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The first troglobitic *Glomeridesmus* from Brazil, and a template for a modern taxonomic description of Glomeridesmida (Diplopoda)

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Abstract

Glomeridesmus spelaeus **n. sp.**, the first Glomeridesmida described from Brazil and only the second known troglobiont of the order, is described from iron caves of the Amazonian. This description is the first in the order Glomeridesmida since 1975, and also the first utilizing modern techniques like SEM. Numerous taxonomic characters, some employed in recent studies of other millipedes, are described, illustrated, and compared for the first time in the Glomeridesmida, building a foundation for future phylogenetic studies, as well as future descriptions of new members of this basal, enigmatic, and still little-known millipede order. The first photographs of a living Glomeridesmida, as well as anecdotal live observations, are presented. The description of *G. spelaeus* is also important from a conservation point of view, since the cave system it inhabits is under anthropogenic pressure due to planned mining activities.

Key words: Glomeridesmida, caves, iron ore, conservation, Neotropics, Brazil

Introduction

The basal most order (Sierwald & Bond 2007) of chilognath millipedes are the Glomeridesmida, sole members of the superorder Limacomorpha (Hoffman 1980). Glomeridesmida are ill-explored and little known, but possess several plesiomorphic traits. Their appearance might come very close to the hypothetical ground-pattern representative of chilognath Diplopoda (Enghoff 1990). Glomeridesmida are intermediate between pill millipedes (subclass Pentazonia) and the remaining millipedes (subclass Helminthomorpha) and are viewed by some authorities as being ancestral to both groups (Hoffman 1982), while they are resolved in most phylogenies as sister taxon to either Glomerida or Sphaerotheriida (Sierwald et al 2003, Sierwald & Bond 2007).

Glomeridesmida are, after the Siphoniulida (two species, Sierwald *et al.* 2003) and Siphonocryptida (six species, Enghoff 2010), the millipedes with the lowest number of described species. The order contained until now only 31 species (26 Glomeridesmidae, 5 Termitodesmidae, Jeekel 2003). In fact, so little is known about this order that the history of its discovery can be reviewed in a few sentences. The first member of the order was described by Gervais in 1844 from Colombia, and no additional species were described until 1894, from Sumatra of all places, as well as the Lesser Antilles (Pocock 1894a, 1894b). Pocock remarked in the first sentence (1894a, p. 36): "Undoubtedly the most interesting and important feature in the Antillean Diplopod fauna brought to light ....is the discovery, or rather rediscovery, of *Glomeridesmus*. This genus has been a puzzle to systematists for upwards of half a century.... " This rediscovery of the order was followed by the description of a few species from Ecuador (Silvestri 1903), Java (Attems 1907) and the Caribbean (Chamberlin 1918, 1922, 1923), as well as the discovery of the enigmatic family Termitodesmidae as obligate commensals of termites in Sri Lanka (Silvestri 1911a, 1911b), India (Hirst 1911, 1913) and Vietnam (Attems 1938). The first male representative of the order Glomeridesmida was not discovered until much later (Loomis 1936), and not formally recognized for another five years (Carl 1941). Before, the extraordinary long ovipositors of the female (see Fig. 3B) were viewed as male penes. Males are still unknown for the family Termitodesmidae, while within the Glomeridesmidae, males are known only for six of the

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26 described species, and apparently rare (Mauriès 1980, Hoffman 1982, Enghoff *et al.* 1993). Later, the anatomy of the Glomeridesmidae was well reviewed and the first (and still only known) *Glomeridesmus* from India was described (Carl 1942). After that date, a few American species were described by Chamberlin and Loomis (e.g. Chamberlin 1918, 1922, 1923, Loomis 1936, 1964, 1975), the first troglobite *Glomeridesmus* was described from Mexico (Shear 1973), and the first 'modern' comprehensive redescription of a *Glomeridesmus* was published (Mauriès 1980).

The Glomeridesmida were previously known from the Caribbean and Middle America from south of the Yucatan peninsula in Mexico, with single records as far south as Ecuador, as well as some places in Asia (India and Sri Lanka, Sumatra and Indochina, Shelley & Golovatch 2011). While records from Canada (Shelley *et al.* 2007) were misidentifications (Shelley, pers. comm.), undescribed representatives of the order were recently found on numerous islands and places in Southeast Asia and Oceania (Shelley 2011). The description of *Glomeridesmus albiceps* Loomis, 1975 was until now the most recent description of a member of the Glomeridesmida. Even the first photographs of (conserved) specimens of Glomeridesmida were just published last year (Shelley 2011). This dearth of descriptions and, despite a monumental work published in the 1940ties (Carl 1942), dearth of knowledge about the anatomy of the order is opposed to its phylogenetic importance for a concise millipede phylogeny (see Wesener & VandenSpiegel 2009), as well as the presence of numerous unnamed species (see Shelley 2011).

In this paper, the first *Glomeridesmus* from Brazil is described, only the second troglobite ever discovered in the Glomeridesmida. This description is used as an impetus to provide a modern taxonomic description utilizing light- and scanning electron microscopy methods on a member of the Glomeridesmida for the first time. It is our hope that our description and numerous illustrations of taxonomic characters will be viewed as a model for future descriptions of Glomeridesmida.

Material and methods

Collection and preservation: A total of 30 specimens were collected from six caves; all located in Curionópolis, Pará, Brazil (Fig. 1): Caves SL31 (E 0650189m/N 9339714m), SL58 (E 0652243m/N 9339216m), SL61 (E 0652512m/N 9338874m), SL93 (E 0651386m/N 9341930m), SL95 (E 651417m/N 9341906m), and SL97 (E 0651411m/N 9339212m).

All specimens were captured with a fine brush and placed in vials containing 70% ethanol. Glomeridesmida were thoroughly visually searched for throughout the floors and walls of the caves. Special attention was also paid to decaying vegetation (e.g. leaves and tree bark) and animal carcasses, though this material was only common near the cave entrances. The largest population observed (cave SL 31) was associated with a bat guano pile in an inner portion of the cave, quite isolated from the external environment.

Photography and scanning electron microscopy (SEM): Living specimens were photographed in the field with a Pentax Optio W30.

For SEM, specimens were dried by transfer through an alcohol series (85%, 90%, 95%, 2x 100%), mounted on sticky-tabs and dried overnight in a desiccator. For observation on a Hitachi S2460 N (based at the ZFMK) they were sputtered with gold for 120 seconds. For observation on a LEO EVO 40 XVP scanning electron microscope (Leo Electron Microscopy) samples were preserved slightly differently: parts from two specimens were mounted on aluminum support stubs, placed on a film of aluminum foil with carbon tape and sputter-covered with gold using a Baltec SCD 050.

Measurements and drawings were made under a stereomicroscope and a *camera lucida* microscope. Dissections were made with fine entomological pins. All images were later modified with Adobe Photoshop CS2 and assembled in plates with Adobe Illustrator CS2.

