

A New Epigeous Species of Troglobius (Collembola: Paronellidae: Cyphoderinae) from Brazil and Notes on the Chaetotaxy of the Genus

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A new epigeous species of *Troglobius* (Collembola: Paronellidae: Cyphoderinae) from Brazil and notes on the chaetotaxy of the genus

Nikolas G. Cipola^{1,*}, José W. de Morais¹, and Bruno C. Bellini²

Abstract

Troglobius albertonoi **sp. nov.** (Collembola: Paronellidae: Cyphoderinae) from the Brazilian Amazon is described and illustrated. The shape of the mucro and unguis resemble those of *T. ferroicus* Zeppelini, Silva & Palacios-Vargas, recently described from Brazil, but the chaetotaxy is distinct. This is the 4th species of the genus and the 3rd from Brazil. Variation within the genus *Troglobius* of the dorsal chaetotaxy and the geographic distribution are discussed, and an identification key to the species is provided. *Troglobius albertonoi* **sp. nov.** is the only known epigeous species of the genus.

Key Words: Amapá; Amazon Biome; Neotropical fauna; taxonomy; troglomorphic springtail; Troglopedetini

Resumo

Troglobius albertonoi **sp. nov.** (Collembola: Paronellidae: Cyphoderinae) da Amazônia Brasileira é descrita e ilustrada. A forma do mucro e unguis da nova espécie assemelham-se com *T. ferroicus* Zeppelini, Silva & Palacios-Vargas, recentemente descrita do Brasil, embora o padrão quetotáxico das espécies sejam claramente distintos. Esta é a quarta espécie descrita do gênero e a terceira proveniente do Brasil. Informações comparativas sobre a quetotaxia dorsal e distribuição do gênero são discutidas e uma chave de identificação para as espécies é fornecida. *Troglobius albertonoi* **sp. nov.** corresponde à primeira espécie epigeica do gênero reportada na literatura.

Palavras Chave: Amapá; Bioma Amazônico; fauna Neotropical; taxonomia; colêmbolos troglomórficos; Troglopedetini

Cyphoderinae (*sensu* Soto-Adames et al. 2008) or Cyphoderidae (*sensu* Jantarit et al. 2014) currently comprise about 130 species in 13 genera, 7 of which recorded in the New World and 4 in Brazil: *Cyphoderus* Nicolet, *Cyphoderodes* Silvestri, *Serroderus* Delamare-Deboutteville, and *Troglobius* Palacios-Vargas & Wilson (Bellinger et al. 2015).

Troglobius is a small genus with 3 species described from caves; 2 from Brazil and 1 from Magadascar (Palacios-Vargas & Zeppelini 1995; Zeppelini et al. 2014). The genus was recently transferred from Troglopedetini (Paronellinae) to Cyphoderinae (*sensu* Soto-Adames et al. 2008), based on absence of eyes, shape of the mucro, and presence of very large scales at the tip of dens, all of which are typical of Cyphoderinae (Zeppelini et al. 2014). *Troglobius* resembles other genera of cyphoderids, such as *Cyphoderus*, in other features: overall body chaetotaxy; developed abdomen IV, when compared with III; antenna IV not subdivided; and ungual shape. However, other species of *Troglobius* are distinctly different, especially by mucro shape, with 2 lamellae (1 or both serrate), whereas *Cyphoder*us has a single dorsal lamella with up to 5 teeth (Yoshii 1987; Palacios-Vargas & Wilson 1990; Jantarit et al. 2014; Zeppelini et al. 2014).

Herein we describe a new epigeous species of *Troglobius* from the Brazilian Amazon, including comments and comparisons on the dorsal chaetotaxy among *Troglobius* species, and an identification key.

Materials and Methods

The specimens were photographed in ethanol gel using a Leica stereomicroscope (M165C) attached to a DFC420 digital camera. Photographs were digitally corrected using Leica Application Suite V3.4.1. Specimens were clarified in potassium dichromate ($K_2Cr_2O_7$) and hydrochloric acid (HCl), and were mounted on glass slides in Hoyer's medium. Drawings were first made using a drawing tube attached to a microscope whereas final drawings were assembled into plates using Adobe Illustrator CS6 software. Types of the new species were deposited in the Invertebrates Collection of the Instituto Nacional de Pesquisas da Amazônia–INPA, Manaus, Amazonas, Brazil.

