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First report of Eucalodiidae in Brazil (Stylommatophora: Urocoptoidea), with the description of a new genus and species

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Abstract. Alto Ribeira Tourist State Park (PETAR) in São Paulo state, southeast Brazil, is renowned for its numerous caves hosting diverse molluscan fauna, including many endemic and cavernicolous species. Collection efforts at PETAR have uncovered a unique terrestrial gastropod from one of these caves. This land snail, exhibiting striking shell morphology, has led to the present description of a new genus and species, *Caerbannogia calida* gen. et sp. nov. Its conchological features, particularly the internal structure of the columella, suggest a classification within Eucalodiidae (Urocoptoidea). Although this superfamily is predominantly distributed in the Caribbean, a few modern and fossil species deemed to belong to it have been identified in Brazil. This discovery marks the first record of the family Eucalodiidae in Brazil.

Key words. Caerbannogia calida gen. et sp. nov., Paleogene, PETAR, subterranean fauna

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Introduction

Cave faunas can be pretty interesting to various disciplines of biology, as they typically count with plenty of endemic species. Many cave-dwelling species exhibit pronounced morpho-anatomical and physiological adaptations to life in darkness. Some taxa can undergo extensive radiation and speciation throughout a cave system, and some taxa can survive within caves while related species go extinct in the "surface world". In Brazil, the subterranean fauna attracts many researchers, and most higher taxa count with plenty of studies (Trajano & Bichuette 2010). However, we are just starting to understand this subterranean snail fauna's diversity and complexity (Salvador *et al.* 2022b).

The Upper Ribeira Valley (Vale do Alto Ribeira), located in São Paulo state, is a well-documented hotspot of subterranean biodiversity in Brazil (Trajano 2000; Trajano *et al.* 2016). The Alto Ribeira karst region features discontinuous

limestone outcrops, leading to the isolation of distinct cave systems (Trajano *et al.* 2016). This area lies at the transition between the Tropical Atlantic and Araucaria Forest domains and is characterized by a humid subtropical climate, with no distinct dry season and mean annual temperatures ranging from 18 to 19 °C (Nimer 1989). The valley harbours one of the last continuous remnants of the Brazilian Atlantic Forest and is famous for its numerous caves (reaching 500 recorded caves). It is also home to one of the most well-known nature parks in the country, the Alto Ribeira Touristic State Park (Parque Estadual Turístico do Alto Ribeira, PETAR), which plays a crucial role in both Atlantic Forest research and ecotourism (Trajano 2000).

The Upper Ribeira Valley, and PETAR in particular, is home to a wide diversity of land and freshwater snails, including a few endemic species (Simone & Moracchioli 1994; Salvador *et al.* 2016; Simone 2016; Bichuette & Trajano 2018). Nevertheless, the molluscan diversity in the

valley has yet to be fully assessed, and more discoveries are expected from the many caves in the area (Salvador *et al.* 2016).

Collection efforts at PETAR have brought to light a terrestrial gastropod of unique morphology from one of the park's caves. It is considered to belong to a new species and a new genus, described herein, and is the first record of the family Eucalodiidae in Brazil.

MATERIALS & METHODS

The studied material originates from the Ressurgência das Areias de Água Quente cave (Fig. 1), which is part of the Areias cave system. This system comprises three caves: Areias de Cima, Areias de Baixo, and Ressurgência das Areias de Água Quente. While Areias de Cima and Areias de Baixo are located within the boundaries of PETAR, the Ressurgência das Areias de Água Quente cave lies outside the park's protected area. Consequently, tourist access to this cave is not regulated by a management plan, and signs of anthropogenic impact are already evident (Bichuette & Trajano 2003) (Fig. 2).

