European Journal of Taxonomy 932: 82–111
https://doi.org/10.5852/ejt.2024.932.2511
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Tavares *et al.*

Research article

urn:lsid:zoobank.org:pub:2597B29F-DF1C-44E0-92AC-7252E6C72E98

New species and records of *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014 (Orthoptera: Gryllidae: Gryllinae) from the Brazilian Amazon rainforest

Gustavo Costa TAVARES [1,*], Beatriz Harumi Kondo OYA [2],
Oscar J. CADENA-CASTAÑEDA [3], Marcus Paulo Alves de OLIVEIRA [4] &
Rodrigo Antônio CASTRO-SOUZA [5]

[1] Universidade Federal do Pará (UFPA), Instituto de Ciências Biológicas (ICB), Laboratório de Invertebrados (LAINV), Grupo de Estudos de Artrópodes da Amazônia (GEAA), Av. Augusto Correa #1, 66075-110, Belém, PA, Brazil.
[2] Universidade Federal do Pará (UFPA), Instituto de Ciências Biológicas (ICB), Laboratório de Invertebrados (LAINV), Av. Augusto Correa #1, 66075-110, Belém, PA, Brazil.
[3] Universidad Distrital Francisco José de Caldas, Grupo de Investigación en Artrópodos "Kumangui", Bogotá, Colombia.
[4] BioEspeleo Consultoria Ambiental Ltda, Lavras, Minas Gerais, Brazil.
[5] Universidade Federal de Mato Grosso (UFMT), Laboratório de Macroecologia e Conservação da Biodiversidade, Departamento de Botânica e Ecologia, Instituto de Biociências, 78060-900, Cuiabá, MT, Brazil.

[*] Corresponding author: gustavoctavares@gmail.com
[2] E-mail: bia.kondo.oya@gmail.com
[3] E-mail: ojccorthoptera@gmail.com
[4] E-mail: marcus@bioespeleo.com.br
[5] E-mail: rodrigodesouzaac@gmail.com

[1] urn:lsid:zoobank.org:author:C1A132DE-8721-4E36-A28D-EFA43A8F1541
[2] urn:lsid:zoobank.org:author:5F07593B-D146-4114-ABE8-8EB593324D39
[3] urn:lsid:zoobank.org:author:410E81C9-E470-425C-9B1E-7175C43D847A
[4] urn:lsid:zoobank.org:author:A154CEC0-04AC-4BA6-9A7E-48C07923D5D3
[5] urn:lsid:zoobank.org:author:06EC4D09-05F6-44C6-9FE2-E43CC14B24C4

Abstract. *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014 is a Neotropical genus of field crickets that inhabits the leaf litter of the Amazon rainforest. The genus has six species and is characterized by the distinct 'zebra' pattern displayed by some of them. The species are recorded in French Guiana, Peru, and Colombia. Here, we describe two new species of the genus from the Brazilian Amazon rainforest, the first record of the genus for Brazil. We expand the records of *Z. guianensis* Desutter-Grandcolas, 2014 and *Z. nouragui* Desutter-Grandcolas, 2014 to Brazil. We also describe but do not name two females corresponding to two new species, provide an up-to-date key for species of *Zebragryllus*, and discuss the potential distribution for the genus.

Keywords. Gryllini, Anurogryllina, cave cricket, Minimum Convex Polygons.

Tavares G.C., Oya B.H.K., Cadena-Castañeda O.J., de Oliveira M.P.A. & Castro-Souza R.A. 2024. New species and records of *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014 (Orthoptera: Gryllidae: Gryllinae) from the Brazilian Amazon rainforest. *European Journal of Taxonomy* 932: 82–111. https://doi.org/10.5852/ejt.2024.932.2511

Introduction

Despite its high diversity, the subfamily Gryllinae, Laicharting, 1781 is mainly found in regions of Africa and Eurasia, and the cosmopolitan tribe Gryllini, Laicharting, 1781 is the only group to occur in the Neotropics (Cigliano *et al.* 2023). However, no representative of this subfamily was ever reported to occur in South American caves.

Zebragryllus Desutter-Grandcolas & Cadena-Castañeda, 2014 is a Neotropical Gryllini genus (subtribe Anurogryllina Randell, 1964) with six species that inhabit the leaf litter of the Amazon region (Desutter-Grandcolas *et al.* 2014). The genus is officially recorded in French Guiana, Colombia, and Peru (Desutter-Grandcolas *et al.* 2014). It is characterized by crickets with a black and white 'zebra' pattern on the hind legs (which can be conspicuous, like in *Zebragryllus wittoto* Desutter-Grandcolas & Cadena-Castañeda, 2014, or even absent, like in *Zebragryllus fuscus* Desutter-Grandcolas, 2014). The male genitalia have a transverse pseudepiphallic sclerite; median lophi moderately elongated, subtriangular, and medially incised; rami notably arched, somehow circular (fused); and pseudepiphallic paramere elongated (Desutter-Grandcolas *et al.* 2014; Cadena-Castañeda *et al.* 2021).

In this work, we describe two new species of *Zebragryllus*, describe but do not name two additional females comprising two new species, and expand the records of *Z. guianensis* Desutter-Grandcolas, 2014 and *Z. nouragui* Desutter-Grandcolas, 2014 to Brazil. In addition, we provide an up-to-date identification key for species of the genus and discuss its potential distribution.

Material and methods

The genitalia were removed and treated with a warm 10% aqueous solution of potassium hydroxide (KOH) for approximately 10–15 minutes to digest and remove muscles and fat. Afterward, they were stored in an 80% ethanol solution, and both body and genitalia morphologies were analyzed under a Leica M205 A stereo microscope equipped with a Leica DFC 450 camera.

The venation terminology followed Desutter-Grandcolas et al. (2017). The nomenclature adopted for the phallic complex followed Desutter (1987), modified in Desutter-Grandcolas (2003) and is defined in the section Abbreviations for measurements and morphological terms.

Measurements of body parts were made using a digital pachymeter and were defined as follows: *total length* (TL) as the distance between the top of the fastigium of vertex and the apex of the supra-anal plate; *length of pronotum* (LP) as the length of a mid-dorsal line between the anterior and posterior margins of the pronotal disk; *width of pronotum* (WP) as the maximum distance between the mid-portion of pronotum lateral lobes; *tegmina* (Tg) as the length of a dorsal line between the base and the apex of tegmina; *hind femur* (HF) as the distance between the base of the hind femur and the apex of genicular lobes; *hind tibia* (HT) as the distance between the base and the apex of the hind tibia; and *ovipositor* (Ov) as the distance from the apex of the subgenital plate and the apex of the ovipositor.

All the type material is deposited in the Entomological Collection of the Museu Paraense Emílio Goeldi (MPEG), in Brazil. Additional non-type specimens were distributed between two institutions, MPEG and Coleção de Invertebrados Subterrâneos de Lavras (ISLA), in the Universidade Federal de Lavras, also in Brazil.

Abbreviations for measurement

HF = hind femur
HT = hind tibia
LP = length of pronotum
Ov = ovipositor
Tg = tegmina
TL = total length
WP = width of pronotum

Abbreviations for morphological terms

A.F. = anal field
Ap.F = apical field
arc = ectophallic arc
CuP. = postcubital
ec.a. = ectophallic apodeme
ec.f. = ectophallic fold
ejv. = ejaculatory vesicle
en.c. = endophallic cavity
H. = harp
L.F. = lateral field
l.l. = pseudepiphallic lateral lophi
M. = mirror
m.l. = pseudepiphallic median lophi
ps.a. = pseudepiphallic apodeme
ps.p. = pseudepiphallic paramere
r. = rami

Institutional abbreviations

ISLA = Coleção de Invertebrados Subterrâneos de Lavras, Universidade Federal de Lavras, Brazil
MPEG = Entomological Collection of the Museu Paraense Emílio Goeldi, Brazil

Potential distribution

The study of species' potential distribution can be facilitated through maps that utilize Minimum Convex Polygons (MCPs) (Mace *et al.* 1992). This method involves creating minimum convex polygons, which are the smallest polygons where no internal angle exceeds 180° and that encompass all occurrence points (IUCN 2021). For the genus *Zebragryllus*, in which most species have few occurrence points (Cigliano *et al.* 2023), we developed an MCP for the genus as a model by using the coordinates of the published records of species, available in Desutter-Grandcolas *et al.* (2014) and Cigliano *et al.* (2023), and new records from this study. The maps were produced using the QGIS software (https://QGIS.org).

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Orthoptera Olivier, 1789
Suborder Ensifera Chopard, 1921
Family Gryllidae Laicharting, 1781
Subfamily Gryllinae Laicharting, 1781
Tribe Gryllini Laicharting, 1781
Subtribe Anurogryllina Randell, 1964

Genus ***Zebragryllus*** Desutter-Grandcolas & Cadena-Castañeda, 2014

Key to males of species of *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014 (adapted from Desutter-Grandcolas et al. (2014))

1. Species with fore and mid legs black and white 5
– Species without contrasted coloration on the fore and mid legs 2

2. Hind femora completely ochre, brown, dark brown, or blackish, but without white marks 3
– Hind femora with only some whitish bands along its outer margin and close to its base .... ***Zebragryllus intermedius*** Desutter-Grandcolas, 2014

3. All femora ochre, tegmina short, not surpassing the fourth tergite 4
– Fore and mid legs all blackish or dark brown. Tegmina well-developed, covering the subgenital plate tip .... ***Z. fuscus*** Desutter-Grandcolas, 2014

4. Tegmina without stridulatory apparatus .... ***Z. aphonus*** Tavares, Oya & Cadena-Castañeda sp. nov.
– Tegmina with stridulatory apparatus .... ***Z. mebengokre*** Tavares, Oya & Cadena-Castañeda sp. nov.

5. Very small species with light ochre hindlegs, making the contrasted coloration less clear. Genitalia with lateral lophi hidden under pseudepiphallic sclerite .... ***Z. nauta*** Desutter-Grandcolas, 2014
– Medium-sized species with a black and white 'zebra' pattern. Genitalia with lateral lophi not hidden under pseudepiphallic sclerite... 6

6. Base of antennae brown (scape + about 30 antennomeres), followed by a short white ring of about ten antennomeres. Maxillary palpi dark brown, fourth joint white .... ***Z. nouragui*** Desutter-Grandcolas, 2014
– Base of antennae white. Maxillary palpi dark brown, fourth joint lighter only dorso-basally 7

7. Harp with 2–4 veins; genitalia with lophi 'foliaceous' .....***Z. guianensis*** Desutter-Grandcolas, 2014
– Male harp with two veins; genitalia with lophi sub-conical .... ***Z. wittoto*** Desutter-Grandcolas and Cadena-Castañeda, 2014

Key to females of species of *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014 (adapted from Desutter-Grandcolas et al. (2014))

1. Species with fore and mid legs black and white; abdomen also black and white (little contrasted in the light brown *Z. nauta* Desutter-Grandcolas, 2014) 3
– Species without contrasted coloration on the fore and mid legs. Abdomen without distinct white tergites 2

2. Hind femora completely ochre, without white marks. Tegmina reaching up to the first abdominal tergite .... ***Zebragryllus aphonus*** Tavares, Oya & Cadena-Castañeda sp. nov.
– Hind femora brown with only some whitish bands along its outer margin and close to its base. Tegmina very short, mostly covered by pronotum ....***Z. intermedius*** Desutter-Grandcolas, 2014

3. Very small species with light ochre hindlegs, making the contrasted coloration less clear. Forewings quite long for the genus, overlapping on the anal area, with many cells between longitudinal veins; third and fourth (partially) tergites lighter than the others but not contrastingly white .... ***Z. nauta*** Desutter-Grandcolas , 2014
– Medium-sized species with a black and white ‘zebra’ pattern. Fore wings absent or short, not reaching the first abdominal tergite 4

4. Base of antennae brown (scape + about 30 antennomeres), followed by a short white ring of about 10 antennomeres. Short and slightly overlapping forewings; abdomen dark brown, metanotum and third tergite with a wide transverse and continuous white stripe ....
.... ***Z. nouragui*** Desutter-Grandcolas, 2014
– Base of antennae white. Apterous or with shorter forewings; abdomen coloration different 5

5. Apterous; posterior margin of metanotum with a white semicircular band covering part of the first tergite anterior margin. Fourth to sixth tergites white in their anterior two/third, except on a short medio-dorsal line, black ....***Z. guianensis*** Desutter-Grandcolas, 2014
– Forewings short, not overlapping; metanotum with a white half ring and a pair of faint whitish bands on fourth and fifth tergites ....***Z. wittoto*** Desutter-Grandcolas & Cadena-Castañeda, 2014

Zebragryllus aphonus Tavares, Oya & Cadena-Castañeda sp. nov.

urn:lsid:zoobank.org:act:C2212D6F-194D-49C7-BA27-B113E0B51C55

Figs 1–5, 16A–C

Diagnosis

Specimens dark (Figs 1A–B, 4A–B). Tympana reduced or absent (Fig. 2A–F). All femora entirely ochre, without the ‘zebra’ pattern (Fig. 2A–C, G–K). Males dorsally with head, pronotum, tegmina, and first abdominal tergite black (Fig. 1A–E); without stridulatory apparatus (Fig. 1E). Comparatively, all the other known species of *Zebragryllus* are easily distinguished for having stridulatory apparatus on the male tegmina. Male genitalia: pseudepiphallic median lophi elongated, conspicuously produced hind- and upwards, very narrow, and apically acute, ventrally with a sharp keel. Pseudepiphallic lateral lophi acute. Pseudepiphallic paramere surpassing the lateral lophi; in ventral view, slightly arched. Ectophallic fold very thin, not reaching the level of the pseudepiphallic paramere apex (Fig. 3A–D). Female with the black coloration extending till the second abdominal tergite (Fig. 4A–D); remaining tergites dark brown; ovipositor straight and almost as long as the hind femora (Fig. 4A, H–I). Female genitalia: copulatory papilla with posterior margin of dorsal surface widely concave, and the anterior margin with medial process emarginated, flanking the spermatheca duct (Fig. 4L); ventral surface acute anteriorly (Fig. 4M); in lateral view, posterior portion taller than anterior one (Fig. 4N).

Etymology

The specific epithet "*aphonus*" refers to the absence of a stridulatory apparatus, which makes the cricket incapable of producing sound.

Type material

Holotype

BRAZIL • ♂; Pará, Cannã dos Carajás, S11C-0033 cave; 6°23′53.5″ S, 50°23′26.5″ W; 16 Aug. 2022; J.P. Alves and D. Souza leg.; except for the right foreleg, all the remaining legs have fallen but are stored in the same specimen vial, one palpus, the subgenital plate, the right tegmen, and the phallic complex were removed but kept in a microvial with the specimen; MPEG.HEX 05050607.

Paratypes

BRAZIL • 1 ♀; same collection data as for holotype; except for the left hindleg, all the remaining legs have fallen but are stored in the same specimen vial, the subgenital plate, the seventh abdominal sternite, and the copulatory papilla were removed but kept in a microvial with the specimen; MPEG.HEX 05050608 • 1 ♂; same collection data as for preceding; S11C-0066 cave; 6°23′53.5″ S, 50°22′58.1″ W; 9 Oct. 2022; except for the left foreleg and right hindleg, all the remaining legs have fallen but are stored in the same specimen vial; MPEG.HEX 05050609.