The labial chaetotaxy and labial papilla system used in the descriptions follows Fjellberg (1999), and subcoxae chaetotaxy follows Yosii (1959). The dorsal chaetotaxy of the head is described following the AMS system of Mari Mutt (1979), Jordana & Baquero (2005), and Zeppelini et al. (2014), based on *Dicranocentrus* Schött, *Entomobrya* Rondani, and *Troglobius*, respectively, whereas body dorsal chaetotaxy follows Szeptycki (1979) and Jantarit et al. (2014) according to *Cyphoderus*. Trunk specialized chaetae (S-chaetae) are presented following Zhang & Deharveng (2015). In abdomen IV chaetotaxy, chaeta De3 (sensu Szeptycki 1979) was considered as D3p, as in Soto-Adames

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2008. Chaetal symbols used to depict follow Fig. 22. Chaetae of uncertain homology are followed by a question mark (?).

Troglobius albertinoi sp. nov. Cipola & Bellini (Figs. 1–30)

DIAGNOSIS

Troglobius albertinoi **sp. nov.** is distinguished by: dorsal head chaetotaxy, with mesochaetae An2a and A2, microchaeta a1 absent; medial region of mesothorax and metathorax lacking macrochaetae; abdomen II and III lacking macrochaetae p5 and p6, respectively; abdomen IV with 2+2 central macrochaetae (A4 and A5), and 1+1 posterior pseudoporus; unguis with 1 unpaired tooth; mucro inner lamella with 1 tooth and dorsal lamella with 8 to 12 teeth.

DESCRIPTION

Size. Total length of holotype 1.35 mm, range 1.18 to 1.52 mm (*n* = 4). Habitus typical of cyphoderids (Fig. 1).

Color. Specimens pale white with several opaque stains on lateral sides of metathorax to abdomen IV. Ocular region without pigments (Fig. 1).

Scales. Oval, elongate, apically rounded or truncate scales covering antennae I and basal half of II, dorsal head, trunk, and ventral face of manubrium and dens (Figs. 2–5, 20a). Legs and ventral tube without scales. Apically rounded strongly ciliate scales covering ventral head (Figs. 6 and 7).

Head. Antennae shorter than body, antennal ratio (n = 4) as I: II: III: IV = 1: 2.03-2.66: 1.03-1.86: 2.61-4.28, holotype 1: 2.21: 1.86: 4.28 (Fig. 1). Antenna IV not annulate or subdivided, without apical bulb, with several ciliate or smooth chaetae of different sizes. Antenna III with 9 large s-blunt chaetae on distal half plus several ciliate or smooth chaetae of different sizes (Fig. 9). Eyes absent (Figs. 1 and 23). Head dorsal chaetotaxy (Fig. 23): antennal series 'An' with 7+7 to 8+8 chaetae (An0, An1a2, An1a, An1, An2a, An2, An3a, and An3), An2 as ciliated or smooth chaeta; An3a present or absent; anterior series 'A' with 4+4 chaetae (A0, A2, A3, and A5), A1 and A4 absent; medio-ocellar series 'M' with 4+4 microchaetae (M1, M2, M3, and M4); sutural series 'S' with 5+5 microchaetae (S0, S2, S3, S4, and S5), S1 absent; post-sutural series 'Ps' with 3+3 microchaetae (Ps2, Ps5, and Ps6?); post-occipital anterior series 'Pa' with 4+4 chaetae (Pa2, Pa3, Pa5, and Pa6), Pa6 as bothriotricum; post-occipital medial series 'Pm' with 1+1 chaetae (Pm1?); post-occipital posterior 'Pp' series with 3+3 chaetae (Pp1, Pp5, and Pp6). Head lateral chaetotaxy (Fig. 23) with 7+7 ciliate chaetae, 4+4 smooth chaetae and 1+1 bothriotrica anteriorly. Clypeus with 9+9 smooth chaetae of different sizes (Fig. 23). Prelabral and labral smooth chaetae formula 4/5, 5, 4; 4 labral anterior chaetae (a1 and a2), 5 median (m0, m1, and m2) and 5 posterior (p0, p1, and p2) (Fig. 23). Head ventral chaetotaxy with smooth chaetae as in Fig. 7. Labial triangle chaetae as in Fig. 8, M1 and r slightly reduced and subequal in size, L2 absent, and M2 anteriorly or laterally to M1; labium with 5 smooth proximal chaetae; labial palp with 5 papillae (A–E), A and C simple, B with 5 papillae, D with 3, and E with 3 papillae and lateral process (inverted) in finger shape (l.p.) smaller than the papilla (Figs. 8 and 10). Maxillary palp with apical papilla and 1 smooth basal chaeta, smaller than the papilla; sublobal plate with 2 smooth chaeta-like projections and a projected lamella (Fig. 11). Right mandible (ventral view) with 4 incisive teeth, left mandible with 5; both mandibles with 5 large molar teeth (Fig. 12). Maxillae with 3 apical teeth and 3 lamellae (Fig. 13).

