

Article

Hidden in the Shadows: *Grunagryllus*, a New Genus of Paragryllina (Orthoptera: Phalangopsidae) Reveals the First Occurrence of the Subtribe in the Brazilian Semiarid [†]

Pedro H. Mendes-Carvalho *  and Rodrigo L. Ferreira 

Centro de Estudos em Biologia Subterrânea, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras CEP 37200-900, Minas Gerais, Brazil; drops@ufla.br

* Correspondence: carvalhopedrohm@gmail.com

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Abstract

Paragryllina currently comprises more than 30 species of predominantly dendrophilous crickets, all previously recorded exclusively from tropical rainforests environments. Over the past three decades, the taxonomy of this subtribe has undergone successive reevaluations, highlighting the need for additional taxonomic studies to improve the understanding of its diversity and distribution patterns. Herein, we describe a new genus and two new species of Paragryllina collected at cave entrances in the Brazilian states of Bahia and Minas Gerais: *Grunagryllus aquaeclarae* gen. et sp. nov. and *G. sanctijosephi* gen. et sp. nov. *Grunagryllus aquaeclarae* gen. et sp. nov. constitutes the first record of the subtribe from the Caatinga, a semi-arid biome endemic to Brazil, considerably expanding the known ecological and biogeographic range of Paragryllina. Both species were recorded in environments currently subjected to multiple anthropogenic threats, particularly mining activities and deforestation. The discovery and description of these taxa contribute substantially to the knowledge of Brazilian Orthoptera diversity and reinforce the importance of subterranean and ecotonal habitats as refuges of poorly known biodiversity.

Keywords: cricket; phallic complex; taxonomy; new species; cave; Caatinga

1. Introduction

Paragryllina Desutter-Grandcolas, 1987 [1], as well as the majority of the other suprageneric groups within Phalangopsidae, has undergone multiple reclassifications, being elevated or reduced to different taxonomic groups several times over the past 35 years (see [2]). This instability reflects our still limited understanding of the phylogenetic relationships among phalangopsid crickets [3,4].

The subtribe (sensu Gorochoy, 2014 [5]) currently comprises 34 species distributed across nine genera [6]: *Aclogryllus* Gorochoy, 2009 [7] (3 spp.), *Alfarogryllus* Cadena-Castañeda, 2021 [2] (1 sp.), *Benoistella* Uvarov, 1939 [8] (2 spp.), *Bolivacla* Gorochoy, 2014 [5] (1 sp.), *Dambachia* Nischk & Otte, 2000 [9] (1 sp.), *Izerskya* Gorochoy, 2019 [10] (1 sp.), *Paragryllus* Guérin-Ménéville, 1844 [11] (14 spp.), *Rumea* Desutter-Grandcolas, 1988 [12] (8 spp.), and *Silvastella* Desutter-Grandcolas, 1992 [13] (3 spp.). These genera are further organized into three suprageneric groups, Benoistellae Desutter-Grandcolas, 1987, Paragryllae Desutter-Grandcolas, 1987, and Rumeae Desutter-Grandcolas, 1988, recently revalidated by Cadena-Castañeda et al. [2].



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Paragryllina are characterized by short palps; forewings bearing a mirror and harp typically crossed by numerous transverse veins; hindwings always present, apically truncated, and longer than the forewings; hind tibiae with at most three pairs of subapical spurs, distally concentrated on both margins; and an ovipositor broadened toward an acute apex, with the dorsal valves partially overlapping the ventral ones [2,12]. Additional diagnostic features are associated with the phallic complex, particularly the shape and length of the pseudepiphallic and endophallic sclerites, and especially the pseudepiphallic parameres, which are among the most taxonomically informative structures and exhibit remarkable morphological diversity, ranging from short to elongated, straight to curved, tubular, or apically branched [2,12]. Benoistellae, Paragryllae, and Rumeae, in turn, are distinguished by the position of the median ocellus, the relative width of the head and fastigium, the venation of the female forewings, the number of subapical spurs on the posterodorsal (inner) margin of the hind tibia, the number of rows of spines on the hind basitarsus, and the degree of development of the pseudepiphallic parameres and ectophallic fold [2,12].

To date, Paragryllina, which are predominantly dendrophilous [14], have been recorded exclusively from tropical rainforests of the Neotropical and Afrotropical regions, as well as the Antilles. Most genera and species, however, occur in the Amazon Rainforest (e.g., [2,7,10,13,15,16]), and only a few species of *Paragryllus* and *Silvastella* are known from the Brazilian Atlantic Forest [17,18]. Furthermore, the three *Paragryllus* species described from the African continent, *P. obscurus* (Scudder, 1869) [19], *P. simplex* Chopard, 1948 [20], and *P. tricaudatus* (Fairmaire, 1858) [21], were likely misassigned to this genus and require re-examination to confirm their taxonomic identity [2]. These African species therefore likely contribute to an artificial expansion of the geographic distribution not only of the genus but also of the subtribe, as Paragryllina is probably restricted to the Americas and the Caribbean.

In this study, we describe a new genus and two new species of Paragryllina, representing the first record of the group from the Caatinga, a semi-arid biome endemic to Brazil. We provide morphological comparisons between the examined specimens and previously described taxa, and discuss the occurrence of Paragryllina in poorly sampled environments, as well as the threats to their habitats.

2. Materials and Methods

Study area. Specimens of *Grunagryllus aquaeclarae* gen. et sp. nov. were collected from caves within the Serra do Ramalho karst complex, in southwestern Bahia, Brazil (Figure 1). The Serra do Ramalho karst lies within an ecotonal belt between two major South American biomes, the Caatinga and the Cerrado, resulting in marked environmental heterogeneity [22]. The regional climate corresponds to a tropical savanna regime (Aw, sensu Köppen), characterized by pronounced seasonality in both precipitation and temperature, with annual rainfall typically ranging from approximately 600 to 650 mm concentrated within a relatively brief wet season, generally spanning November to March, followed by an extended dry season lasting up to seven or eight months [23]. Persistently high temperatures, coupled with elevated evapotranspiration rates, promote a chronic water deficit, a defining feature of the semiarid interior of northeastern Brazil [24].

The landscape is characterized by seasonally dry forests and shrublands composed primarily of drought-adapted, deciduous, and xeromorphic species associated with the Caatinga domain [24]. Interspersed within this matrix are patches of Cerrado-like vegetation, characterized by more open formations with a continuous herbaceous layer and scattered woody elements [24]. At finer spatial scales, variation in vegetation is strongly mediated by edaphic heterogeneity, topographic gradients, and the influence of karst features, which modulate soil development, water retention, and microclimatic conditions.

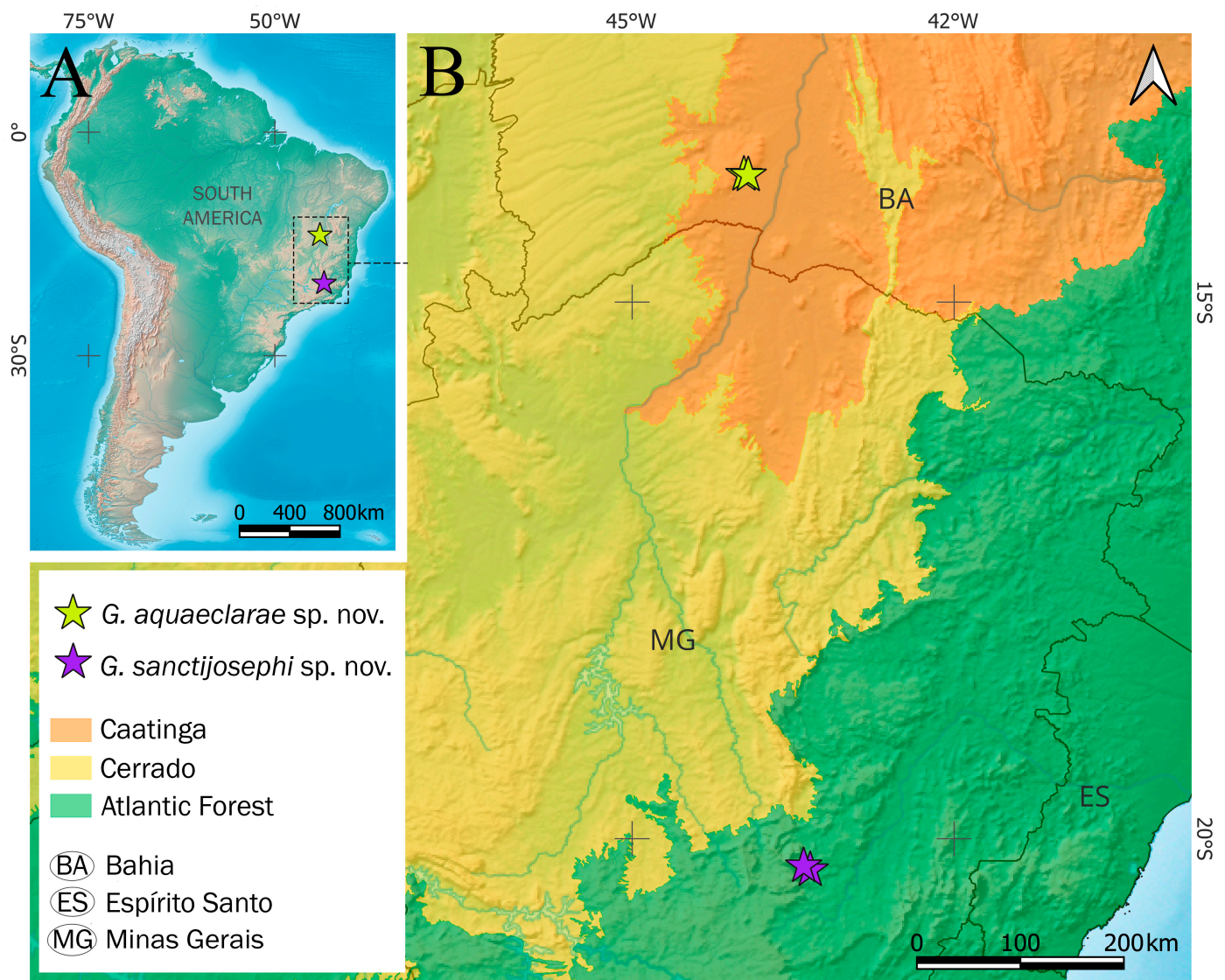


Figure 1. Distribution map of *Grunagryllus* gen. nov. (A) Map of the South American continent, with the known distribution of *Grunagryllus* gen. nov. delimited by a dotted rectangle. (B) Map of the known distribution of *Grunagryllus* gen. nov., with biomes (Caatinga, Cerrado, and Atlantic Forest) distinguished by different colors.

