



RESEARCH ARTICLE

Three new species of the Amazonian millipede genus *Leptherpum* (Polydesmida: Chelodesmidae)

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ABSTRACT. This study concerns the millipede genus *Leptherpum* Attems, 1931, which contains nine valid species distributed across the Amazonian rainforest of northeastern South America. The type species *L. carinovatum* (Attems, 1898) is reexamined based on the type material and high-resolution photographs, including the first scanning electron micrographs of this species. The following three new species are described: *Leptherpum tialaura* sp. nov. from the state of Pará, Brazil; *Leptherpum battirolai* sp. nov. from the state of Amazonas, Brazil; and *Leptherpum buenovillegasi* sp. nov. from the commune of Maripasoula, French Guiana. A brief review of *Leptherpum* taxonomy and geographic distribution is provided, along with a key to males.

KEY WORDS. Brazil, Chelodesmidae, Diplopoda, distribution, French Guiana, Guyana, Neotropical, Suriname, taxonomic key, Venezuela.

INTRODUCTION

Chelodesmidae is the second most speciose family of millipedes, with the majority of the nearly 800 described species found in the Neotropics. Only approximately 350 species have been assigned to a tribe (Hoffman 1980, Pena-Barbosa et al. 2013, Bouzan et al. 2017). Chondrodesmini was proposed by Hoffman (1978) to accommodate five genera characterized primarily by gonopod and gonopod aperture morphology. Among the 21 known tribes, members of Chondrodesmini are defined by small, transversely oval gonopod apertures which do not extend outside of the prozonum; the presence of a rudimentary sternal remnant between the gonopods, which is relatively small relative to body size; coxae with medium to large dorsal apophyses (e.g., Hoffman 1978: figs 1–4) and a cingulum on the lateral side of the falcate acropodite (Hoffman 1978). At present, Chondrodesmini contains seven Neotropical genera (*Alyssa* Hoffman, 1997, *Antrogonodesmus* Hoffman, 1959, *Chondrodesmus* Silvestri, 1897, *Eumastostethus* Hoffman, 1978, *Iphyria* Chamberlin, 1941, *Leptherpum* Attems, 1931, and *Raima* Hoffman, 1978) occurring in northern South America and Central America (Hoffman 2005).

Within the Chondrodesmini, *Leptherpum* Attems, 1931 is characterized by the presence of a large spatulate prefemoral process and the lack of bilobed paramedian processes on the anterior sternites of males as found in the very similar genus *Eumastostethus* (Hoffman 1978). The genus is widely distributed across the Amazonian rainforest of northeastern South America (Hoffman 1966). A number of *Leptherpum* species have been reported from urban areas and may be synanthropic (Golovatch and Hoffman 2004). According to Hoffman (1992), and supported by collection gaps in the known distribution of *Leptherpum*, the genus likely contains many undescribed species.

Attems (1938) included *L. carinovatum* (Attems, 1898), *L. huebneri* (Attems, 1901), and *L. zernyi* Attems, 1931 in *Leptherpum*. Subsequently, Jeekel (1950) described *L. staheli* Jeekel, 1950 as a subspecies of *L. carinovatum*. Jeekel (1963) then revised the genus, adding *L. geijskesi* Jeekel, 1963 and *L. loomisi* Jeekel, 1963 to the genus, and transferred *L. zernyi* to the new genus *Brasi-loschubartia* Jeekel, 1963. In his account of the Polydesmida of the Pacaraima Mountains, Hoffman (1966) provided an updated diagnosis of *Leptherpum*, including the description of *L. jeekeli* Hoffman, 1966, and the transfer of *Polydesmus schomburgkii*

(Erichson, 1848) into *Leptherpum*. Hoffman (1992) transferred *Rachis californicus* Daday, 1891 into *Leptherpum* based on gonopod morphology. The most recent addition to the genus was made by Golovatch and Hoffman (2004) who described *Leptherpum capiberibe* Golovatch & Hoffman, 2004 from Amapá, Brazil.

Currently, the genus includes nine species: *L. californicum* ("South America" without exact locality data); *L. capiberibe* (Brazil); *L. carinovatum* (type species; Brazil, Guyana, French Guiana, Suriname, Venezuela); *L. geijskesi* (Suriname); *L. huebneri* (Venezuela); *L. jeekeli* (Guyana); *L. loomisi* (Suriname); *L. schomburgkii* (Guyana); and *L. staheli* (Guyana).

We revisit *Leptherpum* based on museum specimens and recently collected material, provide a reassessment of the type species, *L. carinovatum*, and describe three new species: *L. battirolai* sp. nov. (Amazonas, Brazil), *L. buenovillegasi* sp. nov. (Maripasoula, French Guiana), and *L. tialaura* sp. nov. (Pará, Brazil). In addition, we include a distribution map for all species along with a key to males.

MATERIAL AND METHODS

The examined material is deposited at the following institutions (curators in parentheses): IBSP, Instituto Butantan, São Paulo, Brazil (A.D. Brescovit); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (M.L. de Oliveira); ZMH, Zoologisches Museum Hamburg, Germany (D. Harms). Other collection abbreviations used in this study are as follows: BMNH, Natural History Museum [formerly British Museum] London, United Kingdom; IEPA, Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Amapá, Brazil; ZMA, Zoological Museum Amsterdam, North Holland, Netherlands. HNHM, Hungarian Natural History Museum, Budapest, Hungary and RMNH, National Museum of Natural History [= Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands (now fused into Naturalis Biodiversity Center [<http://www.naturalis.nl>]).

High-resolution photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereomicroscope. Measurements and extended focal range images were composed with Leica Application Suite version 2.5.0 (Leica Camera, Wetzlar, Germany). Scanning electron micrographs (SEM) were taken using a FEI Quanta 250 SEM with an attached SLR digital camera (Thermo Fisher Scientific) at Instituto Butantan, São Paulo, Brazil. Specimens selected for SEM imaging were cleaned using brushes and an ultrasonic cleaner Q3.8L (Eco-Sonics). The material was dissected and dehydrated through an ascending series of ethanol dilutions (70, 80, 90 and 100%; 15 minutes each), critical point dried, fixed on metal stubs with adhesive copper tape, and sputter coated with gold. All measurements were taken at 20x magnification and are reported in millimeters to an accuracy of two decimal places. Gonopod terminology follows Pena-Barbosa et al. (2013), and vulva terminology follows Koch (2015). Morphological abbreviations used in this study are as follows: (C) cingulum, (Ep) epigyne, (EV) external valve, (IV)

internal valve, (ll) lingual lobes, (me) mentum, (OP) operculum, (Pfp) prefemoral process, (S) solenomere, (SPr) secondary process of the prefemoral process, (stg) gnathochilarial stipes.

The geographic coordinates of the collection sites were obtained directly from the specimen labels or georeferenced in Google Earth Pro v. 7.1. (Alphabet Inc., Mountain View, California).

TAXONOMY

Chelodesmidae Cook, 1895
Chelodesminae Cook, 1895
Chondrodesmini Hoffman, 1978
Leptherpum Attems, 1931

Leptherpum Attems, 1931: 48. Type species: *Leptodesmus carinovatus* Attems, 1898, by original designation; Attems, 1938: 90; Schubart, 1958: 205; Jeekel, 1963: 119; Hoffman, 1966: 542; Jeekel, 1971: 269; Hoffman, 1978: 550; Hoffman, 1980: 153; Hoffman, 1997: 6; Golovatch and Hoffman, 2004: 50; Hoffman, 2005: 69.

Diagnosis. Males of *Leptherpum* differ from those of other Chondrodesmini by the following combination of characters: gonopodal prefemoral process large, concave, with an elongated and slender secondary process (Figs 15, 17); solenomere falcate and not branching (Figs 15–18, 26–28, 32–34, 38–40, 44–46); presence of marginal projections on the caudal edge of the paranota (= posterior margin of paranota with acute projections; Figs 11, 23–25, 35–37, 41–43), except in *L. capiberibe*.

Taxonomic notes. *Leptherpum* species have characteristically shaped paranota, related to the size and position of the peritrematic swelling (Jeekel 1963, Hoffman 1966). The large, prominent marginal projection (or "tooth") of the caudal edge of the paranota forms a caudolateral angle by displacing the peritremata to an anterior position (Jeekel 1963: fig. 33, Hoffman 1966: fig. 3). In *L. loomisi*, the peritremata are elongated, extending directly caudad, forming a small and weakly developed projection along the caudolateral corner of the paranota, as typical for Chelodesmidae (Jeekel 1963: fig. 34).

Distribution. Widespread in the Amazon Rainforest region of Brazil, Guyana, French Guiana, Suriname, and Venezuela.

Composition. Now composed of twelve species: *Leptherpum battirolai* sp. nov.; *Leptherpum buenovillegasi* sp. nov.; *Leptherpum californicum* (Daday, 1891); *Leptherpum capiberibe* Golovatch and Hoffman, 2004; *Leptherpum carinovatum* (Attems, 1898); *Leptherpum geijskesi* Jeekel, 1963; *Leptherpum huebneri* Attems, 1901; *Leptherpum jeekeli* Hoffman, 1966; *Leptherpum loomisi* Jeekel, 1963; *Leptherpum schomburgkii* (Erichson, 1848); *Leptherpum staheli* Jeekel, 1950; *Leptherpum tialaura* sp. nov.