Thorax. Mesothorax dorsal chaetotaxy (Fig. 24) with ciliate chaetae; anterior chaetal collar with 1 macrochaeta, approximately 20 mesochaetae, 13 microchaetae, 1+1 S-microchaetae (ms), and 1+1

Abdomen. Abdomen I dorsal chaetotaxy (Fig. 26) with 5+5 ciliate microchaetae of 'm' series and 1+1 S-microchaetae (ms). Abdomen II dorsal chaetotaxy (Fig. 27) with ciliate chaetae; series 'a' with 4+4 microchaetae, a5 as bothriotricum; series 'm' with 5+5 microchaetae, m2 as bothriotricum, m3 as macrochaeta, and m5 as mesochaeta; series 'p' with 1+1 microchaetae (p7). Abdomen III (Fig. 28) with ciliate chaetae; series 'a' with 5+5 microchaetae, a5 as bothriotricum and 1+1 anterosubmedial sensilla (as); series 'm' with 3+3 microchaetae, m2 and m5 as bothriotrica; series 'p' with 3+3 microchaetae, pm6 as macrochaeta, plus 5+5 unnamed tergal microchaetae and 1+1 S-microchaetae (ms). Abdomen IV (Fig. 29) only with ciliate chaetae; series 'A' with 2+2 macrochaetae (A4 and A5) and 1+1 mesochaetae; series 'B' with 2+2 microchaetae and 1+1 mesochaetae (B6); series 'C' with 4+4 microchaetae and 1+1 mesochaetae (C4); series 'T' with 4+4 microchaetae and 2+2 bothriotrica (T2 and T4); series 'D' with 4+4 microchaetae and 1+1 mesochaetae (De3 renamed); series 'E' with 2+2 macrochaetae (E2 and E3), 2+2 mesochaetae (E4p and E4p2), E4 as bothriotricum and E2p as microchaeta; series 'F' with 2+2 mesochaetae (F2 and F3), and 1+1 microchaetae; series 'Fe' with 2+2 mesochaetae (Fe2p and Fe3), 1+1 microchaetae, plus 1+1 unnamed mesochaetae. Four sensilla present between the series 'A' and 'E' (as, ps, and 2 unnamed). Abdomen V (Fig. 30) with ciliate chaetae; series 'a' with 3+3 microchaetae, a5 as macrochaeta and 1+1 anterosubmedial sensilla (as); series 'm' with 3+3 mesochaetae, m5 as macrochaeta; series 'p' with 4+4 mesochaetae, p3 as macrochaeta and 2+2 accessory sensilla (acc. p4 and acc. p5).

