INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA

Filogenia de Spongiphoridae (Insecta: Dermaptera), taxonomia de Mecomera Audinet-Serville (Sprattinae) e guia ilustrado com um novo método de armazenamento para o estudo das asas de Dermaptera

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Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas, área de concentração em Entomologia.

Manaus, Amazonas
Março de 2021

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R217f Heleodoro, Raphael Aquino
Filogenia de Spongiphoridae (Insecta: Dermaptera), taxonomia de Mecomera Audinet-Serville (Sprattinae) e guia ilustrado com um novo método de armazenamento para o estudo das asas de Dermaptera / Raphael Aquino Heleodoro; orientador José Albertino Rafael. -- Manaus:[s.l], 2021.
83 f.

Tese (Doutorado - Programa de Pós Graduação em Entomologia) -- Coordenação do Programa de Pós-Graduação, INPA, 2021.

1. filogenia. 2. taxonomia. 3. Spongiphoridae. 4. Dermaptera. I. Rafael, José Albertino, orient. II. Título.

CDD: 595.7

Sinopse:

Foi realizado um estudo filogenético e taxonômico de Spongiphoridae. O gênero *Mecomera* foi revisado, Mecomerini e Homotagini foram incluídas em Spongiphorinae; Cosmogeracini, Geracini, Pericomini e Sparattini foram incluídas em Sparattinae. Um novo método para armazenar asas de Dermaptera foi proposto.

Palavras Chave: Neotropical, Taxonomia, Filogenia, Dermaptera.

AGRADECIMENTOS

Gostaria de agradecer, primeiramente, a minha amada esposa e família: minha “marida”, Larissa, minha mãe, Célia, meu Pai, Renato, minha vó, Luzia, minha irmã, Luisa e meu primo-irmão, Victor. Vocês são a base da minha vida.

Em segundo lugar, ao meu orientador, José Albertino Rafael. Gostaria de um dia poder retribuir todas as chances e oportunidades que o senhor me concedeu.

Em terceiro lugar gostaria de agradecer aos irmãos que a vida me deu: Alberto Neto, Diego Mendes, Douglas Campos, João Rafael, Guilherme Alves, Marlus Almeida, Rafael Sobral e Renato Azevedo. Podem ter certeza, vocês foram uma das grandes razões pelas quais eu consegui “atravessar” mais essa batalha.

Em quarto lugar, um agradecimento especial ao grande amigo José Wellington de Morais. Muito obrigado por toda a sabedoria transmitida e por todas as prazerosas conversas e cafés.

Por último, deixo o lugar reservado para agradecer a Deus que, primeiramente, me permitiu que eu me conectasse com Ele e daí em diante me deu forças para continuar.

|俺は海賊王になる（Ore wa kaizoku-ō ni naru)

Uma pequena homenagem a “Mugiwara no Luffy”, que muitas vezes me alegrou e inspirou em momentos muito difíceis.

RESUMO

Os Dermaptera são insetos hemimetábolos terrestres com distribuição cosmopolita. São popularmente conhecidos no Brasil como “Tesourinhas”. Esses animais tem hábitos alimentares diversos e tem preferência por lugares estreitos, onde podem sempre estar em contato com alguma superfície. No mundo, existem cerca de 2.200 espécies, onde cerca de 540 pertencem a Spongiphoridae. Essa família pertence ao grupo dos Eudermaptera, que compreende as tesourinhas que perderam estruturas na genitália masculina. Segundo estudos moleculares recentes, essa família é filogeneticamente e taxonomicamente mal definida, sendo considerada um grupo “lixão”, onde as espécies de Eudermaptera que não tem posicionamento certo são colocadas. Não existe um estudo morfológico robusto acerca da filogenia de Spongiphoridae. Devido a isso, a presente tese objetivou investigar morfologicamente a sistemática de Spongiphoridae. Como resultado, o gênero *Mecomera* Audinet-Serville foi revisado, bem um novo método e guia ilustrado que ensina como abrir e montar asas de Dermaptera foi feito. Esse novo método surgiu da necessidade e dificuldade de abrir as asas das tesourinhas, que são as asas com as dobras mais complexas dentre os insetos. Filogeneticamente, Spongiphoridae resultou como um grupo monofilético, dando suporte a duas grandes subfamílias: Labiinae e Spongiphorinae. Cosmogeracini, Geracini, Pericomini e Sparattini foram transferidos para Labiinae, enquanto Mecomerini, Homotagini e *Strongylolabis* foram transferidos para Spongiphorinae. Todas as tribos aqui trabalhadas foram ilustradas e tiveram sua diagnose atualizada. Ainda, foram encontradas sinapomorfias inéditas para Eudermaptera.

ABSTRACT

The Dermaptera are terrestrials hemimetabolous insects, with cosmopolitan distribution. In Brazil, they are popularly known as “tesourinhas”. These animals have diverse feeding habits and have preference for narrow places, where they can always be in touch with a surface. There are around 2,200 species worldwide, out of which 540 belong to Spongiphoridae. This family is assigned to the Eudermaptera, a group of earwigs which had suffered reduction of structures from male genitalia. According to recent molecular studies, this family is phylogenetically and taxonomically poorly defined, being considered as a “catch-all” group, where the Eudermaptera species which do not have a defined position are assigned. There is no robust phylogeny based on morphological data. Due to it, the present thesis aimed to investigate the systematics of Spongiphoridae with a morphological approach. Resulting, *Mecomera* Audinet-Serville was revised, as well as a guide on how to stretch and preserve the wings of Dermaptera with a new method was published. This new method risen from the need of stretching the earwig wings, which have the most complex folding system among all insects. Phylogenetically, Spongiphoridae resulted as monophyletic and supporting two large subfamilies: Labiinae and Spongiphorinae. Cosmogeracini, Geracini, Pericomini and Sparattini were transferred to Labiinae, whilst Mecomerini, Homotagini and *Strongylolabis* were transferred to Spongiphorinae. All the assigned tribes were illustrated and had their diagnosis updated. Furthermore, new morphological synapomorphies for Eudermaptera were found.

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INTRODUÇÃO GERAL

Dermaptera é uma ordem de insetos popularmente conhecidos no Brasil como tesourinhas ou lacrainhas (Haas, 2012). O nome da ordem é originado no grego derma = pele e pteron = asa e faz referência às tégminas grossas e coriáceas dos indivíduos (Haas, 2012). Os dermápteros são terrestres, caracterizados pelo corpo alongado, geralmente com 3 a 85 mm de comprimento e desenvolvimento hemimetábolo. São, insetos noturnos e podem ocupar diversos hábitats. Graças à tigmotaxia (preferência por estar em contato com superfícies) são comumente encontrados em frestas e espaços estreitos, como debaixo de cascas de árvore ou pedras, em inflorescências e axilas de folhas (Haas, 2012). A dieta dos dermápteros também é diversa e inclui desde fontes animais (predação ou utilização da matéria em decomposição), bem como fontes vegetais. Existem também, espécies que se reproduzem e se alimentam em esterco, como Labia minor (Linneaus, 1758) (Haas, 2012).

Os dermápteros possuem cabeça prognata, sem ocelos; mesotórax curto, mas não fundido com o metatórax; tégmina e asa posterior presentes, comumente reduzidas (raramente ausentes), sendo a asa posterior densamente dobrada e assim possuem o sistema de dobras mais complexo entre os insetos; abdômen com dez segmentos visíveis para machos e ninfas e sete para fêmeas; cercos dos adultos em formato de pinça. A coloração das tesourinhas é relativamente uniforme e predominantemente amarela, marrom e/ou preta (Haas, 2012). No mundo existem aproximadamente 2.200 espécies descritas, sendo 303 registradas na América do Sul (Hopkins et al. 2016) e 135 no Brasil (Vieira et al. 2021). As 2.200 espécies estão distribuídas em 11 famílias de dermápteros recentes (não fósseis): Anisolabididae, Apachyidae, Arixeniidae, Chelisoschidae, Diplatyidae, Forficulidade, Hemimeridae, Karschiellidae, Labiduridae, Pygidicranidae e Spongiphoridae. No Brasil são registradas Anisolabididae, Diplatyidae, Forficulidade, Labiduridae, Pygidicranidae e Spongiphoridae.

Dentre as famílias supracitadas, a única que não possui uma diagnose concisa é Spongiphoridae. Essa família compreende a cerca de 540 espécies no mundo todo e é a única família de Dermaptera que possui um grande grupo de espécies exclusivamente neotropicais: Sparattini (Sparattinae). Essa tribo é subdivida em *Mecomera* Audinet-Serville, 1838 (três espécies) e *Sparatta* Audinet-Serville, 1838 (28 espécies) e é caracterizada pelos indivíduos possuírem o corpo achatado dorsoventralmente, uma adaptação para o local de vida desses insetos, que é debaixo de cascas de árvore caídas em estágio moderado de decomposição. Ambos os gêneros necessitam de revisão.

Spongiphoridae faz parte de Eudermaptera, um grupo de tesourinhas cujo os integrantes sofreram reduções nas estruturas do lado direito da genitália masculina. O órgão fálico dos dermápteros, com exceção de Eudermaptera, possui estruturas pareadas no lado esquerdo e direito.

Em estudos moleculares recentes, tanto Naegle et al. (2016) e Wipfler et al. (2020) consideraram Spongiphoridae como polifilético, além de ser um grupo "lixão", onde diversas espécies de Eudermaptera que não tem posicionamento bem definido são alocadas. No entanto, apesar desses dois estudos concordarem, os dois estudos têm poucas espécies de Spongiphoridae amostradas. Ainda, não existem estudos filogenéticos robustos que estudam essa família do ponto de vista morfológico. Um dos prováveis motivos para isso é o complexo sistema de dobras das asas das tesourinhas, uma estrutura que foi muito pouco estudada dentro de Dermaptera, mas que tem seu valor filogenético já demonstrado por Haas & Kukalová-Peck (2001).

OBJETIVOS

- **Objetivo Geral**
  - Realizar o estudo filogenético de Spongiphoridae e contribuir para sua taxonomia.

- **Objetivos específicos**
  - Revisar *Mecomera;*
  - Verificar a monofilia das subfamílias atuais;
  - Aplicar as mudanças taxonômicas pertinentes que tiverem respaldo na filogenia;
  - Propor um guia para dissecção das asas posterior de Dermaptera.

CAPÍTULO I

Heleodoro, R.A., Alves-Oliveira, J.R., & Rafael, J.A. 2019. *Mecomera* Audinet-Serville, 1839 (Dermaptera: Spongiphoridae): proposal of new diagnosis, descriptions and illustrations for all three-known species. *Zootaxa*, 4577: 117-130.

Zootaxa 4577 (1): 117–130
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4577.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:8EC74D92-C774-4D5D-82D8-E064DE3F7081

Mecomera Audinet-Serville, 1839 (Dermaptera: Spongiphoridae): proposal of new diagnosis, descriptions and illustrations of all three-known species

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Abstract

Mecomera Audinet-Serville, 1839 (Spongiphoridae: Sparattinae) is a neotropical genus with three species: *M. brunnea* Audinet-Serville, *M. chacoensis* (Borelli) and *M. reichardti* Brindle. By comparing specimens of the three *Mecomera* species (types and ordinary material) to their respective original descriptions and drawings, it was determined that the descriptions are over-simplified and the drawings are not fully accurate. To prevent future identification problems, new diagnosis, descriptions and images of the external body and male genitalia of the three *Mecomera* species are provided.

Key words: earwigs, Insecta, Neotropical region, Sparattinae

Introduction

Dermaptera comprises approximately 2.200 species worldwide (Haas 2012), of which 510 belong to Spongiphoridae (Hopkins *et al.* 2016). In Brazil, there are 53 known species of Spongiphoridae, of which 17 belong to Sparattinae (Vieira & Chagas 2017), a well-marked subfamily, recognized by having the body strongly flattened dorsoventrally and with a prominent neck (Brindle 1968, Steinmann 1990). Sparattinae is subdivided into Auchenomini, Chaetospanini and Sparattini; only the latter occurs in the Neotropic region. Sparattini is characterized by having the pronotum not armed and cercus having few short setae (Steinmann 1990). The Sparattinae are divided into two genera: *Sparatta* Audinet-Serville, 1838, with 28 species (14 species occurring in Brazil) and *Mecomera* Audinet-Serville, 1839 with three species: *M. brunnea* Audinet-Serville, 1839, *M. chacoensis* (Borelli, 1912) and *M. reichardti* Brindle, 1971 (Hopkins *et al.* 2016; Vieira & Chagas 2017), of which only *M. chacoensis* does not occur in Brazil.

By analyzing specimens of the three species of *Mecomera* (types and ordinary material), it was observed that the drawings and descriptions presented by previous authors are a bit inaccurate from what the real specimens are. For instance, in the description of *M. reichardti* it is stated that pygidium is dorsally rounded and has two postero-lateral projections, which are subdivided into two lobes each (Brindle 1971). The drawing, in the same work, shows the rounded aspect of the pygidium and its two projections but does not represent the projections as if they were subdivided in two lobes each. This contrast between drawing and description may cause uncertainty while identifying a specimen. Furthermore, by looking at the types of *M. reichardti*, it was noticed that the drawing and the description are over-simplified. Hence, the aim of this work is to provide images and descriptions of the male terminalia and genitalia of all *Mecomera* species.

Material and methods

The non-type material material of *M. brunnea* is deposited at *Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia* (INPA), pinned and stored in Eppendorf vials in 80% alcohol. The type material was not

Accepted by E. Bernard: 20 Feb. 2019; published: 4 Apr. 2019

found at the *Muséum National D'Histoire Naturelle* (MNHN). Type material of *M. reichardti* is deposited at *Museu de Zoologia da Universidade de São Paulo* (MZUSP). Type material from *M. chacoensis* is deposited at the MNHN and non-type material at the Manchester Museum of the University of Manchester (MMUE). Male terminalia were removed and macerated in 85% lactic acid heated at 120ºC for about 45 minutes. The macerated piece was examined in glycerin in cavity slides with a stereomicroscope. After study, each set of genitalia was stored in a microvial with glycerin and associated with the source specimen. Terminology for external morphology follows Haas and Kukalová-Peck (2001) and for terminalia and genitalia follows Kamimura (2014).

Measurements were taken with a digital caliper rule and all of them were made dorsally as following: body length – from base of the head to the apical margin of tergite 10 (ultimate); head width—the maximun distance between left and right lateral margins; pronotum length—measured medially from basal margin to apical margin; pronotum width—the maximum distance between left and right lateral margins; cercus length—from basal margin to apical margin.

Photographs were taken with a Leica DFC500 digital camera fitted on a Leica MZ205 stereomicroscope. The camera was linked to a computer with Leica Application Suite software, used to combine multiple layers of photographs into a single fully focused image. Label data are presented as on labels, with use of square brackets ([ ]) for supplementary information. The identification plate and drawings were made withAdobe Illustrator CS6.

Abbreviations

AP = anal posterior;
BM = medial basivenale;
BR = radial basivenale;
CuA = cubitus anterior;
CuP = cubitus posterior;
MP = media posterior;
S = sternite;
T = tergite;
TF = transverse fold area.

Taxonomy

Mecomera Audinet-Serville, 1839

Mecomera Audinet-Serville, 1839: 53 type species: *Mecomera brunnea* by original designation; Brindle, 1968: 288; Steinmann, 1990: 169 (redescription).

Mecomera brunnea Audinet-Serville, 1839

Figs. 1A–E, 2A–C, 3A–D, 4A–D.

Mecomera brunnea Audinet-Serville, 1839: 54; Brindle, 1968: 288 (redescription, new illustrations); Steinmann, 1990: 170 (redescription); Sakai, 1991 (comparison of descriptions from different authors).
Forficula plana Illiger, in Burmeister, 1838: 752;
Forficula gracilis Blanchard, in Orbigny,1843: 214;
Sparatta apicalis Kirby, 1896: 526;
Sparatta dohrni Kirby, 1903: 68 (new name for *Sparatta plana* Dohrn, 1865, a junior secondary homonymy of *Sparatta plana* (Illiger, 1839)).

Examined material. BR, AM, km 30 Manaus-Caracaraí, NAF 6 AM, 30.iv.1976, Joselita Maria Santos leg. (3♂ **INPA**); BR, AM, Manaus, Est. [highway] BR-174, KM 30, 21.v.1976, Paralupi (1♂, **INPA**); BRASIL, AM, Manaus, Aleixo, Km 7, 14.vi.1977, Joselita Maria Santos leg. (♂ **INPA**); idem, 20.vi.1978 (♂ **INPA**); BRASIL, AM, Manaus, Aleixo, Km 11, 15.ix.1978, A. Y. Harada, Col. (2 ♀ **INPA**); BR, AM, Manaus, Reserva Biológica da Campina, BR 174, 12.iv.2002, Silva AC leg, Manual collecting (♂, ♀ **INPA**); BRASIL, AM, Reserva Extrativista

Unini, 03 bocas, 16–28.vii.2004, manual collecting, A. Silva, leg. (♀ **INPA**); BRASIL, RO [Rondônia], Guaporé, 12°13'19"S–60°32'44"W, 23.iv.2006, J.A. Rafael & F.F. Xavier, Manual collecting (2 ♀ **INPA**) BRASIL, AM [Amazonas], São Paulo de Olivença, 03°28'50"S–68°55'25"W, Campina, 11–14.ix.2005, Malaise trap, J.A. Rafael & F.F. Xavier (2♂**INPA**).

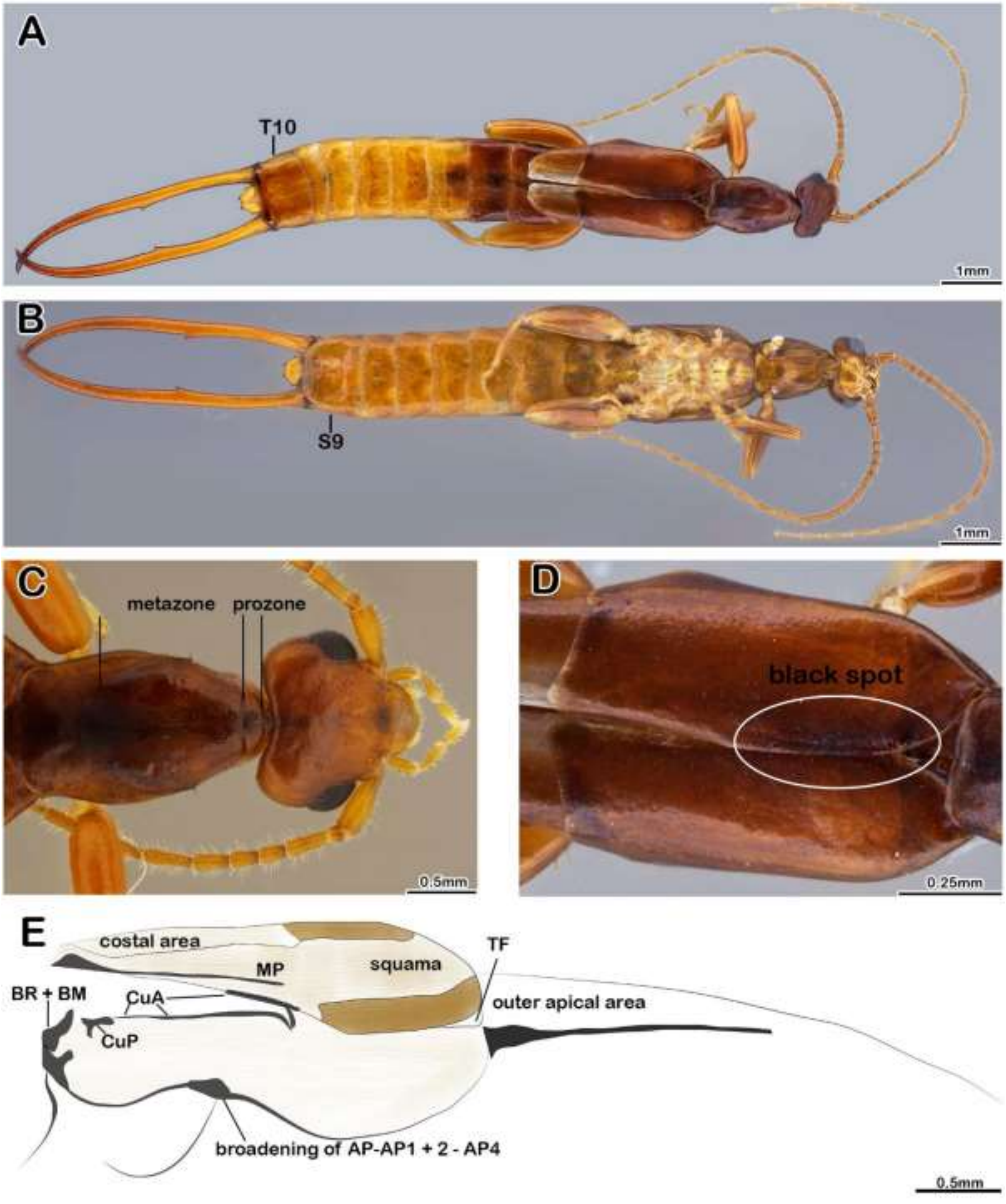

FIGURE 1. *Mecomera brunnea* ♂. A) Habitus in dorsal view; B) Habitus, ventral view; C) Head and pronotum in dorsal view; D) Tegmina in dorsal view; E) Schematic drawing of the base of the posterior wing. Abbreviations: AP = anal posterior, BM = medial basiveinal, BR = radial basiveinal, CuA = cubitus anterior, CuP = cubitus posterior, MP = media posterior, S = sternite, T = tergite, TF = transverse fold area.

Description of male. Proximal half of body (excluding head appendages) dark brown, becoming mainly light brown to yellow towards apex; body shiny (Figs. 1A, B). Measurements (mm) (n=6): body length 9.5–10.0; head width 1–1.2; pronotum length 1.4–1.6; pronotum width 1.0; cercus length 4.2–4.5.

Head cordiform, smooth (Figs. 1A, C). Frons and vertex with inconspicuous postfrontal and coronal sutures. Frons with basal margin inconspicuously sinuous (Figs. 1A, C). Post-ocular area with postero-lateral margin rounded; vertex concave (Figs. 1A, C). Eyes black, diameter slightly less than length of post-ocular area (Figs. 1A, C). Antenna with 22 antennomeres, setose from base to apex, dark yellow from scapus to flagellomere 13, yellow from flagellomere 14 to apex (Figs. 1A, B); scapus 5.5 times longer than pedicel and 1.5 times longer than flagellomere 1 (Fig. 1C). Maxillary and labial palps yellow, setose (Figs. 1B, C).

Pronotum hexagonal, 1.6 times longer when measured at widest point, broadening from base to apex, wider at middle, surface roughened, basal and lateral margins convex, apical margin almost straight; midlongitudinal sulcus conspicuous and deep; prozone 5.2 times shorter than metazone (Figs. 1A, C). Meso- and metanotum covered by tegmina and posterior wings, respectively. Prosternum dark brown with black spots, sternal plate with oblong basal margin, straight lateral margin and conspicuous emargination on apical margin (Fig. 1B). Meso and metasternum light yellow, with several dark brown spots, both striated apically (Fig. 1B). Mesosternum with conspicuous sternal plate, with truncated basal margin, broadening towards sinuous lateral margin and slightly emarginated apical margin (Figs. 1B). Metasternum with inconspicuous sternal plate.

Tegmina elongated, 2.7 times longer than wide, broadening towards apex; with black longitudinal spots mesally at basal third and transversally at extreme apical; surface roughened, postero-laterally emarginated (Figs. 1A, D). Posterior wing almost translucid, covered by small setae. Costal margin straight, with costal area marked by a thin conspicuous line (Fig 1E). Squama with two conspicuous light brown spots, at costal and anal margin (Fig. 1E). BR + BM broadened at base, gradually narrowing towards apex. MP slender, almost reaching the length of the costal area (Fig. 1E) CuA surpassing MP in length, bifurcated at apex (Fig. 1E). CuP with three acute edges, with anal margin conspicuously concave; apex widened (Fig. 1E). TF small, inconspicuous (Fig. 1E). Outer apical area large, approximately half width of the squama (Fig. 1E). Broadening of AP-AP1 +2-AP4 reniform, enlarged (Fig. 1E).

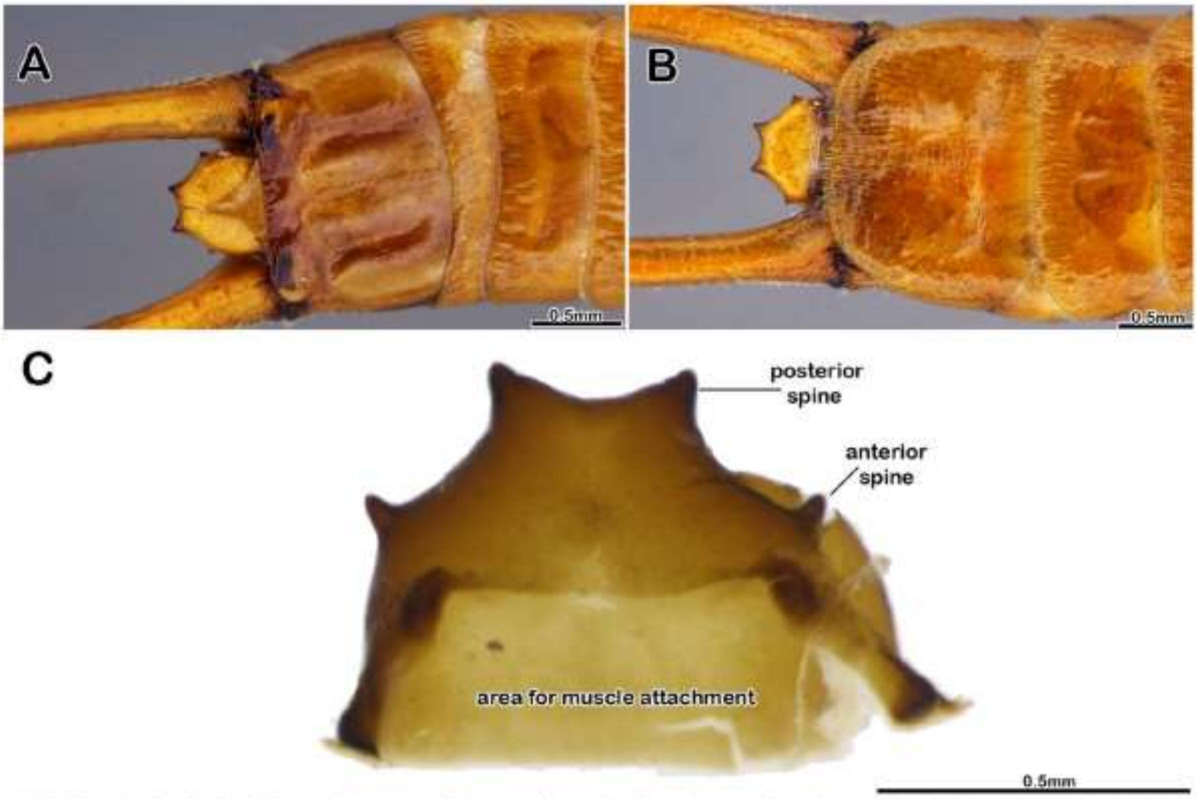

FIGURE 2. Abdominal sclerites of *Mecomera brunnea* ♂. A) Tergites 8–10 and pygidium, dorsal view; B) Sternites 8–9 and pygidium, ventral view; C) Pygidium, ventral view.

