0.393/0.019)
♀	<b>126–192</b> (159/20)	<b>486–750</b> (619/78)	<b>0.308–0.369</b> (0.335/0.020)	<b>0.408–0.556</b> (0.446/0.045)	<b>0.185–0.295</b> (0.217/0.033)	<b>0.098–0.113</b> (0.103/0.006)	<b>0.407–0.472</b> (0.431/0.021)

**Table 2.** Width and length measurements.

	<b>W1</b>	<b>W2</b>	<b>W3</b>	<b>WM</b>	<b>L1</b>	<b>L2</b>	<b>L3</b>	<b>LM</b>
♂	<b>0.437–0.526</b> (0.485/0.033)	<b>0.467–0.554</b> (0.500/0.036)	<b>0.455–0.545</b> (0.488/0.034)	0.491/ 0.032	<b>0.148–0.203</b> (0.173/0.021)	<b>0.150–0.197</b> (0.162/0.020)	<b>0.140–0.183</b> (0.159/0.017)	0.165/ 0.019
♀	<b>0.520–0.620</b> (0.564/0.035)	<b>0.531–0.640</b> (0.569/0.037)	<b>0.517–0.610</b> (0.559–0.032)	0.564/ 0.034	<b>0.172–0.228</b> (0.195/0.018)	<b>0.176–0.209</b> (0.194/0.012)	<b>0.157–0.234</b> (0.194/0.021)	0.194/ 0.017

**Table 3.** Height, apodous segment/gonopodal width, body length measurements.

	H1	H2	H3	HM	AS1	A5W	P5W	BL
♂	<b>0.273– 0.400</b> (0.350/ 0.057)	<b>0.277– 0.418</b> (0.337/ 0.055)	<b>0.295– 0.381</b> (0.336/ 0.036)	0.341/ 0.047	<b>0.394– 0.445</b> (0.423/ 0.022)	<b>0.047– 0.055</b> (0.051/ 0.003)	<b>0.036– 0.043</b> (0.040/ 0.003)	<b>13.368– 28.156</b> (19.251/ 6.305)
♀	<b>0.220– 0.486</b> (0.365/ 0.077)	<b>0.289– 0.488</b> (0.384/ 0.064)	<b>0.295– 0.504</b> (0.370/ 0.079)	0.373/ 0.071	<b>0.412– 0.482</b> (0.451/ 0.024)	-	-	<b>24.541– 40.399</b> (31.055/ 5.474)

the trunk, and are slightly taller, and more convex, in posterior segments—potentially to accommodate the spiraled metenteron.

**Natural history.** *Illacme plenipes* specimens were collected during the day in a small valley adjacent to cattle pasture. The woodland habitat was primarily composed of California live-oak, *Quercus agrifolia* (Fig. 28). Understory flora included ferns (bracken, *Pteridium aquilinum*; California polypody, *Polypodium californicum*; and California maiden-hair, *Adiantum jordanii*), California blackberry (*Rubus ursinus*), and poison oak (*Toxicodendron diversilobum*) (Fig. 29). Specimens were found beneath large moss-covered boulders, typically with a mass > 30 kg (Fig. 30). The mil-



**Figure 28.** Habitat of *I. plenipes*. Top left, view of oak forest where *I. plenipes* were encountered. Top right, close up of oak forest and sandstone pinnacle where *I. plenipes* occur. Bottom, landscape view of oak forest, cattle trails evident (composite stitched image of three photos, image sides slightly distorted).



**Figure 29.** Oak forest understory habitat of *I. plenipes*. Top, base of sandstone pinnacle (from Fig. 28), where specimens were found. Bottom, mossy oak forest—close-up of habitat where *I. plenipes* individuals were encountered.

lipede *Tylobolus uncigerus* (Wood, 1864) (order Spirobolida) was found co-occurring with *I. plenipes* at this locality. Other arthropods encountered include: *Aptostichus* and *Calisoga* trapdoor spiders (Mygalomorphae), *Evalljapyx* (Diplura), and *Promecogna-*



