UC Riverside

UCR Honors Capstones 2020-2021

Title

Systematics of Ectrichodiella Fracker and Bruner, 1924 with description of the first fossil millipede assassin bug (Insecta: Heteroptera: Reduviidae: Ectrichodiinae)

Permalink

https://escholarship.org/uc/item/0zx7m0dj

Author

Bush, Tatiana N.

Publication Date

2022-08-25

Data Availability

The data associated with this publication are not available for this reason: Embargo

eScholarship.org Powered by the California Digital Library
University of California

SYSTEMATICS OF *ECTRICHODIELLA* FRACKER AND BRUNER, 1924, WITH DESCRIPTION OF THE FIRST FOSSIL MILLIPEDE ASSASSIN BUG (INSECTA: HETEROPTERA: REDUVIIDAE: ECTRICHODIINAE)

By

Tatiana Nicole Bush

A capstone project submitted for Graduation with University Honors

May 06, 2021

University Honors
University of California, Riverside

APPROVED

Dr. Christiane Weirauch
Department of Entomology

Dr. Richard Cardullo, Howard H Hays Jr. Chair
University Honors

Abstract

With more than 886 species in ~137 genera, Ectrichodiinae (Hemiptera: Reduviidae) are the largest animal clade of millipede predators. Recent phylogenetic studies have created a framework for our understanding of ectrichodiine evolutionary history, but no fossil species have been described. *Ectrichodiella* Fracker and Bruner, 1924 belongs to the earliest diverging lineage of Ectrichodiinae and a better understanding of the morphology and biodiversity of this genus may provide insights into our understanding of the early evolution of the subfamily. The genus is composed of two described species, *Ectrichodiella minima* (Valdés, 1910) and *Ectrichodiella rafaeli* (Gil-Santana & Coletto-Silva, 2005) from Cuba and Brazil, respectively. Here, three new species of *Ectrichodiella* are described, with two representing extant taxa currently only known from French Guiana (*E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.**), while the third is based on a Dominican amber fossil from the Miocene (*Ectrichodiella electrina* **n. sp.**). Diagnoses, descriptions or re-descriptions, habitus and morphological detail images, an identification key and distribution map are provided. A cladistic analysis based on 43 morphological characters corroborates that *Ectrichodiella* is monophyletic and shows the fossil species to be supported as sister taxon to the two new species. This narrow phylogenetic placement makes *Ectrichodiella electrina*, **n. sp.** a valuable fossil calibration for divergence dating analyses, despite its relatively young age.

Acknowledgements

I would like first to thank my faculty mentor Dr. Christiane Weirauch for her mentorship and wisdom throughout this project. I would also like to thank the Heteropteran Systematics Lab at University of California, Riverside for reviewing the manuscript and teaching me new techniques that came with learning about systematics and heteropterans. Funding was provided by the National Science Foundation (NSF) grant 1655769 (awarded to Dr. Christiane Weirauch)

Table of Contents

Abstract…….2

Acknowledgements……3

Introduction……6

Materials and Methods…….9

Specimens, databasing, and map…….9

Dissections, imaging, measurements……9

Terminology…….10

Species descriptions and cladistic analyses……11

Phylogenetic results and discussion……11

Character list and discussion of character transitions and synapomorphies based on the strict consensus of the two best trees derived from the implied weighting (K=20) analysis…….13

Taxonomy…….20

***Ectrichodiella*……20**

Key to species of *Ectrichodiella*…….22

***Ectrichodiella caballina*, n. sp……. 23**

***Ectrichodiella electrina*, n. sp……. 26**

***Ectrichodiella minima*…….28**

***Ectrichodiella nouraguensis*, n. sp. …….30**

***Ectrichodiella rafaeli*……33**

References…….35

Figure legends……..…….37

Figures 1-11……41

Supplemental Materials……..…51

Introduction

Ectrichodiinae, the millipede assassin bugs, are a diverse assassin bug subfamily (>137 genera, >886 species) of documented or suspected millipede predators (Forthman and Weirauch, 2012). Recent phylogenetic analyses have resulted in first insights into the evolutionary history of the group, including the evolution of aposematic coloration and extreme sexual dimorphism, and the colonization of Madagascar (Forthman and Weirauch, 2018, 2017, 2016). These phylogenies were also the basis for a revised classification that treats the former subfamily Tribelocephalinae as junior synonym of Ectrichodiinae and recognizes five tribes (Forthman and Weirauch, 2017). The worldwide, mostly circumtropical Ectrichodiini include the bulk of millipede assassin bug species (~730 spp.) and are often aposematic and glabrous, while the typically brown and setose Tribelocephalini (~130 spp.) and Abelocephalini (~20 spp.) are restricted to the Old World. The two remaining tribes form the earliest diverging lineage of Ectrichodiinae and consist of the monogeneric Afrotropcial Xenocaucini (8 spp.) (Weirauch et al., 2017) and the Neotropical Tribelocodiini (3 spp.) (Gil-Santana et al., 2013. Weirauch, 2010). Tribelocodiini comprise the monotypic genus *Tribelocodia* Weirauch, 2010 from French Guiana and *Ectrichodiella* Fracker and Bruner, 1924 with two species from Cuba and Brazil, *Ectrichodiella minima* (Valdés, 1910) and *Ectrichodiella rafaeli* (Gil-Santana and Coletto-Silva, 2005), respectively (Gil-Santana et al., 2013). The tribe is set apart from other Ectrichodiinae by a unique combination of morphological features including the tibiae lacking a fossula spongiosa and features of the scutellum (Forthman and Weirauch, 2017). Initially described in the Tribelocephalinae and supported as sister taxon to *Xenocaucus* China and Usinger, 1949, *Tribelocodia* differs from *Ectrichodiella* by the one-segmented tarsus that is fused with the tibia (two-segmented and not fused in *Ectrichodiella*) and a bifid scutellar apex (median scutellar apex and paired lateral processes in *Ectrichodiella*)

(Forthman and Weirauch, 2017; Weirauch, 2010). According to the phylogenetic analysis by Forthman and Weirauch (2017), the monophyly of *Ectrichodiella* is supported by several morphological synapomorphies, including the antennal insertion protected laterally by a small sclerite, the toothlike subapical spine on the scape, and paired ventroapical projections on all femora.

Despite comprising only two described species, the taxonomic history of *Ectrichodiella* is convoluted. The genus was described by Fracker and Bruner (1924) to accommodate *Ectrichodiella cubensis* Fracker and Bruner, 1924. This species was later recognized as a junior synonym of *Ectoiochoda minima* Valdés, 1910, a misspelling of the manuscript name *Ectrichodia minima* Uhler (Bruner and Barber, 1937). *Ectrichodiella rafaeli* was described in a new genus of Reduviinae, *Berengeria* Gil-Santana and Coletto-Silva, 2005 (Gil-Santana and Coletto-Silva, 2005) and later synonymized with *Ectrichodiella* (Gil-Santana et al., 2013). Gil-Santana et al. (2013) also provided documentation of type specimens of *E. minima* and *E. cubensis* and a discussion of the taxonomic history, morphology, and potential phylogenetic affinities of the genus.

While our understanding of the timing of the early evolution of Ectrichodiinae is limited, fossil-calibrated divergence dating analyses by Hwang and Weirauch (2012) and Forthman and Weirauch (2016) suggest that Ectrichodiinae diverged from other assassin bugs in the Late Cretaceous (~75 mya; HPD ~85-65 mya) and Tribelocephalini from Ectrichodiini around 68 mya (HPD ~75-50 mya). While Xenocaucini and Tribelocodiini were not included in these analyses, their phylogenetic position as earliest diverging lineage of Ectrichodiinae makes it likely that they originated in the Late Cretaceous (Forthman and Weirauch, 2017). Biogeographic analyses of Madagascan Ectrichodiini show that this fauna is young and the result of dispersal-driven

colonization (Forthman and Weirauch, 2016). In contrast, given the potential age of Tribelocodiini and the distribution of extant taxa in the Guiana Shield, Amazonia, and the Greater Antilles, vicariance via the Greater Antilles and Aves Ridge (GAARlandia) land bridge (35-32 mya) (Iturralde-Vinent 2006) may have contributed to the biogeographic history of this tribe.

Fossil species provide insights into the evolution of morphological characters and the timing of the diversification of a lineage when analyzed in the context of a phylogenetic framework. While Reduviidae comprise close to 7,000 described extant species, only ~34 fossil species were recognized as belonging to this family by Schuh and Weirauch (2020). Emesinae are best represented (13 spp.) in the fossil record, followed by Holoptilinae (3 spp.), Triatominae (2 spp.), Harpactorinae (2 spp.), Reduviinae (2 spp.), and Centrocnemidinae (2 spp.), while subfamilial placement of the remaining fossil taxa is uncertain. No fossil ectrichodiine taxa have been described. The majority of assassin bug fossils are fairly young (Eocene, Oligocene, and Miocene) and comprise compression fossils from deposits including Florissant, Messel, and Shandong and amber fossils from Baltic and Dominican amber (Schuh and Weirauch, 2020). The recently described *Paleotriatoma* is the first assassin bug from mid-Cretaceous Burmese amber and oldest uncontroversial fossil Reduviidae (Poinar, 2019). While Dominican amber fossils are young (Iturralde-Vinent, 2017), they are easily placed within a given subfamily and tribe and are often part of genera that were described based on extant species. Dominican amber reduviid fossils comprise species of Emesinae, Harpactorinae (Apiomerini), Holoptilinae and Triatominae. Certain extant Emesinae (Wygodzinsky, 1966) and Holoptilinae (CW, pers. obs.) are found around the bases of trees and Apiomerini collect resin for maternal care and prey capture (Forero et al., 2011), circumstances that likely facilitate fossilization in amber.

Ectrichodiinae are often collected from leaf litter (Forthman et al., 2016) or on vegetation (Haviland, 1931), and while most photographs available on iNaturalist.org show millipede assassin bugs on artificial surfaces or the ground, some were taken on tree bark. Their absence from the amber fossil record is therefore somewhat surprising.

We here describe and illustrate three new species of *Ectrichodiella* and provide an updated diagnosis and description of the genus. Two of the new species are extant taxa from French Guiana, the third is the first fossil species of Ectrichodiinae and is from Dominican amber. We conduct a morphology-based phylogenetic analysis of *Ectrichodiella* and outgroups to reconstruct the phylogeny of the genus and to determine the phylogenetic position of the fossil species.

Materials and Methods

Specimens, databasing, and map

One male specimen was examined for each of the three new species (Figs 1-9). The Dominican amber specimen is deposited at the American Museum of Natural History (AMNH) and holotypes of the two extant species at the Muséum national d'Histoire naturelle, Paris, France (MNMH). Since both *E. minima* and *E. rafaeli* are well described and documented, type specimens were not examined. Specimens were given matrix-code labels (unique specimen identifier or USI labels) and specimen data captured using the online Arthropod Easy Capture database housed at the American Museum of Natural History (AMNH) https://research.amnh.org/pbi/locality/. Coordinates were then downloaded from that database and mapped using SimpleMappr [http://www.simplemappr.net/] (Fig. 10).

Dissections, imaging, and measurements

Morphological characters were examined using a Nikon SMZ1000 dissecting microscope. The pygophore of the two extant species was dissected and cleared in ~10% KOH and the aedeagus removed. Genitalic dissections were stored in genitalic vials and re-associated with the specimen after examination and documentation. Habitus and morphological detail photographs (Figs 1-9) were taken using a Leica Z16 APO imaging system with 1.0x and 2.0x objective lenses and the Leica Application Suite (LAS) v4.3 software and compiled using Zerene Stacker v1.04. Photographs were edited and plates assembled in Adobe Photoshop CS6. Measurements were taken from the photographs.

Terminology

Morphological terminology follows Forthman and Weirauch (2016), with modifications.

Abbreviations: **1A**, first anal vein; **alp**, anterior pronotal lobe processes; **as**, antennal shield; **asp**, apical scutellar process; **bp**, basal plate (of aedeagus); **bpe**, basal plate extension; **ca**, carina (median longitudinal of abdomen); **Cu**, cubitus; **DAG1-3**, dorsal abdominal gland 1-3; **exM**, extension of M beyond M+Cu; **gl**, gula; **L2**, labial segment 2 (first visible); **L3**, labial segment 3 (second visible); **L4**, labial segment 4 (third visible); **lr**, lateral ridges (of posterior pronotal lobe); **M**, media; **mp**, midlateral projections of scutellum; **msn**, mesonotum; **mtn**, metanotum; **oc**, ocellus; **pa**, paramere; **pg**, prosternal groove; **ple**, paramedian lobe-like extension on the posterior margin of the posterior pronotal lobe; **pr**, pygophore ridge (median on ventral pygophore surface); **psp**, prosternal stridulatory process; **pt**, pterostigma; **py**, pygophore; **S3-S8**, (abdominal) sternites 3-8; **sas**, subapical spine on antennal scape, **sc**, scutellum; **T1-2**, synterga 1 and 2; **T3-T7**, (abdominal) terga 3-7; **td**, tibial dilation; **ts1, 2**, tarsal segment 1, 2; **vap**, paired ventroapical projections on forefemur.

Species descriptions and cladistic analyses

To assure consistency of species descriptions, descriptive characters and states were organized as an Excel table and then assembled into text sections and edited in Word.