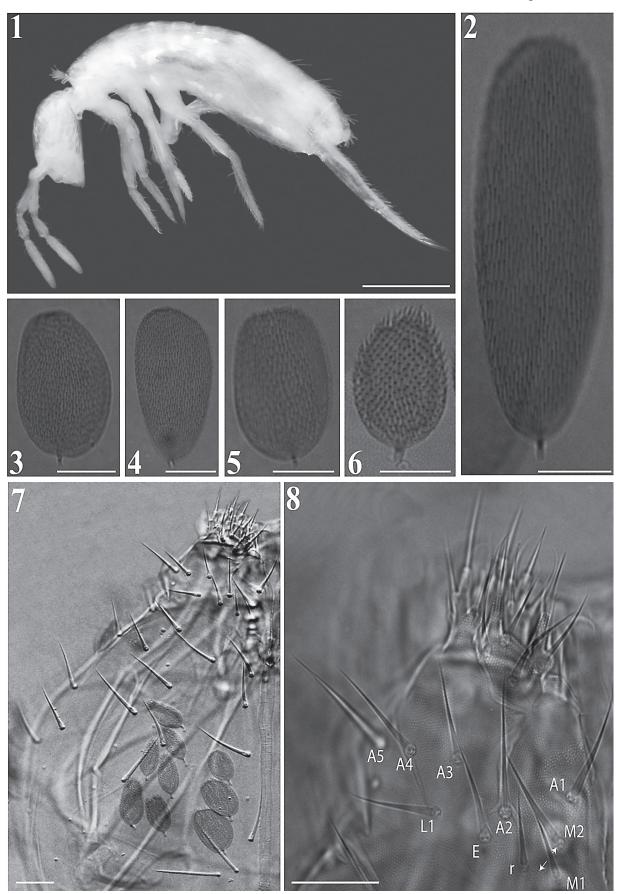
Legs. Subcoxa I with 3 mesochaetae and 2 pseudopores; subcoxa II anterior row (a) with 8 ciliate microchaetae, median row (m) with 2 macrochaetae, 2 mesochaetae, and 1 microchaeta; posterior row (p) with 1 macrochaeta, 1 mesochaeta, and 1 pseudopore; subcoxa III with 6 mesochaetae and 15 ciliate microchaetae of different sizes (Figs. 14–16). Trochanteral organ (Fig. 17) Y-shaped with approximately 11 spine-like chaetae and anteriorly with 8 ciliate chaetae. Unguis (Fig. 18) with 3 teeth; 2 basal winged lanceolate large teeth of equal size, and 1 small median inner tooth. Unguiculi lanceolate with smooth edges, with 1 large outer tooth. Tenent hairs smooth and acuminate. Tibiotar-sus III with a smooth distal seta, near the empodium (Fig. 18).

Collophore. Anterior face with 2+2 ciliate macrochaetae; posterolateral face with 19+19 smooth chaetae (Fig. 19a,b).

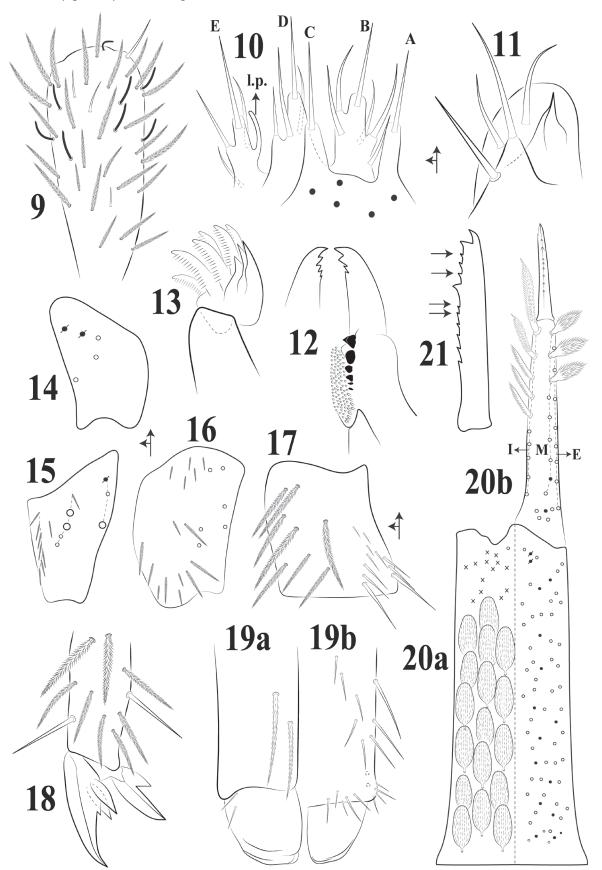
Furcula. Mucro, dens, and manubrium ratio (n = 4) 1: 2.04–2.42: 2.49–3.26, holotype 1: 2.42: 3.26. Anterior face of manubrium with 1+1 apical ciliate chaetae; posterior face with several ciliate and 14 smooth chaetae; manubrial plaque with 2+2 ciliate chaetae and 2+2 pseudopores (Fig. 20a,b). Posterior face of dens with a basal group of 5+5 chaetae, 1+1 smooth and 4+4 ciliate. Rows 3 of posterior chaetae, internal row 'I' with 10+10 ciliate chaetae, 5+5 basal, followed by 3+3 barbulate scale-like chaetae and 2+2 long aristate distal scale-like chaetae; median row 'M' with 9+9 chaetae, 5+5 ciliate and 1+1 smooth and 3+3 distal palpate scale-like chaetae; external row 'E' with 8+8 ciliate chaetae (Fig. 20b). Mucro long with 1 apical tooth on internal lamellae and 8+8 to 12+12 teeth on posterior lamellae (Figs. 20b and 21).