Key to males of *Leptherpum*

1. Anterior edge of paranota of anterior and midbody segments with a prominent acute projection (Hoffman 1966: fig. 3).....
..... *Leptherpum schomburgkii* (Erichson, 1848)

- 1'. Anterior edge of paranota of anterior and midbody segments lacking an acute projection..... 2
2. Peritremata positioned medially on the paranota (Fig. 11) .. 3
- 2'. Peritremata positioned posteriorly on the paranota (Fig. 12)..... 8
3. Posterior margin of some anterior and midbody paranota (e.g. 5, 9, 10) with two well-defined projections (Fig. 24)... 4
- 3'. Posterior margin of anterior and midbody paranota with a single well-defined projection (Fig. 36)..... 5
4. Metazonites essentially smooth and polished (Hoffman 1966: fig. 1)..... *Leptherpum jeekeli* Hoffman, 1966
- 4'. Metazonites granulated (Fig. 9)..... *Leptherpum carinovatum* (Attems, 1898)
5. Prefemoral process of the gonopod elongate, longer than wide; oval (Fig. 32) 6
- 5'. Prefemoral process of the gonopod with subequal proportions; circular (Fig. 26) 7
6. Outer margin of prefemoral process convex; the secondary process curving upward at approximately 45° (Fig. 38); body rings dark red to nearly black (Figs 35–37)..... *Leptherpum buenovillegasi* sp. nov.
- 6'. Outer margin of prefemoral process slightly concave; the secondary process abruptly curving upward, nearly parallel to the solenomere (Figs 44–46); body rings reddish brown (Figs 41–43).....*Leptherpum battirolai* sp. nov.
7. Posterior edges of poriferous paranota emarginate beginning at body ring 15*Leptherpum geijskesi* Jeekel, 1963 (Jeekel 1963: fig. 33)
- 7'. Posterior edges of poriferous paranota emarginate beginning at body ring 10*Leptherpum staheli* Jeekel, 1950 (Jeekel 1950: fig. 4)
8. Marginal projections on the caudal edge of paranota of midbody rings absent (Golovatch and Hoffman 2004: fig. 2).....*Leptherpum capiberibe* Golovatch & Hoffman, 2004
- 8'. Marginal projections on the caudal edge of paranota of midbody rings present (Fig. 24) 9
9. Secondary process of the gonopod robust and spatulate (Fig. 15)..... 10
- 9'. Secondary process of the gonopod slender and only slightly spatulate at apex (Fig. 17) 11
10. Prefemur of post gonopodal legs with a ventroapical projection (arrow; Fig. 47) *Leptherpum huebneri* Attems, 1901
- 10'. Prefemur of post gonopodal legs without a ventroapical projection *Leptherpum californicum* (Daday, 1891)
11. Secondary process arising basally from the prefemoral process *Leptherpum loomisi* Jeekel, 1963 (Jeekel 1950: fig. 5)
- 11'. Secondary process arising medially from the prefemoral process (Fig. 33).....*Leptherpum tialaura* sp. nov.

***Leptherpum carinovatum* (Attems, 1898)**

Figs 3–9, 11, 13, 15–16, 23–28, 53

Leptodesmus carinovatus Attems, 1898: 376, plate 6, figs 127–129, plate 7, fig. 154 (two males syntypes from Manaus (3°04'49.1"S; 60°00'19.4"W), Amazonas, Brazil, Bicego leg., deposited at ZMH, examined). Attems, 1901: 85; Brölemann, 1904: 74; Brölemann, 1909: 64.

Dirhabdophallus carinovatus: Pocock, 1909: 165.

Leptherpum carinovatum: Attems, 1931: 49, fig. 71; Attems, 1938: 91, fig. 104; Jeekel, 1963: 127, figs 39–40; Jeekel, 2009: 24.

Material examined. BRAZIL: Amazonas: Manaus (3°04'49.1"S; 60°00'19.4"W), 2 males syntypes, Bicego leg. (ZMH); 3 males, 1 female, xi.1983–iv.1984, J. Adis leg. (INPA 395); Rio Preto da Eva, Região Metropolitana, (2°41'51.2"S; 59°41'47.4"W), 2 males, 17.viii.2018, A.P. dos Santos leg. (IBSP 8300).

Historical records. GUYANA: Upper Demerara-Berbice: Canister Falls; (4°48'00.0"N; 58°26'00.0"W), Cattle Trail Survey, 1 male, vi.1920, A.A. Abraham leg. (BMNH) (Jeekel, 1963); East Berbice-Corentyne: source of Kutari (= Kutari River) (2°20'34.3"N; 56°52'06.4"W), 2 males, vi.1936, C.A. Hudson leg. (BMNH) (Jeekel, 1963); SURINAME: Sipaliwini: Mt. Janbasigodo, 1 male, 20.xii.1902, P.J. de Kock leg. (RMNH) (Jeekel, 1963); Tugumutu (= Toekoemoetoe) (4°12'00.0"N; 55°54'00.0"W), 1 male, 1 female, 10–14.ii.1903, P.J. de Kock leg. (RMNH) (Jeekel, 1963); Para: Mapane (= Mapane Kreek), savanna forest (5°28'00.0"N; 54°41'00.0"W), 5 males, 1 female, 10.xii.1953, D.C. Geijskes leg. (ZMA) (Jeekel, 1963).

Distribution. Guyana, French Guiana, Suriname, Venezuela, and the Brazilian state of Amazonas (Fig. 53).

Remarks. According to the original description (Attems 1898), the type material of *Leptodesmus carinovatus* includes two male specimens. However, the ZMH storage container has a single male specimen with intact gonopods, and a microvial containing the dissected gonopods of the second male (N. Duperre, pers. comm.).

***Leptherpum californicum* (Daday, 1891)**

Rachis californicus Daday, 1891: 142, plate 7, fig. 12 (male holotype labeled "California" [probably from Guyana, French Guiana, or an adjacent part of Brazil or Venezuela], deposited at HNHM, lost).

Rhachodesmus californicus: Attems, 1940: 466.

Leptherpum californicum: Hoffman, 1992: 61.

Distribution. Unknown.

***Leptherpum capiberibe* Golovatch & Hoffman, 2004**

Fig. 53

Leptherpum capiberibe Golovatch and Hoffman, 2004: 50, figs 1–5 (male holotype from Campus Zoobotânico da Universidade Federal do Amapá (0°02'04.5"N; 51°04'12.6"W), Macapá, Amapá, Brazil, 06.i.1994, J.M. da Rocha leg., deposited at IEPA, not examined).

Distribution. Brazil.

***Leptherpum geijskesi* Jeekel, 1963**

Fig. 53

Leptherpum geijskesi Jeekel, 1963: 121, figs 33, 35 (male holotype from Nassau Mountains (4°47'60.0"N; 54°36'00.0"W), Suriname, iii.1949, D.C. Geijskes leg., deposited at RMNH, not examined); Jeekel, 2009: 71.

Distribution. Suriname.

Leptherpum huebneri Attems, 1901

Leptodesmus hübnerei Attems, 1901: 93, plate 2, figs 22, 23 (male holotype from Süd-Venezuela, deposited at ZMH, not examined). Attems, 1931: 48; Attems, 1938: 91, fig. 105.

Leptodesmus (Leptodesmus) huebneri: Weidner, 1960: 84.

Leptherpum huebneri: Jeekel, 1963: 119.

Leptherpum huebneri: Bueno-Villegas et al., 2019: 163.

Distribution. Venezuela.

Leptherpum jeekeli Hoffman, 1966

Fig. 53

Leptherpum jeekeli Hoffman, 1966: 543, figs 1, 2 (male holotype from Pacaraima Mountains (5°00'00.4"N; 60°59'54.2"W), British Guiana, 9.xi.1932, D. Vesey-Fitzgerald leg., deposited at BMNH, not examined).

Distribution. Guyana.

Leptherpum loomisi Jeekel, 1963

Fig. 53

Leptherpum loomisi Jeekel, 1963: 126, figs 34, 37 (male holotype from Wilhelmina Mountains, line I (3°44'60.0"N; 56°30'00.0"W), Suriname, viii-ix.1943, D.C. Geijskes leg., deposited at RMNH, not examined). Jeekel, 2009: 24.

Distribution. Suriname.

Leptherpum schomburgkii (Erichson, 1848)

Polydesmus schomburgkii Erichson, 1848: 552 (male holotype from British Guiana, R. Schomburgk leg., deposited at ZMB, not examined); Jeekel, 1963: 117.

Polydesmus (Rhacophorus) Schomburgkii: Peters, 1865: 537.

Rhacophorus schomburgkii: Attems, 1938: 200.

Leptherpum schomburgkii: Hoffman, 1966: 547, fig. 3.

Distribution. Guyana.

Leptherpum staheli Jeekel, 1950

Fig. 53

Leptherpum carinovatum staheli Jeekel, 1950: 71, figs 4–5 (male holotype from Wilhelmina Mountains, near the Lucie Rivier (3°44'60.0"N; 56°30'00.0"W), Suriname, 1926, D.S. Fernandes leg., deposited at ZMA, not examined).

Leptherpum staheli: Jeekel, 1963: 125, figs 36, 38; Jeekel, 2009: 24

Distribution. Suriname.

Leptherpum tialaura Bouzan, Means, Ivanov & Brescovit, sp. nov.

