



## ***Coarazuphium tapiaguassu* (Coleoptera: Carabidae: Zuphiini), a new Brazilian troglobitic beetle, with ultrastructural analysis and ecological considerations**

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### **Abstract**

*Coarazuphium tapiaguassu* sp. n. was collected in caves SL 30, SL 31 and SL 35 located in Curionópolis (Pará, Brazil). *C. tapiaguassu* is readily differentiated by the absence of setae on the dorsal surface of the head close to the posterior margin, as the other species of the genus show one, two or three pairs of setae. Taxa of *Coarazuphium* exhibit advanced troglobiomorphic characters in comparison to other Brazilian cave beetles. Increased extra-optic sensory structures, presence of particular sensilla, and sensory and gustatory receptors are characters not detected under routine microscopy and thus require ultrastructural methods for their study. Similar analyses are needed in other epigeal Zuphiini species for a better interpretation of their functional meaning.

**Key words:** *Coarazuphium*, ground beetle, cave dwelling, sensilla, antenna, mouthparts, legs

### **Introduction**

Few Zuphiine species have been reported with adaptive features to the subterranean environment. To date, only four genera featuring troglobitic species have been described. The first record was from the genus *Ildobates*, with troglobitic species *Ildobates neboti* (Español *et al.*, 1966). Recently, molecular data have supported the inclusion of *Ildobates neboti* into Zuphiini (Ribera *et al.*, 2006). Moore (1995) recorded two other new genera of troglobitic Zuphiini—*Speozuphium* and *Speothalpius*—each featuring a new species—*Speozuphium poulteri* and *Speothalpius grayi*, respectively. Both were found in the cave systems of the Nullarbor Plain, Australia. The fourth genus, *Coarazuphium*, is found exclusively in Brazil, with five troglobitic species already described. They are: *C. tessai*, *C. cessaima*, *C. bezerra*, *C. pains* and *C. formoso* (Godoy & Vanin, 1990; Gnaspini *et al.* 1998; Álvares & Ferreira, 2002; Pellegrini & Ferreira, 2011).

Our objective is to describe a new species of troglobitic Zuphiini, *Coarazuphium tapiaguassu*, found in iron ore caves located in the ferriferous formation of Carajás (Pará State, Brazil). This description focuses on an ultrastructural analysis of the antennae, mouthparts, and legs, which were compared with the only species of the same genus (*C. formoso*) for which those data are available. According to Moldovan *et al.* (2004), these structures indicate the degree of adaptation to life in caves. They also provide adequate criteria to identify cave species with otherwise similar morphology.

### **Material and methods**

Twenty specimens were collected in three caves: SL 30 Cave (E 0650160m/N 9339706m; 7 specimens), SL 31 Cave (E 0650189m/N 9339714m; 3 specimens) and SL 35 Cave (E 0650799m/N 9339330m; 10 specimens), all located in Curionópolis, Pará, Brazil.

Carabids were thoroughly searched visually throughout the base and walls of the caves. Special attention was also paid to decaying vegetation (e.g. leaves and tree bark), animal carcasses, and vertebrate feces, though this

material was only common near the cave entrances, where no individuals were found. Carabids were captured with a fine brush and placed in vials containing 70% ethanol. Measurements and drawings were made under a stereomicroscope and a camera lucida microscope. To dissecting male genitalia, fine entomological pins were used. The specimen was prepared in Kayser glycerol gelatin; drawings were made under a Leica MDLS phase contrast microscope. Ultrastructural analyses were carried out with a scanning electron microscope. Parts from another specimen were placed on aluminum support stubs, placed over a film of aluminum foil with carbon tape, sputter-covered with gold (Baltec SCD 050), and observed in a LEO EVO 40 XVP scanning electron microscope (Leo Electron Microscopy).

We followed the criteria of Schneider (1964), McIver (1975), Zacharuk (1980), Kim & Yamasak (1995) and Merivee *et al.* (2000) for naming ultrastructures and assessing their function.

Type specimens are deposited in the Zoology Collection, Seção de Invertebrados Subterrâneos (ISLA 1493 male holotype; ISLA 1494 female paratype 1; ISLA 1495 male paratype 2 and ISLA 1496 male paratype 3), at the Universidade Federal de Lavras (UFLA), Campus Universitário de Lavras, Minas Gerais, Brazil.

## Taxonomy

### Family CARABIDAE Latreille, 1802

### Tribe Zuphiini Bonelli, 1810

### Genus *Coarazuphium* Gnaspini, Vanin & Godoy, 1998

### *Coarazuphium tapiaguassu* sp. n.

(Figs. 1–11).

**Description.** Minimum and maximum morphometric data from paratypes are given in parenthesis. No distinct sexual differences were observed. Female paratype 1 (Fig. 2). A live female specimen is shown in figure 1.

Holotype male. Total length, from the apex of the mandible to the apex of the elytra: 4.14 mm (4.07–4.26), width, from at the widest region of the elytra: 1.29 mm (1.25–1.29). Body pale reddish brown, one paratype is yellowish to pale brown, dorsal integument of the elytra covered with short recumbent hairs.

**Head.** Subtrapezoidal (Fig. 2A) with similar width and length, width/length ratio: 0,96 (0.92–1.0). Maximum width of head at its base, 2.3 (2.2–2.3). Head slightly narrower than pronotum. Dorsal surface with one pair of setae internal to the ocular area and one pair of lateral setae located immediately behind ocular area. Ventral surface with a pair of posterior setae close to median line of head, and an anterior pair, close to margin of gular region (Fig. 2C). Eyes reduced and depigmented, situated laterally at the end of antennal impression of the head.