Specimens of *Grunagryllus sanctijosephi* gen. et sp. nov. were collected from caves located in Mariana municipality, Minas Gerais state, southeastern Brazil (Figure 1). Mariana is located in the Quadrilátero Ferrífero (Iron Quadrangle) of southeastern Minas Gerais, a mineral-rich province dominated by Precambrian lithologies linked to the São Francisco Craton, including quartzites, schists, iron formations, and ferruginous crusts [25]. The regional climate corresponds to the humid subtropical type with dry winters (Cwa), characterized by pronounced rainfall seasonality, with wetter summers and drier winters, annual precipitation generally above 1200 mm, and mean temperature ranging from 18 to 22 °C [26]. Vegetation comprises a complex mosaic including Atlantic Forest remnants, seasonal forests, Cerrado formations, and ferruginous rupestrian grasslands, whose distribution is strongly associated with topographic variation and iron-rich substrates [27].

Map production. The new genus and new species distribution map was made using the free open source QGIS software (v. 3.34.10-Prizen).

Collection and depository. Two males and one female of *Grunagryllus aquaeclarae* gen. et sp. nov. were collected through active searching in the caves Lapa dos Peixes I

(13°48′43.66″ S; 43°57′30.26″ W) and Gruna da Água Escura I (13°49′3.70″ S; 43°57′1.30″ W), located in the Serra do Ramalho karst region, southwestern Bahia, northeastern Brazil, during field surveys conducted in 2017 and 2021. A single adult male and one juvenile of *Grunagryllus sanctijosephi* gen. et sp. nov. were collected in the caves GER-0051 ES (20°17′32.6″ S; 43°22′23.6″ W) and CMR-0207 ES (20°15′21.2″ S; 43°24′06.9″ W), respectively, during two field surveys carried out by the environmental consulting company BioEspeleo in the municipality of Mariana, Minas Gerais, southeastern Brazil. All specimens were preserved in 70% ethanol and deposited in the Collection of Subterranean Invertebrates of Lavras (Coleção de Invertebrados Subterrâneos de Lavras—ISLA), housed at the Center of Studies in Subterranean Biology (Centro de Estudos em Biologia Subterrânea—CEBS).

Morphological analysis. Photographs and morphometric data of the holotypes and paratypes were obtained using an Axiocam 506 color camera (Zeiss, Oberkochen, Germany) coupled to an Axio Zoom V16 stereomicroscope (Zeiss). Measurements were taken using the ZEN 2 Blue Edition (Zeiss) software. Male and female specimens were dissected, and their phallic complexes and copulatory papilla were cleared in an enzymatic solution following Álvarez-Padilla and Hormiga [28] for 24 h prior to imaging using the same equipment. Morphological descriptions were prepared based on observations under a Stemi 2000 stereomicroscope (Zeiss). Terminology for the phallic complex follows Desutter [1], Desutter-Grandcolas [29], and Cadena-Castañeda et al. [2]. Comparisons with other Paragryllina were based on the information available in the literature. In addition, the right forewing of the male paratype of *G. aquaeclarae* gen. et sp. nov. and of the holotype of *G. sanctijosephi* gen. et sp. nov. were detached and mounted on microscope slides for counting the teeth of the stridulatory file under an Axio Lab.A1 microscope (Zeiss), using a mechanical hand tally counter.

Abbreviations. Pseudepiphallos: *med.l*, pseudepiphallic median lophi; *ps.p*, pseudepiphallic paramere; *r.*, rami. Ectophallic invagination: *ect.f*, ectophallic fold; *ect.ap*, ectophallic apodeme. Endophallus: *end.s*, endophallic sclerite. Hind tibia: *ia*, inner apical spur; *is*, inner subapical spur; *oa*, outer apical spur; *os*, outer subapical spur.

3. Results

Taxonomy

Order Orthoptera Olivier, 1789

Suborder Ensifera Chopard, 1921

Superfamily Grylloidea Laicharting, 1781

Family Phalangopsidae Blanchard, 1845

Subfamily Paragryllinae Desutter-Grandcolas, 1987

Tribe Paragryllini Desutter-Grandcolas, 1987

Subtribe Paragryllina Desutter-Grandcolas, 1987

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Type species. *Grunagryllus aquaeclarae* sp. nov.

Diagnosis. Combination of the following characteristics: head longer than wide; vertex with a pair of dark brown stripes extending from the occiput toward the fastigium and diverging at both ends; mirror of the right forewing crossed by two transverse veins; foretibia bearing tympana on both faces; hind tibia with three inner subapical spurs; hind basitarsus with two rows of spines; supra-anal plate with a tripartite modification in the shape of an inverted lowercase omega (ω); phallic complex laterally symmetrical; pseudepiphallic parameres dorsally curved, with the apex dorsoventrally bifurcated, the inner surface concave, and the dorsal projection more developed than the ventral; ectophallic fold and endophallic sclerites weakly developed.

Comparative diagnosis. *Grunagryllus* gen. nov. can be distinguished from all other genera of Paragryllina by the unique combination of characters presented above. It differs from *Benoistella*, *Izerskya*, *Silvastella*, and *Rumea* in having three inner subapical spurs on the hind tibia (Figures 4G–I and 9G–I). It further differs from all other Paragryllina, except *Rumea*, in possessing two rows of spines on the hind basitarsus (Figures 4L and 9L).

Adult males of *Grunagryllus* gen. nov. differ from *Aclogryllus*, *Alfarogryllus*, *Bolivacla*, *Dambachia*, *Paragryllus*, and *Rumea* by having forewings that do not extend beyond the abdomen and a mirror crossed by two transverse veins (Figures 2B, 3A and 8B). Additionally, it differs from *Paragryllus* in lacking a swollen dorsal inner apical spur on the hind tibia (Figures 4J,K and 9J,K), and from *Dambachia* in lacking a modified distal subapical spur on the hind tibia (Figures 4G–K and 9G–K).

The supra-anal plate of *Grunagryllus* gen. nov. is modified, as in *Paragryllus* and *Benoistella lyra* Gorochov, 2009, but differs from both in being tripartite rather than bipartite (Figures 2H,I and 8E).

Regarding the phallic complex, *Grunagryllus* gen. nov. differs from *Dambachia* in having a laterally symmetrical phallic complex (Figures 5 and 10). The pseudepiphallic parameres differ from those of all other Paragryllina in overall shape: they are considerably shorter than in *Aclogryllus* and *Rumea*, dorsally curved, differing from *Benoistella* and *Izerskya*, and do not cross distally, differing from *Paragryllus*. Additionally, the median lophi lack ventral or lateral projections, further distinguishing the new genus from *Alfarogryllus* and *Paragryllus*, respectively. Finally, the ectophallic fold and endophallic sclerites are considerably less developed than in *Aclogryllus* and *Bolivacla*.

Etymology. The generic name *Grunagryllus* is derived from *gruna*, a traditional local term used to refer to caves in the Serra do Ramalho region, southwestern Bahia, where the type species was collected, combined with *gryllus* (Latin for “cricket”), an element commonly associated with cricket taxa, particularly genera assigned to the subtribe Paragryllina. The name thus alludes both to the subterranean habitat in which the type species was collected and to its taxonomic affinities. The gender of the genus is masculine.

Description. Body coloration ranging from beige to light brown, with dark brow or grey spots and stripes; body size varying from approximately 16 to 21 mm (Table 1).

Table 1. Morphological measurements (mm) of adult males and female (type series) of *Grunagryllus aquaeclarae* gen. et sp. nov. (ISLA50485, ISLA50489, ISLA155510) and *G. sanctijosephi* gen. et sp. nov. (ISLA155526).

	ISLA50485 (♂)	ISLA50489 (♂)	ISLA155510 (♀)	ISLA155526 (♂)
Body length	20.59	17.91	18.15	16.88
Compound eye length	1.56	1.57	1.55	1.53
Compound eye width	0.93	0.92	0.92	0.85
Intraocular distance	1.30	1.34	1.40	1.29
Apical maxillary palpomere length	1.48	1.38	1.35	1.36
Head length	1.82	2.07	1.79	1.94
Head width	3.19	3.16	3.36	3.18
Pronotum length	2.61	2.64	2.59	2.64
Pronotum width	3.85	3.80	4.26	3.96
Right forewing length	8.81	9.16	9.63	10.36
Right forewing width	4.38	4.79	3.66	4.76
Stridulatory teeth	-	179	-	208
Left foreleg length	14.86	14.74	15.40	13.83
Left middle leg length	15.15	14.82	14.25	14.28
Left hind femur length	12.02	12.60	12.55	11.02

Table 1. Cont.

	ISLA50485 (♂)	ISLA50489 (♂)	ISLA155510 (♀)	ISLA155526 (♂)
Left hind femur width	3.16	3.37	3.09	3.03
Left hind tibia length	10.50	10.72	10.86	9.27
Left hind basitarsus length	3.46	3.28	3.66	3.33
Ovipositor length	-	-	14.48	-

Head: pubescent; longer than wide in frontal view; compound eyes developed; lateral ocelli closer to each other than to the median ocellus, which is subapical; fastigium bearing long, thick setae and approximately as wide as the antennal scape; maxillary palp short; apical maxillary palpomeres longer than third and fourth palpomeres, broadened at the tip, with the apex rounded.

Thorax: pronotum pubescent, anterior and posterior margins bearing long, thick setae; pronotum anteriorly and posteriorly irregularly dark brown along the anterior and posterior portions, dorsal area separated from the lateral lobes by a sinuous dark brown stripe extending anteroposteriorly; lateral lobes directed anteriorly; metanotum apparently lacking glandular structures; metasternite with posterior margin broadly arched.

Male right forewing: slightly shorter than or as long as the abdomen; darkly colored, with light-colored crossveins; mirror wider than long, crossed by two arched transverse veins; harp with one anteriorly bifurcated crossvein on the left, followed by four or five thick, simple transverse veins decreasing in length from left to right; stridulatory file present, composed of hundreds of closely spaced teeth; apical area present, moderately elongated; lateral field with two thick, parallel, and closely spaced longitudinal veins, and multiple (16–18) dorsoventral crossveins.

Hindwings: translucent; longer than the forewings.

Legs: femora and tibiae with dark brown rings; foretibiae bearing a well-developed oval tympanum on both faces and a pair of ventral apical spurs, the inner longer than the outer; middle tibiae also with two ventral apical spurs; hind tibiae dorsally serrulated on the proximal and median portions, intersubapical spur margins bearing one or no spines; hind tibiae with three inner (is1–is3) and three outer (os1–os3) subapical spurs concentrated on the distal portion of the tibia, inner spurs shorter than the outer; hind tibiae with three outer (oa1–oa3) and three inner (ia1–ia3) apical spurs; dorsal outer apical spur (oa1) shorter than the ventral (oa3), which, in turn, is approximately half the length of the median outer apical spur (oa2); dorsal (ia1) and ventral (ia3) inner apical spurs subequal and approximately half the length of the median inner apical spur (ia2); subapical and apical spurs lacking any modifications; hind basitarsi with two rows of spines, the inner row composed of 3–5 spines and shorter than the outer row, which bears 5–8 spines; hind basitarsi with a pair of ventral apical spurs, the inner longer than the outer; tarsal claws smooth, symmetrical, and more strongly sclerotized at the apex.

Male abdomen: cerci elongated, pubescent, covered with short, elongate and globose setae, the latter concentrated on the proximal portion of the structure; subgenital plate subtriangular, with the distal margin medially emarginate; supra-anal plate trapezoidal, bearing a tripartite modification in the shape of an inverted lowercase omega (ω).