TYPE MATERIAL

Holotype: Brazil, Amapá, Oiapoque Municipality, Amazon forest next to the airport (3.871111°N, 51.806556°W), 13.XI.2014, cols. JA



Figs. 1–8. Troglobius albertinoi sp. nov. (1) Habitus. (2–6) Different shapes of scales: (2) elongate; (3) oval; (4) rounded; (5) truncate; (6) rounded and strongly ciliate. (7) Ventral head chaetotaxy. (8) Labial chaetotaxy. Scale bars: (1) 0.3 mm; (2–6) 0.01 mm; (7–8) 0.02 mm.



Figs. 9–21. Troglobius albertinoi sp. nov. (9) Antenna III chaetotaxy. (10) Labial papilla and proximal chaetae. (11) Maxillary palp. (12) Mandibles. (13) Right maxilla. (14) Subcoxa I. (15) Subcoxa II. (16) Subcoxa III. (17) Trochanteral organ. (18) Hind foot complex. (19a and b) Collophore: (19a) anterior face; (19b) posterior face. (20a and b) Furca (black dots mark smooth chaetae, white circles mark ciliate chaetae, and 'x' symbols mark scales): (20a) manubrium anterior face; (20b) furca posterior face. (21) Mucro (lateral view), arrows indicate present or absent teeth.

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Rafael & FF Xavier Filho, 1 female on slide, deposited at Collection of Invertebrates of INPA under number COLLE 050. Paratypes: 1 male, 4 females, and 1 immature on slides and 15 specimens in alcohol, same locality as holotype, deposited at Collection of Invertebrates of INPA under number COLLE 050.

DISTRIBUTION AND HABITAT

Specimens of *T. albertinoi* **sp. nov.** were found inside decaying wooden trunks in a forested area of the Amazonian phytogeographic domain. The species is possibly myrmecophilous or termitophilus, as are other cyphoderids. The type locality is characterized as: Neotropical Region, northern Brazil, Amapá State, Good's biogeographic zone 26 (Good 1974). The climate of the area following the Köppen–Geiger system is "Am" tropical wet (or monsoon) climate, characterized by wet and dry seasons (Kottek el at. 2006). This is the first non-cave-dweller species of *Troglobius* recorded.

of 1 ungual unpaired tooth; collophore anterior face chaetotaxy with 2+2 long ciliate chaetae; and mucro with 1 tooth on internal lamella and 10 to 12 teeth on dorsal lamella (Table 1). Troglobius albertinoi sp. nov. differs from *T. ferroicus* in the following characters: labial triangle chaetotaxy, with chaeta M1 reduced (normal in T. ferroicus); labial papilla B with 5 papillae, and D and E with 3 (reduced in T. ferroicus); posterior face of dens with smooth chaetae (absent in T. ferroicus) and internal row with 3 types of modified chaetae (only 1 in T. ferroicus). In addition to these characteristics, T. albertinoi sp. nov. differs in: dorsal head chaetotaxy (An2a mesochaeta is only present in the new species); macrochaeta m7? present in mesothorax and mesochaeta m6 in metathorax (both absent in T. ferroicus); abdomen III without macrochaeta p6 (present in T. ferroicus); abdomen IV with chaetae B6 present and posterior margin with 1+1 pseudopores, whereas B6 is absent and there are 4+4 pseudopores in T. ferroicus. Other morphological differences of Troglobius species are presented in Table 1.