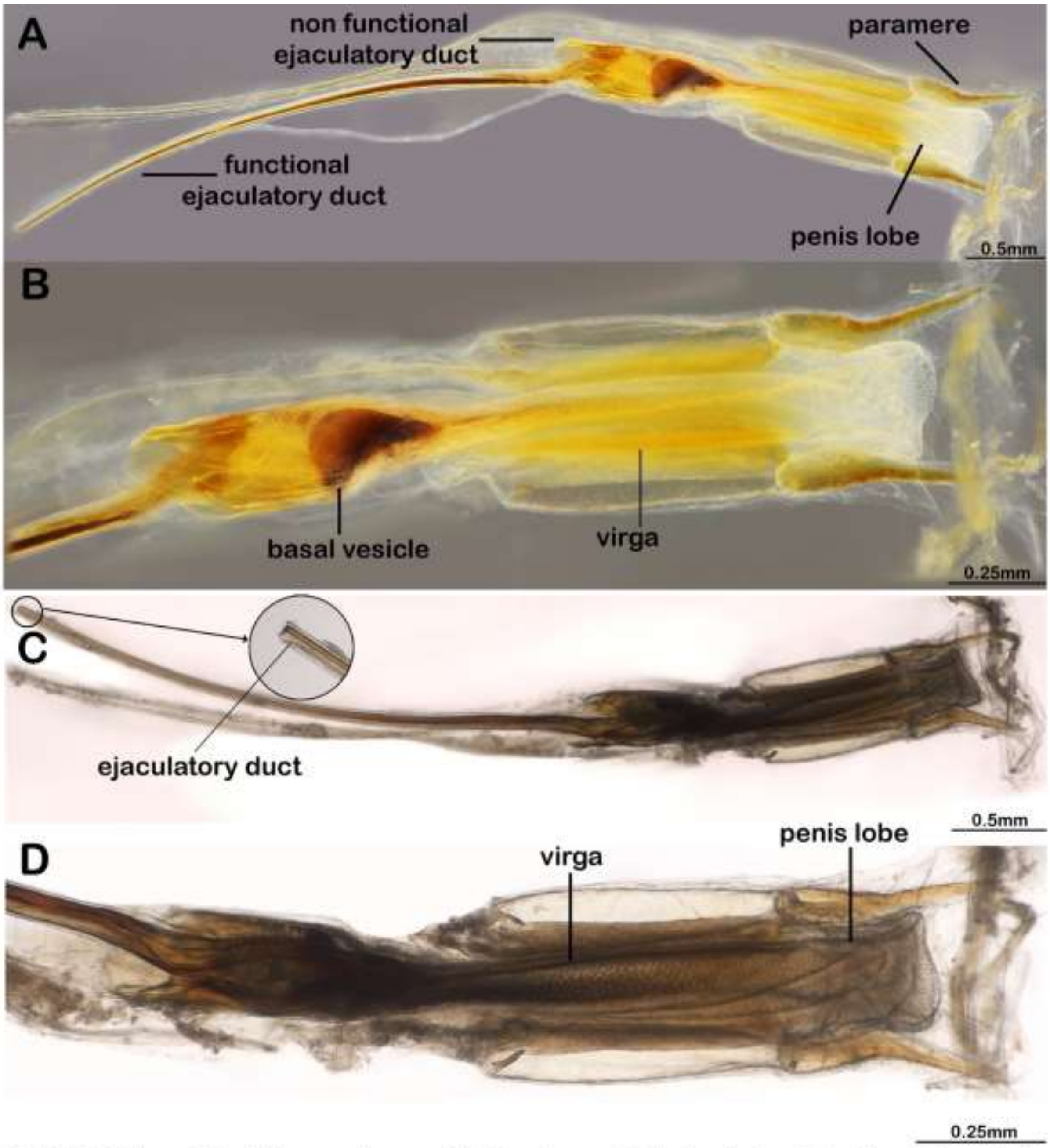

FIGURE 3. Male genitalia of *Mecomera brunnea* ♂ A) Complete genitalia in dorsal view; B) Partial genitalia, excluding ejaculatory duct in dorsal view; C) Complete genitalia in ventral view; D) Partial genitalia, excluding ejaculatory duct in ventral view.

All legs dorsally light brown from base of basal third to apex of medial third, remaininder light yellow. All femora broadened, with small setae. All tibiae and tarsi densely setose (Figs. 1A, B).

Abdomen with lateral margins parallel-sided, dorsally and ventrally covered with small, scattered, smooth setae; all segments apically striated dorsally and ventrally (Figs. 1A, B). Tergites 1–3 not narrowed. Tergites 3–4 dark brown, with inconspicuous glandular folds. Tergites 3–9 rectangular; tergites 3–7 1.7 times wider than long, with apical margin almost straight (Figs. 1A, 2A); tergite 8 2.5 times wider than long, with apical margin concave; tergite 9 four times wider than long, with apical margin concave (Figs. 1A, 2A). Tergite 10 (ultimate) rectangular, 1.5 times wider than long, slightly sinuous laterally and straight apically; apical margin slightly upwardly projected, with dark brown and black spots (Figs. 1A, 2A). Pygidium with four conspicuous acute projections, posterior pair pointing backward and anterior pair pointing downward; concavity between posterior projections shallow (Figs. 1A, 2A–C). Cercus (forceps) light yellow to brown on proximal half, darker at distal half, slender, slightly shorter than abdomen, mesally with one short acute projection pointing downward; margins finely black-pigmented, apex acute (Figs. 1A, B). Abdominal sterna light brown (Fig. 1B). Sternites 2–7 rectangular, with lateral margin somewhat straight, apical margin emarginated, slightly concave (Fig. 1B). Sternite 8 rectangular, 1.3 times longer than wider, slightly sinuous apically (Figs. 1B, 2B). Sternite 9 (penultimate) with lateral margin convex, apical margin slightly concave (Figs. 1B, 2B).

Genitalia with functional ejaculatory ductwell sclerotized, elongated, approximately 2.5 times longer than virga; dark brown (Figs. 3A, C). Basal vesicle reniform, dorsally widened at proximal half, short and slightly elongated at distal half (Fig. 3A, B, D). Virga elongated, reaching base of paramere (Fig. 3A, B). Penis lobe broadened, elongated, covered with small scale-like structure (Figs. 3B–D); apex of penis lobe bilobed, asymmetrical, left lobule larger than right lobule (Figs. 3B, D). Paramere elongated, with basal third bacilliform, slightly widened, gradually narrowing towards apex; apex acute (Figs. 3A–D).

Description of female. Similar to male, but having a broader and longer body, except cercus shorter; additionally with the following differences. Legs homogeneously light brown (Figs. 4A, B). Abdominal tergite 8 (ultimate) trapezoidal, width gradually narrowing laterally, apically straight (Figs. 4A, C). Pygidium trapezoidal, emarginated laterally and posteriorly; apical margin with two dorsal pointed, acute projections (Fig. 4C, D). Cercus (forceps) broader and shorter, length 0.6 times that of abdomen (Figs. 4A, B). Abdominal sterna light yellow basally and slightly darker distally (Fig. 4B). Sternite 7 (penultimate) with, convex lateral margin and strongly convex apical margin (Figs. 4B, D). Measurements (mm) (n=6): body length 1010.4; head width 1–1.3; pronotum length 1.2–1.6; pronotum width 1.1; cercus length 2.8–3.0.

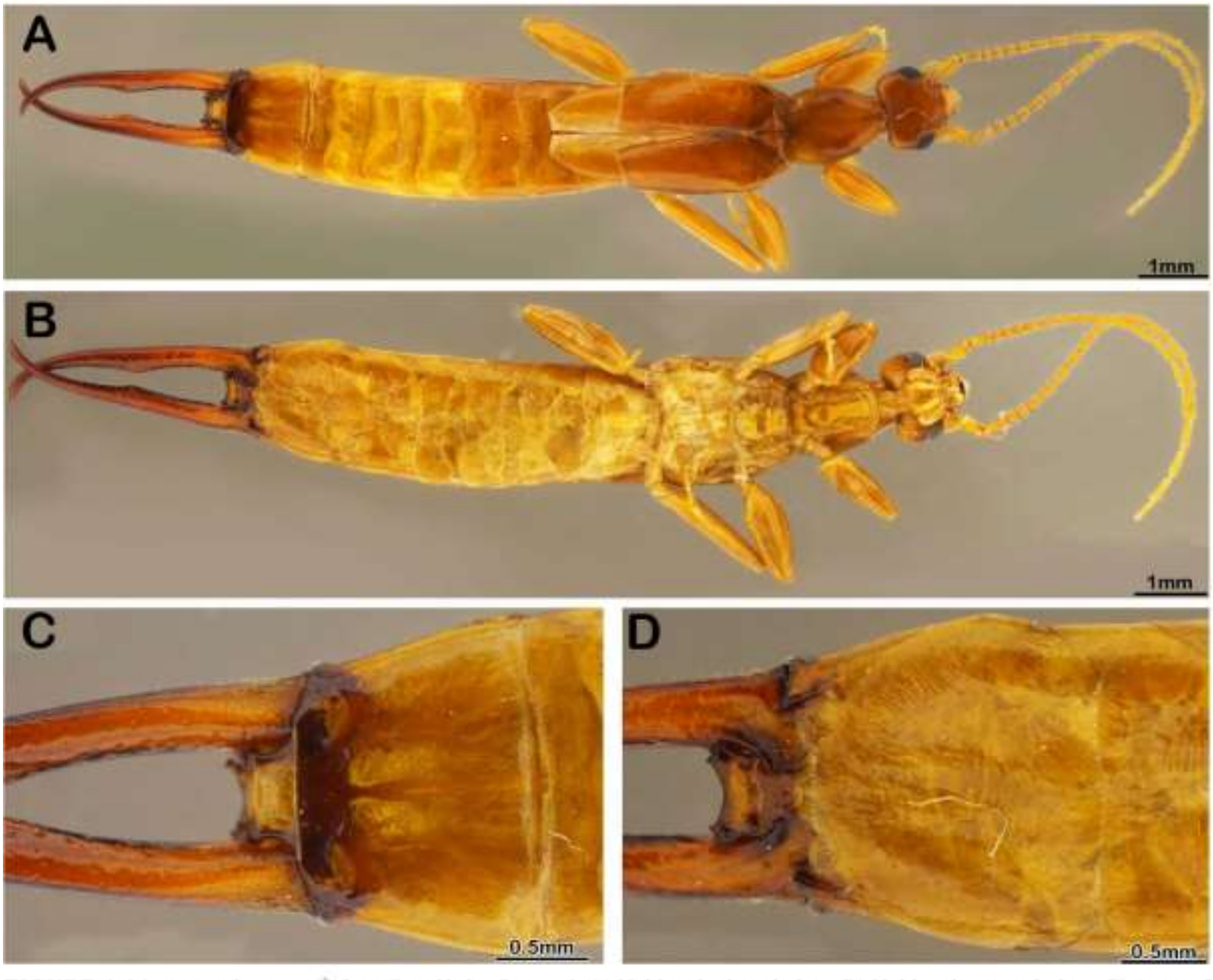

FIGURE 4. *Mecomera brunnea* ♀ from Rondônia, Guaporé. A) Habitus in dorsal view; B) Habitus in ventral view; C) Apex of abdomen, dorsal view; D) Apex of abdomen, ventral view.

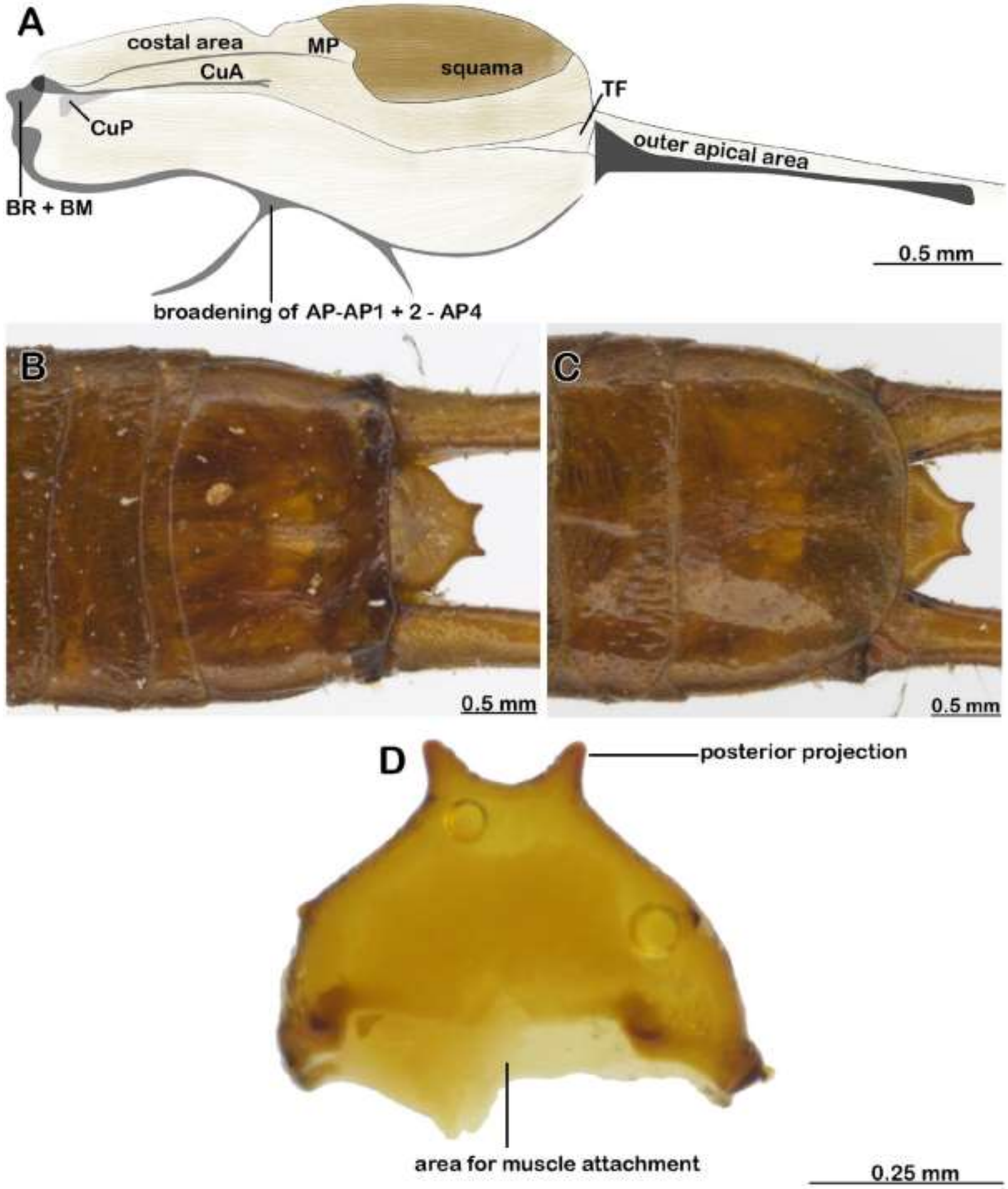

FIGURE 5. Posterior wing, male terminalia and partial genitalia, excluding ejaculatory duct of *Mecomera brunnea* ♂. A) Schematic drawing of the base of the posterior wing B) Tergites 8–10 and pygidium, dorsal view; C) Sternites 8–9 and pygidium, ventral view; D) Pygidium, ventral view. Abbreviations: AP = anal posterior, BM = medial basiveinal, BR = radial basiveinal, CuA = cubitus anterior, CuP = cubitus posterior, MP = media posterior, TF = transverse fold area.

Distribution. Bolivia; Brazil: Amazonas and Rondônia [**new records**]; Colombia; Costa Rica; French Guiana; Nicaragua; Peru.

Variations. There are two patterns of variations within the species: 1) having two different dark brown spots on squama and pygidium bearing four conspicuous projections (as described and illustrated above, Figs. 1E, 2C); 2) having one single large dark brown spot on squama and pygidium bearing two conspicuous projections and two inconspicuous projections (Figs. 5A–D). Furthermore, the following differences on the posterior wing were also noticed in the second pattern (Fig. 5D): costal margin with sinuous concavity at approximately half length; costal area marked by MP. Squama with a single large dark brown spot. MP slender, curved at base, almost reaching the squama spot. CuA slender, reaching at maximum half-length of MP, bifurcated at apex. CuP resembling a boot, with costal and anal margin rounded. BR + BM slender at anal half, widening conspicuously towards costal half. TF large, with almost same length of outer apical area. Outer apical area thin, barely reaching a third of the squama width. Broadening of AP-AP1 + 2-AP4 resembling a triangle.

Remarks. *Mecomera brunnea* differs from *M. reichardti* by the smooth surface of tergites 4–10 (punctate in *M. reichardti* (Figs. 7C, 8A–C)); in *M. brunnea* basal vesicle reniform, widened at proximal half, short and slightly elongated at distal half; basal third of paramere bacilliform and slightly widened (in *M. reichardti* basal vesicle conspicuously slender at proximal half, rounded at distal half; the paramere with basal margin conspicuously rounded, antero-lateral margin concave, postero-lateral margin convex, surface of the penis lobe smooth (Figs. 7D–E)).

Mecomera brunnea differs from *M. chacoensis* in having one mesal projection on each cercus (two or three mesal projections on each cercus in *M. chacoensis*). It is known that Dermaptera species can have intraspecific morphological variation on the cerci, as with *M. chacoensis* (Brindle 1968; Steinmann 1990). However, it is also true that some New World Dermaptera do not have significant variation on the cercus and therefore it can be reliably used for differentiation, as verified for *Mecomera* (Brindle 1968). Due to the relatively high number of specimens analyzed, it is safe to separate males of *M. brunnea* from those of *M. chacoensis* by the number of projections on the cercus.

Mecomera chacoensis (Borelli, 1912)

Figs. 6A–E.

Metasparatta chacoensis Borelli, 1912: 2; Brindle, 1968: 289 (short description and illustrations after Borelli).
Mecomera chacoensis; Steinman 1990: 171 (new combination).

Examined material. Chaco de Santiago Del Estero [Argentina], Bords do Rio Salado Env. Dicaño, E. R. Wagner, 1904 (Holotype ♂ **MNHN**); Venezuela, Yaracuy, Yumare, 1–5.vi.1970 [**new record**].

Diagnosis. Eye diameter about 0.8 times length of post-ocular area (Fig. 6A). Antenna uniformly light brown (Fig. 6A). Tegmina light yellow, translucid (Fig. 6A). Cercus with four to six acute projections, pointing to venter (Fig. 6A). Pygidium dorsally descending from base towards apex; apical margin with four rounded elongated projections, each pointing latero-posteriorly; ventrally flattened (Figs. 6B–C). Basal vesicle of the male genitalia resembling an elongated crab claw, sinuous, bifurcated at apex, forming concavity; connected to a "C" shaped sclerite, strongly sclerotized (Figs. 6D–E). Paramere partially sclerotized, with small membranous area at apex; exterior margin gradually curving, concave; internal margin conspicuously curving, concave; apex straight, thin (Figs. 6D–E).

Description of male. Body light brown to light yellow (Fig. 6A).

Head cordiform, smooth (Fig. 6A). Frons and vertex with inconspicuous postfrontal and coronal sutures. Frons with basal margin inconspicuously sinuous. Post-ocular area with postero-lateral margin rounded; vertex conspicuously concave. Eyes light brown (in dead specimen), diameter about 0.8 times length of post-ocular area (Fig. 6A). Antenna setose from base to apex, light brown (Fig. 6A); scapus 3.4 times longer than pedicel and 1.1 times longer than flagellomere 1. Maxillary and labial palps setose.

Pronotum hexagonal, 1.6 times longer than wide when measured at widest point; broadening from base to apex, wider at middle, roughed surface, apical, basal and lateral margins convex; mid-longitudinal sulcus inconspicuous and shallow; metazone length 11 times that of prozone (Fig. 6A). Meso- and metanotum covered by tegmina and posterior wings, respectively. Sternum light yellow. Prosternum with sternal plate cylindrical, with all margins conspicuously curved. Mesosternum with conspicuous sternal plate, with truncated basal and apical margin, broadening towards sinuous lateral margin. Metasternum with inconspicuous sternal plate.

Tegmina light yellow, translucid, elongated, 2.2 times longer than wide, broadening towards apex; surface roughened, postero-laterally emarginated (Fig. 6A).

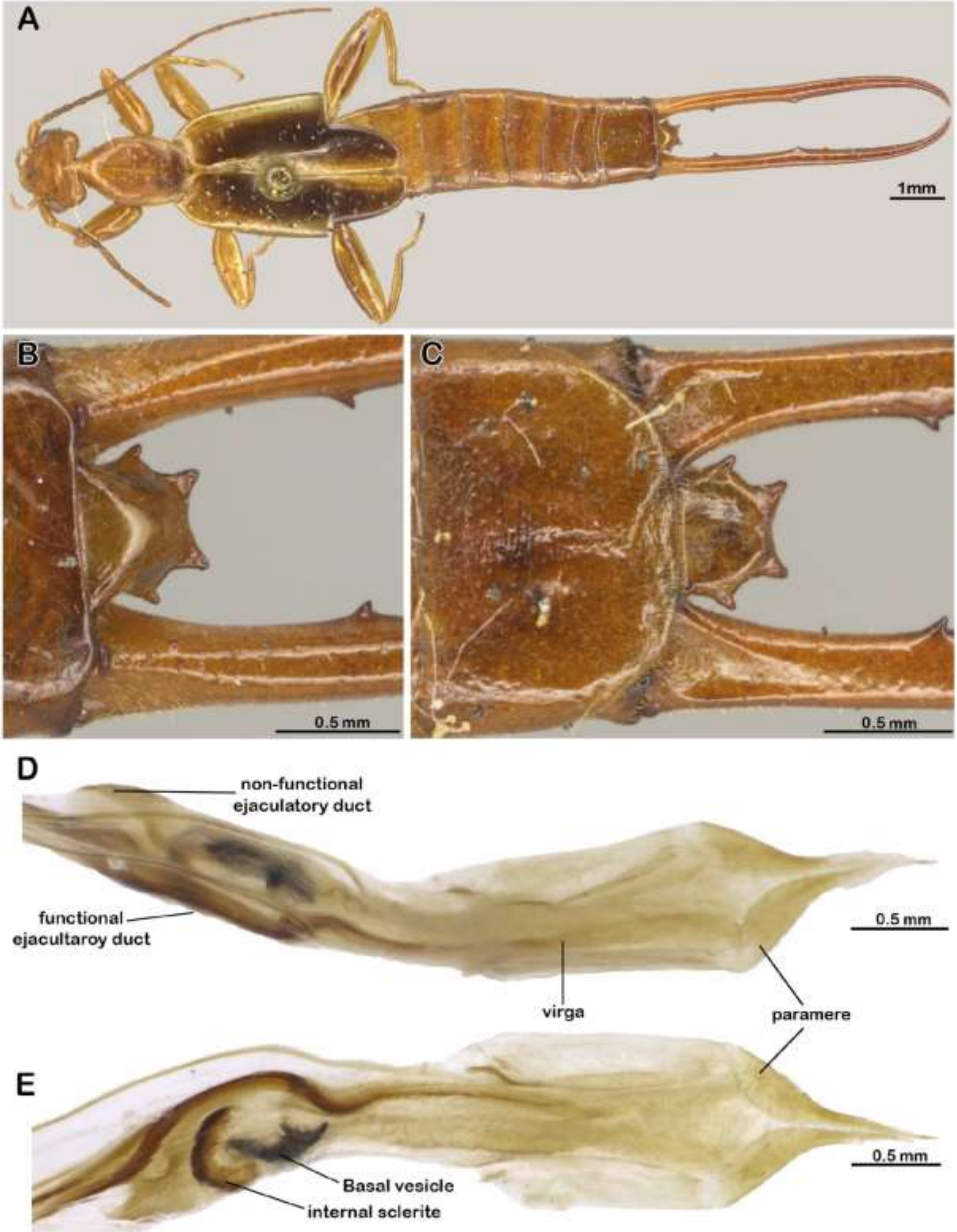

FIGURE 6. *Mecomera chacoensis* ♂. A) Habitus, dorsal view; B) Pygidium and cercus base, dorsal view; C) Pygidium and subgenital plate, ventral view; D) Genitalia, dorsal view; E) Genitalia, ventral view.

All legs shiny, light yellow (Fig. 6A). Posterior legs with conspicuous brown spot dorsally. All femora lacking setae; tibiae and tarsi with setae ventrally.

Abdomen with lateral margins parallel-sided, dorsally and ventrally covered with small, scattered, smooth setae; all segments apically striated dorsally and ventrally. Tergites 1–3 not narrowed. Tergites 3–4 dark brown, with inconspicuous glandular folds. Tergites 3–9 rectangular; tergites 3–7 approximately three times wider than long, with apical margin concave. Tergite 8 approximately 2.5 times wider than long, with apical margin concave (Fig. 6A). Tergite 9 approximately 7.6 times wider than long, with apical margin concave (Fig. 6A). Tergite10 (ultimate) with lateral margins convex, apical margin slightly emarginated with postero-lateral margin projected (Fig. 6A). Pygidium dorsally descending from base towards apex; basal margin straight, lateral margin sinuous, apical margin with four rounded, elongated projections, each pointing latero-posteriorly; the concavity between projections wide, deep; ventrally flattened (Figs. 6B–C). Cercus robust, light brown, gradually curving at apical margin, with four to six acute projections, pointing to venter. Sternites 2–7 rectangular, with lateral margin somewhat straight, apical margin emarginated, slightly concave. Sternite 8 the same, but apical margin straight (Fig. 6C). Sternite 9 (penultimate) "D"-shaped, with lateral margin convex, apical margin inconspicuously emarginated (Fig. 6C).

Male genitalia (Fig. 6D–E) with functional ejaculatory duct right-sided, approximately 5.5 times longer than virga; well sclerotized, elongated dark brown sclerite accompanying the ejaculatory duct longitudinally. Basal vesicle resembling an elongated crab claw, sinuous, bifurcated at apex, forming concavity, connected to a "C"-shaped sclerite, strongly sclerotized. Virga elongated, reaching base of paramere. Penis lobe broad, convex, symmetrical, smooth. Paramere partially sclerotized, with small membranous area at apex; exterior margin gradually curving, concave; internal margin conspicuously curving, concave; apex straight, thin.

Remarks. The "C" shaped sclerite connected to the basal vesicle may be an independent sclerite, despite the two of them being connected. Furthermore, it appears the "C"-shaped sclerite is also connected to the ejaculatory duct.

Mecomera chacoensis differs from *M. reichardti* by the pygidium with four elongated rounded projections (*M. reichardti* with two bifurcated oblong projections). Furthermore, *M. chacoensis* has the basal vesicle resembling a crab claw, slender and sinuous at basal half, bifurcated at apical half (*M. reichardti* has the basal vesicle conspicuously slender at proximal half, rounded at distal half, resembling a comma).

Mecomera reichardti Brindle, 1971

Figs. 7A–E, 8A–D.

Mecomera reichardti Brindle, 1971: 166; Steinmann, 1990: 172 (redescription); Sakai, 1991 (comparison of descriptions from different authors).

Examined material. Holotype: "São Paulo, STO. [Santo] Amaro, SP [São Paulo], 29.vi.1966, E. X. Rabello col." (♂, **MZUSP**). Allotype: same data as holotype (1 ♀, MZUSP). Paratypes: "St. Catharina [Santa Catarina], Blumenau, ii. 1919, H. Luederwaldt" (2♂, 3♀ **MZUSP**); "Same data as holotype (1♀, **MZUSP**)".