A single specimen, an empty shell, was found in 2012; further specimens could not be procured despite extensive searches since. The shell is preserved dry and deposited in the collection of the Laboratório de Estudos Subterrâneos (LES) of the Federal University of São Carlos (São Carlos, SP, Brazil) under registration number

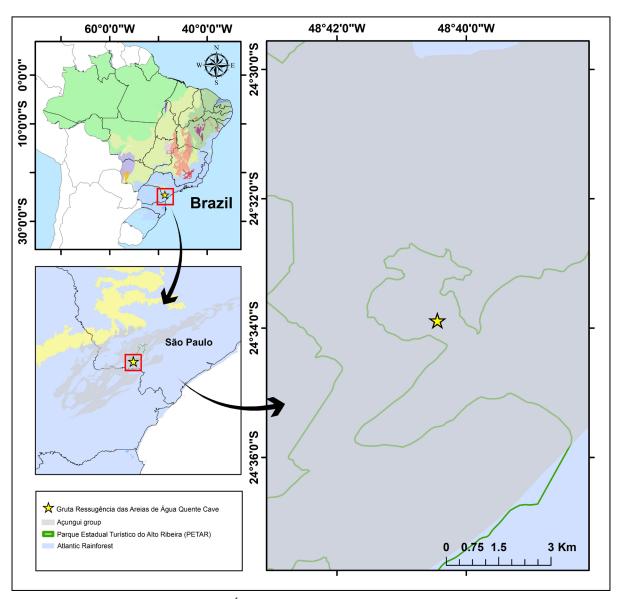


Figure 1. Location of Ressurgência das Areias de Água Quente cave in southeastern Brazil. Map provided by Marcus V.S.A. Duarte.



Figure 2. A, aerial photograph showing signs of deforestation close to the Ressurgência das Areias de Água Quente cave. **B**, **C**, cave entrance with steps for easy access by visitors. **D**, gallery with silt and rocky substrate.

LES 6873. For comparison, fossils of *Brasilennea arethusae* Maury, 1935 were obtained from the collection of the Museu de Zoologia da Universidade de São Paulo (lots MZSP 86322 and 86324).

Computed tomography (CT) scanning was conducted at the Centro para Documentação da Biodiversidade (FFCL-RP-USP, Brazil) using a Phoenix v|tome|x S240 CT & X-Ray System (General Electric, USA) equipped with a digital high-contrast detector DXR250RT and a 240 kV microfocus source. The specimen LES 6873 was scanned under the following parameters: source voltage of 70 kV and current of 200 μ A, 1,200 projections, binning of 1 \times 1, averaging 3 frames with 1 frame skipped, exposure time of 200.09 ms, default offset and gain correction, and a 0.1 mm copper filter. Fossil specimens were scanned using a source voltage of 90 kV and current of 180 μA, 1,200 projections, binning of 1×1 , averaging 4 frames with 1 frame skipped, exposure time of 200.09 ms, default offset and gain correction, and a 0.1 mm copper filter. The resulting 16-bit grayscale images measured 990 × 1,000 pixels. Three-dimensional reconstructions were generated using GE Phoenix Datos X2 software, while visualisation and editing of the 3D models were performed using VGStudio Max 3.0 (Volume Graphics, Germany).

Systematics

Superfamily Urocoptoidea Pilsbry, 1898 (1868)

Family Eucalodiidae Fischer & Crosse, 1873

Genus Caerbannogia gen. nov.

Figure 3

ZooBank identifier. urn:lsid:zoobank.org:act:CB6566A A-7AA0-43C8-9F8D-139D426606D7

Type species. Caerbannogia calida gen. et sp. nov.

Included species. Caerbannogia calida gen. et sp. nov.

Etymology. The name refers to the Cave of Caerbannog, home of the Legendary Black Beast of Arrrghhh, a.k.a. the Rabbit of Caerbannog, in *Monty Python and the Holy Grail*. Grammatical gender: feminine.

Diagnosis. Shell cylindrical-turriform, decollate, narrower towards aperture. Teleoconch sculptured by prosocline ribs, which become stronger and more spaced towards aperture. Whorls with shoulder-like angulation on their apical portion. Body whorl and half of preceding half marked by an extreme narrowing of their median portion. Aperture subcircular, apically elongated. Columellar lamella absent.