Other material

BRAZIL • 1 immature (sex unknown); same locality as for holotype; 6°23′53.5″ S, 50°23′26.5″ W; 15 Feb. 2023; J.P. Alves and D. Souza leg.; ISLA107969 • 1 immature (sex unknown); same collection data as for preceding; S11C-0110 cave; 6°23′55.5″ S, 50°23′23.2″ W; 15 Feb. 2023; ISLA107970 • 1 ♀, immature; same collection data as for preceding; S11C-0110 cave; 6°23′55.5″ S, 50°23′23.2″ W; 16 Aug. 2022; ISLA107971 • 1 ♂, immature; same collection data as for preceding; S11C-0121 cave; 6°22′56.8″ S, 50°23′56.0″ W; 4 Aug. 2022; ISLA107972 • 1 ♂, immature; same collection data as for preceding; S11C-0037 cave; 6°23′28.2″ S, 50°23′33.7″ W; 12 Aug. 2022; ISLA107973 • 1 immature (sex unknown); same collection data as for preceding; S11C-0050 cave; 6°23′58.2″ S, 50°23′8.5″ W; 8 Aug. 2022; ISLA107974 • 2 immatures (sex unknown); same collection data as for preceding; S11C-0092 cave; 6°24′7.2″ S, 50°23′18.7″ W; 17 Aug. 2022; ISLA107975 to 107976.

Description

Male

COLORATION. Specimens very dark (Figs 1A–E, 4A–D). Cephalic capsule, pronotum, and tegmina black (Fig. 1A–E). Abdominal tergites dark brown and posteriorly black (Figs 1B, 4B), each with midline of black punctuations extending from lateral to the dorsolateral portion. Some whitish spots sometimes present on head dorsum (Fig. 1B). Eyes black, ocelli whitish. Scapus and pedicel yellowish, flagellomeres brown. Clypeus and labrum dark brown. Mandibles proximally black and mediodistally reddish-brown (Fig. 1C). Maxillary palpi dark brown, except for whitish ventral areas on mediodistal portion and apex (Fig. 1G). Two first segments of labial palpi dark brown, and last ochre, with tip and ventrodistal portion whitish. Femora entirely ochre, and tibiae dark brown (Fig. 2A–C, G–K) – fore tibia with two inner whitish circular areas on most proximal portion (Fig. 2G). Ventral sclerites of thorax and abdomen ochre, except for brown sternite 8 and male subgenital plate, which are brown (Fig. 1F, I).

HEAD. In frontal view (Fig. 1C), semicircular, almost as wide as high, with eyes slightly produced laterally; ocelli circular and almost aligned to eyes dorsal margin – median ocellus slightly lower. Antennal pits located low on frons, near epistomal suture, and almost on same level as eyes' most ventral border (these last also close to subgenal suture). Clypeus dorsal area notably separated from ventral area by clypeal suture. Ventral area conspicuously constricted laterally, almost half as wide as dorsal area, with median white stripe and transverse dark line on sides. Labrum circular, with pair of incomplete transverse mediolateral sutures. First two segments of maxillary palpi subequal in length; third and fourth as long as first and second together; fifth longer than any other segment, ventrally truncated on mediodistal area (Fig. 1G). In lateral view (Fig. 1D), head convex, with frons slightly tumescent; eyes ovoid, higher than wide. In dorsal view (Fig. 1B), eyes protruding; fastigium subtriangular and apically convex. Scapus wide, almost as wide as half fastigium apex.

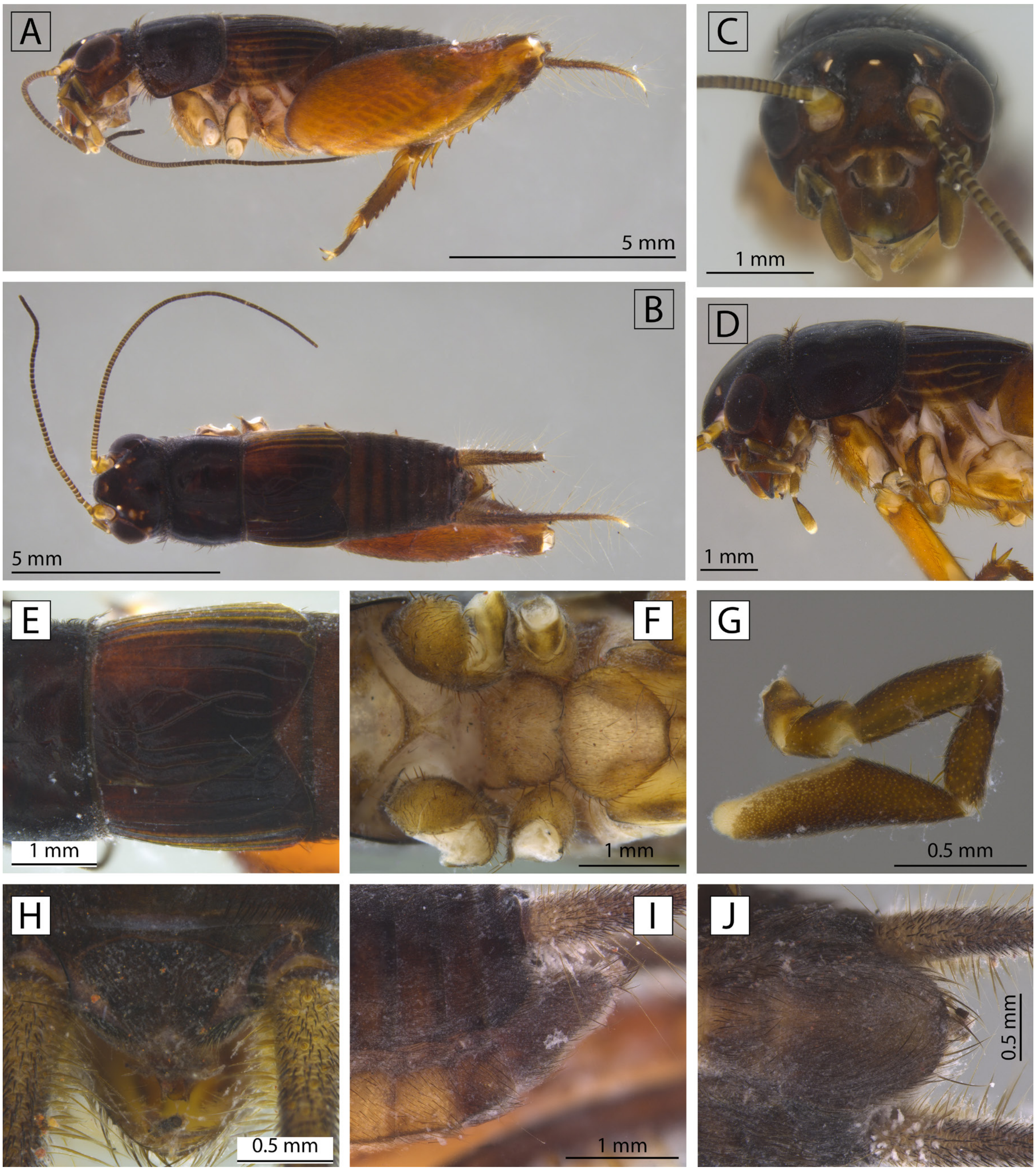

Fig. 1. *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., habitus. **A–F, H–J**. Paratype, ♂, (MPEG.HEX 05050609). **G**. Holotype, ♂ (MPEG.HEX 05050607). **A**. Lateral view. **B**. Dorsal view. **C**. Frons. **D**. Lateral view of head and thorax. **E**. Tegmina. **F**. Sternum. **G**. Maxillary palpi, outer view. **H–J**. Terminalia. **H**. Dorsal view. **I**. Lateral view. **J**. Ventral view.

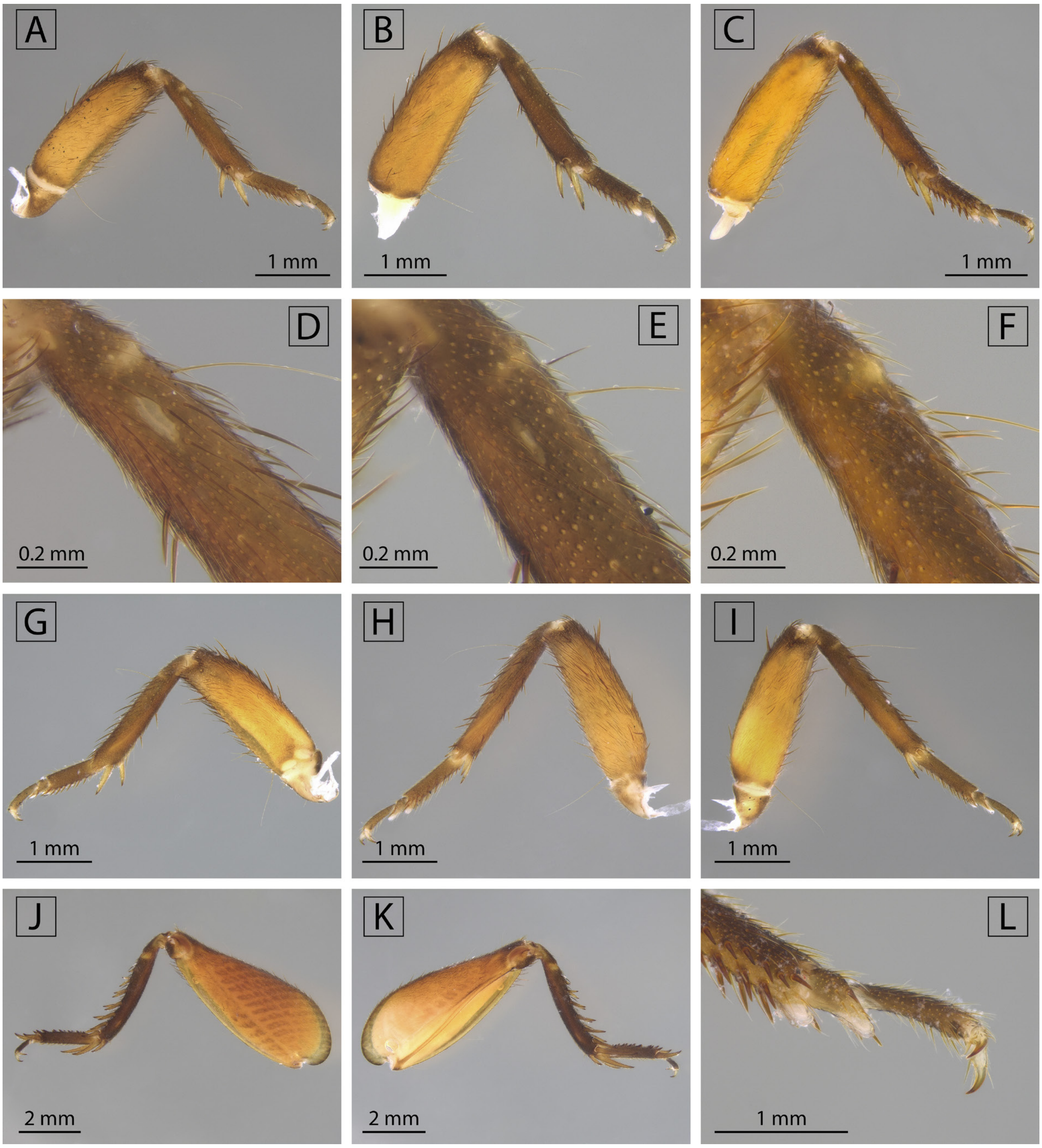

Fig. 2. *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov. legs, outer views of legs. **A**. ♂, paratype (MPEG.HEX 05050609), with reduced tympanum. **B**. ♀, paratype (MPEG.HEX 05050608), very reduced tympanum. **C**. ♂, holotype (MPEG.HEX 05050607), no tympanum. **D**. ♂, paratype (MPEG.HEX 05050609), detail of reduced tympanum. **E**. ♀, paratype (MPEG.HEX 05050608), detail of very reduced tympanum. **F**. ♂, holotype (MPEG.HEX 05050607), detail of the tibia with no tympanum. **G–I**. ♂, holotype (MPEG.HEX 05050607). **G**. Inner view of the fore leg. **H**. Outer view of the mid leg. **I**. Inner view of the mid leg. **J–L**. ♂, paratype (MPEG.HEX 05050609). **J**. Outer view of the hind leg. **K**. Inner view of the hind leg. **L**. First tarsus, in detail.

Thorax. Pronotum wider than long, bearing bristles on margins, with both anterior and posterior dorsal margins slightly concave (Fig. 1B). Lateral lobes almost squared, with anterior and posterior margins almost straight and ventral margin obliquely straight (Fig. 1A, D). Prosternum reduced, triangular, and continuous with conjoint cervical sclerites. Mesosternum sub-squared, with posterior margin slightly bilobed. Metasternum hexagonal, with posterior margin slightly incised (Fig. 1F)

Legs. All femora covered by fine pubescence and some longer bristles (Fig. 2A–C, G–K). Fore and mid tibia with two apical spurs on outer side (Fig. 2A–C, H) and one on inner side (Fig. 2G, I). Tympana reduced (Fig. 2A–B, D–E) or absent (Fig. 2C, F) (different development levels can be found in same