Diagnosis. Head with postero-lateral margin of post-ocular area convex; vertex inconspicuously concave (Figs. 7A–B, 8B–C). Antenna with approximately proximal half light brown, distal half dark brown (Fig. 8C). Eye diameter half the length of the post-ocular area (Fig. 7B). Tegmina and posterior wings dark brown to black (Fig. 7A, 8B, C). Tergites 2–3 conspicuously narrowing (Fig. 8B). Tergite 4 to end of abdomen with punctated surface (Figs. 7C, 8A–C). Male pygidium somewhat rectangular, with two conspicuous bifurcated, oblong projections (Figs. 7C, 8A); female the same, but with pygidium semicircular (Fig. 8D). Basal vesicle conspicuously slender at proximal half, rounded at distal half, resembling a comma; paramere with basal margin conspicuously rounded, antero-lateral margin concave, postero-lateral margin convex (Figs. 7D–E).

Description of male. Body light brown to light yellow (Fig. 7A).

Head with inconspicuous postfrontal and coronal sutures on frons and vertex (Fig. 7A, B). Frons with basal margin convex. Post-ocular area with postero-lateral margin convex; vertex inconspicuously concave. Eyes black (in dead specimen), short, diameter half the length of post–ocular area (Fig. 7B). Antenna setose, light brown; scapus 3.7 times longer than pedicel and 1.6 times longer than flagellomere 1. Maxillary and labial palps setose; pedicel cylindrical, remaining antennomere conical (Fig. 7B).

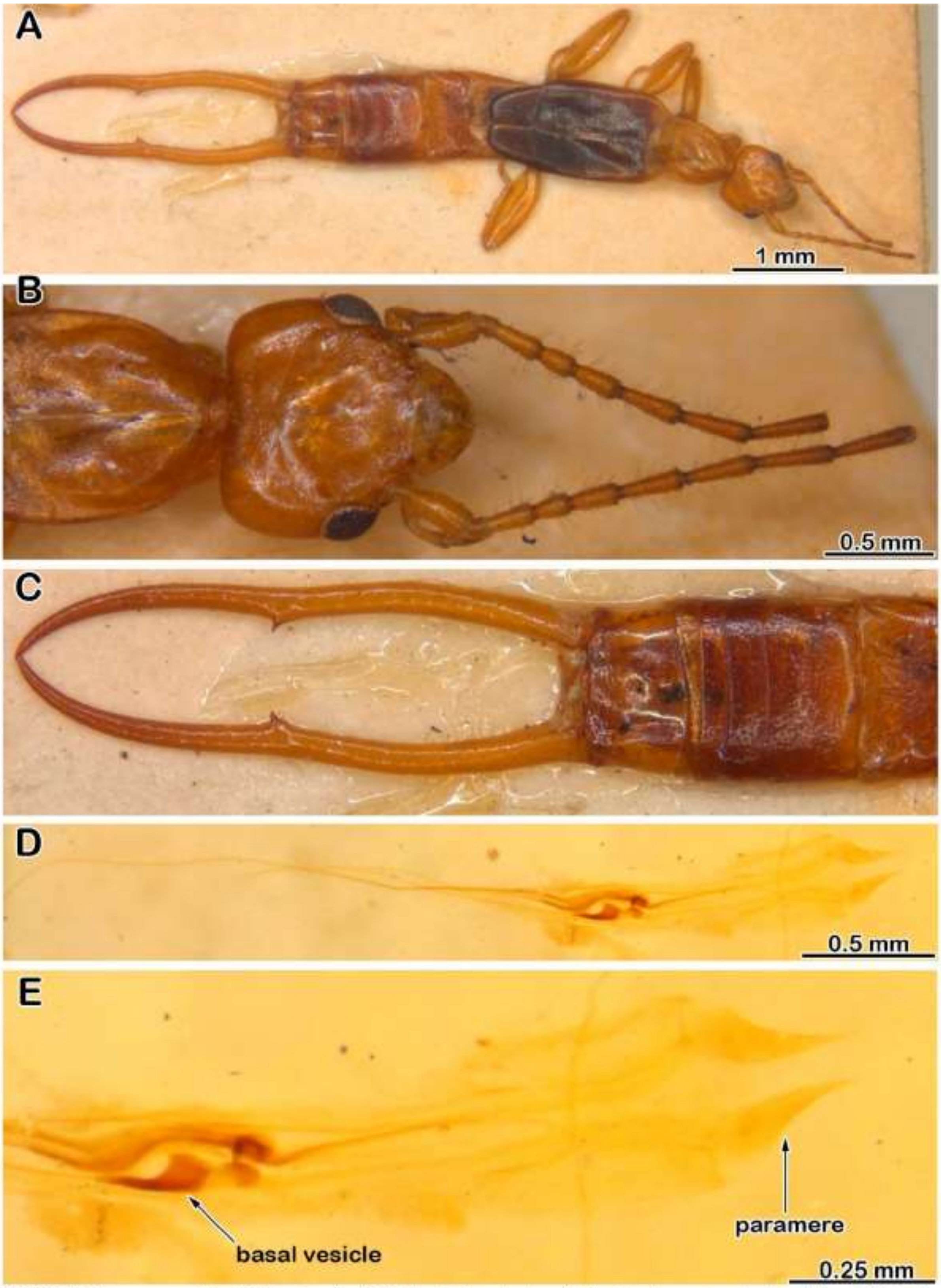

FIGURE 7. *Mecomera reichardti*, holotype ♂. A) Habitus in dorsal view; B) Head and pronotum in dorsal view; C) Tergites 5–10 and cercus, dorsal view; D) Genitalia, ventral view; E) Partial gentalia, excluding ejaculatory duct, ventral view. Photos by MZUSP staff.

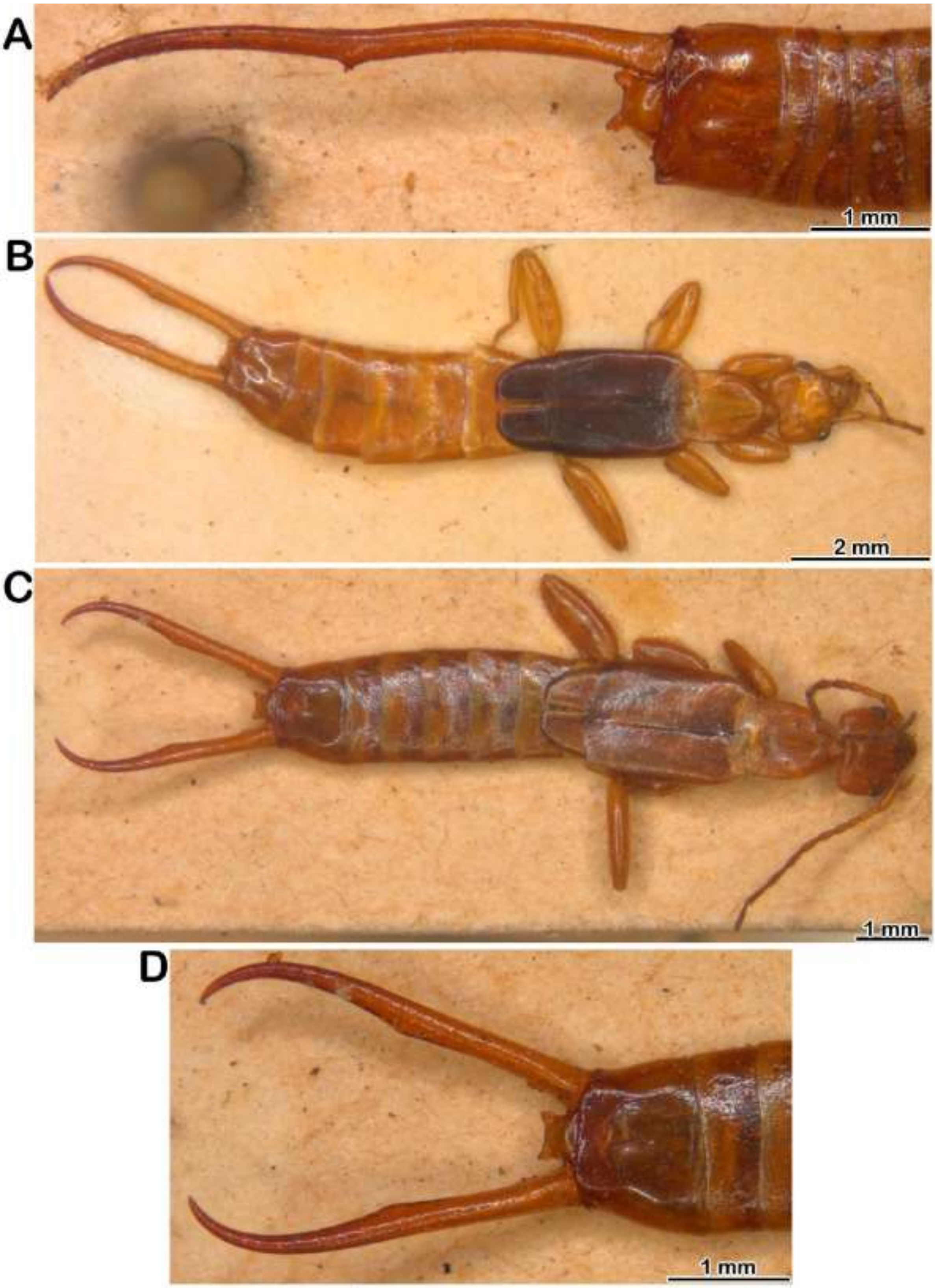

FIGURE 8. *Mecomera reichardti*. A) Paratype ♂, tergites 7–10, pygidium and cercus, dorsal view; B) Paratype ♀, habitus in dorsal view; C) Paratype ♂, habitus in dorsal view; D) Tergites 6–8, pygidium and cercus, dorsal view. Photos by MZUSP staff.

Pronotum hexagonal, 1.3 times longer than wide when measured at widest point; broadening from base to apex, wider at middle, surface roughened, apical, basal and lateral margins convex; mid-longitudinal sulcus inconspicuous and shallow (Fig. 7A). Meso- and metanotum covered by tegmina and posterior wings, respectively.

Tegmina dark brown, thick, elongated, 2.5 times longer than wide, broadening towards apex; surface roughened, postero-laterally straight (Fig. 7A).

All legs shiny, uniformly light yellow (Fig. 6A). Legs lacking setae, except for tarsi on ventral side.

Male abdominal tergites 1–3 conspicuously narrowed (Fig. 7A). Tergites 4–10 with punctate surface (Figs. 7C, 8A). Tergites 5–8 with straight lateral margin, inconspicuously concave apical margins (Figs. 7C, 8A). Tergite 6 rectangular, approximately two times wider than long (Fig. 7C). Tergite 7 rectangular, but about 4.5 times wider than long (Fig. 7C). Tergite 8 rectangular, approximately 6.5 times wider than long (Fig. 7C). Tergite 9 conspicuously narrowed, approximately 6.2 times wider than long, with straight lateral margin and conspicuous concave apical margin (Figs. 7C, 8A). Tergite 10 trapezoidal, without spots, with concave straight lateral margin, conspicuously emarginated apical margin (Figs. 7C, 8A). Pygidium somewhat rectangular, with lateral margin straight, apical margin with two conspicuous bifurcated, oblong projections (Figs. 7C, 8A).

Male genitalia with basal vesicle conspicuously slender at proximal half, rounded at distal half, resembling a comma; paramere with basal margin conspicuously rounded, antero-lateral margin concave, postero-lateral margin convex (Figs. 7D–E).

Female abdomen. Dark brown. Tergites 1–4 conspicuously narrowed (Fig. 8B). Tergites 2–8 with punctate surface (Fig. 8B). Tergites 3–7 rectangular, gradually decreasing in length, with lateral margins straight, apical margins slightly concave (Fig. 8B). Tergite 7 rectangular, 2.8 times wider than long (Fig. 8C). Tergite 8 trapezoidal, narrowing from base to apex, with basal margin slightly sinuous, lateral margin straight, apical margin straight with postero-lateral angle projected upwards (Figs. 8B–C). Pygidium semicircular, with two conspicuous bifurcated oblong projections (Figs. 8B–C).

Variations. The projections on the holotype's pygidium are more distant from each other than in the remaining two male paratypes (Figs. 7C, 8A).

Remarks. Concerning the description of the male terminalia of *M. reichardti*, previous authors misinterpreted the description of the pygidium of this species (Brindle 1971; Steinmann 1990; Sakai 1991). These previous authors described the male pygidium as a structure with a rounded apical margin with two projections. This interpretation might have happened because the holotype's pygidium is partially encompassed by the last abdominal segments, leaving only the apical margin of the pygidium visible. Based on the new illustrations of the holotype specimen, the characterization of the male pygidium is amended and the variations between holotype and paratypes are given above.

Acknowledgments

We thank Alberto da Silva Neto, Diego Matheus de Mello Mendes and Larissa Queiroz for support in the laboratory; to staff from Museu de Zoologia da Universidade de São Paulo (MZUSP); to staff from the Museum of the University of Manchester (MMUE); to staff of the *Muséum National D'Histoire Naturelle*, Paris (MNHN) for all their support. We are grateful to Fabian Haas for type photos. We appreciate the support of the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) and Programa de Apoio a núcleos de Excelência (PRONEX) for grant 016/2006, proc. 1437/2007; to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the award of a fellowship to J.A.R. (grant 300.997/2016-7) and for financial resources MCTI/CNPq/FNDCT Ação Transversal—Redes Regionais de Pesquisa em Biodiversidade e Biotecnologia N ° 79/ 2013 (grant 407.627/ 2013-8).

References

Audinet-Serville, J.G. (1839) *Historie naturelle des insectes. Orthopteres*. Librairie Encyclopédique de Roret, Paris, 53 pp.

Brindle, A. (1968) A revision of the Labiidae (Dermaptera) of the Neo-tropical and Nearctic Regions. 1. Pericominae, Strongylopsalinae, Sparattinae. *Journal of Natural History*, 2, 273–303. https://doi.org/10.1080/00222936800770931

Brindle, A. (1971) Two new species of Dermaptera from Brazil. *Papéis Avulsos de Zoologia*, 23 (20), 165–171.

Haas, F. & Kukalová-Peck, J. (2001) Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *European Journal of Entomology*, 98 (4), 445–510. https://doi.org/10.14411/eje.2001.065

Haas, F. (2012) A Ordem Dermaptera. *In*: Rafael, J.A., Melo, A.R.G., Carvalho, C.J.B., Casari, S.A. & Constantino, R. (Eds.), *Insetos do Brasil: diversidade e taxonomia*. Holos Editora, São Paulo, pp. 1–297.

Hopkins, H., Maehr, M.D., Haas, F. & Deem, L.S. (2016) Dermaptera species file. Version 5.0/5.0. Available from: http://dermaptera.speciesfile.org (accessed 12 July 2018)

Kamimura, Y. (2014) Pre- and postcopulatory sexual selection and the evolution of sexually dimorphic traits in earwigs (Dermaptera). *Entomological Science*, 17, 139–166. https://doi.org/10.1111/ens.12058

Sakai, S. (1991) *Dermapterorum Catalogus XXIII: Iconographia VIII.* Spongiphoridae *I.* Daito Bunka University, Tokyo, 708 pp.

Steinmann, H. (1990) Dermaptera, Part II: Eudermaptera I: Labiidae. *Das Tierreich*, 106, 1–558.

Vieira, R.M. & Chagas, C.B. (2017) Catálogo taxonômico da fauna do Brasil: Dermaptera. Available from http://fauna.jbrj.gov.br/ (accessed 29 October 2018)

CAPÍTULO II

Heleodoro, R.A. & Rafael, J.A. 2020. Dermaptera (Insecta): a guide for hide wing stretching and hind wing preservation. *Zootaxa*, 4532(2): 474-480.

Zootaxa 4732 (3): 474–480
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4732.3.9
http://zoobank.org/urn:lsid:zoobank.org:pub:FDA521A2-1D7B-41CD-ABAA-DB4590D2A9E3

Dermaptera (Insecta): a guide for hind wing stretching and hind wing preservation

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Abstract

The Dermaptera (earwigs) have the most complex folding system of the posterior wing among insects. We provide an illustrated guide describing how to stretch a dermapteran hind wing and mount it on slides in Hoyer's medium.

Key words: earwigs, Insects, Hoyer's medium, methodology

Introduction

Insect wings are a common subject explored in many study areas, such as animal behavior (Katayama *et al.* 2014), biomechanics (Sane 2016), evolution (Haug *et al.* 2014) and especially taxonomy. Many taxonomic works are based on the wing and its associated sclerites (e.g. Orthoptera (Dias *et al.* 2012); Diptera (Vieira & Rafael 2014)) and wings are important in phylogenetic studies, e.g. Dermaptera (Haas & Kukalová-Peck 2001) and Psocoptera (Silva-Neto *et al.* 2016). Regardless of the area, proper study of the wing requires a standard of wing preparation to allow the visualization of the characters. The wings are often are visualized on dorsal view. In some cases (e.g. Ephemeroptera, Odonata, Diptera, Hymenoptera), this preparation requires little effort, as the wing is easy to access and observe. In other cases, however, more effort is required when preparing the specimen to be studied. For instance, several polyneopteran orders have folded wings, requiring them to be unfolded and mounted in a stretched position long enough to finish the study. Examples of these preparations are stretching of Orthoptera wings over foam, with help of pins and pieces of papers and preparation of permanent or semi-permanent slides for Psocoptera.

Earwigs (Dermaptera) wings have the most complex folding system among polyneopterans, making wing unfolding and preparation a challenge. However, dermapteran wing venation and its associated sclerites are important components of earwig study (Haas *et al.* 2000; Haas *et al.* 2012), including major phylogenies and classification (Haas 1995; Haas & Kukalová-Peck 2001). Haas (1995) and Haas & Kukalová-Peck (2001) unfolded wings on a black foam, with pins and paper. Haas *et al.* (2000) cut the wing from the body from a recently killed specimen and stretched it on a slide with Mowiol medium (http://cshprotocols.cshlp.org/content/2006/1/pdb.rec10255), without further information as to how they unfolded the wing.

The lack of details represents an impediment to researchers who are not familiar with earwig morphology, as they are likely to spoil several wings specimen before getting good results. Furthermore, Dermaptera wings have a tendency to curl themselves if no force (such as pins, paper or mountant) is being applied to keep them expanded. It is common to find museum specimens with curled or missing wings, where authors stretched them but did not make that stretching permanent. This is a significant problem with Dermaptera, which have the most complex folding system of the posterior wing among insects. Their curled hind wings are nearly impossible to unfold again.

We present a guide on stretching the hind wing and providing images to help to assist in the effort, and suggest a method of wing preservation.

Accepted by E. Bernard: 3 Jan. 2020; published: 13 Feb. 2020

Material and methods

A total of 32 earwigs were used (5 *Mecomera brunnea*; 1 *Mecomera* sp.; 3 Pygidicranidae sp.; 3 *Pygidicrana v-nigra* Audinet-Serville, 1831; 5 *Spongiphora croceipennis* Audinet-Serville 1831; 5 *Sparatta semirufa* Kirby, 1896; 5 *Spongovostox* sp.; and 5 *Labidura riparia* (Pallas, 1773)). The wings were stretched over a microscope slide holding a drop of Hoyer's medium, after which a cover slip was added and ringed with base coat. After sealing, the slides were stored in an oven at 40C° for 7 days to let the base coat dry. The stretching tool used was a pair of wooden probes with curved and blunt apex. A system of lines, numbers, shapes and colors was created to provide a better understanding of the changes that happen at each step of the stretching process (Figs. 2, 3). Solid green lines represent the wing area that will not be moved in that given step. In contrast, solid red lines represent the wing area that will be moved. The solid green and red lines are the initial conformation of the wing in the given step. The dashed blue lines represent how the wing should look after all the indicated moves have been made, thus indicating the initial position of the next step. Black numbers indicate the initial position of a given wing area and pink numbers indicate where this area should be moved to. Furthermore, the arrow system indicates the direction of the movement (e.g., if the head of the arrow is pointed toward the wing apex, then that point should be moved toward the wing apex) and how that movement should be done. Straight arrows indicated a simple direct pushing and curved arrows indicate one must unfold a point in the indicated direction.

Wing-stretching Procedure

Step 1 (Fig. 1): This is the initial position of the procedure. The ventral aspect is easier and is recommended, as it is possible to directly see all the folding, allows a more precise unfolding and diminishes the odds of tearing the wing. For illustrative purposes, Fig. 1 shows a wing still attached to the body. However, it is much easier to stretch the wing after it is cut off. To optimize imaging, the left legs were removed, but this procedure is not necessary.

Step 2 (Figs. 2A, B): At the initial position of this step, the anal margin (black 1, 2 and 3) of the wing will be found above and covering the costal margin. Push the anal margin of the wing towards its unfolded position (pink 1, 2 and 3). Press the indicated points (black arrow beneath the black numbers) towards where the pink numbers are. To avoid tearing the wing, we recommend alternating the pushing between the three points, pushing each of them a little until the anal margin reaches the final position of the step.

Step 3 (Figs. 2C, D): The initial position consists approximately of half of the wing width folded on top of the other half. This step requires the separation of both halves. Insert the stretching tool inside the gap formed between the two wing halves (black arrow in Fig. 2C). After inserting the tool inside the gap, position it at one of the black curved arrows indicated in Fig. 2D and push this point towards the anal-most margin of the wing. Which point to push will depend on the specimen, as some will be easier at the basal-most point, whilst others are going to be easier at the apical or middle point. However, one point should be chosen between the line formed by the three points to diminish the odds of tearing the wing. At the end of the step, the wing will be approximately doubled in width (Fig. 2E).

Step 4 (Figs. 2E, F): In this step, the anal-most margin of the wing is covering one of the halves unfolded in step 3. This unfolded half contains approximately half of the total length of the wing, which is folded like a fan. Push at the indicated black arrows towards the apical margin of the wing. The unfolded half of step 3 will be pushed from beneath the anal margin and gradually be moved towards the costal margin, until assuming a position like Fig. 3A and B. As in step 2, it is recommended to alternate between the indicated pushing points.

Step 5 (Figs. 3A–B, 3C–D, 3E): From this step onwards, the goal is to unfold the fan formed by half of the length of the wing. By doing so, the other parts of the anal margin are going to be unfolded as well and hence there is no need to directly pushing them. To fulfill this step, start pushing towards the apical margin at the indicated black arrows in Fig. 3B, until the wing resembles Fig. 3C. Then change the pushing points to those indicated in Fig. 3D. When the conformation resembles Fig. 3E, change the direction of the pushing from toward apical margin to toward costal margin. As in Steps 1 and 4, there is no correct order to push and alternation between the points is recommended.

Step 6 (Fig. 3F): In this final step, the costal margin should be pointed upwards and resembling a wall. To fully stretch the wing, fully push the costal margin at the indicated straight black arrows until it adheres to the medium on the slide. Then position the stretch tool underneath the remaining costal margin, still pointed upwards, and unfold it toward and until it touches the slide. After it touches the slide, apply slight force on the costal margin and hold for a few seconds to properly anchor it and prevent it from bending upwards again. The wing should now be finally stretched as in Fig. 4A.

FIGURE 1. Step 1—An earwig (Pygidicranidae sp.) in the initial position of the hind wing stretching process.

Step 7 (Figs. 4A–C): Cover the wing with Hoyer's medium (if it is already not immersed), put on the cover slip and seal it with base coat. However, we recommend imaging the wing after stretching (as in Fig. 4A) and again after cutting the wing from the body (as in Fig. 4B). These images could be important in the case of air bubbles is formed, or if a wing part becomes folded again while the cover slip is being applied. In Fig. 4C, the wing is already covered by the cover slip and sealed, but an air bubble was retained in the right corner of the anal margin. Based on Figs. 4A and 4B, the original state of this corner prior the bubble can be determined. After sealing the slide, it should be cured at least seven days in an oven for 40 C°, to allow proper drying of the base coat and the expulsion of air bubbles.

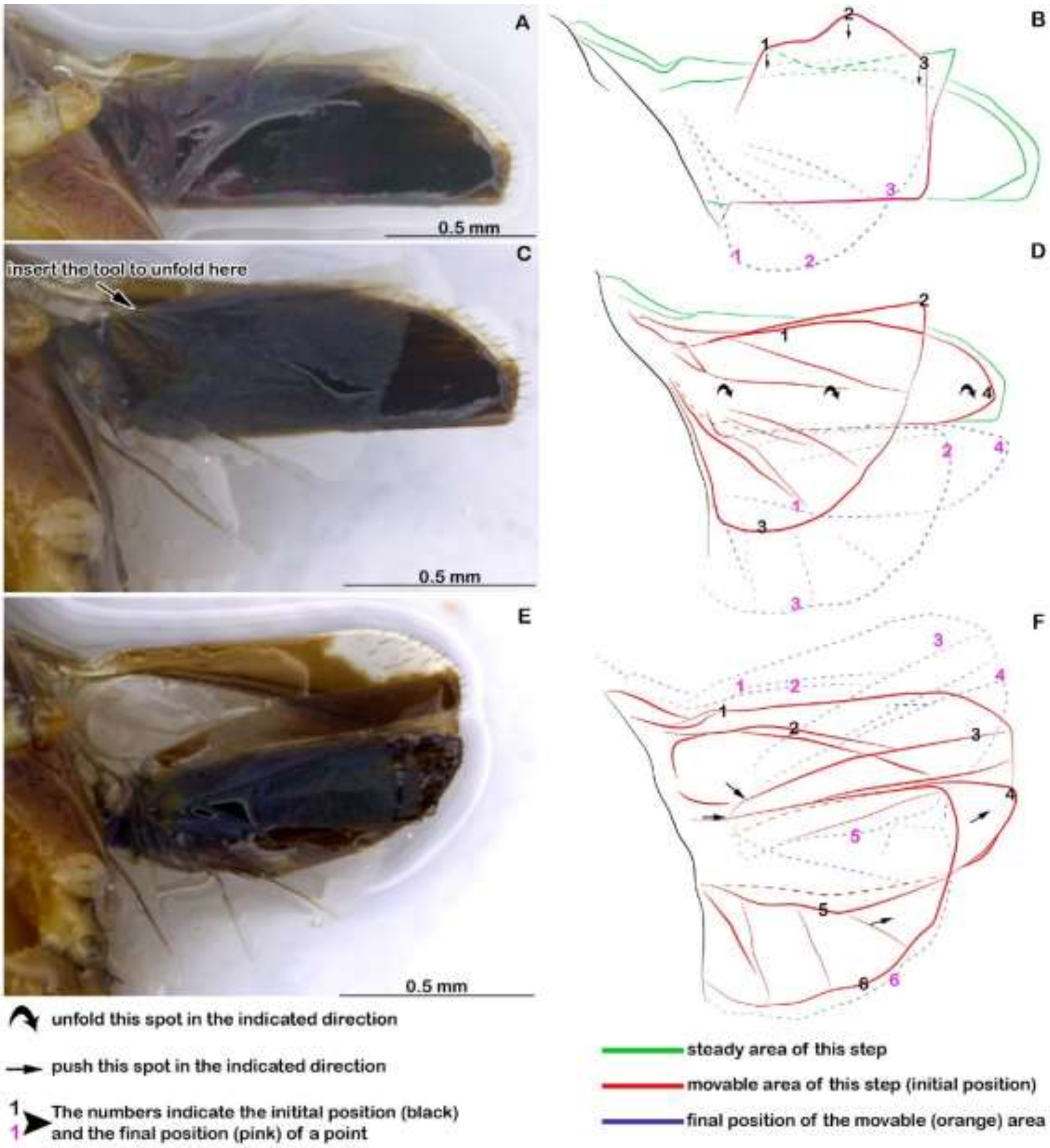

FIGURE 2. Hind wing in the initial steps of the stretching. A, B: Step 2; C, D: Step 3; E, F: Step 4. A) folded wing; B) scheme of Fig. 2A; C) anal area in the initial stretching; D) scheme of Fig. 2C; E) wing with half width stretched; F) scheme of Figure 2E).