The morphological matrix used for phylogenetic analyses is overlapping with characters used for the descriptions. However, unique species-level characters were omitted from the phylogenetic matrix, and additional characters were included that do not vary between species of *Ectrichodiella* and are aimed at testing the monophyly and relationship of *Ectrichodiella*. The morphological matrix was assembled in WinClada ver. 1.00.08 (Nixon, 2002) and comprises 43 morphological characters and 10 taxa: the two described and three new putative species of *Ectrichodiella*, *Tribelocodia ashei* Weirauch (Tribelocodiini), *Tribelocephala* sp. (Tribelocephalini), *Abelocephala* sp. (Abelocephalini), *Xenocaucus ethiopiensis* Weirauch et al., 2017 (Xenocaucini) and *Gibbosella consimilis* Forthman, Chłond, & Weirauch, 2017 (Ectrichodiini). Because of the exceptional preservation of the fossil specimen, all but four of the 43 characters were coded for this taxon. For equal weights (EW) analyses in TNT (Goloboff et al., 2008), we used New Technology Searches, using Sectorial Searches, Ratchet, Drift, and Tree fusing with default settings, and finding the minimum length tree 100 times. For resampling procedures, we employed jackknife with default settings and 1000 replications. A number of characters showed homoplasy in the equal weights analyses, so we down weighted homoplastic characters exploring a range of k-values (20, 12, 9, and 6). We used symmetric resampling procedures with default settings and 1000 replications to assess the robustness of these analyses.

Phylogenetic results and discussion

The equal weights analysis resulted in eight most parsimonious trees (L=80; Ci=68; Ri=69). The eight trees differ in treating *Ectrichodiella electrina* **n. sp.** either as sister taxon to (*Ectrichodiella caballina* **n. sp.** + *Ectrichodiella nouraguensis* **n. sp.**) or to (*E. minima* + *E. rafaeli*), and in relationships among the outgroups. *Ectrichodiella* (98% jackknifing) and (*E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.**) (90%) are highly supported in resampling analyses, but (*E. minima* + *E. rafaeli*) is less well supported (67%). The strict consensus tree collapses *E. electrina* **n. sp.**, (*E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.**), and (*E. minima* + *E. rafaeli*) into a polytomy. The strict consensus tree is provided as Supplemental Fig. S1 with unambiguous character changes shown. The four implied weights analyses resulted in two optimal trees for each analysis, with identical relationships among the four analyses. *Ectrichodiella* is monophyletic, *E. minima* and *E. rafaeli* are sister taxa, and *Ectrichodiella electrina* **n. sp.** the sister taxon to (*E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.**) (Fig. 11). The strict consensus of these two tree collapses relationships in the non-Tribelocodiini outgroups. Resampling values show minor differences between analyses. Resampling values for *Ectrichodiella* are 97% or 98% in all analyses, values for *E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.** are either 92% or 93%, and 70% for (*E. minima* + *E. rafaeli*). With either 41% or 42%, the sister group relationship between *Ectrichodiella electrina* **n. sp.** and the two species from French Guiana is poorly supported in all analyses. Similarly, *Tribelocodia* is recovered as sister taxon to *Ectrichodiella* in all IW analyses, but with very low support (9% or 10%). We use the tree with the best score 1.156 derived from the k=20 IW analysis (Fig. 11) to document unambiguous character state transitions (homoplasy setting: any extra step) and for the "character list and discussion" below.

The three new extant and fossil species are well supported within *Ectrichodiella* in all our analyses. Unfortunately, the phylogenetic position of the Dominican amber fossil *E. electrina* **n.**

sp. is less clear. All implied weights analyses found *E. electrina* **n. sp.** as sister taxon to the two new species from French Guiana, but support for this placement is low; relationships between *E. electrina* **n. sp.,** (*E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.**), and (*E. minima* + *E. rafaeli*) are unresolved in the equal weights analyses. Given these uncertainties, we refrain from using this phylogenetic hypothesis to speculate on the biogeographic history of the group.

Character list and discussion of character transitions and synapomorphies based on the strict consensus of the two best trees derived from the implied weighting (K=20) analysis. Only unambiguous character state changes are discussed. The most recent common ancestor of *Ectrichodiella* is abbreviated as MRCA.

0. Postocular area, shape in dorsal view: (0) narrow; (1) broad. A narrow postocular area is treated as synapomorphy for *Tribelocodia* + *Ectrichodiella*, with a transition to broad in *E. rafaeli*.

1. Posterolateral gular area, shape in lateral view: (0) flat to slightly swollen, conforming to rounded head shape; (1) moderately swollen; (2) distinctly swollen. A distinctly swollen posterolateral gular area (Fig. 2B) is a synapomorphy for *Ectrichodiella*.

2. Labium, relative length of second (L2) and third (L3) segments: (0) L3 about 1/2 as long as L2; (1) L3 about 3/4 as long as L2; (2) about same length. The MRCA was reconstructed as having L3 about 3/4 the length of L2 (Fig. 4A), with transitions to half the length within the genus (Fig. 4C). We were unable to code this character for *E. electrina* **n. sp.**, where it is obscured.

3. Eye, size, in lateral view relative to ventral head margin: (0) not reaching ventral head margin (Fig. 2B); (1) reaching ventral head margin; (2) surpassing ventral head margin. The

reconstruction for the MRCA was ambiguous. Only *E. minima* and *E. electrina* **n. sp.** have eyes that reach the ventral head margin among species of *Ectrichodiella*.

4. Eye, shape in lateral view: (0) reniform; (1) oval. The eye was reconstructed as being reniform in the MRCA of *Ectrichodiella* (Fig. 2B), with one transition to oval in *E. electrina* **n. sp.**

5. Synthlipsis, width relative to eye: (0) synthlipsis 2x width of eye; (1) synthlipsis 3x width of eye; (2) synthlipsis 1.5x width of eye; (3) synthlipsis more than 3x width of eye. The synthlipsis being more than 3x as wide as the eye is a synapomorphy of (*E. minima* + *E. rafaeli*). The synthlipsis is narrower in *E. electrina* **n. sp.** and *E. caballina* **n. sp.** (2x eye width; Fig. 2A) and *E. nouraguensis* **n. sp.** (3x eye width; Fig. 2E).

6. Ocellar lens: (0) absent; (1) present. The presence of the ocellar lens is plesiomorphic for *Ectrichodiella* and was retained in all species (Fig. 2A, C, E).

7. Ocellus, size: (0) small; (1) large. Only *E. rafaeli* among species of *Ectrichodiella* shows a relatively small ocellar size. The ocellus is large in the remaining species (Fig. 2A, C, E). The reconstruction of this feature in the MRCA is ambiguous.

8. Ocellus, located on elevation: (0) absent; (1) present. The ocellus in all species of *Ectrichodiella* except *E. rafaeli* is located on an elevation (Fig. 2B, F), and this was reconstructed as the state in the MRCA of the genus.

9. Ocellar elevation (if present): (0) single median elevation; (1) paired elevations. The ocelli in *E. electrina* **n. sp.** are located on a single, median elevation (Fig. 2C), while those in *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.** are located on separate, paired elevations (Fig. 2A, F).

10. Antennal shield (i.e., antennal insertion shielded laterally by small sclerite): (0) absent; (1) present. The antennal shield (as) is present in all species of *Ectrichodiella* (Fig. 2B, D, F) and a synapomorphy of the genus.

11. Scape of antenna, subapical spine: (0) absent; (1) small; (2) large. A large subapical spine on the antennal scape is a synapomorphy for *E. electrina* **n. sp.**, *E. caballina* **n. sp.**, and *E. nouraguensis* **n. sp.** (Fig. 3B, D, F). The spine is absent in *E. rafaeli* and small in *E. minima*.

12. Flagellomeres, diameter: (0) similar to diameter of pedicel; (1) more slender than diameter of pedicel. Slender flagellomeres are plesiomorphic for *Ectrichodiella* (Fig. 3A, C, E).

13. Anterior and posterior pronotal lobes, relative length: (0) anterior lobe less than 1/2 length of posterior; (1) anterior lobe more than 1/2 length of posterior. The longer anterior pronotal lobe is a synapomorphy for *E. rafaeli* and *E. minima*, and independently derived in *E. electrina* **n. sp.** *Ectrichodiella caballina* **n. sp.**, and *E. nouraguensis* **n. sp.** have a very short anterior lobe (Fig. 5A, E) that is here treated as homologous to the condition seen in the sister taxon *Tribelocodia*.

14. Anterior and posterior pronotal lobes, relative width: (0) anterior lobe less than 1/2 width of posterior; (1) anterior lobe more than 1/2 width of posterior. The MRCA of *Ectrichodiella* had a pronotum with the anterior lobe more than 1/2 the width of the posterior lobe, a feature that was retained in the three new species (Fig. 5A, C, E). The anterior lobe being less than 1/2 the width of the posterior lobe is a synapomorphy for (*E. minima* + *E. rafaeli*).

15. Anterior pronotal lobe, longitudinal depression: (0) absent; (1) present. All species of *Ectrichodiella* except *E. electrina* **n. sp.** show a longitudinal depression on the anterior lobe. The feature was reconstructed as plesiomorphic for the genus in our analysis.

16. Anterior pronotal lobe, pair of glabrous areas posterior to anterior lobe process: (0) absent; (1) present. The glabrous areas (Fig. 5A) are a synapomorphy for *Ectrichodiella* (state in *E. electrina* **n. sp.** unknown).

17. Anterior pronotal lobe, paired, rounded processes on disc: (0) absent; (1) present. Paired rounded processes on the anterior pronotal lobe disc are a synapomorphy for *Ectrichodiella* (Fig. 5A, C, E).

18. Posterior pronotal lobe, coloration: (0) caramel; (1) brown. The MRCA of *Ectrichodiella* was reconstructed as with brown posterior pronotal lobe (Fig. 5A, C, E); the caramel color in *E. minima* is autapomorphic.

19. Posterior pronotal lobe, median groove: (0) absent; (1) present. A longitudinal groove is plesiomorphically present in all species of *Ectrichodiella* (Fig. 5A, C, E).

20. Posterior pronotal lobe, lateral ridges: (0) absent; (1) present. Lateral ridges (lr) are a synapomorphy for the three new species of *Ectrichodiella* (Fig. 5A, C, E).

21. Posterior pronotal lobe, paramedian lobes on posterior margin: (0) shallow; (1) pronounced. Pronounced paramedian lobes are a synapomorphy for *Ectrichodiella*.

22. Prosternal stridulatory process, length: (0) short, not reaching or surpassing posterior margin of procoxal cavity; (1) long, surpassing posterior margin of procoxal cavity. The process is plesiomorphically long in all species of *Ectrichodiella* for which this feature was examined (unknown the two described species).

23. Scutellum, apex: (0) drawn into process; (1) blunt. The optimization of this character is ambiguous, with a median process being present in Tribelocephalini, *Xenocaucus*, and *Ectrichodiella* (Fig. 5A,C, E), while absent in Ectrichodiini and *Tribelocodia*.

24. Scutellum, midlateral projections: (0) absent; (1) paired. All species of *Ectrichodiella* feature distinct paramedian scutellar projections or processes (mp; Fig. 5A-C, E, F). Our analyses found the subapical lateral projections on the scutellum in *Tribelocodia* to be synapomorphic with the projections in *Ectrichodiella*.

25. Scutellum, midlateral projections, size: (0) small; (1) large. The three new species share the large size of the midlateral projection (Fig. 5A, C, E), here treated as plesiomorphic, because it also occurs in *Tribelocodia*. The small size of the projections is synapomorphic for the two described species.

26. Scutellum, midlateral projections, orientation: (0) mostly horizontal; (1) strongly vertical. While the projections are plesiomorphically horizontal in the two described species of *Ectrichodiella* and in *E. electrina* **n. sp.**, the strong vertical orientation (Fig. 5B, F) is a synapomorphy for (*E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.**).

27. Hind trochanter, small tubercles: (0) absent; (1) present. Small tubercles on the hind trochanter are here treated as a synapomorphy for *Ectrichodiella* (unknown in *E. electrina* **n. sp.**) and *Tribelocodia*.

28. Forefemur, paired ventroapical projections: (0) absent; (1) present. Paired ventroapical projections on forefemur are a synapomorphy for *Ectrichodiella* (vap; Fig. 6A, C).

29. Tibia, dilation at apex: (0) absent; (1) present. The tibial apex is dilated (Fig. 6A) in all species of *Ectrichodiella*, except *E. electrina* **n. sp**.; the reconstruction for the MRCA is ambiguous due to the absence of a dilation in *Tribelocodia*.

30. Fossula spongiosa on foreleg: (0) absent; (1) present. The fossula spongiosa is plesiomorphically absent in all species of *Ectrichodiella* (Fig. 6D).

31. Tarsal segmentation: (0) 2-segmented; (1) 3-segmented; (2) 1-segmented. The 2-segmented tarsus (Fig. 6D) is here treated as plesiomorphic for *Ectrichodiella* (shared with *Xenocaucus* and *Abelocephala*).

32. M and Cu (forewing), proximal portion: (0) fused into M+Cu; (1) separate veins. The proximal portions of M and Cu are distinct in the three new species described in this publication, and then fuse in a more distal point (Fig. 7). This is synapomorphic, and in contrast to the two described species that retain the plesiomorphic condition of a completely fused M+Cu.

33. Pterostigma (inflated area on forewing margin anterior to M): (0) slightly inflated; (1) strongly inflated; (2) not inflated. Optimization of the strongly inflated pterostigma is ambiguous for (*E. minima* + *E. rafaeli*) and *E. electrina* **n. sp.** (Fig. 7C, D). The less inflated pterostigma in *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.** (Fig. 7A, B) is synapomorphic.

34. Vestiture of corium: (0) long, simple setae absent; (1) long, simple setae sparse; (2) long, simple setae dense. The long and sparse setation on the forewing is here treated as synapomorphic for *Ectrichodiella* (Fig. 7).

35. Corium, color: (0) uniformly brown; (1) brown with yellow band proximally. While the corium is plesiomorphically brown in the two described species and *E. electrina* **n. sp.** (Fig. 7C),

the brown and yellow patterning in *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.** is a synapomorphy for the two new species (Fig. 7A, B).