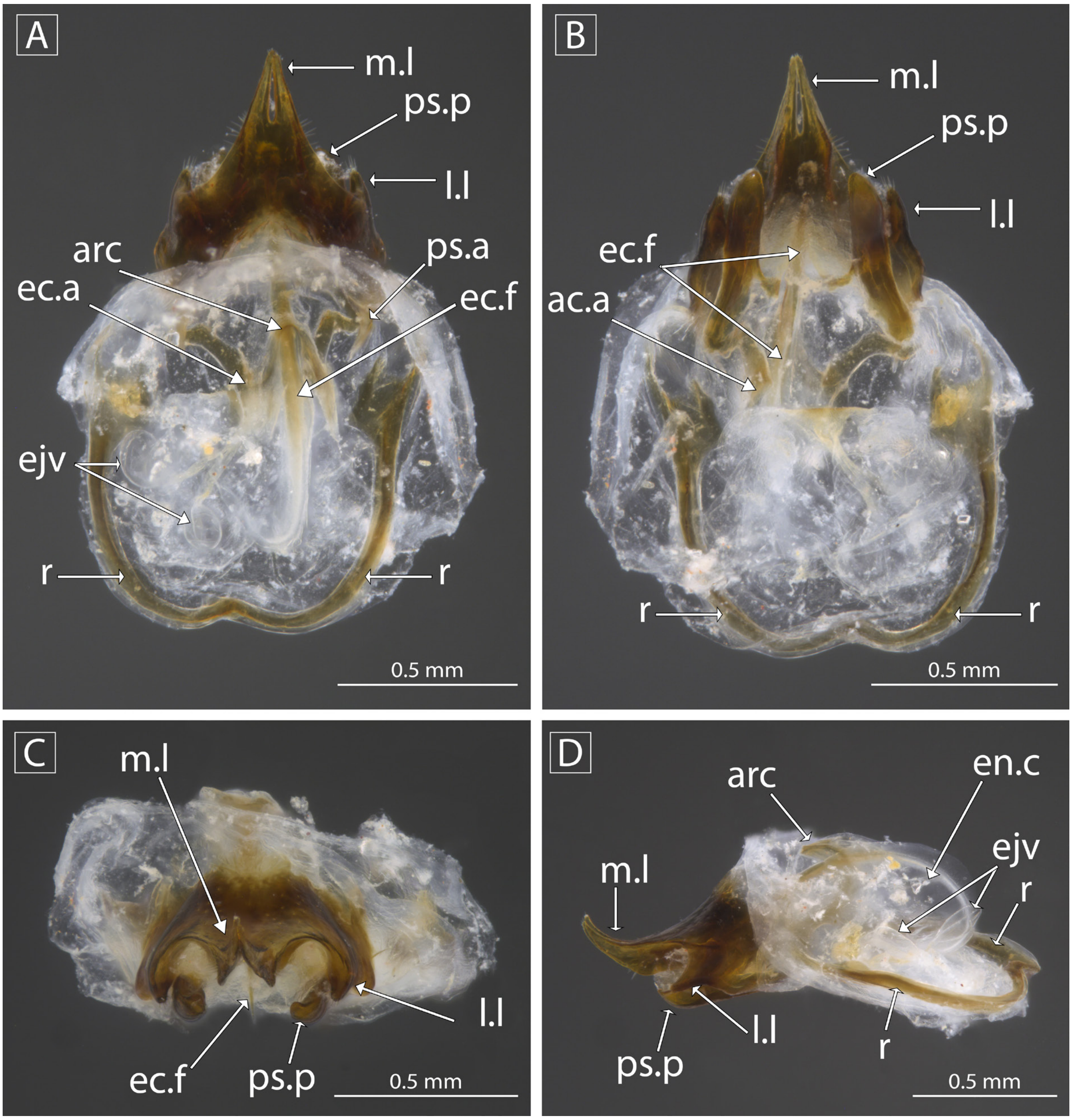

Fig. 3. *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., ♂, holotype (MPEG. HEX 05050607), phallic complex. **A**. Dorsal view. **B**. Ventral view. **C**. Axial view. **D**. Lateral view. Abbreviations: see Material and methods.

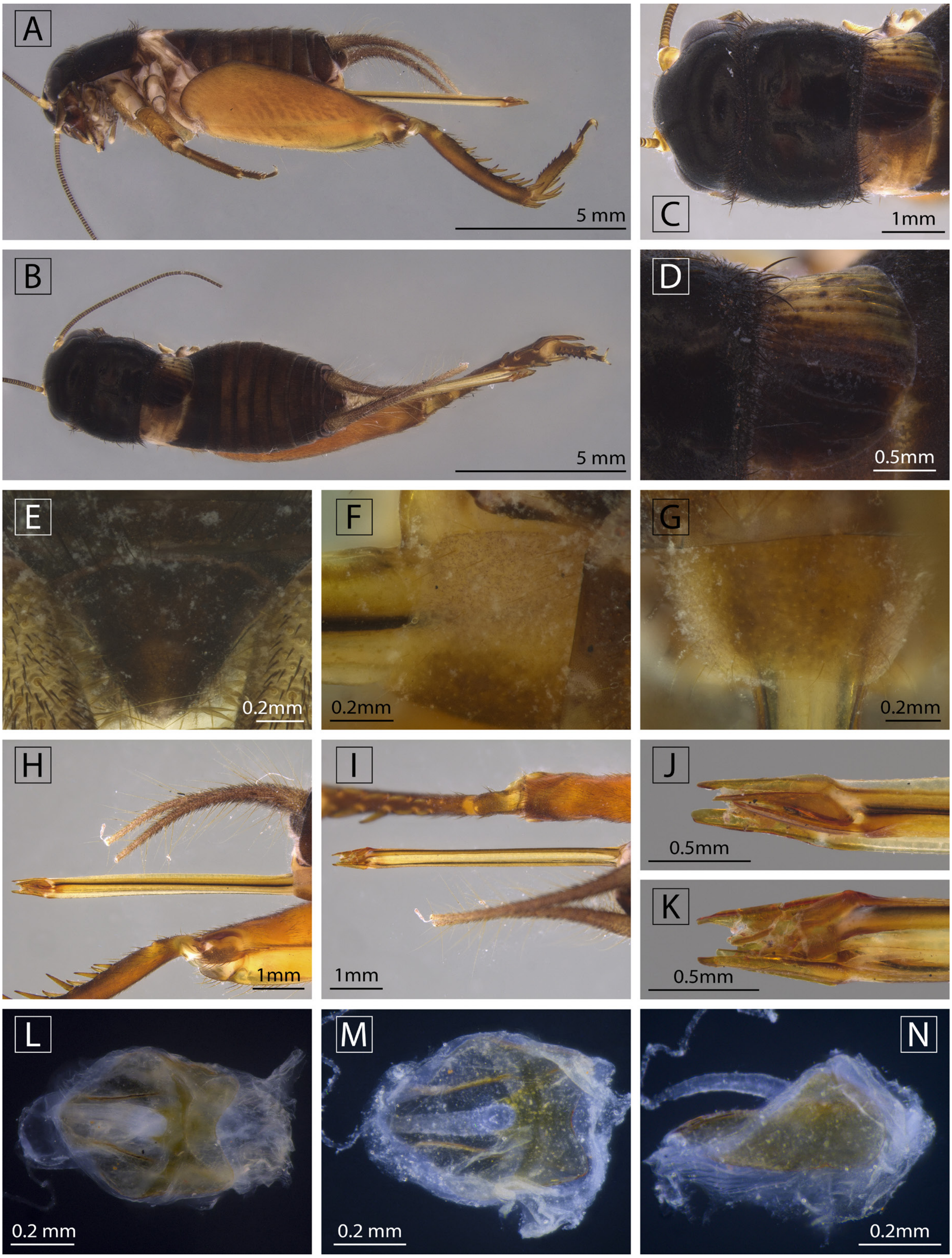

Fig. 4. *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., paratype, ♀ (MPEG.HEX 05050608). **A**–**B**. Habitus. **A**. Lateral view. **B**. Dorsal view. **C**. Dorsal view of head and thorax. **D**. Tegmina. **E**. Supra-anal plate. **F**–**G**. Subgenital plate. **F**. Lateral view. **G**. Ventral view. **H**–**I**. Ovipositor. **H**. Lateral view. **I**. Dorsal view. **J**–**K**. Detail of the ovipositor apex. **J**. Lateral view. **K**. Dorsal view. **L**–**M**. Copulatory papilla. **L**. Dorsal view. **M**. Ventral view. **N**. Lateral view.

specimen). Hind tibia with 6–7 external and 5–6 internal dorsal spurs and three apical spurs on each side (Fig. 2J–K); externally, dorsal and ventral apical spurs equal in length, mid one twice longer; internally, dorsal and mid spurs same-lengthened, ventral one at least three times smaller (Fig. 2J–K). Fore and mid basitarsi covered by strong setae on ventral side (Fig. 2A–C, G–I, L). Hind basitarsi ventrally with setae, dorsally with two rows of spines, and apically with two spurs, outer one smaller (Fig. 2J–K).

Wings. Tegmina short, reaching up to the third tergite, without stridulatory apparatus or transverse veins; lateral field with six longitudinal veins (Fig. 1A–B, D–E). Hind wings absent.

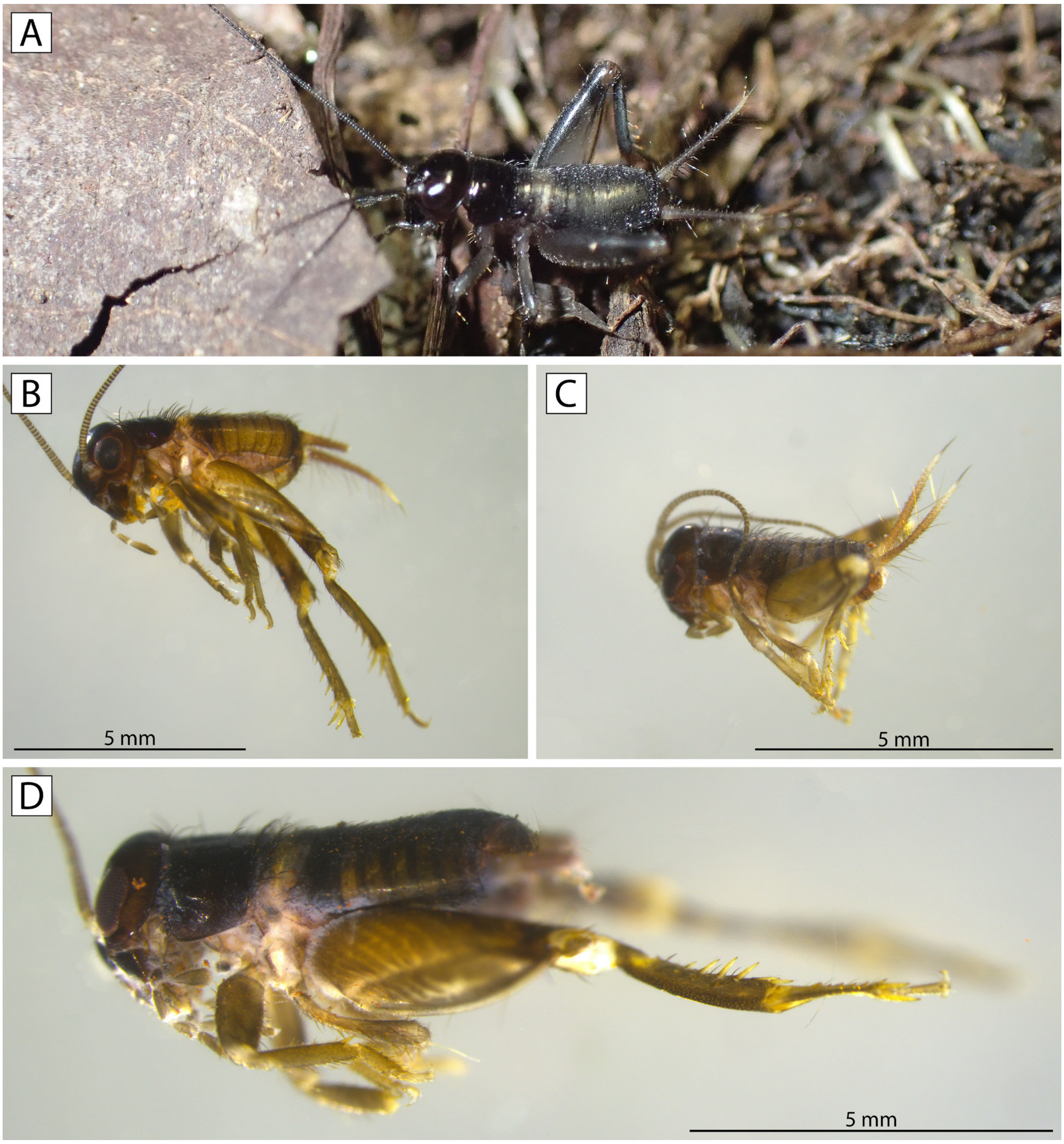

Fig. 5. *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., immatures. **B**. Immature (ISLA 107975). **C**. Immature (ISLA 107976). **D**. Immature (ISLA 107969). **A**. Alive. **B–D**. Alcohol-preserved.

ABDOMEN. Cylindrical, covered with bristles. Male supra-anal plate triangular, medially incised posteriorly and with transverse suture (Fig. 1H). Subgenital plate slightly longer than wide, with widely rounded posterior margin (Fig. 1I–J).

GENITALIA. Pseudepiphallic median lophi conspicuously elongated, notably produced hind- and upwards, very narrow, apically acute (Fig. 3A–B, D), and ventrally with sharp keel (Fig. 3C). Pseudepiphallic lateral lophi triangular, apically acute (Fig. 3D). Pseudepiphallic parameres elongated, surpassing lateral lophi; in ventral view, slightly arched, with rounded apex (Fig. 3B). Pseudepiphallic apodemes acute, incurved (Fig. 3A). Ectophallic fold very thin, not reaching level of pseudepiphallic paramere apex (Fig. 3B). Ectophallic arc very thin and notably curved; in dorsal view, forming 'W' with ectophallic apodemes (Fig. 3A). Rami basally bifid and notably arched along its length, contiguous, and medially incised (Fig. 3A–B).

Female

Similar to males in very dark coloration, with head, pronotum, tegmina, and first two abdominal tergites blackish (Fig. 4A–B). Tegmina reduced, reaching only first abdominal tergite, with only longitudinal veins (Fig. 4C–D). Supra-anal plate notably triangular, with transverse suture (Fig. 4E). Subgenital plate short; in ventral view, wider than long, with posterior margin slightly concave medially (Fig. 4G); in lateral view, higher than long, with posterior margin truncated (Fig. 4F). Ovipositor almost straight, with triangular apex. Dorsal valves dorsally sulcated (Fig. 4H–K).

GENITALIA. Copulatory papilla with posterior margin of dorsal surface widely concave, and anterior margin with medial process emarginated, flanking spermatheca duct (Fig. 4L); ventral surface acute anteriorly (Fig. 4M); in lateral view, posterior portion taller than anterior one (Fig. 4N).

Nymphs

In life, bearing same black coloration as head and pronotum of adults, but abdomen and legs gray (Fig. 5A). When preserved in alcohol, gray body parts become ochre (Fig. 5B–D).

MEASUREMENTS (mm). ♂, holotype. TL: 11.0; LP: 2.0; WP: 3.0; Tg: 2.5; HF: 6.0; HT: 4.0. ♂, paratype. TL: 9.5; LP: 2.0; WP: 2.5; Tg: 3.0; HF: 7.0; HT: 4.0. ♀, paratype. TL: 9.0; LP: 2.0; WP: 3.0; Tg: 1.5; HF: 7.0; HT: 4.0; Ov: 6.5.

Remarks

Zebragryllus aphonus Tavares, Oya & Cadena-Castañeda sp. nov. has quite a unique feature. It is the only known species of the genus in which the male has no stridulatory apparatus. The different development levels of the tympana are also singular to this species. These two characteristics may be adaptations to the caves in which they were found. Still, it is hard to ensure since no phylogenetic study was made and ecological data are lacking. The shape of the pseudepiphallic median lophi is similar to that of *Z. nauta*. However, it differs by the presence of conspicuous pseudepiphallic lateral lophi, which are very reduced and almost inconspicuous in *Z. nauta.* These two species may be related.