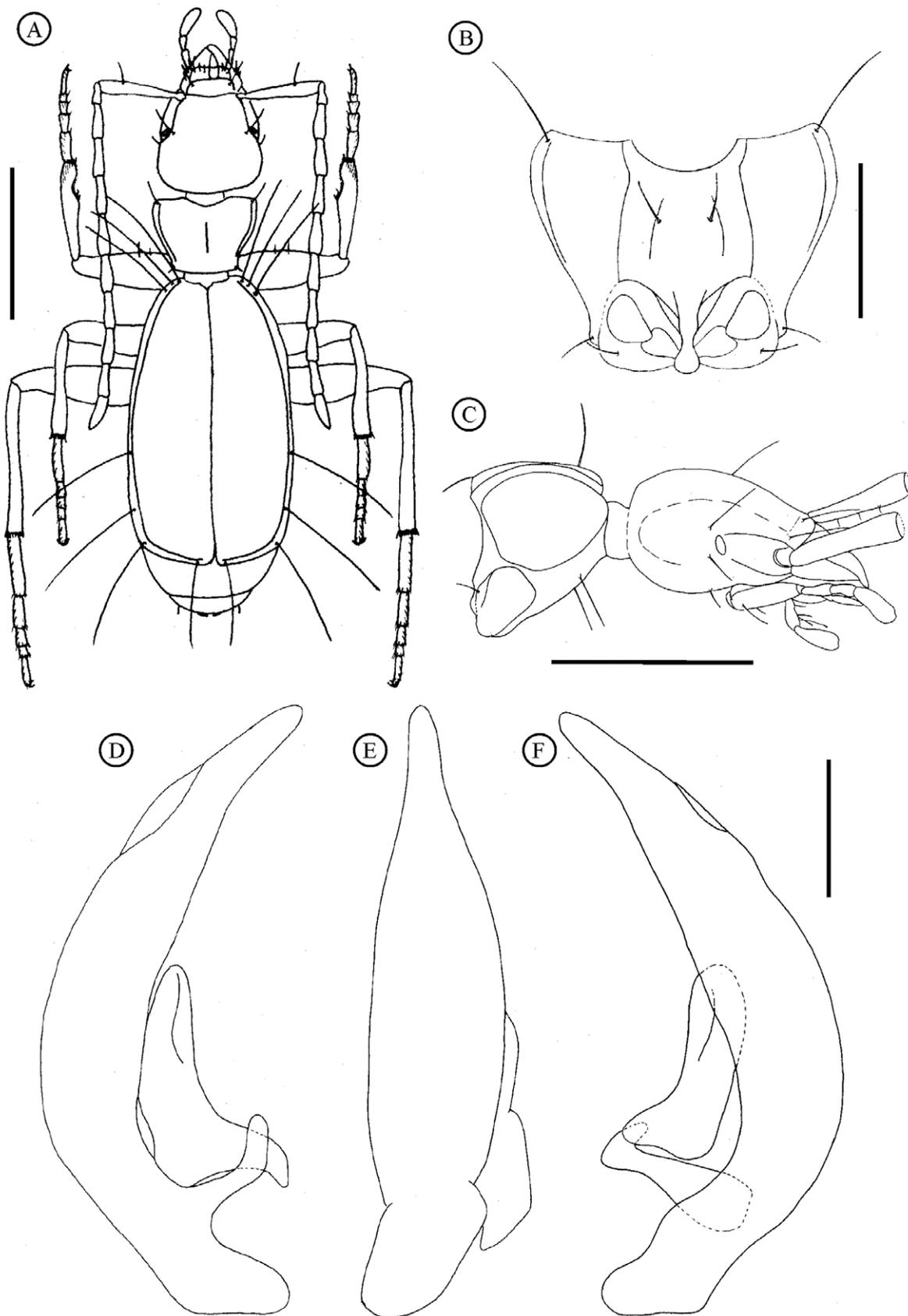


FIGURE 1. Live specimen of *C. tapiaguassu* found in SL 35 cave.

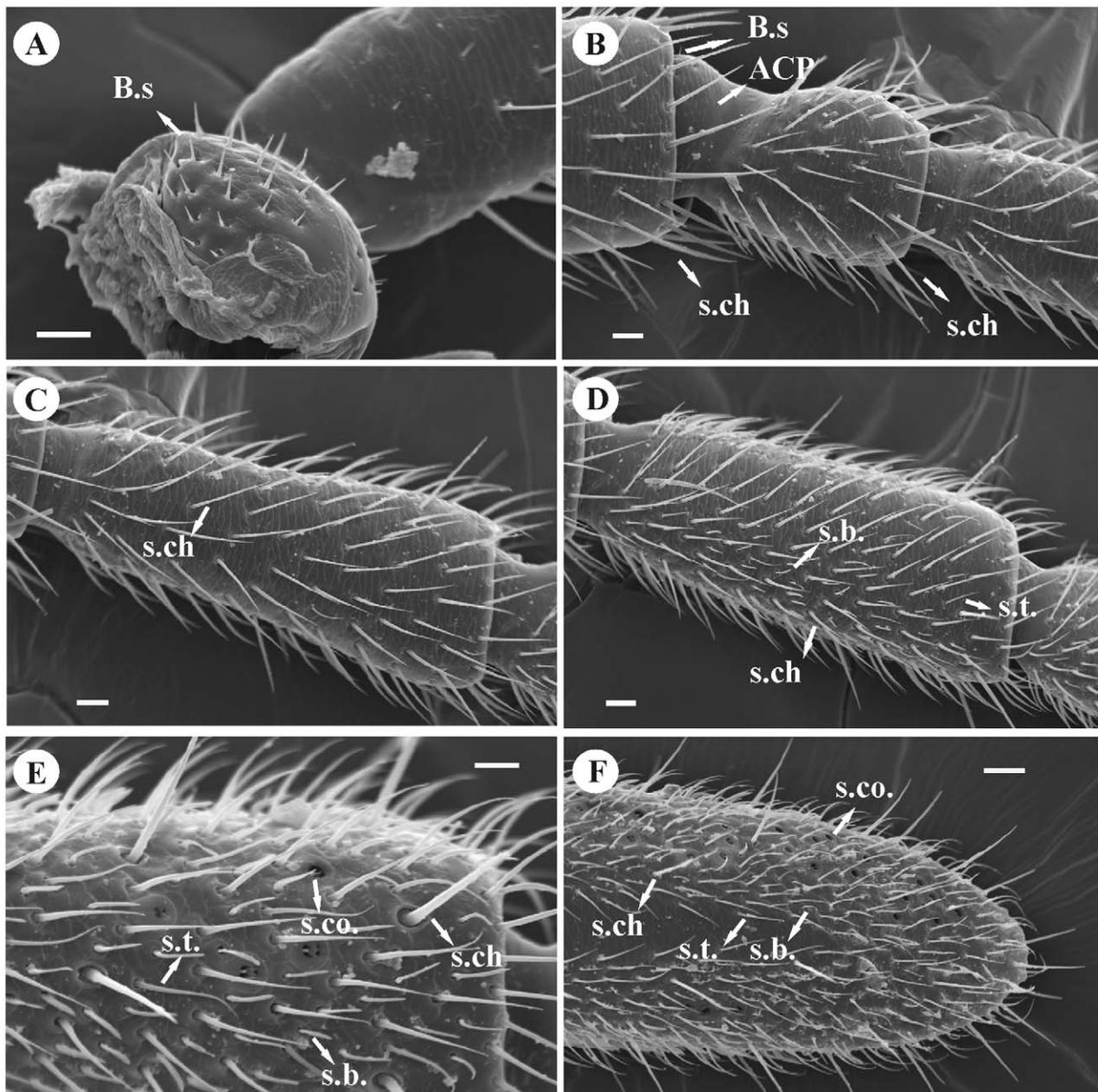
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**FIGURE 2.** *Coarazuphium tapiaguassu*. (A) Habitus from female paratype 1. Bar = 10 mm. (B) Pronotum, ventral view. Bar = 0.5 mm. (C) Head and pronotum lateral view. Bar = 1 mm. (D) Aedeagus, left lateral view. (E) Aedeagus, dorsal view (F) Aedeagus, right lateral view. Bar = 0.25 mm.