Some additional points can be made that will help make the process easier:

- Always hydrate the specimen prior the stretching. We place the entire earwig in a recipient containing boiling water for a few hours. It makes the wing more elastic and less likely to tear.
- Always keep the wing submerged in the Hoyer's medium. It will make easier to move the wing without tearing it.
- When moving a given area, it is preferable to look for a close vein and use it to push that point rather than directly pressing a membranous area and pushing it.

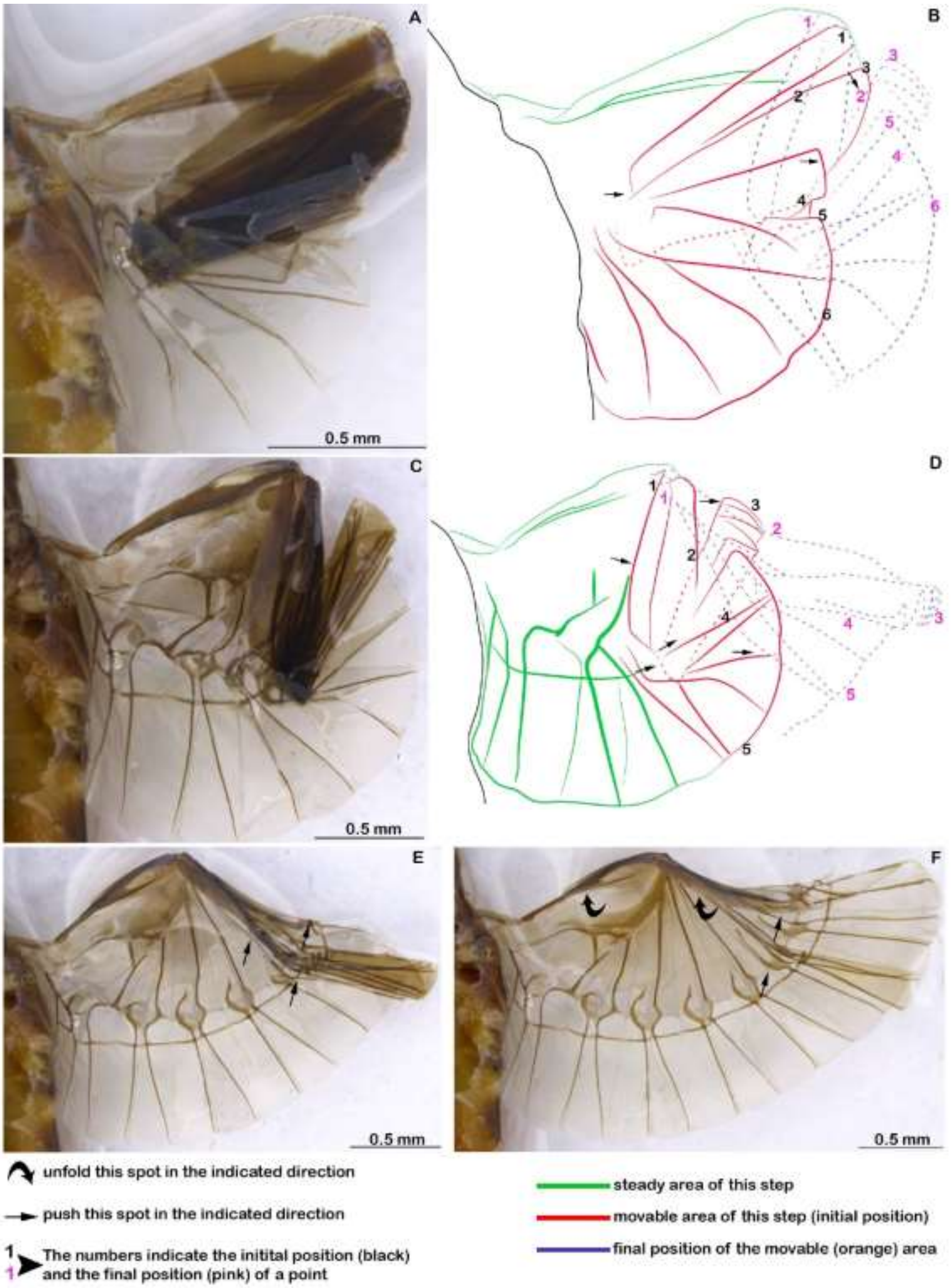

FIGURE 3. Hind wing in the middle steps of the stretching. A–E: Step 5. F: Step 6. A) anal area almost fully stretched; B) scheme of Fig. 3A; C) anal area fully stretched; D) scheme of Fig. 3C; E) posterior margin almost fully stretched; F) anterior and posterior margins almost fully stretched.

- When moving a given point, never press that point against the slide and then push it. Try to gently touch the wing, without exerting too much pressure, and then push it. This tip is especially important for some genera such as *Spongiphora* Audinet-Serville, 1831, which have an extremely thin and fragile hind wing.
- Use an appropriate background color during the stretching process. Some wings will be better observed on a white background, while others will be better on a black background. For wings that are very transparent a black-glass background is helpful.
- Lower the cover slip gently onto the slide, allowing the medium to spread. Once it has settled completely, apply some pressure in the corners as it may stretch the wing even more.

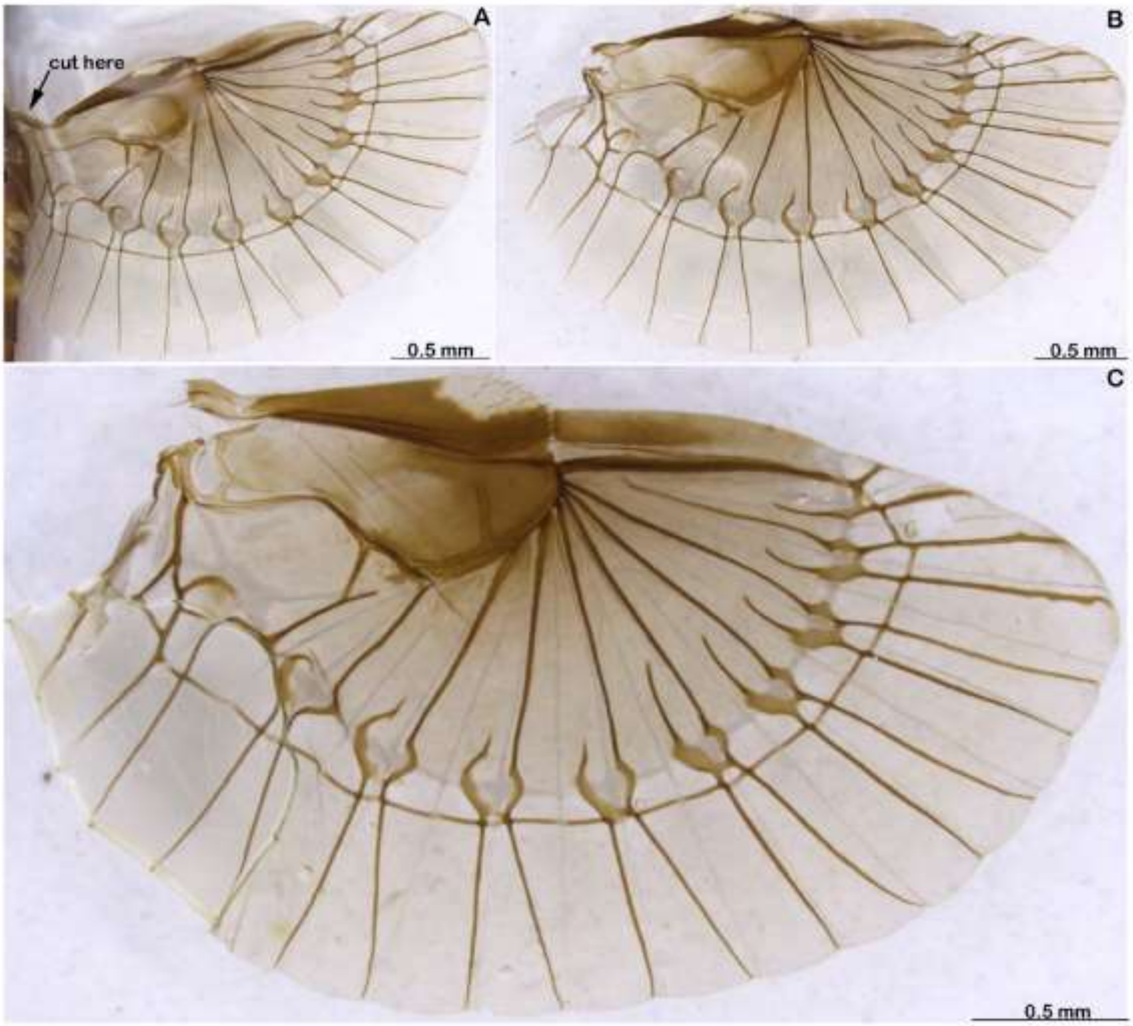

FIGURE 4. Hind wing in the final steps of the stretching. A–C: Step 7. A) wing fully stretched and attached to body; B) the same but separated from the body; C) wing covered by a cover slip.

Method applicability and Hoyer's medium for wing preparation

We tested the described method with small specimens (e.g., *Spongovostox* sp. total body length approximately 5 mm) and larger ones (e.g., *P. v-nigra* total body length approximately 45 mm). The *P. v-nigra* wing almost reached the limit of the slide's width thus indicating that larger specimens, such as *Apachyus faeae* De Bormans, 1894, would also require a larger slide. Despite that, we consider this a proper method to be used for any Dermaptera specimen.

Hoyer's medium was chosen for three reasons: 1) it can be used to mount specimens that are rehydrated; 2) it is an accessible medium, as it can be manufactured with widely available ingredients. The recipe is well known (Anderson 1954; Cold Spring Harbor Protocol 2011); 3) it is a medium widely used for soft-bodied arthropods (such as Collembola Glance 1956; Palacios-Vargas & Castaño-Meneses 2002; Cipola *et al*. 2019). It is imperative to seal the mounted slides after curing, due to Hoyer's medium being considered as a semi-permanent medium if left exposed to the atmosphere.

References

Anderson, L.E. (1954) Hoyer's Solution as a rapid permanent mounting medium for Bryophytes. *The Byologist*, 57, 242–244. https://doi.org/10.2307/3240091

Cipola, N.G., Morais, J.W. & Bellini. (2018) New subgenus and four species of *Lepidocyrtus* Bourlet (Collembola, Entomobryidae, Lepidocyrtinae) from Amazon. *Insect Systematics & Evolution*, 50 (2), 1–46. https://doi.org/10.1163/1876312X-0002184

Cold Spring Harbor Laboratory Press (2011) Hoyer's Medium, Cold Spring Harbor Protocols. Available from: http://cshprotocols.cshlp.org/content/2012/1/pdb.prot067371.short (accessed 06 September 2019)

Dias, P., Rafael, J.A. & Naskrecki, P. (2012) A Taxonomic Revision of The Neotropical Genus *Aegimia* Stål, 1874 (Orthoptera, Tettigonniidae, Phaneropterinae). *Journal of Orthoptera Research*, 21, 109–132. https://doi.org/10.1665/034.021.0108

Glance, G. (1956) Slide Mountinf of Collembola. *Annals of the Entomological Society of America*, 49 (2), 132–133. https://doi.org/10.1093/aesa/49.2.132

Haas, F. (1995) The phylogeny of Forficulina, a suborder of the Dermaptera. *Systematic Entomology*, 20, 85–98.

Haas, F., Gorb, S. & Wootton, R.J. (2000) Elastic joints in dermapteran hind wings: materials and wing folding. *Arthropod Structure & Development*, 29, 137–146. https://doi.org/10.1016/S1467-8039(00)00025-6

Haas, F., Hwen, J.T.C. & Tang, H.B. (2012) New evidence on the mechanics of wing unfolding in Dermaptera (Insecta). *Arthropod Systematics & Phylogeny*, 70, 95–105.

Haas, F. & Kukalová-Peck, J. (2001) Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *European Journal of Entomology*, 98, 445–509. https://doi.org/10.14411/eje.2001.065

Haug, J.T., Haug, C. & Garwood, R.J. (2016) Evolution of insect wings and development—new details from Palaeozoic nymphs. *Biological Reviews*, 91, 53–69. https://doi.org/10.1111/brv.12159

Katayama, N., Abbott, J.K., Kjærandsen, J., Takahashi, Y. & Svensson, E.I. (2014) Sexual selection on wing interference patterns in *Drosophila melanogaster*. *Proceedings of the National Academy of Sceinces of the United States of America*, 111, 15144–15148. https://doi.org/10.1073/pnas.1407595111

Palacios-Vargas, J.G. & Castaño-Meneses, G. (2002) Collembola associated with *Tillandsia violaceae* (Bromeliaceae) in Mexican Quercus-Abies forests. *Pedobiologia*, 46, 395–403. https://doi.org/10.1078/0031-4056-00147

Sane, S.P. (2016) Neurobiology and biomechanics of flight in miniature insects. *Current Opinion on Neurobiology*, 41, 158–166. https://doi.org/10.1016/j.conb.2016.09.008

Silva-Neto, A.M., Aldrete, A.N. & Rafael, J.A. (2016) Phylogenetic relationships of the genera of Ptiloneuridae (Psocodea, 'Psocoptera', Epipsocetae) and a test on the monophyly of *Brasineura* Silva-Neto & García Aldrete and *Loneuroides* García Aldrete. *Zootaxa*, 4150 (1), 73–84. https://doi.org/10.11646/zootaxa.4150.1.4

Vieira, R.M. & Rafael, J.A. (2014) *Longivena,* a new robberfly genus from Brazil (Diptera, Asilidae, Asilinae). *ZooKeys*, 443, 119–138. https://doi.org/10.3897/zookeys.443.8324

CAPÍTULO III

Heleodoro, R.A. & Rafael, J.A. Systematics of the Spongiphoridae (Dermaptera): first morphological evidences for monophyly, with new synapomorphies for the Eudermaptera and taxonomy of the subfamilies

. *Manuscrito a ser enviado para Zoologischer Anzeiger*.

REJEIÇÃO PARA FINS DE NOMENCLATURA

Os atos nomenclaturais utilizados neste trabalho tem a finalidade do exercício e aprendizagem das práticas taxonômicas de Zoologia e sua avaliação pela banca avaliadora. Esta tese de doutorado não deve ser considerada como publicação válida para fins de nomenclatura zoológica. Essa recomendação é mencionada no Código Internacional de Nomenclatura Zoológica (edição 1999), capítulo três, artigo 8.2 e 8.3.

Systematics of the Spongiphoridae (Dermaptera): first morphological evidences for monophyly, with new synapomorphies for the Eudermaptera and taxonomy of the subfamilies

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Abstract. The Spongiphoridae is a group of earwigs (Dermaptera) that belongs to the Eudermaptera group (earwigs that do not have paired structures at the male genitalia). The family is cosmopolitan and currently do not have a precise diagnosis. Furthermore, the phylogenetic studies (all molecular based) so far have been pointing towards a possible polyphyly and thus considering the Spongiphoridae as a "catch-all" group. Concerned by the lack of broad morphological phylogenies, we decide to investigate whether the body characters of this family would corroborate with the previous molecular studies or would result differently. As a result of a morphological phylogeny using the parsimony, we found out that the Spongiphoridae is a monophyletic group, supported by five synapomorphies (from mandible, wings and legs). We also found support for Eudermaptera monophyly and a new subfamily arrangement, as follows: Cosmogeracini **stat**. **nov**., Geracini **stat**. **nov**., Nesogastrini **stat**. **nov**. and Pericomini **stat**. **nov**. had the status of subfamily changed to tribe; Mecomerini **trib**. **nov**. and *Homotagini* **trib**. **nov**. are described. Furthermore, *Filolabia* is transferred from Spongiphorinae to Labiinae: Labiini.

Key words: earwigs, parsimony, Spongiphorinae, systematics.

Introduction

The Spongiphoridae is a group of earwigs (Dermaptera) that are distributed all over the world, with the exception of the poles (Haas 2012). Currently, the family is organized according to Engel & Haas (2007) classification with over 500 species distributed in 13 subfamilies, namely: Caecolabiinae, Cosmogeracinae, Geracinae, Isopyginae, Labiinae, Nesogastrinae, Pericominae, Ramamurthiinae, Rudracinae, Sparattinae, Spongiphorinae, Strongylopsalinae and Vandicinae. Most of these species are extant, but there are fossil records in the Geracinae (in the fossil genus *Nesogerax* Engel, 2016) Labiinae (in the extant genus *Paralabella* Steinmann, 1990) and Spongiphorinae (in the extant genus *Marava* Burr, 1911).

The family is assigned to belong to the Eudermaptera, a group of earwigs which do not have paired male genitalia as a result of the loss of the structures that were located at the left side (Kamimura, 2014). The Eudermaptera is composed by the Forficulidae (distinguished by the second tarsomere cordiform), the Chelisochidae (distinguished by an elongation at the second tarsomere) and the Spongiphoridae being the only family without a clear diagnostic character.

Phylogenetically, the Spongiphoridae is considered to be polyphyletic. Jarvis et al. (2005) recovered *Auchenomus* (Sparattinae) and *Irdex* (Spongiphorinae) as a sister-group to the remaining Eudermaptera and *Labia* Leach, 1815 (Labiinae) and *Nesogaster* Verhoeff, 1902 (Nesogastrinae) outside Eudermaptera in a clade with Carcinophorinae (Anisolabididae). Kocarek et al. (2013) added two more species of epizoic Dermaptera upon Jarvis et al. (2005) dataset and obtained the same abovementioned results for Spongiphoridae. Naegle et al. (2016), working with both Jarvis (2005) and Kocarek (2013) datasets, added 6 Spongiphoridae species to their analyses, recovering the same clades as previous authors, but also recovering *Paralabella* (Labiinae), *Chaetospania* (Sparattinae) and *Spongovostox* (Spongiphorinae) Burr, 1911 in a new monophyletic clade inside the Eudermaptera and *Marava* (Spongiphorinae) as sister-group of Arixeniidae. The results of Naegle et al. (2016) also indicates the paraphyly of Labiinae, Sparattinae and Spongiphorinae as well as the relationship of parts of these three subfamilies. All of these works combined molecular and morphological data, although the morphological characters came from the phylogeny of Haas & Kukalová-Peck (2001) (which only had a single Spongiphoridae species), without the addition of new characters. More recently, Wipfler et al. (2020) using phylogenomics and morphological data from literature recovered *Nesogaster* as sister-group of Forficulidae and *Labia* as sister-group of Chelisochidae. Despite agreeing with the polyphyly of Spongiphoridae, Wipfler et al. (2020) obtained considerably different results from previous authors, as all Spongiphoridae species were recovered inside the Eudermaptera.

All of the abovementioned works agree upon the lack of morphological support for the Spongiphoridae, considering the family as a "catch-all" group. However, we believe these assumptions have issues that must be tackled. First, all of these works used morphological characters that were sampled with the goal of testing other taxa but not specifically Spongiphoridae. For instance, Haas & Kukalová-Peck (2001) had the goal of testing the monophyly of Dermaptera as well as to check the relationship of the families, whilst in Schneider & Klass (2013) (used in Wipfler et al. 2020 dataset) the authors studied the female genitalia aiming for Eudermaptera. The problem here is that these datasets aimed for supra-familiar level, which naturally causes the characters to be more informative at supra-familiar level. The second problem is that all of these works did not try to sample new characters besides those recorded in the literature, automatically excluding the possibility of finding new characters and excluding the possibility of re-interpretation of these previous characters. For instance, Haas & Kukalová-Peck (2001) summed up the tarsi of all spongiphorids in "normal, not elongated", which we consider to be incorrect as they ignored features such as shape, presence/absence of setae and other features that might indicate a common ancestor. The third problem is the low number of species/genera used in these works to infer the relationship of over 500 Spongiphoridae species. For instance, Naegle et al. (2016), which is the dataset with the highest number of Spongiphoridae, used 12 species from 9 genera and 4 subfamilies (the family comprised 28 genera in 11 subfamilies), thus excluding about 2/3 of the family total known diversity. Furthermore, these 12 species are mostly from the Old World, with only a single species from the New World. In short, these three problems together mean that the family is underestimated in terms of species richness, morphology and geographical distribution.

Thus, we decided to investigate the monophyly of the Spongiphoridae by using the poorly explored parsimony and body characters. Our goals are: 1) increase the taxonomic and sampling effort of Spongiphoridae and verify if the polyphyly remains; 2) test these taxa with characters from the literature and new ones; 3) test if the subfamilies found in taxonomic arrangement of Engel & Haas (2007) are monophyletic; 4) apply the taxonomic changes found in our phylogenetic analyses.

Material and Methods

Material origin, dissection methods and terminology

The material of the present study belongs to the Natural History Museum - NHM (UK, London), the Entomological Collection of the Manchester Museum - MUE (UK, Manchester), the *Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia* – INPA (Brazil, Manaus) the entomological collection of the *Museu Nacional do Rio de Janeiro* - MNRJ (Brazil, Rio de Janeiro).

All the dissected specimens were submerged in water for at least 24 hours to allow for a proper softening of the body parts. The mouthparts were dissected with pins and tweezers, whilst the wings followed the protocol available at Heleodoro & Rafael (2020). For the male genitalia, the entire abdomen was separated from the body and immersed in lactic acid heated at 100 Cº for about an hour to dissolve fat and muscles. Afterwards, the genitalia were separated from the abdomen and stored in microvials containing glycerin. The dissected body, the male genitalia and slides containing the wings (as well as labels) were all stored in the same recipient, a tube made for storing slides to prevent the loss of the body parts.

The morphology of the head follows Haas & Gorb (2004), for the wing Haas & Kukalová-Peck (2001) and for the male terminalia and genitalia Kamimura (2014). Photographs were taken with a Leica DFC500 digital camera fitted on a Leica MZ205 stereomicroscope. The camera was linked to a computer with Leica Application Suite software, used to combine multiple layers of photographs into a single fully focused image. Photos were edited on Adobe Photoshop CS6 and Adobe Illustrator CS6.

Phylogeny

For the phylogeny, we built the character matrix with the Winclada ver. 1.00.8 (Nixon, 2002) and then transferred to the Tree Analysis Using New Techonology (TNT) ver. 1.5-beta software (Goloboff et al. 2003), where the analyses were conducted. The “Traditional Search” was used, using the Tree Bisection and Reconnection method with 1,000 replications and saving 10,000 trees per replication. Our analyses included 59 body characters, from all tagma, which were treated as unordered, with same weighting and their construction followed the recommendations made by Sereno (2007). The terminals of our analyses are all species and we included 72 species in total, out of which 66 are from Spongiphoridae and 6 are from other families (three from Forficulidae, one from Chelisochidae, one from Anisolabididae and one from Labiduridae).

The ingroup is composed solely by Spongiphoridae species, which we sampled following two criteria: 1) include as much genera and subfamilies as possible, in order to obtain a broader taxonomic sampling and avoid the underestimation of Spongiphoridae diversity; 2) include all genera that were previously tested in other phylogenies. We analyzed a total of 28 genera out of the 37 and 6 subfamilies out of the eleven. We could not sample all subfamilies of the Spongiphoridae, as we could not find specimens of the Isopyginae Rudracinae, Ramamurthiinae and Vandicinae. Furthermore, the literature data of these subfamilies is scarce (as well as photos and illustrations), thus impeding their character sampling. In addition, we analyzed photos from the Caecolabiinae, but due to the lack wings of these specimens we decided to not include them in our analyses as most of the data would be uninformative. However, we treated this subfamily in the taxonomy section and addressed its position in the Spongiphoridae. For the same reason as Caecolabiinae, the few fossil taxa of Spongiphoridae were not included in our analyses, although we address them in our discussion. The outgroup is composed by Anisolabididae (Carcinophorinae) and Labiduridae, as they were recovered together with Spongiphoridae in previous hypothesis, and Chelisochidae and Forficulidae, for being the closest groups to Spongiphoridae in the Eudermaptera. The Bremer support was provided above the nodes to indicate their robustness. In the results, we provided two images of our most—parsimonious tree: one with our proposal of taxonomic arrangement overlapped over the nodes and another one overlapping the taxonomy of Engel & Haas (2007), but we highlight that both trees are the same and are our results. The samples characters are given below:

Head characters

1) Head conformation: dorso-ventrally not flattened (0); dorso-ventrally flattened (1) (Fig. 3A)
2) Head coloration in relation to pronotum: concolor (0); different (1) (Figs. 5A, B).
3) Depression at head frons: absent (0); present (Fig. 5C) (1).
4) Latero-apical portion of vertex: not elevated (0); elevated (Fig. 5D) (1)
5) Depression at head vertex: absent (0); present (Fig. 5F) (1).

6) Position of the mandibular mola: overlapping the mesal protuberance (Fig. 5H) (0); not overlapping the mesal protuberance (Fig. 5G) (1).
7) Apical margin of the mandibular mola: smooth (Fig. 5J) (0); with small-teeth-like protuberances (Fig. 5I) (1).
8) Gula shape: distinctly wider than long, slender aspect (Fig. 5M) (0); distinctly as wide as long, broad aspect (Fig. 5K, L) (1).
9) Eye length in relation to length of tempers: eye length at maximum 1.5 times shorter than tempers (Fig. 5E) (0); eye length at least two times shorter than tempers (Fig. 5D) (1); eye length longer than tempers (Fig. 5N) (2).
10) Base of flagellomeres: not constricted (0); constricted (1).
11) Antennomeres 4-5: shortened (Fig. 6A) (0); elongated (Fig. 6B) (1).
12) General coloration of antennomeres 6-11: concolor to antennomeres 3-5 (0); different from antennomeres 3-5 (1).

Thorax and legs characters

13) Thorax conformation: dorso-ventrally not flattened (0); dorso-ventrally flattened (1) (Fig. 5A).
14) Latero-basal margin of pronotum: not projected (0); projected (Fig. 6C) (1).
15) Apical margin of the pronotum: convex (0); straight (Fig. 6D) (1).
16) Long setae of the pronotum: absent (0); present (Fig. 5E) (1). These setae are exclusively of the Pericominae and are conspicuously different in length and shape from other pronotum setae of other genera.
17) Ventral surface of all femurs: with setae (Fig. 6G) (0); without setae (Fig. 6F) (1). It is important to highlight that the Forficulidae has several minute setae and if not observed carefully, it might seem the ventral surface does not have setae (Fig. 6G).
18) Shape of second tarsomere in ventral view: ellipsoidal (0); cordiform (Fig. 6H) (1).
19) Base of second and third tarsomere: not constricted (Fig. 6I) (0) constricted (Figs. 6J, K) (1). There are tarsomeres with a more conspicuous constriction than others, such as in example of *Purex* and *Barygerax* (Figs. 6J, K).
20) Arolium: absent (0); present Fig. 6K) (1).

