DANIELA SANTOS MARTINS SILVA

ESTUDOS TAXONÔMICOS, CLADÍSTICOS E MORFOLÓGICOS DE TETRIGÍDEOS (INSECTA: ORTHOPTERA: CAELIFERA: TETRIGOIDEA) NEOTROPICAIS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Doctor Scientiae*.

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Kátia Costa

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(Orientador)

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Nota: a presente tese não constitui publicação no sentido do artigo 9 do Código Internacional de Nomenclatura Zoológica. Nomes das espécies que ainda não foram formalmente publicados constituem, portanto, nomina nuda.

Note: the present thesis should not be considered as a publication in the sense of article 9 of International Code of Zoological Nomenclature. Names of species that have not yet been formally published are, therefore, considered as nomina nuda.

SUMÁRIO

RESUMO

SILVA, Daniela Santos Martins, D.Sc., Universidade Federal de Viçosa, agosto, 2018. **Estudos Taxonômicos, Cladísticos e Morfológicos de tetrigídeos (Insecta: Orthoptera: Caelifera: Tetrigoidea) Neotropicais**. Orientador: Carlos Frankl Sperber. Coorientadores: Marcelo Ribeiro Pereira e Fernando Campos De Domenico.

Tetrigídeos são gafanhotos que se distinguem dos demais táxons de Caelifera principalmente pelo pronoto que recobre parcialmente ou completamente o abdômen e pela fórmula tarsal 2-2-3. Atualmente esta família inclui cerca de 1900 espécies em 280 gêneros em oito subfamílias: Batrachideinae Bolívar, 1887, Cladonotinae Bolívar, 1887, Discotettiginae Hancock, 1907, Lophotettiginae Hancock, 1909, Metrodorinae Bolívar, 1887, Scelimeninae Bolívar, 1887, Tetriginae Rambur, 1838 e Tripetalocerinae Bolívar, 1887. Embora seja um grupo representativo e de ampla distribuição, os tetrigídeos ainda são pouco estudados e muitas questões morfológicas e taxonômicas ainda não estão resolvidas. Para os táxons Neotropicais, está situação é ainda mais preocupante visto que existem poucos espécimens coletados e quase todas as espécies tipos estão depositadas em museus norte-americanos ou europeus. Assim, em virtude da ausência de informações específicas para este grupo, acesso limitado ao material tipo e morfologia do complexo fálico pouco estudada, revisões são limitadas e hipóteses filogenéticas ausentes. O presente estudo teve como objetivo propor a organização e revisão taxonômica de grupos Neotropicais, realizar a primeira análise cladística de uma subfamília de tetrigídeos e investigar a razão pela qual o complexo fálico neste grupo não foi incorporado às descrições taxonômicas. Este estudo se dividiu em três partes: (i) revisões taxonômicas de uma espécie da subfamília Metrodorinae, da subfamília Lophottetiginae e a proposta de duas novas tribos Neotropicais para membros da família Cladonotinae: Chorophyllini **n. trib**. e Mucrotettigini **n. trib**; (ii) uma filogenia morfológica da subfamília Batrachideinae com 28 espécies e 71 caracteres, que indicou que este grupo é monofilético e (iii) uma proposta do uso de dados do complexo fálico de tetrigídeos na determinação de espécies a partir de dados da literatura.

ABSTRACT

SILVA, Daniela Santos Martins, D.Sc., Universidade Federal de Viçosa, August, 2018. **Taxonomic, Cladistic and Morphological studies of Neotropical tetrigids (Insecta: Orthoptera: Caelifera: Tetrigoidea)**. Adviser: Carlos Frankl Sperber. Co-advisers: Marcelo Ribeiro Pereira and Fernando Campos De Domenico.