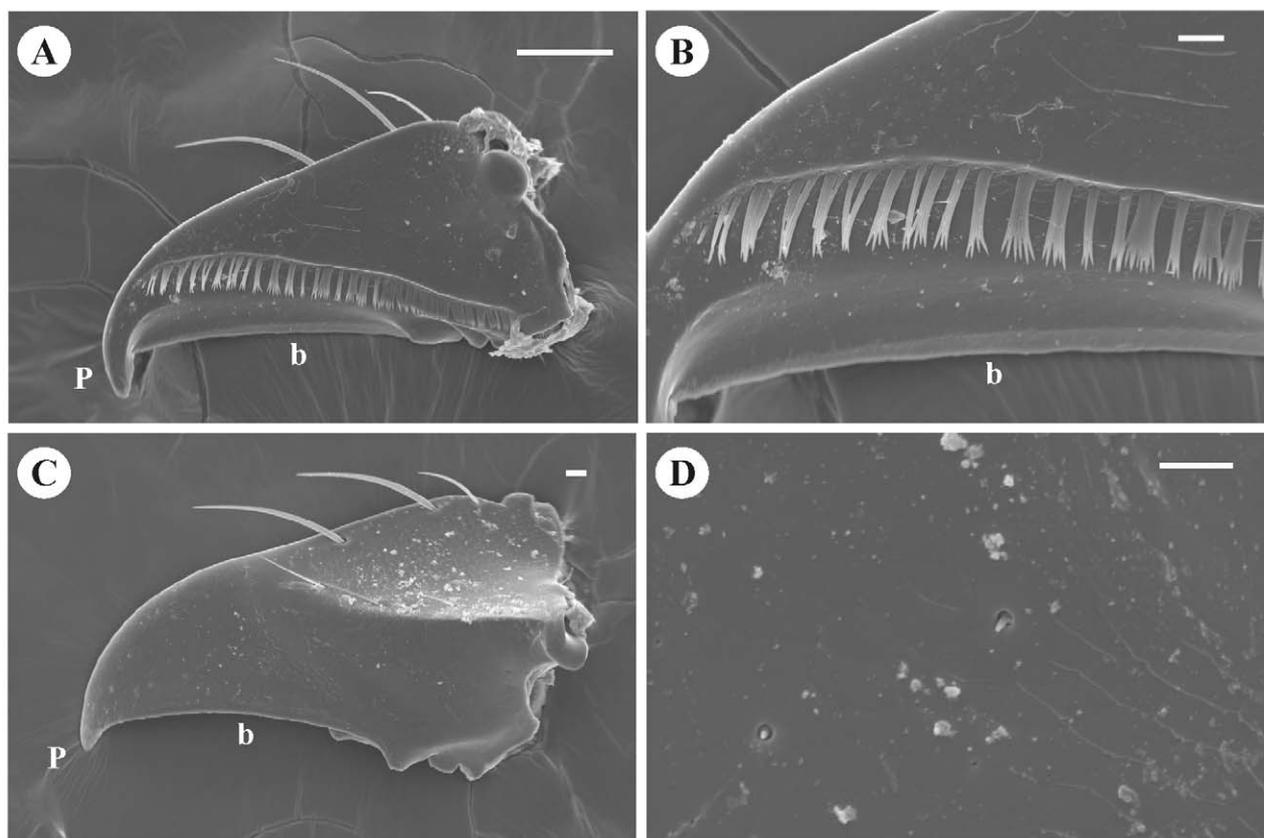
**FIGURE 3.** Scanning electron micrograph showing antennal segments and sensilla in paratype 1 *C. tapiaguassu*. s.ch. show sensilla chaetica, s.t. trichoid sensilla, s.b. sensilla basiconica, s.co. coeloconic sensilla. ACP, appendages of cuticular plates. (A) Back view from the attachment on the head and scape. Bar = 20  $\mu$ m. (B) Pedicel insertion on the scape. Bar = 20  $\mu$ m. (C) Third antennomere. Bar = 20  $\mu$ m. (D) Fourth antennomere. Bar = 20  $\mu$ m. (E) Eighth antennomere. Bar = 10  $\mu$ m. (F) Terminal antennomere. Bar = 20  $\mu$ m.

**Antennae.** Antennae filiform and flagellar, (Fig. 2A) 3.22 mm (3.15–3.40), 5.44 (5.0–5.41) times longer than pronotum; first antennomere elongate, shorter than 2–4 together. First antennomere with a long bristle close to the middle. Antennomeres are almost round in cross-section, except for the tip of the terminal, which is laterally flattened (Fig. 3F).

Sensilla on the antennae of the paratype 2 were examined. The sensilla chaetoid (s.ch) (sensory bristles or spines) are present in all antennomeres, and are the most abundant (Figs. 3B–F). Trichoid sensilla (s.t.) (sensory hairs) can be found on the 4<sup>th</sup> to 11<sup>th</sup> antennomeres. Basiconic sensilla (s.b.) (sensory pegs or cones) are present on the 4<sup>th</sup> to 11<sup>th</sup> antennomeres. Some Böhm sensilla (B.s.) (sensory pit-pegs) are also present found in areas opposite the intersegmental membrane between head and scape, as well as between scape and pedicel on the scape and pedi-

cel bases, respectively (Figs. 3A–B). Coeloconic sensilla (s.co.), (sensory pit-pegs) can be found on the 5<sup>th</sup> to 11<sup>th</sup> antennomeres (Figs. 3E–F). Appendages of cuticular plates (ACP) were abundant at the bases of all antennomeres, close to the intersegmental joints (Fig. 3B).

**Mouthparts.** Sensilla on the mandible, maxilla, labial palpus, labrum, and clypeus of the paratype 1 were examined. The mandible is acutely bent inwardly at its tip. On the ventral side, longitudinal rows of setae are present (Figs. 4A–B). On the dorsal surface, a series of hair sensilla projects from the submolar region to near the cuticular processes (Figs. 4C–D).



**FIGURE 4.** Scanning electron micrograph showing mandible from paratype 1 *C. tapiaguassu*. P = principal tooth; b = masticator border. (A) Ventral view from left mandible. Bar = 100  $\mu$ m. (B) A close-up on ventral view from left mandible. Bar = 20  $\mu$ m. (C) Dorsal view from right mandible. Bar = 20  $\mu$ m. (D) A close dorsal view from right mandible. Bar = 10  $\mu$ m.