We believe this species is facultative to a cave-dwelling way of life or caviculous (sensu Desutter-Grandcolas *et al.* 1998), foraging on forest ground during the nights and passing the day inside the caves or cavities at ground level. We believe in this assumption since adult and immature stages were found inside caves as field work was carried out during the day. This species may also inhabit or take refuge in pores or voids on the soil, characteristic microhabitats of the environment where it was collected. The structure of the landscape is known as Banded Ferruginous Formations, which are iron formations composed of alternated bands of jaspilite and ore bodies rich in iron. In this area, extensive iron ore plateaus are formed, comprising superficial ferrugineous breccia, also known as canga formation. A metallophilic savannah covers the canga formations on the plateaus and mountains, while typical tropical vegetation of the Amazon rainforest covers the slopes. The highly porous canga formations result from the removal of silica and carbonates due to the tropical rains, which causes the dissolution and chemical change found in iron ore, forming several interconnected small spaces in the canga formations – the voids (Ferreira *et al.* 2018).

Zebragryllus aphonus Tavares, Oya & Cadena-Castañeda sp. nov. was collected in seven caves in the municipality of Canaã dos Carajás, located in the east region of Pará State, Brazil (Fig. 16A–C). The caves are coded as S11C-0033, S11C-0037, S11C-0050, S11C-0066, S11C-0092, S11C-0110, S11C-0121. They are situated in the Amazon rainforest and are part of the federal conservation unit "Floresta Nacional de Carajás" (FLONA) (Carmo & Kamino 2015). They are located within the "Grão-Pará" geological group, known for its iron-ore lithology. This region is popularly known as "Serra dos Carajás", which comprises vast plateaus separated by depressions in the landscape, dividing it into three regions: Serra Norte, Serra Leste, and Serra Sul (Carmo & Kamino 2015). The seven caves where the specimens were collected are situated in the "Serra Sul" plateaus region (Fig. 16).

Zebragryllus mebengokre Tavares, Oya & Cadena-Castañeda sp. nov.

urn:lsid:zoobank.org:act:E5A449C1-D5DD-4C2A-944E-1CB4C33F60E1

Figs 6–9, 16A, D–E

Diagnosis

Species with head and pronotum dark brown, abdomen dorsally brown, and all legs ochre (Figs 6A–D, 7A–H). Males with stridulatory apparatus well developed but with a small harp subdivided into two smaller cells (Fig. 6E). Tympana well developed on the fore tibia outer surface (Figs 6A, 7A–C). Male genitalia: pseudepiphallic median lophi notably elongated and robust, conspicuously produced hindwards (greatly surpassing pseudepiphallic lateral lophi), apically acute and ventrally with round keel. Pseudepiphallic lateral lophi acute and short. Pseudepiphallic paramere not surpassing lateral lophi; in ventral view, triangular, robust, and with oblique hyaline area basally. Ectophallic fold large, greatly surpassing pseudepiphallic lateral lophi (Fig. 8A–D).

Etymology

The specific epithet is an homage to the indigenous community that lives in the type-locality area, the Mebêngôkre, which is the self-denomination of natives known in Brazil as the Kayapó people. The name is an indigenous word of the Macro-Jê linguistic trunk and is established as a noun in apposition.

Type material

Holotype

BRAZIL • ♂; Pará, Conceição do Araguaia, Área 4; 7°59′52.6″ S, 49°22′27.1″ W; 20–26 Nov. 2021; F.V. Arruda and R.P.S. Almeida leg; Pitfall epigéico [epigeic pitfall]; all left legs, one palpus, and the phallic complex were removed but kept in a microvial with the specimen; MPEG.HEX 05050458.

Other material

BRAZIL • 1 ♀, immature; Pará, Conceição do Araguaia, Área 2; 7°55′31.7″ S, 49°24′11.5″ W; 24–31 Jul. 2021; pitfall epigéico [epigeic pitfall]; MPEG.HEX 05050459.

Description

Male

Coloration. Species ochre with cephalic capsule and pronotum dark brown; abdominal tergites, eighth abdominal sternite, and subgenital plate brown; sternum and all the remaining abdominal sternites ochre (Fig. 6A–D, F, J). Eyes black, lateral ocelli whitish, median ocellus ochre; clypeus and labrum brownish,

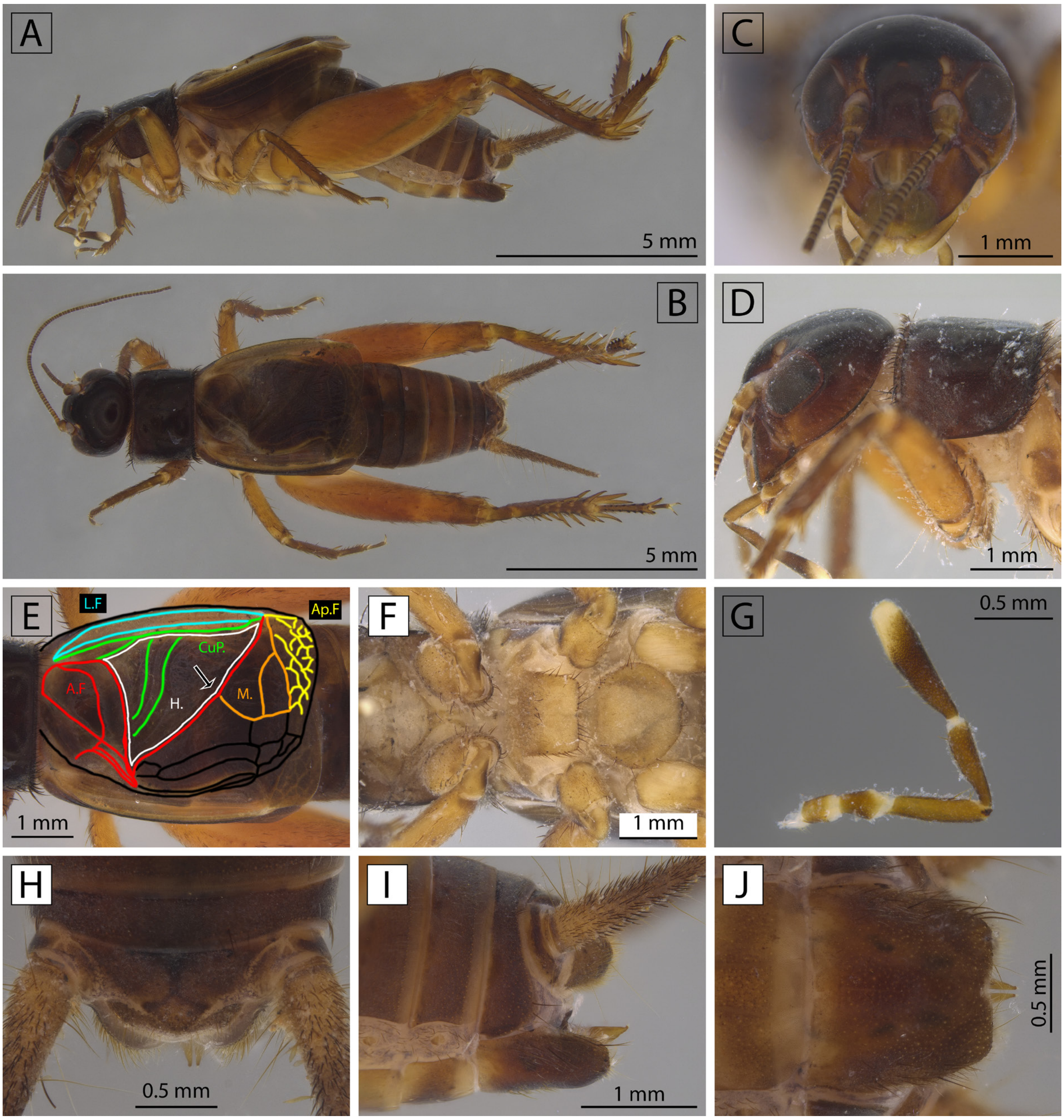

Fig. 6. *Zebragryllus mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov., holotype, ♂ (MPEG. HEX 05050458). **A–B**. Habitus. **A**. Lateral view. **B**. Dorsal view. **C**. Frons. **D**. Lateral view of head and thorax. **E**. Tegmina, arrow = angle of the forewing mirror. **F**. Sternum. **G**. Maxillary palpi, outer view. **H**. Supra-anal plate. **I**. Terminalia, lateral view. **J**. Subgenital plate. Abbreviations: see Material and methods.

and mandibles slightly darker (Fig. 6C); maxillary palpi brown, last segment slightly darker except for whitish tip (Fig. 6G); labial palpi brown. All legs ochre, with slightly darker tibia (Fig. 7A–H).

Head. In frontal view, semicircular, slightly higher than wide, with eyes not laterally protruding; all three ocelli circular and almost at same level of eyes dorsal margin – median ocellus slightly lower. Antennal pits located near mid-level of eyes. Clypeus dorsal portion notably separated from ventral portion by clypeal suture. Ventral portion conspicuously constricted laterally, almost half as wide as dorsal portion, with median white stripe and transverse dark line on sides. Labrum circular, with pair of incomplete transverse mediolateral sutures. First two segments of maxillary palpi subequal in length; third and fourth each as long as first and second together; fifth longer than any other segment, with ventral margin slightly arched, dorsal margin straight, and apex rounded. Distal portion of each maxillary palpomere whitish (Fig. 6G). In lateral view, head notably convex, but frons not tumescent; eyes ovoid, and higher than wide (Fig. 6D). In dorsal view, eyes protruding, with trapezoid and apically truncated fastigium (Fig. 6B). Scapus wide, almost as wide as half of fastigium.

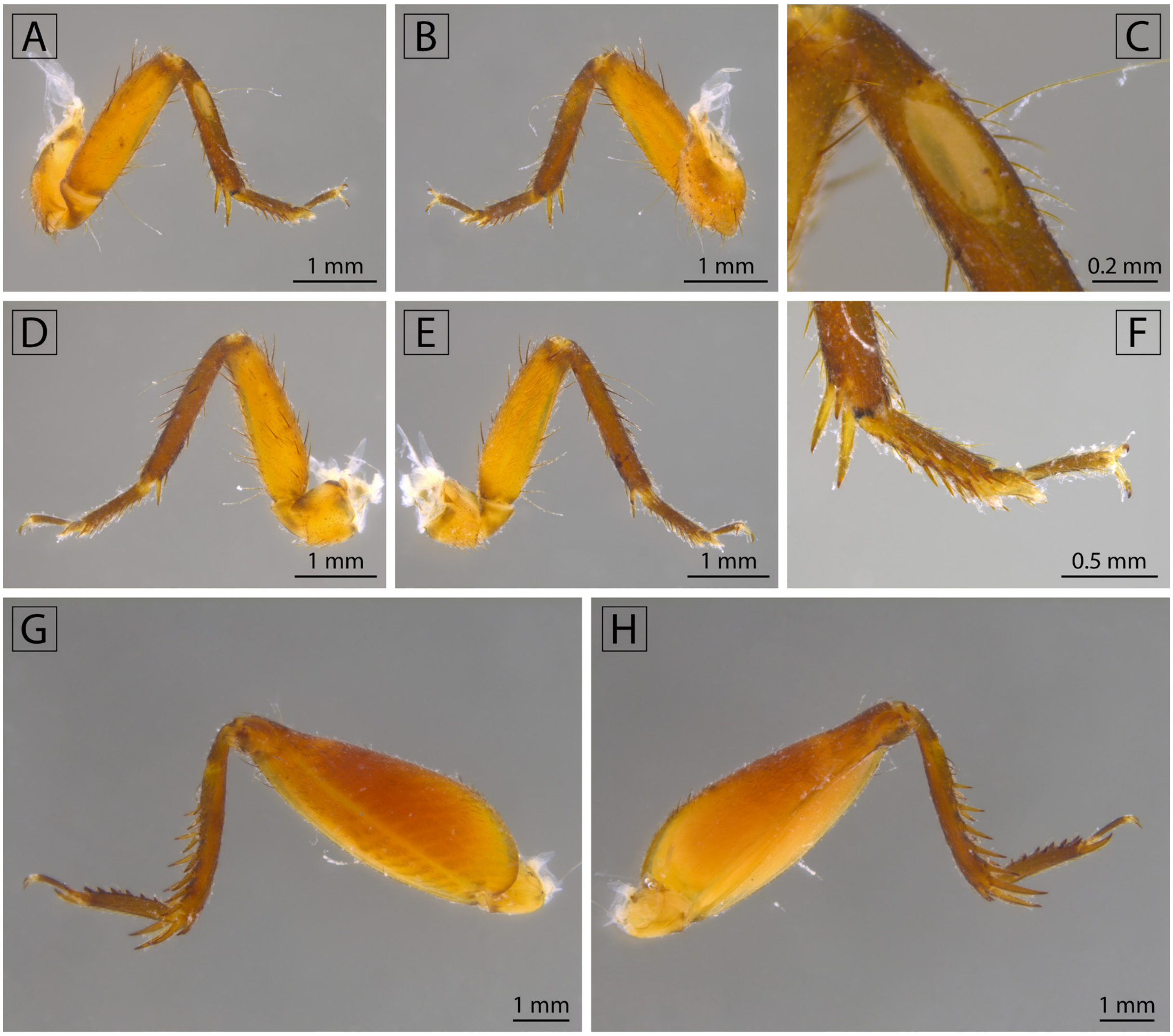

Fig. 7. *Zebragryllus mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov., holotype, ♂ (MPEG. HEX 05050458), legs. **A–B**. Fore leg. **A**. Outer view. **B**. Inner view. **C**. Tympanum, in detail. **D–E**. Mid leg. **D**. Outer view. **E**. Inner view. **F**. First tarsus, in detail. **G–H**. Hind leg. **G**. Outer view. **H**. Inner view.

THORAX. Pronotum wider than long, bearing bristles on margins and posterior area of lateral lobes, with both anterior and posterior dorsal margins slightly concave. Lateral lobes almost squared, with anterior and posterior margins straight and ventral margin obliquely straight. Prosternum reduced, triangular, and continuous with conjoint cervical sclerites. Mesosternum sub-squared, with posterior margin slightly bilobed. Metasternum hexagonal, with postero-lateral margins convex and posterior margin straight (Fig. 6F).

LEGS. All femora covered by fine pubescence and some longer bristles (Fig. 7A–B, D–E, G–H). Fore and mid tibia with two apical spurs on outer side (Fig. 7A, D) and one on inner side (Fig. 7B, E).