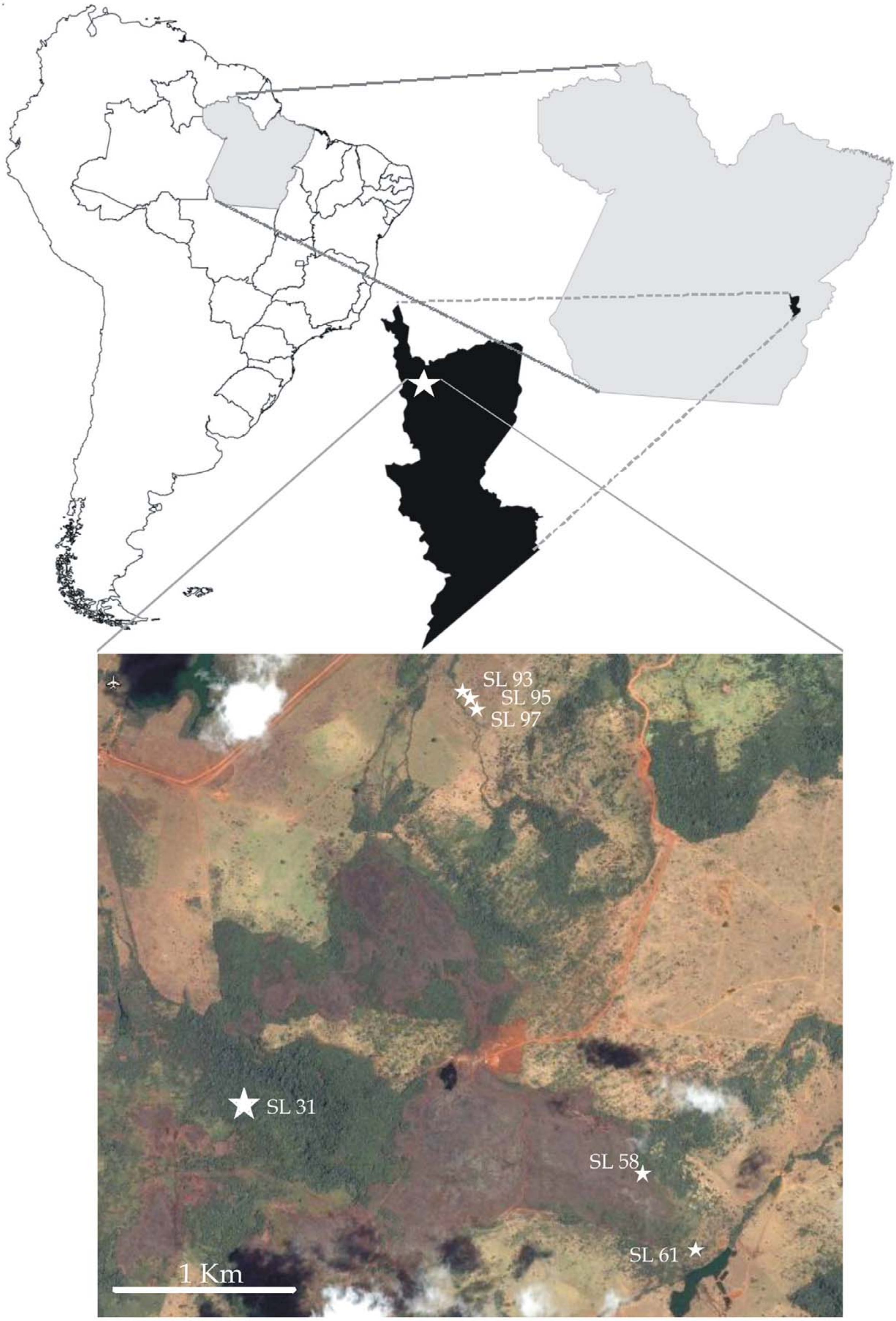

FIGURE 1. Distribution map of *Glomeridesmus spelaeus* **n. sp.**. Stars and SL # refer to caves. Specimens were found year-round in SL31 (type locality), in the other caves only during wet season.

Taxonomy

Superorder Limacomorpha Pocock, 1894

Comment: Comprising the single order Glomeridesmida

Order Glomeridesmida Latzel, 1884

Family Glomeridesmidae Latzel, 1884

Zephroniodesmidae Cook, 1895: 2

Comment: A monogeneric family (Jeekel 2003, Shear 2011).

Characters: Females with 36 pair of legs, 20 tergites plus anal shield; males with 35 leg pairs, 19 tergites plus anal shield (see Hoffman 1982, Enghoff *et al.* 1993). Males with 20 tergites and 37 leg pairs are supposed to exist but have not yet been discovered (Carl 1942).

Head without ocelli, but with large, circular organ of Tömösváry (Fig. 3D). Genae (head sclerites below the antennae) absent. Antennae long, slender, with seven joints and an apical disc carrying four long, slender apical cones (Fig. 3F). The mandible seems to consist of a sutureless fused cardo and stipites (Fig. 3C), confirming earlier observations (Carl 1942).

Each body segment composed of tergite forming a semicircle, one large laterotergite ('pleurite') on each side, and two coxosternites with stigma and tracheal apodeme (Fig. 3A, 4A, B). As in earlier papers on the phylogeny of Pentazonia (Wesener & VandenSpiegel 2009), we follow here Snodgrass' view of the so-called pleurites as laterotergites (Snodgrass 1958). Tergites generally soft, weakly calcified, not divided into pro-, meso- and metazona, but with numerous (5–10) longitudinal striae (Fig. 6A, B, E). Lateral tips of last 3–5 tergites always(?) projecting posteriorly, overlapping following tergites with a sharp-edged tip (Fig. 6A, B). Ozopores for secretion of defense fluid absent.

Development hemianamorphic, leg and tergite development apparently decoupled (Enghoff *et al.* 1993). Last leg pair of males (either 33rd, 34th or 35th) modified to telopods (Fig. 8A, B, 9A, B). Last leg in females, as well as second last in males, characteristically modified, with undivided large sternal plate (Fig. 7A), tarsus posteriorly protruding above anal shield (Fig. 7B). Starting at the mid-body each odd-numbered coxa (e.g. 11, 13, 15) with eversible coxal pouch (Fig. 4A, C).

Gonopores in both sexes located on posterior side of coxa 2. Females with long ovipositors (misinterpreted as 'penes' by earlier authors) forming long (up to half of body length), eversible, membranous tubes (Fig. 3B). Male gonopore consisting of two small sclerotized plates located mesally on the coxa (Fig. 5A, B).

Telopods (only known from 7 species) divided into a syncoxite with inner horns (Fig. 8A) and a 4-jointed telopod. Joint 2 at apico-mesal margin with a species-specific (?) membranous field, joint 3 elongated into immovable finger located laterally (see Wesener & VandenSpiegel 2009: fig. 37) or posteriorly (Fig. 9A) of joint 4, which forms the movable finger and carries a prominent apical spine (Fig. 9A, B, D).

The complete inner morphology remains unstudied (see discussion below).

Genus *Glomeridesmus* Gervais, 1844

Javadesmus Verhoeff, 1929: 1377 (synonymized by Carl 1942)
Zephroniodesmus Pocock, 1894: 476 (synonymized by Loomis 1936)

Comment: The position of the new species in the genus *Glomeridesmus* is based on habitus and head characteristics (Silvestri 1911).

Glomeridesmus spelaeus Iniesta & Wesener, new species

Material examined: Holotype: 1 Male (ISLA 1906) SLQ31 EU, Brazil, Pará, Curionópolis, iron cave SL 31, E 0650189m, N 9339714m, in bat guano pile far from entrance, Zampaulo, R.A. coll.

Paratypes: 1 M (fragmented, ZFMK MYR 0936), 1 F (ZFMK MYR 0937), '1758', same data as holotype; 3 M (fragmented, ISLA 1758, ISLA 1759, fragmented ISLA 3837); 5 F (ISLA 1928, ISLA 1929, ISLA 1930, ISLA 1931, fragmented ISLA 3838); 4 juv. (ISLA 1932, ISLA 1933, ISLA 1934, ISLA 1935).