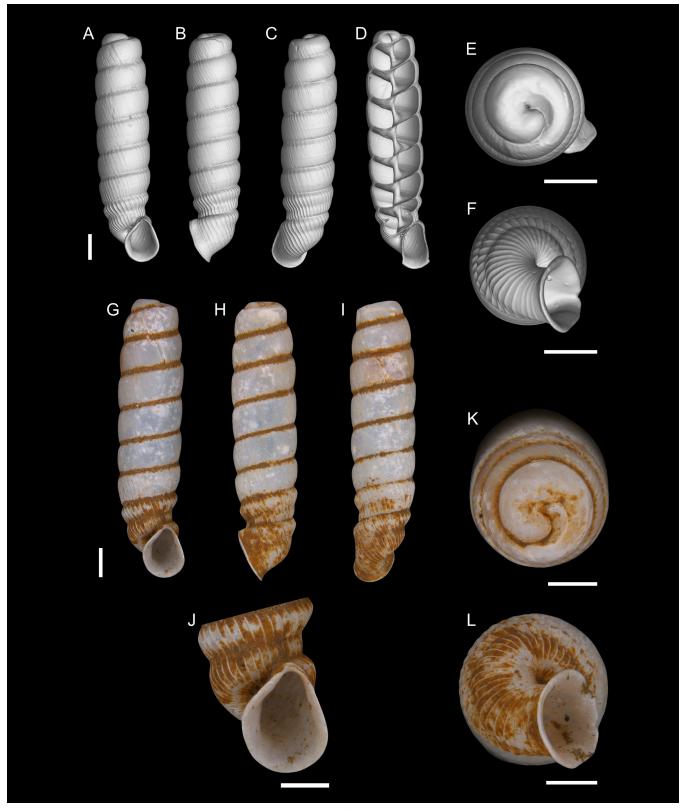


Figure 3. Caerbannogia calida gen. et sp. nov., holotype (LES 6873); scale bars = 1 mm. A–F, 3D reconstruction of micro-CT images (voxel size = 11.75 μm). G, H, stereomicroscope photographs. A–C, G–I, entire shell in apertural, lateral, and dorsal views, respectively. D, internal structure of the shell. E, K, shell in apical view, showing detail of decollate spire top. F, L, shell in abapical view. J, detail of aperture.

Description. See species entry below.

Classification. The classification of *Caerbannogia* gen. nov. in Urocoptoidea (and Eucalodiidae specifically, which was formerly a subfamily of Urocoptidae) can be explained by the morphological features of the shell and the close resemblance to other members of the group. The cylindrical-turriform shell (often decollated) is typical of both Eucalodiidae and Urocoptidae, although a decollate spire top (Fig. 3E, K) is more of a rule in the former; the hollow columella typically lacking a lamella (Fig. 3D) is one of the diagnostic features of Eucalodiidae (Zilch 1960; Schileyko 1999a). The subcircular apically elongated aperture (Fig. 3J) is also widespread among members of Eucalodiidae, and the shoulder-like angulation and the narrowing of the body whorl can be seen, respectively (and in a very attenuated manner), in genera such as Coelocentrum Crosse & Fischer, 1872 and Eucalodium Crosse & Fischer, 1868 (Zilch 1960; Schileyko 1999a; Uit de Weerd 2008).

The Eucalodiidae are distributed in the Caribbean, Mexico, and Guatemala (Zilch 1960), so it is also necessary to compare *Caerbannogia* gen. nov. to the other Brazilian representatives of Urocoptoidea, namely: *Habeas* Simone, 2013 and the Paleogene fossils *Brasilennea* Maury, 1935 and "*Brachypodella*" britoi (Ferreira & Coelho, 1971).

The shoulder-like angulation on the whorls of the shell of Caerbannogia gen. nov. is somewhat reminiscent of the genus Habeas (Fig. 4A, B), which also contains some cave-dwelling species (Salvador et al. 2022b; Simone 2022). This sinistrally shelled genus was originally classified in Diplommatinidae (Caenogastropoda; Simone 2013) but was later transferred to Urocoptidae based on conchological and anatomical similarities (Simone 2022). Nevertheless, when the latter author compared the anatomical features (Simone 2022), most of his positive comparisons were with genera that he considered to be Urocoptidae but that have long been classified as either Eucalodiidae or Holospiridae (Uit de Weerd 2008; Thompson 2012). Thus, *Habeas* likely belongs to one of these two families and the procurement of genetic data should clarify its position. Case in point, even though the shell of Habeas is sinistral, it more closely resembles members of Holospiridae (or even Epirobiidae) than Urocoptidae proper, being particularly reminiscent of Coelostemma Dall, 1895, some Holospira Martens, 1860, and Epirobia Strebel & Pfeiffer 1880. There is no information, however, on the internal structure of the columella of Habeas spp. or the presence/absence of a columellar lamella (Simone 2022).