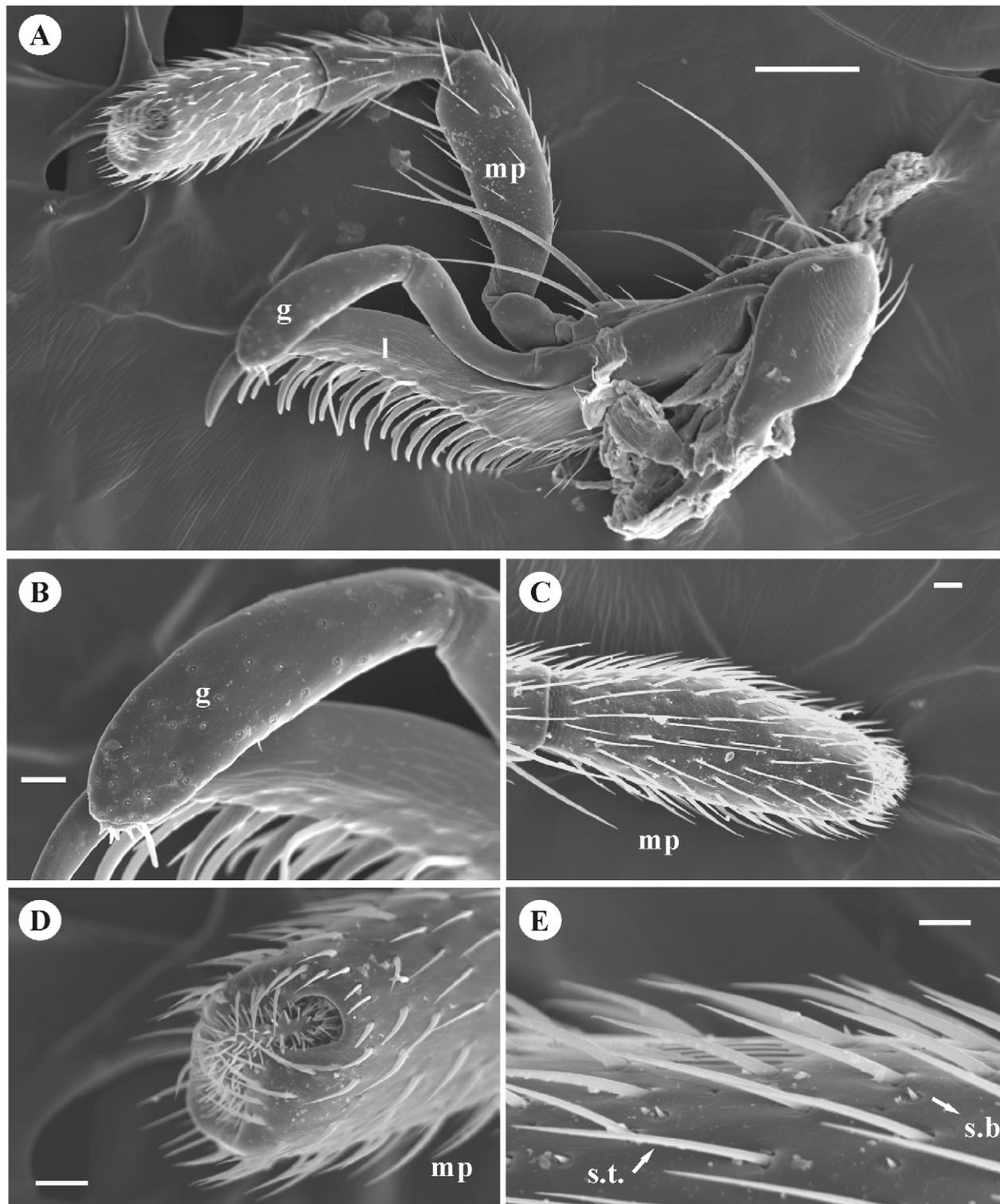
The maxilla basically consists of the lacinia, maxillary palp, and galea (Figs. 5A). The lacinia is shorter than the galea, with an acute and curved end, with rows of long setae and cuticular processes. The galea is biarticulated, composed of 2 segments, with different types of basiconic sensilla. These sensilla become more abundant near the apex of the last segment (Fig. 5B). The four-palpomere from maxillary palp is long and filiform with spaced basiconic sensilla present on the surfaces of the segments. Trichoid sensilla are distributed along the maxillary palp, and they become more abundant and smaller on the last segment (Figs. 5C–D). There are also grooves in this segment that may indicate a sensory organ or gustatory receptors (Fig. 5E).

The labium has one pair of small setae and one pair of long setae near the labial palpi (Fig. 6A), which has some long hairs within. The types of sensilla on the three-segmented labial palpomeres are the same as those on the maxillary palpomeres (Fig. 6B). The labrum is quadrangular and presents tree pairs of setae in dorsal margin (Figs. 7A–B).

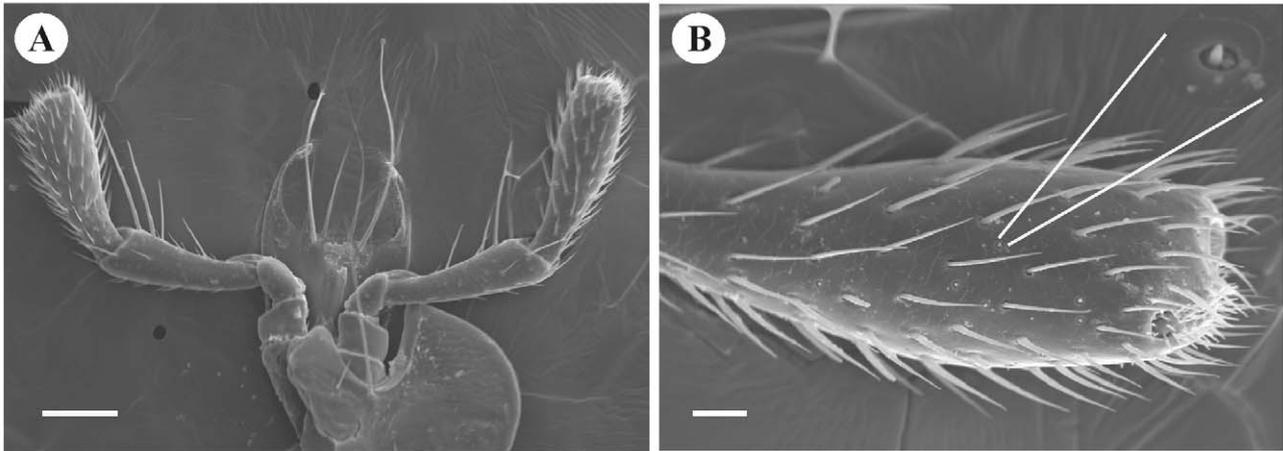
**Pronotum.** Shape trapezoidal, 1.38 (1.28–1.35) times wider than long (Figs. 2A–B). Maximum width close to anterior angle and as wide as head. Anterior and posterior angles are acute. Dorsal surface (Fig. 2A) with two pairs of erect setae: one close to the anterior angle of the pronotum and the other, shorter, close to the posterior angle. Ventral surface with one pair of anterior setae medially located (Fig. 2B).