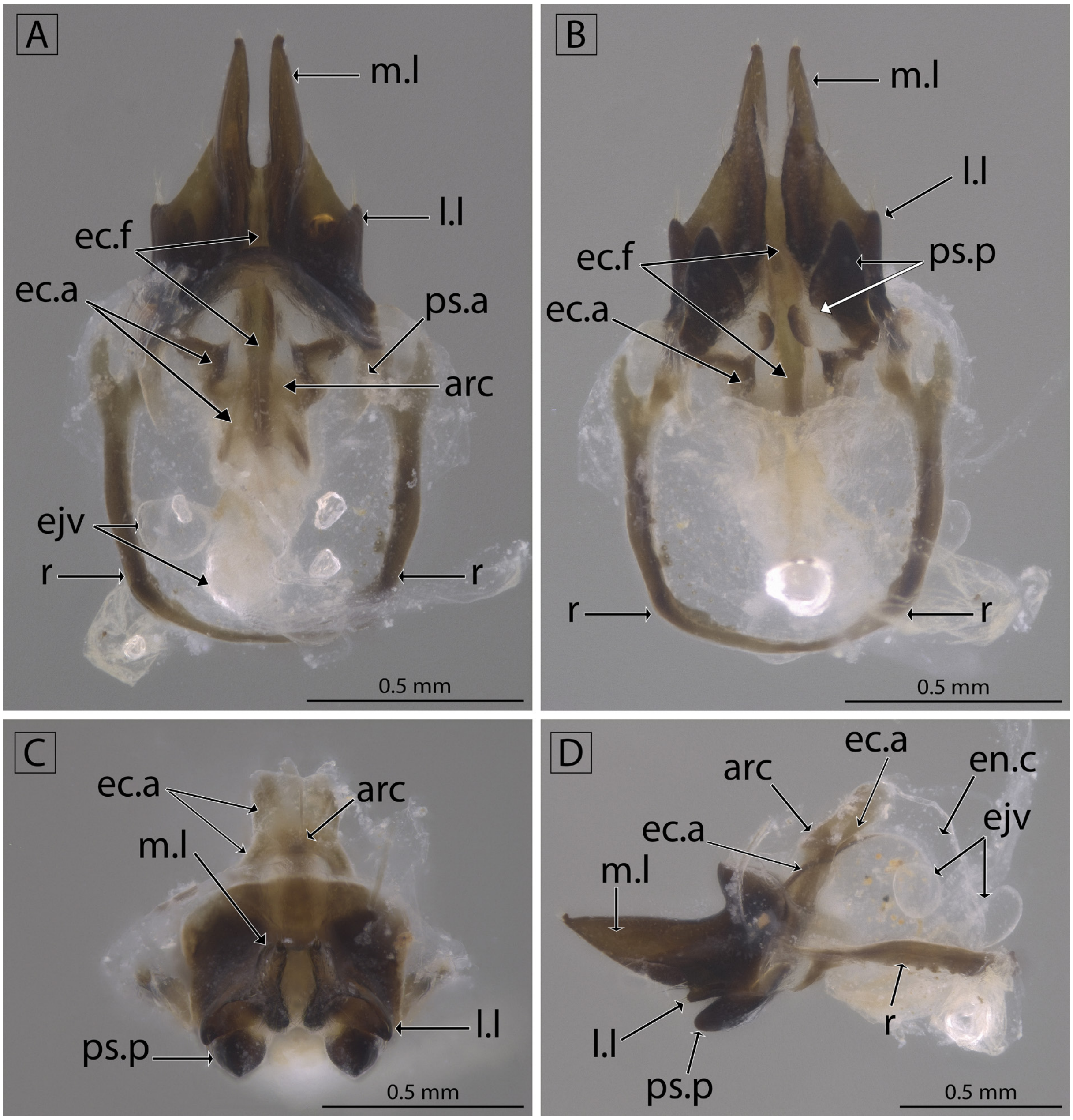

Fig. 8. *Zebragryllus mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov., holotype, ♂ (MPEG. HEX 05050458), phallic complex. **A**. Dorsal view. **B**. Ventral view. **C**. Axial view. **D**. Lateral view. Abbreviations: see Material and methods.

Tympana large, opened on fore tibia outer surface (Fig. 7A, C). Hind tibia with six outer and five inner dorsal spurs, and three apical spurs on each side (Fig. 7G–H); externally, dorsal and ventral apical spurs equal in size, and mid one twice longer; internally, dorsal and mid spurs equal in size, and ventral one at least three times smaller (Fig. 7G–H). Fore and mid basitarsi covered by strong setae on ventral side (Fig. 7A–B, D–F). Hind basitarsi ventrally with setae, dorsally with two rows of spines, and apically with two spurs, outer one smaller (Fig. 7G–H).

WINGS. Tegmina reaching up to fourth abdominal tergite, with stridulatory apparatus present; harp divided by two transverse veins; mirror short, divided into two longitudinal cells; apical field reticulated (Fig. 6E); angle of mirror formed almost at middle of harp posterior vein (Fig. 6E, arrow). Hind wings absent.

Fig. 9. *Zebragryllus mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov., ♀, immature (MPEG.HEX 05050459). **A**. Lateral view. **B**. Dorsal view.

ABDOMEN. Cylindrical, covered with fine bristles. Male supra-anal plate subtriangular (Fig. 6H). In ventral view, subgenital plate slightly longer than wide, with widely bilobed posterior margin (Fig. 6J); in lateral view, with rounded posterior margin (Fig. 6I).

GENITALIA. Pseudepiphallic median lophi conspicuously elongated, notably produced hind- and upwards, very robust, apically acute (Fig. 8A–B, D), and ventrally with rounded keel (Fig. 8C). Pseudepiphallic lateral lophi short, with apical bristles (Fig. 8D). Pseudepiphallic parameres not surpassing lateral lophi; in ventral view, subtriangular, robust (Fig. 8B, black arrow), and with oblique hyaline area basally (Fig. 8B, white arrow). Pseudepiphallic apodeme acute and incurved (Fig. 8D). Ectophallic fold large, greatly surpassing pseudepiphallic lateral lophi (Fig. 8B). Ectophallic apodemes large and twisted, forming large dorsal plate with ectophallic arc (Fig. 8A). Rami basally bifid and notably arched along its length, contiguous (Fig. 8A–B).

MEASUREMENTS (mm). ♂, holotype: TL: 11.0; LP: 2.0; WP: 2.5; Tg: 4.5; HF: 6.0; HT: 3.5.

Female

Unknown.

Nymph female

The coloration is very similar to the adult male but lighter (Fig. 9A–B).

Remarks

This species also has quite unique male genitalia, with very long pseudepiphallic median lophi. The only known species with elongated pseudepiphallic median lophi are *Z. nauta* and *Z. aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., but *Z. mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov. has the most extended and most robust pseudepiphallic median lophi of all species of *Zebragryllus*.

The locality where the species was collected is in a transition zone between two large biomes, the Cerrado-Amazonia transition, considered the world's largest ecotone (Torello-Raventos *et al.* 2013; Marques *et al.* 2020) (Fig. 16A–C). Marked seasonality and highly dynamic vegetation, comprising a mosaic of Cerrado, Amazon rainforest, and ecotonal forest vegetations, with high tree mortality and turnover levels, characterize this zone (Marimon *et al.* 2014; Morandi *et al.* 2015; Passos *et al.* 2018; Marques *et al.* 2020).

Zebragryllus sp. 1
Figs 10–11

Diagnosis

This female is similar to that of *Z. wittoto*, *Z. guianensis*, and *Z. nouragi* by the 'zebra' pattern on the hind legs (Figs 10A–B, 11J–K). The fore and mid legs have only a few whitish areas on the base of the femora and dorsal surface of the tibia (Fig. 11E–F, H–I). The tympanum is widely open on the outer face proximal portion of the fore tibia (Fig. 11E, G). However, it differs from the species mentioned above in the longer tegmina, reaching up to the second abdominal tergite (Fig. 10C–D), which is more similar to *Z. nauta.* The first two segments of maxillary palpi are small and subequal in length; the third and fourth are as long as the first and second together; the fifth is longer than any other segment, with the ventral margin slightly arched and the medio-distal portion obliquely truncated, dorsal margin straight and the apex rounded. The only whitish area of the maxillary palpi is the ventral surface of the medio-distal portion; the remaining is dark (Fig. 11D). The abdomen is mostly black but has whitish bands on the anterior and posterior margins of each tergite (Fig. 10A–B). The supra-anal plate is subtriangular, with a distal margin rounded (Fig. 10E). The subgenital plate is similar to that of *Z. nouragi*, with the posterior margin sinuous in lateral view and concave in ventral view (Fig. 10F–G). The ovipositor is straight and very short, shorter than the hind tibia, with a triangular apex (Fig. 10A–B, 10H–I), similar to *Z. guianensis*. The copulatory papilla is quite unique, with an ovoid shape, laterally sinuous, and a more membranous dorsal portion (Fig. 11A–B).

Material examined

BRAZIL • 1 ♀; Pará, Conceição do Araguaia, Área 2; 7°55′31.7″ S, 49°24′11.5″ W; 9–12 Sep. 2022; E.B. Feiras and R.P.S. Almeida leg; Pitfall epigéico [epigeic pitfall]; MPEG.HEX 05050460.

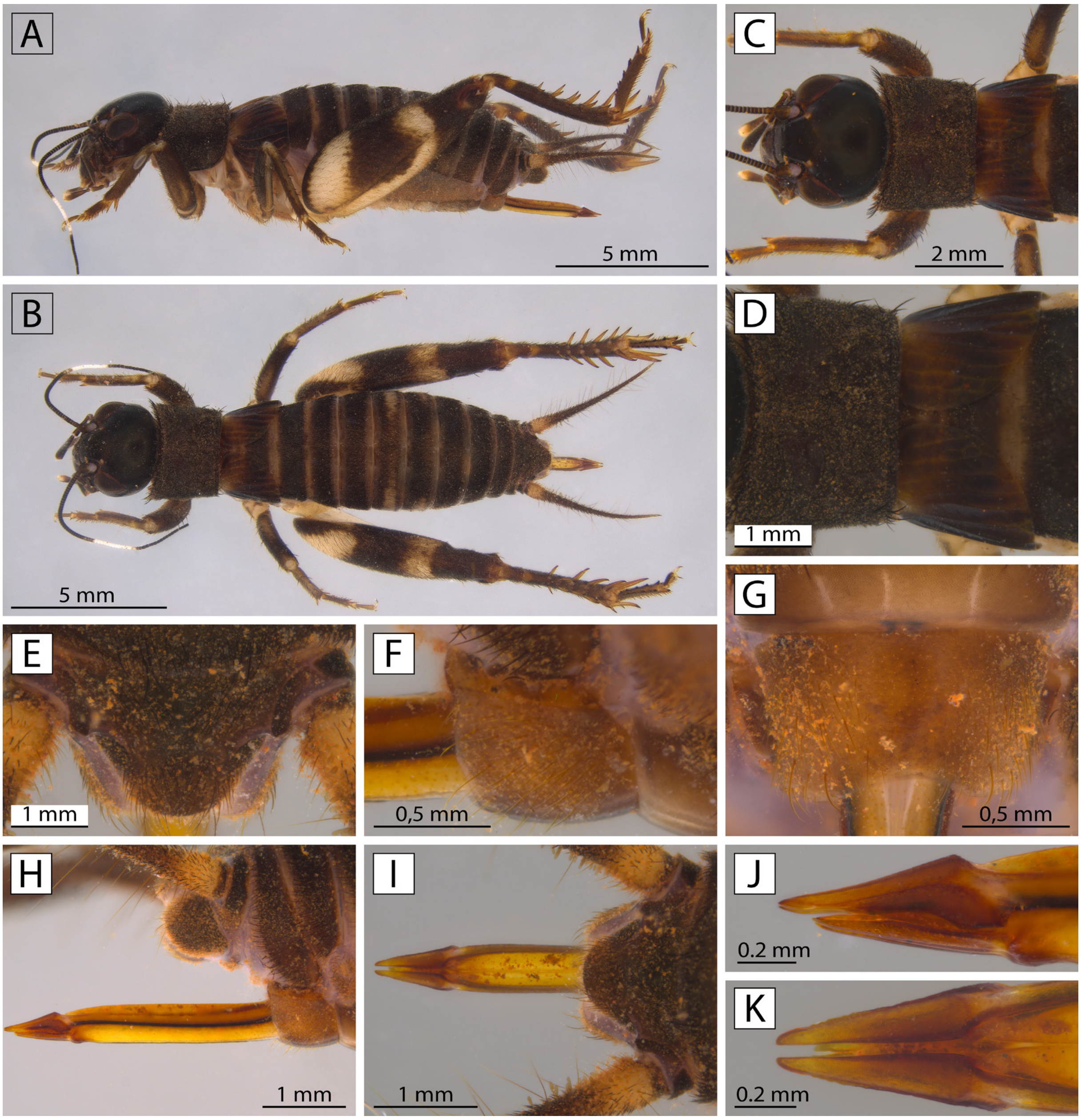

Fig. 10. *Zebragyllus* sp. 1, ♀ (MPEG.HEX 05050460). **A–B**. Habitus. **A**. Lateral view. **B**. Dorsal view. **C**. Head and thorax in dorsal view. **D**. Tegmina. **E**. Supra-anal plate. **F–G**. Subgenital plate. **F**. Lateral view. **G**. Ventral view. **H–I**. Ovipositor. **H**. Lateral view. **I**. Dorsal view. **J–K**. Detail of ovipositor apex. **J**. Lateral view. **K**. Dorsal view.

Description

Measurements (mm). ♀. TL: 15.0; LP: 2.0; WP: 3.0; Tg: 2.0; HF: 8.0; HT: 4.5; Ov: 3.5.

Zebragryllus sp. 2
Figs 12–13

Diagnosis

This female is very similar to that of *Z. aphonus* Tavares, Oya & Cadena-Castañeda sp. nov. in the body shape (Fig. 12A–B). Still, it is quickly differentiated in the legs darker chromatic pattern (Figs 12A–B, 13E–H). This species does not have the genus characteristic 'zebra' pattern on the hind legs or