Tegmina and posterior wing characters

21) Parallel-longitudinal yellowish band of the tegmina: absent (0); present (1).
22) Groove of the fustis: absent (0); present (1). This character was modified from Haas & Kukalová-Peck (2001).

23) Squama length: with at least 75% of coastal area length (Fig. 3M) (0); reaching at maximum 70% of the coastal area length (Figs. 4L, N, P). There are variations from 70% and bellow (there are *Sparatta* species which barely reach 55% of coastal area length) and from 75% and above (for instance *Purex*, which reaches nearly 80%). So far, there are no specimens within the 71%-74% interval.
24) Apical margin of the squama: truncated (Fig. 6L) (0); rounded (Fig. 6N) (1).
25) Length of the squama's setae: moderate (0); conspicuously long (1). The length of the *Irdex* squama setae is conspicuously longer than remaining genera.
26) Coloration of posterior wing while resting: uniform (0); with yellowish spots near anterior margin (1).
27) Coastal area coloration of the posterior wing: translucid (Figs. 6L, M, O) (0); pigmented (Figs 6N, P) (1).
28) Semi-trapezoidal reentrance at coastal area near squama: absent (0); present (Fig. 6O) (1).
29) Media posterior vein: reaching the squama (0); ending before the squama (Fig. 6L) (1). This character was modified from Haas & Kukalová-Peck (2001).
30) Cubital anterior vein: reaching the squama (0); ending before the squama (Fig. 6L) (1). This character was modified from Haas & Kukalová-Peck (2001).
31) Anal posterior 3+4 vein: present (Fig. 6P) (0); absent (1).
32) Anojulgal cell: closed (Fig. 7B) (0); open (Fig. 7A) (1).
33) Area of the anojulgal cell in relation to the area of the julgal cell: both cells with nearly the same area (Fig. 7B) (0); anojulgal cell smaller than julgal cell (Fig. 7C) (1); anojulgal cell larger than julgal cell (Fig. 7A) (2). This character was modified from Haas & Kukalová-Peck (2001).
34) Position of the julgal cell in relation to anojulgal cell: julgal cell above anojulgal cell (Fig. 5A) (0); julgal cell sided to anojulgal cell (Figs. 7B, C) (1).
35) Shape of the anal posterior 3 vein before the apical broadening: straight (0); slightly curved (1); strongly curved (2).
36) Shape of the apical broadening of the anal posterior 4: rounded (Fig. 7C) (0); acute (Fig. 7B) (1).
37) Apical broadening of the anal posterior 4: pointing towards apical area of the wing (Fig. 5D) (0); pointing towards posterior area of the wing (Figs. 7A-C) (1).
38) Outer apical area width: gradually narrowing (Fig. 7F) (0); constant (Fig. 7E) (1). This is a synapomorphy of the Geracinae. The constant width gives the outer apical area of this group a widened aspect, whilst in the remaining Dermpatera it has a slender aspect.

39) Length of the ring-cross vein 1: with same length as ring-cross vein 3(0); at least 1.5 times shorter than ring-cross vein (Fig. 7G) (1).
40) Coloration of the radiating branches 3, 4 and 5 of the anal area: not outstanding from remaining veins (0); outstanding from remaining veins (Fig. 7H) (1). The coloration of these three veins in the Eudermaptera is conspicuously more intense than in remaining veins.
41) Posterior half of the radiating branches 6,7 and 8: straight (0); curved (Fig. 7H) (1).
42) Position of the ring-cross vein 19: aligned with the line formed among the ring-cross veins 1-17 (Figs. 7I, J) (0); not aligned with the line formed among the ring-cross veins 1-17 (Fig. 8A) (1).
43) Broadenings of the anal radiating branches in relation to the broadenings of the intermediary veins: connected (0); not connected (Fig. 7H) (1). This character was modified from Haas & Kukalová-Peck (2001).

Abdomen characters

44) Abdomen conformation: dorso-ventrally not flattened (0); dorso-ventrally flattened (Fig 5A).
45) Shape of tergite 10: rectangular, not flattened (Fig. 8B) (0); dome-shaped, flattened (Fig. 8C) (1).
46) Dorsal protuberances of the tergite 10: absent (0); present (Fig. 8B) (1).
47) Latero-apical margin of tergite 10: without depression (Fig. 8B) (0); with depression (Fig. 8D) (1).
48) Apical margin of tergite 10: smooth (Fig. 6D) (0); striated (Fig. 8B) (1).
49) Dorsal protuberances of cercus: absent (0); present (Fig. 8B) (1).
50) Basal blade of cercus: slender (0); conspicuously widened (Fig. 8D) (1).
51) Serrated projections at apical third of cercus: absent (0); present (Fig. 8E) (1).
52) Male pygidium extension: absent (0); present (1). When the extension present, easily seen from dorsal view, surpassing tergite 10 (Figs 8B, D). We coded this character only at males due to lack of female specimens for most species.
53) Male pygidium shape: sub-triangular (Fig. 8G) (0); sub-trapezoidal (Fig. 8F) (1). We coded this character only at males due to the lack of female specimens for most species.
54) Aspect of the paramere of the male genitalia: dorso-ventrally not flattened (Fig. 8I) (0); dorso-ventrally flattened (Figs. 8H, J) (1).
55) Symmetry of the paramere: symmetrical (0); asymmetrical (Fig. 8H) (1).
56) Width of the Paramere of the male genitalia: constant from base to apical third, where it narrows (Fig. 6I) (0); conspicuously wider at anterior half (Fig. 8H, J) (1).

57) Basal margin of the paramere of the male genitalia: truncated (Figs. 8H, I) (0); rounded (Figs. 8J) (1).
58) Apical third of the paramere of the male genitalia: not elongated (0); elongated (Fig. 8J) (1).
59) Emargination at apical third of the paramere of the male genitalia: absent (0); present (Fig. 8H) (1).

Results and Discussion

Our analyses recovered a single most-parsimonious tree, which is displayed bellow (Fig. 1A). Right afterwards, we repeated our tree and substituted our taxonomic proposal by the one from Engel & Haas (2007) to visually facilitate the comprehension of the taxonomic changes (Fig. 1B). In both figures, the colored names and bars equals the new familiar and tribal proposal of our work in Fig. XA, whilst it equals the familiar and subfamiliar proposal of Engel & Haas (2007) in Fig. XB.

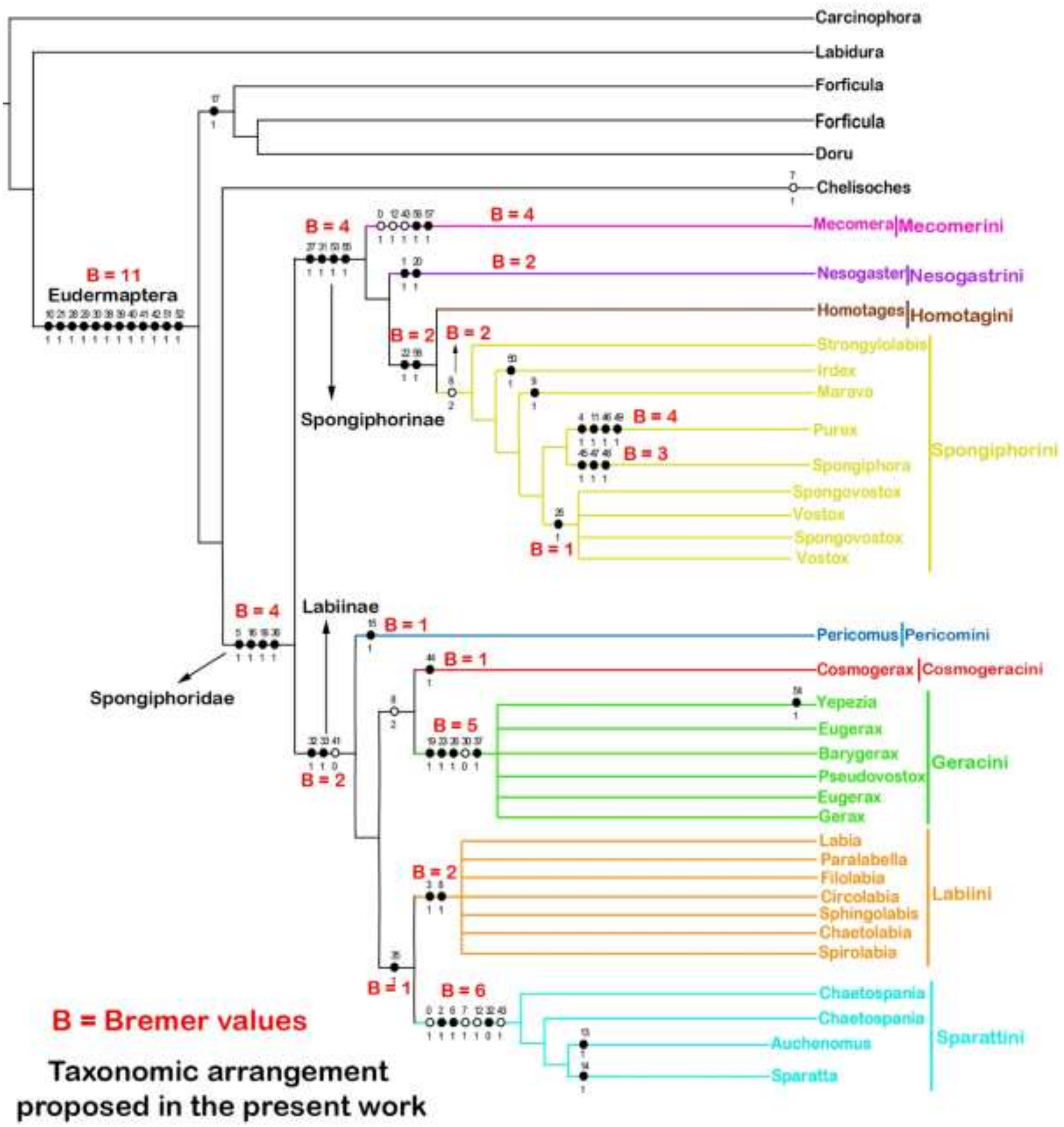

Figure 1 - Single most-parsimonious tree from the phylogenetic analysis displaying the current taxonomic arrangement of Spongiphoridae.

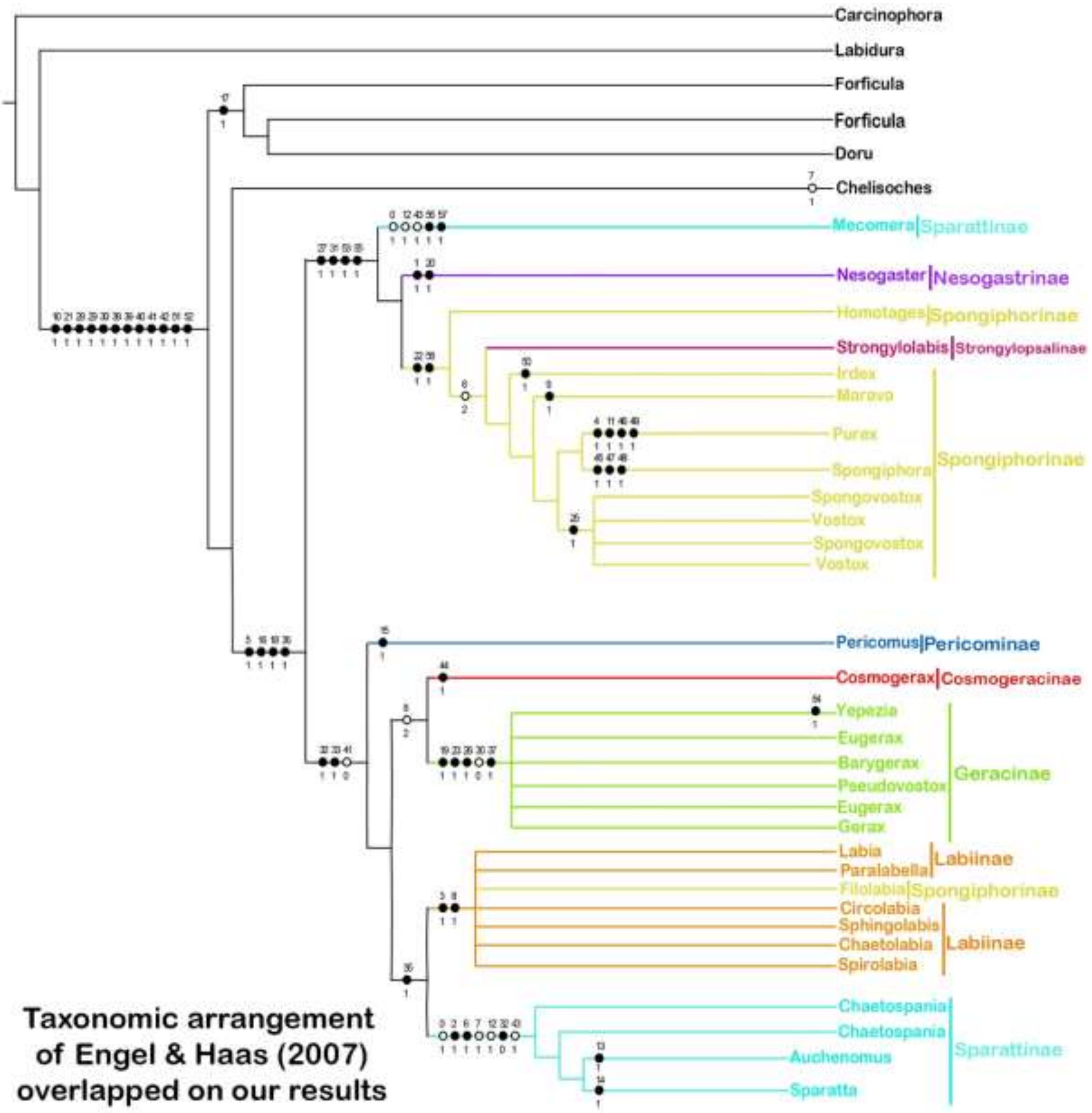

Figure 2 - Single most-parsimonious tree from the phylogenetic analysis displaying the Taxonomy of Engel & Haas (2007) overlapped in our results.

Recovered Topology

Eudermarptera (Bremer = 11) was recovered as a monophyletic group with 12 synapomorphies: antenomeres 4-5 elongated (character 11:1), groove of the fustis present (character 22:1); media posterior vein ending before the squama (character 29:1); cubital anterior vein ending before the squama (character 30:1); ring-cross vein 1 at least 1.5 times shorter than ring-cross vein 3 (character 39:1); coloration from radiating branches 3, 4 and 5 outstanding from remaining veins (character 40:1); posterior half of radiating branches 6, 7 and

8 (character 41:1); broadenings of the radiating branches connected to broadening of intermediary branches (character 43:1); pygidium with extension (character 52:1) and pygidium subtrapezoidal (character 52:1).

Spongiphoridae (the ingroup) was recovered as a monophyletic group (Bremer = 4) supported by four synapomorphies: mandibular mola not overlapping the mesal protuberance (character 6:1), ventral surface of femurs without setae (character 17:1); base of second tarsomere constricted (18:1); apical broadening of anal posterior 4 pointing towards posterior area of the wing (character 37:1). Probing in the internal relationships of the Spongiphoridae, the family was subdivided into two major clades which we considered to be two subfamilies: Spongiphorinae and Labiinae

Spongiphorinae (Bremer = 4) is supported by four synapomorhies: semi-trapezoidal reentrance near the squama present (character 28:1); anojulgal cell open (character 32:1); paramere of the male genitalia flattened (54:1); paramere of the male genitalia conspicuously wider at anterior half (character 56:1). Labiinae (Bremer = 2) is supported by two synapomorphies and one homoplasy: anojugal cell smaller than julgal cell (character 33:1); julgal cell sided to anojugal cell (character 34:1); ring-cross vein 19 aligned with previous ring-cross veins (homoplasy – character 42:0).

Inside the Spongiphorinae, Mecomerini (Bremer = 4) was recovered as the sister-group of the remaining spongiphorines, supported by three homoplasies: head, thorax and abdomen dorso-ventrally flattened (characters 1:1; 13:1 and 44:1) and two synapomorphies: basal margin of the paramere rounded (character 57:1) and apical third of the paramere elongated (character 58:1). Nesogastrini (Bremer = 2) was recovered as the sister group of Spongiphorini based on two synapomorphies: head coloration different from pronotum (character 2:1) and presence of parallel-longitudinal yellowish band (character 21:1). Spongiphorini (Bremer = 2), which included *Irdex*, *Homotages*, *Marava*, *Purex*, *Spongiphora*, *Spongovostox*, *Strongylolabis* and *Vostox*, is supported by two synapomorhies: squama length at maximum of 70% of the coastal area length (character 23:1) and apical third of male genitalia emarginated (character 59:1).

Inside the Labiinae, Pericomini (Bremer = 1) was recovered as the sister group of the remaining Labiinae. Internally, Cosmogeracini (Bremer = 1) and Geracini (Bremer = 5) form a monophyletic clade which is a sister-group of another monophyletic clade formed by Labiini (Bremer = 2) and Sparattini (Bremer = 6). The Cosmogeracini is sustained by a single synapomorphy, the flattened tergite 10 (character 45:1), whilst the Geracini is sustained by four synapomorphies: arolium present (character 20:1), apical margin of the squama rounded (character 24:1), coastal area pigmented (character 27:1), outer apical area of the posterior wing with constant width (character 37:1); Geracini also bear a homoplasy: the anal posterior 3+4 present (31:1). The clade formed by Labiini + Sparattini is sustained by the acute broadening of anal posterior 4 (character 36:1). The Labiini is sustained by the latero-apical portion of the vertex elevated (character 4:1) and the short eye which is at maximum 1.5 times as long as the temper (character 9:1). The Sparattini is sustained by three synapomorphies: frons depressed (character 3:1), apical margin of the mandibular mola with small-teeth-like protuberance (character 7:1) and anojulgal cell and julgal cell with nearly same area (character 33:0). Furthermore, three homoplasies sustain the clade: the dorso-ventrally flattened head, thorax and abdomen (character 33:1).

Eudermaptera monophyly

Our findings are the first external morphological characters to corroborate the monophyly of Eudermaptera. These evidences contrast with previous results of Naegle et al. (2016), which recovered *Labia* sp., *Nesogaster aculeatus* and *Sphingolabis* sp. outside the Eudermaptera. That would mean that the only morphological character supporting the Eudermaptera (loss and reduction of genitalia structures) up to that point would be a case of extreme convergence. If this would be proven true, considering our results, not only the shift in the genitalia, but also shifts in the mandible, legs, wings and abdomen would have to be explained by convergence or several independent cases of reversion or parallelism, which is a scenario we consider unlikely to have happened.

Bilinski et al. (2014) analyzed the ovaries of *Irdex chapmani* Brindle, 1980 and *Chaetospania borneensis* (Dubrony, 1879) and concluded that the first species has the morphology of the ovaries closer to Anisolabididae and Labiduridae, whilst the later has the ovary morphology closer to remaining Eudermaptera. Due to this difference, the authors agreed with the hypothesis of a polyphyletic Spongiphoridae. This hypothesis is contradictory to the results of Naegle et al. (2016), in which recovered both abovementioned genera closer to Eudermaptera than to the Anisolabididae and Labiduridae. As can be seen in our topology, our results do not support the hypothesis proposed by Bilinski et al. (2014). The authors did not consider the ovary morphology of *Irdex chapmani* as result of reversion, a case in which we consider much more likely to have happened, given the evidence for a morphological affinity we presented here.

Concerned by sampling bias, we verified through photos if the synapomorphies of Eudermaptera characters are stable in other members of the Chelisochidae (*Adiathetus tenebrator* (Kirby, 1891); *Hamaxas nigrorufus* Burr, 1907) and Forficulidae (*Allodahlia scabriuscula* (Audinet-Serville, 1838); *Elaunon bipartitus* (Kirby, 1891); *Eparchus biroi* (Burr, 1902); *Forficula lurida* Fischer 1853) and concluded that they are stable. Concerned with the constancy of the character 53, the male pygidium shape, we also verified some Anisolabididae (*Anisolabis* Fieber, 1853 Euborellia Burr, 1909 *Neolabis* Brindle, 1981), Diplatyidae (identified to family level), Pygidicranidae (identified to family level) and Labiduridae (*Forcipula gariazzi* Borelli, 1900; *Labidura riparia* from Japan) and concluded that the subtriangular pygidium is present at these taxa, indicating a clear lineage distinction between the Eudermaptera and the remaining extant Dermaptera that have the pygidium not fused to tergite 10.

Due to the results of Naegle et al. (2016) and Wipfler et al (2020), we also verified the pygidium of Arixeniidae and Hemimeridae. For the arixeniids, the pygidium is conspicuously subtrapezoidal, as for the hemimerids, we also consider it to be subtrapezoidal despite being fused to tergite 10. It is possible to confirm the subtrapezoidal aspect by observing the structure via its ventral aspect. This is an interesting finding, as it is possibly one of the few morphological characters that may indicate ancestry between the epizoic families and the remaining Eudermaptera. We attempted to include these two epizoic families in our analyses, but the lack of wings and extremely modified body hindered the establishment of homologies.

One exception to our proposed synapomorphies of Eudermaptera lies in the Diplatyidae: the elongated antennomeres 4-5. The members of this family seem to have a stable distribution of the elongated antennomeres, as in our dataset. However, based on the other synapomorphies, we hypothesize that this is a case of adaptative convergence.

Spongiphoridae monophyly

Our analyses provided the first evidence of monophyly for the family, based on a robust taxon sampling. Interestingly, as in Chelisochidae and Forficulidae, the legs provided synapomorphies for the family: the lack of setae at the ventral side of the femur and the second tarsomere having a constriction at base. In Chelisochidae, the second tarsomere has a conspicuous projection, whilst the shape of the second tarsomere in Forficulidade is distinctly cordiform. For some reason, the second tarsomere seems to adapt in the different groups of Dermaptera and therefore should be investigated outside the Eudermaptera. An example can be seen in Haas & Gorb (2004), where the authors illustrated several tarsi from different Dermaptera species, demonstrating a richness of shapes of the second tarsomere. Curiously, the second tarsomere of *Hemimerus vosseleri* Rehn & Rehn, 1936 illustrated by the authors is similar to that of *Apterygida albipennis*, indicating a possible hint of relationship.

The wings played an important role in our analyses, as in many different insect orders. In terms of family-level, the anal region of the wing is the one with the highest number of adaptations. We found patterns for Spongiphoridae and Chelisochidae, suggesting that each family have their own morphology. Furthermore, our wing characters sustained the division of the family in two subfamilies as well as clustered Labiini and Sparattini. Haas & Kukalová-Peck (2001) already demonstrated that this is arguably the region of the posterior wing which is more derived in Dermaptera in relation to other insect orders. Hence, we encourage further Dermaptera studies to investigate this area, as it has a great potential for synapomorphies, as well as for diagnostic characters for taxonomists.

Besides the mandibular molar not overlapping the mesal protuberance of the left mandible, we attempted to establish several patterns in family-level in search for synapomorphies at the mandible. Unfortunately, what we could perceive is that this structure, at least for Spongiphoridae, has a considerable degree of plasticity. In many genera, the presence/absence of setae, position of the sutures/sulci, position of the condyles and many other features, were not constant, with great variation. We also used morphometrical tests over the mandible, but did not get any result. This might be linked and indicate an unexplored diversity of diet and foraging habitat of the Dermaptera, in which for most species we do not have such level of information.

Subfamilies and tribes

The subfamily/tribe levels are the ones which had more changes in relation to the taxonomy of Engel & Haas (2007). Our results solved the problem of several tribes, such as Pericomini and Geracini, which consisted of several small taxa which had no connection between each other, without a clear hypothesis of relationship. With our results, we connected all current tribes under a subfamily, serving as base for future works guide their hypothesis and an improvement towards a more comprehensive taxonomy of the Dermaptera.

Naegle et al. (2016) recovered our proposal of Spongiphorini as paraphyletic, with *Irdex* and and *Spongovostox* being recovered separately. These two genera have similarities that are too specific to be considered as independent, such as the emargination of the paramere of the male genitalia and the open anojulgal cell. Naegle et al. (2016) also recovered *Auchenomus* and *Chaetospania* as independent lineages, but the unique morphology of the mandible, genitalia and wings suggests that these genera belong to the same lineage. Haas & Gorb (2004) mentioned that the arolium of the Geracini could be explained by convergence. This hypothesis falls in the light of our results, as the Geracini also strongly uniform morphology of the wings, suggesting ancestry between these species.

Despite having a Bremer support of 1, we consider the Comosgeracini as a well-supported group. The flattened tergite 10 is a unique feature among Dermaptera, suggesting a well-delimited and conspicuous lineage.

Mecomera was recovered as the sister-group of the Spongiphorinae. The remaining Sparattinae (*sensu* Engel & Haas, 2007) genera (*Auchenomus*, *Chaetospania* and *Sparatta*) were recovered as a monophyletic group and represent the true taxonomic configuration of the Sparattini, as it was a solid and robust group. These results mean that the dorso-ventrally flattened body of the abovementioned genera is a product of environmental pressure, as they live under tree bark of fallen trees. This was a hypothesis risen by Srivastava (1995), but the author thought that the Old World *Auchenomus* and *Chaetospania* would form one group and the New World *Mecomera* and *Sparatta* would form another, based on the geographical distribution of the genera.

Another possible synapomorphy of the Spongiphorinae clade is the size of the paramere, in which Steinman (1990) already characterized as “small parameres”. In fact, the total length of the paramere when compared to the total length of the genitalia is conspicuously shorter in this clade when compared to the paramere of the Labiinae clade. The problem is that we found several punctual exceptions in the other major clade, as in the example of *Labia*, which has a really short paramere. We tried to code this relative length of the paramere in several different ways but had no success. Still, we would like to outline this peculiar aspect of the paramere and encourage future investigations.

Chaetospania, *Spongovostox* and *Vostox*

For these three genera, we could not find synapomorphic characters. They all have more than 20 species and have a considerable amount of variation in their morphology. However, in the case of *Spongovostox* and *Vostox*, they also have morphologically similar species. It is likely that these three genera are "catch-all" groups and have more than three genera clustered, thus requiring a dedicated study solely from themselves.

Fossil records

The fossil records of the Spongiphoridae dates from the early Miocene. From the records of *Marava neli* Engel, 2019, *Nesogerax polytrichum* Engel, 2016 and *Paralabella primigenia* Engel, 2016 *Marava*, we can verify that the constriction at the second and third tarsomere and the trapezoidal pygidium are already present (Engel, 2016a, b; 2019). Furthermore, we can see the large and characteristic eyes of Spongiphorinae and the small eyes of the Labiinae, from the *Marava neli* and *Paralabella primigenial*, respectively. These findings demonstrate that the proposed characters of our phylogeny are present in extant and extinct lineages of the Eudermaptera and Spongiphoridae, thus strengthening the idea of a morphologic constancy.

Taxonomy

Spongiphoridae Verhoeff, 1902

Spongiphoridae Verhoeff, 1902; Srivastava 1995 (Synonymy with Labiidae); Engel & Haas 2007 (Family-group names of Dermaptera).

Labiidae Burr, 1909: Brindle 1968 (Pericominae, Strongylopsalinae and Sparattinae revision); Brindle 1968 (Geracinae and Labiinae revision); Brindle 1971 (Spongiphorinae revision); Steinmann 1990 (keys for genera and species); Srivastava 1995 (Synonymy with Spongiphoridae).