**Elytra.** Elytra are free (Fig. 2A), together 1.71 (1.74–1.79) times longer than wide. Maximum width nearly one third the distance from the apex and 1.52 (1.48–1.54) times wider than pronotum. Apex of elytra is not sinuous.

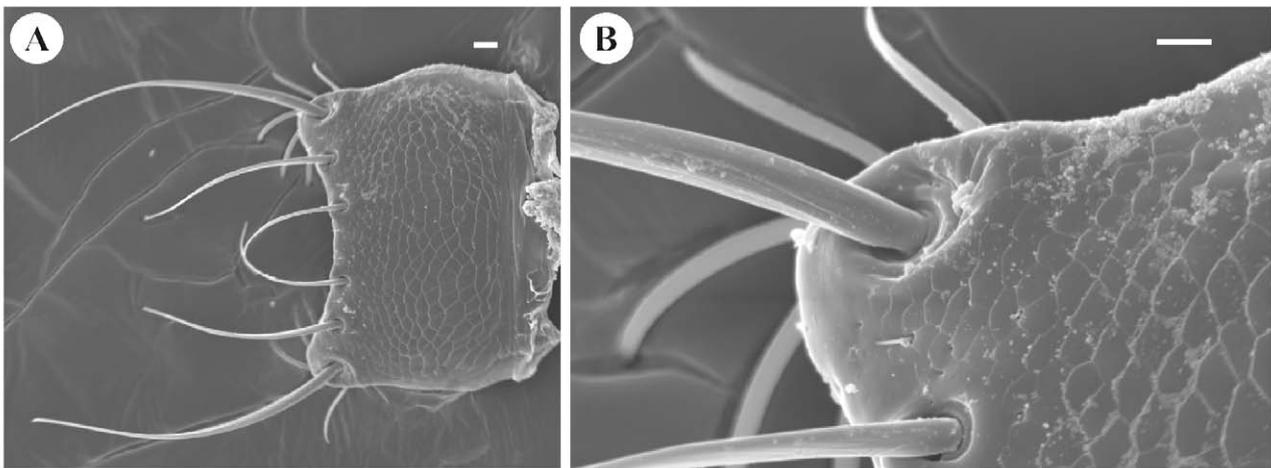
Seven large setae in each elytron: 3 close to the anterior angle, 2 marginal in posterior half, and 2 on posterior margin. Hind wings absent. Abdominal sterna 1–5, glabrous, sixth sternum with a small pair of setae close to its posterior margin.



**FIGURE 5.** Scanning electron micrograph showing maxilla from paratype 1 *C. tapiaguassu*. m.p. = maxillary palp; g = galea; l = lacinia. (A) Right maxilla, ventral view. Bar = 100  $\mu$ m. (B) Right galea, ventral view. Bar = 20  $\mu$ m. (C) Left maxillary palp. Bar = 20  $\mu$ m. (D) A view from the apical maxillary palp. Bar = 20  $\mu$ m. (E) Close-up on maxillary palp, view of a probable sensilla organ. Bar = 10  $\mu$ m.



**FIGURE 6.** Scanning electron micrograph showing labium with labial palpus from paratype 1 *C. tapiaguassu*, l.p. = labial palp. (A) Labium, ventral view. Bar = 100  $\mu\text{m}$ . (B) Apex of distal palpomere. Bar = 20  $\mu\text{m}$ .