**Figure 30.** Sandstone microhabitat of *I. plenipes*. Top left, 50 kg sandstone from 29.xi.2005 rediscovery locality of *I. plenipes*; one ♀ with 666 legs was discovered from beneath the stone (scale bar = 5 cm, hand shovel shown for scale). Bottom left, 30 kg sandstone from the 16.xii.2007 locality, two ♀ (specimen #: SPC001187, MIL0020) were discovered below the stone (scale bar = 5 cm, 15 cm ruler shown for scale). Top right, surface close up of sandstone from 16.xii.2007 locality with ♂ *I. plenipes*, not collected (scale bar = 5 mm). Bottom right, surface close up of sandstone from 29.xi.2005 locality with ♂ *I. plenipes* (specimen #: SPC000924, scale bar = 5 mm). Millipedes shown in right two pictures were found clinging to the surface of the stone.

*thus* ground beetles (Carabidae). *Edaphic setting*: Specimens collected in 2007 were found beneath a large stone (Fig 30, about 30 kg). When the stone was removed, individuals were seen corkscrewing outward into the cavity from the soil (Fig. 31). The soil, consisting of moist small-grained substrate, was dark chocolate brown in coloration and somewhat sandy (Fig. 31). The soil did not contain clay particles and seemed to drain water quickly. During the 16 December 2007 collections, soil moisture extended 15 cm below the surface.

**Distribution.** *Illacme plenipes* is only known from a small area, ca. 4.5 km in diameter, in the northwestern foothills of the Gabilan Range in San Benito County, California.



**Figure 31.** Subterranean soil microhabitat of *I. plenipes*. Left, sandstone crater; dotted line indicates crater's edges, arrows indicate two ♀ *I. plenipes* shown *in situ* upon removal of stone (specimen #: SPC001187, MIL0020—lower individual with anterior trunk segments embedded in soil, upper individual with middle segments embedded in soil). Bottom middle, close up of lower individual from left image. Top right, dark sandy soil from microhabitat. Bottom right, close up of soil showing sandy grain structure.

## Discussion

### “The acme of plentiful feet”

The pattern by which *I. plenipes* add segments and subsequently legs post-embryonically between developmental stadia is referred to as anamorphosis (Enghoff et al. 1993). Based on the large number of legs and considerable variation in leg and segment count among adults, anamorphosis likely continues for an indeterminate period, extending well beyond the attainment of sexual maturity (Enghoff et al. 1993; Marek and Bond 2006). Millipedes generally use their numerous legs to burrow between and through obstacles that they encounter (Hopkin and Read 1992; Manton 1954). A leg pair acts to push and propel the myriapod forward, and with two leg-pairs per segment (diplosegments in millipedes represent a fusion of two primordial segments), millipedes create a stronger thrust for a relatively compact body. Millipedes with heavily calcified cuticles and rather incompressible bodies composed of rigid rings (e.g., the Spirobolida and Spirostreptida), burrow through the soil by brute leg force, ramming and bulldozing with a smooth rounded head and collum. In contrast, many millipedes

with flexible cuticles and compressible bodies, which are composed of free sternites and pleurites (e.g., other Siphonophorida and *I. plenipes*), move through the soil by squeezing flexible anterior segments forward by leg force and subsequently telescoping posterior segments forward and repeating, i.e. the borer millipedes (Hopkin and Read 1992; Manton 1961). The anterior segments in these millipedes are tapered, most noticeably in the Polyzoiiida, and bore and wedge to facilitate movement through the soil. With *I. plenipes*, the numerous legs presumably impart greater motive force to push within a subterranean microhabitat, and to cling tightly to the surface of sandstone boulders (as described below).