Type species: *Spongiphora croceipennis* Audinet-Serville, 1831, by monotypy.

Included taxa

Caecolabiinae

Caecolabia Brindle, 1975 (Fig. 3A)

Labiinae

Cosmogeracinini **stat. nov.**

Cosmogerax Hebard, 1933 (Fig. 3B)

Geracini **stat. nov.**

Barygerax Hebard, 1917 (Fig. 3D)

Eugerax Hebard, 1917 (Fig. 3C)

Gerax, Hebard 1917 (Fig. 3F)

Nesolabia Hincks, 1957

Pseudovostox Borelli, 1926 (Fig. 3E)

Yepezia Brindle, 1982

Labiini

Chaetolabia Brindle, 1972

Circolabia Steinmann, 1987

Isolabella Verhoeff, 1902

Filolabia Steinmann, 1990 (Fig. 3I)

Labia Leach, 1815 (Fig. 3G)

Paralabella Steinmann, 1990 (Fig. 3J)

Paraspania Steinmann, 1985

Sphingolabis de Bormans, 1883 (Fig. 3H)

Spirolabia Steinmann, 1987

Pericomini **stat. nov.**

Parapericomus Ramamurthi, 1967

Pericomus Burr, 1911 (Fig. 4A)

Sparattini **stat. nov.**

Auchenomus Karsch, 1886 (Fig. 4B)

Chaetospania Steinmann, 1990 (Fig 4C)

Sparatta Audinet-Serville, 1839 (Fi. 4D)

Isopyginae

Isopyge Borelli, 1931

Ramamurthiinae

Ramamurthia Steinmann, 1975

Rudracinae

Rudrax Srivastava, 1995

Spongiphorinae

Mecomerini **tribe**. **nov**.

Mecomera Audinet-Serville, 1839 (Fig. 4E)

Nesogastrini **stat. nov.**

Nesogaster Verhoeff, 1902 (Fig. 4F)

Spongiphorini

Irdex Burr, 1911

Homotages Burr, 1909 (Fig. 4G)

Formicilabia Steinmann, 1990

Marava Burr, 1911 (Fig. 4H)

Pseudomarava Steinmann, 1990

Purex Burr, 1911 (Fig. 4I)

Spongiphora Burr, 1911 (Fig. 4J)

Spongovostox Burr, 1911 (Fig. 4K)

Strongylolabis Steinmann, 1986

Vostox Burr, 1911 (Fig. 4L)

Strongylopsalinae

Strongylopsalis Burr, 1900

Vandicinae

Vandex Burr, 1911

Incertae saedis

Paratages sakaii Srivastava, 1987

Family name notes: despite not being taxonomy works, up until recently it is possible to find papers using the name Labiidae (Thouvenot 2011; Silva et al. 2016). This may have happened due to the poor treatment Srivastava (1995) gave to the synonymy between Spongiphoridae (senior) and Labiidae (junior). The authors solely expressed the nomenclatural act at the title while identifying the family as "Spongiphoridae (= Labiidae)", without further explanations inside the remaining content. The reason is that Spongiphoridae has priority over Labiidae for being older (1902 and 1909, respectively). Engel & Haas (2007) recognized the problem that publications were being published with both names, but did not recognized Labiidae as a synonym of Spongiphoridae.

Diagnosis. Left mandible with mesal protuberance not overlapping mandibular mola (Fig. 5G). Ventral surface of the femur without seatae (Fig. 6F). Second tarsomere diamond-shaped in lateral view (Figs. 6J, K). Second and third tarsomere constricted at base (Figs. 6J, K). Anal posterior 3 slightly curved up to the apical broadening (Figs. 6A-C). Apical broadening of the anal posterior 4 pointing towards apical area of the posterior wing (Fig. 7A-C). Male pygidium conspicuous, distinctly surpassing tergite 10 (Fig. 8D).

Description. Coloration: variable in tones of brown, black and yellow. Species body may be glabrous (*Homotages*) or densely hairy (*Pericomus*). *Head*. Sutures inconspicuous (*Spongiphora*) or conspicuous (*Sparatta*); vertex emarginated (*Irdex*) or straight (*Cosmogerax*). Antenna hairy. Compound eye globose, longer than tempers (*Spongiphora),* slightly shorter than tempers (*Mecomera*) or conspicuously shorter than tempers (Labiini). Left mandible with mesal protuberance not overlapping mandibular mola. Mandibular mola smooth (*Spongiphora*) or with small-teeth-like protuberances (Sparattini). Mandibles with mandibular mola glabrous (*Nesogaster*) or hairy (*Strongylopsalis*). Gula with slender aspect (*Cosmogerax*) or with a widened aspect (Sparattini).

Thorax. Pronotum mostly subquadratic (*Sphingolabis*) or subtrapezoidal (*Nesogaster*), but also hexagonal (*Mecomera*) and subretangular (*Auchenomus*). Prosternum subrectangular, mesosternum subquadratic (*Spongovostox*) or subrectangular (*Spongiphora*), metasternum subrectangular, wide, conspicuously larger than mesonotum.

Legs. All legs with setae at latero-ventral margin. All femora robust, conspicuously tall in lateral view, without setae at ventral surface. Tibiae slender. Tarsomere 1 always the longest, with exception of *Mecomera*, which the longest is the third tarsomere. Tarsomere 2 diamond-shaped in lateral viewm, always being the shortest. Tarsomere 3 baciliform. Tarsomeres 2 and 3 emarginated at basal third.

Wings. Tegmina – With latero-ventral margin curling the posterior wing (*Sphingolabis*) or not curling; when not curling, the latero-ventral margin widened (*Spongiphora*) or inconspicuous, thin (*Sparatta*). Apical margin conspicuously emarginated (*Spongiphora*) or straight (*Cosmogerax*).

Posterior wing – hyaline (*Irdex*) or pigmented (*Sparatta*). Radial vein inconspicuous. Media posterior and Cubital anterior veins not reaching the squama. Anal posterior 3 slightly curved up to the apical broadening. Julgal anterior and posterior present. Apical broadening of the anal posterior 4 pointing towards apical area of the posterior wing. Radiating branches 3, 4 and 5 of the anal area with coloration outstanding from remaining veins.

Abdomen. Long, conspicuously longer than tegmina (*Sparatta*) or shortened, as long or shorter than tegmina (Geracinae). Glandular folds inconspicuous (*Cosmogerax)* or conspicuous (*Spongiphora*). Tergite 10 mostly wider than long, subrectangular, but also as wide as long, quadratic (*Sparatta*). Subgenital plate with varied shape. Male pygidium variable in shape, but always conspicuous and surpassing tergite 10. Female pygidium conspicuous or inconspicuous, with different or similar morphology to male pygidium. Cercus simple, not armed (*Pseudovostox*) or strongly armed (*Purex* and *Irdex*); conspicuously longer than abdomen (*Spongiphora croceipennis*), as long as abdomen (*Sphingolabis*) or conspicuously shorter than abdomen (*Yepezia*). Male genitalia with great variation on morphology.

Remarks. The second tarsomere is enough to distinguish the Eudermaptera families: Forficulidade if cordiform, Chelisochidae if bearing a projection and Spongiphoridae if having a constriction at basal third. Another useful feature is to check the pygidium, large, conspicuous and notably surpasses the tergite 10 in Spongiphoridae. However, there are few cases of Chelisochidae (*Hamaxas*) and Forficulidae (*Apterygida albipennis* (von Muhlfeld, 1825)).

Caecolabiinae Steinmann, 1990

Fig. 3A.

Type species: *Caecolabia gomyi* Brindle, 1975 by original designation.

Diagnosis. Compound eye and wings absent (Fig. 3A).

Remarks. This subfamily was well described at Steinmann (1990). We could only examine specimens (types) through photos and due to this we did not include it in our phylogeny. However, we could confirm the position of the subfamily within Spongiphoridae due to the presence of the diamond-shaped second tarsomere and the conspicuous and wide pygidium.

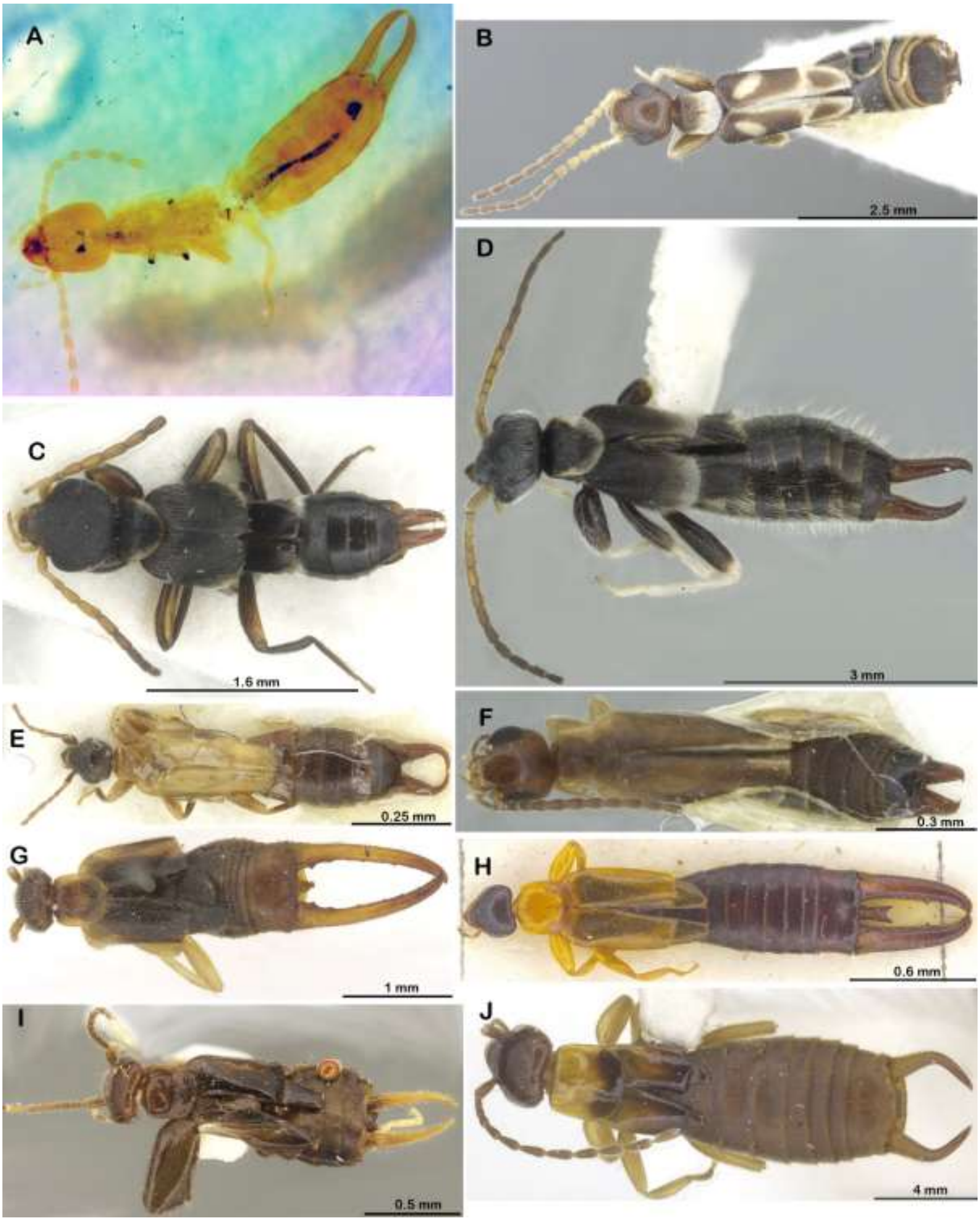

Figure 3. Diversity of Spongiphoridae. A) Holotype of *Caecolabia gomyi* (Caecolabiinae), Fiji - MNHN; B) *Cosmogerax diagonalis* (Cosmogeracini), Panama - MUE; C) *Eugerax salcedoi* (Geracini), Venezuela - MUE; D) *Barygerax venezuelicum* (Geracini), Venezuela - MUE; E) *Pseudovostox bicolor* (Geracini), Phillipines - MUE; F) *Gerax phantasma* (Geracini), Panama - MUE; G) *Labia minor* (Labiini), Sri Lanka - NHM; *Sphingolabis semifulva* (Labiini), Java -

NHM; I) *Filolabia exigua* (Labiini), Brazil, Pará - MPEG; J) *Paralabella dorsalis* (Labiini), Antilles - NHM. All photos from Authors, except for *Caecolabia gomyi*, which is a courtesy of Tony Robillard, *Muséum national d'Historie naturelle*, France.

Labiinae Burr, 1911

Labiinae Burr, 1911; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Labia minor* (Linneaus, 1758) by subsequent designation (Steinmann 1990).

Diagnosis. Anojulgal cell closed, sided to julgal cell (Figs. 7B, C). Anojulgal cell with approximately same area or smaller than julgal cell. Ring-cross vein 19 aligned with the line formed with previous ring-cross veins (Figs. 7I, J). Paramere of the male genitalia conspicuously wider at anterior half, gradually narrowing from there, not flattened (Fig. 8I).

Description. Body size varying from the shortest Dermaptera (*Eugerax poecilum*, 3 mm) to specimens with more than 30 mm long (*Auchenomus, Sparatta*). Body of most specimens hairy. *Head*. Variable, frons with (Sparattini) or without (remaining) depression. Specimens having eyes longer than tempers (Cosmogeracini, Geracini) and having eyes shorter than tempers (Sarattini, Labiini). Head sutures conspicuous. Mandibles hairy, with minute and thin mesal protuberance.

Thorax. Pronotum longitudinally elongated, with variable shape, always narrower than head. Prozone of the pronotum conspicuously elevated. Outline of pronotum well-marked.

Wings. Tegmina with width constant and apex not emarginated. Posterior wing pigmented, with well-marked veins. Anojulgal cell closed, sided to julgal cell. Anojulgal cell with approximately same area or smaller than julgal cell. Ring-cross vein 19 aligned with the line formed with previous ring-cross veins. Apical curvature of Anal Posterior 4 rounded (Cosmogeracini, Geracini and Pericomini) or acute (Labiini, Sparattini).

Abdomen. Cercus shorter or as long as abdomen, with exception of *Sparatta* and *Auchenomus*, which have some species with cercus longer than abdomen. Paramere of the male genitalia conspicuously wider at anterior half, gradually narrowing from there, not flattened.

Remarks. Due to the large eyes of the Cosmogeracini and Geracini, these two tribes may be wrongly identified as Sponghiphorinae. These taxa may be differentiated by the cercus, notably shorter than the abdomen at the Cosmogeracini and Geracini and longer or little shorter than the abdomen at Spongiphorinae.

Cosmogeracini Brindle, 1982 **stat. nov.**

Fig. 3B

Cosmogeracinae Brindle, 1982; Steinmann 1990 (revision).

Type species: *Cosmogerax formica* (Hebard, 1933), by original designation.

Diagnosis. Pronotum with lateral margin emarginated, apical margin with middle point pronounced; prozone and metazone colored differently (Fig. 3B). Tegmina with conspicuous light-yellow spot (Fig 3B). Tergite 10 flattened, dome-shaped (Fig. 8C).

Description. Body hairy, generally dark-brown or black with several light-yellowish or whitish spots. Short species, varying from 5 mm to 7 mm of length. *Head*. Robust, with large compound eye longer than temper. Antenna with approximately anterior half with light-colored tones and posterior half with dark-colored tones.

Thorax. Pronotum with lateral margin emarginated, apical margin with middle point pronounced; prozone and metazone colored differently.

Wings. Tegmina longitudinally elongated, always wider than pronotum, each bearing conspicuous light-yellow spot. Posterior wing at rest reaching tergite 5. Veins well pigmented. Squama hairy. Apical curvature of Anal Posterior 4 rounded.

Abdomen. Tergites laterally convex, with large portion dark-tone colored followed by thin portion light-tone colored. Tergite 10 flattened, dome-shaped. Cercus notably shorter than abdomen, dorsoventrally flattened.

Geracini Brindle, 1971 **stat. nov.**

Figs 3C-F,

Geracinae Brindle, 1971; Steinmann 1990 (revision).

Type species: *Gerax phantasma* Hebard, 1917, by original designation.

Diagnosis. Arolium present (Fig. 6K). Apical margin of the squama rounded (Fig. 6M, N, P). Vein anal posterior 3 +4 present (Fig. 6P). Coastal area of the posterior wing pigmented (Figs. 6N, P). Outer apical area of the posterior wing with constant width from base to apex (Fig. 7E).

Description. General coloration varying among dark-brown, light-brown, light-yellow and black. Body minutely setose, varying from 3 mm to 12 mm. *Head*. Sutures inconspicuous. Compound eye large, longer than temper, black. Antenna uniformly colored. Mandible glabrous, with minute mesal protuberance.

Thorax. Pronotum variable in shape, conspicuously narrower than head. Prozone of pronotum colored differently from metazone.

Wings. Tegmina longitudinally elongated, except for *Eugerax* and *Barygerax*, with apex never emarginated. Apical margin of the squama truncated. Vein anal posterior 3 +4 present. Arolium present. Coastal area of the posterior wing pigmented. Outer apical area of the posterior wing with constant width from base to apex.

Abdomen. Visually narrower than thorax. Tergite 10 rectangular, wider than long. Cercus shorter than abdomen.

Remarks. Although sharing characters with the Cosmogeracini (such as the large compound eye, reduced size and having a short cercus in relation to abdomen), the synapomorphies of both subfamilies are too well-marked and support the existence of two related tribes.

Labiini Burr, 1909

Figs. 3G-J

Type species: *Labia minor* Linneaus, 1758 by original designation.

Diagnosis. Latero-apical portion of the vertex elevated (Fig. 5D). Compound eye at least two times shorter than temper (Fig. 5D). Apical broadening of the vein anal posterior 4 acute (Fig. 7b).

Description. General body coloration dark brown and black. Body hairy. *Head*. Conspicuously wider than pronotum. Sutures inconspicuous. Latero-apical portion of the vertex elevated. Compound eye at least two times shorter than temper.

Thorax. Pronotum conspicuously narrower than tegmina, except for some *Paralabella* species; subquadratic, with posterior margin conspicuously convex. Pronotum coloration uniform, sometimes with spots as in *Parallabella* and *Labia*. Legs with uniform coloration, light-yellow or dark-brown.

Wings. Tegmina widened, visually elongated in *Labia*, with apical margin truncated, with coloration uniform, without spots. Apical broadening of the anal posterior 4 acute. Broadenings of radiating branches and intermediary veins with acute shape.

Abdomen. Tergites conspicuously separated from each other (*Sphingolabis*) or projecting over each other, with condensed aspect (*Labia*, *Paralabella*). Tergite 10 rectangular, wider than long. Cercus as long as abdomen (*Sphingolabis*).

Pericomini Burr, 1911 **stat. nov.**

Fig. 4A

Pericominae Burr, 1911; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Pericomus tenuipes* Burr, 1905 by monotypy.

Diagnosis. Body setae long and conspicuous (Fig. 4A).

Description. This tribe is well-described at Steinmann (1990).

Remarks. The setae of these tribe members are unique among the Spongiphoridae.

Sparattini Verhoeff, 1902 **stat. nov.**

Figs. 4B-D

Sparattinae Verhoeff, 1902; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Sparatta pelvimetra* Audinet-Servile, 1839 by original designation. *Diagnosis*. Body dorso-ventrally flattened (Fig 4B-D, 5A). Gula as wide as long, with broad aspect (Fig. 5L). Head frons depressed (Fig. 5C). Apical margin of mandibular mola rugged (Fig. 5I). Anojulgal cell and julgal cell with nearly same area (Fig. 7B). Apical broadening of vein anal posterior 4 acute (Fig. 7B).

Description. General coloration varying between light-brown, light-yellow, dark-brown and black. Body hairy or glabrous, strongly dorso-ventrally depressed with strong elongated aspect.

Head. Sutures conspicuous, with frons depressed. Antenna with anterior and posterior half colored differently in tones of brown, yellow and black. Gula as wide as long, with broad aspect. Head frons depressed. Apical margin of mandibular mola with conspicuous small-teeth-like protuberances.

Thorax. Pronotum subquadratic or subrectangular, with posterior margin varying in convex and straight; as wide as head. Femur frequently differing in color with remaining leg. Tarsi ventrally densely setose or with few long setae.

Wings. Tegmina conspicuously larger than pronotum, with apical margin emarginated or truncated. Veins well-pigmented, conspicuous. Anojulgal cell and julgal cell of the posterior wing with nearly same area. Apical broadening of the anal posterior 4 acute.

Abdomen. Tergites distinct from each other. Tergite 10 rectangular, wider than long or longer than wide. Cercus and pygidium varying in shape. Subgenital plate widened. Paramere of the male genitalia slender.

Remarks. This tribe may be misidentified as the previously congeneric *Mecomera* (currently transferred to Spongiphorinae), as their members also have a flattened body. The tribe and the genus can be differentiated by the pronotum, which in the Sparattini is subquadratic or subrectangular, whilst in *Mecomera* it is semi-ellipsoidal.

Spongiphorinae Verhoeff, 1902

Spongiphorinae Verhoeff, 1902; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Spongiphora croceipennis* Audinet-Servile, 1831 by original designation.

Diagnosis. Coastal area of the posterior wing with semi-trapezoidal reentrance near the squama (Fig. 6O). Anojulgal cell of the posterior wing open, larger than julgal cell (Fig. 7A). Ring-cross vein 19 of the posterior wing not aligned, but under the line formed with previous ring-cross veins (Fig. 8A). Paramere of the male genitalia dorsoventrally flattened, having constant width until apical third where it narrows (Figs. 8H, J).

Description. Varying in size, from at least 10 mm (some *Spongovostox* species) to more than 40 mm (*Spongiphora*, *Homotages*, *Vostox*). Body robust with coloration mostly dark- or light-brown, but also tones of yellow and black, mostly lustrous but sometimes opaque. Hairy (*Purex*) or glabrous (*Homotages*). *Head*. Robust, with apical margin at vertex mostly convex, sometimes nearly straight. Compound eye slightly shorter than temper (*Mecomera*, *Homotages* and *Nesogaster*) or conspicuously longer than temper (*Irdex*, *Marava*, Spongiphora, *Spongovostox* and *Vostox*). Sutures conspicuous or inconspicuous. Mesal protuberance of the mandible conspicuous.

Thorax. Pronotum with variable shape, often having apical margin convex, nearly as wide as head, with sutures conspicuous. Legs robust and elongated, with variable lenght of the tarsi.

Wings. Tegmina developed or absent. Posterior wing developed, reduced or absent (*Marava* species). Tegmina wider than pronotum and head, with apex often emarginated. Posterior wing weakly pigmented. Coastal area of the posterior wing with semitrapezoidal reentrance near the squama. Anojulgal cell of the posterior wing open, larger than julgal cell. Ring-cross vein 19 of the posterior wing not aligned, but under the line formed with previous ring-cross vein. Squama as long as coastal area (Spongiphorini) or conspicuously shorter (Mecomerini and Nesogastrini).

Abdomen. Parallel sided, wide. Tergites overlapping each other or conspicuously separated. Tergite 10 rectangular, wider than long. Paramere of the male genitalia dorsoventrally flattened, having constant width until apical third where it narrows, subtriangular.

Mecomerini **trib**. **nov**.

Fig. 5E

Mecomera Audinet-Serville, 1839; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Mecomera brunnea* Audinet-Serville, 1839, by original designation.

Included taxon:

Mecomera Audinet-Serville, 1839

Diagnosis. Body dorsoventrally flattened (Fig. 5E). Pronotum hexagonal (Fig. 5E).

Description. The genus and species were sufficiently described at Steinmann (1990) and Heleodoro & Rafael (2019), respectively.

Remarks. This tribe can be easily differentiated with the remaining Spongiphorinae by the flattened body.

Nesogastrini Verhoeff, 1902 **stat**. **nov**.

Fig. 4F

Nesogastrinae Verhoeff, 1902; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: *Nesogaster dolichus*, by monotypy.

Included taxon:

Nesogaster Verhoeff, 1902

Diagnosis. Body glabrous, conspicuously lustrous (Fig. 2F). Head reddish, pronotum with other coloration (Fig. 2F). Tegmina with parallel-longitudinal yellow band (Fig. 2F).

Description. This tribe is well described throughout the works of Brindle (1971) and Steinmann (1990).

Spongiphorini Verhoeff, 1902

Figs. 4E-L

Spongiphorinae Verhoeff, 1902; Brindle 1971 (revision), Steinmann 1990 (revision).

Type species: Type species: *Spongiphora croceipennis* Audinet-Servile, 1831 by original designation.

Diagnosis. Squama nearly as long as coastal margin (Fig. 6M). Compound eye longer than temper (except for *Homotages*) (Fig. 5N). Emargination at apical third of male genitalia (except for *Homotages*) (Fig. 8H).

Description. This tribe is extensively described at Brindle (1971) and Steinmann (1990).

Figure 4. Diversity of Spongiphoridae. A) *Pericomus ater* (Pericomini), Panama - MUE; B) *Auchenomus longiforceps* (Sparattini), Madagascar - NHM; C) *Chaetospania feae*, Sumatra - NHM (Sparattini); D) *Sparatta* sp. nov. (Sparattini), Colombia - INPA; E) *Mecomera* sp. nov. (Spongiphorini), Brazil, Piracicaba - ESALq; F) *Nesogaster amoenus* (Spongiphorini), Sumatra - NHM; G) *Homotages feae* (Spongiphorini), Himalaya - MUE; H) *Marava moreirai* (Spongiphorini), Brazil, Rio de Janeiro - NHM; I) *Purex frontalis* (Spongiphorini), Venezuela

- MUE; J) *Spongiphora buprestoides* (Spongiphorini), Brazil, Rio de Janeiro - MNRJ; K) *Spongovostox alter* (Spongiphorini), Congo - NHM; *Vostox brunneipenis* (Spongiphorini), Brazil, Rio de Janeiro - NHM. All photos from Authors.