Phallic complex: pseudepiphallic median lophi (med.l) posteriorly rounded, densely covered with long setae, and with a median emargination approximately square or rectangular in shape, with moderately sclerotized margins; med.l lacking lateral projections; pseudepiphallic parameres (ps.p) well developed, with the apex dorsoventrally bifurcated, the inner surface concave, and the dorsal projection more developed than the ventral one, curving posteriorly and inward as a broad hook; ectophallic fold (ect.f) reduced; ectophallic

apodemes (ect.ap) well developed; endophallic sclerite (end.s) shaped like an inverted V, with a pair of less sclerotized apodemes extending outwardly.

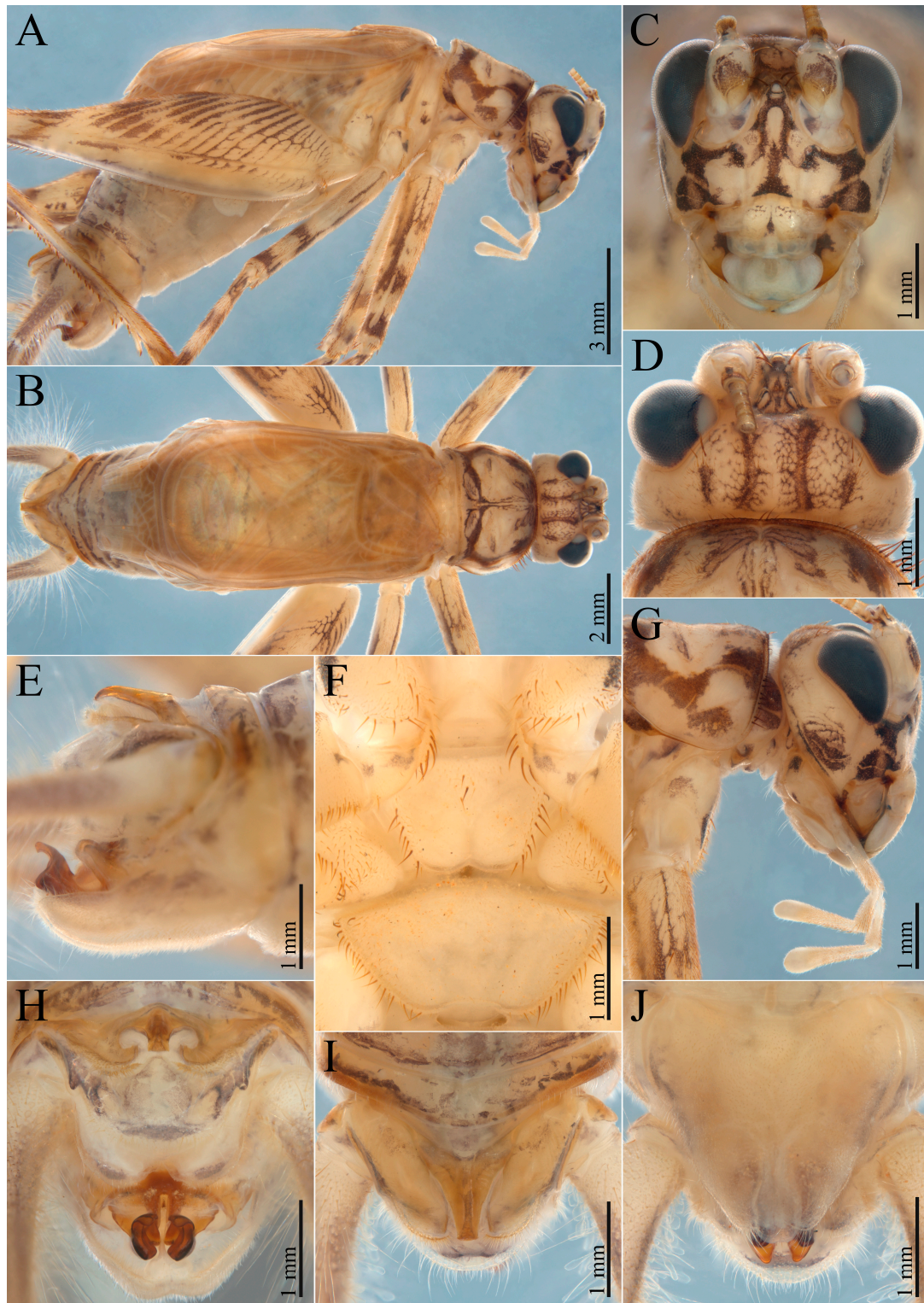


Figure 2. Adult male (ISLA50485, holotype) of *Grunagryllus aquaeclararum* gen. et sp. nov. (A) Body, lateral view; (B) body, dorsal view; (C) head, frontal view; (D) head, dorsal view; (E) abdominal tip, lateral view; (F) meso- and metasternite, ventral view; (G) head and pronotum, lateral view; (H) abdominal tip, axial view; (I) supra-anal plate, dorsal view; (J) subgenital plate, ventral view.

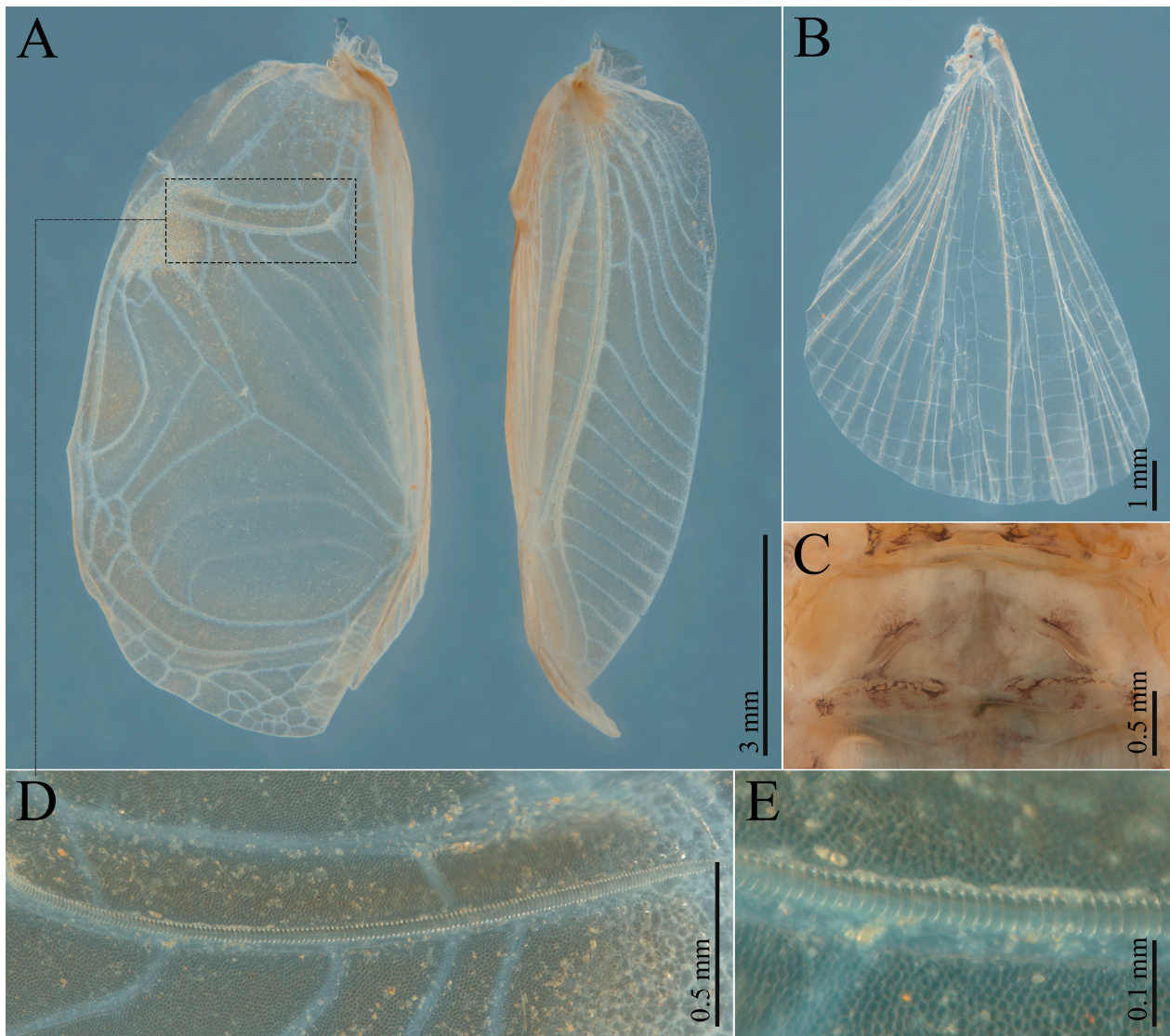


Figure 3. Wings and metanotum of adult male (ISLA50489, paratype) of *Grunagryllus aquaeclarae* gen. et sp. nov. (A) Right forewing, dorsal (left) and lateral (right) views; (B) right hind wing; (C) metanotum, dorsal view; (D) stridulatory file, ventral view; (E) stridulatory file teeth, ventral view.

Female right forewing: also darkly colored, with light-colored anastomotic crossveins; lacking specialized areas, except for the lateral field.

Female abdomen: subgenital plate longer than wide, with a deep distal emargination; supra-anal plate trapezoidal and proximally elevated, bearing what appears to be an underdeveloped version of the modification observed in adult males; ovipositor slightly curved dorsally, longer than the hind femur.

Copulatory papilla: subtriangular, with a strongly sclerotized median dorsal carina; anterior ventral margin slightly arcuate.

***Grunagryllus aquaeclarae* sp. nov. Mendes-Carvalho & Ferreira**

(Table 1; Figures 2–7)

Comparative diagnosis. *Grunagryllus aquaeclarae* gen. et sp. nov. differs from *G. sanctijosephi* gen. et sp. nov. by the absence of a broad dark brown stripe in the transitional area between the vertex and gena, extending from the compound eye toward the occiput (present in the latter species) (Figure 2D,G); less conspicuous dark brown markings on the

frons (Figure 2C); a clypeus bearing a single narrow median dark brown spot rather than multiple irregular dark brown spots (Figure 2C); a more developed tripartite modification of the supra-anal plate, covering nearly its entire surface (covering approximately one third in *G. sanctijosephi* sp. nov.) (Figure 2E,H,I); a narrower apical portion of the pseudepiphallallic parameres (Figure 5D); apical portion of the pseudepiphallallic parameres differently shaped, with the inner concavity bearing a leaf-shaped carina (Figure 5F); and ectophallic apodemes longer and more developed (Figure 5B,C).