36. Corium, vein color: (0) uniformly yellow; (1) brown and yellow; (2) uniformly brown. The uniform yellow coloration of the veins in *E. minima* and *E. rafaeli* is synapomorphic, as are the yellow and brown patterning in *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.** (Fig. 7A, B).

37. Lateral margin of laterotergite 1+2: (0) with small spine; (1) with large, curved spine; (2) only slightly expanded; (3) without spine. None of the outgroups feature a spine or distinct expansion on laterotergite 1+2. The size of the spine varies among species of *Ectrichodiella*. While the laterotergite is only slightly expanded in the three new species, the spine is large in *E. rafaeli*, and small in *E. minima*.

38. Dorsal abdominal scent gland (DAG) I ostioles in adults: (0) absent; (1) present. The DAG I ostioles are present (Fig. 8C) in species of *Ectrichodiella* (as are the ostioles of DAG II and III), but it is unclear if they are synapomorphic or plesiomorphic (absent in *Tribelocodia*).

39. Connexivum, color pattern: (0) uniformly brown or yellow; (1) with contrasting brown and yellow markings. The contrasting connexival color pattern is a synapomorphy for *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.** (Fig. 8A, E).

40. Posterior margin of tergum 7 (male): (0) straight; (1) indented; (2) slightly rounded. The posterior margin of tergum 7 shows some homoplastic transitions among species of *Ectrichodiella* and can be used to distinguish the two new species from French Guiana (Fig. 8A, E).

41. Sternum 8 (male), posterior margin: (0) strongly sinuous; (1) slightly sinuous; (2) straight. This feature shows species-diagnostic differences between *Ectrichodiella* species but does not group together species (Fig. 9A, H, P).

42. Pygophore, shape of posterior margin: (0) rounded; (1) straight; (2) slightly rounded. Similar to the preceding character, the posterior pygophore margin differs among species of *Ectrichodiella* (Fig. 9A, H, P).

Taxonomy

Ectrichodiella Fracker and Bruner, 1924

Figs 1–11

Type species: *Ectrichodia minima* Valdés, 1910

Revised diagnosis. Recognized among Ectrichodiinae by the small size, antennal insertion with antennal shield (Fig. 2B, F), posterolateral gular area very swollen in lateral view (Fig. 2B), anterior pronotal lobe with pair of processes on disc and glabrous areas posterior to processes (Fig. 5A, C, E), pronounced paramedian lobe-like extension on posterior pronotal margin (Fig. 5A, C, E), scutellum with apex drawn into process (Fig. 5A, C, E), midlateral scutellar projections (Fig. 5A-C, E, F), forefemur with paired ventroapical projections (Fig. 6A, C), absence of fossula spongiosa on foreleg and mid leg (Fig. 6D), 2-segmented tarsi (Fig. 6D), strongly inflated pterostigma in some species (Fig. 7C), sparse long vestiture on corium, and dorsal abdominal scent gland (DAG) ostioles 1–3 in adults present (Fig. 8C).

Re-description. Male. Macropterous, small body size (length clypeus to abdomen margin: 3.31-3.74). COLORATION: body and appendages brown to caramel or yellow; hemelytron and veins brown and/or yellow; connexivum either uniformly colored or with contrasting yellow and brown bands. VESTITURE: head with light colored setation; antennal vestiture longer or shorter than 2x diameter of antennal segment, light or dark; thorax with light colored hairs, scutellum with long or short, thin, yellow setae; small tubercles on hind trochanter; hemelytra with sparse setation. STRUCTURE: HEAD: antennal insertion protected laterally by antennal shield; interocular sulcus pronounced anterior to ocelli; synthlipsis 2x, 3x or more than 3x as wide as eye; posterolateral gular area in lateral view very swollen; eye reniform or oval in lateral view, reaching or jot reaching ventral head margin in lateral view; paired hemispherical elevations between eyes present or absent; ocelli large or small, on shared or paired elevation(s) or on flat dorsal head surface. Antenna: scape with or without subapical spine; scape and pedicel thickened; flagellomeres more slender than pedicel. Labium: fairly stout, with third segment ¾ or ½ length of second segment. THORAX: pronotum bell shaped in dorsal view, with anterior lobe shorter and narrower than posterior lobe; anterior margin rounded or straight; anterior lobe with or without longitudinal depression, with paired, rounded processes on disc and pair of glabrous areas posterior to processes; posterior pronotal lobe with or without lateral ridges and with paramedian lobes on posterior margin; scutellum triangular with apex drawn into process; midlateral scutellar projections small or large, horizontal or strongly vertical. Leg: hind trochanter with small tubercles; forefemur with paired ventroapical projections; fossula spongiosa on foreleg and mid leg absent; foretibia dilated apically, with foretibial comb; tarsi 2-segmented. Hemelytra: membrane with 2 closed cells (MCu and Cu1A cells) of unequal size, with distal margin of CuA1 cell fairly straight (Fig. 7A, B, D) or slightly curved, distal margin of

MCu cell curved; proximal portion of M+Cu separated or fused; pterostigma strongly to slightly inflated. ABDOMEN: lateral margin of laterotergite 1+2 slightly expanded or with small or large, curved spine; ostioles of dorsal abdominal scent glands (DAG) 1–3 present in adults; posterior margin of tergum7 straight, indented, or slightly rounded; posterior margin of sternum 8 straight or slightly or strongly sinuous (Fig. 9A, H). Genitalia (Fig. 9): Pygophore rounded (Fig. 9P) or more elongate and with sinuous lateral margins (Fig. 9A, B, H, I), ventral surface with distinct setation and ridges along midline in some species (Fig. 9H), posterior margin of pygophore straight (Fig. 9H) or rounded (Fig. 9O). Aedeagus simple and slender (Fig. 9D–G, K–N).

Key to species of *Ectrichodiella*

1. Lateral margin of laterotergite 1+2 with large, curved spine; ocelli not on elevation …… *E. rafaeli* (Gil-Santana and Coletto-Silva, 2006)

- Lateral margin of laterotergite 1+2 with small spine or only slightly expanded; ocelli on elevation ……..…….2

2. Midlateral projection of scutellum small, posterior pronotal lobe without lateral ridges, lateral margin of laterotergite 1+2 with small spine ……...……...…… *E. minima* (Valdés, 1910)

- Midlateral projection of scutellum large (Fig. 5B, C, F), posterior pronotal lobe with lateral ridges (Fig. 5A, C, E), lateral margin of laterotergite 1=2 slightly expanded …..……3

3. Ocelli on shared elevation (Fig. 2C), midlateral scutellar projections mostly horizontal (Fig. 5C), pygophore rounded (Fig. 9P) ……...…… *E. electrina*, **n. sp.**

- Ocelli on individual elevations (Fig. 2A, E), midlateral scutellar projections strongly vertical (Fig. 5B, F), pygophore more elongate and with sinuous lateral margins (Fig. 9D, K) .....……4

4. Yellow coloration on hemelytron largely restricted to proximal part of veins (Fig. 7A), pygophore ventrally along midline without transverse ridges (Fig. 9A)……..... *E. caballina*, **n. sp.**

- Yellow coloration on hemelytron on proximal part of veins and in adjacent cells (Fig. 7B), pygophore ventrally along midline with transverse ridges (Fig. 9H: pr)… *E. nouraguensis*, **n. sp.**

Ectrichodiella caballina, **n. sp.**

Figs 1A-C, 2A, B, 3A, B, 4A, B, 5A, B, 6A, C, 7A, 8A, B, 9A-G

Diagnosis. Recognized among species of *Ectrichodiella* by the large subapical spine on scape (Fig. 3B), eye in lateral view not reaching ventral head margin, about 1/2 height of head (Fig. 2B), ocelli large and on paired elevations (Fig. 2A), third labial segment about 3/4 length of second (Fig. 4A), large and vertical midlateral scutellar projections (Fig. 5B), M and Cu separate at base of hemelytron (Fig. 7A), slightly inflated pterostigma (Fig. 7A), yellow coloration on hemelytron largely restricted to proximal part of veins and narrow areas surrounding veins (Fig. 7A), lateral margin of laterotergite 1+2 only slightly expanded, posterior margin of tergum 7 indented (Fig. 8A), and posterior margin of sternum 8 slightly sinuous (Fig. 9A).

Description. MALE: Macropterous, small body size. Measurements of holotype (in mm): habitus length to posterior wing margin: 3.94; habitus length to abdomen margin: 3.74; head length excluding neck: 0.77; head greatest width: 0.98; head anteocular: 0.24; head postocular:

0.29; synthlipsis: 0.57; scape: 0.87; second labial segment: 0.48; third labial segment: 0.32; thorax length: 1.25; anterior pronotal lobe greatest length: 0.16; posterior pronotal lobe greatest length: 0.54; scutellum greatest length: 0.39; abdomen length: 1.97; greatest width at abdomen: 1.84. COLORATION: Body brown; eye dark brown; antennal hair color light; thorax dark brown, with posterior pronotal lobe brown; legs yellow with brown band on femur; hemelytron with corium brown with yellow band, proximally, with veins brown and yellow, yellow coloration on hemelytron largely restricted to proximal part of veins (Fig. 7A) with suture yellow. VESTITURE: head with thin, short, white hair covering ventral surface, with thin, medium length yellow hair sparsely behind eyes and dorsally; labium hairs thin, small, yellow; antenna hair under 2x the diameter of antenna segment, thorax with yellow, thin, medium length hairs sparse on the anterior and dorsal side with white thin hair on the ventral and anterior sides; scutellum with short yellowish hairs lining sides; small tubercles on hind trochanter; hemelytra with sparse, yellow, short, hairs; connexivum with yellow short hairs on ventral side. STRUCTURE: HEAD: antennal insertion protected laterally by a small sclerite; interocular sulcus most pronounced middle of head; width of synthlipsis 3x eye width (Fig. 2A); posterolateral gula area in lateral view very swollen. Antenna: scape with large subapical spine (Fig. 3B); scape and pedicel thickened; diameter of flagellomeres less than diameter of pedicel. Eye: relatively large, in lateral view reniform, eye height about 0.5 height of head (Fig. 2B), in ventral view quarter spherical; 2 hemispherical elevations between eyes; ocellar lens present; ocelli large, on individual elevation; groove between ocelli. Labium curved at second labial segment (first visible), third labial segment (second visible segment) is 0.75 size of second labial segment (first visible segment) (Fig.4A), fourth labial segment (third visible) reaching thorax. THORAX: pronotum bell shaped, with surface smooth; anterior edge straight; pronotal

longitudinal depression on posterior lobe; anterior pronotal lobe less than half length and more than half width of posterior pronotal lobe; pronotal longitudinal depression on anterior lobe present, lateral ridges present; anterior lobe with paired, rounded processes on disc (Fig. 5B alp), with pair of glabrous areas on anterior pronotal lobe posterior to anterior lobe process; prosternal stridulatory process long, surpassing posterior margin of procoxal cavity; scutellum triangular, with apex drawn into spine; paramedian scutellar processes, with two large, strongly vertical, midlateral projections (Fig. 5B). Leg: paired ventroapical projections on forefemur (Fig. 6C); fossula spongiosa on foreleg absent; tibia dilation at tip; tibial comb at distal margin of tibia; tarsi 2-segmented. Hemelytra: 2 closed cells of unequal size; proximal portion of M+Cu separated (Fig. 7A); pterostigma slightly inflated. ABDOMEN: lateral margin of laterotergite 1+2 only slightly expanded; dorsal abdominal scent gland (DAG) I ostioles in adults present; sternites 4 through posterior margin of sternite 7 keeled; posterior margin of tergum 7 indented (Fig. 8A). Genitalia: sternum 8 posterior margin slightly sinuous (Fig. 9A); shape of pygophore posterior margin slightly rounded, with hair around outside.

Female. Unknown.

Etymology. The species is named after the Montagnes des Chevaux ("Horse Mountains") in French Guiana where the holotype was collected, after Latin adjective caballinus, -a, um referring to a horse.

Distribution. Only known from French Guiana.

Discussion. *Ectrichodiella caballina* **n. sp.** and *E. nouraguensis* **n. sp.** closely resemble each other with respect to overall habitus, color pattern, lateral ridges on the posterior pronotal lobe and size and vertical orientation of the midlateral scutellar projections. *Ectrichodiella caballina*

n. sp. is distinguished from *E. nouraguensis* **n. sp.** by the smaller eye size, wing color pattern, and details of the male genitalia among other features.

Material examined. FRENCH GUIANA: Guyane: Montagnes des Chevaux; 31 Jan 2010; SEAG; Holotype; (UCR_00127901) (MNMH).

Ectrichodiella electrina, **n. sp.**

Figs 1G, H, 2C, D, 3C, D, 5C, D, 7C, D, 8C, D, 9O, P

Diagnosis. Scape with large subapical spine; ocelli large and raised on a shared elevation; tibia dilation at tip absent; proximal portion of M+Cu separated; pterostigma strongly inflated; posterior margin of tergum 7 slightly rounded; sternum 8 posterior margin straight; pygophore posterior margin round.