### Natural history

The diet of *I. plenipes* is unknown. Given the shape of its mouthparts, the typical millipede diet in which decaying organic matter is mechanically fragmented is unlikely for the species. *Illacme plenipes* possesses a comb-like structure on the posterior margin of the labrum and an open triangular tooth-lined “mouth” formed by an orifice through the labrum (Fig. 7a, b; Fig. 8a, b; Mb-805580; Mb-805588). The mouthparts are composed of the stylet-like mandibles and the gnathochilarium (structures observed between 500–2000× with a scanning electron microscope and the mandibles through the translucent head capsule at 400× with a compound microscope). These mouthparts are tightly appressed and tapered anteriorly to a rounded point. Given that the mandibles appear stylet-like, and assuming the mouthparts are moveable, a functional hypothesis for feeding is that the gnathochilarium hinges open, the mandibles are protruded to pierce plant and/or fungal tissue, and then the tooth-lined mouth is used to suck out the fluid contents. The teeth and labral comb could serve to filter particulates exceeding a certain size. Other Colobognath millipedes with somewhat reduced mouthparts, for example species of the family Andrognathidae, feed on fungus or other live plant or soft organic matter (Gardner 1974). Manton (1961) described the feeding of captive siphonophorids *Siphonophora portoricensis* Brandt, 1837 and *Siphonophora* (= *Siphonocybe*) *hartii* (Pocock, 1894) and observed individuals probing decayed vegetation with their beaked proboscises, after tapping the material with their antennae. Fungi were not observed associated with *I. plenipes*, as they are often with species of Platydesmida. However, live plant tissues, especially fine grass roots that are often confused with *I. plenipes*, were abundant where specimens were encountered and are a potential food source. The enteric anatomy of *I. plenipes* indicates a water or nutrient-poor diet. Individuals of the species possess a regularly spiraled metenteron, which is similar to glomeridan millipedes and a diverse range of animals (e.g., snails and loricariid catfish with spiraled digestive tracts). A spiraled metenteron coupled with the extreme number of segments lengthens the digestive tract and hence the body. This lengthening might function to increase the absorptive surface area in order to extract maximum benefit from a water or nutrient-deficient diet. (It is uncertain whether the spiraling is restricted to the metenteron, a structure concerned with water resorption

via the Malpighian tubules, or a combination of the metenteron and mesenteron.) Alternatively, a long trunk may function to store additional eggs, and potentially evolved under fecundity selection. Consistent with this hypothesis, *I. plenipes* are sexually size dimorphic: female maximum length (BL) and maximum width (BM) is 1.43-fold and 1.16-fold greater than male length and width.

Based on natural history observations of *I. plenipes* in the field, individuals are always found approximately 10 – 15 cm beneath the soil, or clinging to the surface of large sandstones. The great number of legs may benefit a deep subterranean lifestyle clinging to sandstone. *Illacme plenipes* has bifurcate claws on anterior legs and two separate claws, coterminal on the tarsal apex (in lieu of the abifurcation), on posterior legs. In several millipede species, e.g. *Cylindroiulus fimbriatus* Enghoff, 1982 and *Dolistenus savii* Fanzago, 1874, the additional claws serve a stone-clinging function for surface adherence and an epilithic lifestyle (Enghoff 1983; Manton 1961). *Illacme plenipes* has large eversible sacs, structures that have also been implicated in surface clinging in petrophilic colobognath millipedes (Manton 1954; 1961). On the dorsal surface of the millipede, setae secrete a silk-like substance, which appears sticky, and may be used for clinging to the stone surface. The secretions seem to increase with handling, perhaps alternatively indicating an anti-predatory function (Shear 2008; Youngsteadt 2008). The silk may also function as a soil shedding mechanism to allow efficient burrowing, or as a means to ensnare parasites or debris particles (Youngsteadt 2008). The chemical composition of the silk is unknown. While millipedes in seven other orders of Diplopoda produce a silk-like substance from various body structures, its threads are not true silk composed of protein (one order produces silk from openings on the legs, one order from metatergal setae like *I. plenipes*, 4 orders from epiproctal spinnerets, and one order from both metatergal and epiproctal setae). In contrast with the silk's origin from the setal tip in *I. plenipes* (Fig. 18, Mb-805600), the other seven orders appear to produce silk from pores located at the setal base (Shear 2008). The diverse locations where silk originates in millipedes (legs, epiprocts, metatergal setae), suggests independent origins and precludes homology (Shear, 2008). The extrusive sticky appearance of *I. plenipes*' silk-like secretion may indicate a mucopolysaccharide identity, as is the composition of epiproctal silk spun by millipedes in the order Polydesmida (Adis et al. 2000; Shear 2008).