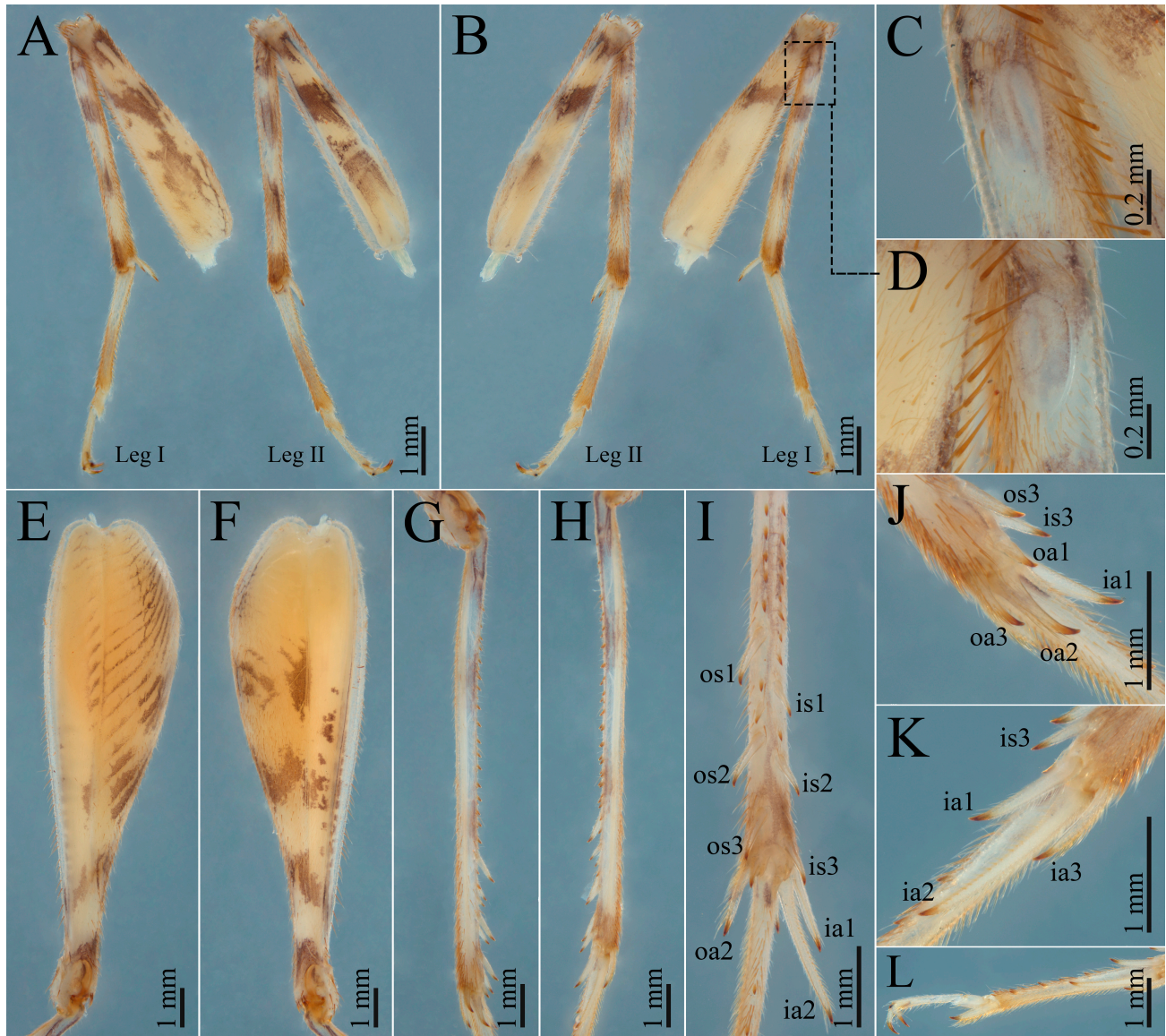


Figure 4. Legs of adult male (ISLA50489, paratype) of *Grunagryllus aquaeclarae* gen. et sp. nov. (A) Left fore and middle legs, posterior view; (B) left fore and middle legs, anterior view; (C) tympanum on the foretibia, posterior (outer) view; (D) tympanum on the foretibia, anterior (inner) view; (E) left hind femur, anterior (outer) view; (F) left hind femur, posterior (inner) view; (G) left hind tibia, anterior (outer) view; (H) left hind tibia, posterior (inner) view; (I) left hind tibia, dorsal view; (J) left hind tibia, anterior (outer) apical spurs; (K) left hind tibia, posterior (inner) apical spurs; (L) left hind tarsus. Abbreviations: ia, inner apical spur; is, inner subapical spur; oa, outer apical spur; os, outer subapical spur.

Etymology. The specific epithet *aquaeclarae* derives from the Latin *aquae* (“of water”) and *clarae* (“clear, bright”), meaning “of clear waters.” The name refers to the caves of the

Água Clara Cave System, where the type series was collected. The epithet is to be treated as a noun in apposition.

Material examined. Holotype (ISLA50485), male ♂, Lapa dos Peixes I cave (13°48'43.66" S; 43°57'30.26" W), São Felix do Coribe, Bahia, Brazil, R.F.V. Cerqueira leg., 14 October 2017; condition: antennae and cerci broken, phallic complex dissected and stored alongside the specimen. Paratype (ISLA50489), male ♂, same data as the holotype; condition: fore and hind wings, fore, middle and hind left legs, fore right leg, and left cercus detached, phallic complex dissected, all structures stored alongside the specimen. Paratype (ISLA155510), female ♀, Grana da Água Escura I cave (13°49'3.70" S; 43°57'1.30" W), Carinhanha, Bahia, Brazil, R.L. Ferreira leg., 17 September 2021; condition: right hind leg missing, cerci and antennae broken, right foreleg detached, copulatory papilla dissected, both stored alongside the specimen.

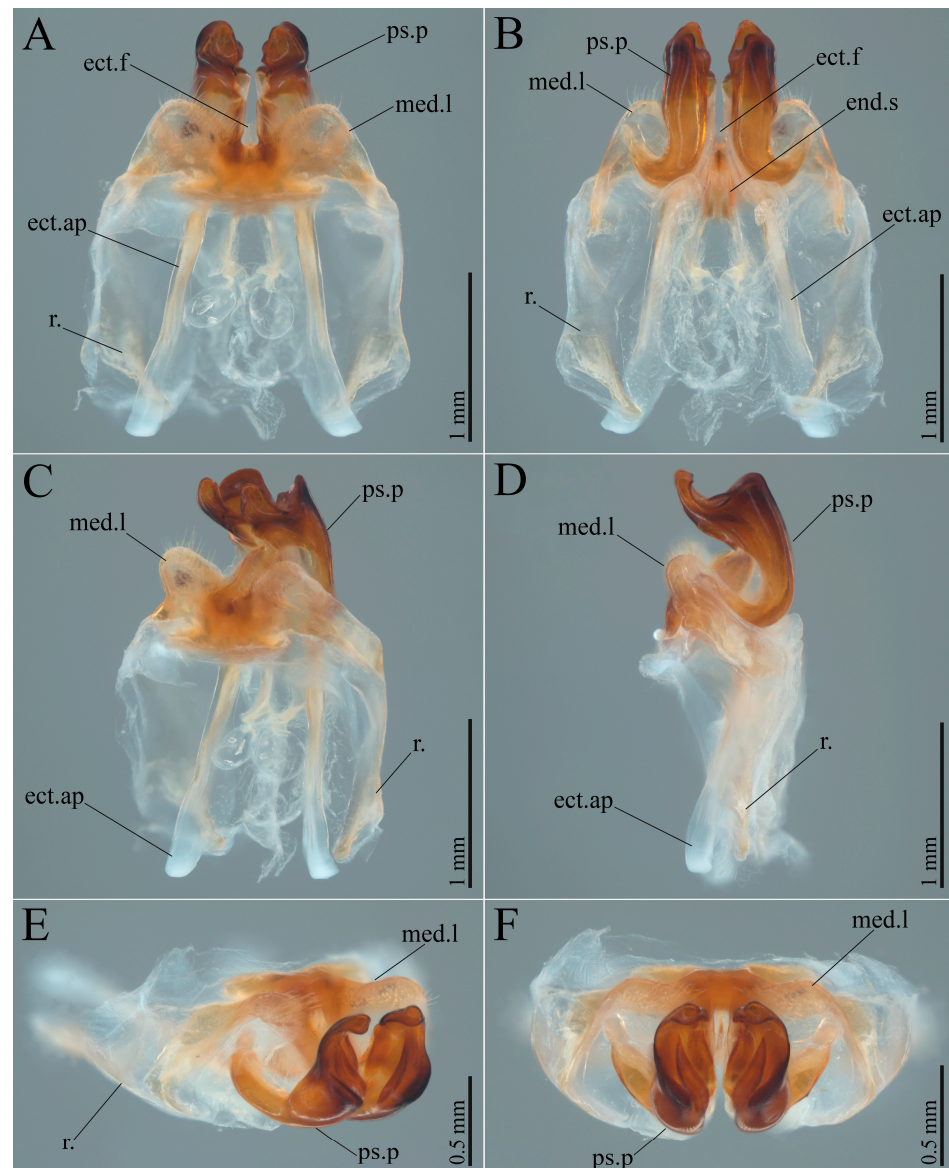


Figure 5. Phallic complex of adult male (ISLA50485, holotype) of *Grunagryllus aquaeclarae* gen. et sp. nov. (A) Dorsal view; (B) ventral view; (C) dorsolateral view; (D) lateral view; (E) lateroaxial view; (F) axial view. Abbreviations: *med.l*, pseudepiphallallic median lophi; *ps.p*, pseudepiphallallic paramere; *r.*, rami; *ect.f*, ectophallic fold; *ect.ap*, ectophallic apodeme; *end.s*, endophallic sclerite.