Description. MALE: Dimensions (in mm): habitus length to posterior wing margin: unknown because of flexed forewing; habitus length to abdomen margin: 3.31; head length excluding neck: 0.41; head greatest width: 0.62; head anteocular: 0.12; head postocular: 0.13; synthlipsis: 0.34; scape: 0.43; second labial segment (1st visible): unknown; third labial segment (2nd visible): unknown; thorax length: 1.04; anterior pronotal lobe greatest length: 0.16; posterior pronotal lobe greatest length: 0.35; scutellum greatest length: 0.27; abdomen length: 1.77; greatest width at abdomen: 1.26. Macropterous, small body size. COLORATION: Body brown; ocelli bright; antennal hair dark; thorax dark brown, with posterior pronotal lobe brown; legs dark; hemelytron with corium uniformly brown, with veins uniformly brown; connexivum uniformly dark brown. VESTITURE: head with short hairs; antenna hair under 2x the diameter of antenna segment; thorax with short dark hairs; small tubercles on hind trochanter unknown;

connexivum with dark hair on ventral side. STRUCTURE: HEAD: antennal insertion protected laterally by a small sclerite; width of synthlipsis is 2x the eye size; posterolateral gula area in lateral view very swollen. Antenna: scape with large subapical spine (Fig. 3D); scape and pedicel thickened; diameter of flagellomeres smaller than diameter of pedicel. Eye: large; in lateral view oval, reaching ventral head surface; in ventral view hemispherical; 2 hemispherical elevations between eyes; ocellar lens present; ocelli large, on shared elevation (Fig. 2C). Labium: curved; relative length of second labial segment (first visible) and third labial segment (second visible) unknown; last segment reaching anterior margin of thorax. THORAX: pronotum bell shaped; anterior edge rounded; posterior pronotal lobe with median groove; anterior pronotal lobe more than half length of and more than half width of posterior pronotal lobe; lateral ridges present (Fig. 5C); anterior lobe with paired, rounded processes on disc; prosternal stridulatory process long; scutellum triangular, with apex drawn into spine; paramedian scutellar processes, with two large, mostly horizontal, midlateral projections. Leg: paired ventroapical projections on forefemur unknown; fossula spongiosa on foreleg absent; tibia dilation at tip absent (Fig. 5D); tibial comb at distal margin of tibia unknown; tarsi 2-segmented. Hemelytra: 2 closed cells of unequal size; proximal portion of M+Cu separated; pterostigma strongly inflated (Fig. 7C). ABDOMEN: lateral margin of laterotergite 1+2 only slightly expanded; dorsal abdominal scent gland (DAG) I ostioles in adults present (Fig. 8C); sternites 1 through posterior margin of sternite 7 keel unknown; posterior margin of tergum 7 slightly rounded (Fig. 8D). Genitalia: sternum 8 posterior margin straight; pygophore posterior margin round (Fig. 9P), with hair around outside.

Female. unknown

Etymology. The species name refers to the Latin feminine gender for “amber” referring to the type of fossilization.

Distribution. Dominican Republic, Dominican Amber.

Discussion. *Ectrichodiella electrina* **n. sp.** is unambiguously classified as part of *Ectrichodiella* shown by the morphology-based phylogenetic analysis in this study. *Ectrichodiella electrina* **n. sp.** was recovered as sister taxon to either *E. minima* and *E. rafaeli* or *E. caballina* **n. sp.** and *E. nouraguensis* **n. sp.**. *Ectrichodiella electrina* **n. sp.** is unique in the tibia dilation at tip absent and the pygophore posterior margin round.

Material examined. DOMINICAN REPUBLIC; Dominican Amber specimen, Oligo-Miocene (AMNH_DR-14-405) (AMNH).

Ectrichodiella minima (Valdés, 1910)

Ectrichodia minima Uhler (manuscript name)

Ectoiochoda (sic) *minima* Valdés, 1910

Ectrichodiella cubensis Fracker and Bruner, 1924

Ectrichodiella minima Bruner and Barber, 1937

Revised diagnosis. Antenna with small subapical spine on scape; scutellum with 2 small, mostly horizontal midlateral projections; lateral ridges absent; lateral margin of laterotergite 1+2 with small spine; proximal portion of M+Cu fused; pygophore posterior margin round.

Re-description. MALE: Dimensions (in mm): habitus length to posterior wing margin 4.17. COLORATION: Body yellow; eye brown; antennal hair light; thorax caramel; legs brown; hemelytron with corium uniformly brown, with veins uniformly yellow; connexivum uniformly dark yellow. VESTITURE: head covered with fringe of short white hairs; antenna hair greater than 2x the diameter of antenna segment; thorax with fringe short whitish hairs on anterior margin, sutures covered by dense fringe of short white pubescence; pronotum with short, dense, pubescence; scutellum with long thin yellowish hairs; small tubercles on hind trochanter; hemelytra with veins and cuneal area with sparse long, thin yellow hair; abdomen with long hair. STRUCTURE: HEAD: antennal insertion protected laterally by a small sclerite; interocular sulcus most pronounced near ocelli; width of synthlipsis more than 3x the eye size; posterolateral gula area in lateral view very swollen. Antenna: scape with small subapical spine; scape and pedicel thickened, diameter of flagellomeres smaller than diameter of pedicel. Eye: large, in lateral view reniform reaching ventral head surface; 2 hemispherical elevations between eyes; ocellar lens present; ocelli large, on individual elevations. Labium: third labial segment (2nd visible) is 0.75 length of second labial segment (1st visible). THORAX: pronotum bell shaped, with surface smooth, anterior edge rounded; posterior pronotal lobe with median groove; anterior lobe more than half length and less than half width of posterior lobe; lateral ridges absent; anterior lobe with paired, rounded, processes on disc present, with pair of glabrous areas on posterior corners absent; prosternal stridulatory process length unknown; scutellum triangular, with apex drawn into spine; paramedian scutellar processes present, with two small, mostly horizontal, midlateral projections. Leg: paired ventroapical projections on forefemur; fossula spongiosa on foreleg absent; tibia dilation at tip; tibial comb at distal margin of tibia; tarsi 2-segmented. Hemelytra: 2 closed cells of unequal size; proximal portion of M+Cu fused;

pterostigma strongly inflated. ABDOMEN: lateral margin of laterotergite 1+2 with small spine; dorsal abdominal scent gland (DAG) I ostioles in adults present; distal sternites keeled; connexivum with rim along entire length; posterior margin of tergum 7 straight. Genitalia: hairs down middle ventrally; pygophore posterior margin round.

Female. Unknown

Distribution. Cuba.

Discussion. See Gil-Santana et al. (2013).

Material examined. CUBA: Santiago: Palma Peak, Sierra Maestra, 1386 m, 10 Jul 1922 - 20 Jul 1922, S. C. Bruner & C. H. Ballou, Holotype of Junior Synonym, 1; (UCR_ENT 00008147) (USNM).

Ectrichodiella nouraguensis, **n. sp.**

Figs. 1D-F, 2E, F, 3E, F, 4C, D, 5E, F, 6B, D, 7B, 8E, F, 9H-N)

Diagnosis. Scape with large subapical spine; eye height about 0.6 height of head; ocelli small, on individual elevations; third labial segment (second visible) is 0.5 length of second segment; yellow coloration on hemelytron on proximal part of veins and in adjacent cells; posterior margin of tergum 7 straight; sternum 8 posterior margin strongly sinuous with ridges along the middle ventrally.

Description. MALE: Dimensions (in mm): habitus length to posterior wing margin: 3.64; habitus length to abdomen margin: 3.32; head length excluding neck: 0.52; head greatest width: 0.63; head anteocular: 0.14; head postocular: 0.13; synthlipsis: 0.49; scape: 0.79; second labial

segment (1st visible): 0.48; third labial segment (2nd visible): 0.35; thorax length: 1.12; anterior pronotal lobe greatest length: 0.16; posterior pronotal lobe greatest length: 0.44; scutellum greatest length: 0.31; abdomen length: 1.68; greatest width at abdomen: 1.6. Macropterous, small body size. COLORATION: Body dark brown; eye dark brown; antennal hair color light; thorax dark brown with posterior pronotal lobe brown; legs yellow with band of brown on femur, hemelytron with corium brown with yellow band proximally with veins brown and yellow, yellow coloration on hemelytron on proximal part of veins and in adjacent cells (Fig. 7B); connexivum medium brown, and patterned with contrasting brown and yellow markings, with suture yellow. VESTITURE: head with light yellow colored hair, with fringe of white hairs behind eyes, labium hairs small, yellow, thin; antenna hair greater than 2x the diameter of the antenna segment; pronotum sparse short yellow hairs laterally; thorax with short, fine, yellowish hairs ventrally; scutellum long thin yellow hairs along sides; small tubercles on hind trochanter; hemelytra with sparse, short, yellow, hairs; connexivum with yellow short hairs on ventral side. STRUCTURE: HEAD: antennal insertion protected laterally by a small sclerite; interocular sulcus most pronounced at middle of head; width of synthlipsis 2x eye size; posterolateral gula area in lateral view very swollen (Fig. 2E). Antenna: scape with large subapical spine (Fig. 3F); scape and pedicel thickened; diameter of flagellomere smaller than diameter of pedicel. Eye: large, in lateral view reniform, eye height about 0.6 height of head, in ventral view quarter spherical; 2 hemispherical elevations between eyes; ocellar lens present; ocelli small, on individual elevations (Fig. 2E); groove between ocelli. Labium: second labial segment (first visible) curved, third labial segment (second visible) is 0.5 length of second segment (Fig. 4C), fourth segment (third visible) reaching thorax. THORAX: pronotum bell shaped with surface smooth, anterior edge rounded, anterior pronotal lobe less than half length of posterior pronotal

lobe and more than half width of posterior pronotal lobe; lateral ridges present (Fig. 5E); anterior lobe with paired, rounded process on disc present; with pair of glabrous areas posterior to anterior lobe process; prosternal stridulatory process long, surpassing posterior margin of procoxal cavity; scutellum triangular with apex drawn into spine; paramedian scutellar processes, with two large, strongly vertical, midlateral projections (Fig. 5F). Leg: paired ventroapical projections on forefemur; fossula spongiosa on foreleg absent, tibia dilation at tip (Fig. 6A td); tibial comb at distal margin of tibia; tarsi 2-segmented. Hemelytra: 2 closed cells of unequal size; proximal portion of M+Cu separated; pterostigma slightly inflated (Fig. 7B). ABDOMEN: lateral margin of laterotergite 1+2 only slightly expanded; dorsal abdominal scent gland (DAG) I ostioles in adults present; sternites 4 through posterior margin of sternite 7 keeled; posterior margin of tergum 7 straight (Fig. 8E). Genitalia: sternum 8 posterior margin strongly sinuous; pygophore posterior margin straight, with ridges along the middle ventrally (Fig. 9H), hair around outside.

Female. unknown

Etymology. The species is named for Nouragues Nature Reserve in French Guiana where it was collected.

Distribution. French Guiana.

Discussion. See discussion under *E. caballina* **n. sp.**

Material examined. FRENCH GUIANA: Cayenne: Regina, Pararé, Nouragues Nat. Res.; 4.03800, -52.67286; 70 m (230 ft); 01 Nov 2009; SEAG; Holotype; (UCR_ENT 00127900) (MNMH).

Ectrichodiella rafaeli (Gil-Santana and Coletto-Silva, 2005)

Revised diagnosis. Antenna without subapical spine; ocelli not elevated; eye small; lateral ridges absent; proximal portion of M+Cu fused; proximal portion of M+Cu fused; lateral margin of laterotergite 1+2 with large, curved spine.

Re-description. FEMALE: Dimensions (in mm): habitus length to posterior wing margin 3.8. COLORATION: Body brownish; eye dark; antennal hair light; thorax darker, with posterior pronotal lobe caramel; legs reddish; hemelytron with corium uniformly brown, with veins uniformly yellow; connexivum uniformly dark yellow, with suture intersegmental sutures white. VESTITURE: head covered posteriorly and ventrally with white fringe hairs; labium with short, light colored hairs; antenna hair under 2x the diameter of the antenna segment; thorax with covered with long, fine yellowish hairs and short whitish hairs on anterior margin; pronotum brown with many long, thin hairs; scutellum with short hairs; small tubercles on hind trochanter; hemelytra with sparse fine hairs; abdomen with first sternite with fringe of short white hairs, others with sparse long bright hairs; connexivum with long bright hairs mainly on margin. STRUCTURE: HEAD: antennal insertion protected laterally by a small sclerite present, with subapical spine on scape absent; width of synthlipsis more than 3x the eye size; posterolateral gula area in lateral view very swollen. Antenna: scape without subapical spine; scape and pedicel thickened, diameter of flagellomeres smaller than diameter of pedicel. Eye: small, in lateral view reniform, above ventral head margin; 2 hemispherical elevations between the eyes absent; ocellar lens present; ocelli small; not elevated. Labium curved at third segment (second visible); third labial segment (second visible) is 0.5 length of second labial segment (first visible); last segment (third visible) reaching anterior margin of thorax. THORAX: pronotum bell shaped, with surface granulose on lateral sides of anterior lobe; anterior edge rounded; posterior lobe with median

groove; anterior lobe more than half length and less than half width of posterior, pronotal longitudinal depression on anterior lobe present; lateral ridges absent; anterior lobe with paired, rounded processes on disc present, with pair of glabrous areas on posterior corners present; prosternal stridulatory process length unknown; scutellum triangular with apex drawn into spine; paramedian scutellar processes, with two small, mostly horizontal, midlateral projections present. Leg: paired ventroapical projections on forefemur; fossula spongiosa on foreleg absent; tibia dilated at tip, with tibial comb at distal margin; tarsi 2-segmented. Hemelytra: 2 closed cells of unequal size; proximal portion of M+Cu fused; pterostigma strongly inflated. ABDOMEN: lateral margin of laterotergite 1+2 with large, curved spine; dorsal abdominal scent gland (DAG) I ostioles in adults present; sternites 1–5 keeled; connexivum with crest on inner margin.

Male. Unknown

Distribution. Brazil.

Discussion. See Gil-Santana et al. (2013).

Material examined. Only photographs were seen.

References

Bruner, S.C., Barber, H.G., 1937. Additional notes on Cuban Reduviidae (Hemiptera-Heteroptera). Memorias la Soc. Cuba. Hist. Nat. 11, 181–190.