Other material examined: 3 F (ISLA 3814, ISLA 3815, ISLA 3816), Brazil, Pará, Curionópolis, iron cave SL 31, E 0652243m/N 9339216m, Zampaulo, R.A. coll. same data as holotype; 2 F (ISLA 3817, ISLA 3818), 1 M (ISLA 3819) Brazil, Pará, Curionópolis, iron cave SL 31, E 0652243m/N 9339216m, Zampaulo, R.A. coll. same data as holotype; 4 F (ISLA 3824, ISLA 3825, ISLA 3826, ISLA 3827), Brazil, Pará, Curionópolis, iron cave SL 58, E 0652243m/N 9339216m, Zampaulo, R.A. coll. 29.i.2011; 1 F (ISLA 3820) Brazil, Pará, Curionópolis, iron cave SL 61, E 0652512m/N 9338874m, Zampaulo, R.A. coll. 10.i.2011; 2 F (ISLA 3828, ISLA 3829), Brazil, Pará, Curionópolis, iron cave SL 93, E 0651386m/N 9341930m, Zampaulo, R.A. coll. 17.i.2011; 1 F, (ISLA 3823), Brazil, Pará, Curionópolis, iron cave SL 95, E 651417m/N 9341906m, Zampaulo, R.A. coll. 03.ii.2011; 2 F, (ISLA 3821, ISLA 3822), Brazil, Pará, Curionópolis, iron cave SL 97, E 0651411m/N 9339212m, Zampaulo, R.A. coll. 04.xii.2011;

Diagnosis. White, translucent body (Fig. 2) shared with *G. sbordonii* Shear, 1974 from Mexico, the only other known troglobitic species of the order. *G. spelaeus* **n. sp.** differs from *G. sbordonii* in the presence of sclerotized knobs with mechanoreceptorical(?) setae on tergites (smooth and glabrous in *G. sbordonii*), larger size (~ 5 mm body length in *G. sbordonii*), antennae more densely pilose than in *G. sbordonii* (which could be a perspective error), joint 3 of telopod in oral (anterior) view not overlapping joint 4, as well as other telopod characteristic (provided drawing of *S. sbordonii* [Shear 1974, fig. 2] difficult to compare with our SEM images). Location and shape of projection (immovable finger) of joint 3, posteriorly instead of laterally of joint 4, appears to be unique for the order (Fig. 9A, B, D), albeit telopods are only known from <1/3 of described *Glomeridesmus* species.

Etymology. Species epithet is a noun in apposition, as a reference to the Latin word *spelaeus*, meaning “cave”.

Description. *Measurements*: (largest) adult females (20+AS tergites, 35+1 leg pairs): length: 8.6 mm; width (midbody): 2.3 mm.

Males (19+AS tergites, 33+1+T leg pairs, holotype male): length: 7.2; width (midbody): 2.1; (32+1+T, n =2): length: 5.4, width: 1.6; (31+1+T, n=1): length: 6.3, width: 1.9.

Colour: translucent white.

Head: General shape: typical for the family (Figs 3C, E). Epicranium glabrous; frons, clypeus and labrum with several isolated setae. Both antennae widely separated by a distance (300 µm) longer than twice the width of the first antennal joint. Genae (area below the antennae) almost non-existant, but basal joint of mandible large and visible in dorsal view. Antennal base and organ of Tömösváry surrounded by sclerotized rim (Fig. 3D, E). Antennae consisting of seven joints, each covered with numerous setae (Fig. 3E). Joints 4–6 slightly flattened, apically much wider than basally, wider than long (Fig. 3C, E). Apical disc carrying four long (40 µm) apical cones; sensilla basiconicae seem to be absent (Fig. 3F). Tömösváry organs slightly larger than antennal base. Of well-rounded oval shape, interior covered by sclerotized plate (Fig. 3D). Gnathochilarium with very broad gula (hypostoma). Cardines very small, separated from basal part of gnathochilarium. Mentum basally towards gula with a transverse elevated area, completely fused with laminae linguales (Fig. 3G). Stipites laterally with single sclerotized ledge. Whole surface of gnathochilarium covered with few, isolated setae. Stipites apically with 2, lamello-mentum with 4 extra-long setae. Lateral palpi thin, carrying 4 or 5 sensory cones; inner palpi very wide, carrying several dozen long, tube-shaped sensory cones; central pads large, mesally touching one another, in ventral view also covered with numerous long, tube-shaped sensory cones.

Mandible: with single, densely pilose basal joint (Fig. 3C). Apical part not investigated.

Trunk: Collum (tergite 1): wider than head, shape similar to following tergites.

Tergites 2–19 (20): very thin, decalcified and difficult to distinguish from one another. Size of tergites first increasing until tergite 8, than slowly decreasing more posteriorly. Each tergite divided by 8–10 longitudinal striae, each stria projecting with a toothed margin above more posterior stria (Fig. 6B). Distances between striae expanding towards posterior margin (Fig. 6E). Posterior margin with single row of large sclerotized knobs (Fig. 6A, B, D). Knobs accompanied by longer sensorial setae (Fig. 6C). Surface of tergites covered by a sparse field of very short setae (Fig. 6B). Tergites at apico-lateral corner with 2 or 3 striae and denser rows of short setae (Fig. 6B). Tergite 12 onwards posterior-lateral edge pronounced into a sharp-edged tip, becoming a longer, spine like process at second last tergites. Last tergite at posterior margin towards anal shield without (male) or with (female) single row of short spines. Limbus (posterior margin of tergite) smooth, without any structures (Fig. 5D). Endotergum (underside of posterior margin of tergite) smooth area without any specific structures (Figs 5F). Anterior margin of tergite smooth, without any structures. (Fig. 5D, E). Latero-tergites of rectangular shape, posterior margin overlapping first third of subsequent latero-tergite (Fig. 4A). Anterior and posterior sides longer than mesal and lateral ones (Fig. 4D, E). Mesal side with a rounded angle towards coxosternite, marginal brim here extraordinarily thick; midbody latero-tergite with an elevated marginal brim engulfing all but posterior margin (Fig.4D, E). Posterior margin with a single row of short and slender spines. Marginal rim covering more than anterior third of latero-tergite, descending in 3 steps. Surface area not covered by marginal rim (posterior 2/3) reticulated. Whole surface of latero-tergite very sparsely covered by isolated setae (Fig. 4D, E). Latero-tergite similar to one another, but last latero-tergite on posterior margin with a well-rounded indentation, providing space for the movements of the last leg.

FIGURE 2. *Glomeridesmus spelaeus*, living specimens. First published pictures of living Glomeridesmida. arrows point to eggs and and intestine. Note the large eggs. Intestine not straight tube but folded.