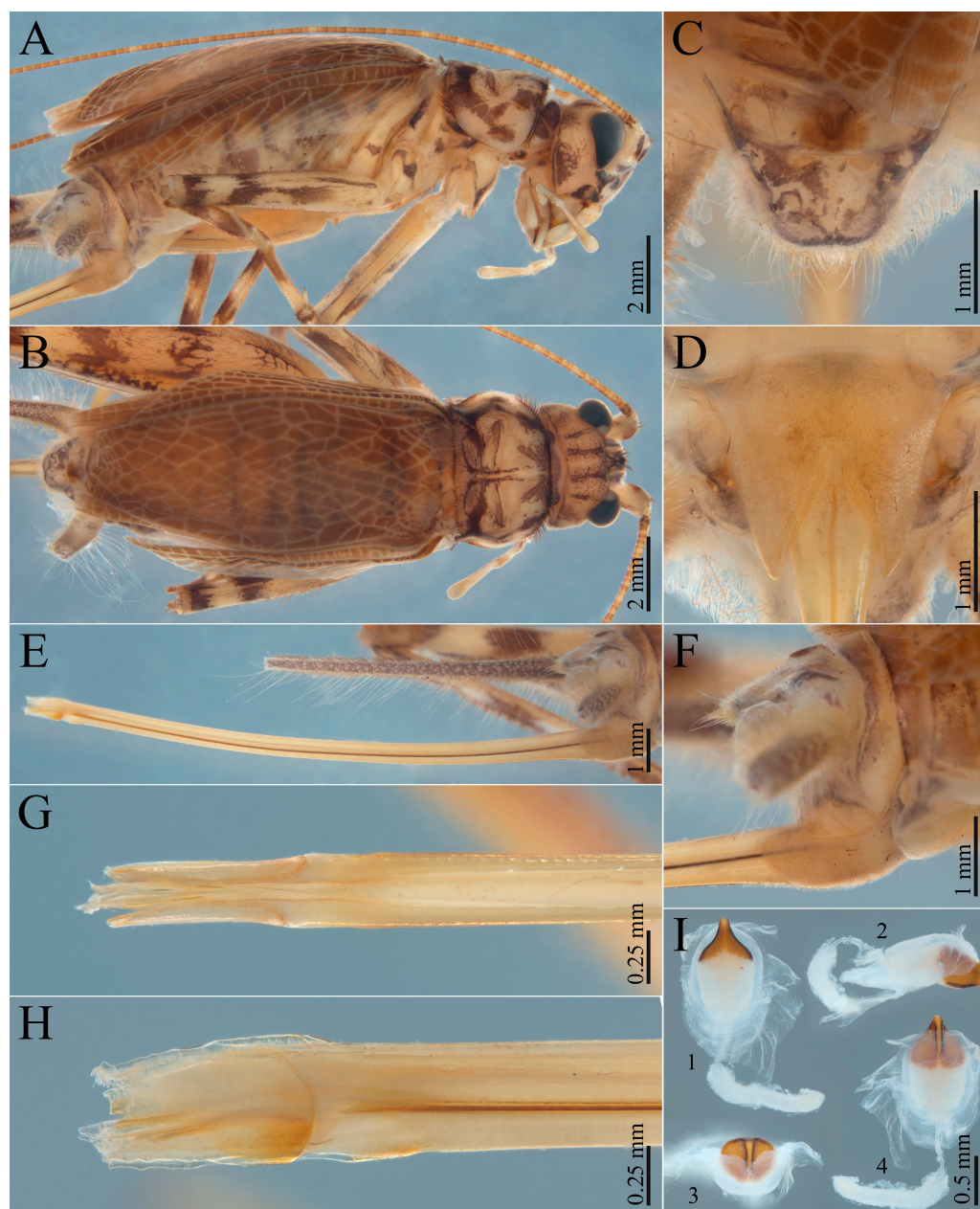


Figure 6. Adult female (ISLA155510, paratype) of *Grunagryllus aquaeclaræ* gen. et sp. nov. (A) Body, lateral view; (B) body, dorsal view; (C) supra-anal plate, dorsal view; (D) subgenital plate, ventral view; (E) ovipositor, lateral view; (F) abdominal tip, lateral view; (G) ovipositor apex, dorsal view; (H) ovipositor apex, lateral view; (I) copulatory papilla, (1) ventral, (2) lateral, (3) axial, and (4) dorsal views.

Description. Body coloration beige, with dark grey spots and stripes.

Head (Figure 2A–D,G): pubescent; longer than wide in frontal view; compound eyes developed; antennal scape with a dark brown spot anteriorly; lateral ocelli closer to each other than to the median ocellus, which is subapical; fastigium bearing long, thick setae and approximately as wide as the antennal scape; vertex with a pair of dark brown stripes extending from the occiput toward the fastigium and diverging at both ends, area between the compound eye and the occiput with a dark brown spot; transitional area between vertex and gena without a broad dark brown stripe extending from the compound eye toward the occiput; gena with a posteromedian dark brown spot; frons with a pair of broad, irregular lateral dark brown stripes extending from the compound eye to the clypeus, a median dark

brown stripe with a central interruption roughly in the shape of an inverted triangle, lateral stripes connected to the median stripe through a pair of small dark brown spots; clypeus with a single median spot; labrum whitish, without a dark brown spot; mandibles with a median dark brow spot, continuous with the color pattern of the frons; maxillary palp short; apical maxillary palpomeres longer than third and fourth palpomeres, broadened at the tip, with the apex rounded.



Figure 7. Habitat and live specimens of *Grunagryllus aquaeclarae* gen. et sp. nov. (A) Cave entrance, Água Clara Cave System, Serra do Ramalho region; (B) adult female of *G. aquaeclarae* gen. et sp. nov.; (C) adult male of *G. aquaeclarae* gen. et sp. nov.

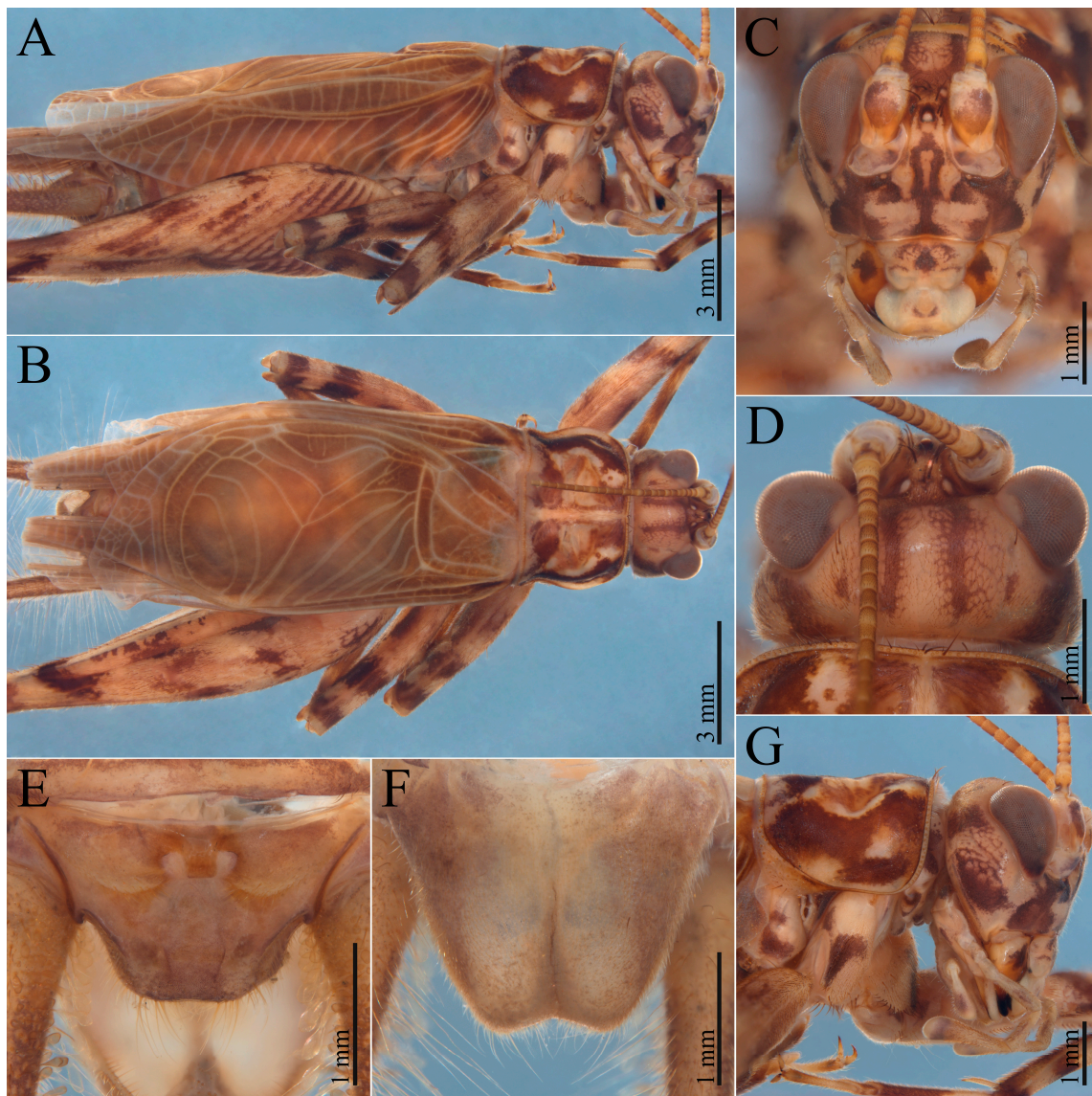


Figure 8. Adult male (ISLA155526, holotype) of *Grunagryllus sanctijosephi* gen. et sp. nov. (A) Body, lateral view; (B) body, dorsal view; (C) head, frontal view; (D) head, dorsal view; (E) supra-anal plate, dorsal view; (F) subgenital plate, ventral view; (G) head and pronotum, lateral view.

Thorax (Figures 2A,B,F,G, and 3C): pronotum pubescent, anterior and posterior margins bearing long, thick setae; pronotum anteriorly and posteriorly irregularly dark brown along the anterior and posterior portions, dorsal area separated from the lateral lobes by a narrow sinuous dark brown stripe extending anteroposteriorly; lateral lobes directed anteriorly; metanotum apparently lacking glandular structures; metasternite with posterior margin broadly arched.

Male right forewing (Figures 2A,B, and 3A,D,E): slightly shorter than or as long as the abdomen; darkly colored, with light-colored crossveins; mirror wider than long, crossed by two arched transverse veins; harp bearing one anteriorly bifurcated crossvein on the left, followed by four (paratype ISLA155510) or five (holotype, ISLA50485) thick, simple transverse veins decreasing in length from left to right; stridulatory file present, composed of 179 closely spaced teeth ($n = 1$); apical area present, moderately elongate; lateral field with two thick, parallel, and closely spaced longitudinal veins, and multiple (16–18) dorsoventral crossveins. **Male left forewing**: similar to the right forewing but mirrored, less sclero-

tized, and with less conspicuous venation; stridulatory file absent. Hindwings (Figure 3B): translucent; longer than the forewings.