Forero, D., Choe, D.-H., Weirauch, C., 2011. Resin gathering in Neotropical resin bugs (Insecta: Hemiptera: Reduviidae): Functional and comparative morphology. J. Morphol. 272. https://doi.org/10.1002/jmor.10907

Forthman, M., Chłond, D., Weirauch, C., 2016. Taxonomic monograph of the endemic millipede assassin bug fauna of Madagascar (Hemiptera: Reduviidae: Ectrichodiinae), Bulletin of the American Museum of Natural History. https://doi.org/10.1206/amnb-928-00-01.1

Forthman, M., Weirauch, C., 2018. Phylogenetic comparative analysis supports aposematic colouration–body size association in millipede assassins (Hemiptera: Reduviidae: Ectrichodiinae). J. Evol. Biol. 31. https://doi.org/10.1111/jeb.13288

Forthman, M., Weirauch, C., 2017. Millipede assassins and allies (Heteroptera: Reduviidae: Ectrichodiinae, Tribelocephalinae): total evidence phylogeny, revised classification and evolution of sexual dimorphism. Syst. Entomol. 42. https://doi.org/10.1111/syen.12232

Forthman, M., Weirauch, C., 2016. Phylogenetics and biogeography of the endemic Madagascan millipede assassin bugs (Hemiptera: Reduviidae: Ectrichodiinae). Mol. Phylogenet. Evol. 100. https://doi.org/10.1016/j.ympev.2016.03.011

Forthman, M., Weirauch, C., 2012. Toxic associations: A review of the predatory behaviors of millipede assassin bugs (Hemiptera: Reduviidae: Ectrichodiinae). Eur. J. Entomol. 109. https://doi.org/10.14411/eje.2012.019

Fracker, S.B., Bruner, S.C., 1924. Notes on some Neotropical Reduviidae. Ann. Entomol. Soc. Am. 17, 163–174. https://doi.org/10.1093/aesa/17.2.163

Gil-Santana, H.R., Baena, M., Grillo, H., 2013. *Berengeria* Gil-Santana & Coletto-Silva, a junior synonym of *Ectrichodiella* Fracker & Bruner, with new records and taxonomic notes on Ectrichodiinae from Brazil, and with keys to Ectrichodiinae and Reduviinae genera of the New World (Hemiptera: Heteroptera: Reduviidae). Zootaxa 3652, 60. https://doi.org/10.11646/zootaxa.3652.1.2

Gil-Santana, H.R., Coletto-Silva, A., 2005. *Berengeria rafaeli*, gen. nov., sp. nov. de Reduviinae da Reserva Ducke, Estado do Amazonas, Brasil (Hemiptera-Heteroptera, Reduviidae). Acta Amaz. 35, 297–300. https://doi.org/10.1590/s0044-59672005000200019

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics. 24, 774–786. https://doi:10.1111/j.1096-0031.2008.00217.x

Haviland, M.D., 1931. The Reduviidae of Kartabo, Bartica district. Zoologica 129–154.

Hwang, W.S., Weirauch, C., 2012. Evolutionary history of assassin bugs (Insecta: Hemiptera: Reduviidae): Insights from divergence dating and ancestral state reconstruction. PLoS One 7. https://doi.org/10.1371/journal.pone.0045523

Iturralde-Vinent, M.A., 2006. Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. International Geology Review. 48, 791–827. https://doi:10.2747/0020-6814.48.9.791

Iturralde-Vinent, M.A., 2017. Overview of the geology of Cuba. Acta Geologica Sinica - English Edition. 91, 22–22. https://doi:10.1111/1755-6724.13160

Nixon, K.C., 2002. WinClada ver. 1.00.08. Published by the author, Ithaca, NY, USA.

Poinar, G., 2019. A primitive triatomine bug, *Paleotriatoma* metaxytaxa gen. et sp. nov. (Hemiptera: Reduviidae: Triatominae), in mid-Cretaceous amber from northern Myanmar. Cretac. Res. 93, 90–97. https://doi.org/10.1016/j.cretres.2018.09.004

Schuh, R.T., Weirauch, C., 2020. True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History (Second Edition). Siri Scientific Press.

Weirauch, C., 2010. *Tribelocodia ashei*, new genus and new species of Reduviidae (Insecta: Hemiptera), has implications on character evolution in Ectrichodiinae and Tribelocephalinae. Insect Syst. Evol. 41. https://doi.org/10.1163/187631210X497308

Weirauch, C., Forthman, M., Grebennikov, V., Baňař, P., 2017. From Eastern Arc Mountains to extreme sexual dimorphism: systematics of the enigmatic assassin bug genus *Xenocaucus* (Hemiptera: Reduviidae: Tribelocephalinae). Org. Divers. Evol. 17. https://doi.org/10.1007/s13127-016-0314-2

Wygodzinsky, P., 1966. A monograph of the Emesinae (Reduviidae, Hemiptera). Bull. Am. Museum Nat. Hist. 133, 1–616.

Figure legends

Fig. 1 Dorsal, lateral, and ventral habitus. **A-C.** *E. caballina* **n. sp.**; **D-F.** *E. nouraguensis* **n. sp.**; **G, H.** *E. electrina* **n. sp.**

Fig. 2 Dorsal **(A, C, E)** and lateral **(B, D, F)** head structures. **A, B.** *E. caballina* **n. sp.**; **C, D.** *E. electrina* **n. sp.**; **E, F.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states

used in cladistic analysis. **as**, antenna protection sclerite; **gl**, gula; **L2**, labial segment 2 (first visible); **L3**, labial segment 3 (second visible); **L4**, labial segment 4 (third visible); **oc**, ocelli; **sas**, subapical spine on antenna.

Fig. 3 Antenna morphology **(A, C, E)** and subapical spine **(B, D, F)**. **A, B.** *E. caballina* **n. sp.**; **C, D.** *E. electrina* **n. sp.**; **E, F.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **sas**, subapical spine on antenna.

Fig. 4 Lateral **(A, C)** and ventral **(B, D)** labium structures. **A, B.** *E. caballina* **n. sp.**; **C, D.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **L2**, labial segment 2 (first visible); **L3**, labial segment 3 (second visible); **L4**, labial segment 4 (third visible); **psp**, prosternal stridulatory process.

Fig. 5 Dorsal **(A, C, E)** and lateral **(B, D, F)** thorax structures. **A, B.** *E. caballina* **n. sp.**; **C, D.** *E. electrina* **n. sp.**; **E, F.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **alp**, anterior lobe processes; **asp**, apex scutellum spine; **lr**, lateral ridges; **mp**, midlateral projections; **msn**, mesonotum; **mtn**, metanotum; **pg**, prosternal groove; **ple**, paramedian lobe-like extensions on the posterior margin of the posterior pronotal lobe; **sc**, scutellum; **ts1**, tarsal segment 1; **ts2**, tarsal segment 2.

Fig. 6 Leg structures **A.** Leg, **B.** Trochanter, ventral view; **C.** Paired ventroapical projections, ventral view; **D.** Tarsi and claws, lateral view. **A, C.** *E. caballina* **n. sp.**; **B, D.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **td**, tibial dilation; **ts1**, tarsal segment 1; **ts2**, tarsal segment 2; **vap**, paired ventroapical projections.

Fig. 7 Hemelytron morphology. **A.** *E. caballina* **n. sp.**; **B.** *E. nouraguensis* **n. sp.**; **C, D.** *E. electrina* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **1A**, first anal vein; **Cu**, cubitus; **exM**, extension of M beyond M+Cu; **M**, medius; **pt**, pterostigma.

Fig. 8 Ventral **(A, C, E)** and lateral **(B, D, F)** abdomen structures. **A, B.** *E. caballina* **n. sp.**, **C, D.** *E. electrina* **n. sp.**, **E, F.** *E. nouraguensis* **n. sp.** Numbers refer to characters and character states used in cladistic analysis. **DAG1**, dorsal abdominal gland 1; **DAG2**, dorsal abdominal gland 2; **DAG3**, dorsal abdominal gland 3; **py**, pygophore; S3-8, sterna 3-8; **T1-2**, synterga 1 and 2; **T3-7**, terga 3-7.

Fig. 9 Dorsal, ventral, and lateral pygophore morphology. **A-G.** *E. caballina* **n. sp.**; **A.** Ventral external morphology, **B-D.** Pygophore ventral, dorsal, lateral views respectively, **E-G.** Aedeagus dorsal, lateral, ventral views respectively; **H-N.** *E. caballina* **n. sp.**, **H.** Ventral external morphology, **I-K.** Pygophore ventral, dorsal, lateral views respectively, **L-N.** Aedeagus dorsal, lateral, ventral views respectively; **O, P.** Ventral external morphology *E. electrina* **n. sp.**, . Numbers refer to characters and character states used in cladistic analysis. **bp**, basal plate; **bpe**, basal plate extension; **ca**, carina; **pa**, paramere; **pr**, pygophore ridges; **py**, pygophore; **S8**, sternite 8.

Fig. 10 Distribution map of *Ectrichodiella* species.

Fig. 11 Phylogenetic hypothesis of *Ectrichodiella* based on all five ingroup species and five outgroups and 43 morphological characters. The tree shown is the strict consensus tree of the two best trees derived from the implied weights analysis with the k-value of 20. Values shown underneath branches are jackknife values.

Supplemental Material

Fig. S1 Phylogenetic hypothesis of *Ectrichodiella* based on all five ingroup species and five outgroups and 43 morphological characters. The tree shown is the strict consensus tree which collapsed *E. electrina* **n. sp.**, (*E. caballina* **n. sp.** + *E. nouraguensis* **n. sp.**), and (*E. minima* + *E. rafaeli*) into a polytomy. Values shown underneath branches are jackknife values.

Table. S1 Matrix formed from 43 morphological characters of the five ingroups and five outgroups. – represents unknown characters.

Figure 1.

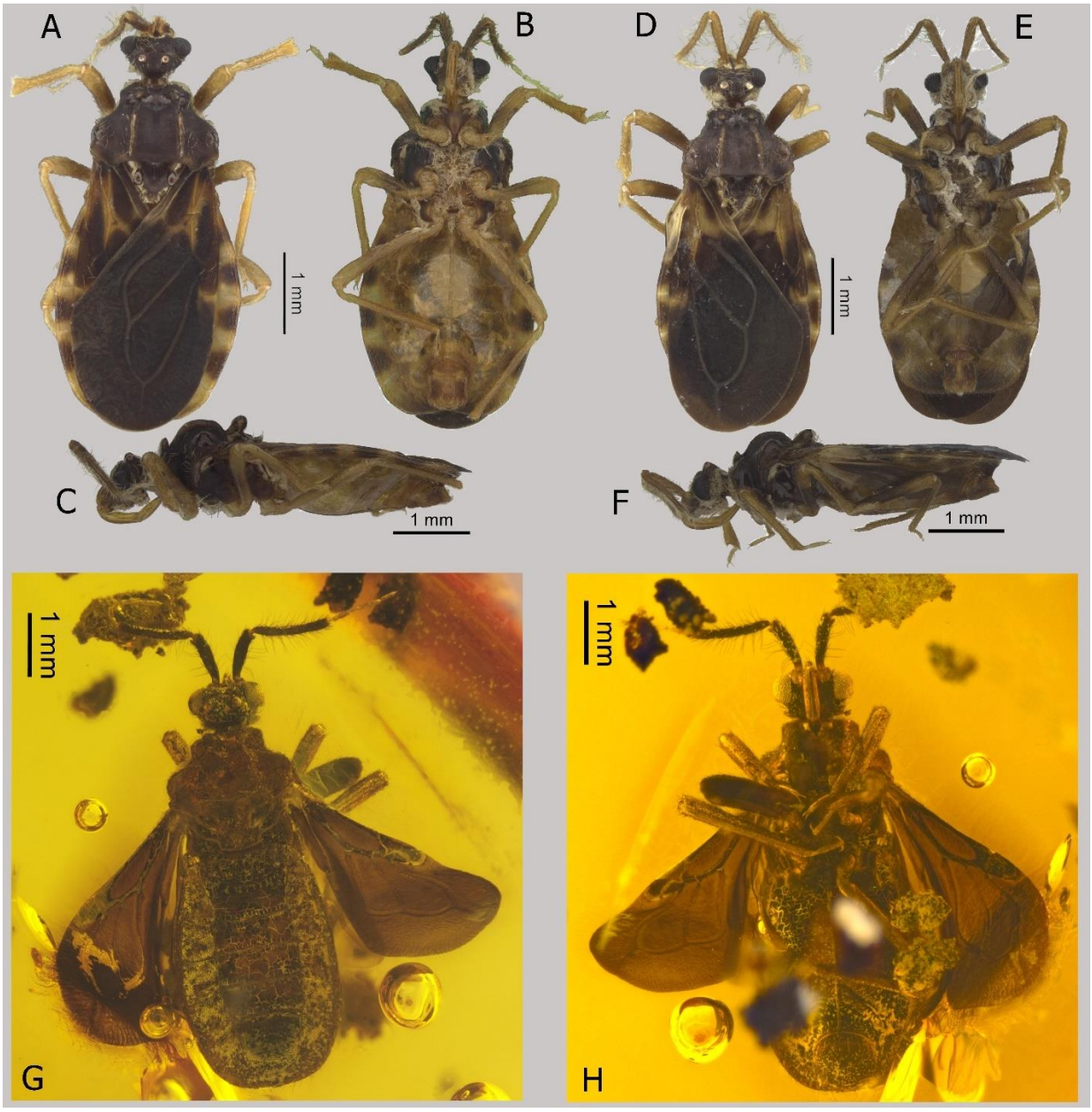


Figure 2.