In contrast with the smooth exoskeleton of the bulldozer millipedes, *I. plenipes*' has a multiplicity of projections and cuticular ornaments including anchor-shaped spikes, discoidal tubercles, long silk-secreting setae and jagged body plates. Several of these projections (e.g., the peculiar anchor-shaped spikes—Fig. 17a, Mb-805601) have been documented in other taxa in the Siphonophorida and Julida (Akkari et al. 2011; Read and Enghoff 2009). In a survey of Siphonophorida from Brazilian collections, Read and Enghoff (2009, Fig. 4) provide SEMs that document an individual with similar appearing tergal sculpture, including anchor-shaped spines, discoidal metatergal tubercles, long (possibly silk-secreting) setae, and two shape classes of prozonital tubercles. The prozonital microsculpture of *I. plenipes* also appears to correspond in shape and location with several taxa of Polydesmida (Akkari and Enghoff 2011; Mesibov 2012). In the Polydesmida, like *I. plenipes* (and other taxa in the Siphonophorida), the pro-

zonital microsculpture is divided into two shape classes: a smooth scaly texture anterior to the prozonital transverse ridge and a rugged knobby surface, with discoidal tubercles or spherical knobs posterior to the ridge. The presence of spherical knobs and other cuticular ornaments in certain families of Polydesmida appear to reflect major evolutionary groups in the order (Akkari and Enghoff 2011). The function of the cuticular ornaments in *I. plenipes* is uncertain. Authors have suggested several hypotheses for the function of various projections including a locking mechanism for volvation, in the case of the anchor-shaped spike in Julida, and maintaining a cloak of soil for camouflage, in the case of branching tree-shaped setae in Polydesmida (Shear, 1977).

### Evolutionary relationships

The widely scattered distribution of modern Siphonorhinidae, predominately in the Southern Hemisphere except with *I. plenipes* in North America, indicates that their most recent common ancestor likely predates the breakup of Pangaea more than 200 million years ago. A phylogeny for Siphonorhinidae, or any taxa in the four orders of Colobognatha, does not exist, except for a recent species phylogeny of the genus *Brachycybe* in the order Platydesmida (Brewer et al. 2012). Even though the number of COI barcodes for the Colobognatha is low and the region may not be ideal for recovering the ancient divergences between the colobognath taxa represented here (likely > 200 mya), we inferred a preliminary phylogeny with the COI nucleotides using a maximum likelihood tree search in RAxML ver. 7.0.3 (Stamatakis 2006). We recovered monophyletic Platydesmida and Siphonophorida with *S. lyttoni* sister to *I. plenipes*. When *Polyzonium germanicum* (Polyzoniida) was included in the RAxML analysis and visualized in an unrooted tree, it occurred on an intervening branch between Siphonophorida and Platydesmida clades. (*Polyzonium* COI barcoding sequences from Spelda et al. 2011).

The paleoendemic species *I. plenipes* is the sole representative of the family in the Western Hemisphere. Remaining genera in the family occur primarily in the Old World tropics in Wallacea, Sundaland, Himalayas (*Siphonorhinus* species), Indo-Burma (*Kleruchus olivaceus* and *Siphonorhinus* species), and Maputaland-Pondoland-Albany (*Nematozonium filum*). The closest relative of *I. plenipes* is uncertain. The present day range of Siphonorhinidae may be the remnant of an ancient and widespread tropical distribution across Pangaea. The most likely sister taxon to *I. plenipes* is *Nematozonium filum* from South Africa, as they share a number of anatomical similarities. Among the known species of Siphonorhinidae, a South African species is a probable candidate for closest relative based on other close relationships between co-distributed taxa, for example the flightless Californian beetle genus *Promecognathus* and its close relatives in the tribe Axiniidiini in South Africa (Erwin 1985; McKay 1991). *Nematozonium filum* and *I. plenipes* share posterior gonopods divided into 2-3 thin articles (three in *I. plenipes* and two plus a small spine in *N. filum*), and each millipede is very long and spindly (Attems 1951; Shelley and Hoffman 2004). Known *I. plenipes* specimens compose a maximum of 192 segments and *N. filum*, 182 segments. (However, some species of the family Siphonophoridae also reach