Figs 1–2, 10, 12, 14, 17–18, 19–22, 29–34, 53

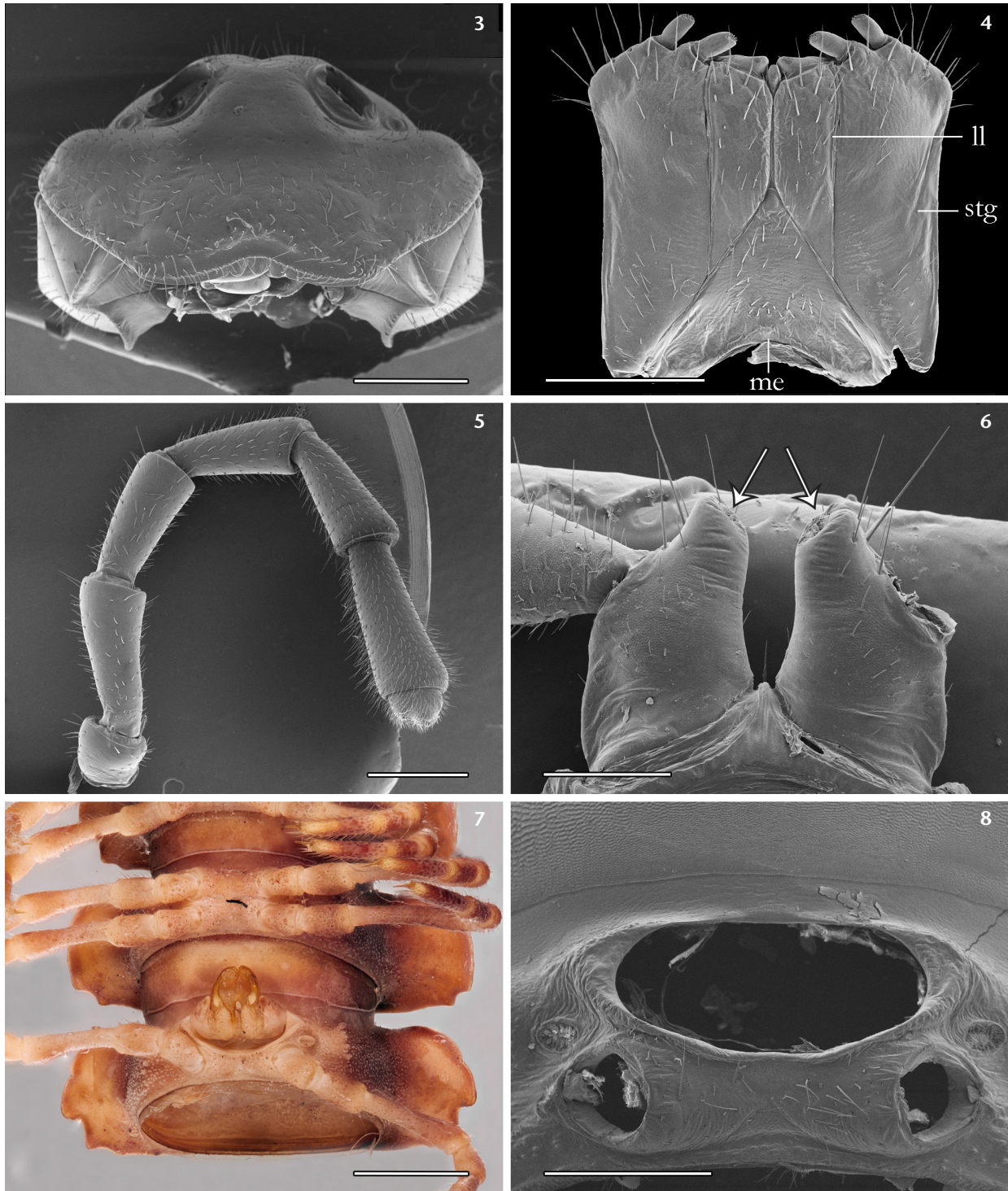
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Diagnosis. Adult males differ from all other species of the genus by the following combination of characters: secondary process of the gonopod slender, only slightly spatulate at apex, arising medially from the prefemoral process of the gonopod (Figs 32–34); presence of small tooth on the posterior border of the midbody paranota.

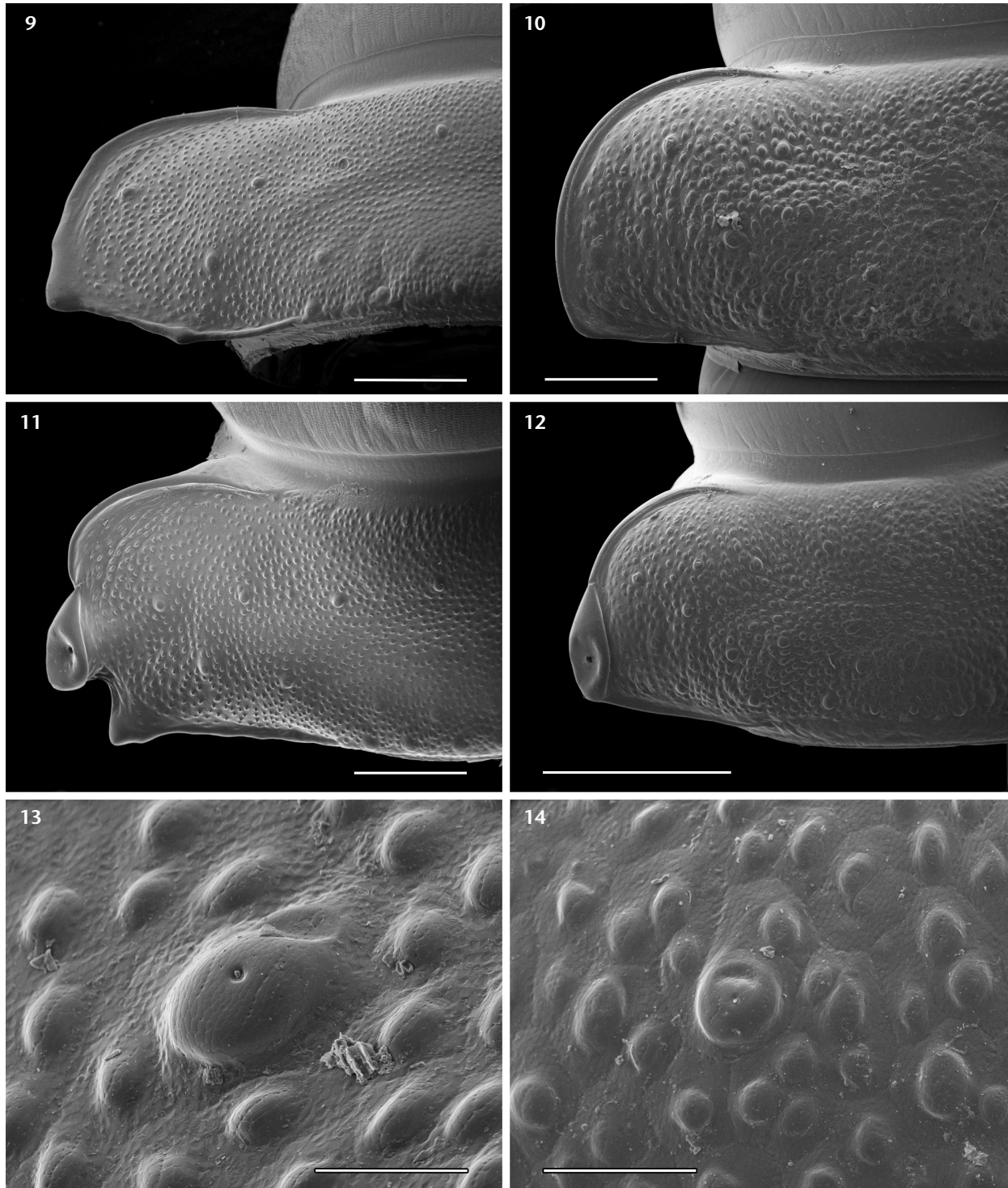
Description. Male (Holotype, IBSP 7972). Coloration (preserved in 70% ethanol): head and antennae reddish brown, 7th antennomere and labrum yellowish; body and paranota tips reddish brown (Figs 1–2, 29–31); legs reddish brown (Figs 2, 29–31); telson dark reddish (Fig. 31). Head: labrum and clypeus covered with sparse setae; two (1+1) small setae between the antennal sockets and two (1+1) above the antennae; vertex of the head with two (1+1) setae; incisura lateralis suboval. Antennae: almost reaching the 4th body ring; 5th, 6th and 7th antennomeres with a grouping of basiconic sensilla in small clusters on the distal and external margin. Body rings: absence of a sulcus on the metaterga; cuticle with several small tubercles scattered across the metazonites (Fig. 14); metazonites with scattered large tubercles in addition



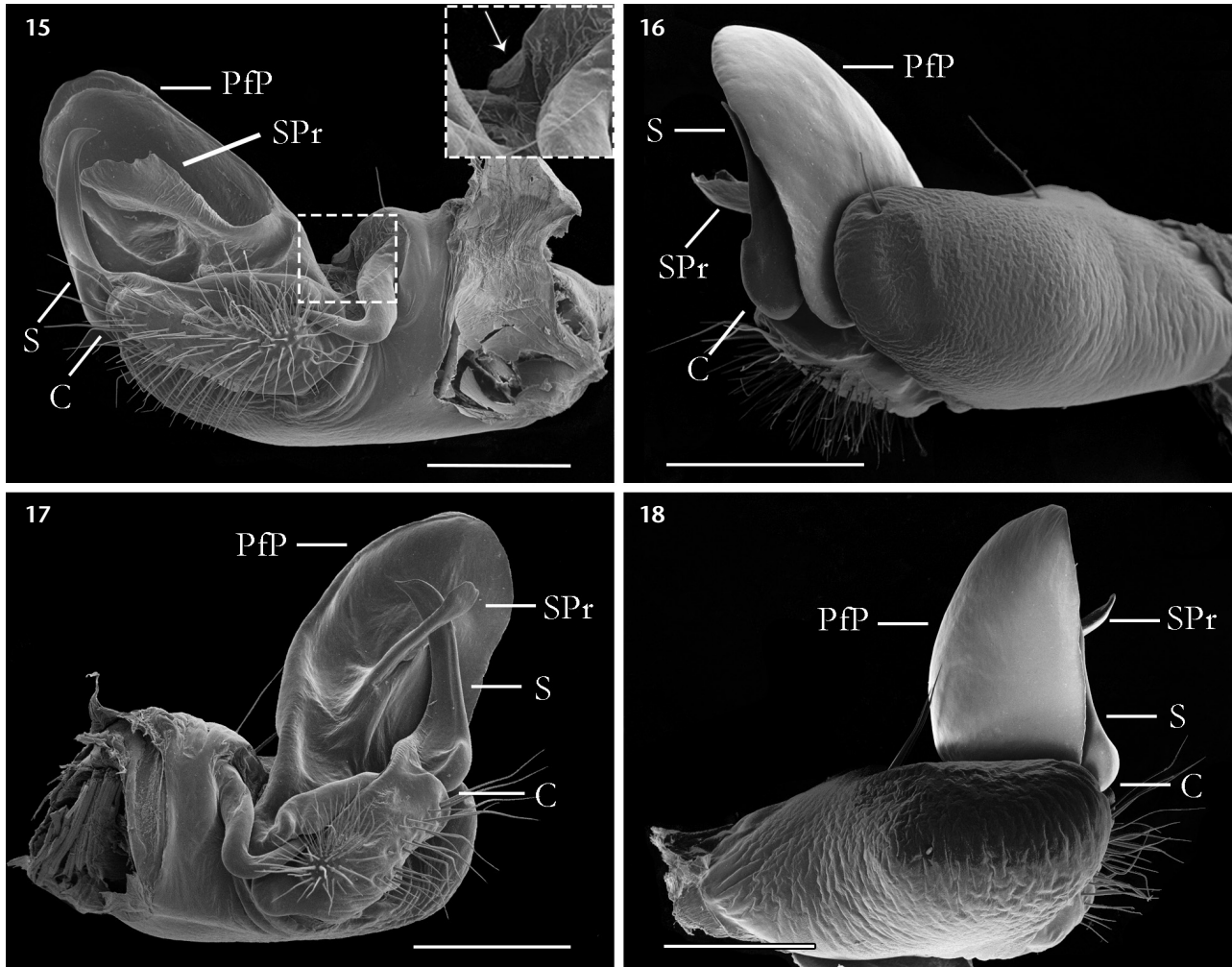
Figures 1–2. Habitus of living *Leptherpum tialaura* sp. nov. Photo: G. Puerto.