Tetrigids are grasshoppers which are distinguished from the other Caeliefa mainly by pronotum covering partial-in parts or completely the abdomen, and tarsal formula 2-2-3. Currently, the family includes 1900 species within 280 genera within eight subfamilies: Batrachideinae Bolívar, 1887, Cladonotinae Bolívar, 1887, Discotettiginae Hancock, 1907, Lophotettiginae Hancock, 1909, Metrodorinae Bolívar, 1887, Scelimeninae Bolívar, 1887, Tetriginae Rambur, 1838 and Tripetalocerinae Bolívar, 1887. Although it is a representative and widely distributed group, tetrigids are still poorly studied and many morphological and taxonomic questions remain unresolved. For Neotropical taxa, this situation is even more worrying since there are few specimens collected and almost all species typesare deposited in North American or European museums. Thus, due to the absence of specific information for this group, limited access to the type material and poorly known morphology of the phallic complex, reviews are limited and phylogenetic hypotheses are unknown. The present study aimed to propose the taxonomic organization and revision of Neotropical groups, to indicate the first cladistic analysis of a subfamily of tetrigids and to investigate the reason why the phallic complex in this group did not incorporate the taxonomic descriptions. This study was divided into three parts: (i) taxonomic revisions of one species of the subfamily Metrodorinae of the subfamily Lophottetiginae and the proposal of two new Neotropical tribes for members of the family Cladonotinae: Chorophyllini **n. trib**. and Mucrotettigini **n. trib**; (ii) a morphological phylogeny of the subfamily Batrachideinae with 28 species and 71 characters, indicating that this group is monophyletic and (iii) a proposal of the use of phallic complex data of tetrigids in the determination of species from data of the literature.

INTRODUÇÃO GERAL

Os ortópteros possuem aproximadamente 28.100 espécies conhecidas (Cigliano *et al.* 2018), sendo os Polyneoptera mais representativos em riqueza de espécies (Grimaldi & Engel 2005). Apresentam uma diversidade morfológica e de habitats que os permitem serem modelos biológicos para estudos estruturais (Snodgrass 1929, 1935; Uvarov 1966; Chapman 2013; Baccetti 1987), biacústicos (Otte 1970) e evolucionários (Alexander & Otte 1967). São distinguidos dos demais insetos por possuírem duas características: presença de criptopleura (extensão lateral do pronoto sobre os escleritos pleurais, com exceção de Proscopiidae) e terceiro par de pernas com estruturas associadas ao salto. Essa ordem é dividida em duas subordens, Ensifera que engloba os grilos, paquinhas e esperanças (Gryllidea e Tettigoniidea) e Caelifera, com os gafanhotos e mané-magros (Tridactylidea e Acrididea) (Cigliano *et al.* 2018) (Fig. 1).

A subordem Caelifera é a segunda maior linhagem de Orthoptera (Cigliano *et al.* 2018) e este taxon se destaca por possuir uma série de características que o separam dos ensiferos como: antenas curtas (menos de 30 antenômeros com exceção de Tanaoceridae) e com comprimento inferior a soma do comprimento da cabeça ao pronoto (com exceção de Tanaoceridae); segmentos antenais filiformes, em alguns grupos achatados e raramente clavados distalmente; alados, porém existem grupos que não possuem asas; tegmina quando presente do tipo pergaminosa cobrindo as asas ou dispostas lateralmente ao corpo (Rehn & Grant 1961); produção de sons quando presente, geralmente ocorre devido à fricção fêmur-tegmina, fêmur-abdômen (Pneumoridae) e menos frequentemente tegmina-asa (Rehn & Grant 1961; Otte 1970); tímpanos quando presentes posicionados lateralmente no primeiro segmento do abdômen; ovipositor formado por quatro valvas curtas, externas e duas abrigadas na base das valvas externas; fórmula tarsal variante de 3-3-3, 2-2-3 (Tetrigidae) e 1-1-1 (Cylindrachetidae); cercos curtos e não articulados (com exceção de Tridactyloidea); placa subgenital dos machos sem estilos (Rehn & Grant 1961).