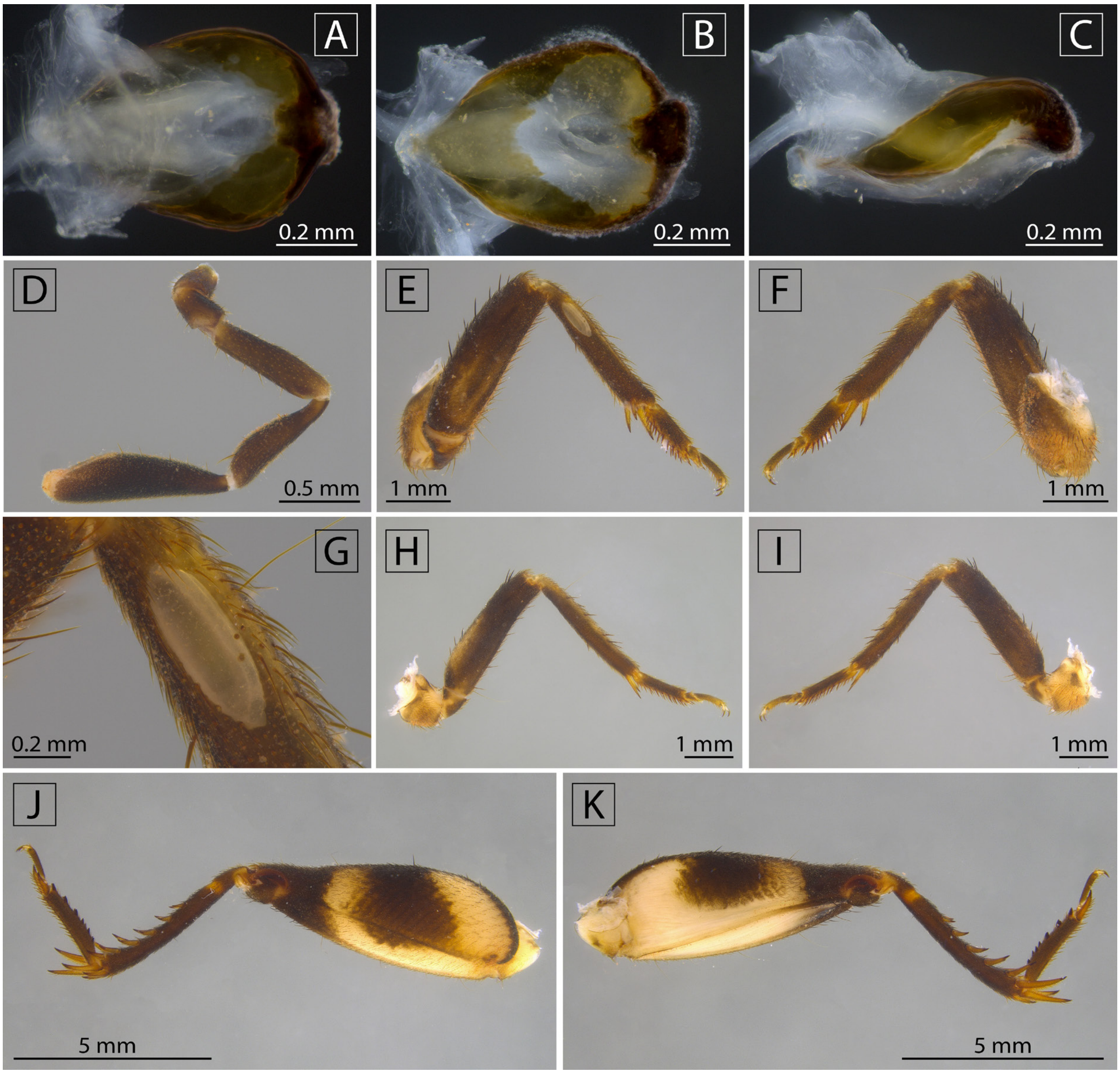

Fig. 11. *Zebragryllus* sp. 1, ♀ (MPEG.HEX 05050460). **A**–**C**. Copulatory papilla. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view. **D**. Maxillary palpus, outer view. **E**–**F**. Fore leg. **E**. Outer view. **F**. Inner view. **G**. Tympanum, in detail. **H**–**I**. Mid leg. **H**. Outer view. **I**. Inner view. **J**–**K**. Hind leg. **J**.Outer view. **K**. Inner view.

abdomen either (Figs 12A–B, 13E–H). Other differences easily noted are the longer tegmina (Fig. 12A–D), the large tympana on the outer faces of the fore tibia (Fig. 13E, in detail), and the tiny tympana on the inner face (Fig. 13F, in detail). The fore and hind (mid legs lost) legs have no whitish areas (Fig. 13E–F). The maxillary palpi are similar to the species described above but differ by the slightly concave fifth segment's dorsal surface and the slightly longer truncated-medio-distal portion (Fig. 13D). The abdominal tergites are dark brown, with no whitish areas (Fig. 12A–B). The supra-anal plate is

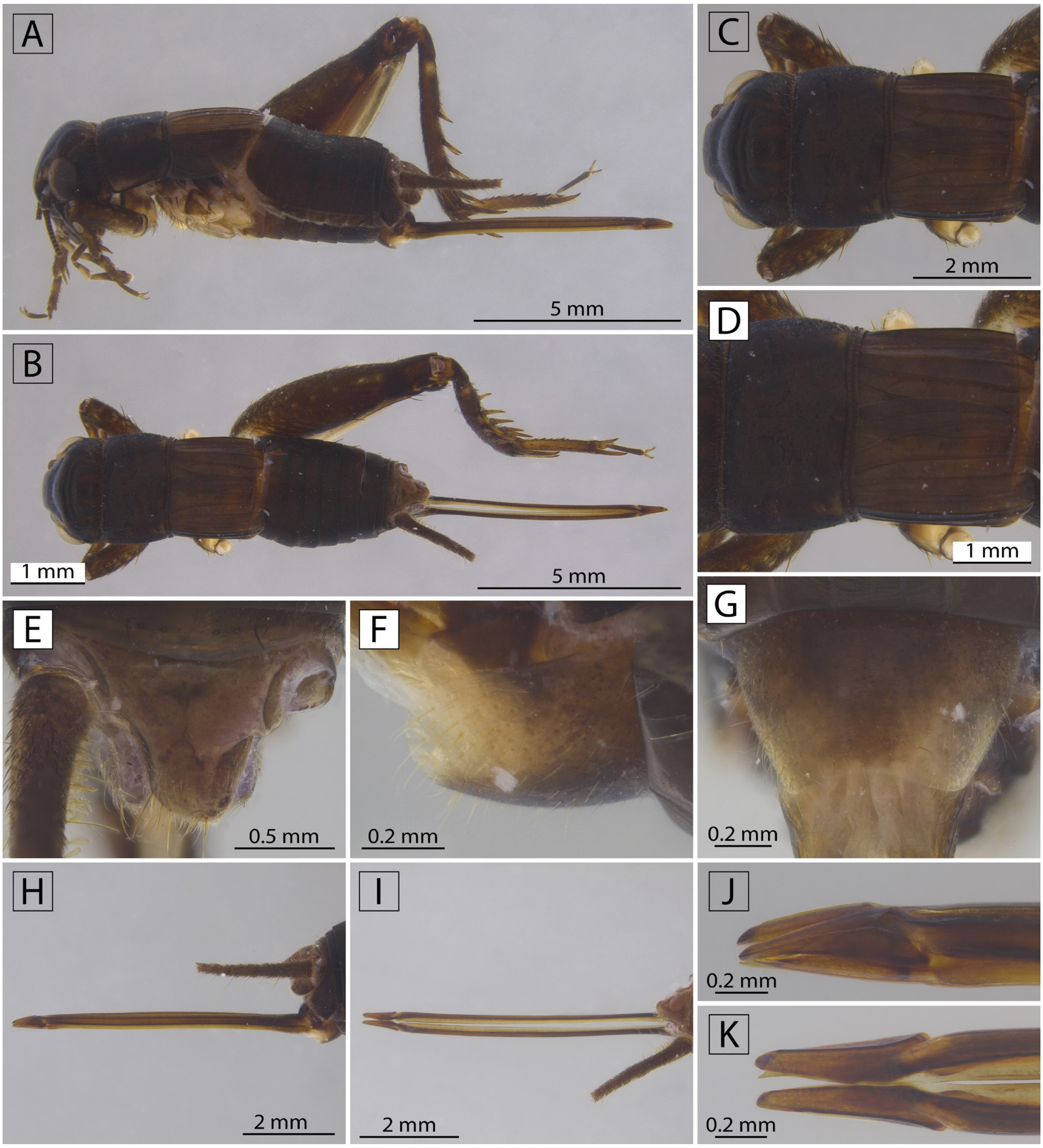

Fig. 12. *Zebragryllus* sp. 2, ♀ (MPEG.HEX 05050476). **A**–**B**. Habitus. **A**. Lateral view. **B**. Dorsal view. **C**. Head and thorax in dorsal view. **D**. Tegmina. **E**. Supra-anal plate. **F**–**G**. Subgenital plate. **F**. Lateral view. **G**. Ventral view. **H**–**I**. Ovipositor. **H**. Lateral view. **I**. Dorsal view. **J**–**K**. Detail of ovipositor apex. **J**. Lateral view. **K**. Dorsal view.

subtriangular, with a distal margin rounded, somewhat longer and wider than in *Z. aphonus* Tavares, Oya & Cadena-Castañeda sp. nov. (Fig. 12E). The subgenital plate is similar to that of the female from Cayenne in Desutter-Grandcolas *et al.* (2014) (see Desutter-Grandcolas *et al.* 2014, Fig. 6Q–R), with the distal margin convex in lateral view and concave in ventral view (Fig. 12F–G). The ovipositor is also similar to that of *Z. aphonus* Tavares, Oya & Cadena-Castañeda sp. nov. but darker (Fig. 12H–I), and almost straight, with a triangular apex bearing scale-like texture on the dorsal surface (Fig. 12J–K). The dorsal valves dorsally sulcated (Fig. 12H–I). The copulatory papilla is also similar to the female from Cayenne in Desutter-Grandcolas *et al.* (2014) (see Desutter-Grandcolas *et al.* 2014: Fig. b'–d') but is more cylindrical and not dorsoventrally flat, like in most species of the genus (Fig. 13A–C).

Material examined

BRAZIL • 1 ♀; Tocantins, Araguatins, Fazenda Estiva; 7°55′31.7″ S, 49°24′11.5″ W; 27 Mar. 2022; pitfall; MPEG.HEX 05050476.

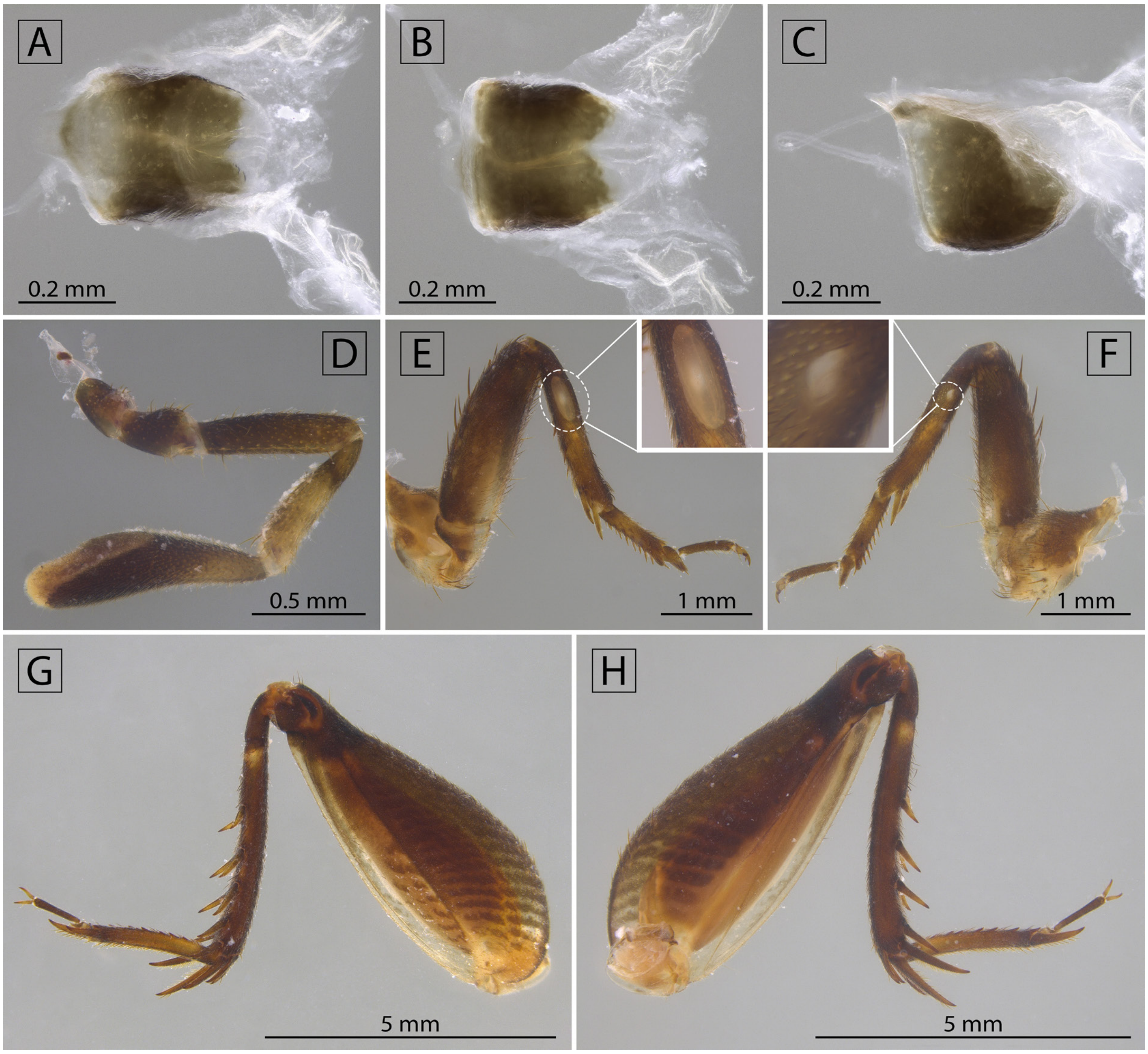

Fig. 13. *Zebragryllus* sp. 2, ♀ (MPEG.HEX 05050476). **A–C**. Copulatory papilla. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view. **D**. Maxillary palpus, outer view. **E–F**. Fore leg, tympanal aperture, in detail. **E**. Outer view. **F**. Inner view. **G–H**. Hind leg. **G**. Outer view. **H**. Inner view.

Description

Measurements (mm). ♀. TL: 9.5; LP: 1.5; WP: 2.7; Tg: 2.3; HF: 6.5; HT: 4.8; Ov: 6.5.

New records

This is the first time that *Zebragyllus* has been recorded in Brazil. Two new species are being added to the genus, and two known species are recorded: *Z. guianensis* (Figs 14A–H, 16A) and *Z. nouragui* (Figs 15A–H, 16A). These two species were only known from their type locality, in French Guiana, where they live in sympatry, and here we extend their distribution (Fig. 16A). Five males and five females of *Z. guianensis* were collected in the Floresta Nacional de Caxiuanã, municipality of Melgaço, Pará State. Two males, two adult females, and one juvenil specimens of *Z. nouragui* were collected in Juruti, Pará State. It is plausible that these species occur in Brazil as these two localities are in Northern Pará State, near the boundary between Brazil and French Guiana, but on the other side of the great Amazon River. Floresta Nacional de Caxiuanã is about 630 km south of the Réserve Naturelle Nationale des Nourages (type locality), and Juruti is about 770 km southwest (Fig. 16A). The other species of *Zebragryllus* are only recorded in Peru and Colombia. So we expect these known species and new ones to also occur in Brazil as their distribution is unexplored.

The males of *Z. nouragui* studied here have a different chromatic pattern of the hind femora, a variation of the populations described by Desutter-Grandcolas *et al.* (2014). The paired whitish oblique bands described for the species, like those seen in the female hind femora (Fig. 15C), are absent, and only the ventral whitish band is displayed (Fig. 15A).

Species of *Zebragryllus* may occur in very low populations since just a few specimens were collected, even in considerable collection efforts, like in Floresta Nacional de Caxiuanã. This site was monitored for two years, with monthly armed pitfall traps in a 2-acre area. The area was divided into several parcels of 1 m², each with a pitfall trap installed in the center. Even so, only ten specimens of *Z. guianensis* were captured.