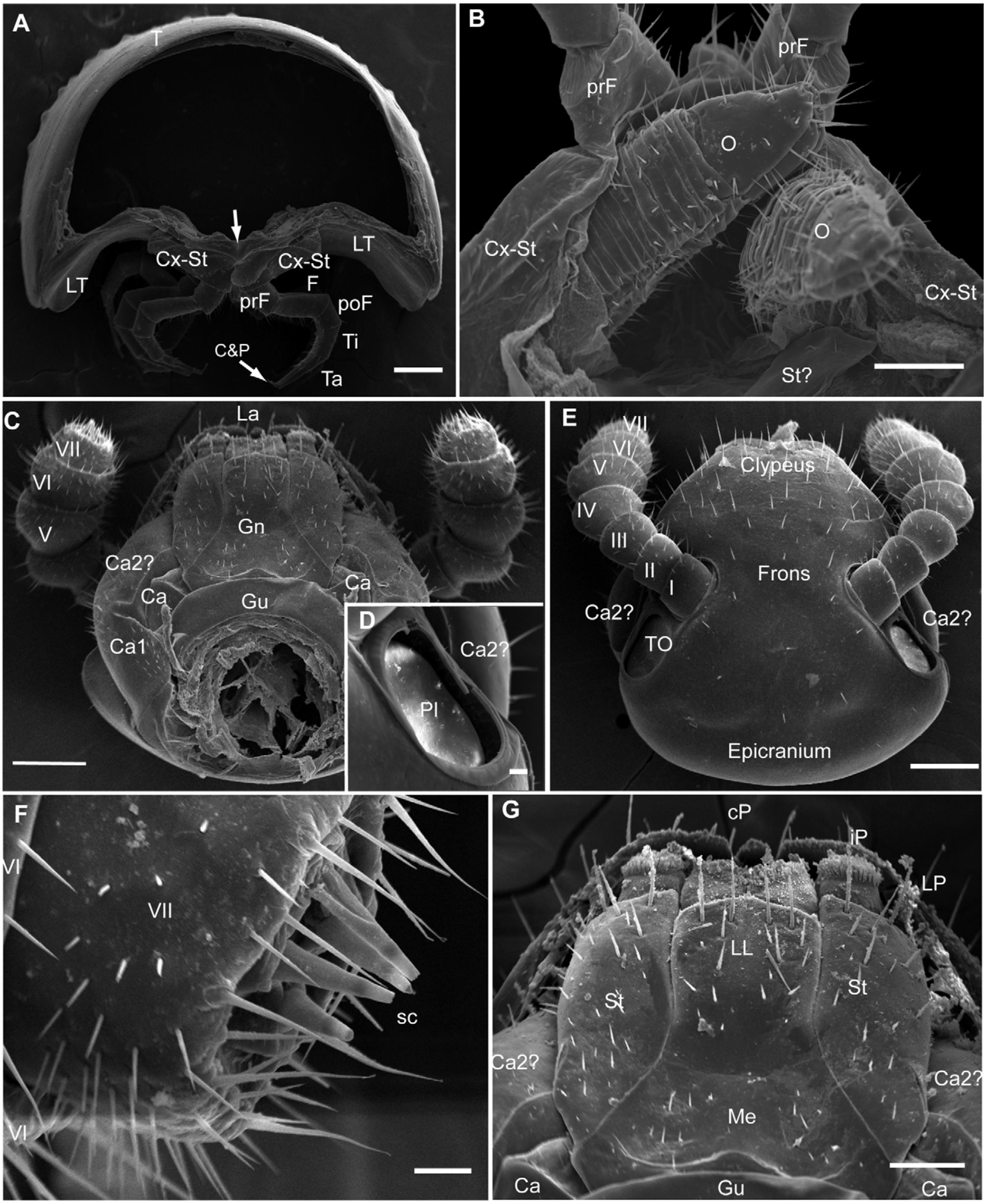

FIGURE 3. *G. spelaeus* **n. sp.**, paratype female (ISLA 3837), SEM. **A**: midbody segment, anterior (oral) view; **B**: coxosternites and prefemur of 2nd leg with ovipositor, posterior view; **C**: head, ventral view; **D**: right organ of Tömösváry, lateral view; **E**: head, dorsal view; **F**: antenna, antennomere 7 and disc, lateral view; **G**: gnathochilarium, underside. **Abbreviations**: C&P = tarsal claw and paranychium; Ca = cardines of gnathochilarium; Ca1 = cardo, basal mandible joint 1; Ca2? = either cardo (joint 1) or stipites (joint 2) of mandible; cP = central pads, modified central palpi; Cx-St = coxosternite; F = femur; Gn = gnathochilarium; iP = inner palpi; La = labrum; LL = lamella linguales; LP = lateral palpi; LT = latero-tergite; Me = mentum; O = ovipositor; Pl = plate covering organ of TO; poF = postfemur; prF = prefemur; St = stipes of gnathochilarium; sc = apical cones; St? = sternite?; T = tergite; Ta = tarsus; Ti = Tibia; TO = organ of Tömösváry; roman numerals refer to number of antennomeres. **Scale bars:** A = 200 µm; B = 100 µm; C = 200 µm; D = 20 µm; E = 200 µm; F = 20 µm; G = 100 µm.

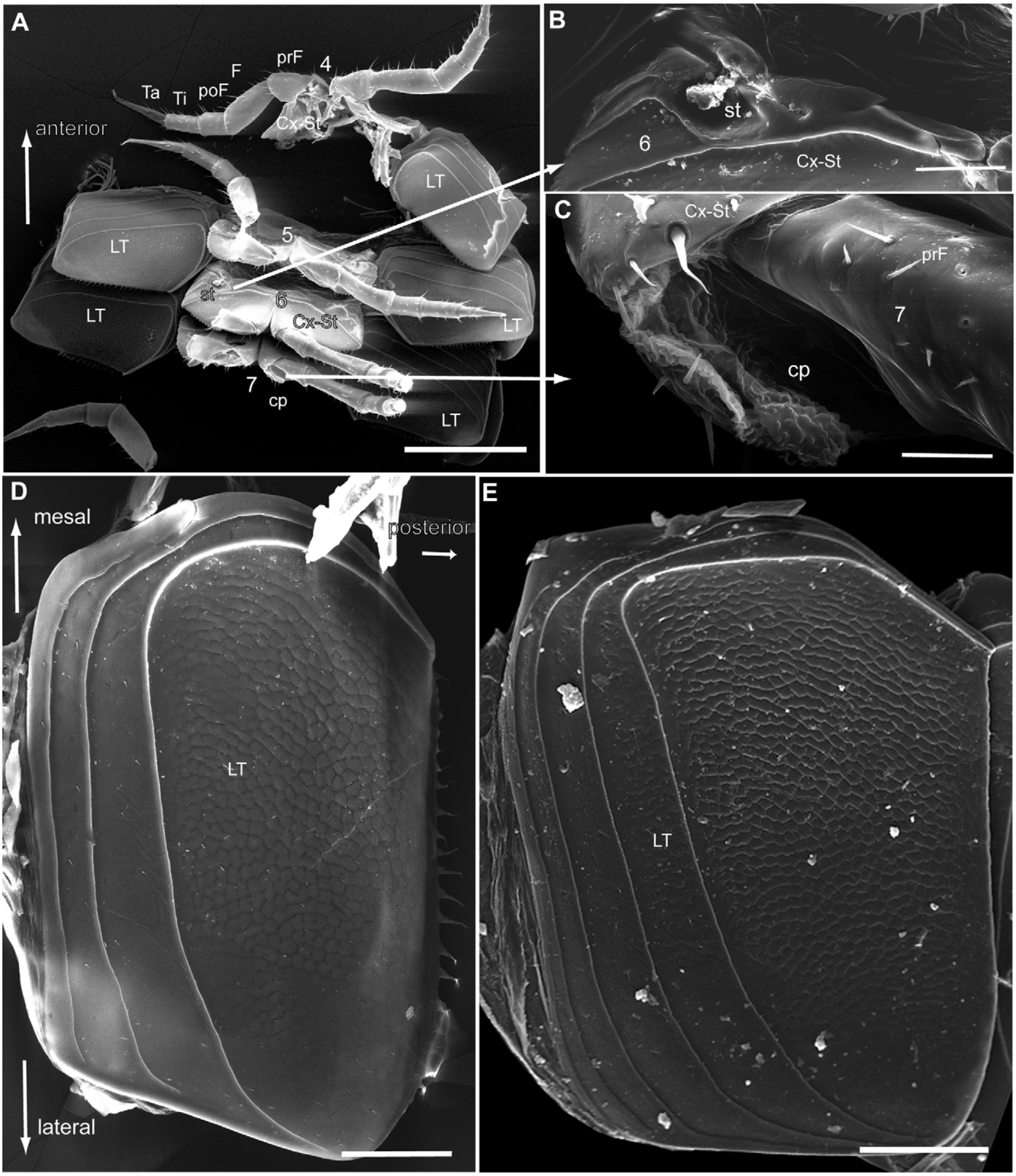

FIGURE 4. *G. spelaeus* **n. sp.**, A–D paratype male (ZFMK Myr0936), E paratype female (ISLA 3838) SEM. **A**: leg pairs 4–7 with latero-tergites; **B**: coxosternite 6 with stigma opening; **C**: coxal pouch 7; **D**: midbody latero-tergite of male; **E**: endbody latero-tergite female. **Abbreviations**: cp = coxal pouch; Cx-St = coxosternite; F = femur; LT = latero-tergite; poF = postfemur; prF = prefemur; st = stigma; Ta = tarsus; Ti = Tibia; numbers refer to leg pair number. **Scale bars:** A = 500 µm; B = 80 µm; C = 30 µm; D = 100 µm; E = 100 µm.