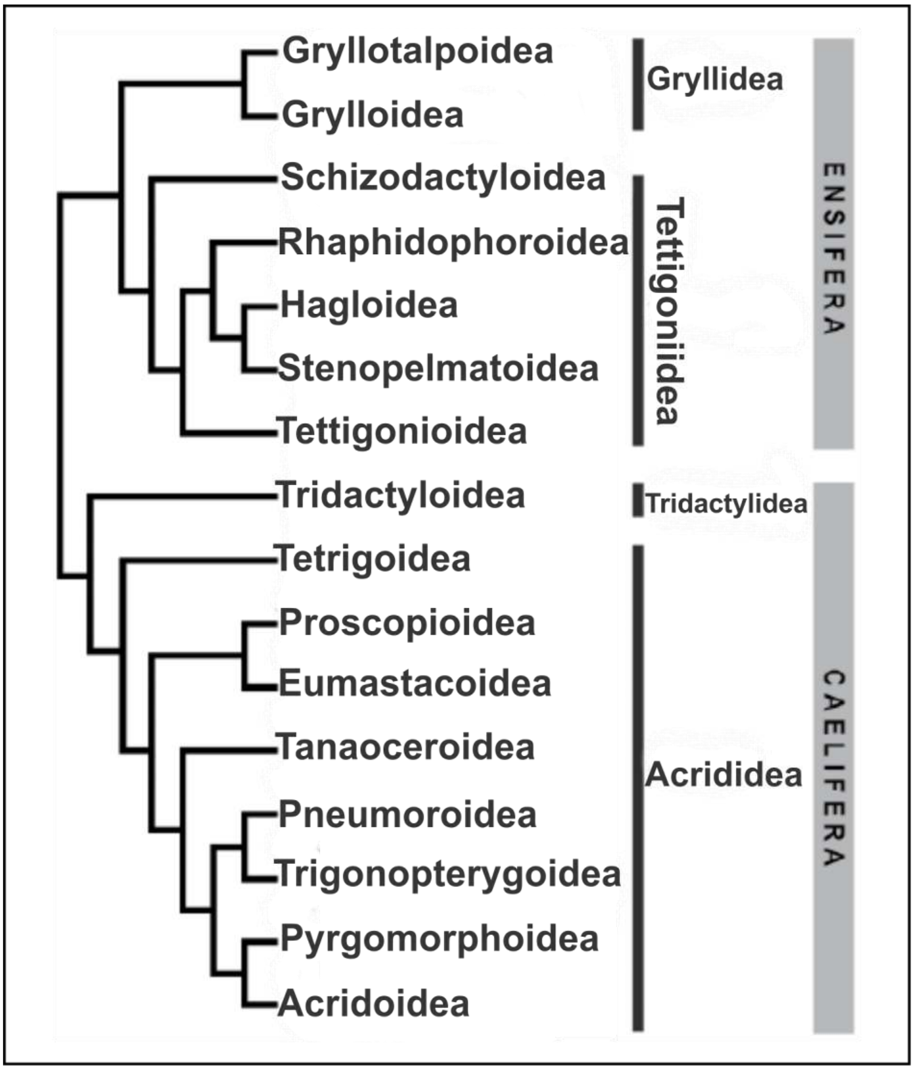

Figura 1. Relação filogenética entre as superfamilias de Orthoptera. Adaptado de Song *et al*. (2015) e Song (2018).

Com características tão abrangentes, essa subordem necessitou ser subdividida para melhor comportar a diversidade de gafanhotos e atualmente possui duas infraordens: (i) Tridactylidea composta pelas superfamílias Dzhajloutshelloidea (fóssil) e Tridactyloidea e (ii) Acrididea, que é composta por Acridomorpha e Tetrigoidea (Cigliano *et al*. 2018). O grupo abordado neste estudo foram os membros da superfamília Tetrigoidea, que possui apenas a família Tetrigidae Rambur, 1838 (também conhecidos como *tetrigids*, *pygmy locusts, pygmy grasshoppers; pygmy unicorns; pygmy giraffhoppers; grouse locusts; dornschrecken*) e as seguintes características os distinguem dos gafanhotos Acridomorpha (ver Hancock 1902; Nabour 1929; Dirsh 1961; Hartley 1962; Amédgnato 1976; Flook & Rowell 1997):