Figures 3–8. General somatic features of *L. carinovatum* (Attems, 1898). (3) male (IBSP 8300), head, oral view; (4) male (IBSP 8300), gnathochilarium, ventral view; (5) male (IBSP 8300), antenna, lateral view; (6) male (IBSP 8300), coxae of 2nd pair of legs, showing the gonopores, ventral view; (7) male syntype (ZMH), detail of body rings 6–7, ventral view; (8) male (IBSP 8300), body ring 7, detail of gonopod aperture, ventral view. The arrows point to the gonopores. Scale bars: 3–5, 8 = 1 mm; 6 = 500 μ m; 7 = 2.5 mm.



Figures 9–14. General somatic features of *Leptherpum* Attems, 1931. (9), (11), (13) *L. carinovatum* (IBSP 8300), male, metazonites, dorsal view; (9) body ring 8; (11) body ring 9; (13) detail of tubercles of body ring 9; (10), (12), (14) *Leptherpum tialaura* sp. nov. (male holotype, IBSP 7972), metazonites, dorsal view; (10) body ring 8; (12) body ring 9; (14) detail of tubercles of body ring 9. Scale bars: 9–11 = 1 mm; 12 = 2 mm; 13 = 100 μ m; 14 = 200 μ m.



Figures 15–18. Gonopodal features of *Leptherpum* Attems, 1931. (15) *L. carinovatum* (IBSP 8300), male, right gonopod, mesal view; (16) *L. carinovatum* (IBSP 8300), male, left gonopod, ectal view; (17) *L. tialaura* sp. nov. (IBSP 7952), male, left gonopod, mesal view; (18) *L. tialaura* sp. nov. (IBSP 7952), male, right gonopod, ectal view. The arrow refers to the spiniform process. Scale bars: 15–18 = 500 μ m.

to a well-defined and easily recognized horizontal row of large tubercles along the posterior margin region (Figs 10, 12, 29, 30). Sternite of fourth segment with a pair of acute projections; sternite of fifth segment with a triangular swelling; sternite of sixth segment with two pairs of small, acute projections, becoming more conspicuous along the post-gonopodal sternites. Paranota: anterior border rounded, posterior border sub-rectangular (Figs 10, 12); metazonites 5–7 with a small “tooth” on the posterior border. Ozopore arrangement: 5, 7, 9, 10, 12, 13, 15–19 (following the typical polydesmidan pore formula); ozopores surrounded by peritremata and facing up at an angle of 45°; peritremata oval and positioned posteriorly on the paranota (Fig. 12). Legs without modifications, except for a conspicuous dorsal lobe on the prefemur. Telson: triangular (Fig. 31); epiproct with (3+3) macrosetae on the dorsal side supported by small projections; two

pairs (2+2) of spinnerets, superior pair more closely positioned to each other as compared to the inferior one; paraprocts each with two macrosetae; hypoproct subtriangular with one pair (1+1) of macrosetae. Subtriangular gonopore on coxae of second leg-pair (Fig. 6, arrows). Gonopod aperture transversely oval, as typical for the genus, small, with a lateral pair of sclerotized triangular slit to accommodate the gonopods (Fig. 8).

Total length: 74.00. Total width: 8.56. Antennomere lengths (1–7): 0.83; 1.92; 1.83; 1.65; 1.51; 1.75; 0.32. Podomere lengths (1–7): 0.68; 0.95; 2.57; 0.91; 1.00; 1.96; tarsal claw 0.43. Gonopod aperture: length 0.87, width 1.87. Telson length 1.80. Gonopod: length 1.61, width 1.62. Gonocoxae: length 0.72, width 1.52. Telopodite: length 1.61, width 0.72. Gonopods (Figs 17–18, 32–34): gonocoxae subequal to the length of the telopodite, globose, greatly expanded on the ectal side (Fig. 34),

with a small spiniform process; two macrosetae on dorsal side; prefemoral region ventrally positioned and setose, same length as the solenomere (Fig. 17); prefemoral and acropodite regions separated by a cingulum basally (C; Figs 17–18); prefemoral process (PFP; Fig. 17) typical for the genus (e.g., large and concave; spoon-shaped), longer than the solenomere, containing a medially positioned elongate and slender secondary process (Figs 17–18); solenomere falciform, carrying the seminal groove to apical point (S; Fig. 17).

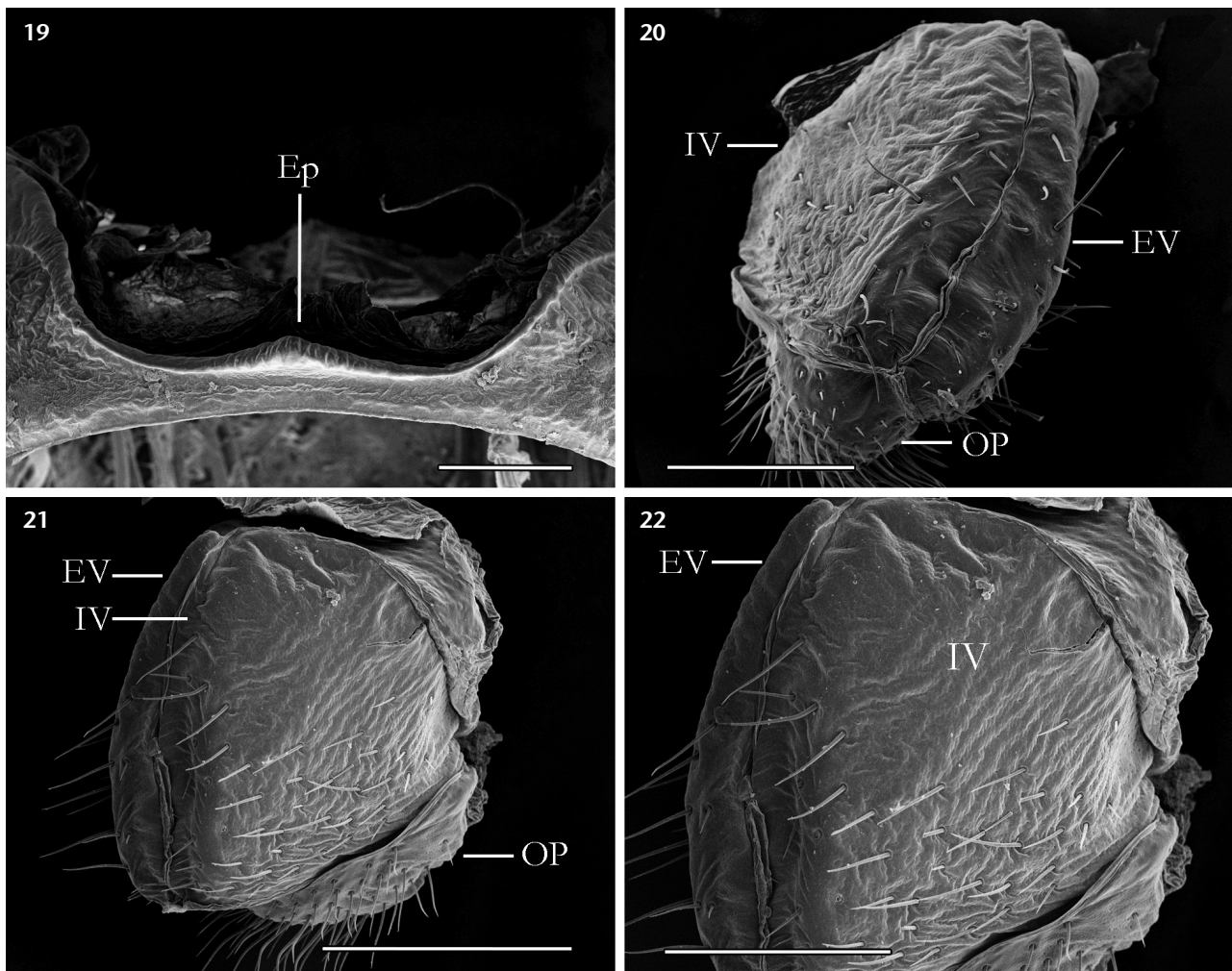
Female (Paratype, IBSP 3751). Coloration as in male (Figs 1–2, 29–31). Sternites wider than in males; sternal projections less conspicuous, present only on the posterior portion of the last segments. Metazonites without a “tooth” on the posterior border. Ozopores of segments 5, 7, and 8 positioned medially on paranota.