Zebragryllus guianensis Desutter-Grandcolas, 2014

Figs 14, 16A

Material examined

BRAZIL • 4 ♂♂, 2 ♀♀; Pará, Melgaço, FLONA Caxiuanã, ECFPn-ESECAFLOR; 1°43′35″ S, 51°26′36″ W; Mar. 2012; D.A. Cunha leg; MPEG.HEX 05050461, MPEG.HEX 05050462, MPEG.HEX 05050463, MPEG.HEX 05050464, MPEG.HEX 05050465, MPEG.HEX 05050466 • 1 ♂; same collection data as for preceding; Apr. 2012; MPEG.HEX 05050467 • 2 ♀♀; same collection data as for preceding; May. 2012; MPEG.HEX 05050468 to 05050469 • 1 ♀; same collection data as for preceding; Feb. 2012; MPEG.HEX 05050470.

Zebragryllus nouragui Desutter-Grandcolas, 2014

Figs 15, 16A

Material examined

BRAZIL • 2 ♂♂, 1 ♀; Pará, Juruti, Barroso; 2°27′41.7″ S, 56°00′11.6″ W; 8–15 Aug. 2006; D.F. Candiani and N.F. Lo-Man-Hung leg.; pitfall; MPEG.HEX 05050471, MPEG.HEX 05050472, MPEG.HEX 05050473 • 1 ♀; same collection data as for preceding; Mutum, 2°36′45.7″ S, 56°11′38.2″ W; 14–18 Dec. 2012; pitfall; MPEG.HEX 05050474 • 1 ♀, immature; same collection data as for preceding; MPEG.HEX 05050475.

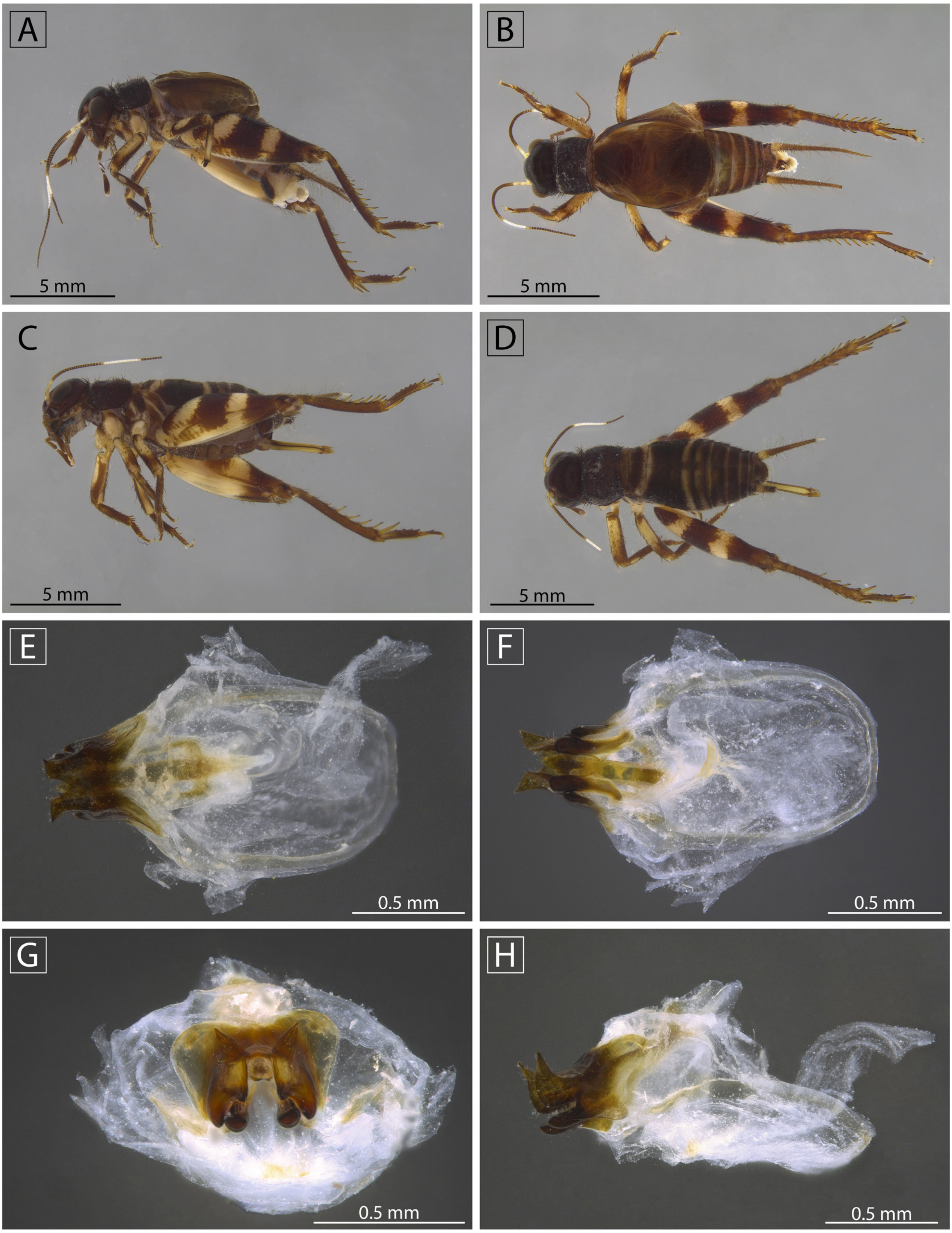

Fig. 14. *Zebragryllus guianensis* Desutter-Grandcolas, 2014 . **A–B**. ♂ (MPEG.HEX 05050467), habitus. **A**. Lateral view. **B**. Dorsal view. C–D. ♀ (MPEG.HEX 05050469), habitus. **C**. Lateral view. **D**. Dorsal view. **E–H**. ♂ (MPEG.HEX 05050461), phallic complex. **E**. Dorsal view. **F**. Ventral view. **G**. Axial view. **H**. Lateral view.

Discussion

The genus *Zebragryllus* and a potential move towards a cave-dwelling lifestyle

Although cave orthopterans were initially a neglected fauna, some caves can host a diverse and endemic fauna of Orthoptera Olivier, 1789 and other taxa (Howarth 1972) and the observation of morphological regressive adaptations (troglomorphism) in their species stands out (Vandel 1965; Deharveng & Bedos 2018; Taylor 2019). These adaptations involve the presence of isolated or combined characteristics, such as eye reduction, loss of pigmentation, significant decrease in body size, wing reduction, and loss of tympanum compared to other species inhabiting surface environments (Vandel 1965; Desutter-Grandcolas *et al.* 1998; Di Russo & Sbordoni 1998; Deharveng & Bedos 2018). On the other hand, an increase in certain characteristics can also be observed, such as the elongation of appendages (legs and antennae) (Vandel 1965; Deharveng & Bedos 2018), the elongation of wings (Campos *et al.* 2023), and even an increase in body size (Vandel 1965; Carvalho *et al.* 2023). Additionally, it is important to emphasize that troglomorphism is not always related to troglobitic lifestyles (whether regressive or progressive), and the general theory of troglomorphism can lead to misguided interpretations of certain characters if not properly tested (see Desutter-Grandcolas 1997). The adaptations related to a cave-dwelling life need to be individually investigated (Desutter-Grandcolas 1997; Deharveng & Bedos 2018) once they may present different patterns depending on the biological entity being investigated, and natural selection, sexual selection, and/or genetic drift may potentially generate distinct patterns of morphological adaptations within the same group.

The presence of pre-adaptations in surface ancestors would be a first step towards colonizing cave environments, as demonstrated by Desutter-Grandcolas in a series of studies using Phalangopsidae as a model (see Desutter-Grandcolas *et al.* 1998). In this sense, an 'erroneous' analysis could consider as troglomorphic those characteristics that are actually pre-adaptations already present in surface ancestors. So, an investigation based on a phylogenetic context becomes a methodological requirement when the study focuses on crickets that have colonized caves (Desutter-Grandcolas 1997).

In the case of *Zebragryllus aphonus* Tavares, Oya & Cadena-Castañeda sp. nov., due to its discovery being based solely on collections in caves and upon observing for the first time the absence of a stridulatory apparatus, wing reduction, and different levels of tympanum development in this species, we may hypothesize, at least, two potential scenarios to be tested in the future: i) these characteristics represent adaptations selected in relation to the subterranean lifestyle of ferruginous cave-dwelling and a network of small channels (see Carmo & Kamino 2015; Ferreira *et al.* 2018); or ii) they are pre-adaptations selected related to a lifestyle in compact environments, such as leaf litter, tree cracks, and rocks. However, we still lack sufficient evidence, and the caves where this species was found are not extensively developed, often less than 10 meters in length. Thus, only evolutionary studies and descriptions of yet-unknown species within this genus will provide a better understanding of these findings and validate some of these hypotheses.

Minimum Convex Polygons for the genus *Zebragryllus* and distribution

Due to many locations in the Amazon Rainforest not having been inventoried or accurately studied from the taxonomic perspective of the genus *Zebragryllus*, there are still significant gaps in our taxonomic knowledge and geographic distribution of its species. To address this situation, we used the Minimum Convex Polygons map, which allowed us to identify these little-studied areas for the entire genus in a practical manner (Fig. 17).

Once all the known species records are placed in the Amazon rainforest or in transition zones between Amazon and Cerrado (Fig. 16), the polygon traced a probable distribution restricted to this biome, at most on the boundaries of the transition zones (Fig. 17). However, the known records undeniably

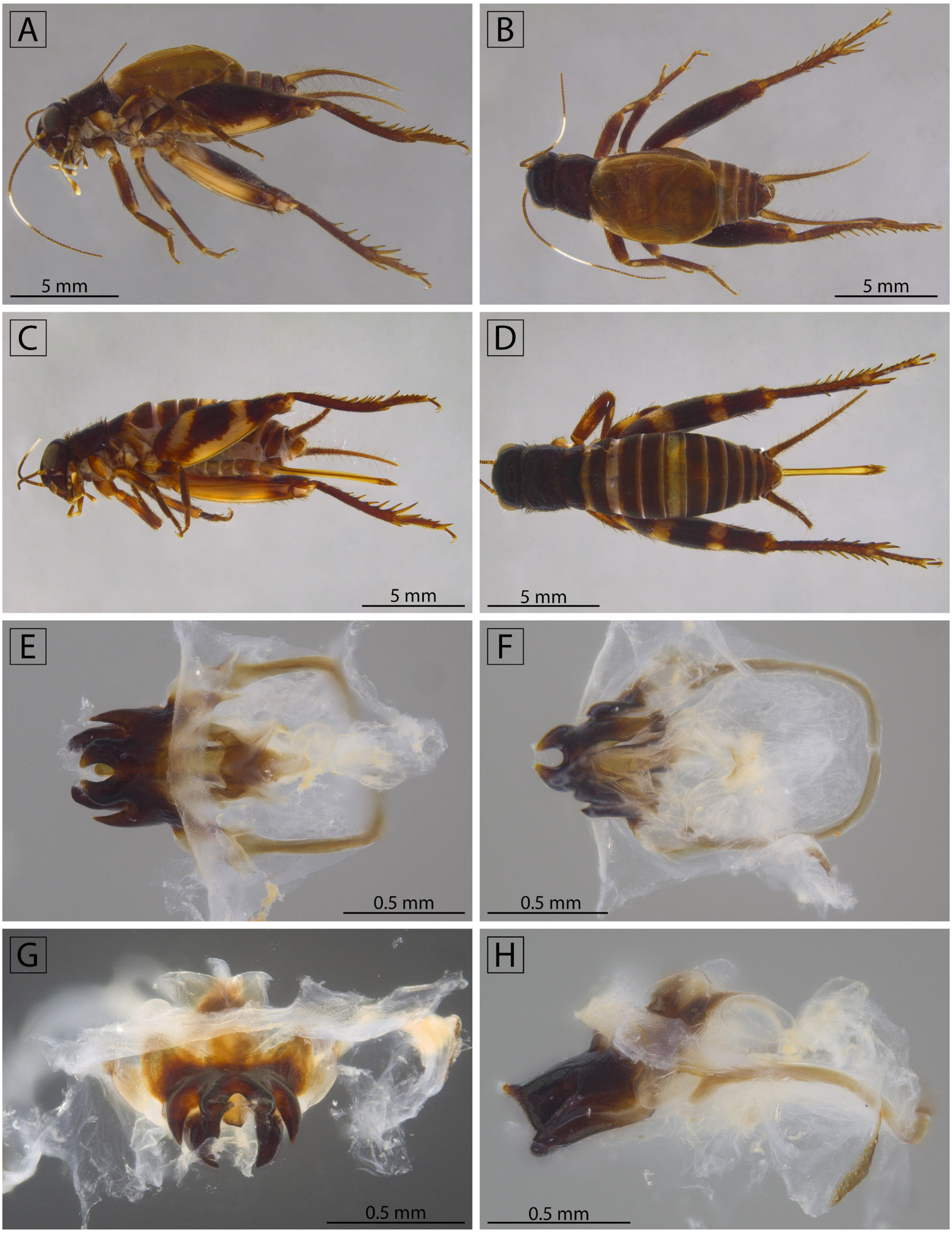

Fig. 15. *Zebragryllus nouragui* Desutter-Grandcolas, 2014. **A**–**B**. ♂ (MPEG.HEX 05050471), habitus. **A**. Lateral view. **B**. Dorsal view. **C**–**D**. ♀ (MPEG.HEX 05050473), habitus. **C**. Lateral view. **D**. Dorsal view. **E**–**H**. ♂ (MPEG.HEX 05050472), phallic complex. **E**. Dorsal view. **F**. Ventral view. **G**. Axial view. **H**. Lateral view.

reveal species from Oriental Amazonia and Occidental Amazonia. The two sets of points are too distant, and an enormous knowledge gap extends in the middle, a Wallacean shortfall (see Hortal *et al.* 2015). Obviously, more collection efforts are needed to address this issue, and other new species will probably be discovered.