(i) pronoto recobrindo parcialmente ou completamente o abdômen, com forma variável e em certos grupos ornamentado (Figs. 2, 3);

(ii) proesterno disposto como um colar que envolver as peças bucais (*sternomentum*) (Fig. 2A);

(iii) tegmina, quando presente, reduzida e disposta lateralmente ao corpo (Fig. 3C, D, F, G);

(iv) asa, quando presente, com região anal expandida;

(v) órgão timpânico ausente;

(vi) formula tarsal 2-2-3 (Fig. 2B, C);

(vii) arólio ausente (Fig. 2B, C);

(viii) órgãos genitais masculinos são compostos por duas camadas que estão alojadas abaixo de placas quitinosas pareadas (Fig. 2D, E);

(ix) órgão fálico em repouso direcionado a região anterior do corpo e

(x) ovos com o formato de garrafa de vinho (*wine-bottle-shaped*), cilíndricos e com uma extremidade afilada.

Atualmente a família Tetrigidae é composta pelas subfamílias Batrachideinae Bolívar, 1887 (Fig. 3A); Cladonotinae Bolívar, 1887 (Fig. 3B); Discotettiginae Hancock, 1907 (Fig. 3C); Lophotettiginae Hancock, 1909 (Fig. 3D); Metrodorinae Bolívar, 1887 (Fig. 3E); Scelimeninae Bolívar, 1887 (Fig. 3F); Tetriginae Serville, 1838 (Fig. 3G) e Tripetalocerinae Bolívar, 1887 (Fig. 3H) (Cigliano *et al.* 2018). Estas oito subfamílias apresentam aproximadamente 250 gêneros e 1900 espécies (Cigliano *et al.* 2018) descritas.

Batrachideinae (Fig. 3A) são tetrigídeos caracterizados pelo fêmur anterior com cristas dorsais em pelo menos parte do comprimento femoral; fêmur mediano com cristas longitudinais; espermateca da fêmea com dois divertículos sendo o dorsal mais longo e o ventral menos expandido (Grant 1962, 1966). Entre as oito subfamílias, os batrachideines possuem as características diagnósticas mais bem estabelecidas, havendo algumas sugestões de mudança hierárquica que elevasse este grupo ao nível de família (Kevan 1982; Rowell & Flook 1998).

Os batrachideíneos apresentam intensa diversificação nas regiões tropicais, em especial na região Neotropical na qual encontramos a maioria dos gêneros conhecidos: *Batrachidea* Serville, 1838; *Cranotettix* Grant, 1955; *Eutettigidea* Hancock, 1914; *Halmatettix* Hancock, 1909; *Lophoscirtus* Bruner, 1911; *Paurotarsus* Hancock, 1900; *Plectronotus* Morse, 1900; *Puiggaria* Bolivar, 1887, *Rehnidium* Grant, 1956; *Scaria* Bolivar, 1887 and *Tettigidea* Scudder, 1862 (Cigliano *et al.* 2018).