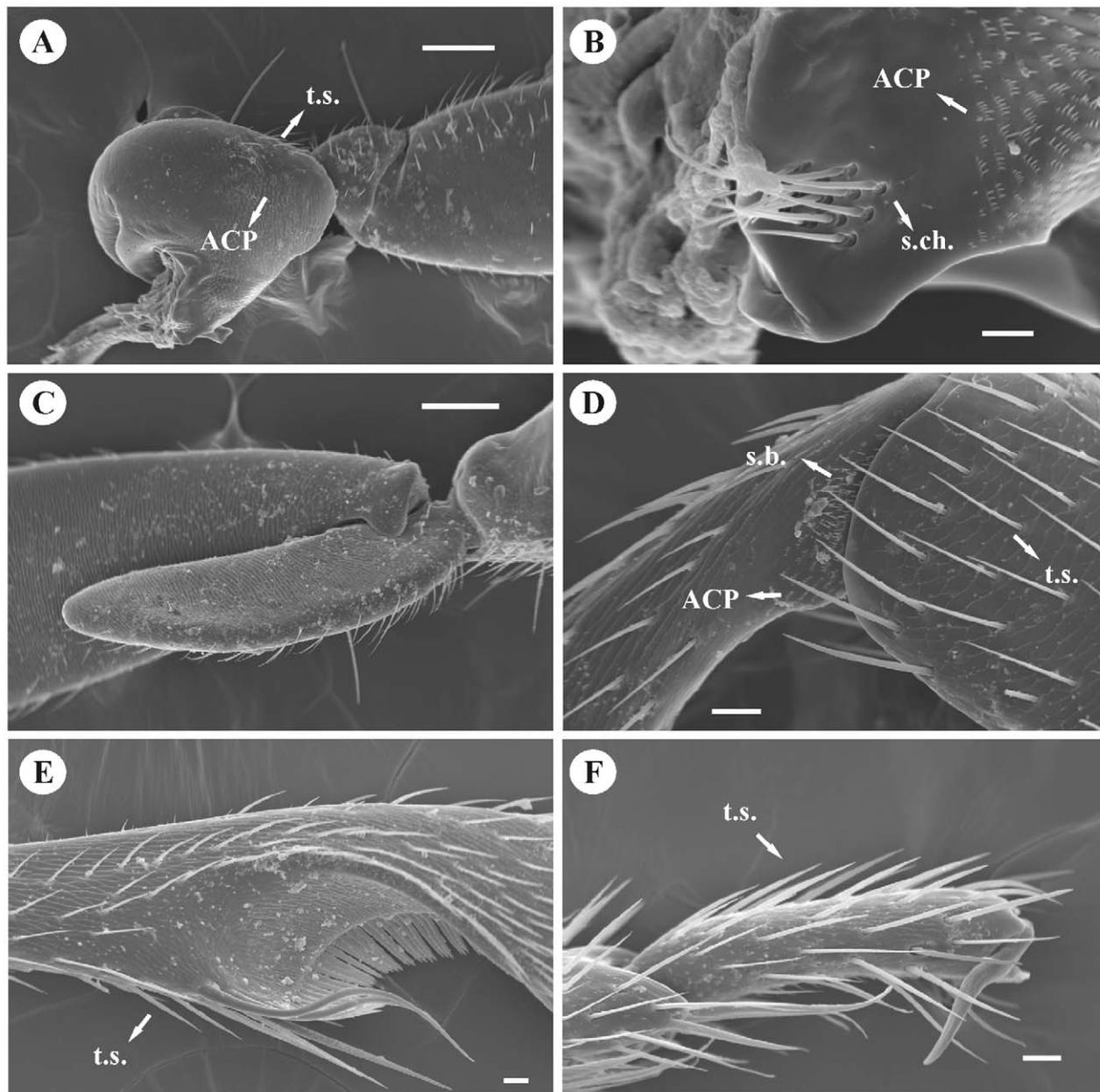


**FIGURE 7.** Scanning electron micrograph showing labrum from paratype 1 *C. tapiaguassu*. (A) Dorsal view of the labrum. Bar = 20  $\mu\text{m}$ . (B) Close-up on apical setae insertion in the labrum. Bar = 10  $\mu\text{m}$ .

**Legs.** Procoxa with one pair of setae at posterior margin (Fig. 2B); meso and metacoxa with one pair of setae close to the anterior margin. Pro-, meso- and metatrochanter bear one medial setae. Profemur with long and short setae. Profemur 1.04 (0.90–1.12) mm, as long as the mesofemur and 0.90 (0.68–0.75) times the length of metafe-mur. Protibia 1.15 (1.0–1.09) as long as the mesotibia and 0.61 (0.68–0.79) times the length of metatibia. Protibia 1.21 (1.15–1.60) times longer than protarsus. Mesotibia 0.90 (1.0–1.2) times the length of mesotarsus and metatibia 1.1 (1.04–1.21) times longer than the metatarsus. First tarsomere almost equal to tarsomeres 2–4 together. Length of protibia and tarsus together 2.63 (2.29–2.65) times the length of the pronotum. Mesotibia and tarsus length 2.63 (2.59–2.56) times, and metatibia and tarsus length 3.94 (2.72–3.65) times the length of pronotum.

The ultrastructural analysis showed that the coxal segment has 3 types of sensilla: one type is the sharply pointed long trichoid sensilla (s.t.). The other type, the appendages of cuticular plates (ACP) are abundant on the procoxae, covering all the procoxae tissue (Figs. 8A–B). Some sensilla chaetica were also observed in the basal part of the coxae (Fig. 8B). The trochanter also bears trichoid sensilla (Fig. 8C). On the femur, trichoid sensilla are regularly distributed on the whole surface (Figs. 8D–E). ACP are abundant at the base of the protibia, close to the intersegmental joint, where there is also an aggregate of basiconic sensilla (Fig. 8D). The protibia also has a row of trichoid sensilla, which become more abundant at the apex, and spaced basiconic sensilla occur at its border (Fig. 8E). The tarsus has abundant trichoid sensilla (Fig. 8F).

**Aedeagus.** Dorsally curved and elongate, presently the biggest and longest aedeagus among *Coarazuphium* species, with some protuberance at the apices (Figs. 2D–F). Left paramere about two times longer than wide, right paramere slighter curved and elongate.



**FIGURE 8.** Scanning electron micrograph showing proleg segments and sensilla in paratype 1 *C. tapiaguassu*. (A) Back view of coxae and trochanter. Bar = 100  $\mu\text{m}$ . (B) Close-up on back portion from coxae. Bar = 10  $\mu\text{m}$ . (C) Trochanter. Bar = 100  $\mu\text{m}$ . (D) Tibia insertion on femur. Bar = 20  $\mu\text{m}$ . (E) Close-up on tibia. Bar = 20  $\mu\text{m}$ . (F) Apical tarsomere and claw. Bar = 20  $\mu\text{m}$ .

**Etymology.** The epithet is from the tupi-Guarani word (Indian Brazilian language) tapiaguassu (Tapiaguaçu), meaning those of large penis.

**Differential diagnosis.** All characteristics of *C. tapiaguassu* are consistent with the description of the genus *Coarazuphium*, except for the non-sinuuous margin of the elytra, which was already observed in *C. pains*. Álvares & Ferreira (2002) suggested that this character be reconsidered for the genus, because it is not present in specimens of *C. pains*. This new troglobite species of *Coarazuphium* differs from the others by the absence of setae on the dorsal surface of the head, near the posterior margin; the other species feature one, two or three pairs of setae. Furthermore, the aedeagus is larger and longer than in other all *Coarazuphium* species.

**Key to species of the genus *Coarazuphium***(modified from Gnaspini *et al.*, 1998 and Pellegrini and Ferreira, 2011).

1. Eyeless; maximum width of elytra at middle ..... *C. cessaima* Gnaspini *et al.*, 1998.
- Eyes very reduced; maximum width of elytra near apex ..... 2
2. Posterior margin of the elytra not sinuate ..... 3
- Posterior margin of the elytra sinuate ..... 4
3. Posterior angle of pronotum rounded, posterior base sinuate ..... *C. pains* Álvares & Ferreira 2002.
- Posterior angle of pronotum marked, posterior base not sinuate ..... *C. tapiaguassu* sp. n. Pellegrini & Ferreira, 2011.
4. One pair of dorsal setae at the posterior border of head; head wider (ratio = 1.2) than pronotum ..... *C. tessai* (Godoy & Vanin, 1990).
- Two pairs of dorsal setae at the posterior border of head; head almost as wide as pronotum ..... 5
5. Head much narrower than elytra (0.55), with two pairs of setae on dorsal surface ..... *C. bezerra*, Gnaspini *et al.*, 1998.
- Head slightly narrower than elytra (0.71), three pairs of setae on dorsal surface ..... *C. formoso*, Pellegrini & Ferreira, 2011.

**Habitat, ecological considerations and threats.** The caves where the specimens were collected are located in a complex iron ore outcrop known locally as “Serra Leste” or “Serra Pelada”. There are distinct lithotypes in the area, with caves associated with superficial ferruginous breccia (canga formation), iron ore and ferricretes. More than 100 caves are known to exist in the area, but the species was found in only three caves, all formed in the canga. Those caves are quite small, with sizes ranging from 25.5 meters (SL 31) to 39.9 meters (SL 35). However, all of those caves are connected to a huge net of small channels (canaliculi), typically found in the canga formation, which considerably enhances the habitats for the subterranean fauna in iron ore caves (Souza-Silva *et al.*, 2011).