While the overall shell shape of *Caerbannogia* gen. nov. is mostly different to the pupiform or teardrop-shaped shells

of Brasilennea spp., there is a striking similarity among them. The shells of *Brasilennea* spp. also display the extreme constriction of the median portion of the body whorl (Maury 1935; Salvador & Simone 2013). That constriction is even more extreme in Brasilennea spp., with a second narrowed region between the first one and the umbilicus (Fig. 4C–G). It is presently impossible to say whether this similarity indicates kinship or is more likely, perhaps, a convergent trait. Salvador et al. (2011) classified Brasilennea in Cerionidae, which is considered the sister taxon to Eucalodiidae + Urocoptidae (although with low support), with Holospiridae and Epirobiidae branching off earlier in a polytomy (Uit de Weerd 2008). Nevertheless, our analysis of specimens of type species Brasilennea arethusae using CT scanning to observe the internal structure of the lamella (Fig. 4F, G; further images available in Supplementary File 1) can add more information to that discussion. The CT images show a wide hollow columella with a strong columellar lamella present throughout the body whorl. That feature is typical of Holospiridae and, in particular, of Holospira, a genus that contains species with very similarly shaped shells to Brasilennea (Zilch 1960). Considering the age of this fossil, that would be in line with the basalmost branching off of Holospiridae within Urocoptoidea (Uit de Weerd 2008). Nevertheless, some members of Cerionidae also bear a short columellar lamella (Schileyko 1999b). Thus, it is difficult to assess which of these modern taxa a Paleogene fossil would be better classified in. Brasilennea spp. has other unique features such as its "double lip" (Salvador et al. 2011; Salvador & Simone 2013) that further confound classification, and these unique fossils could even belong to an extinct urocoptoid branch of their own.

The shell of Caerbannogia gen. nov. has a superficial similarity to that of the fossil species "Brachypodella" britoi, particularly in its more typical urocoptoid cylindrical-turriform shape and the presence of axial ribs (Fig. 4H, I). Nevertheless, "Brachypodella" britoi has a much more acuminated spire than Caerbannogia gen. nov., resulting in a very different overall shell shape. "Brachypodella" britoi was found in the same outcrop as Brasilennea spp. in Itaboraí Basin. Its holotype has been destroyed and the species is known only from other fragmentary specimens, including portions of the early spire whorls and what is tentatively identified as the body whorl and a fragmented aperture (Salvador & Simone 2013) (Fig. 4H, I). Still, it is a markedly different shell shape in contrast to Brasilennea. Originally, Ferreira & Coelho (1971) assigned the fossil species to Brachypodella Beck, 1837 (Urocoptidae) based on superficial similarities to extant species of the genus. Salvador & Simone (2013)