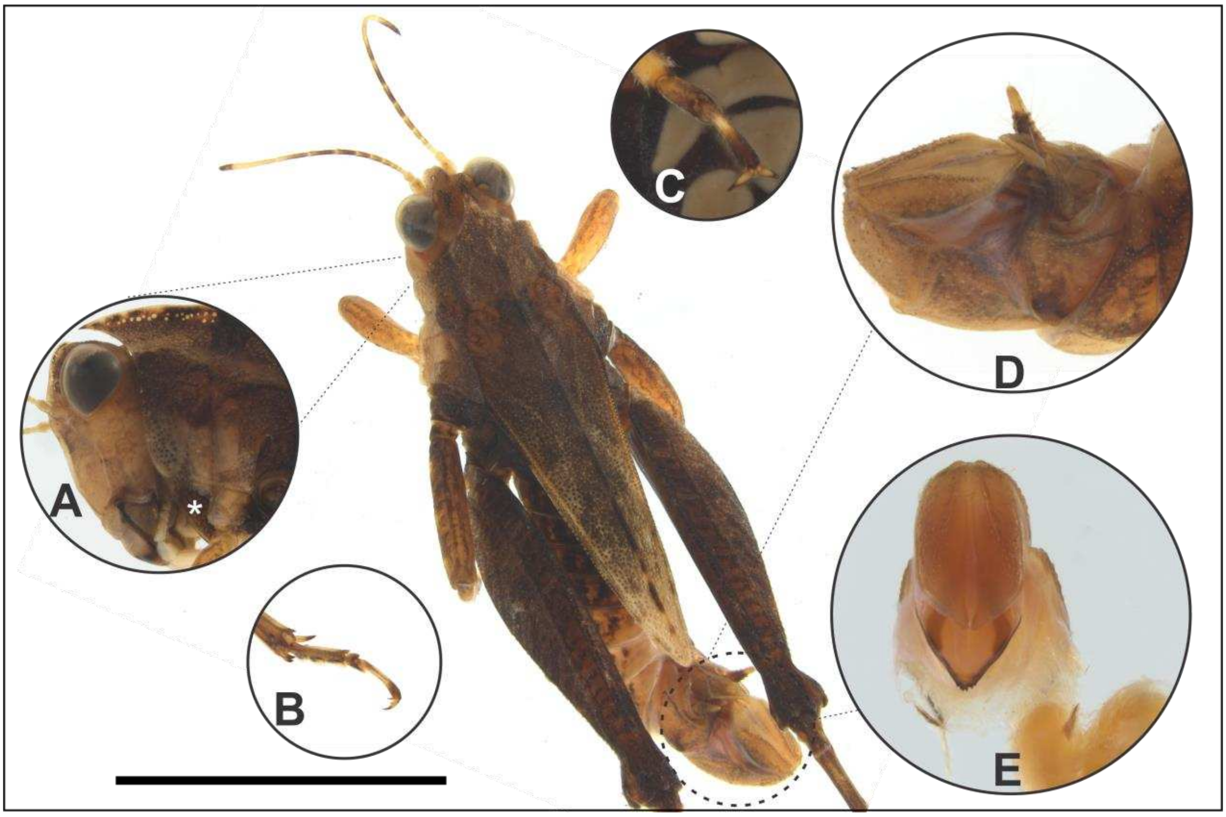

Figura 2. Características diagnósticas de tetrigídeos exemplificadas em *Halmatettix* sp. com pronoto não recobrindo completamente o abdômen, (A) cabeça em vista lateral com asterisco indicando o proesterno (*sternomentum*), (B) tarsos do primeiro e segundo pares de pernas com três segmentos, (C) tarsos do terceiro par de pernas com dois segmentos, (D) terminalia em vista lateral com placas quitinosas pareadas e (E) terminalia em vista dorsal com placas quitinosas pareadas e órgãos do complexo fálico. Escala: 5 mm.

Algumas espécies de *Tettigidea* e o gênero *Paxilla* Bolivar, 1887 também são encontrados na região Neártica se expandindo para a região Neotropical (Cigliano *et al*. 2018). Na África são conhecidos dois gêneros: *Ascetotettix* Grant, 1956 e *Phloeonotus* Bolívar, 1887 e na Ásia e regiões do Pacifico (incluindo a Austrália, Nova Guiné e Oceania) apresentam mais seis gêneros: *Bufonides* Bolívar, 1898; *Palaioscaria* Günther, 1936; *Saussurella* Bolívar, 1887; *Vilma* Steinmann, 1973; *Vingselina* Sjöstedt, 1921 e *Wiemersiella* Tumbrinck, 2014.