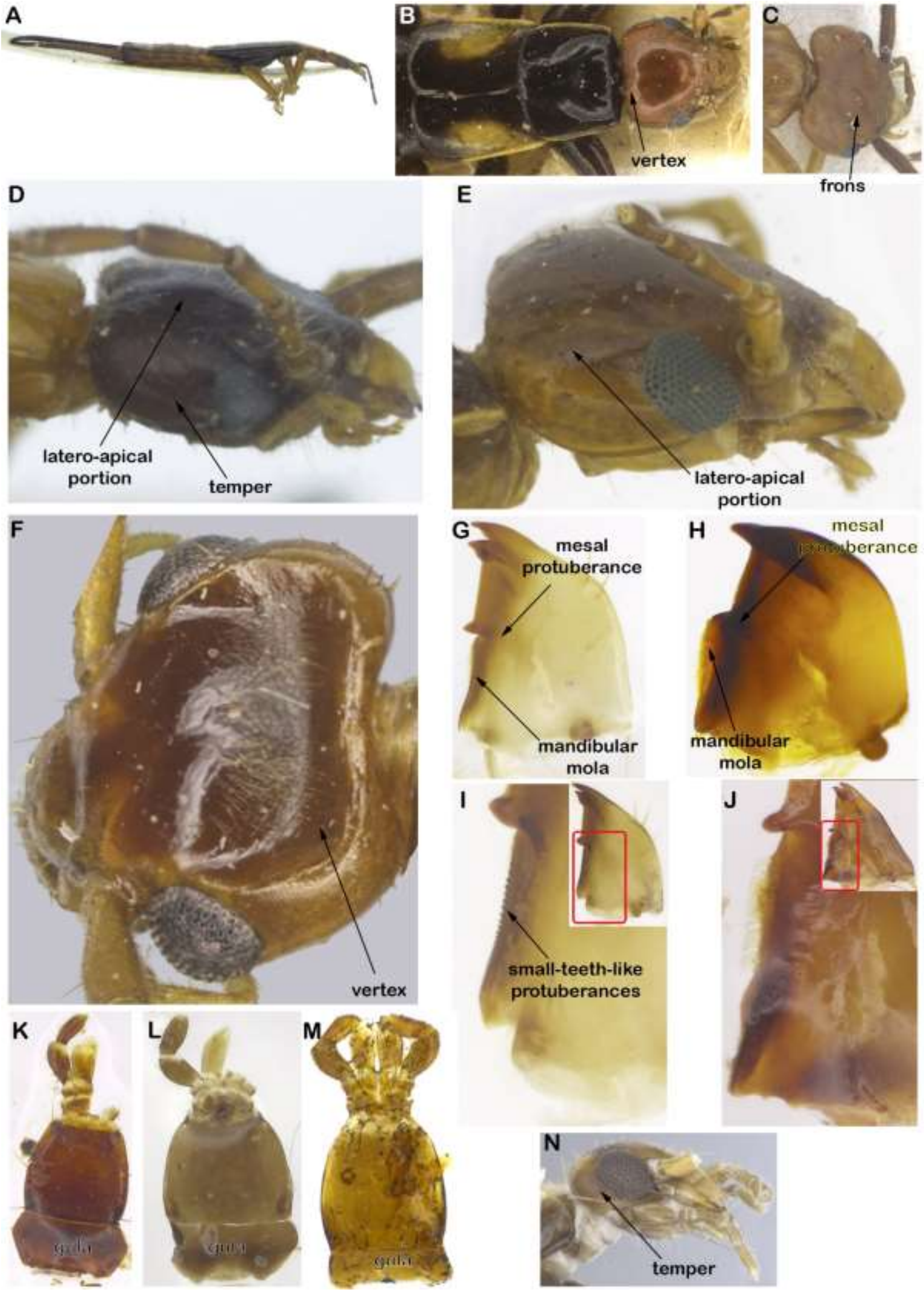

Figure 5. Morphological characters. A) *Spongiphora semirufa*, lateral view; B) *Nesogaster amoenus*, head and thorax, dorsal view; C) Head of *Sparatta* sp., dorsal view; D) head of

Sphingolabis semifulva, lateral view; E) Head of *Nesogaster* sp., lateral view; F) head of *Purex frontalis*, dorsal view; G) left mandible of *Auchenomus javanus*, ventral view; H) left mandible of *Forficula* sp., ventral view; I) left mandible of *Sparatta* sp., ventral view; J) left mandible of *Spongiphora bogotensis*, ventral view; K) mouthparts of *Chelisoches morio*, ventral view; L) mouthparts of *Sparatta* sp., ventral view; M); mouthparts of *Vostox* sp.; N) head of *Cosmogerax diagonalis*, lateral view. All photos from Authors.

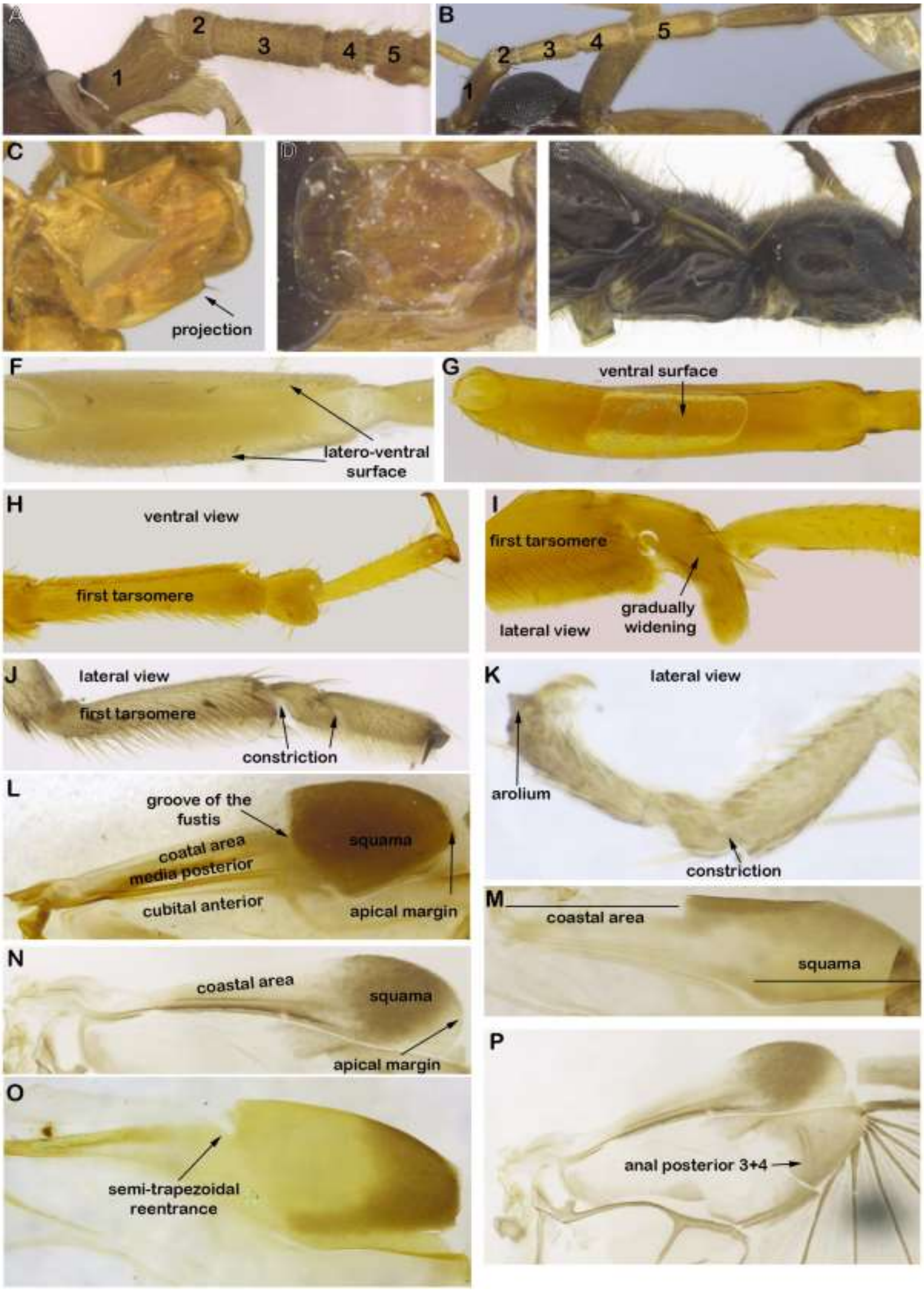

Figure 6. Morphological characters. A) Basal antennomeres of *Labidura riparia*; B) Basal antennomeres of *Purex sinuatus*; C) pronotum of *Auchenomus longiforceps*, dorsal view; D)

pronotum of *Sparatta bormansi*; E) *Pericomus* sp., head and pronotum, lateral view; F) hind femur of *Chaetospania* sp., ventral view; G) hind femur of *Forficula* sp., ventral view; H) tarsomeres of *Forficula* sp., ventral view; I) tarsomeres of *Forficula* sp., lateral view; J) tarsomeres of *Purex frontalis*, lateral view; K) tarsomeres of *Barygerax esau*., lateral view; L) anterior portion from posterior wing of *Chelisoches morio*; M) anterior portion from posterior wing of *Irdex nitidipenis*; N) anterior portion of wing from posterior wing of *Barygerax esau*; O) anterior portion from posterior wing of *Nesogaster aculeatus*; P) anterior portion from posterior wing of *Yepezia venezuelica*. All photos from Authors.

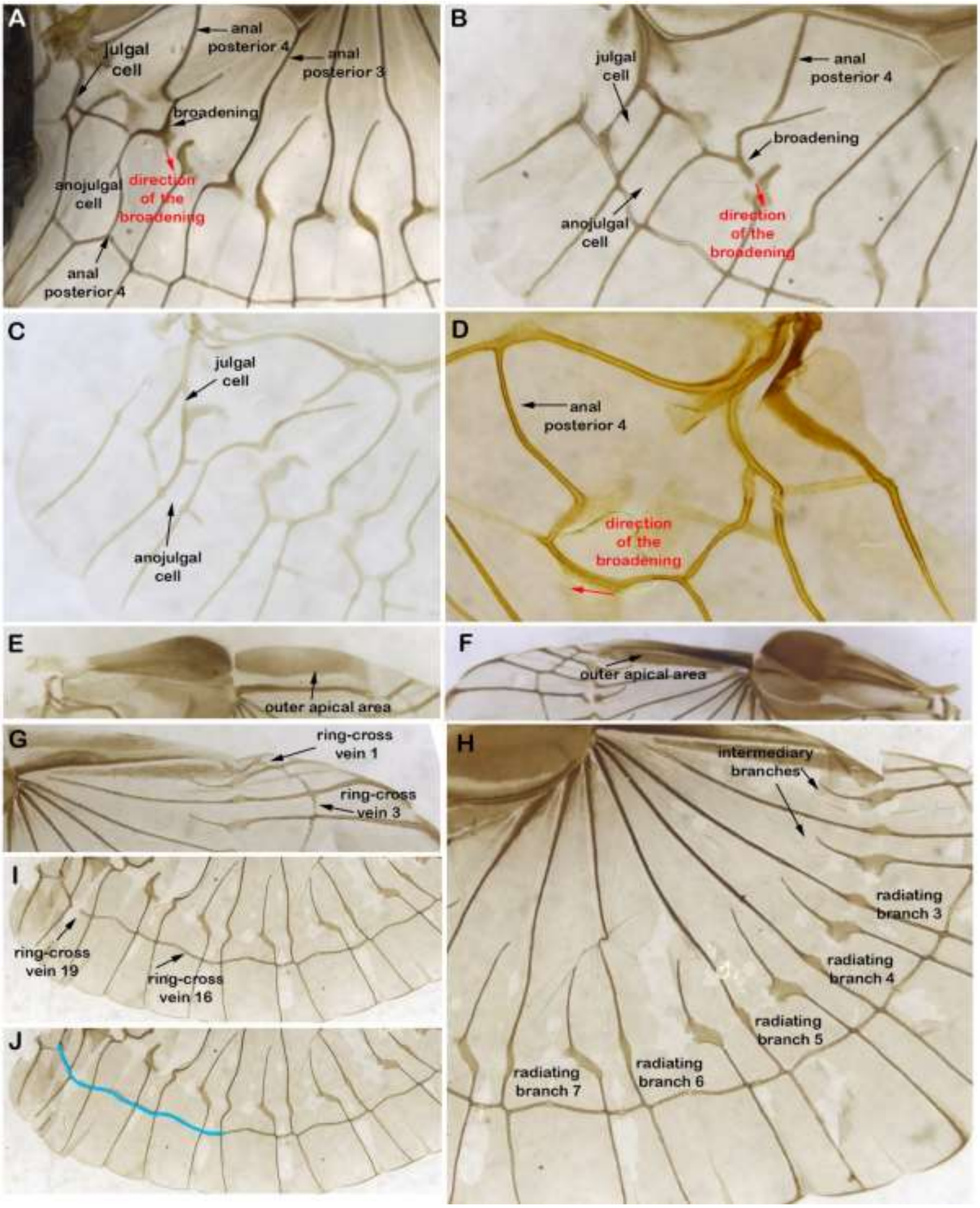

Figure 7. Morphological characters. A) Posterior portion from posterior wing of *Homotages feae*; B) Posterior portion from posterior wing of *Sparatta w-signatta*; C) Posterior portion from posterior wing of *Cosmogerax guatemalensis*; D) Posterior portion from posterior wing of *Forficula* sp.; E) Anterior portion from posterior wing of *Eugerax nigrinum*; F) Anterior portion from posterior wing of *Spongovostox*; G) Anterior portion from posterior wing of *Sparatta* sp.;

H) Anal region from posterior wing of *Sparatta* sp.; I) Posterior portion from posterior wing of *Sparatta* sp.; J) Posterior portion from posterior wing of *Sparatta* sp. All photos from Authors.

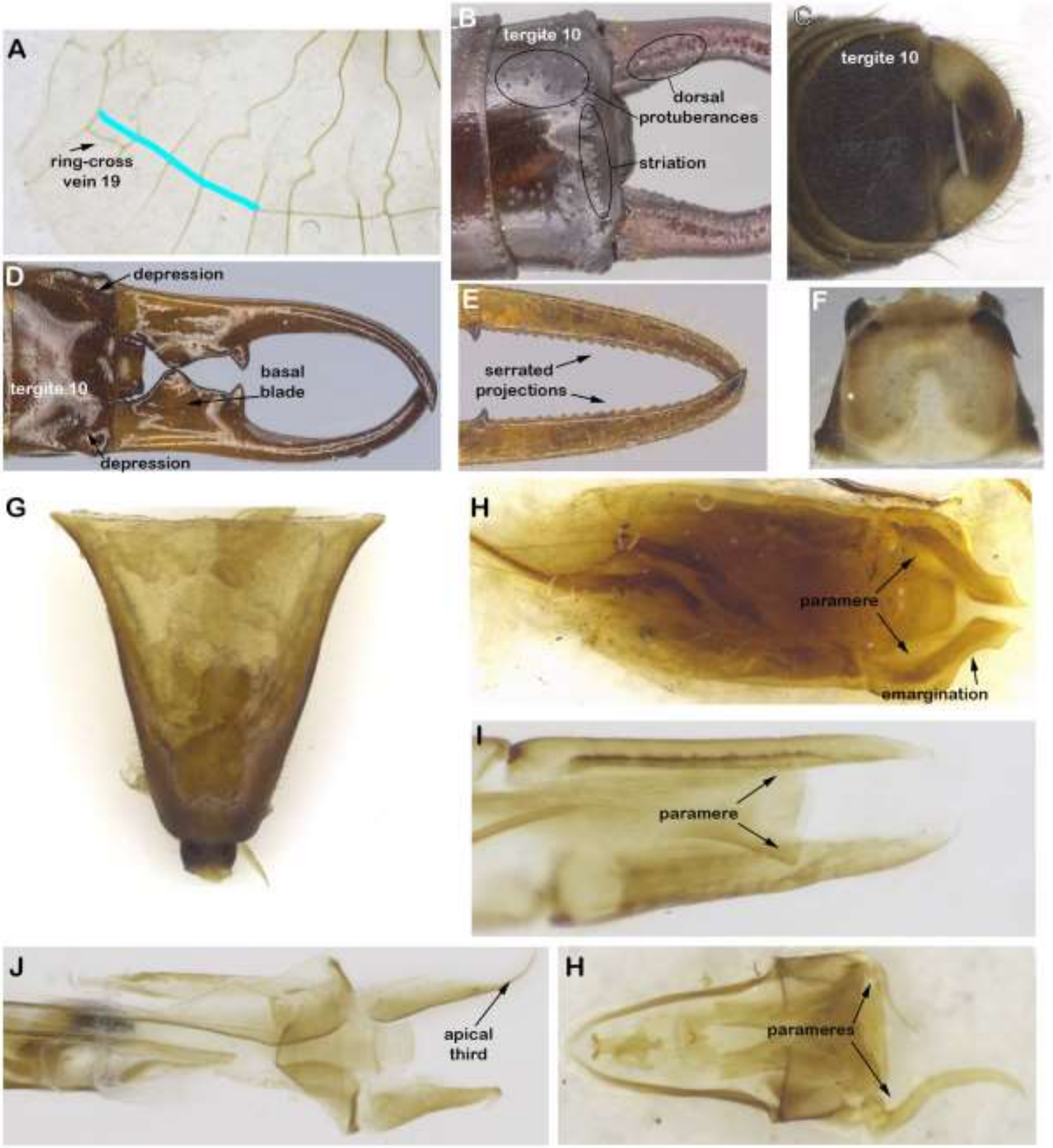

Figure 8. Morphological characters. A) Posterior portion from posterior wing of *Spongiphora croceipennis*; B) Tergite 10 and base of cercus of *Spongiphora bogotensis*, dorsal view; C) Tergite 10 and cercus of *Cosmogerax diagonalis*, dorsal view; D) Tergite 10 and cercus of *Purex frontalis*, dorsal view; E) Cercus apex of *Irdex nitidipennis*, dorsal view; F) Male pygidium of *Spongiphora croceipennis*, anterior view; G) Male pygidium of *Spongiphora croceipennis*, posterior view; H) male genitalia of *Spongiphora bogotensis*; I) apex of the male

genitalia from *Chaetospania* sp.; J) Male genitalia of *Mecomera* sp.; H) male genitalia of *Yepezia venezuelica*. All photos from Authors.

Acknowledgements

We are grateful to Alberto Neto, Diego Mendes, Larissa Queiroz, João Rafael and Rafael Sobral for their help. A special thanks to Tony Robillard for taking photos. Furthermore, we would like to thank Fabian Haas, Michael Engel and Yoshitaka Kamimura for all their help and insight on the Dermaptera systematics and Evolution. We also thank Conselho Nacional de Desenvolvimento Científico e Tecnologico (CNPq) for the productivity in research fellowship to J.A.R. (grant 300.305/2007e9) and for financial resources from Chamada MCTI/CNPq/ FNDCT Açao Transversal ~ e Redes Regionais de Pesquisa em Biodiversidade e Biotecnologia N◦ 79/2013 (grant 407.627/2013-8), Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM, grant 016/2006) and Programa de Apoio a núcleos de Excelência PRONEX, proc. 1437/2007). Furthermore, we would like to thank the MNHN, MNRJ, NHM and INPA for granting access to the material of this work.

References

Brindle, A., 1968. A revision of the Labiidae (Dermaptera) of the Neo-tropical and Nearctic Regions. 1. Pericominae, Strongylopsalinae, Sparattinae. Journal of Natural History. 2, 273–303.

Brindle, A., 1971. A revision of the Labiidae (Dermaptera) of the Neo-tropical and Nearctic regions. II. Geracinae and Labiinae. Journal of Natural History. 5(2), 155–182.

Brindle, A., 1982. Dermaptera from Venezuela. Part 4. A new subfamily, a new genus, and new species of Labiidae. Boletín de Entomología Venezolana. 2(4), 33–43.

Burr, M., 1909. Note on the classification of the Dermaptera. Deutsche Entomologische Zeitschrift. 1909, 320–328.

Engel, M.S., 2016. The earwig genus *Paralabella* Steinmann in amber from the Dominican Republic, with remarks on the classification of Burr's Eocene Dermaptera. Entomologist's Monthly Magazine. 152, 121–130.

Engel, M.S., 2017. The first fossil occurrence for the earwig subfamily Geracinae (Dermaptera). Entomologist's Monthly Magazine. 153, 31–43.

Engel, M.S., 2019. A new species of spongiphorine earwig in Miocene amber from the Dominican Republic (Dermaptera: Spongiphoridae). Palaeoentomology. 02, 560–565. https://doi.org/10.11646/palaeoentomology.2.6.3

Engel, M.S. & Haas, F., 2007. Family-Group Names for Earwigs (Dermaptera). American Museum Novitates. 3567, 1–20.

Goloboff, P., Farris, J., Nixon, K.T.N.T., 2003. TNT: Tree Analysis Using New Technology. Program and Documentation (available from the authors).

Haas, F., 2012. A Ordem Dermaptera. in: Rafael, J. A., Melo, A. R. G., Carvalho, C. J. B., Casari, S. A. & Constantino, R. (Eds.), Insetos do Brasil: diversidade e taxonomia. Holos Editora, São Paulo, pp. 297.

Haas, F. & Gorb, S., 2004. Evolution of locomotory attachment pads in the Dermaptera (Insecta). Arthropod Structure & Development. 33, 45–66. ttps://doi.org/10.1016/j.asd.2003.11.003.

Haas, F. & Kukalová-Peck, J., 2001. Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships withing Neoptera (Insecta). European Journal of Entomology. 98, 445–509.

Heleodoro, R.A., Alves-Oliveira, J.R., Rafael, J.A., 2019. Mecomera Audinet-Serville, 1839 (Dermaptera: Spongiphoridae): proposal of new diagnosis, descriptions and illustrations of all three-known species. Zootaxa. 4577, 117–130.

Heleodoro, R.A. & J.A. Rafael 2020., Dermaptera (Insecta): a guide for hind wing stretching and hind wing preservation. Zootaxa. 4732, 474–480.

Hopkins, H., Maehr, M. D., Haas, F., Deem, L. S., 2016. Dermaptera species file. Version 5.0/5.0. Available from http://dermaptera.speciesfile.org. (06/03/2021). Doi: https://doi.org/10.11646/zootaxa.4577.1.7

Kamimura, Y., 2014. Pre- and postcopulatory sexual selection and the evolution of sexually dimorphic traits in earwigs (Dermaptera). Entomological Science. 17, 139–166. doi:10.1111/ens.12058

Naegle, M.A., Mugleston, J.D., Bybee, S.M., Whiting, M.F., 2016. Reassessing the phylogenetic position of the epizoic earwigs (Insecta: Dermaptera). Molecular Phylogenetics and Evolution. 100, 382–390. DOI: 10.1111/syen.12420

Nixon, C.K., 2002. WinClada Ver. 1.00.08, p. 28. Published by author, Ithaca. Steinmann, H., 1990. Dermaptera, Part II: Eudermaptera (I): Labiidae. Das Tierreich, 106, 1–558.

Srivastava, G.K., 1995. On the classification of Spongiphoridae (=Labiidae) with a list of species. Zoological Survey of India. 95, 71–105.

Verhoeff, K.W., 1902. Über Dermapteren. 1. Aufsatz: Versuch eines neuen, natürlicheren Systems auf vergleichend-morphologischer Grundlage und über den Mikrothorax der Insecten. Zoologischer Anzeiger. 25, 181–208

Wipfler, B, Koehler, W., Frandsen, P.B., Donath, A., Liu, S., Machida, R., Misof, B., Peters, R.S., Shimizu, S., Zhou, X., Simon, S., 2020. Phylogenomics changes our understating about earwig evolution. Systematic Entomology. 1–11.

Figure captions

Figure 1. Single most-parsimonious tree from the phylogenetic analysis displaying the current taxonomic arrangement of Spongiphoridae.

Figure 2. Single most-parsimonious tree from the phylogenetic analysis displaying the Taxonomy of Engel & Haas (2007) overlapped in our results.

Figure 3. Diversity of Spongiphoridae. A) Holotype of *Caecolabia gomyi* (Caecolabiinae), Fiji - MNHN; B) *Cosmogerax diagonalis* (Cosmogeracini), Panama - MUE; C) *Eugerax salcedoi* (Geracini), Venezuela - MUE; D) *Barygerax venezuelicum* (Geracini), Venezuela - MUE; E) *Pseudovostox bicolor* (Geracini), Phillipines - MUE; F) *Gerax phantasma* (Geracini), Panama - MUE; G) *Labia minor* (Labiini), Sri Lanka - NHM; *Sphingolabis semifulva* (Labiini), Java - NHM; I) *Filolabia exigua* (Labiini), Brazil, Pará - MPEG; J) *Paralabella dorsalis* (Labiini), Antilles - NHM. All photos from Authors, except for *Caecolabia gomyi*, which is a courtesy of Tony Robillard, *Muséum national d'Historie naturelle*, France.

Figure 4. Diversity of Spongiphoridae. A) *Pericomus ater* (Pericomini), Panama - MUE; B) *Auchenomus longiforceps* (Sparattini), Madagascar - NHM; C) *Chaetospania feae*, Sumatra -

NHM (Sparattini); D) *Sparatta* sp. nov. (Sparattini), Colombia - INPA; E) *Mecomera* sp. nov. (Spongiphorini), Brazil, Piracicaba - ESALq; F) *Nesogaster amoenus* (Spongiphorini), Sumatra - NHM; G) *Homotages feae* (Spongiphorini), Himalaya - MUE; H) *Marava moreirai* (Spongiphorini), Brazil, Rio de Janeiro - NHM; I) *Purex frontalis* (Spongiphorini), Venezuela - MUE; J) *Spongiphora buprestoides* (Spongiphorini), Brazil, Rio de Janeiro - MNRJ; K) *Spongovostox alter* (Spongiphorini), Congo - NHM; *Vostox brunneipenis* (Spongiphorini), Brazil, Rio de Janeiro - NHM. All photos from Authors.

Figure 5. Morphological characters. A) *Spongiphora semirufa*, lateral view; B) *Nesogaster amoenus*, head and thorax, dorsal view; C) Head of *Sparatta* sp., dorsal view; D) head of *Sphingolabis semifulva*, lateral view; E) Head of *Nesogaster* sp., lateral view; F) head of *Purex frontalis*, dorsal view; G) left mandible of *Auchenomus javanus*, ventral view; H) left mandible of *Forficula* sp., ventral view; I) left mandible of *Sparatta* sp., ventral view; J) left mandible of *Spongiphora bogotensis*, ventral view; K) mouthparts of *Chelisoches morio*, ventral view; L) mouthparts of *Sparatta* sp., ventral view; M); mouthparts of *Vostox* sp.; N) head of *Cosmogerax diagonalis*, lateral view. All photos from Authors.

Figure 6. Morphological characters. A) Basal antennomeres of *Labidura riparia*; B) Basal antennomeres of *Purex sinuatus*; C) pronotum of *Auchenomus longiforceps*, dorsal view; D) pronotum of *Sparatta bormansi*; E) *Pericomus* sp., head and pronotum, lateral view; F) hind femur of *Chaetospania* sp., ventral view; G) hind femur of *Forficula* sp., ventral view; H) tarsomeres of *Forficula* sp., ventral view; I) tarsomeres of *Forficula* sp., lateral view; J) tarsomeres of *Purex frontalis*, lateral view; K) tarsomeres of *Barygerax esau*., lateral view; L) anterior portion from posterior wing of *Chelisoches morio*; M) anterior portion from posterior wing of *Irdex nitidipenis*; N) anterior portion of wing from posterior wing of *Barygerax esau*; O) anterior portion from posterior wing of *Nesogaster aculeatus*; P) anterior portion from posterior wing of *Yepezia venezuelica*. All photos from Authors.

Figure 7. Morphological characters. A) Posterior portion from posterior wing of *Homotages feae*; B) Posterior portion from posterior wing of *Sparatta w-signatta*; C) Posterior portion from posterior wing of *Cosmogerax guatemalensis*; D) Posterior portion from posterior wing of *Forficula* sp.; E) Anterior portion from posterior wing of *Eugerax nigrinum*; F) Anterior portion from posterior wing of *Spongovostox*; G) Anterior portion from posterior wing of *Sparatta* sp.; H) Anal region from posterior wing of *Sparatta* sp.; I) Posterior portion from posterior wing of *Sparatta* sp.; J) Posterior portion from posterior wing of *Sparatta* sp. All photos from Authors.