ETYMOLOGY

REMARKS

Troglobius albertinoi **sp. nov**. is most similar to *T. ferroicus* Zeppelini, Silva & Palacios-Vargas and shares the following characters: presence

The new species was named after the Brazilian entomologist Dr. José Albertino Rafael, who also collected the specimens.

Key to World Species of Troglobius

- 1'.— Abdomen IV without macrochaetae A5 and E2; unguis without unpaired teeth; mucro inner lamella without teeth *T. coprophagus* Palacios-Vargas & Wilson, 1990 (Madagascar)

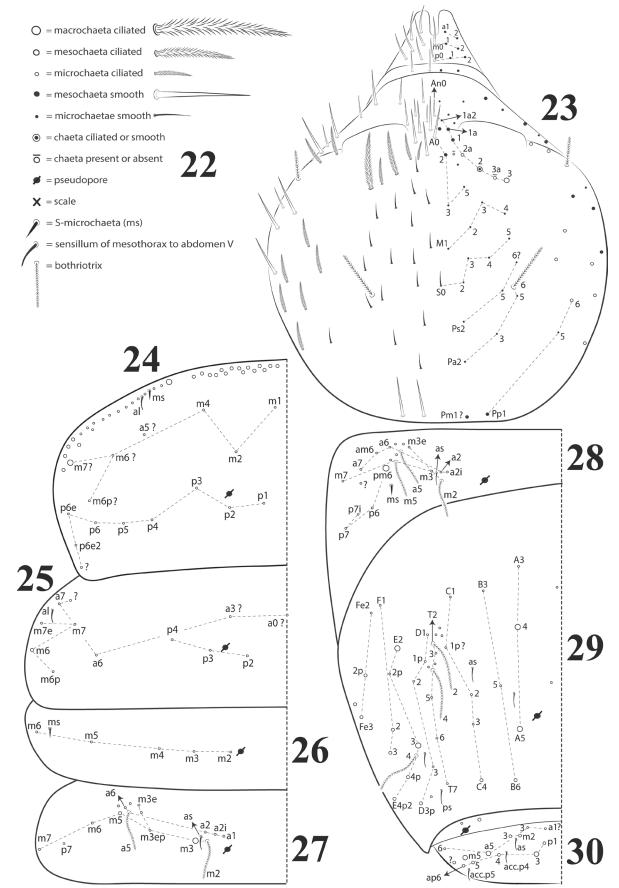
Discussion

Given that *Troglobius* is a small genus, now with 4 species, characteristics such as number of ungual teeth and mucro shape were the main features for comparisons among the species (Palacios-Vargas & Wilson 1990; Palacios-Vargas & Zeppelini 1995; Zeppelini et al. 2014). However, details of the dorsal chaetotaxy can also contribute to the separation of the species (see Table 1). In fact, dorsal chaetotaxy is useful to distinguish other cyphoderids, such as *Cyphoderus*, and taxa of Entomobryoidea (Szeptycki 1979; Jantarit et al. 2014).

The interpretation of the chaetal homology can be confusing (as presented by Szeptycki 1979), and therefore some chaetae were possibly mistakenly named in the other 3 species of *Troglobius* (Zeppelini et al. 2014). Here we provide another point of view of the chaetae of these 3 species (Figs. 31–39). On the head, chaeta S5 was possibly confused for S4, at least in *T. brasiliensis*, and M1 for S1 in all species (Figs. 31–33). We believe this last mistake was due to the proximity of M1 to the sutural series, and this condition among paronellids may have led to other past mistaken interpretations (e.g., Soto-Adames et al. 2014). Here we considered this chaeta as M1 because it fits revisions and new descriptions of other Entomobryidea, such as Jordana