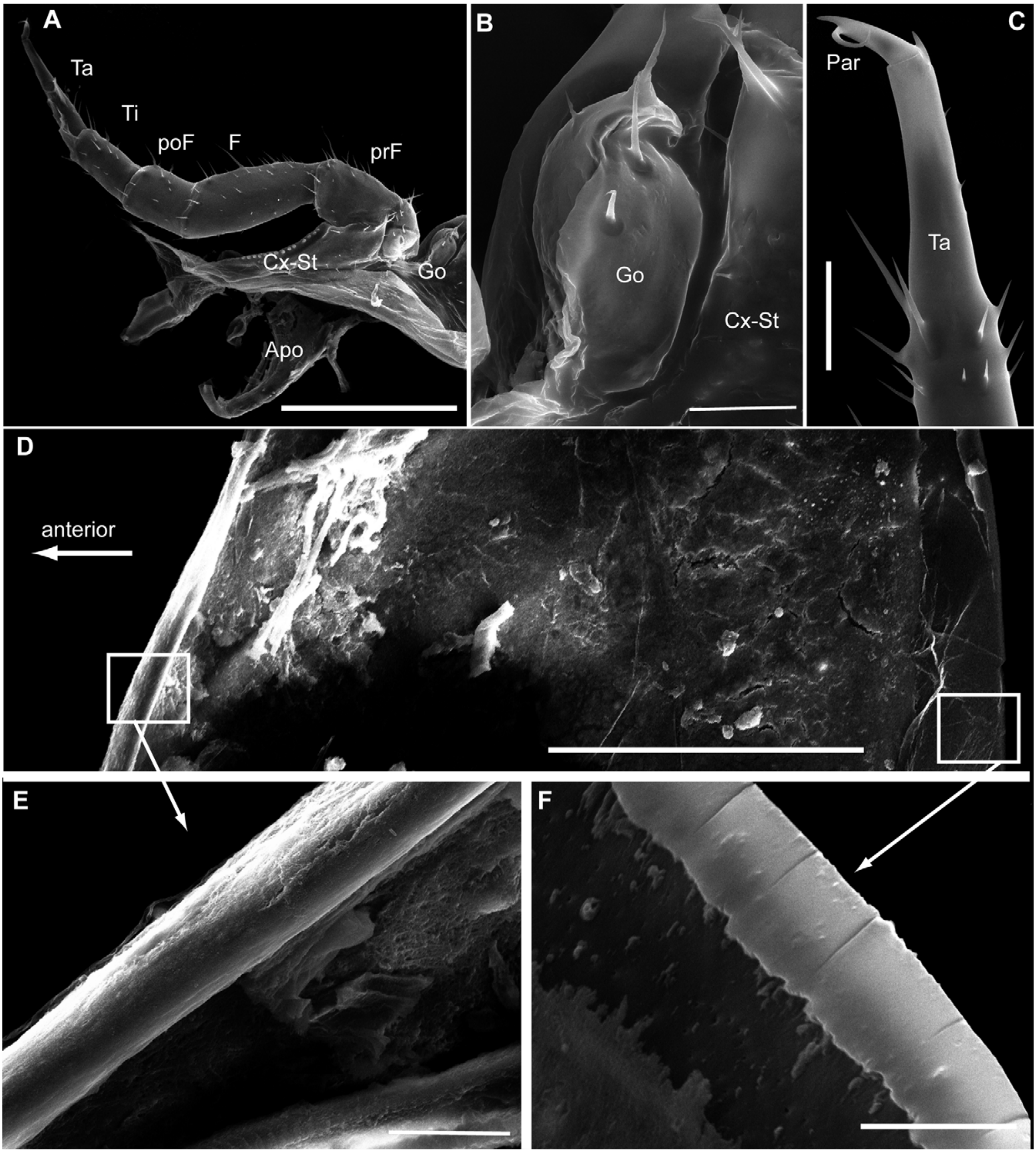

FIGURE 5. *G. spelaeus* **n. sp.**, paratype male (ZFMK Myr0936), SEM. **A**: right male leg 2, posterior view; **B**: gonopore; **C**: tarsus 2 with tarsal claw, apical spine and paranychium; **D**: midbody tergite, underside; **E**: detail of anterior margin of underside; **F**: detail of posterior margin of underside, 'endotergum'. **Abbreviations**: Apo = tracheal apodeme; Cx-St = coxosternite; F = femur; Go = gonopore; Par = paranychium; poF = postfemur; prF = prefemur; Ta = tarsus; Ti = Tibia. **Scale bars:** A = 300 µm; B = 30 µm; C = 60 µm; D = 200 µm; E = 20 µm; F = 8 µm.