Figure 8. Morphological characters. A) Posterior portion from posterior wing of *Spongiphora croceipennis*; B) Tergite 10 and base of cercus of *Spongiphora bogotensis*, dorsal view; C) Tergite 10 and cercus of *Cosmogerax diagonalis*, dorsal view; D) Tergite 10 and cercus of *Purex frontalis*, dorsal view; E) Cercus apex of *Irdex nitidipennis*, dorsal view; F) Male pygidium of *Spongiphora croceipennis*, anterior view; G) Male pygidium of *Spongiphora croceipennis*, posterior view; H) male genitalia of *Spongiphora bogotensis*; I) apex of the male genitalia from *Chaetospania* sp.; J) Male genitalia of *Mecomera* sp.; H) male genitalia of *Yepezia venezuelica*. All photos from Authors.

Anex I – Examined material

Arixeniidae

Arixena sp.: “Malaya: Selangor, near Kepong, D. R. Audy” [♂**NHM**]

Chelisochidae

Chelisoches morio: “Java” [♀3♂**NHM**]

Hemimeridae

Hemimerus bouvieri: “Tanganyiaka, Terr Bukoba, 1921” [3♂**NHM**]

Forficulidae

Doru sp.: “Brasil, Natal, Rio Grande do Norte, Cidade Nova, 15.vi.2013” [♂**INPA**]

Forficula auricularia: “Bolivia, La Paz, Cota-Cota, 23.ii.2005, Jaime Rodriguez” [♂**INPA**]

Forficula sp.: “Panama, Barro Colorado Island, light trap, 3.ii.1975” [5♂**INPA**]

Cosmogeracini

Cosmogerax diagonalis: “Panama, Barro Colorado Island, light trap, ground level, 9.ii.1977” [♂**NHM**], “idem, 18.iv.1978” [♂**MUE**]; “Idem, 24.viii.1977” [2♂**MUE**]

Cosmogerax guatemalensis: “Panama, Barro Colorado Island, light trap, tree canopy, 29.ix.1977” “Idem, 20.x.1977” [♂**MUE**]; “Idem, 21.ix.1978” [♂**MUE**]

Cosmogerax sp. 1: “Panama, Barro Colorado Island, light trap, tree canopy, 16. x.1977” [♂**MUE**], “idem, 15.xii.1977” [♂**MUE**]

Geracini

Barygerax venezuelicum: “Venezuela, Aragua, Rancho Grande, 25.vii.1969” [♂**PARATYPE MUE**]; “Idem, 30.vii.1969” [♀♂**PARATYPE MUE**]; “Idem, 22.x.1974” [♂**NHM**]

Eugerax nigrinum: “Venezuela, Aragua, Rancho Grande, 12-17.v.1973” [♂**PARATYPE MUE**] “Idem, 21.v.1975” [♂**NHM**]

Eugerax poecilum: “Venezuela, Caracas” [2♂**MUE**]; “Panama, El Valle, xi.1946” [♂**MUE**]

Eugerax salcedoi: “Venezuela, Aragua, Rancho Grande, 19.vii.1973” [♂**MUE**]

Gerax phantasma: “Panama, Barro Colorado Island, light trap, ground level, 3.ii.1975” [♂**NHM**]; “Idem, 5.xii.1977” [♂♀**MUE**]; “Idem, 14.v.1978” [♂**MUE**]; “Idem, 14.v.1978” [♀♂**MUE**]; “Venezuela, Aragua, Rancho Grande, 14.vii.1976” [♀**MUE**]

Pseudovostox bicolor: “Memungan, Mindanao” [♀♂**MUE**]

Pseudovostox africanus: “Nigeria, Zaria, Samaru, 26.v.1973” [2♀**MUE**]

Yepezia venezuelica: “Venezuela, Carabobo” [♂**PARATYPE MUE**]; “Venezuela, Cerro Galicia, 18.xi.1971” [♂**MUE**]

Homotagini

Homotages feae: “Himalaya, Chakrata, 17.vi.1956” [♀3♂**MUE**]

Labiini

Circolabia arcuata: “Chimbo, 1.000, viii. 1997, Rosenberg” [♂**NHM**]; “Tabasco” [♂**NHM**]

Chaetolabia tetragona: “São Tomé, ix.1949” [♂**NHM**]; “West Africa, São Thomé Island, 8.xi.1932, W.H.T. Tams.” [♂**NHM**]

Filolabia exígua: “Brasil, Pará, Benevides, PA 408 km 06, 20.vi.1980” [♂**MPEG**]

Labia minor: “Exp. G. Frey. Mus. Nigeria, Kamerun, Bechyne, 1955-56” [♂**NHM**]; “3180, Sri Lanka, Ceylon Niet, 1982” [♂**NHM**];

Paralabella curvicauda: “Indian Ocean, Cocos Keeling Island, C.A., Gibson Hill, 1949” [♂**NHM**]; “Thafo, Gana” [♀**NHM**]”

Paralabella dorsalis; “Antilles [♂**NHM**]”

Sphingolabis hawaiiensis: “Solomon Is., Bougainville, Kokure, 690 m, 13.vi.1956” [♂**MUE**]; “New Mebrides, Malacuba: Amok, 17.ix.1958” [♂**MUE**]

Sphingolabis semifulva: “Java” [2♂**NHM**]

Spirolabia pillicornis: “Sri Lanka, Kanneliya Jungle, 11.x.1973” [♂**MUE**]

Nesogastrini

Nesogaster aculeatus: “Papua: Kokoda, viii, 1933” [♂**NHM**]; Papua: Kokoda, viii, 1934” [♂**NHM**]

Nesogaster amoenus: “Sumatra, Mount Sago” [♂**NHM**]

Nesogaster tristes: “New Caledonia, Paompai, 12.ix.1914” [♀♂**NHM**]

Pericomini

Pericomus ater: “Panama, Fortuna Forest, 30.x.1976” [♂**MUE**];

Parapericomus sp.: “Sorawak, Gunong Mulu National Park, iv.1978, P. Chapman, Deer Water Cave, beneath pebbles, with faeces of cave swifters, near stream” [♂**NHM**]

Sparattini

Auchenomus javanus: “Solomon Islands, xi.1954” [♀♂**NHM**]

Auchenomus longiforceps: “Madagascar” [2♂**NHM**]

Auchenomus hincksi: “India: Kallas, 5.xi.1963” [♂**NHM**]

Auchenomus setulosus: “Sarawak, East Malaysia, 4th division, Baram District. Gunong Mulu National Park., 27.ii.1978” [♂**NHM**];

Auchenomus sp.: “Madagascar” [♂**NHM**]

Chaetospania feae: “Sumatra, Mount Sago” [2♂**NHM**]

Chaetospania gardineri: “Seychelles” [♀♂**NHM**]

Chaetospania rodens: “Kilimandjaro, Kibonoto” [♂**NHM**]

Chaetospania stilleta: “S. India, Madura Distrc., Shembaganur” [4♀**NHM**]

Chaetospania thoracica: “Seychelles” [♀♂**NHM**]

Chaetospania villica: “Zululand: Eshowe, 31.vi.1926 [♂**NHM**]

Sparatta bolivari: “Peru, Ucayali” [♂**NHM**]

Sparatta bormansi: “Mex: Veracruz, Fortin de Las Flores, 28.xii.1963” [♂**MUE**]

Sparatta dentifera: “Guyane, Noveau Chantier” [♀2♂**NHM**]

Sparatta flavipenula: “El Limon, 200, Tamps., Mexico, 30.xii,1968” [♀**MUE**]

Sparatta incerta: “Argentina, 1945” [♂**MUE**]; “Venezuela, Aragua, El Limon, 450 m, 22.viii.1968; [♂**MUE**]; “Peru, Loreto, Estiron, Rio Amapiyacu, 9.xii.1961, B. Malkin leg” [♂**MUE**]

Sparatta nigrina: “Brazil, Rio de Janeiro, Floresta da Tijuca, 1857” [♂**NHM**]; “Argentina, 12-29.i.1941” [♂**MUE**]; “Canindé, Rio Gurupí, Pará, Brasil, vi.1963” [♂**MUE**]

Sparatta pelvimetra: “Burr col., 1915-120” [♂**NHM**]; “Brazil, Itatiaya, 700m, 12.vi.1935, Zikan col.” [♀**MUE**]; “Barueri, Estado de São Paulo, Brazil, 12.iii.1967” [♂**MUE**]

Sparatta quinquepunctata: “Est. Ecol. da Boracéia, Salesópolis, SP., Brazil, 6.xi.1968” [♀♂**MUE**]

Sparatta rufina: “Minas Gerais, Brasil” [♂**NHM**]; “Brazil, Santa Catarina, Nova Teutônia, july-sept. 1972. Fritz Plaumann” [♂**NHM**]

Sparatta schotti: “Brazil, Caguaratuba, São Paulo, 1962” [♂**MUE**]

Sparatta semirufa: “Brazil, Nova Teutonia, 1948” [♂**MUE**]

Spongiphorini

Homotages feae: “Nepal, Bhichuk, 8.x.1984” [♂**MUE**]

Irdex nitidipennis: “South India, 3500 m, Anamalai Hills, Cinchora, iv.1957, leg. P.S. Nathan” [3♂**MUE**]; “Mindanad: P.I., 20 km SW, Davas, 7.xi.1963 [♂**MUE]**

Irdex pygidiata: “Gunung Sindur, Sumatra, 1925” [3♂**MUE**]

Irdex wittmeri: “km 87 von, 1680 m, Phuntsholing” [♀♂**PARATYPE MUE**]

Marava bidentata: “Guatopo, Miranda, Venezuela, 25.viii.1965” [♀**MUE**]

Marava furia: “Venezuela, Bolivar, El Hormiguero, Meseta de Nuria, 500 m, 13-17.xii.1974” [♀♂**MUE**]

Marava griveaudi: “Madagascar, Forest de Zombitsy, near Sakaraha, 650m, 16.xii.1959” [♂**MUE**]

Marava machupicchuensis: “Torentoy Canyon (Base Machu-picchu), 2000 m, vi-vii.1964, B. Malkin” [♂**PARATYPE MUE**]

Marava moreirai: “Rio” [♂**NHM**]

Marava nítida: “Java” [♂**NHM**]

Marava pygidiata: “Panama, Fortuna Wet Forest, at light, 1050 m, 25-29.ix.1957” [♀♂**PARATYPE MUE**]

Marava pallida: “Panama, Barro Colorado Island, light trap, ground level, 8.ix.1978” [2♂**PARATYPE MUE**]

Marava pulchella: “Florida, Lake Placid, Archbeld Bio., Sta., 23-31.v.1964, R.W. Hodges” [♀3♂**MUE**]

Marava rodundata: “México, Pozo Melendez, S. Taxco, 9.vi.1966” [♂**MUE**]

Marava rogersi: “Panama, Fortuna Wet Forest, at light, 1050 m, 19.ix.1957” [4♂**MUE**]

Marava townesi: “Guatemala, 376156, primavera, 1065, under bark, 18.i.1937” [♂**PARATYPE MUE**]

Purex divergens: “Peru, Rio Ucayali” [♀2♂**NHM**]

Purex esquivelae: “Venezuela, Aragua, Rancho Grande, x.1953” [♂**MUE**]; “Idem, 29.x.1969” [♀**MUE**]; “Idem, 4.vi.1974” [♂**MUE**];

Purex frontalis: “Venezuela, Aragua, Rancho Grande, 4.vi.1974” [♀3♂**NHM**]

Purex pulchellus: ““Venezuela, Aragua, Rancho Grande, 21.x.1976” [♀♂**NHM**]

Purex remotus: “Panama, Fortuna Wet Forest, at light, 1050 m, 20.vii.1977” [♀2♂**NHM**]

Purex sinuatus: “Venezuela, Aragua, Rancho Grande, x.1969” [♂**MUE**], [♂**NHM**]; Idem, 26.v.1970” [♂**NHM**]; “Idem, 19.x.1972” [♂**NHM**]

Spongiphora buprestoides: “Bolivia, 1100m, Cochabamba, xi.1980, leg. F. Walz” [♂**MUE**]; Hda. Mosela, Peru, Rio Oxabamba, vi.1955” [5♀**MUE**]

Spongiphora bogotensis: “Brazil, Santa Catarina” [♂**NHM**]

Spongiphora bormansi: “21.i.1939, Brazil, Santa Catarina” [♂**MUE**]; “Brazil, Itatiaya, 700m, 5.x1938, Zikan, at light” [♂**MUE**]; “Brasilia” [2♂**NHM**]

Spongiphora croceipennis: “Itatiaya, iv.1932, D. Mendes” [6♂**MNRJ**]; “Zapote, Guatemala” [♀2♂**NHM**];

Spongiphora prolixa: “Panama, Alto Lino, 1300 m, near Boquete, Chiriqui, ii.1977” [♀**NHM**]; male without collection data [♂**NHM**]; “Mexico, Frontera Tabasco” [♂**NHM**]

Spongiphora salvadorensis: “El Salvador: Mt. San Salvador, 4000-6400 m, 8.vii.1968” [♂**PARATYPE MUE**]

Spongovostox aloysiisabaudiae: “Beni Ituri Forest, Belge Congo, x.1946, T.H.E. Jackson” [♂**MUE**]

Spongovostox alter: “Lulua: Sandoa, vii.1932, F.G. Overlaet, vii.1932” [♂**NHM**]

Spongovostox burgeoni: “Panama, Barro Colorado Island, light trap, ground level, 26.viii.1977” [♀3♂ **MUE**]

Spongovostox carli: “S. India, Anamalai Hills, Cinelona, 3500 m, iv.1959, coll. P.S. Nathan” [2♀3♂**MUE**]

Spongovostox escheri: “S. India, Coimbatore, Valparai, 3500 ft, ii-iii.1988, coll. P.S. Nathan” [♂**MUE**]

Spongovostox ghiliani: “Dominica, 22.x.1964” [♂**MUE**]

Spongovostox mirei: “Ebolowe, St de Nkoemvone, iii.1970” [♂**MUE**]; Beling, 5.ii.1963, H. Coiffait, ar. Light” [♀♂**MUE**]

Spongovostox quadrimaculatus: “Brazil, Amazonas, Maraguá, 15.vii.1930” [♂**MUE**]

Spongovostox schwarzi: “Guyane Franç” [♂**NHM**]

Spongovostox semiflavus: “Ceylon: Kan. Dist., 5miNW, Mahiyangana, 30.iii-9.iv.1971, P. & P. Spangler” [♂♀**MUE**]

Spongovostox victoriae: “Sidney” [♂♀**MUE**]

Strongylopsalis berlandi: “Rwanda” [♂**NHM**]

Vostox apicedentatus: “Tucson” [♂**MUE**]

Vostox bertonii: “Paraguay” [♂**MUE**]; “Argentina, Tartagal, 21.vii.1919” [♀♂**MUE**]

Vostox bolivianus: “Colombia, Maniquira, Boyaca, 1230m, 1975” [♀2♂**MUE**]

Vostox brunneipennis: “Rio de Janeiro, 1856” [♂**NHM**]; “Mexico, Acaponeta, 26.xi.1948” [3♂**MUE**]

Vostox dentatus: “Panama, Fortuna Wet Forest, at light, 1050 m, 4-11. x.1956” [2♀ **MUE**]; “Idem, 2.vi.1977” [♂**MUE**]; “Idem, 16.ix-vi.x.1978” [2♂**MUE**]

Vostox dugueti: “Mexico, Baja California, Sur Second, Bahia de Los Muertos, 29.vii.1971, H.G. Real & R.E. Main” [♂**MUE**]

Vostox magnus: “Panama, 1300m, Alto Lino, near boguete, Chiriqui, 12.vii.1978, Dr. Henk Wolda, STR” [♂**PARATYPE MUE**]

Vostox ocellatus: “Venezuela, Aragua, Rancho Grande, La Trilla Periquito, ii.1975” [♂**PARATYPE MUE**];

Vostox punceteipennis: “Panama, Barro Colorado Island, light trap, ground level, 8-20.v.1978” [2♂**MUE**]

Annex 2 – Phylogeny data matrix

Table 1 – Data matrix of the phylogeny.

Species	1									10										20										30										40										50									59
Carcinophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Labidura riparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelisoches morio	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	-	0	0	0	1	1	1	0	2	0	2	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Forficula auricularia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	-	0	0	0	1	1	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Forficula sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	-	0	0	0	1	1	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Doru sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	-	0	0	0	1	1	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Cosmogerax diagonalis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Cosmogerax guatemalensis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Barygerax venezuelicum	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Eugerax nigrinum	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Eugerax poecilum	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Gerax phantasma	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pseudovostox africanus	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Yepezia venezuelica	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Chaetolabia tetragona	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Circolabia arcuata	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Labia minor	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Paralabella dorsalis	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Paralabella curvicauda	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sphingolabis semifulva	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sphingolabis hawaiiensis	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Spirolabia pilicornis	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Filolabia exigua	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1		0	0	0	0	0
Nesogaster aculeatus	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	-	0	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1
Nesogaster amoenus	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	-	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1
Nesogaster tristes	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	-	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1
Pericomus ater	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Parapericomus sp.	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Auchenomus javanus	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Auchenomus longiforceps	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Auchenomus setulosus	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Auchenomus hincksi	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Auchenomus sp.	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1		0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0

Species	1									10										20											30										40										50									59
Chaetospania feae	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Chaetospania gardineri	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Chaetospania stilleta	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Chaetospania rodens	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Chaetospania dentifera	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta incerta	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta nigrina	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta pelvimetra	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta schotti	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta semirufa	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Sparatta rufina	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	-	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Mecomera brunnea	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Mecomera chacoensis	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Mecomera reichardti	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Mecomera spn.	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Strongylolabis berlandi	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Homotages feae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Irdex nitidipennis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Irdex pygidiata	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1 1
Irdex wittmeri	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Marava moreirai	0	0	0	0	0	1	0	0	2	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Marava nitida	0	0	0	0	0	1	0	0	2	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2 2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Purex frontalis	0	0	0	0	1	1	0	0	2	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1

Purex sinuatus	0	0	0	0	1	1	0	0	2	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1
Spongiphora bogotensis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1
Spongiphora croceipennis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1
Spongiphora bormansi	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1
Spongiphora buprestoides	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	0	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1
Spongovostox quadrimaculatus	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Spongovostox alter	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Spongovostox mirei	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Spongovostox oweni	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1

Species	**1**									**10**										**20**										**30**										**40**										**50**									**59**
Spongovostox schwarzi	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox apicedentatus	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox bruneipennis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox duguetti	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox magnus	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox dentatus	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1
Vostox puncteipennis	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	-	1	0	1	1	1	1	1	2	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1

SÍNTESE

Previamente ao presente trabalho, Spongiphoridae era considerada polifilética, sem caracteres diagnósticos concisos. Com o que foi apresentado, fica demonstrado que a morfologia possui fortes indícios de ancestralidade comum entre as espécies de Spongiphoridae. Além disso, graças as imagens e diagnoses propostas, diversos grupos de pessoas (não necessariamente taxonomistas) podem agora identificar espécimes dessa família, ainda que o maior nível taxonômico alcançado seja o de subfamilia. O pigidio conspícuo em vista dorsal permite uma identificação rápida, bem como a análise do formato do segundo tarsômero, da morfologia das mandíbulas ou das asas possibilitam uma identificação mais precisa. Além disso, é a primeira vez que a taxonomia de Spongiphoridae está alinhada com sua evolução. Dessa maneira, é muito provável que o presente trabalho influencie trabalhos futuros. É importante também destacar que esse é o único trabalho com uma considerável quantidade de fotos, tanto de espécimes quanto de estruturas de Spongiphoridae, auxiliando assim na popularização desse grupo negligenciado.

Outro importante avanço foi o guia ilustrado para dissecção e armazenamento de asas de Dermaptera. Sendo a Ordem com o padrão de dobras mais complexos entre os insetos, dissecar uma asa de Dermaptera sem a mentoria de alguém é um grande desafio. Com esse novo guia, esperamos que cada vez mais pessoas venham a se interessar por dermapteros, bem como tenham sucesso caso tentem dissecar uma asa. Outra vantagem do guia ilustrado é possibilitar que menos espécimes sejam destruídos durante a dissecção, algo muito comum durante a fase de aprendizagem.

Referências Bibliográficas

Anderson, L.E., 1954. Hoyer's Solution as a rapid permanent mounting medium for Bryophytes. The Byologist. 57, 242–244. https://doi.org/10.2307/3240091

Brindle, A., 1968. A revision of the Labiidae (Dermaptera) of the Neo-tropical and Nearctic Regions. 1. Pericominae, Strongylopsalinae, Sparattinae. Journal of Natural History. 2, 273–303.

Brindle, A., 1971. A revision of the Labiidae (Dermaptera) of the Neo-tropical and Nearctic regions. II. Geracinae and Labiinae. Journal of Natural History. 5(2), 155–182.

Brindle, A., 1982. Dermaptera from Venezuela. Part 4. A new subfamily, a new genus, and new species of Labiidae. Boletín de Entomología Venezolana. 2(4), 33–43.

Burr, M., 1909. Note on the classification of the Dermaptera. Deutsche Entomologische Zeitschrift. 1909, 320–328.

Cipola, N.g., Morais, J.W. & Bellini, B., 2018. New subgenus and four species of *Lepidocyrtus* Bourlet (Collembola, Entomobryidae, Lepidocyrtinae) from Amazon. Insect Systematics & Evolution. 50 (2), 1–46.

Dias, P., Rafael, J.A. & Naskrecki, P., 2012. A Taxonomic Revision of The Neotropical genus *Aegimia* Stål, 1874 (Orthoptera, Tettigonniidae, Phaneropterinae). Journal of Orthoptera Research. 21, 109–132. https://doi.org/10.1665/034.021.0108

Engel, M.S., 2016. The earwig genus *Paralabella* Steinmann in amber from the Dominican Republic, with remarks on the classification of Burr's Eocene Dermaptera. Entomologist's Monthly Magazine. 152, 121–130.

Engel, M.S., 2017. The first fossil occurrence for the earwig subfamily Geracinae (Dermaptera). Entomologist's Monthly Magazine. 153, 31–43.

Engel, M.S., 2019. A new species of spongiphorine earwig in Miocene amber from the Dominican Republic (Dermaptera: Spongiphoridae). Palaeoentomology. 02, 560–565. https://doi.org/10.11646/palaeoentomology.2.6.3

Engel, M.S. & Haas, F., 2007. Family-Group Names for Earwigs (Dermaptera). American Museum Novitates. 3567, 1–20.

Glance, G., 1956. Slide Mountinf of Collembola. *Annals of the Entomological Society of America*, 49 (2), 132–133. https://doi.org/10.1093/aesa/49.2.132

Goloboff, P., Farris, J., Nixon, K.T.N.T., 2003. TNT: Tree Analysis Using New Technology. Program and Documentation (available from the authors).

Haas, F., 2012. A Ordem Dermaptera. in: Rafael, J. A., Melo, A. R. G., Carvalho, C. J. B., Casari, S. A. & Constantino, R. (Eds.), Insetos do Brasil: diversidade e taxonomia. Holos Editora, São Paulo, pp. 297.

Haas, F. & Gorb, S., 2004. Evolution of locomotory attachment pads in the Dermaptera (Insecta). Arthropod Structure & Development. 33, 45–66. ttps://doi.org/10.1016/j.asd.2003.11.003.

Haas, F., Hwen, J.T.C. & Tang, H.B., 2012. New evidence on the mechanics of wing unfolding in Dermaptera (Insecta). Arthropod Systematics & Phylogeny. 70, 95–105.

Haas, F. & Kukalová-Peck, J., 2001. Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships withing Neoptera (Insecta). European Journal of Entomology. 98, 445–509.

Haug, J.T., Haug, C. & garwood, R.J., 2016. Evolution of insect wings and development—new details from Palaeozoic nymphs. Biological Reviews. 91, 53–69. https://doi.org/10.1111/brv.12159

Heleodoro, R.A., Alves-Oliveira, J.R., Rafael, J.A., 2019. Mecomera Audinet-Serville, 1839 (Dermaptera: Spongiphoridae): proposal of new diagnosis, descriptions and illustrations of all three-known species. Zootaxa. 4577, 117–130.

Heleodoro, R.A. & J.A. Rafael 2020., Dermaptera (Insecta): a guide for hind wing stretching and hind wing preservation. Zootaxa. 4732, 474–480.

Hopkins, H., Maehr, M. D., Haas, F., Deem, L. S., 2016. Dermaptera species file. Version 5.0/5.0. Available from http://dermaptera.speciesfile.org. (06/03/2021). Doi: https://doi.org/10.11646/zootaxa.4577.1.7

Kamimura, Y., 2014. Pre- and postcopulatory sexual selection and the evolution of sexually dimorphic traits in earwigs (Dermaptera). Entomological Science. 17, 139–166. doi:10.1111/ens.12058

Katayama, N., Abbott, J.K., Kjærandsen, J., Takahashi, Y. & Svensson, E.I., 2014. Sexual selection on wing interference patterns in *Drosophila melanogaster*. *Proceedings of the* National Academy of Sceinces of the United States of America. 111, 15144–15148. https://doi.org/10.1073/pnas.1407595111

Naegle, M.A., Mugleston, J.D., Bybee, S.M., Whiting, M.F., 2016. Reassessing the phylogenetic position of the epizoic earwigs (Insecta: Dermaptera). Molecular Phylogenetics and Evolution. 100, 382–390. DOI: 10.1111/syen.12420

Nixon, C.K., 2002. WinClada Ver. 1.00.08, p. 28. Published by author, Ithaca. Steinmann, H., 1990. Dermaptera, Part II: Eudermaptera (I): Labiidae. Das Tierreich, 106, 1–558.

Palacios-Vargas, J.G. & Castaño-Meneses, G., 2002. Collembola associated with *Tillandsia violaceae* (Bromeliaceae) in Mexican Quercus-Abies forests. Pedobiologia. 46, 395–403.

Sane, S.P., 2016. Neurobiology and biomechanics of flight in miniature insects. Current Opinion on Neurobiology, 41, 158–166. https://doi.org/10.1016/j.conb.2016.09.008

Silva-Neto, A.M., Aldrete, A.N. & Rafael, J.A., 2016. Phylogenetic relationships of the genera of Ptiloneuridae (Psocodea, ‘Psocoptera’, Epipsocetae) and a test on the monophyly of *Brasineura* Silva-Neto & garcía Aldrete and *Loneuroides* garcía Aldrete. Zootaxa. 4150 (1), 73–84.
https://doi.org/10.11646/zootaxa.4150.1.4

Srivastava, G.K., 1995. On the classification of Spongiphoridae (=Labiidae) with a list of species. Zoological Survey of India. 95, 71–105.

Verhoeff, K.W., 1902. Über Dermapteren. 1. Aufsatz: Versuch eines neuen, natürlicheren Systems auf vergleichend-morphologischer Grundlage und über den Mikrothorax der Insecten. Zoologischer Anzeiger. 25, 181–208

Vieira, R.M. & Rafael, J.A., 2014. *Longivena*, a new robberfly genus from Brazil (Diptera, Asilidae, Asilinae). ZooKeys. 443, 119–138. https://doi.org/10.3897/zookeys.443.8324

Vieira, R.M., Chagas, C.B., Heleodoro, R.A., 2021. Dermaptera. In: Catálogo Taxônomico da Fauna do Brasil. PNUD. <httpp://fauna.jbrj.gov.br/fauna/faunadibrasil/126> Acesso em: 06/03/2021.

Wipfler, B, Koehler, W., Frandsen, P.B., Donath, A., Liu, S., Machida, R., Misof, B., Peters, R.S., Shimizu, S., Zhou, X., Simon, S., 2020. Phylogenomics changes our understating about earwig evolution. Systematic Entomology. 1–11.