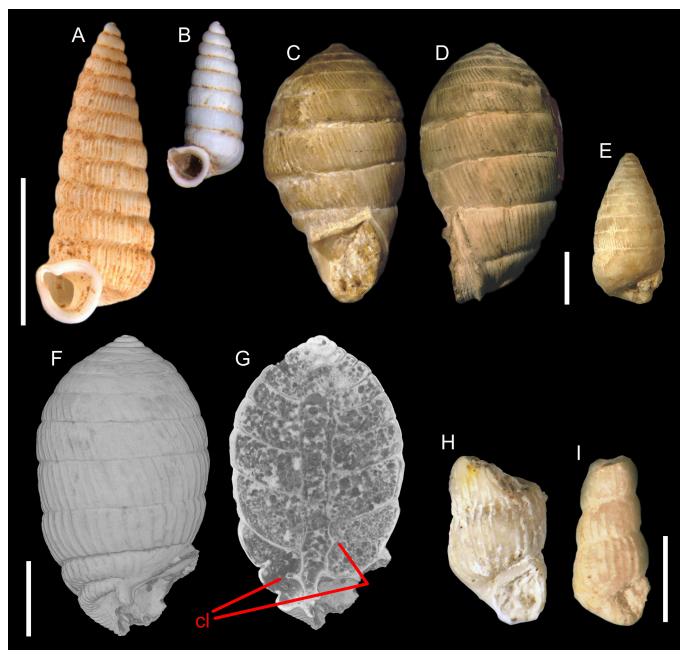


Figure 4. Examples of other Brazilian Urocoptoidea. **A, B,** *Habeas* spp., to scale; scale bar = 5 mm. **A,** *Habeas corpus* Simone, 2013, holotype MZSP 110000 (shell height = 10.3 mm). **B,** *Habeas data* Simone, 2013, holotype MZSP 106810 (shell height = 5.7 mm). Holotype has been fragmented since the original description (cf. Birckolz *et al.*, 2016). **C–E,** *Brasilennea* spp., to scale; scale bar = 5 mm. **C–D,** *Brasilennea arethusae* Maury, 1935, holotype AMNH 24237 (shell height = 23.5 mm). **E,** *Brasilennea guttula* Salvador & Simone, 2012, holotype MCT 6940-I (shell height = 13.5 mm). **F, G,** CT images of specimen MZSP 86322 (shell height = 21 mm) of *Brasilennea arethusae*; scale bar = 5 mm. **F,** 3D reconstruction of the specimen (voxel size = 22 μm). **G,** longitudinal section showing the internal structure of the shell, with an indication of the columellar lamella (cl). **H, I,** fragmentary fossils (type specimens) of "*Brachypodella*" *britoi* Ferreira & Coelho, 1971, to scale; scale bar = 2 mm. **H,** paratype #1 MNRJ 5026-I (shell height = 4 mm). **I,** paratype #2 MNRJ 5026-I (shell height = 4 mm).

argued that the specimens of "Brachypodella" britoi lacked the diagnostic features of that genus (e.g., a keel on the body whorl; Schileyko 1999a) and would likely belong to a new genus. Those authors refrained from describing a new genus due to the poor condition of the fossils and proposed to use the genus name within quotes to indicate its uncertain allocation. A more recent study estimated that the modern genus *Brachypodella* appeared around 20 million years ago (Uit de Weerd *et al.* 2016), significantly younger than the fossils from Itaboraí Basin (*ca.* 53–50 Ma; Woodburne *et al.* 2014). Thus, we agree that "*Brachypodella*" *britoi* represents a distinct genus of Urocoptoidea belonging to either Holospiridae or, more plausibly, Eucalodiidae. Nevertheless, we also refrain from formally describing a new genus at this time.

Caerbannogia calida sp. nov.

Figure 3

ZooBank identifier. urn:lsid:zoobank.org:act:62468153-AF40-45CE-80F3-08BFC89FBD75

Type material. LES 6873 (holotype; M.E. Bichuette leg., 29.ix.2012).

Type locality. Brazil, São Paulo state, Iporanga municipality, Ressurgência das Areias de Água Quente cave; 24°33′45″ S, 048°40′18″ W.

Etymology. From the Latin for "warm", an allusion to the type locality, "Água Quente" ("warm water").

Diagnosis. Same as genus (see above).

Description. Shell. Small, dextral, cylindrical-turriform. Shell multiwhorled, with whorls of similar size to one another. Spire top decollate (Fig. 3E, K); protoconch unknown. Colour seemingly white to pale beige. Spire narrow but appearing somewhat bulging in comparison to the rest of the shell, as the final whorls become narrower towards the aperture. Teleoconch sculptured by prosocline axial ribs bands, which become stronger and more spaced on the lower whorls (Fig. 3A-C). Suture well defined, positioned slightly obliquely to the columellar axis. Whorl profile lightly convex; whorls display a weak shoulder-like angulation on their apical portion, close to the suture (more easily observed in CT images; Fig. 3A-C). Body whorl and half of the preceding whorl are marked by an extreme narrowing of their median portion. Aperture subcircular, prosocline, with its apical portion acuminated (Fig. 3J); aperture relatively large in relation to body whorl. Peristome slightly thickened and reflected. Shell rimate (Fig. 3F, L). Internal structures. Columella (Fig. 3D) hollow, thin and sinuous, with its median portion slightly raised; columellar lamella absent. The narrowing of the body whorl and half of the preceding whorl produces, on the interior surface of the shell, a pronounced spiral lamella-like structure (Fig. 3D). Measurements. Holotype: 8 whorls; shell height = 7.86 mm: shell width = 1.89 mm.

Distribution. Known only from the type locality.

Remarks. The location where the holotype was found (and its presumed habitat) is close to the cave entrance in a riverbank sediment, in silt and rocky substrate. This context suggests the possibility of post-mortem transportation; however, given the shell's small size and fragility, significant post-mortem transportation is unlikely. Thus, there is currently no definitive evidence to ascertain whether this species is troglobitic or troglophilic (cf. criteria of Trajano & Carvalho 2017). Nevertheless, considering that it represents the sole known member of its family in Brazil and that it was never found on surface environments in the best-sampled state in the country (Salvador 2019; Machado et al. 2023), we can exclude accidental occurrence and hypothesise that the species is likely at least troglophilic.