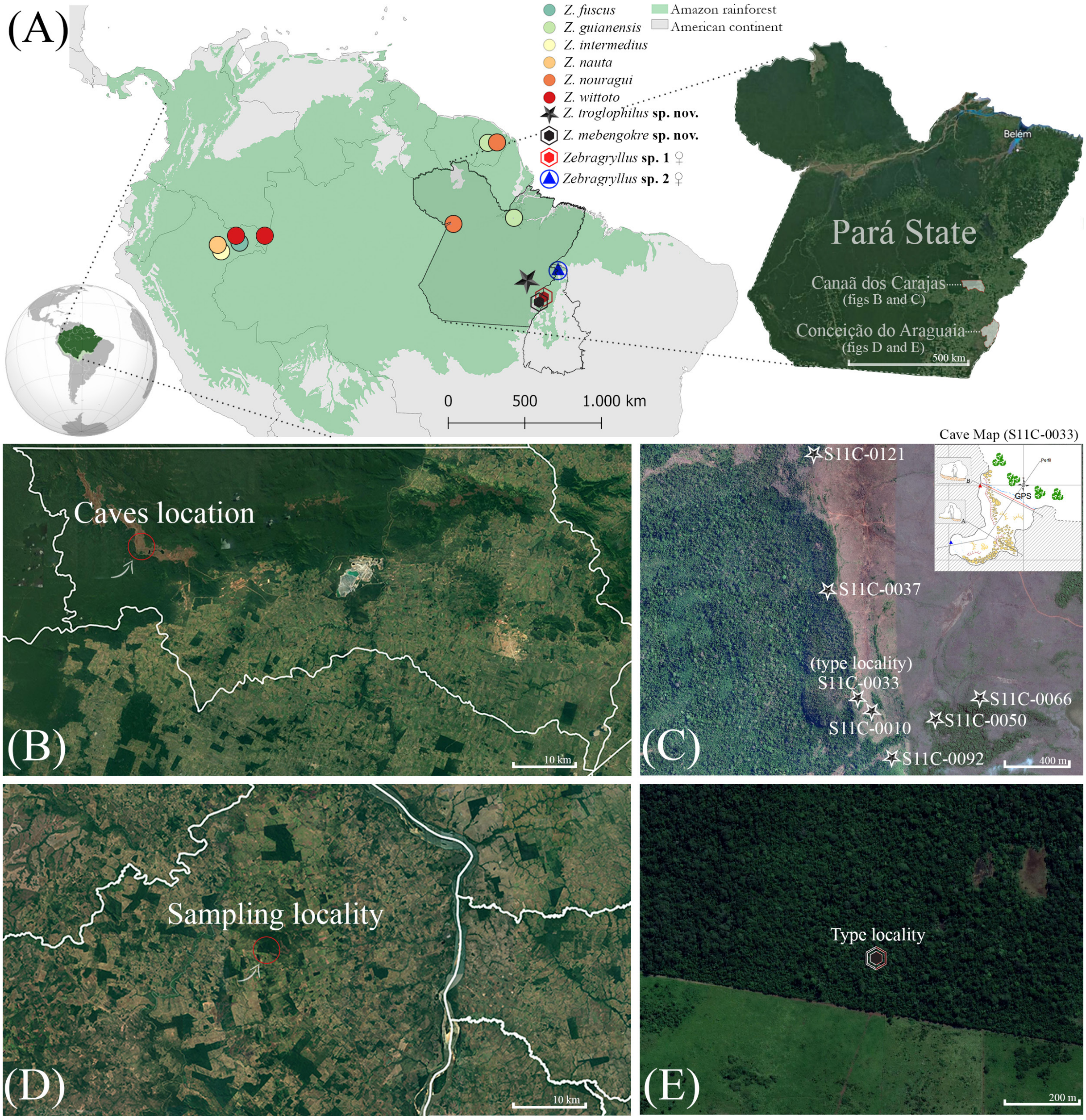

Fig. 16. Distribution of species of *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014. **A**. In the Amazon rainforest of South America, with emphasis on the states of Pará and Tocantins, and the two municipalities that serve as new type localities. **B–C**. Limits of the Canaã dos Carajás municipality with a highlight on the region where seven caves are located, inhabited by *Z. aphonus* Tavares, Oya & Cadena-Castañeda sp. nov. **D–E**. Limits of the Conceição do Araguaia municipality with a highlight on the sampling site where *Z. mebengokre* Tavares, Oya & Cadena-Castañeda sp. nov. was found.

Acknowledgments

We want to thank the companies DBO Engenharia e Horizonte Minerals and BioEspeleo Consultoria Ambiental Ltda, the Museu Paraense Emílio Goeldi, and the dear friends Heitor Antunes and Dr Rony Peterson Santos Almeida for ceding the material studied here. G.C. Tavares and O.J. Cadena-Castañeda would like to thank the Orthopterists' Society for the financial support provided by the OSF Grants, which allowed the purchase of equipment that significantly improved the quality of this work. This work was financed in part by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação Amazônia de Amparo a Estudos e Pesquisas (FAPESPA) (processes CNPq 421693/2022-3 and FAPESPA 2023/157870).

References

Cadena-Castañeda O.J., Rodríguez M.C.V., Gonzalez G.R.D. & López V.H.G. 2021. Studies on Neotropical crickets: A new Anurogryllina genus (Orthoptera: Gryllidae: Gryllinae). *Zootaxa* 4985 (3): 371–380. https://doi.org/10.11646/zootaxa.4985.3.4

Campos L.D. de, Bolfarini M.P., Suemitsu M.M., Borghezan L.M.C. & Souza-Dias P.G.B. 2023. Living in the darkness: a new cave cricket species of the genus *Endecous* Saussure (Orthoptera, Grylloidea, Phalangopsidae) from Serra da Bodoquena in Mato Grosso do Sul state, Brazil. *Zootaxa* 5285 (2): 325–336. https://doi.org/10.11646/zootaxa.5285.2.6

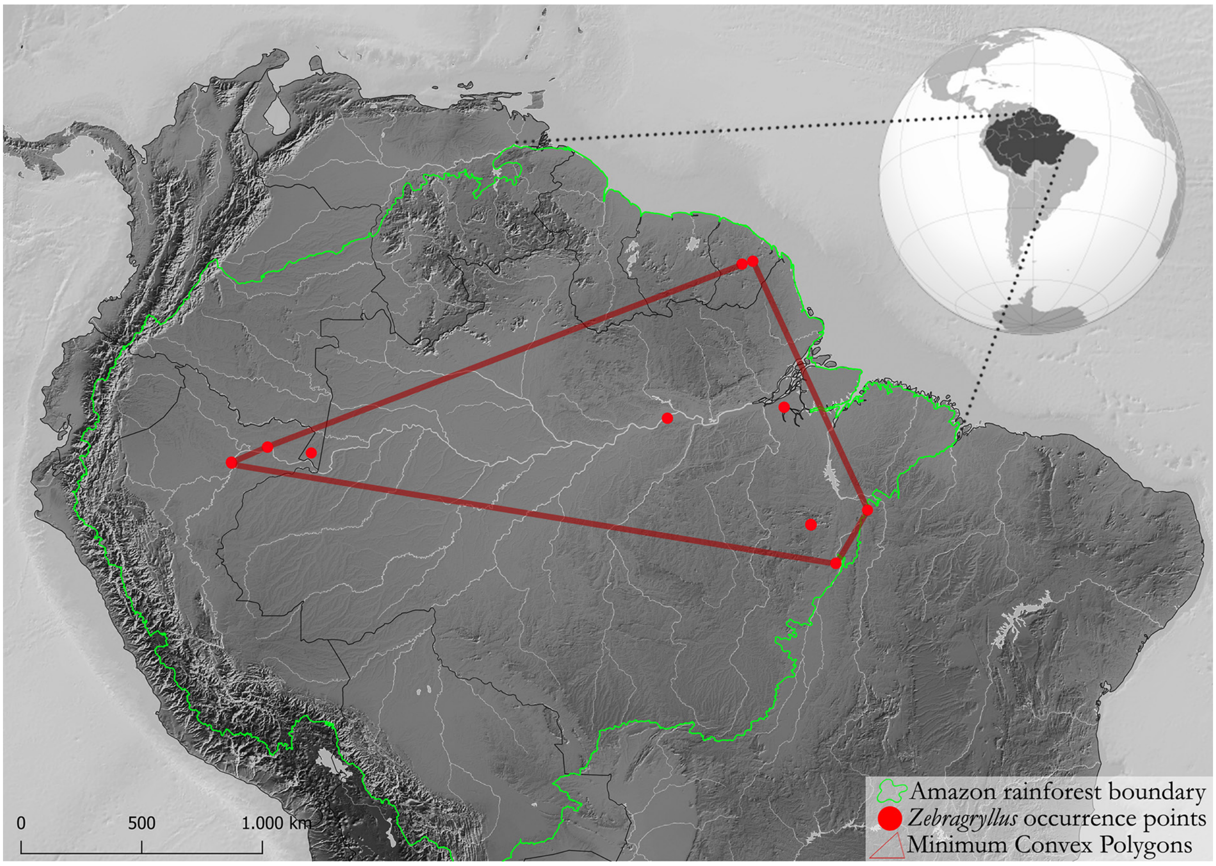

Fig. 17. Potential distribution of the genus *Zebragryllus* Desutter-Grandcolas & Cadena-Castañeda, 2014, using the Minimum Convex Polygons (MCPs).

Carmo F.F. do & Kamino L.H.Y. 2015. *Geossistemas Ferruginosos do Brasil: Áreas Prioritárias Para Conservação da Diversidade Geológica e Biológica, Patrimônio Cultural e Serviços Ambientais*. Belo Horizonte, Brazil.

Carvalho P.H.M., Junta V.G.P., Castro-Souza R.A. & Ferreira R.L. 2023. Three new cricket species and a new subgenus of *Endecous* Saussure, 1878 (Grylloidea: Phalangopsidae) from caves in northeastern Brazil. *Zootaxa* 5263 (1): 1–39. https://doi.org/10.11646/zootaxa.5263.1.1

Cigliano M.M., Braun H., Eades D.C. & Otte D. 2023. Orthoptera species file. Available from http://orthoptera.speciesfile.org [accessed 23 Oct. 2023].

Deharveng L. & Bedos A. 2018. Diversity of terrestrial invertebrates in subterranean habitats. *In*: Moldovan O.T., Kováč Ľ. & Halse S. (eds) *Cave Ecology*: 107–172. Springer, Cham.

Desutter-Grandcolas L. 1997. Are troglobitic taxa troglobiomorphic? A test using phylogenetic inference. *International Journal of Speleology* 26 (1/2): 1–19. https://doi.org/10.5038/1827-806x.26.1.1

Desutter-Grandcolas L., Di Russo C. & Sbordoni V. 1998. II – faune souterraine II., 4 – Insecta, 56 – Ortóptera, B – Grylloidea. *In*: Juberthie C. & Decu V. (eds) *Encyclopaedia Biospeleologia*: 989–1001. Fabbro Saint-Girons.

Desutter-Grandcolas L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* 32 (6): 525–561. https://doi.org/10.1046/j.1463-6409.2003.00142.x

Desutter-Grandcolas L., Cadena-Castañeda O.J., Jaiswara R. & Anso J. 2014. *Zebragryllus* Desutter-Grandcolas & Cadena-Casteñada, n.gen. a new Gryllinae genus from Eastern and Western Amazonia, South America (Orthoptera, Grylloidea, Gryllidae). *Zootaxa* 3768 (1): 1–22. https://doi.org/10.11646/zootaxa.3768.1.1

Desutter-Grandcolas L., Jacquelin L., Hugel S., Boistel R., Garrouste R., Henrotay M., Warren B.H., Chintauan-Marquier I.C., Nel P., Grandcolas P. & Nel A. 2017. 3-D imaging reveals four extraordinary cases of convergent evolution of acoustic communication in crickets and allies (Insecta). *Scientific Reports* 7 (1): 7099. https://doi.org/10.1038/s41598-017-06840-6

Desutter L. 1987. Structure et évolution du complexe phallique des Gryllidea (Orthoptera) et classification des genres Nétropicaux de Grylloidea, Première Partie. *Annales de la Société entomologique de France* 23 (3): 213–239.

Ferreira R.L., de Oliveira M.P.A. & Silva M.S. 2018. Subterranean Biodiversity in Ferruginous Landscapes. *In*: Moldovan O.T., Kováč Ľ. & Halse S. (eds) *Cave Ecology*: 435–447. Springer, Cham.

Hortal J., de Bello F., Diniz-Filho J.A.F., Lewinsohn T.M., Lobo J.M. & Ladle R.J. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Howarth F.G. 1972. Cavernicoles in lava tubes on the Island of Hawaii. *Science* 175 (4019): 325–326. https://doi.org/10.1126/science.175.4019.325

IUCN 2021. Mapping standards and data quality for the IUCN Red Spatial Data. *Report* 19: 30.

Mace G.M., Collar N., Cooke J., Gaston K., Ginsberg J., Leader Williams N., Maunder M. & Milner-Gulland E.J. 1992. The development of new criteria for listing species on the IUCN Red List. *Species* 5 (1): 16–22.

Marimon B.S., Marimon-Junior B.H., Feldpausch T.R., Oliveira-Santos C., Mews H.A., Lopez-Gonzalez G., Lloyd J., Franczak D.D., de Oliveira E.A., Maracahipes L., Miguel A., Lenza E. & Phillips O.L.

2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. *Plant Ecology and Diversity* 7 (1–2): 281–292. https://doi.org/10.1080/17550874.2013.818072

Marques E.Q., Marimon-Junior B.H., Marimon B.S., Matricardi E.A.T., Mews H.A. & Colli G.R. 2020. Redefining the Cerrado–Amazonia transition: implications for conservation. *Biodiversity and Conservation* 29 (5): 1501–1517. https://doi.org/10.1007/s10531-019-01720-z

Morandi P.S., Marimon-Junior B.H., De Oliveira E.A., Reis S.M., Valadão M.B.X., Forsthofer M., Passos F.B. & Marimon B.S. 2015. Vegetation succession in the cerrado-amazonian forest transition zone of Mato Grosso state, Brazil. *Edinburgh Journal of Botany* 73 (1): 83–93. https://doi.org/10.1017/S096042861500027X

Passos F.B., Marimon B.S., Phillips O.L., Morandi P.S., das Neves E.C., Elias F., Reis S.M., de Oliveira B., Feldpausch T.R. & Marimon Júnior B.H. 2018. Savanna turning into forest: concerted vegetation change at the ecotone between the Amazon and "Cerrado" biomes. *Revista Brasileira de Botanica* 41 (3): 611–619. https://doi.org/10.1007/s40415-018-0470-z

QGIS.org 2023. Open Source Geographic Information System. Available from https://www.qgis.org/en/site/ [accessed 15 Jul. 2023].

Di Russo C. & Sbordoni V. 1998. II – faune souterraine II., 4 – Insecta, 56 – Ortóptera, A – Gryllacridoidea. *In*: Juberthie C. & Decu V. (eds) *Encyclopaedia Biospeologica*: 979–987. Fabbro Saint-Girons.

Taylor S.J. 2019. Orthoptera. *In*: White B., Culver D.C. & Pipan T. (eds) *Encyclopedia of Caves. Third Edition*: 779–783. Elsevier, The Netherlands.

Torello-Raventos M., Feldpausch T.R., Veenendaal E., Schrodt F., Saiz G., Domingues T.F., Djagbletey G., Ford A., Kemp J., Marimon B.S., Hur Marimon Junior B., Lenza E., Ratter J.A., Maracahipes L., Sasaki D., Sonké B., Zapfack L., Taedoumg H., Villarroel D., Schwarz M., Quesada C.A., Yoko Ishida F., Nardoto G.B., Affum-Baffoe K., Arroyo L., Bowman D.M.J.S., Compaore H., Davies K., Diallo A., Fyllas N.M., Gilpin M., Hien F., Johnson M., Killeen T.J., Metcalfe D., Miranda H.S., Steininger M., Thomson J., Sykora K., Mougin E., Hiernaux P., Bird M.I., Grace J., Lewis S.L., Phillips O.L. & Lloyd J. 2013. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. *Plant Ecology and Diversity* 6 (1): 101–137. https://doi.org/10.1080/17550874.2012.762812

Vandel A. 1965. *Biospeleology: The Biology of Cavernicolous Animals*. First Edition. Pergamon Press, Oxford.

Manuscript received: 7 December 2023
Manuscript accepted: 4 January 2024
Published on: 24 April 2024
Topic editor: Tony Robillard
Section editor: Ming Kai Tan
Desk editor: Eva-Maria Levermann