Posterior margin of vulvae opening with a small rounded epigyne (Ep; Fig. 19). Vulvae oval in ventral view (Fig. 20); sub-

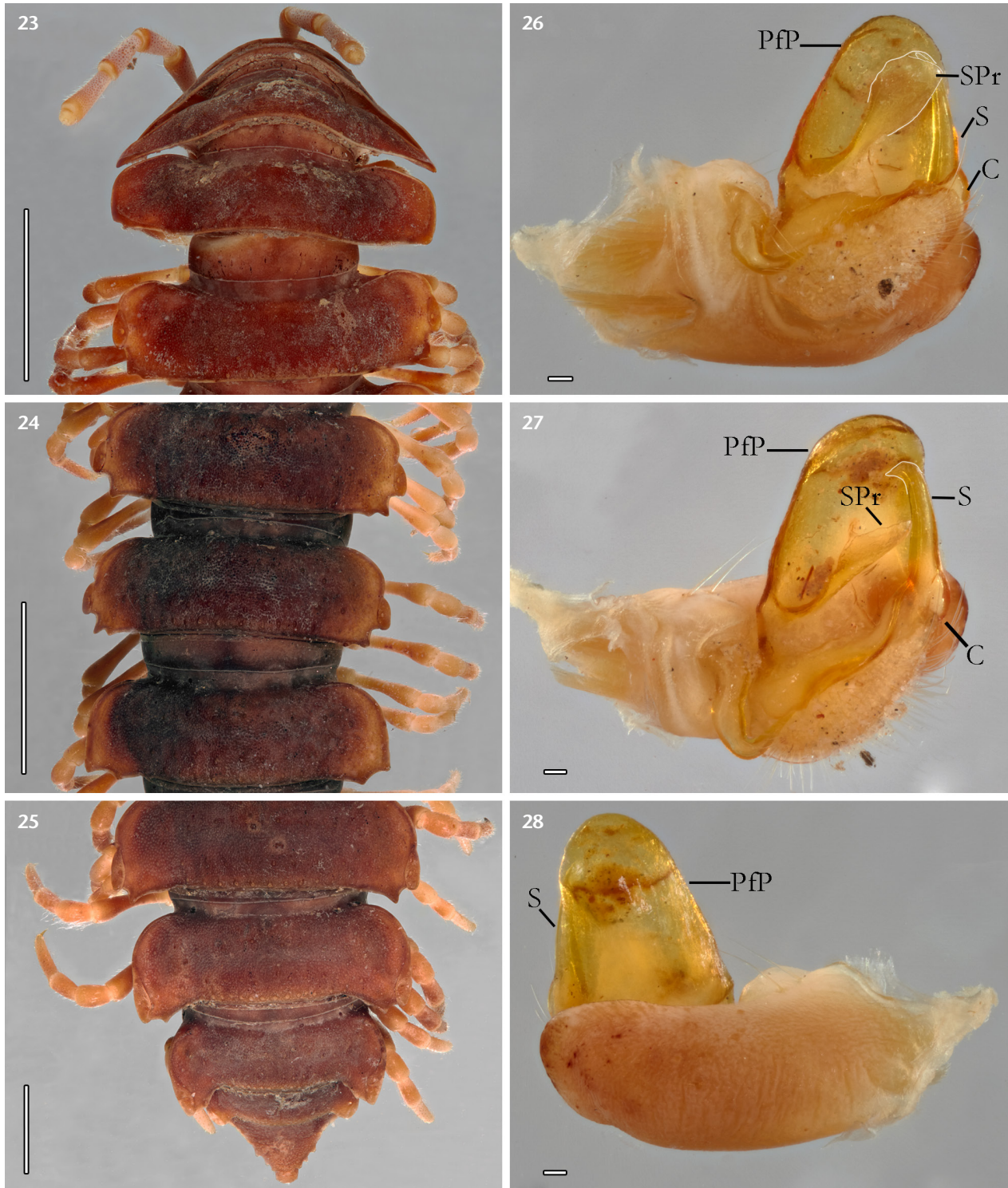
triangular in lateral view (Figs 21, 22). Total length: 66.70. Total width: 8.11. Width of posterior margin of vulvar aperture 1.74. Vulvae: length 0.76, width 0.50. External valve: length 0.56, width 0.25. Internal valve: length 0.55, width 0.24. Operculum: length 0.22, width 0.41. Both valves with scattered setae (Figs 21, 22). Operculum broad and densely setose (OP; Figs 20, 21).

Type material. Holotype: male from Km 83, FLONA do Tapajós (3°31'01"S; 55°04'23"W), Belterra, Pará, Brazil, 28.x.2010, A.D. Brescovit leg. (IBSP 7972). Paratypes: 1 male, same data as for holotype (IBSP 13365); 1 female from Mata do Butantan (2°38'9"S; 54°56'13"W), Belterra, v.2010, A.D. Brescovit et al. leg. (IBSP 3751); 1 male from FLONA do Tapajós, Belterra, x.2011, A.D. Brescovit leg. (IBSP 4544); 1 male from FLONA do Tapajós, Belterra, 16–20.x.2013, A.D. Brescovit leg. (IBSP 8302).

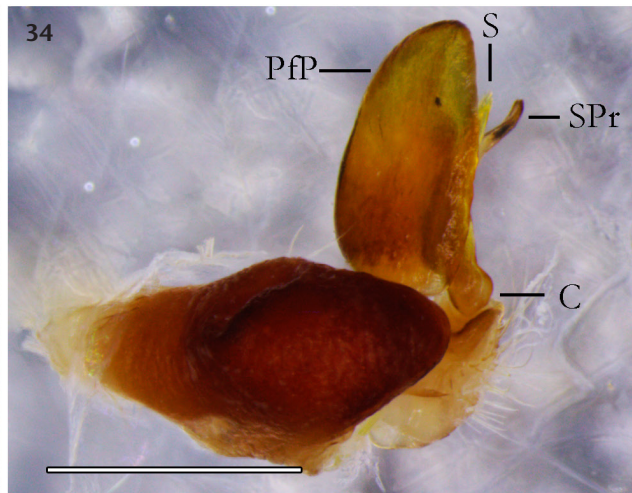
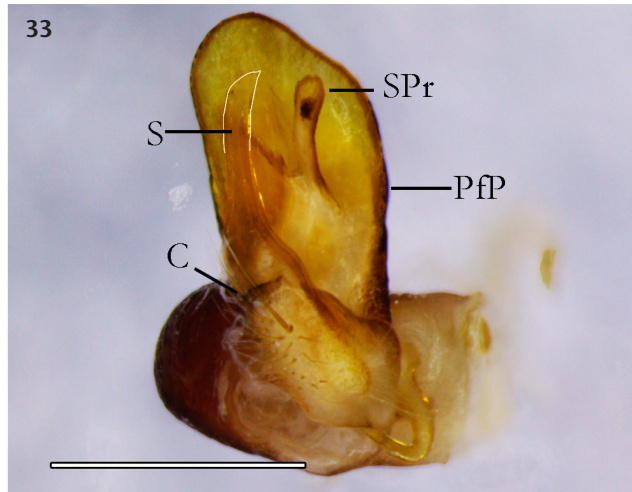
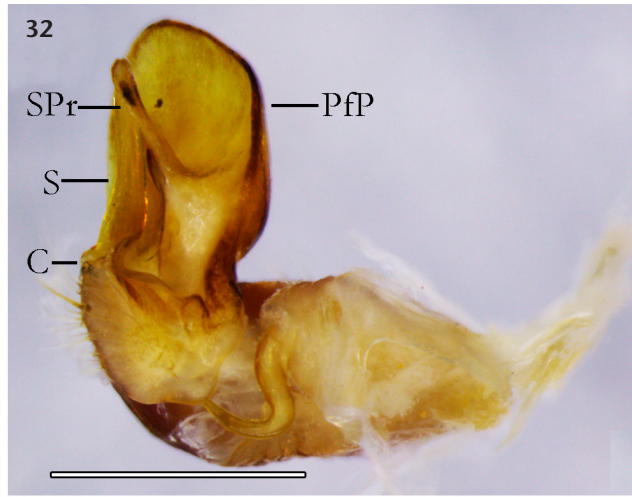
Additional material examined. BRAZIL: Pará: Belterra, FLONA do Tapajós (3°31'01"S; 55°04'23"W), 1 female, 10–13.



Figures 19–22. *Leptherpum tialaura* sp. nov. (IBSP 4130), female. (19) epigyne, ventral view; (20) left vulva, ventral view; (21), (22) right vulva, ventrolateral view. Scale bars: 19 = 500 μ m; 20 = 300 μ m; 21–22 = 400 μ m.



Figures 23–28. *Leptherpum carinovatum* (Attems, 1898), male syntype (ZMH). (23) anterior body rings, dorsal view; (24) midbody rings, dorsal view; (25) posterior body rings, dorsal view; (26), (27) left gonopod, mesal view, different gonopod tilt degrees; (28) left gonopod, ectal view. Scale bars: 23–24 = 5 mm; 25 = 2.5 mm; 26–28 = 100 μ m.



Figures 29–34. *Leptherpum tialaura* sp. nov., male holotype (IBSP 7972). (29) anterior body rings, dorsal view; (30) midbody rings, dorsal view; (31) posterior body rings, dorsal view; (32) right gonopod, mesal view; (33) right gonopod, ventral view; (34) right gonopod, ectal view. Scale bars: 29–34 = 1 mm.

xii.2012, C.S. Costa et al. leg. (IBSP 4130); 1 female, x.2011, A.D. Brescovit et al. (IBSP 4543); 1 male, 2018, H. Chalkidis leg. (IBSP 7912); Belterra, APA Aramaná (2°37'57.96"S; 54°57'44.16"W), 1 female, v.2010, A.D. Brescovit leg. (IBSP 3945); 1 male, 01.viii.2018, A.D. Brescovit and G. Puerto leg. (IBSP 8118); 2 females, 11.iv.2019, A.D. Brescovit and G. Puerto leg. (IBSP 8552); Belterra, Mata do Butantan (2°38'9"S; 54°56'13"W), 3 males, 01–05.v.2011, Equipe IBSP leg. (IBSP 7952); 2 males, v.2010, A.D. Brescovit et al. leg. (IBSP 13366); Belterra, Comunidade São Pedro, Km 50, BR 163 (2°45'11.3"S; 54°54'01.6"W), 1 male, 18.viii.2019, A.D. Brescovit leg. (IBSP 7963); 2 juveniles, 07.iv.2019, A.D. Brescovit leg. (IBSP 8558); Santarém, Comunidade do Cedro, Km 933, BR 163 (2°27'30.9"S; 54°42'39.5"W), 1 male, A.D. Brescovit and G. Puerto leg. (IBSP 8303); Km 933, 1 female, 17.viii.2019, A.D. Brescovit and G. Puerto leg. (IBSP 8017); Medicilândia, Cave Limoeiro (52°47'25.49"W; 03°30'43.8"S), 1 juvenile, 24–26.vii.2012, R. Pinto da Rocha leg. (IBSP 4198).