Discussion

Cave environments in Brazil have been singled out as a promising source for the discovery of new species of gastropods (Salvador 2019; Machado *et al.* 2023; Salvador *et al.* 2024). The presently studied snail is an example of that and also an extremely interesting case from both biodiversity and biogeographic perspectives.

While the finding of representatives of Urocoptoidea in Brazil, so far removed from the core distribution of the group, has been surprising (Simone 2022; Machado et al. 2023), the newly discovered Caerbannogia calida gen. et sp. nov. and the Paleogene fossils of Itaboraí (Salvador & Simone 2023; Salvador et al. 2018) paint a more solid (if still confusing) picture of the presence of this superfamily in Brazil. To summarize the taxonomic discussion presented above, we have: (1) Caerbannogia gen. nov. classified in the Eucalodiidae, thus representing the first record of the family in Brazil; (2) Habeas is likely a member of Eucalodiidae as well (although it could also belong to Holospiridae); (3) "Brachypodella" britoi also likely belongs to Eucalodiidae; (4) Brasilennea could be either a Cerionidae or Holospiridae, or even belong to a lineage of its own.

This scenario represents a tentative classification based on the currently available evidence. If the presence of urocoptoid families is further confirmed in Brazil (e.g., by molecular evidence), it would be interesting to explore what this could mean for the clade's biogeography and history on the continent, as well as the role, if any, of subterranean environments in that history. For instance, it would be good to investigate whether the Brazilian urocoptoids represent a single "foray" into South America (as in the clausiliid subfamily Peruiniinae; Uit de Weerd & Gittenberger 2013) or if they are the result of multiple independent colonisations

events, or even if they are relicts of a once more widespread clade, as observed in other gastropod (e.g., Tomichiidae: Salvador et al. 2022a; Salvador & Bichuette 2024) and subterranean arthropod taxa (e.g., isopods and opilionids: Pérez-González et al. 2017; López-Orozco et al. 2024). In any event, this study is a timely reminder that PETAR and its numerous caves are home to several endemic species across multiple taxa, many still unknown, which face different degrees of threats (Birckolz et al. 2016; Simone 2016; Trajano et al. 2016). The type-locality of Caerbannogia calida gen. et sp. nov., Ressurgência das Areias de Água Quente cave, is located outside PETAR with easy access (Fig. 2). Thus, the main threat to the cave is visitation without proper management and control, as well as the deforestation of surrounding areas (Trajano 2000; Bichuette & Trajano 2003) (Fig. 2).

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REFERENCES

- BICHUETTE ME, TRAJANO E. 2003. A population study of epigean and subterranean *Potamolithus* snails from southeast Brazil (Mollusca: Gastropoda: Hydrobiidae). *Hydrobiologia* **505**: 107–117. doi: 10.1023/b:hydr.0000007299.26220.b8
- BICHUETTE ME, TRAJANO E. 2018. Diversity of *Potamolithus* (Littorinimorpha, Truncatelloidea) in a high-diversity spot for troglobites in southeastern Brazil: role of habitat fragmentation in the origin of subterranean fauna, and conservation status. *Subterranean Biology* **25**: 61–88. doi: 10.3897/subtbiol.25.23778
- BIRCKOLZ CJ, SALVADOR RB, CAVALLARI DC, SIMONE LRL. 2016. Illustrated checklist of newly described (2006–2016) land and freshwater Gastropoda from Brazil. *Archiv* für *Molluskenkunde* **145**: 133–150. doi: 10.1127/arch.moll/145/133-150
- FERREIRA CS, COELHO ACS. 1971. Novos gastrópodes pulmo-