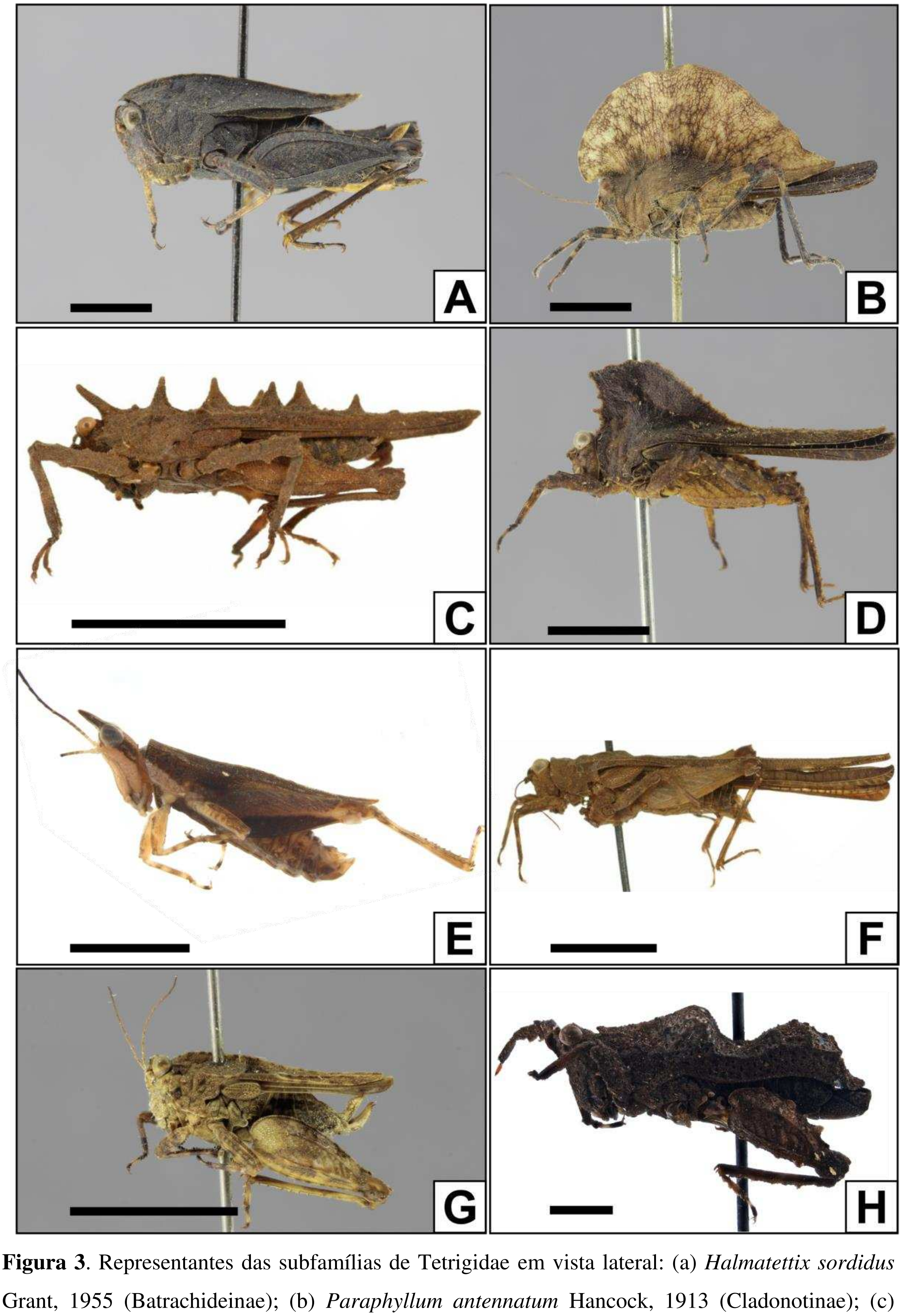

Figura 3. Representantes das subfamílias de Tetrigidae em vista lateral: (a) *Halmatettix sordidus* Grant, 1955 (Batrachideinae); (b) *Paraphyllum antennatum* Hancock, 1913 (Cladonotinae); (c) *Discotettix belzebuth* (Serville, 1838) (Discotettiginae) foto: Josef Tumbrinck; (d) *Lophotettix hancocki* (Bruner, 1910) (Lophotettiginae); (e) *Metopomystrum muriciense* Silva & Skejo, 2017

(Metrodorinae); (f) *Falconius gestroi* Bolívar, 1898 (Scelimeninae) foto: Josef Tumbrinck; (g) *Paratettix cingalensis* (Walker, 1871) (Tetriginae) e (h) *Tripetaloceroides tonkinensis* (Günther, 1938) (Tripetalocerinae) foto Bruckner Harald. Escala: A, B, D, G = 0,5 cm; C = 1 cm; E = 0,5 cm; F= 0,5 cm; H = 2 mm.