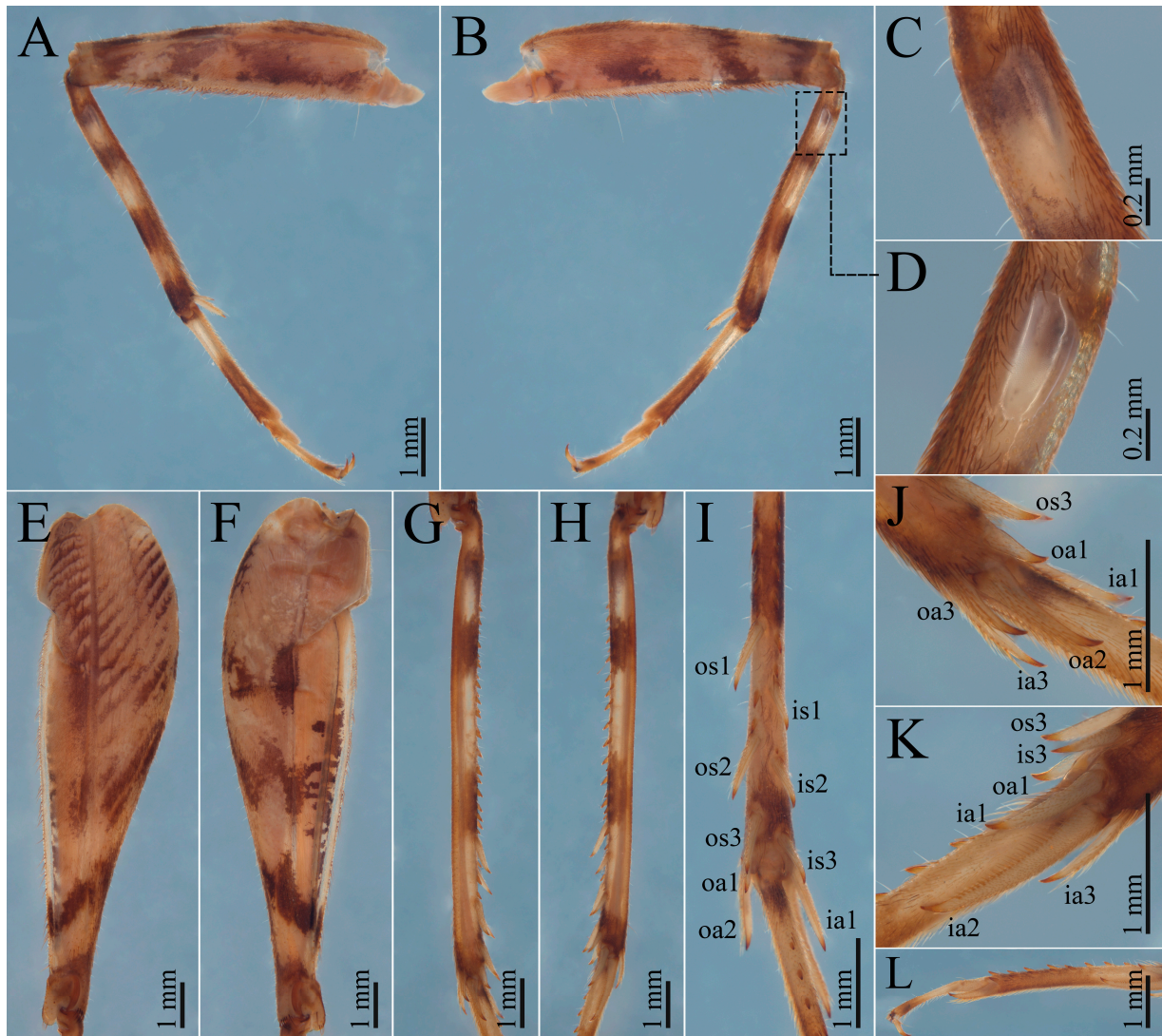


Figure 9. Legs of adult male (ISLA155526, holotype) of *Grunagryllus sanctijosephi* gen. et sp. nov. (A) Left foreleg, posterior view; (B) left foreleg, anterior view; (C) tympanum on the foretibia, posterior (outer) view; (D) tympanum on the foretibia, anterior (inner) view; (E) left hind femur, anterior (outer) view; (F) left hind femur, posterior (inner) view; (G) left hind tibia, anterior (outer) view; (H) left hind tibia, posterior (inner) view; (I) left hind tibia, dorsal view; (J) left hind tibia, anterior (outer) apical spurs; (K) left hind tibia, posterior (inner) apical spurs; (L) left hind tarsus. Abbreviations: *ia*, inner apical spur; *is*, inner subapical spur; *oa*, outer apical spur; *os*, outer subapical spur.

Legs (Figure 4A–L): femora and tibiae with dark brown rings; foretibiae bearing a well-developed oval tympanum on both faces and a pair of ventral apical spurs, the inner longer than the outer; middle tibiae also with two ventral apical spurs; hind tibiae dorsally serrulated on the proximal and median portions, intersubapical spur margins bearing one or no spines; hind tibiae with three inner (*is1*–*is3*) and three outer (*os1*–*os3*) subapical spurs concentrated on the distal portion of the tibia, inner spurs shorter than the outer; hind tibiae with three outer (*oa1*–*oa3*) and three inner (*ia1*–*ia3*) apical spurs; dorsal outer apical spur (*oa1*) shorter than the ventral (*oa3*), which, in turn, is approximately half the length of the median outer apical spur (*oa2*); dorsal (*ia1*) and ventral (*ia3*) inner apical spurs subequal and approximately half the length of the median inner apical spur (*ia2*); subapical and

apical spurs lacking any modifications; hind basitarsi with two rows of spines, the inner row composed of 3–5 spines and shorter than the outer row, which bears 5–8 spines; hind basitarsi with a pair of ventral apical spurs, the inner longer than the outer; tarsal claws smooth, symmetrical, and more strongly sclerotized at the apex.

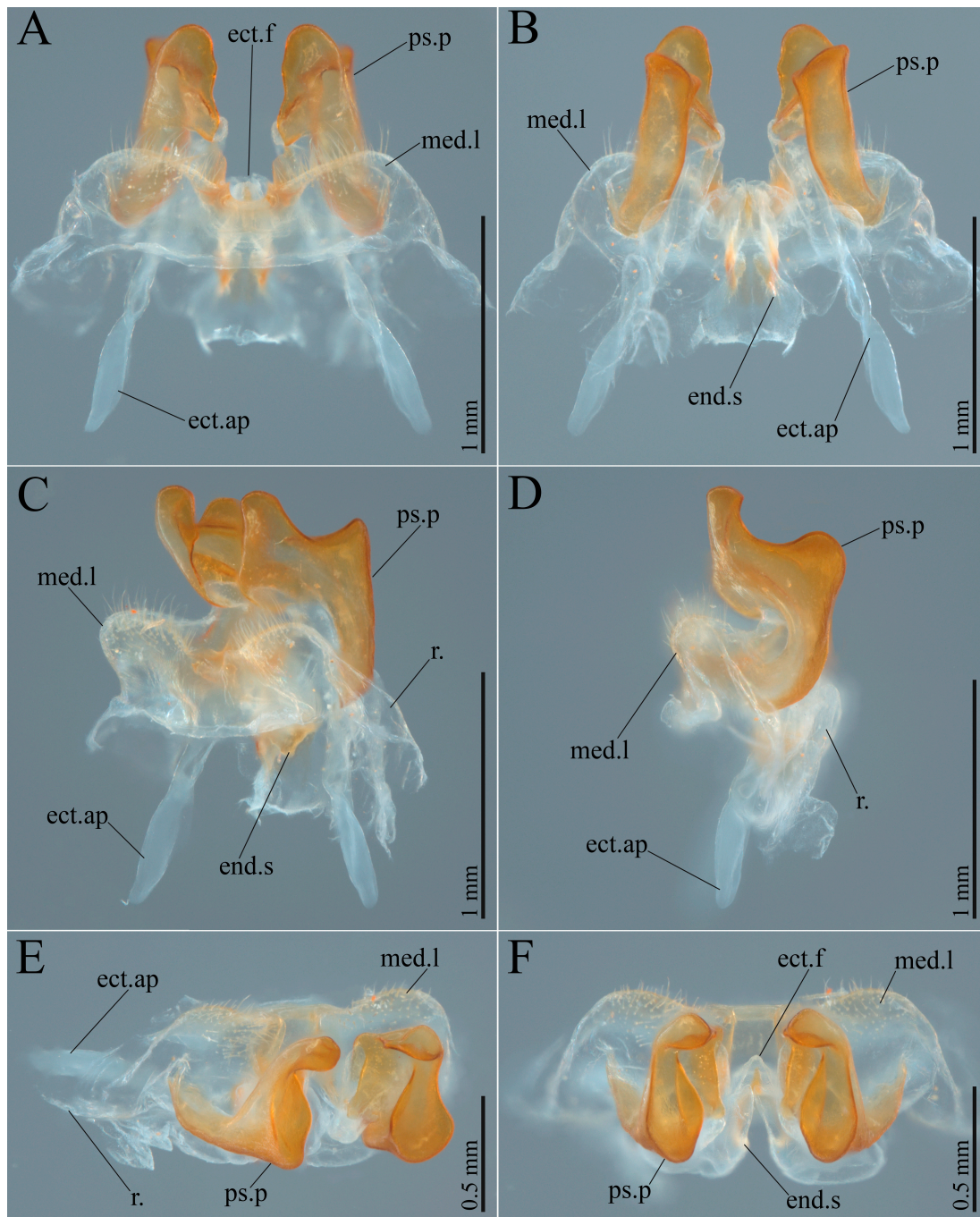


Figure 10. Phallic complex of adult male (ISLA155526, holotype) of *Grunagryllus sanctijosephi* gen. et sp. nov. (A) Dorsal view; (B) ventral view; (C) dorsolateral view; (D) lateral view; (E) lateroaxial view; (F) axial view. Abbreviations: *med.l*, pseudepiphallic median lophi; *ps.p*, pseudepiphallic paramere; *r.*, rami; *ect.f*, ectophallic fold; *ect.ap*, ectophallic apodeme; *end.s*, endophallic sclerite.

Male abdomen (Figure 2A,B,E,H–J): cerci elongated, pubescent, covered with short, elongate and globose setae, the latter concentrated on the proximal portion of the structure; subgenital plate subtriangular, with the distal margin medially emarginate; supra-anal

plate trapezoidal, bearing a tripartite modification in the shape of an inverted lowercase omega (ω) covering almost entirely the dorsal surface of the supra-anal plate.

Phallic complex (Figure 5A–F): pseudepiphallic median lophi (med.l) posteriorly rounded, densely covered with long setae, and with a median emargination approximately rectangular in shape, with moderately sclerotized margins; med.l lacking lateral projections; pseudepiphallic parameres (ps.p) well developed, with the apex dorsoventrally bifurcated, the inner surface concave with a conspicuous leaf-shaped carina, and the dorsal projection more developed than the ventral one, curving posteriorly and inward as a broad hook with a tapered apex; ectophallic fold (ect.f) reduced; ectophallic apodemes (ect.ap) well developed, longer than the rami, which curve inward, over the ect.ap; endophallic sclerite (end.s) shaped like an inverted V, with a pair of less sclerotized apodemes extending outwardly.

Female right forewing (Figure 6A,B): also darkly colored, with light-colored anastomotic crossveins; lacking specialized areas, except for the lateral field.

Female abdomen (Figure 6A–H): subgenital plate longer than wide, with a deep distal emargination; supra-anal plate trapezoidal and proximally elevated, bearing what appears to be an underdeveloped version of the modification observed in adult males; ovipositor slightly curved dorsally, longer than the hind femur, with a yellowish coloration that may indicate the specimen had recently molted; apex broken.

Copulatory papilla (Figure 6I): subtriangular, with a strongly sclerotized median dorsal carina; anterior ventral margin slightly arcuate.

Ecological remarks. Specimens of *Grunagryllus aquaeclarae* gen. et sp. nov. were recorded within caves of the Água Clara Cave System (ACCS), a hydrologically integrated karst network located along the eastern margin of the Serra do Ramalho massif (Figure 11A). The ACCS comprises a series of large, interconnected conduits, including the Água Clara (13,880 m), Índios (510 m), Lapa dos Peixes I (9320 m), and Lapa dos Peixes II (2100 m) caves (Figure 11B). A detailed account of the geological structure and hydrological dynamics of the ACCS is provided by Ferreira et al. [30].