beyond 182 segments, e.g., *Siphonophora millepeda* Loomis, 1934 with 190 segments). Individuals of *K. olivaceus* and *Siphonorhinus* species have bifurcate posterior gonopods (i.e. without a spine as in *N. flum*), fewer segments, and a shorter and more compact body form. Siphonorhinid millipedes, studied sporadically over the last 80 years by different taxonomists concentrating on various geographic faunas, are ideal candidates for a modern synthesis and molecular phylogenetics. For example *Siphonorhinus*, as is certainly the case for *Siphonophora*, seems to be a taxonomic dumping ground for long and spindly Siphonophorida without a bird-like beak or paranota (Jeekel 2001). The diversity of anatomical forms in the Siphonophorida, in particular the Siphonorhinidae, is quite conserved compared to other diplopod taxa. Compared to other Colobognatha, somatic anatomical diversity across lineages is low and indicates that early Siphonophorida may have appeared similar to present day species. This suggests that contemporary habitats, and current environmental factors affecting body shape, may have been similar to those in which early Siphonophorida taxa occurred. *Illacme plenipes* and related lineages may have persisted unchanged in a mild, constant habitat for hundreds of millions of years. This idea raises fascinating questions about climate and habitat constancy where Siphonorhinidae occur (its six regions also happen to be global biodiversity hotspots), and also important concerns about the conservation of the species and co-inhabitants that may have persisted in these mild climates that are now currently threatened by global climate change.

### Local biogeography

The influence of the marine layer and thick inland fog, which creates a unique climate for the area, may have contributed to a stable environment for *I. plenipes*. Areas with high probability of occurrence (Fig. 1) also receive a frequent layer of fog (Johnstone and Dawson 2010). The fog extends into the Monterey Basin and Salinas Valley and is nearly superimposable with the area of highest probability of occurrence on the DM (Appendix V). Rainfall is very seasonal where *I. plenipes* occurs, falling predominately between the months of November and March (when individuals were encountered). Cool, wet winters are punctuated by warm, dry summers when the habitat is much drier, and soil beneath stones is nearly devoid of moisture. Although surveys were not conducted during the summer, individuals are less likely encountered at this time, and probably in a reduced state of activity deep underground. Of the nine localities specifically surveyed for additional populations of *I. plenipes*, only one, the ranch locality near San Juan Bautista, housed a second population. These localities were initially chosen according to similarity with the 2005 locality near San Juan Bautista, and not as a result of the DM that was constructed for this study. All of the localities searched were indicated as low probability in the DM except Alum Rock, where specimens were not found, and the San Bautista ranch. Habitat suitability may be influenced by the presence of fog and/or the particular edaphic conditions and geology of the localities. Niche-based distribution modeling typically does not include edaphic factors or the geology of the area, and individuals of *I. plenipes* were always found in areas with arkose sandstone. The three habitats

where individuals were encountered overlay marine arkosic sandstone deposits between the Vergeles and San Andreas faults (Dibblee et al. 1979). High probability of *I. plenipes* occurrence is also present in the areas around the southern Monterey Bay and Salinas Valley that overlay more recent surficial alluvial deposits. While the probability of occurrence is high in these unsampled areas, the edaphic setting indicates lower suitability. The soils of the Monterey Basin and Salinas Valley are composed of alluvial sediments and fine-grained deposits, lacking the large arkose sandstones and boulders that *I. plenipes* may be specially adapted to. Nonetheless, there is a present-day low overall probability of occurrence of *I. plenipes* in the area, or of any other native soil dweller for that matter, since the Salinas Valley is heavily influenced by agriculture and development.