Distribution. Known only from the Brazilian state of Pará (Fig. 53).

Etymology. The species epithet is a reference to the nickname of Laura Cristina de Souza, a distinguished Biology professor in the city of Belterra, Pará, and a great friend.

Leptherpum buenovillegasi Bouzan, Means, Ivanov & Almeida, sp. nov.

Figs 35–40, 53

<https://zoobank.org/CDFBE356-72E5-4445-8B80-76195CEA10B6>

Diagnosis. Adult males differ from all other species of the genus by the following combination of characters: prefemoral process longer than wide, oval; secondary process spatulate, arising from the basal inner margin of the prefemoral process (Fig. 39) and curving upward at approximately 45°; color of body rings dark red to black (Figs 35–37).

Description. Male (Holotype, INPA 396). Coloration (preserved in 70% ethanol): head and antennae dark reddish; labrum lighter than the head; 7th antennomere yellowish; body and paranota tips dark red, nearly black (Figs 35–37); legs reddish brown, lighter than paranota (Fig. 36); telson dark reddish (Fig. 37). Head: with several thin setae; incisura lateralis suboval. Antennae: almost reaching the 5th body ring; 5th, 6th and 7th antennomere with a grouping of basiconic sensilla in small clusters on the distal and external margin. Body rings: cuticle with several small tubercles scattered across the metazonites; some larger tubercles along the posterior edge region of the metazonites, distributed in two nearly horizontal rows; large tubercles barely noticeable on the last segments (Fig. 37). Sternites with several thin elongate setae; sternite of sixth segment with two pairs of small, acute projections, becoming more conspicuous along the post-gonopodal sternites. Paranota: anterior border rounded; posterior border sub-rectangular (Fig. 35–37); metazonites 6, 8, 11, and 14 with small “tooth” on the posterior border (Fig. 36). Ozopore arrangement: 5, 7, 9, 10, 12, 13, 15–19 (following the

typical polydesmidan pore formula); ozopores surrounded by peritremata, positioned medially on paranota; peritremata suboval, projected laterally (Fig. 36). Legs without modifications, except for a conspicuous dorsal lobe on the prefemur. Telson: triangular (Fig. 37); epiproct with (3+3) macrosetae on the dorsal side supported by small projections; two pairs (2+2) of spinnerets, superior pair more closely positioned to each other as compared to the inferior one; paraprocts each with two macrosetae; hypoproct triangular with one pair of macrosetae supported by small triangular projections. Gonopod aperture transversely oval, as typical for the genus, small, with a lateral pair of sclerotized triangular slit to accommodate the gonopods (Fig. 8).

Total length: 55.30. Total width: 8.13. Antennomere lengths (1–7): 0.68; 1.77; 1.53; 1.38; 1.29; 1.61; 0.31. Podomere lengths (1–7): 0.49; 0.89; 2.34; 0.80; 0.82; 1.44; tarsal claw 0.26. Gonopod aperture: length 0.85, width 1.88. Telson length: 1.07. Gonopod: length 1.65, width 1.74. Gonocoxae: length 0.67, width 1.46. Telopodite: length 1.60, width 0.77. Gonopods: gonocoxae subequal to the length of the telopodite, globose, projected on the ectal side (Fig. 40); with a small spiniform process; two macrosetae present on the dorsal side and two additional macrosetae present on the terminal portion of the ectal side. Prefemoral region ventrally positioned and setose, approximately 1/2 the length of the solenomere (Figs 38, 39). Prefemoral and acropodite regions separated by a cingulum basally (C; Figs 38–40). Prefemoral process (Pfp; Fig. 38): longer than wide; longer than the solenomere; containing a thin (Fig. 38) and spatulate (Fig. 39) secondary process on the inner margin of its basal portion. Solenomere falciform, carrying the seminal groove to apical point (S; Figs 38–40).

Female. Unknown.

Type material. Holotype: male from Crique Alama (2°13'40.6"N; 54°27'58.1"W), Maripasoula, French Guiana, 08.iii.2015, alt. 595m, V. Vedel leg. (INPA 396).

Distribution. Known only from Maripasoula, French Guiana (Fig. 53).

Etymology. The specific epithet is a patronym in honor of Dr. Julián Bueno Villegas for his friendship and outstanding contributions to our knowledge of millipedes.

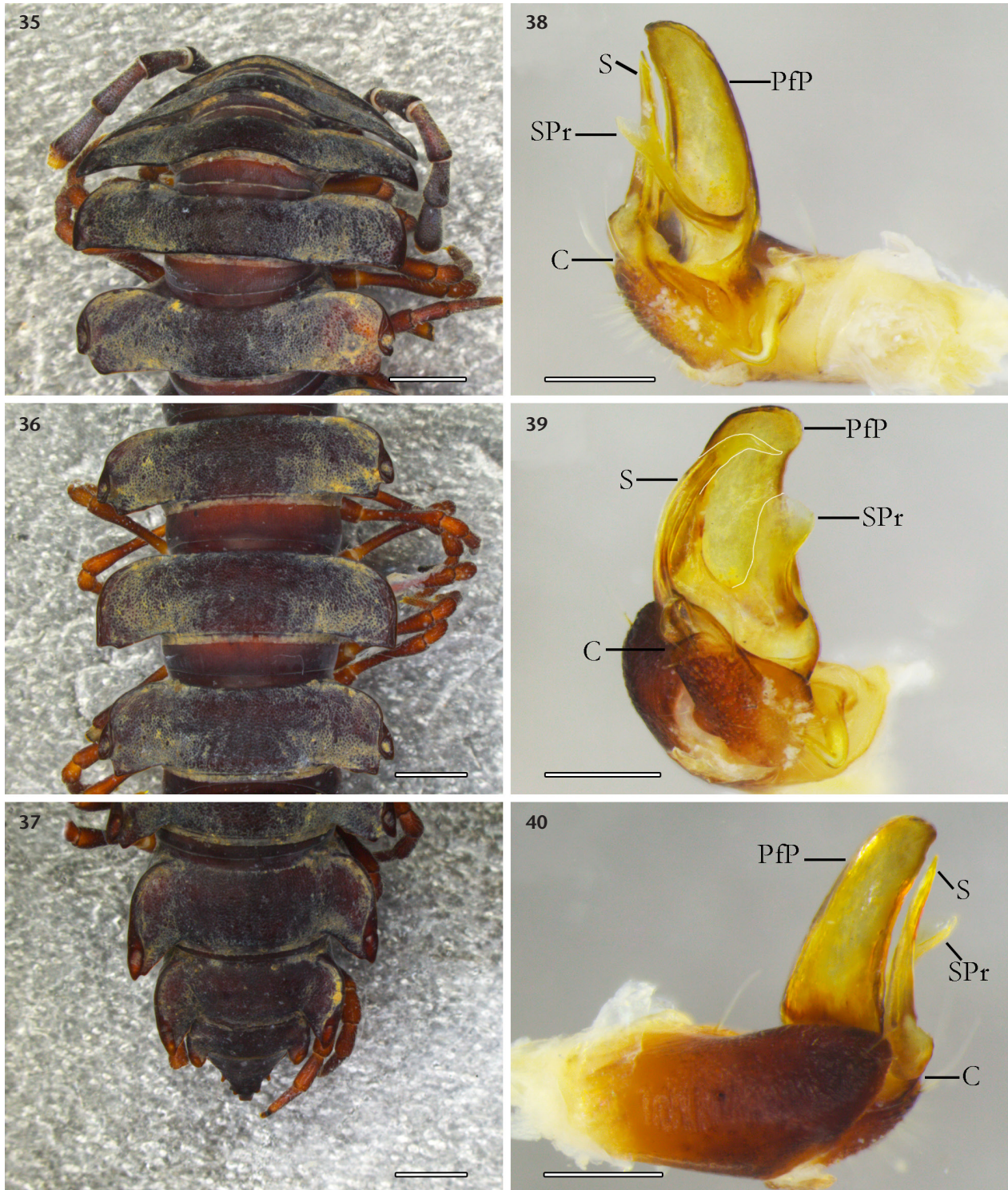
Leptherpum battirolai Bouzan, Means, Ivanov & Brescovit, sp. nov.