- nados da Bacia calcária de São José de Itaboraí, RJ, Brasil. Geocronologia. *Anais da Academia Brasileira de Ciências* **43** (suppl.): 463–472.
- LÓPEZ-OROZCO CM, CAMPOS-FILHO IS, CORDEIRO LM, GALLÃO JE, CARPIO-DÍAZ YM, BORJA-ARRIETA R, BI-CHUETTE ME. 2024. First amphibious Crinocheta (Isopoda, Oniscidea) from the Neotropics with a troglobitic status: a relictual distribution. *ZooKeys* 1192: 9–27. doi: 10.3897/zookeys.1192.114230
- MACHADO FM, MIRANDA MS, SALVADOR RB, PIMENTA AD, CÔRTES MO, GOMES JAJ, MIYAHIRA IC, AGUDO-PADRÓN I, OLIVEIRA CDC, CAETANO CHS, COELHO PRS, D'ÁVILA S, ARRUDA EP, ALMEIDA SM, GOMES SR, ALVIM J, FILHO HG, FERREIRA-JÚNIOR AL, MARQUES RC, MARTINS I, SOUZA LS, ARRUDA JO, CAVALLARI DC, SANTOS SB, PEDRO NC, SALLES ACA, DORNELLAS APS, LIMA TC, AMARAL VS, SILVA FS, PASSOS FD, THIENGO SS, LEITE TS, SIMONE LRL. 2023. How many species of Mollusca are there in Brazil? A collective taxonomic effort to reveal this still unknown diversity. *Zoologia* 40: e23026. doi: 10.1590/s1984-4689.v40.e23026
- MAURY CJ. 1935. New genera and new species of fossil terrestrial Mollusca from Brazil. *American Museum Novitates* **764**: 1–15. http://hdl.handle.net/2246/4568
- NIMER E. 1989. Climatologia do Brasil. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, 427 pp.
- PÉREZ-GONZÁLEZ A, CECCARELLI FS, MONTE BGO, PROUD DN, DASILVA MB, BICHUETTE ME. 2017. Light from dark: A relictual troglobite reveals a broader ancestral distribution for kimulid harvestmen (Opiliones: Laniatores: Kimulidae) in South America. *PLOS ONE* **12**: e0187919. doi: 10.1371/journal.pone.0187919
- SALVADOR RB. 2019. Land snail diversity in Brazil. *Strombus* **25**: 10–20.
- SALVADOR RB, BICHUETTE ME. 2024. *Idiopyrgus* Pilsbry, 1911 (Gastropoda, Tomichiidae): a relict genus radiating into subterranean environments. *Zoosystematics and Evolution* **100**: 1543–1556. doi: 10.3897/zse.100.136428
- SALVADOR RB, SIMONE LRL. 2013. Taxonomic revision of the fossil pulmonate mollusks of Itaboraí Basin (Paleocene), Brazil. *Papéis Avulsos de Zoologia* **53**: 4–56. doi: 10.1590/s0031-10492013000200001
- SALVADOR RB, CABRERA F, MARTÍNEZ S, MIQUEL SE, SIMONE LRL, CUNHA CM. 2018. Annotated catalogue of the fossil Hygrophila and Eupulmonata (Mollusca: Gastropoda) from South America (Cretaceous Neogene). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 289: 249–280. doi: 10.1127/njgpa/2018/0760
- SALVADOR RB, MIRANDA MS, SILVA FS, OLIVEIRA CDC, ARRUDA JO, CAVALLARI DC, GOMES SR, LA PASTA A, PENA MS, OVANDO XMC, ROSA RM, SALLES ACA, SANTOS SB, SIMONE LRL, MACHADO FM. 2024. Checklist of the terrestrial gastropods of Brazil. *Journal of Conchology* **45**: 141–185. doi: 10.61733/jconch/4516
- SALVADOR RB, ROWSON B, SIMONE LRL. 2011. Rewriting the