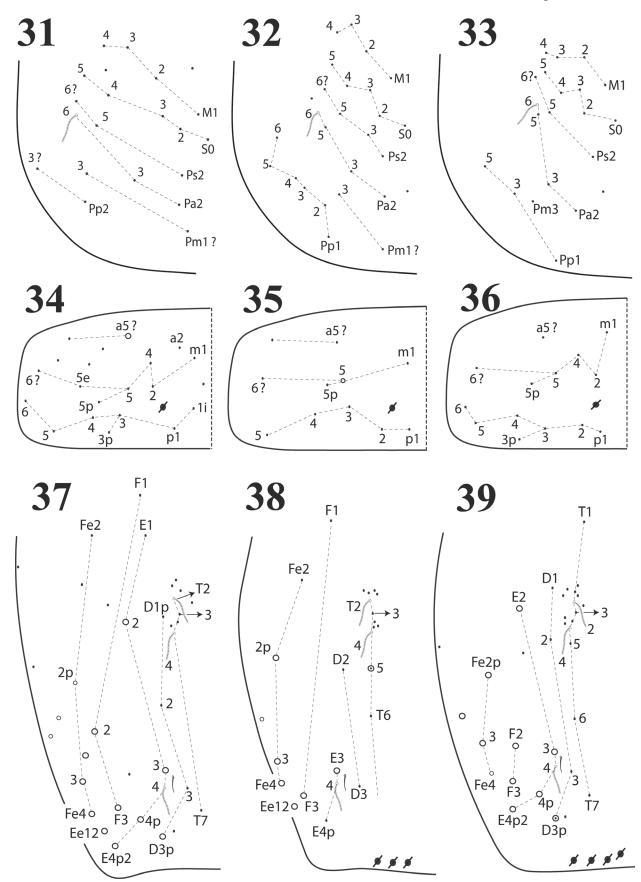
& Baguero (2005), Soto-Adames (2008), and Cipola et al. (2014). On the mesothorax, Troglobius species are very similar to Cyphoderus (see Szeptycki 1979: 150; and Jantarit et al. 2014), and we believe 5 chaetae of the 'm' series were confused in the other 3 species (m1, m2, m4, m5, and m6?). All Troglobius species lack m3, as do some Cyphoderus species (Jantarit et al. 2014). On abdomen IV, 11 chaetae (T6, D3, D3p, E3, E4, E4p, E4p2, F2, F3, Fe3, and Fe4) plus the posterior bothriotricum were also misinterpreted between series 'T' to 'Fe' (Figs. 31-39). In fact, this last bothriotricum was given 3 different names in revisions of Entomobryoidea (see Szeptycki 1979; Soto-Adames 2008; Jantarit et al. 2014; Soto-Adames et al. 2014). Observations on 1st and 2nd instars of Cyphoderus (see Szeptycki 1979: 214, Figs. 295 and 296.) and Seira (Soto-Adames 2008: 22, Figs. 74 and 76) suggest this secondary bothriotricum has independent origins (D3 in Entomobryidae and E4 in Cyphoderinae). This feature should be investigated in future revisions because the position of the bothriotricum is similar in all Entomobryoidea, and possibly homologous.

The detailed chaetotaxy of *Troglobius* species presents a large number of homologies with *Cyphoderus* (see Jantarit et al. 2014), suggesting a close phylogenetic relationship between the genera. On the other hand, characteristics of the idiochaetotaxy can be used to diagnose *Troglobius* among the Cyphoderinae, such as: dorsal head chaetotaxy



Figs. 22–30. Troglobius albertinoi sp. nov. dorsal chaetotaxy. (22) Symbols used in detailed chaetotaxy schemes. (23) Head. (24) Mesothorax. (25) Metathorax. (26) Abdomen II. (27) Abdomen II. (28) Abdomen III. (29) Abdomen IV. (30) Abdomen V.