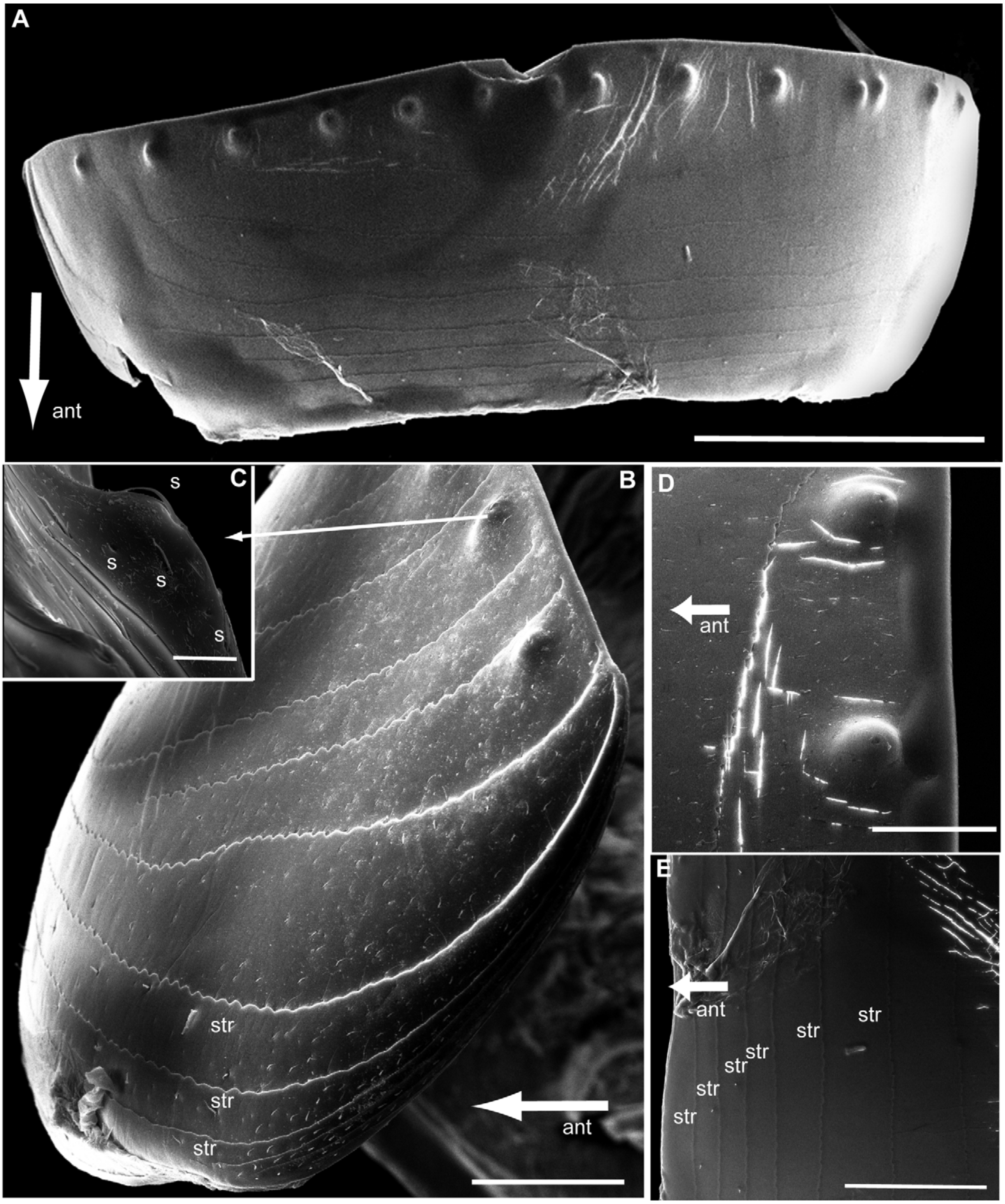

FIGURE 6. *G. spelaeus* **n. sp.**, paratype male (ZFMK Myr0936), SEM, midbody tergite. **A**: dorsal view; **B**: lateral view; **C**: sclerotized knob with setae; **D**: posterior margin, 'limbus'; **E**: anterior margin. **Abbreviations**: ant = anterior; s = (sensorial) seta; str = stria; arrow points to oral side. **Scale bars:** A = 500 µm; B = 100 µm; C = 10 µm; D = 100 µm; E = 200 µm.

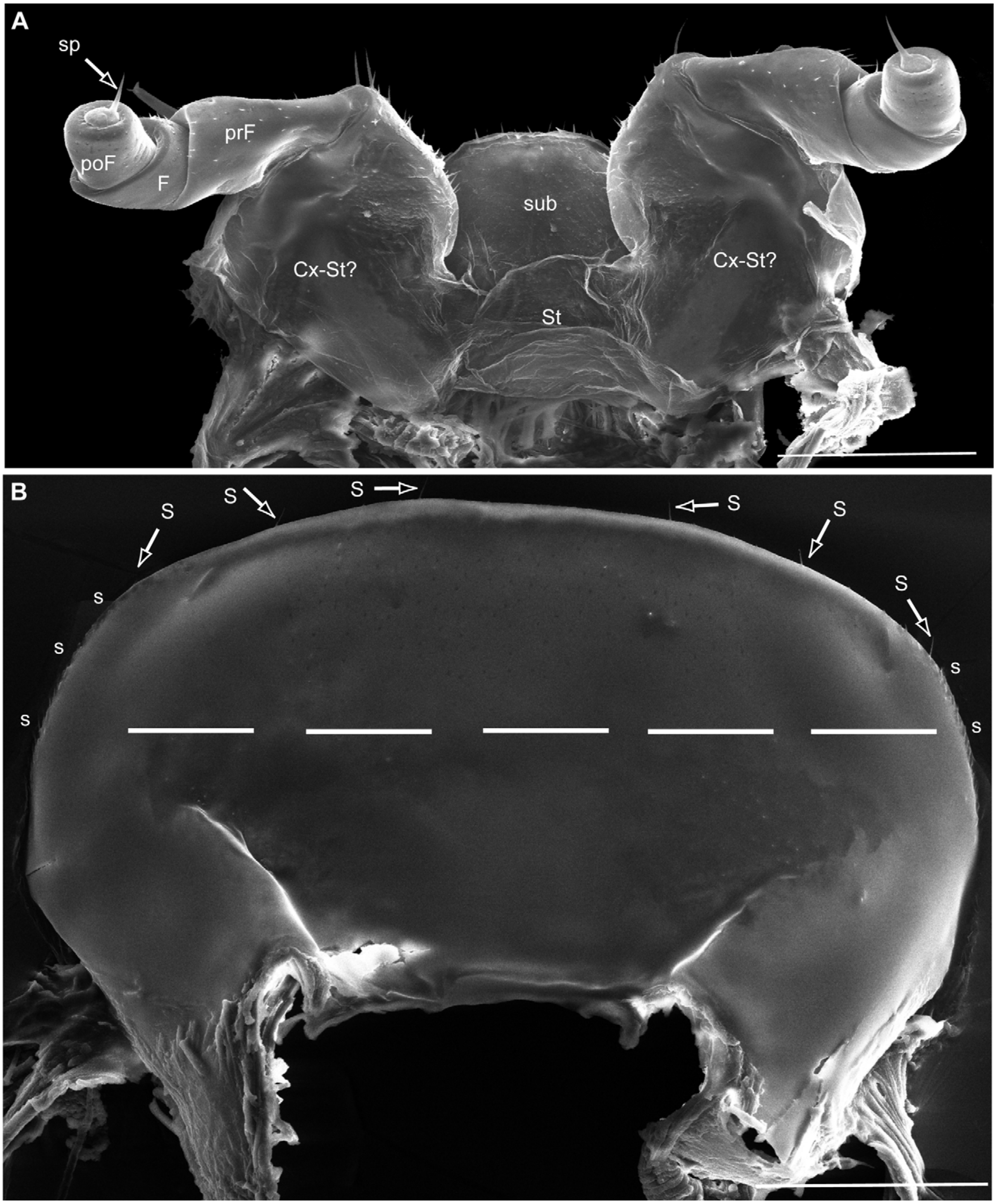

FIGURE 7. *G. spelaeus* **n. sp.**, paratype male (ZFMK Myr0936), SEM. **A**: last pair of walking legs (34) in oral view with sternite and subanal plate; **B**: anal shield, dorsal view, line marks part covered by last tergite (19). **Abbreviations**: Cx-St? = coxosternite; F = femur; poF = postfemur; prF = prefemur; s = field of small setae; S = isolated long setae, sp = spine-like claw; St = sternite; sub = subanal plate. **Scale bars** = 200 µm.

Trunk appendages: Coxosternite(?) serrated at apico-lateral margin (Fig. 5A, 4A). Sternal part more elevated, located basal and lateral of coxal part. Spiracle opening of anterior side in baso-lateral corner of coxosternite (Fig. 4A, B). Starting at coxosternite 7, each odd-numbered coxa up to pair 29 (male) or 31 (female) apically with an eversible coxal pouch posteriorly of prefemur (Figs 4A, C). Legs elongated and slender (Fig. 4A, 5A). Femur 2.5

times longer than wide, tarsus 5.5 times longer than wide. Coxa apically and mesally with few longer setae; prefemur apically, mesally and laterally with 3 or 4 longer setae; prefemur on mesal margin at midpoint with one very long seta, around 20 smaller setae oriented towards mesal margin; station of postfemur and tibia similar to prefemur (Fig. 5A). Tarsus with larger setae only in basal half, a pair of long spines present, tip with one apical spine, an elongated, weakly curved apical claw with basal flexible paranychium, twice as long as claw (Fig. 5C). Penultimate leg with coxosternite narrow, with stigma opening and sternal part located below instead of lateral of coxal part. Ultimate leg pair modified, consisting of coxosternite and 3 podomeres (Fig. 7A). Last two podomeres extending postero-laterally (confused with telopod by previous authors). Both legs widely separated from each other, connected by large plate (sternite?). Coxosternite large, almost as long as 3 podomeres combined. Podomere three apically with a large, long spine (Fig. 7A).

Anal shield: glabrous, with well-rounded edge (Fig. 7B). On lateral side with slightly serrated margin and line of small (sensorial?) setae (Fig. 7B). Subanal plate located behind last pair of legs, large and hyaline.