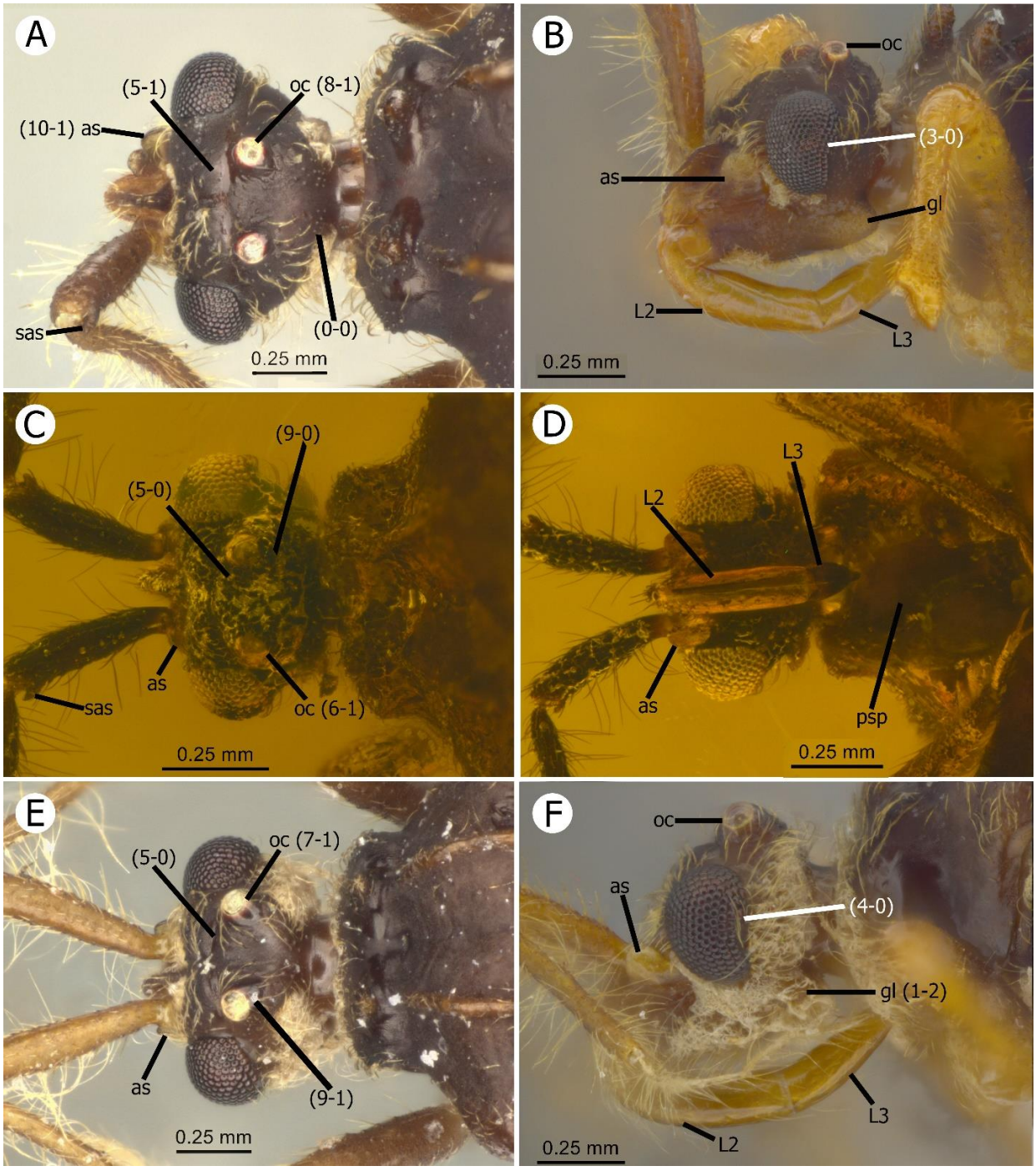

A
(5-1)
oc (8-1)
(10-1) as
sas
(0-0)
0.25 mm
B
oc
(3-0)
as
gl
L2
L3
0.25 mm
C
(9-0)
(5-0)
as
sas
oc (6-1)
0.25 mm
D
L3
L2
as
psp
0.25 mm
E
(5-0)
oc (7-1)
as
(9-1)
0.25 mm
F
oc
as
(4-0)
gl (1-2)
L3
L2
0.25 mm

Figure 3.

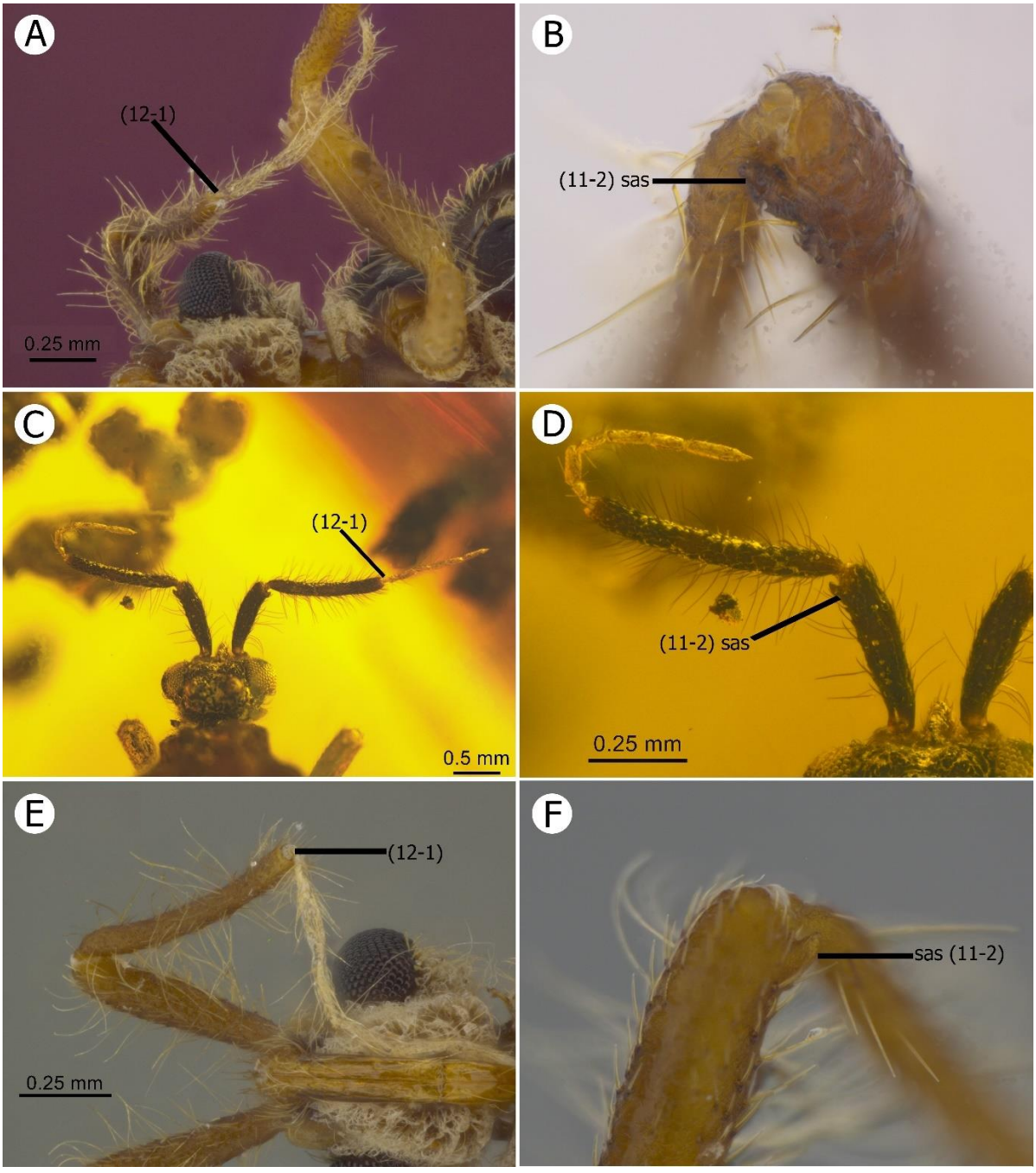

A
(12-1)
0.25 mm
B
(11-2) sas
C
(12-1)
0.5 mm
D
(11-2) sas
0.25 mm
E
(12-1)
0.25 mm
F
sas (11-2)

Figure 4.

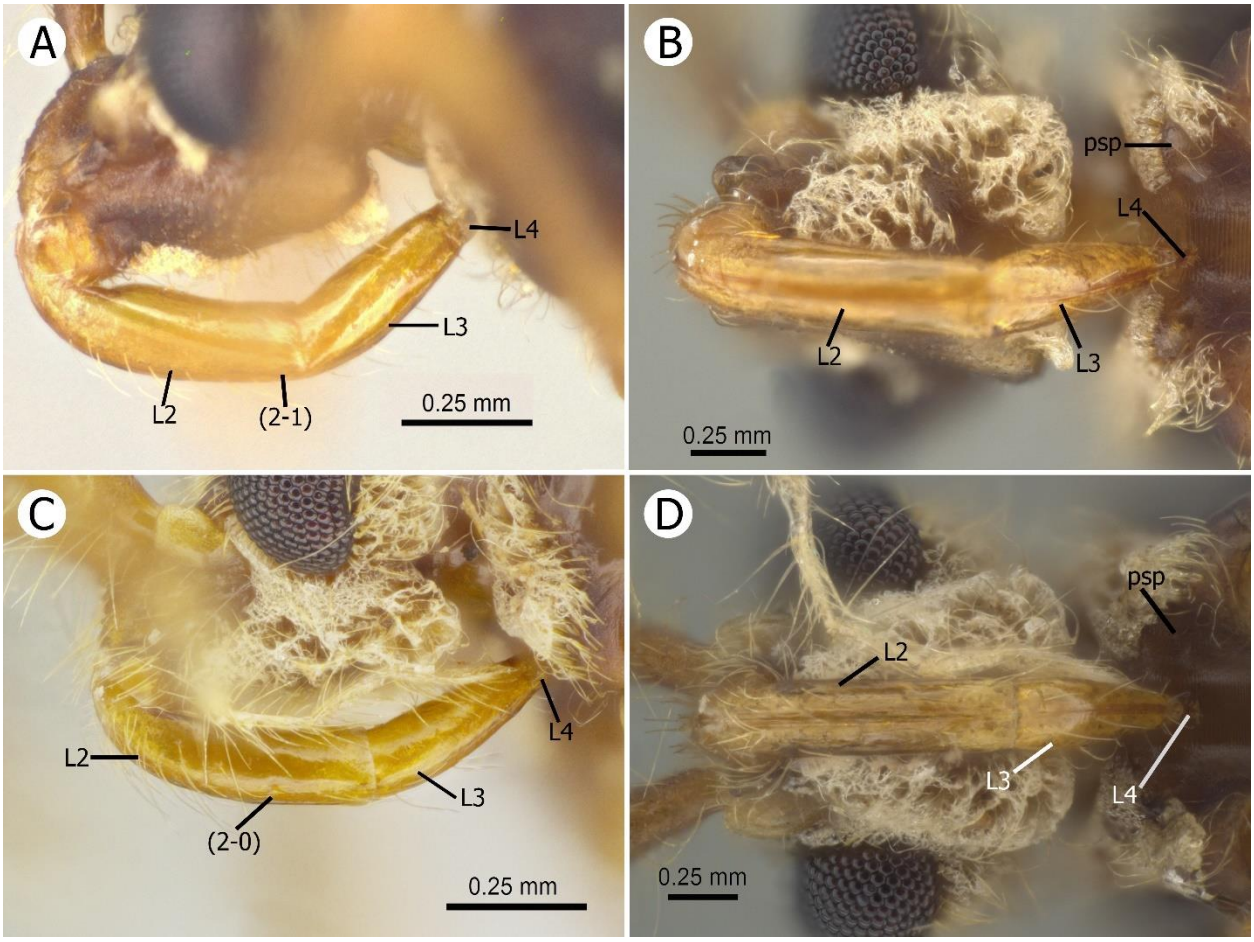

A
L4
L3
L2
(2-1)
0.25 mm
B
psp
L4
L2
L3
0.25 mm
C
L4
L2
L3
(2-0)
0.25 mm
D
psp
L2
L3
L4
0.25 mm

Figure 5.