In all cases, the individuals were found in the inner portion of the caves. In two caves (SL 31 and SL 35), the conditions of those inner parts differ greatly from those observed in the entrance chamber. Those areas are usually aphotic and very moist. In these two caves, individuals were observed during both wet and dry seasons. In contrast, in cave SL 30, with a more “unstable” atmosphere, specimens were collected only in the dry season.

Most species of *Coarazuphium* usually do not hide in microhabitats. Rather, they freely walk over the soil or rocky substrates, which indicates at least a reduction in their cryptobiotic behavior. This was observed at least for *C. formoso*, *C. pains* and *C. cessaima* (Ferreira, personal observations; Álvares & Ferreira, 2002; Pellegrini & Ferreira, 2011). *C. tapiaguassu*, however, shows a quite different behavior. All observed specimens were found by turning rocks in the cave floor. They were all hidden under such rocks. For this reason, no individual was observed feeding, and their diet could not be determined.

Of the 17 specimens collected in SL 31 and SL 35 caves, five had fungal mycelia attached to appendages or elytra, belonging to a species of Laboulbeniales (Ascomycota) (Fig. 9A–C). Unfortunately, the fungal species was not identified up to the present moment, but it could represent a new species, considering the host specificity of such fungi group.

To date, *Coarazuphium* species have been found only in limestone caves. Three of these species were present in the Bambuí Speleological Province (Godoy & Vanin, 1990; Gnaspini *et al.*, 1998; Álvares & Ferreira, 2002). The other two were found at Una Speleological Province (Gnaspini *et al.*, 1998; Pellegrini & Ferreira, 2011). The species described here is the first *Coarazuphium* found in iron ore caves, in the ferriferous formation of Carajás (Lindenmayer *et al.* 2001) (Fig. 10).

Although the original epigeal physiognomy in the area was the Amazon rainforest, most of the forest formations have been removed over the last four decades. The external system (outside the cave) consists mainly of pastures. Furthermore, the area is also threatened by mining activities, which can destroy the caves when extracting iron ore.

**Discussion**

To date, Zuphiini troglomorphic genus *Ildobates*, *Speozuphium* and *Speothalpius*, shows very advanced troglobite characteristics, more developed than in *Coarazuphium*. However, Gnaspini & Trajano (1994) suggested that *Coarazuphium* have the most advanced character states related to troglomorphy among all Brazilian cave beetles. In fact, troglomorphisms shown by many temperate species are usually more developed than those in species from the tropics, as shown in *Ildobates*, *Speozuphium* and *Speothalpius*.



**FIGURE 9.** *Coarazuphium tapiaguassu* specimen infected by fungi Laboulbeniales (Ascomycota). (A) *C. tapiaguassu* infected. (B) Detail on metafemur. (C) Scanning electron micrograph showing fungi Laboulbeniales attached to femur. Bar = 40  $\mu$ m.

The less troglomorphic traits observed in *Coarazuphium* species, when compared to other troglotic Zuphiini, might be due to at least two factors: Brazilian *Coarazuphium* species could be more recent troglotites, and, in this case, they had less time for structural regression. In the other hand, some *Coarazuphium* species (especially *C. tapiaguassu*) lives in very superficial caves. A study comparing eyes from carabids with different degree of adaptation for cave life suggested that troglotite species living in superficial underground systems, utilize dim light stimuli for orientation in space and/or time, and the evolutionary regression of eyes could be stopped at distinct functional and morphological states (Bartkowiak *et al.*, 1991). Accordingly, *Coarazuphium* species associated to shallow subterranean habitats (as iron ore caves) could maintain vestigial eyes, which would allow them to detect (and avoid) sunlight, preventing deleterious effects of such radiation.

Some troglomorphisms, such as eyes and pigment reduction and elongated appendages, can be observed under routine stereomicroscope analysis (Figs. 2A–F). However, more advanced technologies may be required to find other troglomorphic traits. For instance, the increased number of non-optic sensory structures, like hair sensilla, could not be detected via traditional microscopic examination, thus requiring ultrastructural scrutiny.

According to McIver (1975), hair sensilla are the most abundant, widespread and extensively investigated type of cuticular mechanoreceptor that may function as well as chemoreceptors. Unfortunately, of the five known species of *Coarazuphium*, only *C. formoso* (Pellegrini & Ferreira, 2011) has been studied with regard to these structures. The species *C. formoso* and *C. tapiaguassu* did not differ significantly with regard to most ultrastructural features, although some differences in the distribution pattern of the coeloconic sensilla were recognized. In *C. tapiaguassu*, those sensilla occur from the fifth antennomere to the tip of the antennae, while in *C. formoso* they are present from the fourth antennomere to the tip of the antennae. According to Zacharuk (1980), the most probable functions for these sensilla are chemo-, thermo- or hygroreception. The presence of coeloconic sensilla in a lesser

number of antennomeres than observed in *C. formoso* can indicate that the latter species is likely more specialized in searching for water (or moist areas). Considering that *C. formoso* specimens are found in dry caves in the Caatinga formation (Brazilian semi-arid biome), they could be better adapted to the search for moist areas, while *C. tapiaguassu* is found in more humid systems.