Sexual characters: Female: second coxae on posterior side with prominent ovipositors of medium length (Fig. 3B). Coxa protruding mesally as a short lobe. Ovipositors basally supported by an undivided plate (sternite?). Ovipositors of medium length, in largest females protruding posteriorly up to leg 7. Ovipositor divided into a basal part consisting of several layers of (eversible?) half-rings, each carrying isolated setae in a regular distance to one another, and an apical part with the opening (Fig. 3B). In the basal part, half rings are anteriorly and posteriorly interrupted by two different, more slender tubes, also consisting of rings, running along the whole length of the ovipositor. Apical part complex, consisting of apparently four larger plates, each arising out of a tube of rings. All four apical plates covered by longer setae (Fig. 3B).

Male: second coxa with gonopore located mesally (Fig. 5A, B). Gonopore consisting of two sclerotized, apically intertwined plates forming a slit-like opening in basal half (Fig. 5B). Apical part of both plates with 2 or 3 longer setae. Male telopod consisting of syncoxite with inner horns and 4 podomeres (Fig. 8A). Syncoxite engulfing the basal podomeres laterally and in anterior view, medially rising into a smooth glabrous process (Fig. 8A). Process apically with two long inner horns; horns basally only divided by suture, more apically completely separated, diverging and later overlapping one another (Fig. 8A). Each horn apically consisting of sclerotized lateral margins that work like a frame holding more membranous folds covering the median part of the tip (Fig. 8A).Whole surface of horns covered by isolated, minute setae.

Podomere 1 largest and most massive. Podomere 2 basally wide, apically tapering, mesally with a large, swollen, membranous area (Fig. 8A, B, 9A, B). Membranous area well rounded, in anterior view consisting of several inverse membranous folds (Fig. 8C), in posterior aspect with scale like and well-rounded sclerotized teeth (Fig. 9C). Podomere 3 long and slender, 2 times longer than wide, in anterior view smooth and glabrous (Fig. 8A, B). Posterior aspect of podomere 3 in apical part with slender, finger-shaped and well-rounded process, the immovable finger (Fig. 9A, B, D). Immovable finger protruding up to 3/4 of length of podomere 4, the movable finger (Fig. 9D). Movable finger slender and glabrous, at apex with single long spine (Fig. 9D).

Discussion

Evaluation of taxonomic characters in the Glomeridesmida: In the past, descriptions of *Glomeridesmus* species were based on dubious somatic characters, species were most often separated by head morphology, body size, coloration and geography alone (*e.g.* Loomis 1964). Males were not known before 1936 (Loomis) and not thoroughly described until later (Carl 1941). Therefore, descriptions of the telopods, 'the' species-specific characters in the related orders Glomerida and Sphaerotheriida, are rare and comparisons absent. Males are apparently rare in *Glomeridesmus* populations, so numerous species were described from female material only. In fact, telopods are only known from eight species of Glomeridesmida. A comparison of the telopods of the described seven species with those of *Glomeridesmus spelaeus* described here highlights the usefulness of telopods as taxonomic characters. No future *Glomeridesmus* species should be described without a telopod illustration.

Female ovipositors, while prominent, seem not to carry much valuable information. The ovipositors of the Brazilian *G. spelaeus* (Fig. 3B) seem to be identical with the ones of the Indian *G. indus* Carl, 1942.

Other somatic characters employed by Loomis, mainly the shape of the organ of Tömösváry, as well as color patterns, seem to be useful. Body size is, because of the anamorphic development and the still almost unknown lifecycle (Enghoff *et al.* 1993), a difficult character. Apparently mature females with eggs occur in different sizes, evidently indicating post-maturity molts (as observed in Glomerida and Sphaerotheriida). The presence or absence of coxal pouches (Fig. 4C), especially on which leg pair they start, seems to be an important character, but well preserved specimens are necessary. The presence of or absence of a fringe of spines on the posterior margin of the laterotergites also has to be treated with care, since spines are both present (Fig. 4D) and absent (Fig. 4E) in *G. spelaeus*.

FIGURE 8. *G. spelaeus* **n. sp.**, paratype males, SEM, telopod, anterior view. **A**: left telopod with syncoxite and inner horns (ZFMK Myr0936); **B**: right telopod, podomeres 2–4, (ISLA 3838); **C**: right telopod, podomere 2, detail of swollen membranous area (ZFMK Myr0936). **Abbreviations**: IH = inner horns; mem = membranous area; roman numerals refer to podomere number. **Scale bars:** A = 300 µm; B = 30 µm; C = 50 µm.

The last (or second last in males) modified leg pair (Fig. 7A) seems to be relatively poor in characters, but more comparisons between different species are necessary to evaluate this character.

Unfortunately, no good characters could be found on the tergites (Figs 6A) neither on the underside (the endotergum, Fig. 5D), which is a viable character in giant pill-millipede taxonomy (Sphaerotheriida; Wesener 2009), nor on the surface (the limbus, Fig. 6D), which is an important character in several millipede orders (Akkari & Enghoff 2011).

Habitat, ecological considerations and threats. The caves where the specimens were collected are located in a complex iron ore outcrop regionally known as “Serra Leste”, or “Serra Pelada”. There are different litho-types in the region, with caves associated to the superficial ferruginous breccia (canga formation), to the iron ore and to ferricretes. Although there are more than 100 caves known in the area, Glomeridesmida were found only in six caves. These caves are quite small, with sizes varying from 21.5 meters (SL 95) to 49 meters (SL 93), although the biggest population was associated with cave SL31, with a depth of 25.5 meters. All of the caves are connected by a large net of small channels ('canaliculi'), typically found in the canga formation, which considerably enlarges the habitat for the subterranean fauna in iron ore caves (Souza-Silva *et al.* 2011).

In all cases, the individuals were found in the inner portions of the caves, which have very different conditions from those near the entrances. The inner portions of the caves are usually aphotic and very moist. Specimens were found in both dry and rainy seasons only in cave SL 31 (08.vi.2010, 04.xii.2011). In the other caves, which all possess a more "unstable" atmosphere, specimens were also only found during the rainy period (December and January 2011).