- fossil history of Cerionidae (Gastropoda, Pulmonata): new family assignment of the Brazilian Paleocene genus *Brasilennea* Maury, 1935. *Journal of Molluscan Studies* 77: 445–447. doi: 10.1093/mollus/eyr021
- SALVADOR RB, SILVA FS, BICHUETTE ME. 2022a. Phylogenetic position of the relict South American genus *Idiopyrgus* Pilsbry, 1911 (Gastropoda, Truncatelloidea), with the description of two new cave species. *Zoosystematics and Evolution* **98**: 365–375. doi: 10.3897/zse.98.90797
- SALVADOR RB, SILVA FS, CAVALLARI DC, CUNHA CM, BI-CHUETTE ME. 2022b. Cave-dwelling gastropods (Mollusca: Gastropoda) of Brazil: state of the art and conservation. *Zoologia* **39**: e21033. doi: 10.1590/s1984-4689.v39.e21033
- Schileyko AA. 1999a. Treatise on Recent terrestrial pulmonate molluscs. Part 3. *Ruthenica* Supplement 2: 263–436.
- Schileyko AA. 1999b. Treatise on Recent terrestrial pulmonate molluscs. Part 4. *Ruthenica* Supplement 2: 437–564.
- SIMONE LRL. 2013. *Habeas*, a new genus of Diplommatinidae from central Bahia, Brazil (Caenogastropoda), with description of three new species. *Journal of Conchology* **41**: 519–525.
- SIMONE LRL. 2016. A new species of the genus *Gonyostomus* from Brazil. *Spixiana* **39**: 11–13.
- SIMONE LRL. 2022. Review of the genus *Habeas* from Brazil, with description of four new species and in which anatomical features revealed that they belong to Urocoptidae (Eupulmonata, Stylommatophora). *Malacologia* **64**: 269–286. doi: 10.4002/040.064.0209
- SIMONE LRL, MORACCHIOLI N. 1994. Hydrobiidae (Gastropoda: Hydrobioidea) from the Ribeira Valley, S.E. Brazil, with descriptions of two new cavernicolous species. *Journal of Molluscan Studies* **60**: 445–459. doi: 10.1093/mollus/60.4.445
- THOMPSON FG. 2012. The land snail genus *Epirobia* and allied genera in México and Central America, with the description of a new family, the Epirobiidae (Gastropoda, Pulmonata, Urocoptoidea). Bulletin of the Florida Museum Of Natural History 51: 167–215. doi: 10.58782/flmnh.yqei8069
- Trajano E. 2000. Cave faunas in the Atlantic tropical rain forest: composition, ecology, and conservation. *Biotropica* **32**: 882–893. doi: 10.1111/j.1744-7429.2000.tb00626.x
- Trajano E, Bichuette ME. 2010. Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa. *Subterranean Biology* 7: 1–16.
- Trajano E, Carvalho MR. 2017. Towards a biologically meaningful classification of subterranean organisms: a critical

- analysis of the Schiner-Racovitza system from a historical perspective, difficulties of its application and implications for conservation. *Subterranean Biology* **22**: 1–26. doi: 10.3897/subtbiol.22.9759
- Trajano E, Gallão JE, Bichuette ME. 2016. Spots of high diversity of troglobites in Brazil: the challenge of measuring subterranean diversity. *Biodiversity and Conservation* **25**: 1805–1828. doi: 10.1007/s10531-016-1151-5
- UIT DE WEERD D. 2008. Delimitation and phylogenetics of the diverse land-snail family Urocoptidae (Gastropoda: Pulmonata) based on 28S rRNA sequence data: a reunion with *Cerion. Journal of Molluscan Studies* **74**: 317–329. doi: 10.1093/mollus/eyn023
- UIT DE WEERD DR, GITTENBERGER E. 2013. Phylogeny of the land snail family Clausiliidae (Gastropoda: Pulmonata). Molecular Phylogenetics and Evolution 67: 201–216. doi: 10.1016/j.ympev.2013.01.011 Uit de Weerd D, Robinson DG, Rosenberg G. 2016. Evolutionary and biogeographical history of the land snail family Urocoptidae (Gastropoda: Pulmonata) across the Caribbean region. *Journal of Biogeography* 43: 763–777. doi: 10.1111/jbi.12692
- WOODBURNE MO, GOIN FJ, RAIGEMBORN MS, HEIZLER M, GELFO JN, OLIVEIRA EV. 2014. Revised timing of the South American early Paleogene land mammal ages. *Journal of South American Earth Sciences* **54**: 109–119. doi: 10.1016/j. jsames.2014.05.003
- ZILCH A. 1960. Gastropoda von Wilhelm Wenz. Teil 2. Euthyneura. In: Schindewolf OH (Ed.) *Handbuch der Paläozoologie*. Gebrüder Borntraeger, Berlin, 401–835.

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SUPPLEMENTARY MATERIAL

Supplementary File 1. Additional CT scan images of *Caerbannogia calida* gen et. sp. nov. (holotype LES 6873) and *Brasilennea arethusae* Maury, 1935 (specimens MZSP 86322 and 86324A). Available at https://doi.org/10.61733/jconch/4549s