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Figs. 31–39. Troglobius species chaetotaxies (re-interpreted from Zeppelini et al. 2014). (31–33) Head dorsal chaetotaxy: (31) T. brasiliensis; (32) T. coprophagus; (33) T. ferroicus. (34–36) Mesothorax dorsal chaetotaxy: (34) T. brasiliensis; (35) T. coprophagus; (36) T. ferroicus. (37–39) Abdomen IV dorsal chaetotaxy: (37) T. brasiliensis; (38) T. coprophagus; (38) T. coprophagus; (39) T. ferroicus.

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Table 1. Comparison between the main morphological characteristics of *Troglobius* species. Macrochaeta 'mac', mesochaeta 'mes', microchaeta 'mic', chaeta absent '--', pseudopore 'psp', smooth 'S', ciliate 'C', barbulate 'B', palmate 'P', aristate 'A'.

| | | Troglobius species | | | |
|-----------------------|------------------|---------------------|--------------|-------------|-----------|
| Features | | albertinoi sp. nov. | brasiliensis | coprophagus | ferroicus |
| Dorsal head | An2a | mes | _ | _ | _ |
| | A0 | mes | mic | ? | mes/mic |
| | A1 | - | mic | mic | _ |
| | A2 | mes | mic | mic | mic |
| | Ps3 | - | mic | mic | _ |
| | Pm1 | mes | _ | mes | _ |
| | Pm3 | - | _ | mic | mic |
| | Pp1 | mes | _ | mic | mic |
| | Pp2 (mac) | — | _ | mic | — |
| Mesothorax | m5 | _ | mic | mac | mic |
| Metathorax | a6 | mic | mac | mac | mic |
| | р3 | mic | mac | mic | mic |
| Abdomen II | m3 | mac | _ | mac | mac |
| | р5 | _ | mac | _ | mic |
| Abdomen III | p6 | mic | mac | mac | mac |
| | pm6 | mac | mic | mac | mac |
| Abdomen IV | A5 | mac | mac | mic | mac |
| | B6 | mes | mic | mic | - |
| | C4 | mes | mic | _ | mic |
| | E2 | mac | mac | - | mac |
| | F2 | mac | mic | — | mac |
| | posterior margin | 1psp 1mes; 1mic | _ | Зрѕр | 4psp |
| Trochanteral organ | | 11 | 30 | 16 | 34 |
| Ungual unpaired teeth | | 1 | 2 | 0 | 1 |
| Collophore chaetotaxy | anterior | 2C | 2S | 2S | 2C |
| | posterior | 19S | 2C; 24S | 135 | 12C; 13S |
| Dens posterior face | internal | 5C; 3B; 2A | 21C | 9P; 1B | 21P |
| | median | 5C; 1S; 3P | 22C | 2B; 11C | 1P; >25C |
| | external | 8C | 19C | 11B | >25C |
| Mucro lamella teeth | internal dorsal | 1 | 14 | 0 | 1 |
| | | 8—12 | 12-14 | 19 | 10-15 |

without pseudopores in frontal region (present in *Cyphoderus*), 'M' series with 4+4 microchaetae (M1, M2, M3, and M4), S0 always present and S1 always absent; abdomen I without macrochaetae; abdomen IV with A4 as macrochaeta and B4 as microchaeta or absent (the opposite is seen in *Cyphoderus*), 1 sensillum near bothriotricum E4, and posterior region with or without pseudopores (Figs. 29, 37–39).

Other characteristics based on tergal specialized chaetae (S-chaetae) may also be useful in distinguishing cyphoderid genera, because these characteristics are useful to distinguish several Entomobryidae taxa (Zhang & Deharveng 2015). The pattern of trunk S-chaetae (mesothorax to abdomen V) in *Cyphoderus* is 2,1/1,2,3,4,3 (Jantarit et al. 2014: 5), whereas in *Troglobius* it is 2,1/1,1,2,4,3.

The discovery of an epigeic species of *Troglobius* helps to explain the distribution of cave species in distant areas of South America and Africa. Neotropical species have a distinct morphology compared to *T. coprophagus*, especially abdomen IV chaetotaxy and ungual and mucronal shapes. These data could point to two distinct lineages of *Troglobius*: one Neotropical and the other Paleotropical. Discovery of other African species could shed light on this discussion and reveal if the particular morphology of *T. coprophagus* is a pattern among Paleotropical taxa.

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