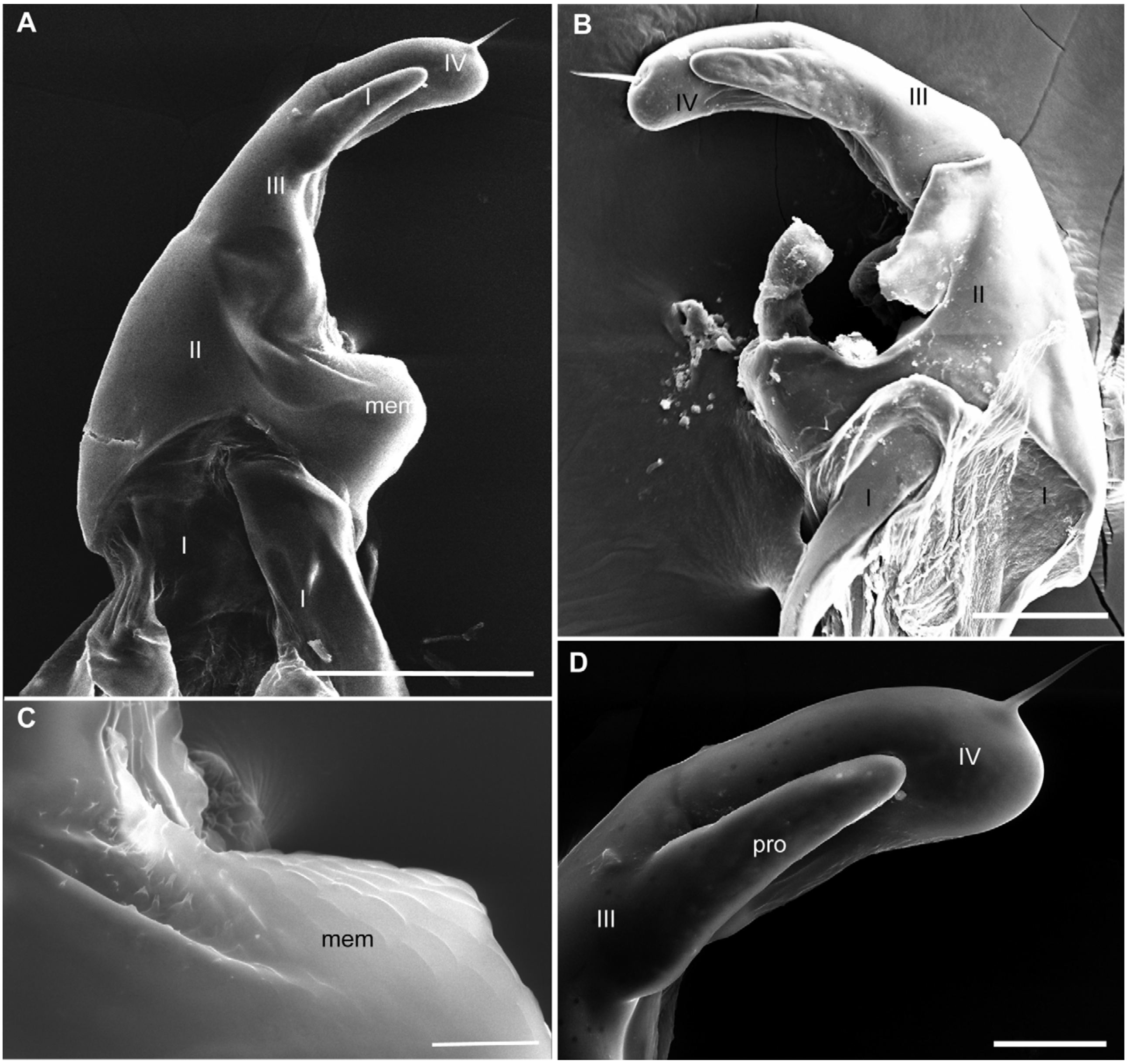

FIGURE 9. *G. spelaeus* **n. sp.**, paratype males, SEM, telopod, posterior view. **A**: right telopod, podomeres 2–4 (ZFMK Myr0936); **B**: left telopod, podomeres 2–4 (ISLA 3838); **C**: right telopod, podomere 2, detail of swollen membranous area (ZFMK Myr0936); **D**: right telopod, detail of podomere 3 & 4(ZFMK Myr0936). **Abbreviations**: mem = membranous area; pro = process of podomere 3; roman numerals refer to podomere number. **Scale bars:** A = 100 µm; B = 100 µm; C = 20 µm; D = 40µm.

In cave SL31 the population was associated with a large bat guano pile. Some specimens were hidden inside small tunnels dug by them in the guano pile. Despite the fact that the delicate nature of the animals does not seem consistent with burrowing, some specimens, raised in laboratory conditions, have buried themselves in a compact guano substrate, brought from one of the caves. These specimens have dug directly into the guano, producing small passages in which they sheltered themselves. In all other caves, the few observed specimens were freely walking on the cave floor. Due to their transparency, it was possible to see their sediment-filled intestines (similar to silt sediment present in the cave floor, Fig. 2A, B, C). They apparently feed directly on the cave sediment, since their feces have the same color as such sediment, although having a pasty consistency (Fig. 2C). The intestine does not appear to be a single tube, as postulated in the past (Hoffman 1982), but a more complex structure.

Although the original epigean physiognomy of the area was Amazon rainforest, most of the forest formations were removed in recent decades. Today, the external system is mainly represented by pastures. Furthermore, the area is also seriously threatened by mining activities. In 2011 a mining company began to exploit iron ore in the outcrop formation where some of the caves are located (Figure 10). Although no cave has been destroyed yet, they are threatened by indirect effects of such activities (such as rock collapses and siltation). Furthermore, in the future, some caves could be destroyed by the extraction of the iron ore.

From 1991 until 2008, all Brazilian caves were protected by law (decree law nº 99.556). However, the legislation was altered (decree law nº 6.640), and the Brazilian caves now can be destroyed by different activities (especially mining). With the intention of defining which caves can be destroyed and which should be preserved, government officials created categories (based on biological and geological criteria) that define the status of each cave. To assure the preservation of a cave in Brazil, it is necessary, from a biological point of view, that it possesses at least an endemic troglobitic or rare species. Therefore, the description of *Glomeridesmus spelaeus*, besides contributing to the knowledge of subterranean Glomeridesmida diversity, ensures the preservation of some caves and its surroundings.

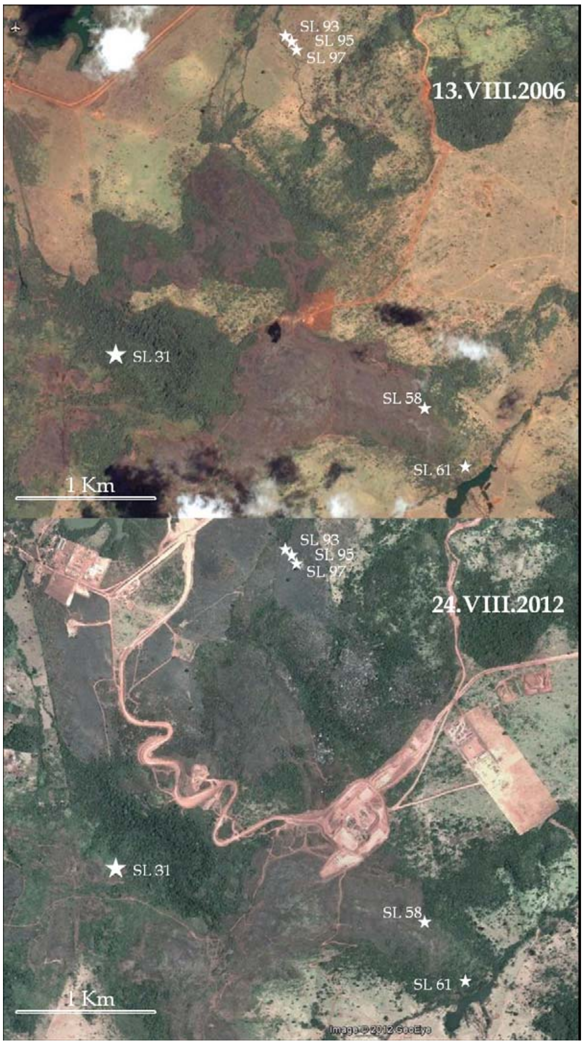

Figure 10. Habitat of *Glomeridesmus spelaeus* sp. n. In the top, the landscape in August of 2006. In the bottom, the same area, in August of 2012, in which is remarkable the habitat destruction due to mining activities (images from Google Earth).

Outlook on Glomeridesmida systematics. The taxonomic status, especially of the SE Asian and Indian Glomeridesmida is still unclear (Shelley 2011), it is unlikely that American and Asian Glomeridesmida belong to the same genus. Several more *Glomeridesmus*, especially from SE Asia, await their description (Shelley & Golovatch 2011), while others (especially from middle America) might be discovered to be synonyms once male specimens, still known only from a small portion of the described species, can be compared. It is surprising that a number of (undescribed) Glomeridesmida have now been discovered on 'Darwinian' (of volcanic origin) islands (Shelley & Golovatch 2011). Either Glomeridesmida have better dispersal abilities than other millipede groups, or these findings are the results of human induced dispersal, a question that can only be answered by a proper taxonomic description of these island *Glomeridesmus*.

The explicitly detailed description of *Glomeridesmus spelaeus* provides future descriptions and redescriptions of Glomeridesmida with a robust framework of which characters are of systematic importance. While numerous character systems needs to be explored and compared in a much more detail, we hope to provide a first step towards a more comprehensive understanding of one of the least known arthropod orders, the Glomeridesmida.

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