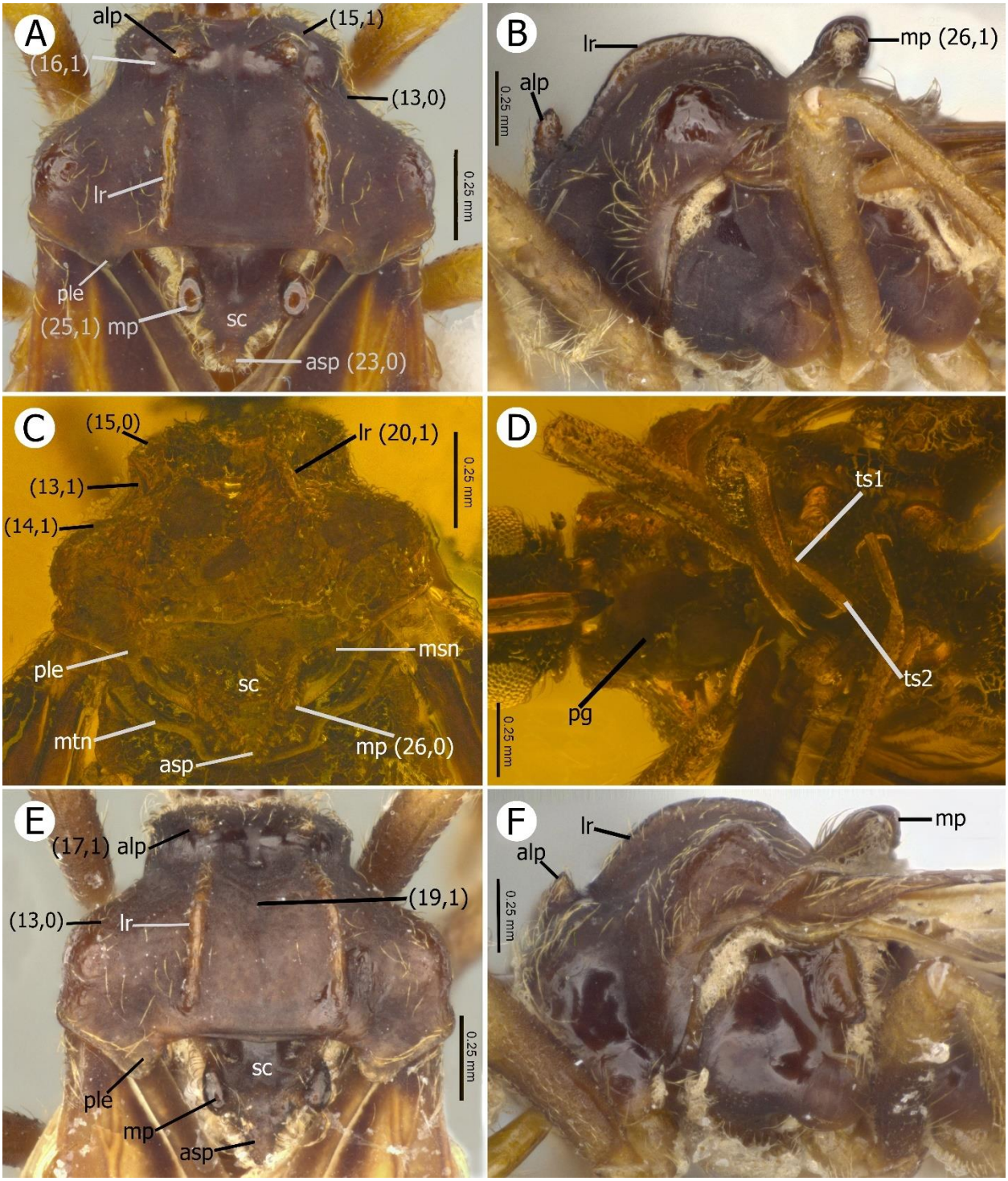

A
alp
(15,1)
(16,1)
(13,0)
lr
0.25 mm
ple
(25,1) mp
sc
asp (23,0)
B
lr
mp (26,1)
alp
0.25 mm
C
(15,0)
lr (20,1)
(13,1)
(14,1)
0.25 mm
msn
ple
sc
mtn
mp (26,0)
asp
D
ts1
ts2
pg
0.25 mm
E
(17,1) alp
(19,1)
(13,0)
lr
0.25 mm
sc
ple
mp
asp
F
lr
mp
alp
0.25 mm

Figure 6.

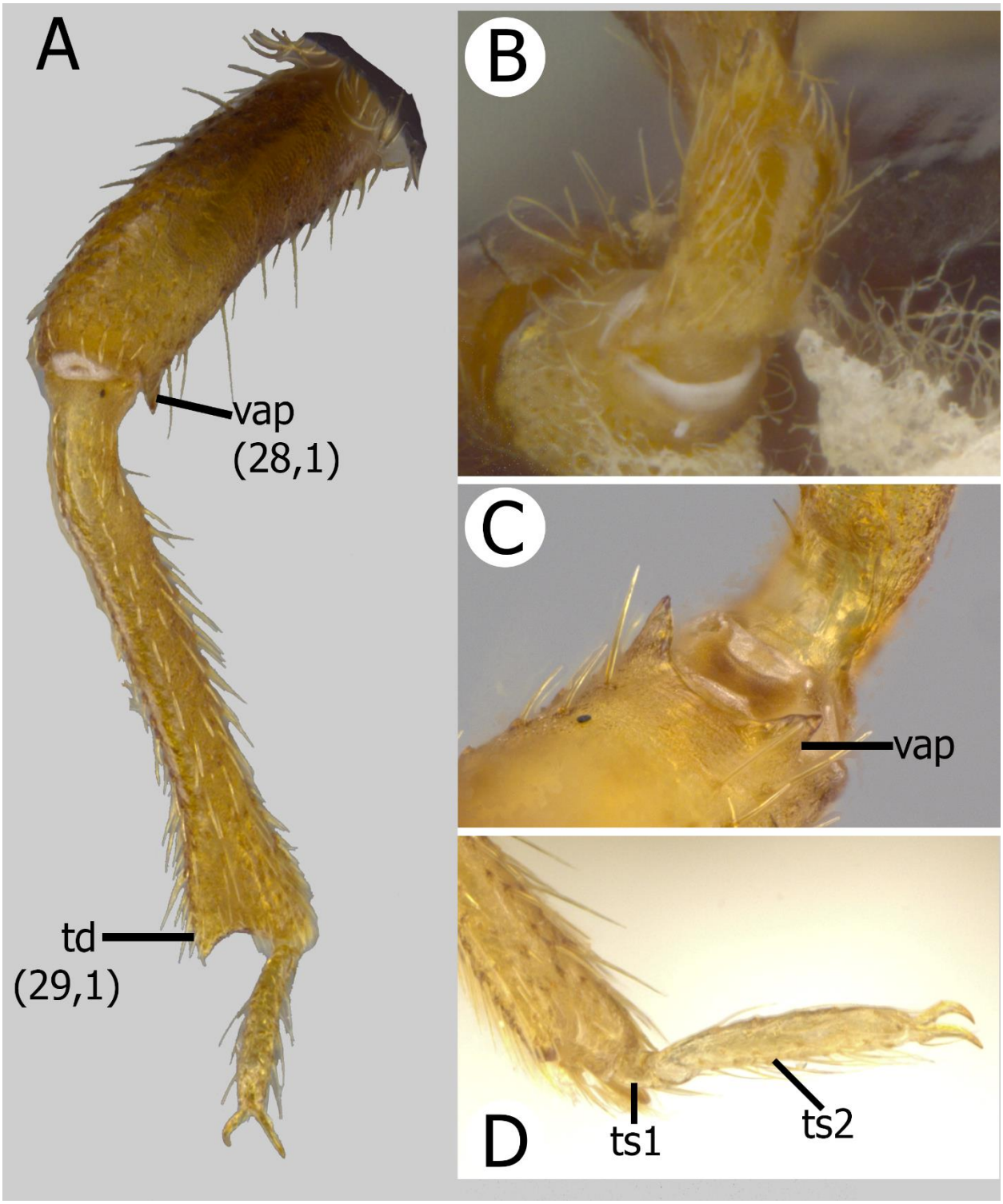


Figure 7.

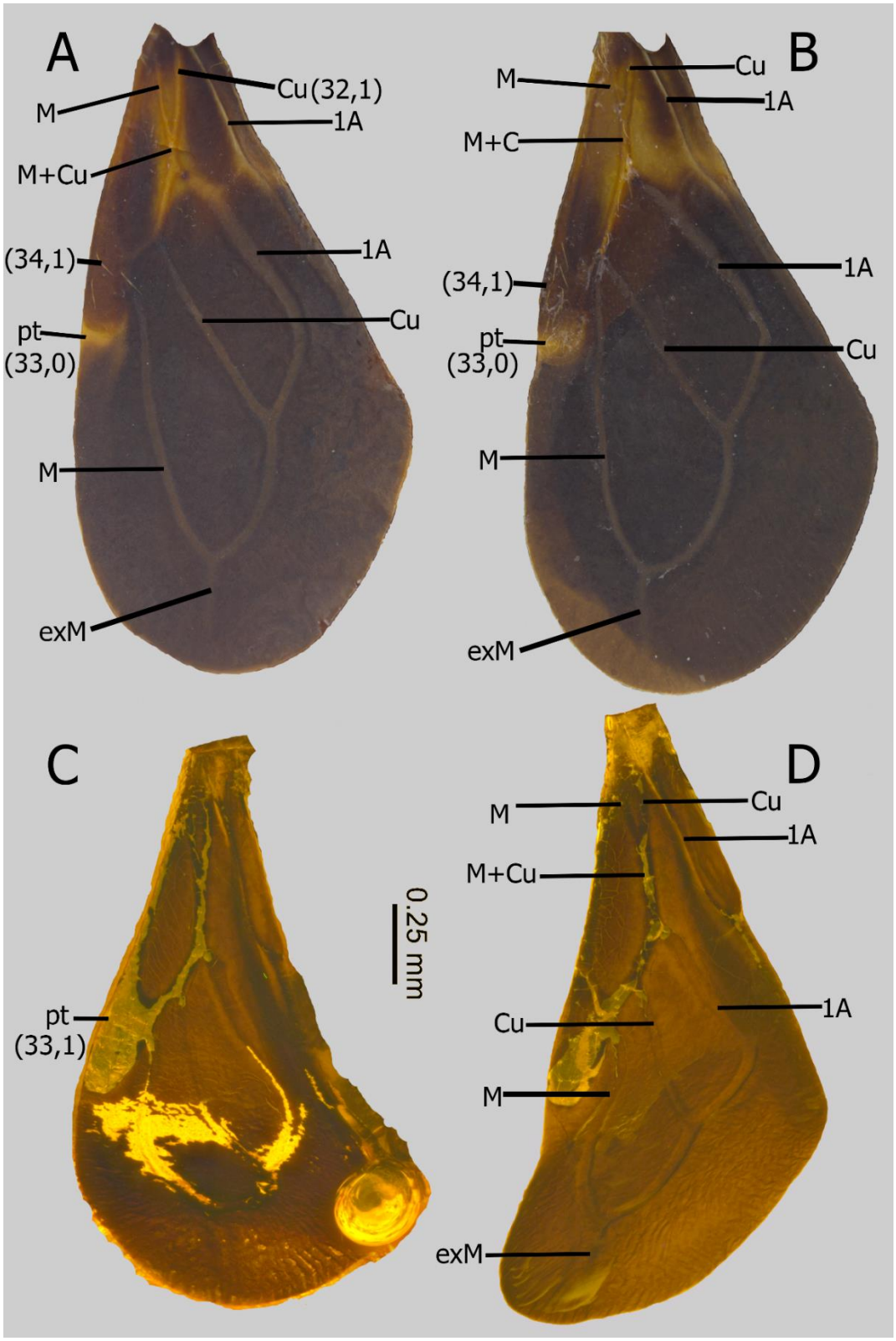

A
M
Cu(32,1)
1A
M+Cu
(34,1)
1A
pt
(33,0)
Cu
M
exM
B
M
Cu
1A
M+C
(34,1)
1A
pt
(33,0)
Cu
M
exM
C
pt
(33,1)
0.25 mm
D
M
Cu
1A
M+Cu
Cu
1A
M
exM

Figure 8.

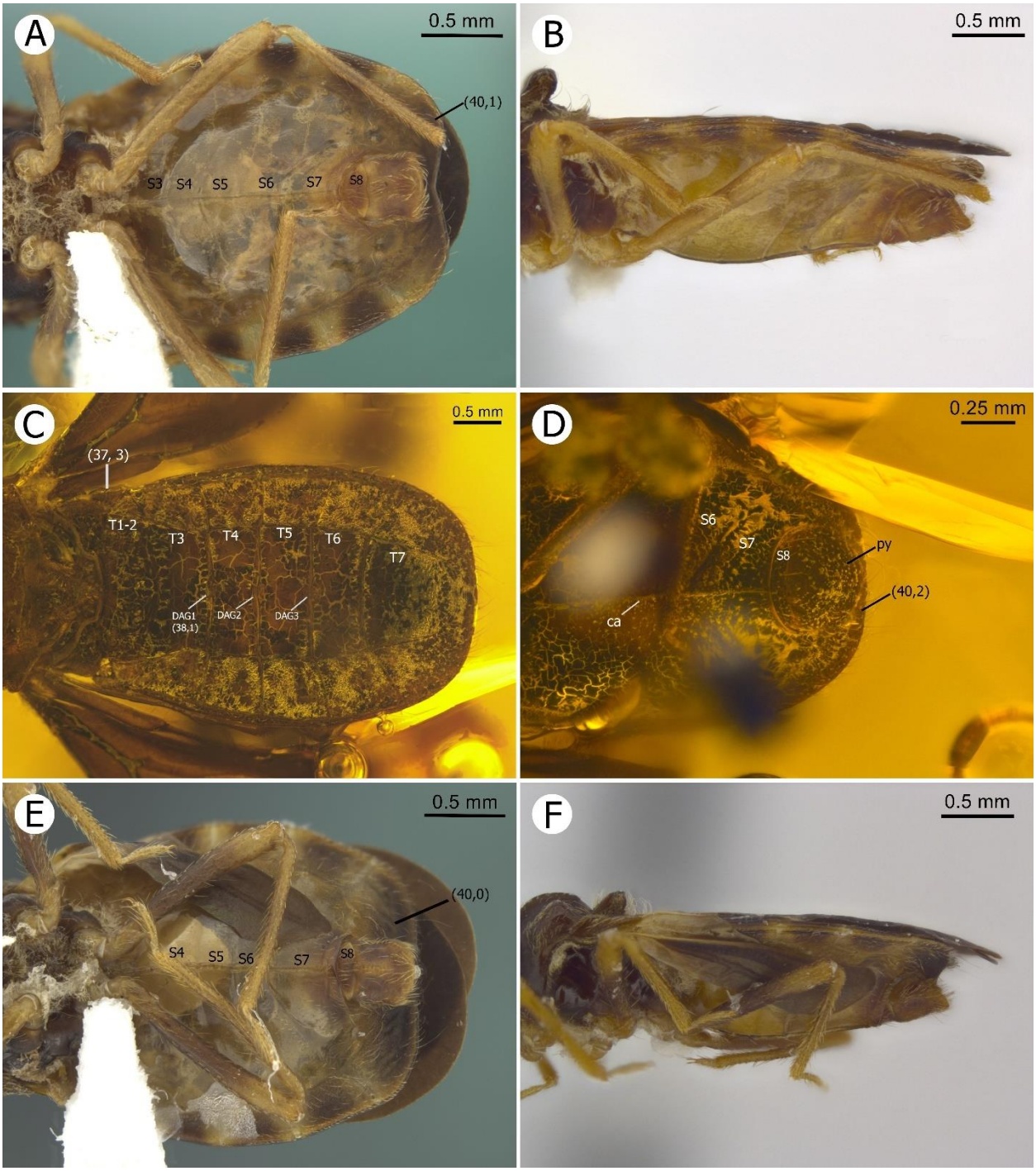

A
0.5 mm
(40,1)
S3
S4
S5
S6
S7
S8
B
0.5 mm
C
0.5 mm
(37, 3)
T1-2
T3
T4
T5
T6
T7
DAG1
(38,1)
DAG2
DAG3
D
0.25 mm
S6
S7
S8
py
(40,2)
ca
E
0.5 mm
(40,0)
S4
S5
S6
S7
S8
F
0.5 mm

Figure 9.