Figs 41–53

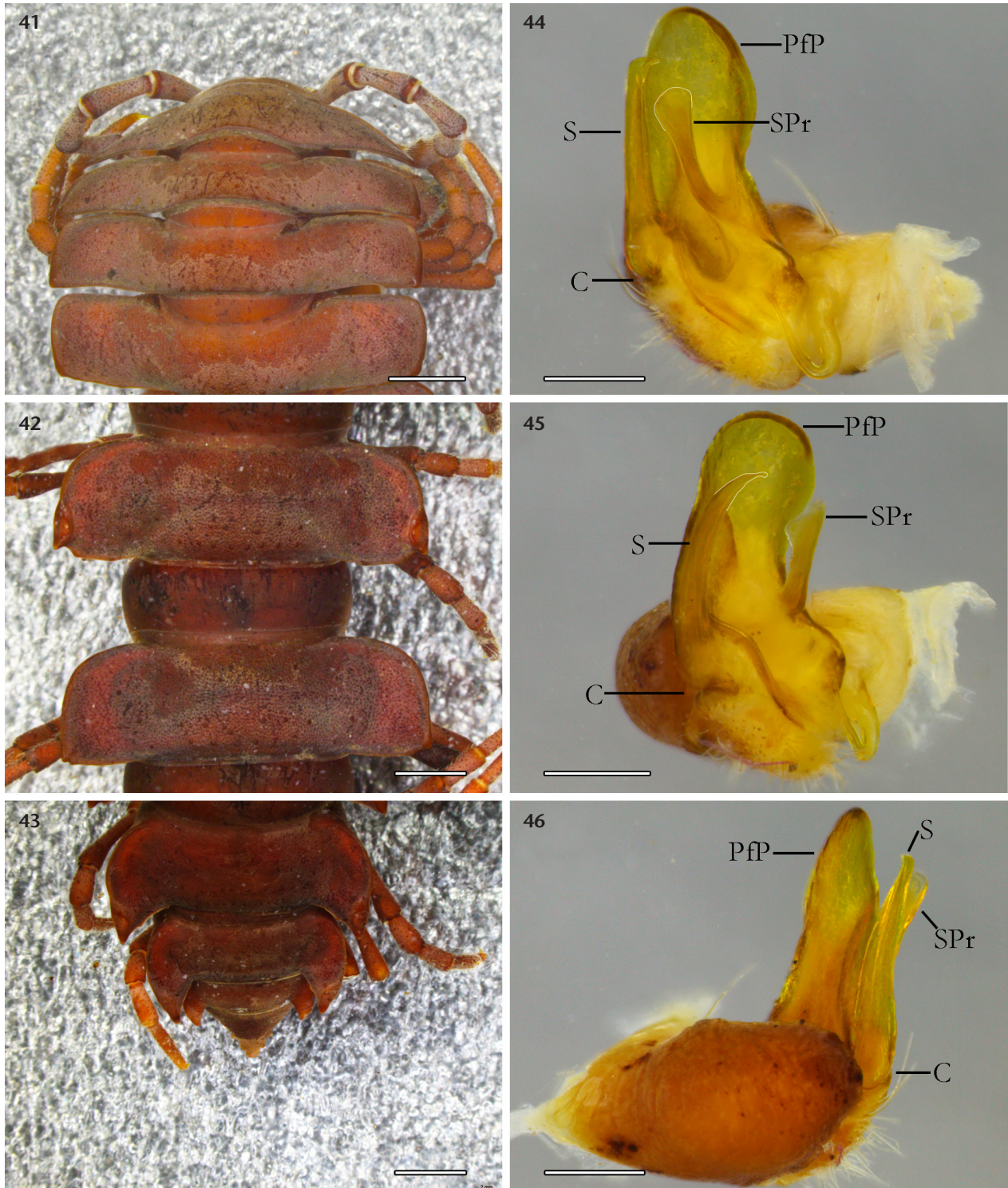
<https://zoobank.org/D68616D4-B1E9-461E-AA90-E21846619F17>

Diagnosis. Adult males differ from all other species of the genus by the following combination of characters: prefemoral process longer than wide, oval; secondary process spatulate, arising from the basal inner margin of the prefemoral process and abruptly curving upward, nearly parallel to the solenomere (Figs 44, 45); prefemur of post-gonopodal legs with a ventroapical projection (Fig. 47); color of body rings light red to red (Figs 41–43).

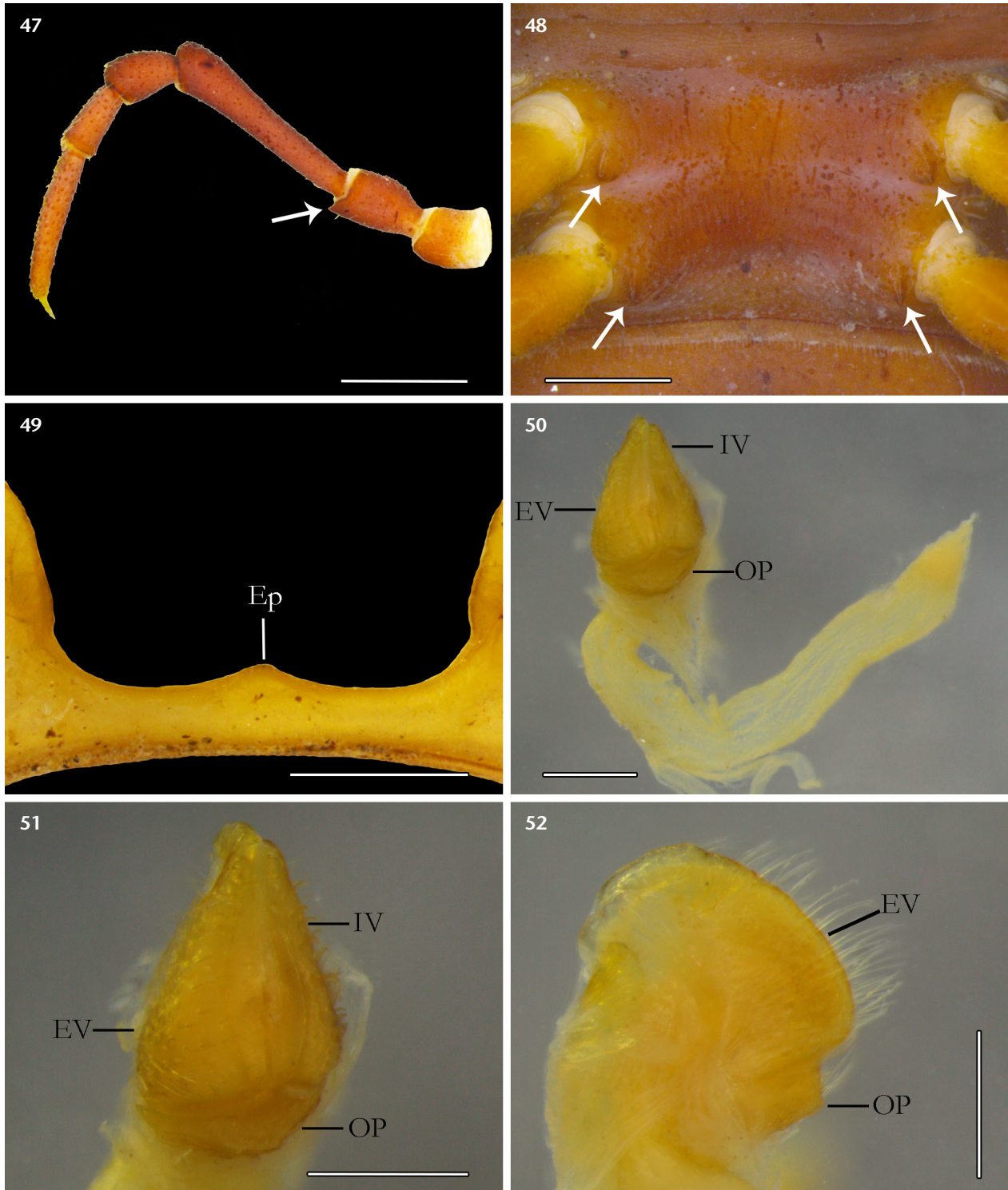
Description. Male (Holotype, INPA 397). Coloration



Figures 35–40. *Leptherpum buenovillegasi* sp. nov., male holotype (INPA 396). (35) anterior body rings, dorsal view; (36) midbody rings, dorsal view; (37) posterior body rings, dorsal view; (38) right gonopod, mesal view; (39) right gonopod, ventral view; (40) right gonopod, ectal view. Scale bars: 35–37 = 2 mm; 38–40 = 500 μ m.



Figures 41–46. *Leptherpum battirolai* sp. nov., male holotype (INPA 397). (41) anterior body rings, dorsal view; (42) midbody rings, dorsal view; (43) posterior body rings, dorsal view; (44) right gonopod, mesal view; (45) right gonopod, ventral view; (46) right gonopod, ectal view. Scale bars: 41–43 = 2 mm; 44–46 = 500 μ m.



Figures 47–52. *Leptherpum battirolai* sp. nov. (47), (48) male holotype (INPA 397). (47) leg of body ring 8, lateral view; (48) sternite of body ring 10, ventral view; (49)–(52) female paratype (INPA 398). (49) epigyne, ventral view; (50), (51) right vulva, ventral view; (52) right vulva, lateral view. Scale bars: 47 = 2 mm; 48–49 = 1 mm; 50–51 = 500 μ m.