A subfamília **Cladonotinae** (Fig. 3B) é um grupo polifilético (Skejo & Bertner 2017) caracterizado pela carena fascial da costa frontal ampla e consequentemente, escutelo mais largo que o escapo (Tumbrinck 2014). Na região Neotropical, a diversidade de espécies é restrita as sub-regiões das Grandes Antilhas (Cuba, Jamaica, Hispaniola (formado pelo Haiti and Republica Dominicana) e Porto Rico (baseado nas bioregiões de Morrone 2014)) cujos gêneros são: *Antillotettix* Perez–Gelabert, 2003; *Armasius* Perez–Gelabert & Yong, 2014; *Bahorucotettix* Perez–Gelabert, Hierro & Otte, 1998; *Choriphyllum* Serville, 1838; *Cubanotettix* Perez–Gelabert, Hierro & Otte, 1998; *Cubonotus* Perez–Gelabert, Hierro & Otte, 1998; *Haitianotettix* Perez–Gelabert, Hierro & Otte, 1998; *Hottettix* Perez–Gelabert, Hierro & Otte, 1998; *Mucrotettix* Perez–Gelabert, Hierro & Otte, 1998; *Phyllotettix* Hancock, 1902; *Sierratettix* Perez–Gelabert, Hierro & Otte, 1998; *Tiburonotus* Perez–Gelabert, Hierro & Otte, 1998 e *Truncotettix* Perez–Gelabert, Hierro & Otte, 1998 (Perez–Gelabert *et al*. 1998; Perez–Gelabert 2003; Perez–Gelabert & Yong 2014; Cigliano *et al*. 2018).

Nesta região, com exceção das espécies que possuem pronoto com formato foliar, as espécies são caracterizadas pelo tegumento granuloso e presença de tubérculos fastigiais (também denominados carinula transversal do vértice) (ver Heads *et al*. 2014). Na América do Sul, os cladonotíneos se limitam a apenas dois gêneros conhecidos *Cota* Bolivar, 1887 e *Eleleus* Bolivar, 1887 (Cadena–Castaneda & Cardona Granda 2015; Cigliano *et al*. 2018).

Na África e Madagascar, temos *Afrolarcus* Gunther, 1979; *Dasyleurotettix* Rehn, 1904; *Hippodes* Karsch,1890; *Pelusca* Bolivar, 1912; *Lepocranus* Devriese, 1991; *Microthymochares* Devriese, 1991; *Thymochares* Rehn, 1929 (Gunther 1979, Devriese 1991, Cigliano et al 2018). Para a Australia, temos registo de apenas dois gêneros: *Peraxelpa* Sjöstedt, 1932 e *Tepperotettix* Rehn, 1952 (Cigliano *et al*. 2018). As regiões onde a diversidade de espécies se destaca são a Ásia (India, Indochina, China) e ilhas do sudeste asiático (Filipinas, Sumatra, Java, Nova Guiné, Nova Caledonia entre outras) nas quais podemos encontrar *Aspiditettix* Liang, Chen, Li & Chen, 2009; *Austrohancockia* Gunther, 1938; *Boczkitettix* Tumbrinck, 2014; *Cladonotella* Hancock, 1909; *Cladonotus* Saussure, 1862; *Deltonotus* Hancock, 1904; *Devriesetettix* Tumbrinck, 2014; *Diotarus*