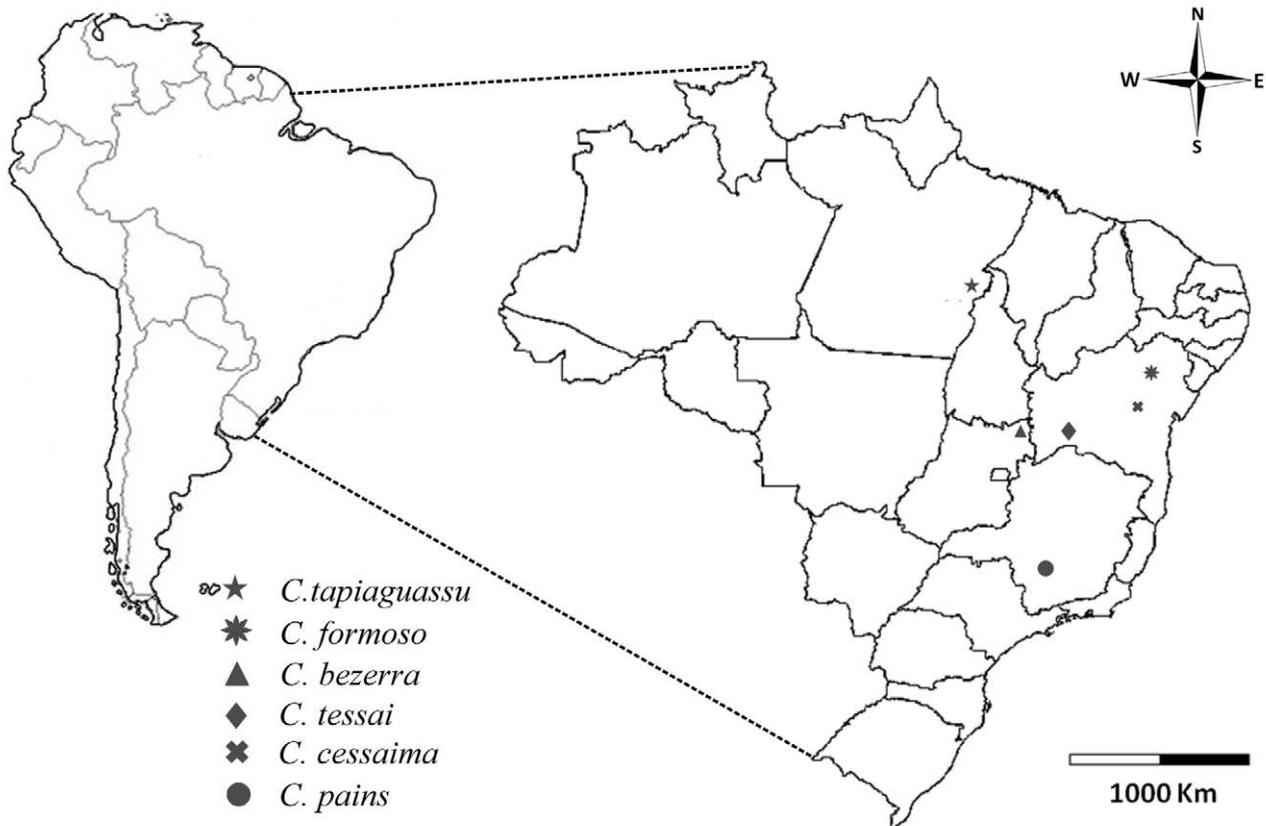


FIGURE 10. Geographic distribution of *Coarazuphium* species in Brazil.

A study comparing Cholevinae (Leiiodidae) species showed notable mouthpart modifications, indicating adaptation to cave life (Moldovan *et al*, 2004). The authors stated that mouthpart differences among Cholevinae species offer useful characters for taxonomy, especially in cave species with otherwise homogeneous morphology. However, the differences in ultrastructural characters observed among Cholevidae may be attributed to taxonomic issues (the compared species belong to different genera), or may even be due to different degrees of adaptation to life in caves (some species were troglaphiles, while other, troglobites).

The ultrastructural analysis of *C. tapiaguassu* and *C. formoso* showed only minor differences between the two species. The observed similarities are perhaps due to their close relationship or, additionally, to similar selective pressures during their evolution. Unfortunately, little is known concerning ultrastructure of other *Coarazuphium* species, which precludes more efficient comparisons. However, given the differences in their macrostructures, it is plausible to assume that are constraints to morphological diversification in *Coarazuphium* species imposed by their adaptation to cave life. However, only with the intensification of morphological studies (including ultrastructural analysis of the remaining species in the genus) and molecular approaches, it will be possible to obtain more data on the phylogeny of the species in this genus, and on their evolution in the subterranean habitats.

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## References

- Álvares, E.S.S. & Ferreira, R.L. (2002) *Coarazuphium pains*, a new species of troglotic beetle from Brazil (Coleoptera, Carabidae, Zuphiini). *Lundiana*, 3, 41–43.
- Bartkowiak, D., Tschardt, T. & Weber, F. (1991) Effects of stabilizing selection in the regressive evolution of compound eyes in hypogean carabid beetles. *Mémoires de Biospéologie*, 18, 19–24.
- Español, F. (1966) Interesantes descubrimientos bioespeleológicos en la provincia de Castellón. *Publicaciones del Instituto de Biología Aplicada de Barcelona*, 40, 67–79.
- Gnaspini, P. & Trajano, E. (1994) Brazilian cave invertebrates, with a checklist of troglomorphic taxa. *Revista Brasileira de Entomologia*, 38, 549–584.
- Gnaspini, P., Vanin, S.A. & Godoy, N.M. (1998) A new genus of troglotic carabid beetles from Brazil (Coleoptera, Carabidae, Zuphiini). *Papéis Avulsos de Zoologia*, S. Paulo, 40, 297–309.
- Godoy, N.M. & Vanin, S.A. (1990) *Parazuphium tessai*, a new cavernicolous beetle from Bahia, Brazil (Coleoptera, Carabidae, Zuphiini). *Revista Brasileira de Entomologia*, 34, 795–799.
- Kim, J.L. & Yamasaki, T. (1996) Sensilla of *Carabus (Isiocarabus) fiduciaris saishutoicus* Csiki (Coleoptera: Carabidae). *International Journal of Insect Morphology and Embryology*, 25, 153–172.
- Lindenmayer, Z.G., Laux, J.H. & Teixeira, J.B.G. (2001) Considerações sobre a origem das formações ferríferas da formação Carajás, Serra dos Carajás. *Revista Brasileira de Geociências*, 31, 21–28.
- McIver, S.B. (1975) Structure of cuticular mechanoreceptors of arthropods. *Annual Review of Entomology*, 20, 381–397.
- Merivee, E., Ploomi, A., Rahi, M., Bresciani, J., Ravn, H.P., Luik, A. & Sammelselg, V. (2000). Antennal sensilla of the ground beetle *Bembidion properans* Steph (Coleoptera: Carabidae). *Micron*, 33, 429–440.
- Moldovan, O.T., Branko, J. & Erichsen, E. (2004) Adaptation of the mouthparts in some subterranean Cholevinae (Coleoptera, Leiodidae). *Natura Croatica*, 13, 1–18.
- Moore, B.P. (1995) Two remarkable new genera and species of troglotic Carabidae (Coleoptera) from Nullarbor Caves. *Journal of the Australian Entomological Society* 34, 159–161.
- Pellegrini, T.G. & Ferreira, R.L. (2011) Ultrastructural analysis of *Coarazuphium formoso* (Coleoptera: Carabidae, Zuphiini), a new Brazilian troglotic beetle. *Zootaxa*, 2866, 39–49.
- Ribeira, I., Montagud, S., Teruel, S. & Bellés, X. (2006) Molecular data supports the inclusion of *Ildobates neboti* Español in Zuphiini (Coleoptera: Carabidae: Harpalinae). *Entomologica Fennica*, 17, 207–213.
- Souza-Silva, M., Martins, R.P. & Ferreira, R.L. (2011) Cave lithology determinig the structure of the invertebrate communities in the Brazilian Atlantic Rain Forest. *Biodiversity and Conservation*, 20, 1713–1729.
- Schneider, D. (1964) Insect antennae. *Annual Review of Entomology*, 9, 103–22.
- Zacharuk, R.Y. (1980) Ultrastructure and function of insect chemosensilla. *Annual Review of Entomology*, 25, 27–47.