### Conservation

*Illacme plenipes* is threatened by extinction as a result of its restricted geographical distribution, narrow microhabitat requirements, seasonal rarity, and low observed population numbers. Natural populations are threatened by habitat loss due to rampant development and intense land use in the area (agricultural, industrial, transit and housing), climate change, invasive species, and potential for over-collecting. The restricted location of *I. plenipes*, limited to the gap between the Santa Cruz Mountains and Gabilan Range at the eastern fog limit, may be due to edaphic requirements (soils composed of sandstone or other native formations in the area: San Lorenzo Formation or Dacitic volcanic rocks), or extirpation due to the heavy agricultural influence around Monterey Basin and the Salinas Valley since the 1800s. In contrast with habitat degradation from development and farming, the presence of cattle does not appear to negatively affect *I. plenipes*. At each locality where *I. plenipes* was discovered, there was noticeable influence of cattle on the habitat. Boulders under which *I. plenipes* occurred were sometimes a meter away from deep cattle hoof prints. The most serious impacts that *I. plenipes* faces are human-induced habitat loss and climate change. As suggested by the distribution model and *I. plenipes*' apparent dependence on marine layer fog (likely influencing moisture and stability of its habitat), the documented 33% reduction in coastal California fog due to higher atmospheric and ocean temperature since the early 1900s (Johnstone and Dawson 2010) may severely impact the species and hasten its extinction. The few locations where *I. plenipes* exist are unique storehouses of this evolutionary relict, and potentially other ancient lineages that await discovery.

### Morphbank annotations

(Published at [www.morphbank.net](http://www.morphbank.net)):

<http://www.morphbank.net/?id=805574>

<http://www.morphbank.net/?id=805575>

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<http://www.morphbank.net/?id=805628>

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## Appendix I

Movie of ♀ *I. plenipes* (specimen # SPC000931) with 662 legs showing live movement and head shape. Individual filmed in a glass petri dish with a Nikon Coolpix 995 digital camera mounted to a Leica 12.5 stereomicroscope. (doi: 10.3897/zookeys.241.3831.app1). File format: Apple QuickTime Movie (MOV).

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**Citation:** Marek PE, Shear WA, Bond JE (2012) A redescription of the leggiest animal, the millipede *Illacme plenipes*, with notes on its natural history and biogeography (Diplopoda, Siphonophorida, Siphonorhinidae). *ZooKeys* 241: 77–112. doi: 10.3897/zookeys.241.3831.app1

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## Appendix II

Movie of ♀ *I. plenipes* (specimen # SPC000930) with 666 legs showing very slow, nearly imperceptible locomotion. Individual filmed on an oak leaf with a Nikon Coolpix 995 digital camera. (doi: 10.3897/zookeys.241.3831.app2). File format: Apple QuickTime Movie (MOV).

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## Appendix III

Movie of ♀ *I. plenipes* (specimen # SPC000930) with 666 legs showing very slow, nearly imperceptible locomotion. Individual filmed on a cardboard sheet with the same method described in Appendix II. (doi: 10.3897/zookeys.241.3831.app3). File format: Apple QuickTime Movie (MOV).

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## Appendix IV

Movie of ♀ *I. plenipes* (specimen # SPC000931) with 662 legs showing live motion and rapid, independent antennal movement. The species is blind and presumably relies on the antennae to sense its environment. Individual filmed in a glass petri dish with the same method described in Appendix I. (doi: 10.3897/zookeys.241.3831.app4). File format: Apple QuickTime Movie (MOV).

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## Appendix V

Times lapse series of visible satellite images of Monterey Bay, California, showing the occurrence of fog extending into the Monterey Basin and Salinas Valley. (doi: 10.3897/zookeys.241.3831.app5). File format: Apple QuickTime Movie (MOV).

**Explanation note:** Times lapse series of 330 visible satellite images of Monterey Bay, California, recorded every 15 mins by the GOES-15, Geostationary Operational Environmental Satellite (U.S. National Environmental Satellite, Data, and Information Service) from 10-18 September 2012. Contour lines = 61 m (200 ft). Images provided by the U.S. Naval Research Laboratory, Monterey, California <http://www.nrlmry.navy.mil/NEXSAT.html>

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## Appendix VI

Images of ♀ *I. plenipes* (specimen # MIL0020) with 618 legs. Individual photographed with a Nikon D40 dSLR and a 60 mm 1:2.8 AF-S macro lens. (doi: 10.3897/zookeys.241.3831.app6). File format: JPEG Interchange Format (JPG).

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