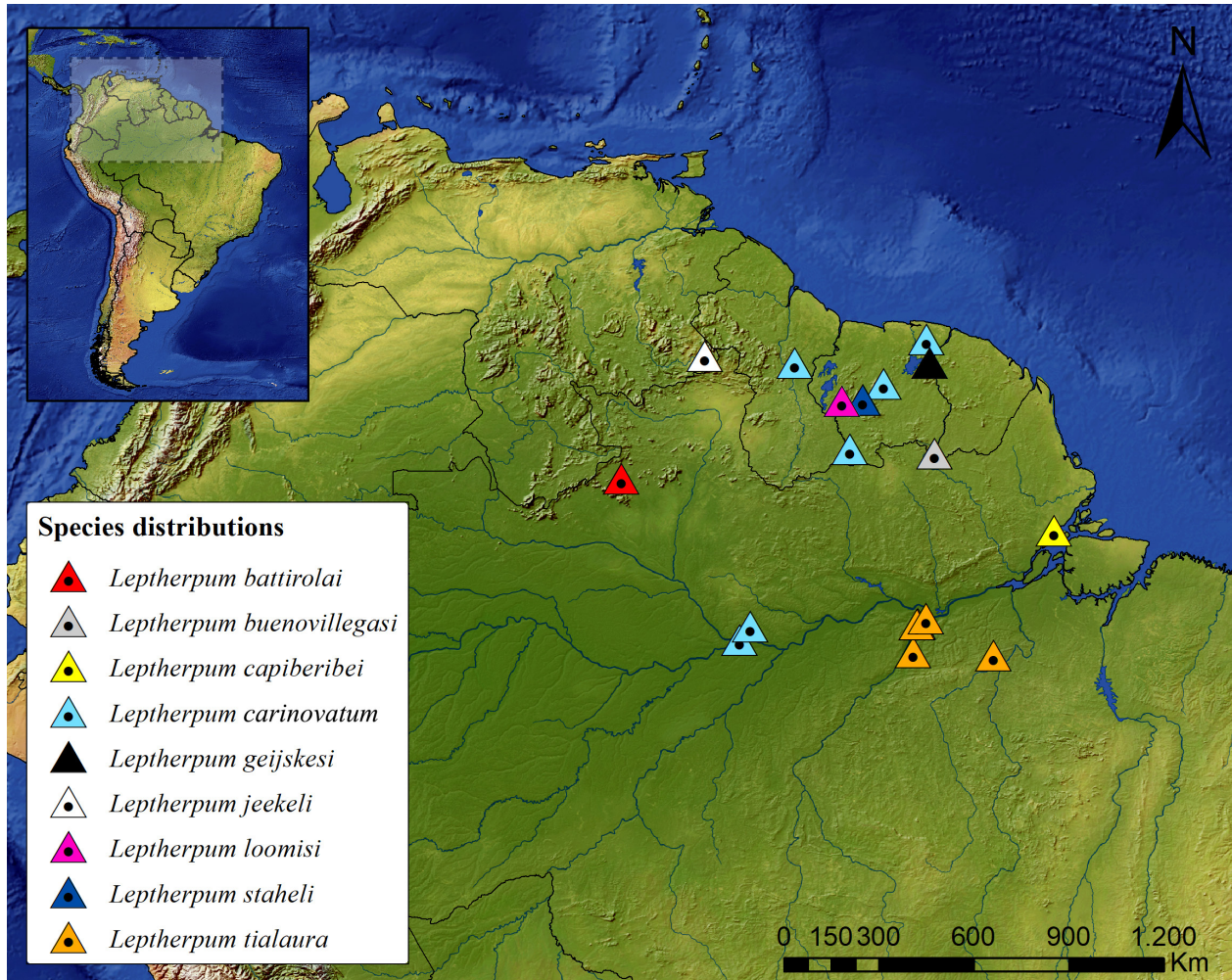


Figure 53. Distribution map of *Leptherpum* Attems, 1931 species. Taxa without precise geographic coordinates, i.e., *L. californicum*, *L. huebneri*, and *L. schomburgkii*, are not shown.

(preserved in 70% ethanol): head and antennae reddish brown; body and paranotal tips reddish brown (Figs 41–43); legs reddish brown (Figs 41, 47); telson dark reddish (Fig. 43). Head: labrum and clypeus setose; two (1+1) small setae between the antennal sockets and two additional (1+1) setae above the antennae; vertex of the head with two (1+1) setae; incisura lateralis suboval. Antennae: almost reaching the 5th body ring; 5th, 6th and 7th antennomere with a grouping of basiconic sensilla in small clusters on the distal and external margins. Body rings: metaterga with a slight horizontal sulcus; metazonites with several small tubercles; some larger tubercles present along the posterior edge region of the metazonites, distributed in two nearly horizontal rows (Figs 41, 42). Sternites of anterior body rings with thin elongate setae; sternite of sixth segment with two pairs of small, acute projections, becoming more conspicuous along the post-gonopodal sternites (arrows; Fig. 48). Paranota: anterior border rounded,

posterior border sub-rectangular; metazonites 6–7, 9–12, and 15–17 with small “tooth” on the posterior border (Figs 42, 43). Ozopore arrangement: 5, 7, 9, 10, 12, 13, 15–19 (following the typical polydesmidan pore formula); ozopores surrounded by peritremata, positioned medially on the paranota; peritremata subtriangular, projected laterally (Fig. 42). Legs: prefemur of post-gonopodal legs with a ventroapical projection (arrow; Fig. 47). Telson: triangular (Fig. 43); epiproct with (4+4) macrosetae on the dorsal side supported by small projections; two pairs (2+2) of spinnerets, superior pair more closely positioned to each other as compared to the inferior one; paraprocts each with two macrosetae; hypoproct subtriangular with one pair of macrosetae supported by small triangular projections. Gonopod aperture transversely oval, as typical for the genus, small, with a lateral pair of sclerotized triangular slits to accommodate the gonopods (Fig. 8).

Total length: 67.30. Total width: 10.52. Antennomere lengths (1–7): 0.56; 1.97; 1.95; 1.72; 1.88; 1.91; 0.38. Podomere lengths (1–7): 0.69; 1.19; 3.22; 0.99; 1.08; 2.36; tarsal claw 0.41. Gonopod aperture: length 0.90, width 2.05. Telson length 1.25. Gonopod: length 1.94, width 1.78. Gonocoxae: length 0.87, width 1.47. Telopodite: length 1.92, width 0.94. Gonopods: gonocoxae subequal to the length of the telopodite, globose, projected on the ectal side (Fig. 46); without a spiniform process; two macrosetae on dorsal side. Prefemoral region ventrally positioned and setose, subequal in size to solenomere (Fig. 44). Prefemoral and acropodal regions separated by a cingulum basally (C; Figs 45, 46). Prefemoral process (Pfp; Fig. 44): narrow medially, spoon-shaped apically; longer than the solenomere; containing an elongated and slender secondary process on the inner margin of its basal portion (Figs 44–46); secondary process wider at apex. Solenomere falciform; carrying the seminal groove to apical point (S; Figs 44–46).

Female (Paratype, INPA 398). Color light brown, lighter than in males. Legs yellowish. Sternites wider than in males. Larger tubercles mainly distributed in three horizontal rows on the metazonites; metazonites with a slight “tooth” on the posterior border of the majority of paranota. Ventroapical projections of the prefemur of the post-gonopodal legs, more conspicuous than those of males.

Posterior margin of vulvar opening with a rounded epigyne (Fig. 49). Vulvae oval in ventral view (Figs 50, 51), suboval in lateral view (Fig. 52). Total length: 73.10. Total width: 10.48. Width of the posterior margin of the vulvar aperture 2.29. Vulvae: length 1.02, width 0.66. External valve: length 0.80, width 0.36. Internal valve: length 0.71, width 0.29. Operculum: length 0.22, width 0.55. Both valves with scattered setae. Operculum broad with scattered setae (OP; Fig. 51) and less projected forward than apical valves in lateral view (OP; Fig. 52).

Type material. Holotype: male from Parque Estadual Serra do Aracá (1°30'29.7"N; 63°21'38.7"W), Barcelos, Amazonas, Brazil, 12.viii.2008, A.A. Nogueira leg. (INPA 397). Paratypes: 1 male, 1 female, same data as for holotype, 14.viii.2008, A.A. Nogueira leg. (INPA 398).

Distribution. Known only from the Brazilian state of Amazonas (Fig. 53).

Etymology. The specific epithet is a patronym in honor of Dr. Leandro Dênis Battirola for his vast contribution to our knowledge of Amazonian millipedes, and for the kind help he has provided to the authors over the years.

DISCUSSION

Traditionally, members of the two most speciose genera of Chondrodesmini, *Chondrodesmus* and *Leptherpum*, have been considered to exhibit highly conserved gonopod morphology, with most of the variability across species occurring in peripheral structures, e.g., metazonites (Jeekel 1963, Hoffman 1978, 2005, Golovatch and Hoffman 2004). While some gonopodal characters (e.g., solenomere) within *Leptherpum* do exhibit homogeneity across species, others, such as the shape and structure

of the prefemoral and secondary processes, were found to show a detectable and diagnostic degree of variability among the majority of species (Figs 26–28, 32–34, 38–40, 44–46).

Hoffman (1978) described the monotypic genus *Eumastostethus* Hoffman, 1978 to accommodate the species *E. cuisinieri* Hoffman, 1978, from Venezuela, and placed it within Chondrodesmini. Males of *Eumastostethus* are characterized by the presence of bilobed processes on the anterior sterna, paranota with projections directed caudad, and gonopods with a spatulate prefemoral process containing a falcate process and a broad laminate process. Notably, the species *E. cuisinieri* was originally identified as an undescribed species of *Leptherpum* by J. Carl (Hoffman 1978: 543) but subsequently described as *Eumastostethus* (Hoffman 1978). Based on our examination of *Leptherpum*, the morphology of the gonopods and paranota of *E. cuisinieri* resembles that of *Leptherpum*, including a clear similarity with the paranota of *L. schomburgkii* (Hofmann 1966: fig. 3). Nevertheless, only through examination of the *Eumastostethus* type material would it be possible to either confirm a putative relationship between these genera or support the transference of *E. cuisinieri* to *Leptherpum*. Molecular phylogenetics is needed to more clearly elucidate the relationships within the Chondrodesmini.

Although northern South America is a biologically diverse region, its millipede diversity remains largely unknown (Hoffman et al. 2002). The genus *Leptherpum* has received little taxonomic attention, with a single species described over the last five decades (Golovatch and Hoffman 2004). The new *Leptherpum* records provided here suggest that this genus is widely distributed throughout the Amazonian rainforest, and that the likelihood of discovering additional *Leptherpum* species remains high. It is our hope that the current taxonomic treatment will inspire further investigations into the diversity and biology of *Leptherpum*, and other millipede groups, across the threatened and rapidly disappearing Amazonian rainforest.

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Author Contributions

RSB and LFMI conceived the manuscript; RSB, LFMI, JCM, KI and TMA analyzed the specimens. ADB collected specimens in field.



RSB described the new species. RSB and LFMI carried out the microscope work and wrote the manuscript with support from JCM, KI, TMA and ADB. All authors discussed the results and approved the final version of the manuscript.

Competing Interests

The authors have declared that no competing interests exist.

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