Individuals of *G. aquaeclarae* gen. et sp. nov. were observed exclusively in entrance-associated sectors, particularly in Lapa dos Peixes I (Figure 7A), Gruta dos Índios and Gruta da Água Escura I caves (Figure 11B). Specimens were typically found resting on cave walls within disphotic zones (Figure 7B,C), where light levels are reduced but not entirely absent. Individuals remained motionless in the presence of approaching observers, allowing close inspection, but responded to minor disturbances with abrupt jumping movements toward sheltered microhabitats, indicating a combination of low baseline activity and rapid escape responses. Notably, no specimens were recorded in aphotic zones, suggesting that the species does not occupy the deeper, permanently dark sectors of the caves. Instead, its occurrence appears to be restricted to ecotonal environments near cave entrances.

Although several caves in the surrounding region were surveyed, *G. aquaeclarae* gen. et sp. nov. was detected only within the ACCS. This pattern may indicate a geographically restricted distribution, potentially encompassing both subterranean and adjacent epigeal habitats, or alternatively, a species that utilizes cave entrances opportunistically as refuges. However, the relatively high number of individuals observed in the three occupied caves (despite the limited number of collected specimens) suggests that these entrance zones are not used sporadically, but rather constitute regularly exploited microhabitats. It is important to emphasize that adjacent surface environments were not included in the sampling design, preventing a comprehensive assessment of the species' full distributional range. Further studies are needed to better understand the ecological relationship between the new species and subterranean environments.

***Grunagryllus sanctijosephi* sp. nov. Mendes-Carvalho & Ferreira**

(Table 1; Figures 8–10)

Comparative diagnosis. *Grunagryllus sanctijosephi* gen. et sp. nov. differs from *G. aquaeclarae* gen. et sp. nov. by the presence of a broad dark brown stripe in the transitional area between the vertex and gena, extending from the compound eye toward the occiput (absent in the latter species) (Figure 8D,G); more conspicuous dark brown markings on the frons (Figure 8C); a clypeus bearing multiple irregular dark brown spots rather than a single narrow median dark brown spot (Figure 8C); a less developed tripartite modification of the supra-anal plate, covering approximately one third of its surface (covering nearly its entire surface in *G. aquaeclarae* sp. nov.) (Figure 8E); a broader apical portion of the pseudepiphallallic parameres (Figure 10D); apical portion of the pseudepiphallallic parameres differently shaped, with the inner concavity lacking a leaf-shaped carina (Figure 10F); and ectophallic apodemes shorter and less developed (Figure 10B,C).

Etymology. The specific epithet *sanctijosephi* derives from the Latin *sancti* (“of Saint”) and *josephi* (“of Joseph”), meaning “of Saint Joseph.” The name refers to International Workers’ Day, traditionally associated with Saint Joseph the Worker, on which the holotype was fortuitously discovered among material deposited in the Collection of Subterranean Invertebrates of Lavras (ISLA). The epithet is to be treated as a noun in apposition.

Material examined. Holotype (ISLA155526), male ♂, GER-0051 cave (20°17′32.6″ S; 43°22′23.6″ W), Mariana, Minas Gerais, Brazil, R.A. Castro-Souza leg., 10 October 2018; condition: antennae and cerci broken, right forewing detached, left hind femur slightly damaged, abdominal apex damaged prior to the present study, phallic complex previously dissected and stored alongside the specimen. Other material examined: (ISLA155527), juvenile male ♂, CMR-0207 cave (20°15′21.2″ S; 43°24′06.9″ W), Mariana, Minas Gerais, Brazil, R.A. Castro-Souza leg., 3 July 2019.

Description. Body coloration light brown, with dark brown spots and stripes; body size slightly smaller than *G. aquaeclarae* gen. et sp. nov.

Head (Figure 8A–D,G): pubescent; longer than wide in frontal view; compound eyes developed; antennal scape with a dark brown spot anteriorly; lateral ocelli closer to each other than to the median ocellus, which is subapical; fastigium bearing long, thick setae and approximately as wide as the antennal scape; vertex with a pair of dark brown stripes extending from the occiput toward the fastigium and diverging at both ends, area between the compound eye and the occiput with a dark brown spot; transitional area between vertex and gena with a broad dark brown stripe extending from the compound eye toward the occiput; gena with a posteromedian dark brown spot; frons with a pair of broad, irregular lateral dark brown stripes extending from the compound eye to the clypeus, a median dark brown stripe with a central interruption roughly in the shape of an inverted triangle, lateral stripes connected to the median stripe through a pair of conspicuous dark brown spots; clypeus with multiple brown spots; labrum light yellow, with a small dark brown spot; mandibles with a median dark brown spot, continuous with the color pattern of the frons; maxillary palp short; apical maxillary palpomeres longer than third and fourth palpomeres, broadened at the tip, with the apex rounded.

Thorax (Figure 8A,B,G): pronotum pubescent, anterior and posterior margins bearing long, thick setae; pronotum anteriorly and posteriorly irregularly dark brown along the anterior and posterior portions, dorsal area separated from the lateral lobes by a broad sinuous dark brown stripe extending anteroposteriorly; lateral lobes directed anteriorly; metanotum apparently lacking glandular structures; metasternite with posterior margin broadly arched.

Male right forewing (Figure 8A,B): as long as the abdomen; darkly colored, with light-colored crossveins; mirror wider than long, crossed by two arched transverse veins; harp

bearing one anteriorly bifurcated crossvein on the left, followed by four thick, simple transverse veins decreasing in length from left to right; stridulatory file present, composed of 208 closely spaced teeth ($n = 1$); apical area present, moderately elongate; lateral field with two thick, parallel, and closely spaced longitudinal veins, and multiple (16–18) dorsoventral crossveins. Male left forewing: similar to the right forewing but mirrored and less sclerotized; stridulatory file absent; mirror crossed by two arched transverse veins, the posterior one incomplete, not reaching the left margin and instead connected to the posterior margin by two short longitudinal veins. Hindwings: translucent; longer than the forewings.

Legs (Figure 9A–L): femora and tibiae with dark brown rings; foretibiae bearing a well-developed oval tympanum on both faces and a pair of ventral apical spurs, the inner longer than the outer; middle tibiae also with two ventral apical spurs; hind tibiae dorsally serrulated on the proximal and median portions, intersubapical spur margins bearing one or no spines; hind tibiae with three inner (is1–is3) and three outer (os1–os3) subapical spurs concentrated on the distal portion of the tibia, inner spurs shorter than the outer; hind tibiae with three outer (oa1–oa3) and three inner (ia1–ia3) apical spurs; dorsal outer apical spur (oa1) shorter than the ventral (oa3), which, in turn, is approximately half the length of the median outer apical spur (oa2); dorsal (ia1) and ventral (ia3) inner apical spurs subequal and approximately half the length of the median inner apical spur (ia2); subapical and apical spurs lacking any modifications; hind basitarsi with two rows of spines, the inner row composed of 5 spines and shorter than the outer row, which bears 8 spines; hind basitarsi with a pair of ventral apical spurs, the inner longer than the outer; tarsal claws smooth, symmetrical, and more strongly sclerotized at the apex.

Male abdomen (Figure 8E,F): cerci elongated, pubescent, covered with short, elongate and globose setae, the latter concentrated on the proximal portion of the structure; subgenital plate subtriangular, with the distal margin medially emarginate; supra-anal plate trapezoidal, bearing a tripartite modification in the shape of an inverted lowercase omega (ω) covering one third of the dorsal surface of supra-anal plate.

Phallic complex (Figure 10A–F): pseudepiphallic median lophi (med.l) posteriorly rounded, densely covered with long setae, and with a median emargination approximately square in shape, with moderately sclerotized margins; med.l lacking lateral projections; pseudepiphallic parameres (ps.p) well developed, with the apex dorsoventrally bifurcated, the inner surface concave, and the dorsal projection more developed than the ventral one, anteroposteriorly broadened, curving posteriorly and inward as a broad hook; ectophallic fold (ect.f) reduced; ectophallic apodemes (ect.ap) well developed; endophallic sclerite (end.s) shaped like an inverted V, with a pair of less sclerotized apodemes extending outwardly.

Female: Unknown.

Ecological remarks. Specimens of *Grunagryllus sanctijosephi* gen. et sp. nov. were recorded in two quartzite caves situated on a mountaintop and surrounded by shrub and arboreal campo rupestre vegetation [31]. As the specimens were collected during environmental licensing surveys conducted by biologists associated with environmental consulting companies, detailed information on the ecology and behavior of the species is unfortunately unavailable. As with *G. aquaeclarae* gen. et sp. nov., further studies will be necessary to clarify the ecological relationship between the new species and subterranean environments.

4. Discussion

Taxonomic affinities and biogeographic distribution of Paragryllina

Grunagryllus gen. nov. shares morphological features with all three suprageneric groups currently recognized within Paragryllina. With Benoistellae, it shares forewings

shorter than or approximately as long as the abdomen, a mirror crossed by two transverse veins, a subapical median ocellus, and a fastigium as wide as the first antennomere. With *Paragryllae*, it shares a head longer than wide in frontal view and the presence of three subapical spurs on the posterior (inner) face of the hind tibia. Finally, similarities with *Rumeae* include the presence of two rows of spines on the dorsal surface of the hind basitarsus.

The overall structure of the phallic complex, particularly the pseudepiphallic sclerites, suggests affinities between *Grunagryllus* gen. nov. and *Benoistella* (Benoistellae), *Bolivacla* (Paragryllae), and, to a lesser extent, *Izerskya* (Benoistellae). In comparison, the dorsally curved pseudepiphallic parameres resemble those observed in *Paragryllus* (Paragryllae). Furthermore, the copulatory papilla shows similarities to that of *Benoistella*. The ovipositor, however, cannot be compared with those of other genera because its apex is damaged and may not accurately represent the morphology of the species.

Given this combination of characters, *Grunagryllus* gen. nov. cannot presently be assigned with confidence to any of the suprageneric groups within Paragryllina. Additional phylogenetic studies will be necessary to clarify the evolutionary relationships between these taxa. Nevertheless, the description of new taxa remains essential for such investigations, as taxonomic studies provide the foundation for recognizing and interpreting the true morphological diversity of the group.

Similarly to Strogulomorphina Desutter-Grandcolas, 1988 [32], Paragryllina exhibits significant gaps in its known geographic distribution. All previously described species have been recorded from rainforest environments, and some genera have been hypothesized to represent regional endemics, such as *Benoistella* in the Guiana Shield [16]. Until now, no representatives of the subtribe had been documented from drier or more open biomes, such as the Caatinga, an endemic Brazilian semiarid biome. In this context, caves may provide environmental conditions, particularly high humidity, comparable to those found in rainforests, potentially contributing to the persistence of taxa typically associated with humid environments, such as Paragryllina, within dryer biomes like the Caatinga. A similar hypothesis was proposed by de Campos et al. [33] for species of *Eidmanacris* Chopard, 1956 (Phalangopsidae, Phalangopsinae), whose distribution extends from the Atlantic Forest into drier environments (Cerrado). Nonetheless, additional sampling efforts, including surveys in epigeal habitats, are needed to determine the actual distribution of *G. aquaeclarae* gen. et sp. nov. and to assess the extent to which caves function as refuges for the species in the Serra do Ramalho region.