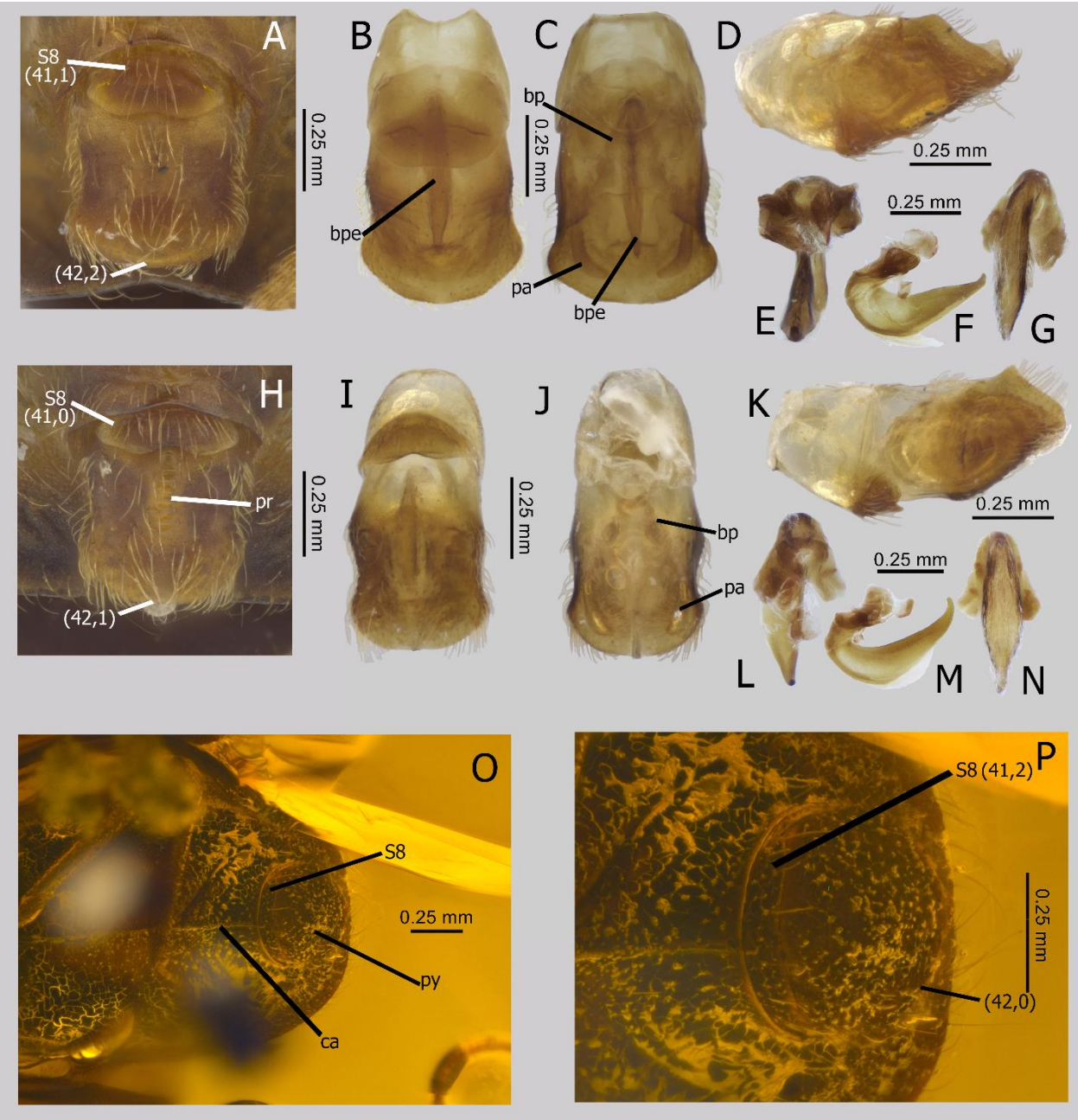

A
S8
(41,1)
(42,2)
B
bpe
0.25 mm
C
bp
pa
bpe
0.25 mm
D
0.25 mm
E
F
G
0.25 mm
H
S8
(41,0)
pr
(42,1)
I
0.25 mm
J
bp
pa
0.25 mm
K
0.25 mm
L
M
N
0.25 mm
O
S8
0.25 mm
py
ca
P
S8 (41,2)
0.25 mm
(42,0)

Figure 10.

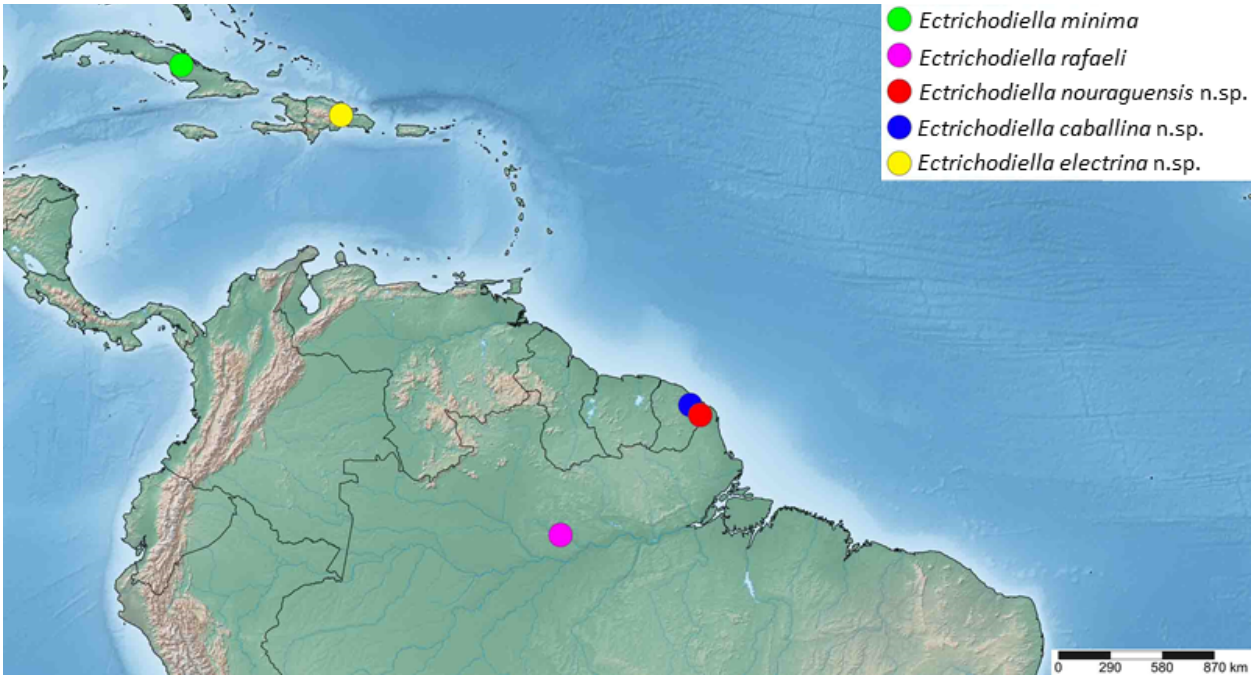
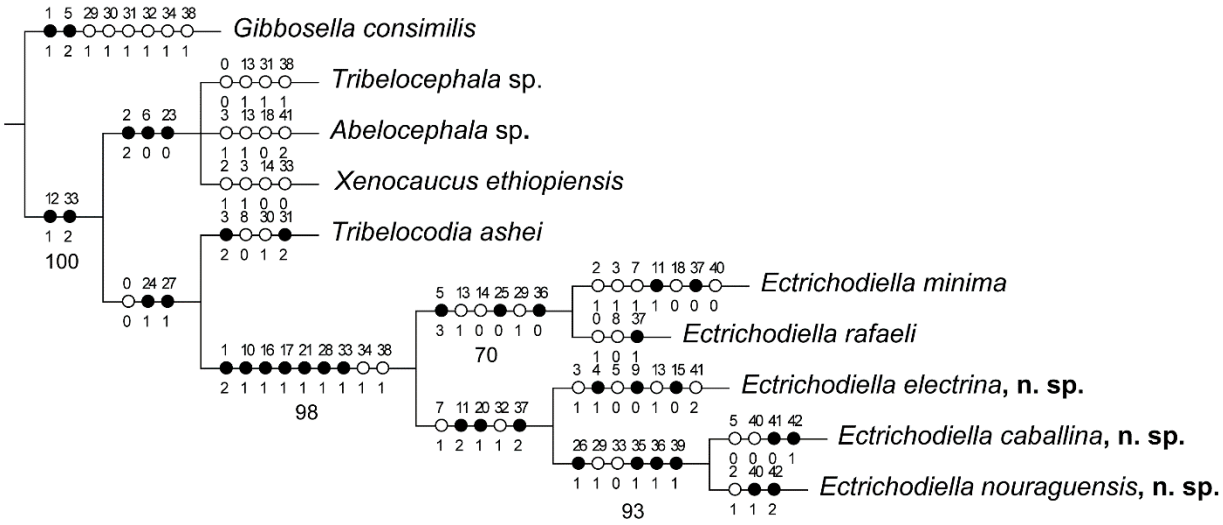
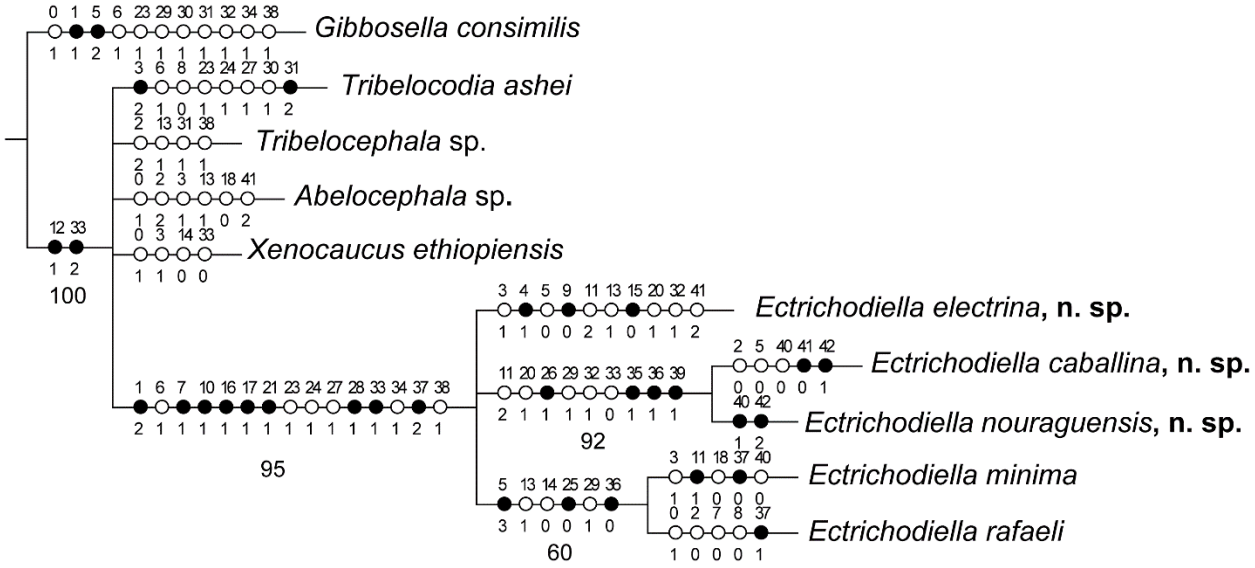


Figure 11.



Supplemental Figure S1.



Supplemental Table S1.

```
                                  0    5    10   15   20   25   30   35   40
                                  |    |    |    |    |    |    |    |    |
Ectrichodiella minima             02110311111111101110101-110011100011000100-0
Ectrichodiella rafaeli            120003100-10-101111101-110011100011001100---
Ectrichodiella nouraguensis n. sp.  020000111112101111111111111111100101112110001
Ectrichodiella caballina n. sp.   021001111112101111111111111111100101112112112
Ectrichodiella electrina n. sp.   02-1101110121110-1111111110--00011102210220
Tribelocodia ashei                00-201100-001011001100-111010012020023002-0
Tribelocaphala sp.                0020010---00-11-001100-00--0000102-023102-0
Abelocaphala sp.                  1021010---001111000100-00--0000002002300220
Xenocaucus ethiopiensis           1011010---001001001100100--0000000002300210
Ectrichodiini Gibbosella conisimilis 11-002101-000011001100110--00111101023102-0
```