The Caatinga remains comparatively underexplored when contrasted with the Amazon and Atlantic Forest biomes [34–36], particularly regarding its invertebrate fauna [37]. Accordingly, broader sampling efforts in poorly surveyed regions will be essential for improving current knowledge of the diversity and distribution of Paragryllina. The description of *G. aquaeclarae* gen. et sp. nov. and *G. sanctijosephi* gen. et sp. nov., therefore, represents an important contribution to the understanding of Brazilian biodiversity, particularly with regard to its Orthoptera fauna.

Threats and conservation

Human visitation within the Água Clara Cave System (ACCS) caves is currently limited, resulting in relatively low levels of direct disturbance to subterranean habitats. In contrast, the surrounding areas have undergone increasingly intense anthropogenic transformation in recent years [30]. Large portions of native vegetation have been removed for agricultural expansion and charcoal production (Figure 12A,B), a deforestation trend that has recently intensified throughout the Caatinga as a whole [38]. In the absence of data on the occurrence of this species in external habitats, the extent to which these disturbances affect its populations remains uncertain. Targeted surveys in epigeal environments surrounding the caves where *G. aquaeclarae* gen. et sp. nov. was originally found

are therefore essential to clarify its distribution and to support a robust evaluation of its conservation status.

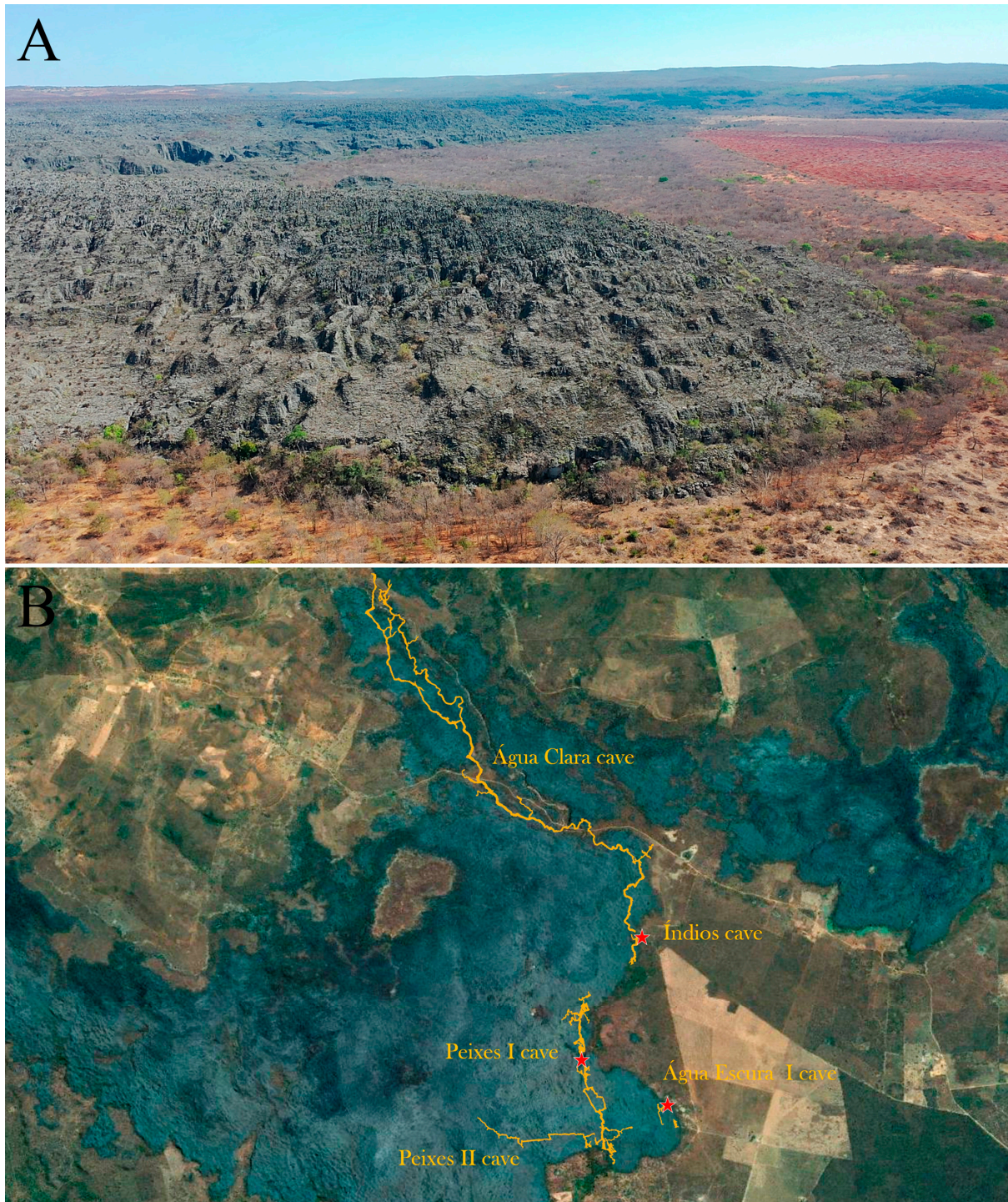


Figure 11. Serra do Ramalho karst, Bahia, Brazil. (A) Aerial view of the Serra do Ramalho karst; (B) satellite view of the Serra do Ramalho karst, with caves from the Água Clara Cave System highlighted.

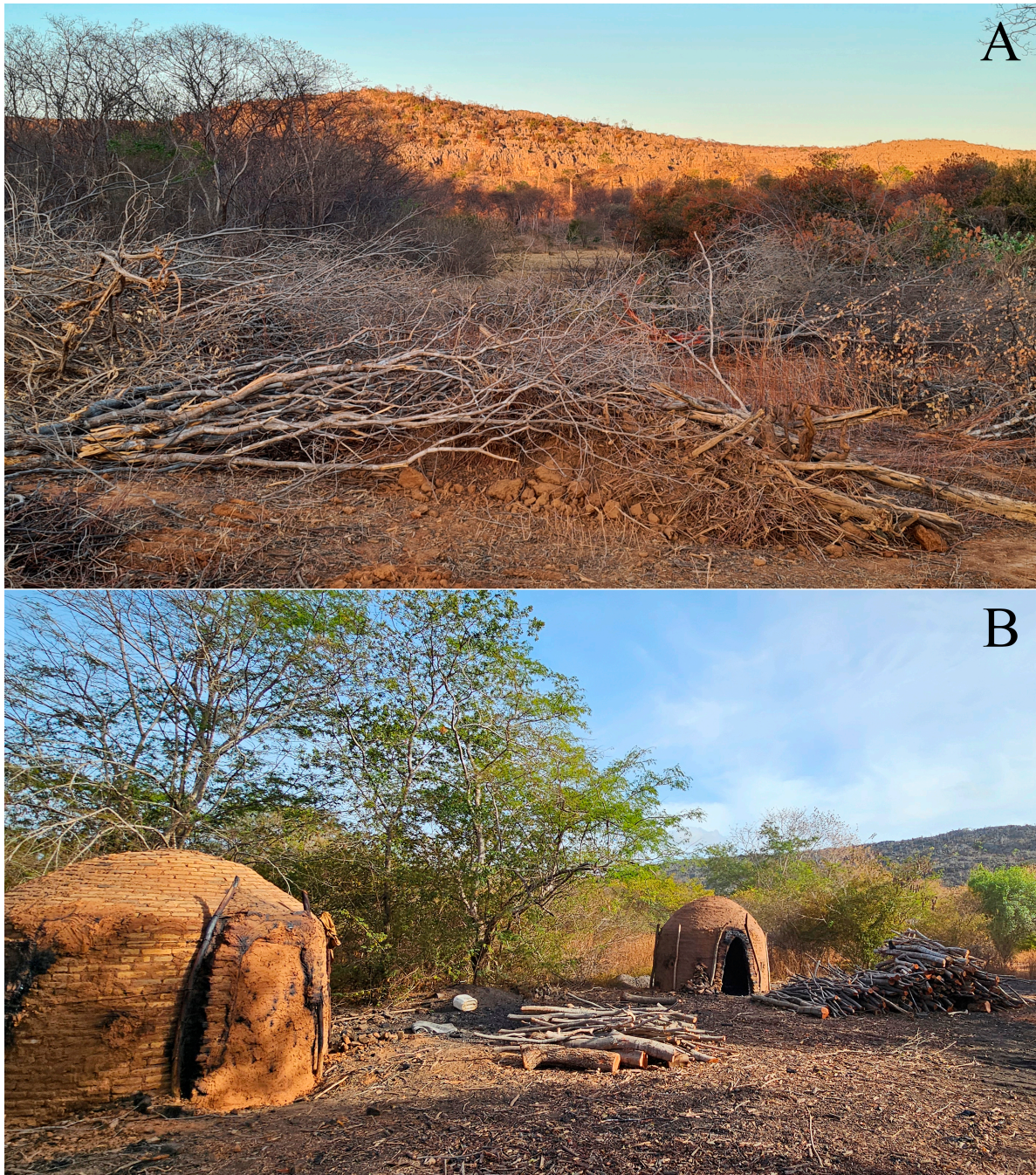


Figure 12. Anthropogenic threats to *Grunagryllus aquaeclarae* gen. et sp. nov. (A) Deforestation; (B) charcoal production.

The ACCS represents a major center of subterranean diversity. Ferreira et al. [30] documented 31 cave-restricted species and identified the system as one of the most significant hotspots of subterranean biodiversity in South America. Subsequent surveys have substantially expanded this number, with new inventories increasing the count to 41 species [39], and more recent efforts raising it further to 53 [40]. This rapid accumulation of records highlights both the exceptional biological value of the system and the likelihood that its diversity remains underestimated. The surrounding seasonally dry forests and shrublands in Serra do Ramalho massif likely harbor high levels of biodiversity, as do its subterranean environments. In light of this, the implementation of urgent conservation measures is strongly warranted. We recommend the establishment of a formally protected area encompassing not only the cave system itself but also its recharge zones, associated

catchment micro-basins and surrounding epigean habitats, coupled with effective regulatory frameworks to ensure the long-term integrity of this highly sensitive and biologically unique karst ecosystem.

Finally, the municipality of Mariana, within the Quadrilátero Ferrífero, constitutes one of the most important iron ore extraction areas in Brazil and has undergone substantial environmental alteration due to long-term mining activities. The advance of open-pit extraction has led to the removal and fragmentation of native vegetation, accelerated erosive processes, and the progressive reduction of ferruginous outcrop ecosystems (“cangas”), which support highly specialized and endemic biota [27]. Mining activities have also affected regional hydrology by altering surface drainage, increasing sediment transport, and introducing suspended material and metallic contaminants into aquatic systems [41].

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Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author. Specimens were deposited in the Collection of Subterranean Invertebrates of Lavras (ISLA), Lavras, at the Center of Studies in Subterranean Biology (CEBS), Federal University of Lavras (UFLA), Minas Gerais State, Brazil.

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Abbreviations

The following abbreviations are used in this manuscript:

med.l	pseudepiphallic median lophi
ps.p	pseudepiphallic paramere
r.	rami
ect.f	ectophallic fold
ect.ap	ectophallic apodeme
end.s	endophallic sclerite
ia	inner apical spur
is	inner subapical spur
oa	outer apical spur
os	outer subapical spur

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