Stal, 1877; *Dolatettix* Hancock, 1907; *Epitettix* Hancock, 1907; *Eurymorphopus* Hancock, 1907; *Fieberiana* Kirby, 1914; *Gestroana* Berg, 1898; *Gignotettix* Hancock, 1909; *Hancockella* Uvarov, 1940; *Holoarcus* Hancock, 1909; *Hymenotes* Westwood,1837; *Hypsaeus* Bolivar, 1887; *Ichikawatettix* Tumbrinck, 2014; *Ingrischitettix* Tumbrinck, 2014; *Misythus* Stal, 1877; *Nesotettix* Holdhaus, 1909; *Oxyphyllum* Hancock, 1909; *Paraphyllum* Hancock, 1913; *Piezotettix* Bolivar, 1887; *Planotettix* Tumbrinck, 2014; *Potua* Bolivar, 1887; *Pseudohyboella* Gunther, 1938; *Pseudepitettix* Zheng, 1995; *Stegaceps* Hancock, 1913; *Tondanotettix* Willemse, 1928; *Tuberfemurus* Zheng, 1992; *Willemsetettix* Tumbrinck, 2014 e *Yunnantettix* Zheng, 1995 (Cigliano *et al.* 2018).

Em Cladonotinae há uma única tribo Xerophyllini Günther, 1979 (Cigliano *et al.* 2018) na qual pesquisas recentes indicam que pode se tratar de uma subfamília a parte dos cladonotines (Silva *et al. in press*). Este grupo se distingue dos demais cladonotines por apresentarem a base das antenas situadas abaixo dos olhos compostos, fêmures anteriores e medianos ornados ou carenados (Günther 1979; Devriese 1999). Atualmente este grupo comporta quinze gêneros: *Acmophyllum* Karsch, 1890; *Astyalus* Rehn, 1939; *Bidentatettix* Zheng, 1992; *Cladoramus* Hancock, 1907; *Morphopoides* Rehn, 1930; *Morphopus* Bolívar, 1905; *Pantelia* Bolívar, 1887; *Paulytettix* Devriese, 1999; *Royitettix* Devriese, 1999; *Sanjetettix* Devriese, 1999; *Seyidotettix* Rehn, 1939; *Tettilobus* Hancock, 1909; *Trachytettix* Stål, 1876; *Trypophyllum* Karsch, 1890 e *Xerophyllum* Fairmaire, 1846 (Cigliano *et al.* 2018).

Discotettiginae (Fig. 3C) são tetrigídeos asiáticos caracterizados por catorze segmentos com dois ou três antenômeros próximos ao ápice achatados ou foliáceos (Hancock 1907). Este grupo atualmente possui uma tribo Discotettigini Hancock, 1907 formada por apenas um gênero, *Discotettix* Costa, 1864 e outros cinco gêneros sem posicionamento em tribos: *Arulenus* Stål, 1877; *Flatocerus* Liang & Zheng, 1984; *Hirrius* Bolívar, 1887; *Kraengia* Bolívar, 1909 e *Phaesticus* Uvarov, 1940 (Cigliano *et al.* 2018).

Lophotettiginae (Fig. 3D) é uma subfamília Neotropical com apenas um gênero *Lophotettix* Hancock, 1909 caracterizado pelas antenas achatadas, mas não foliáceas com formato dos antenômeros alargados da base ao ápice, com 11 antenômeros (com um segmento apical agudo), pronoto elevado comprimido formando uma crista ou foliáceo, não recobrindo a cabeça, em algumas espécies a elevação do pronoto é translúcido (Hancock 1909; Barranco 2010).

Metrodorinae (Fig. 3E) é um dos maiores grupos de tetrigídeos em numero de espécies e são encontrados distribuídos na região Neotropical, Etiópiana, Oriental e

Australiana onde atualmente é composta por cinco tribos: Amorphopini Günther, 1939 (composto pelos gêneros Neotropicais *Amorphopus* Serville, 1838; *Eomorphopus* Hancock, 1907 e *Platythorus* Morse, 1900); Cleostratini Bolívar, 1887 (*Cleostratus* Stål, 1877; *Indomiriatra* Tinkham, 1939; *Metopomystrum* Günther, 1939; *Miriatroides* Zheng & Jiang, 2002; *Procytettix* Bolívar, 1912; *Pseudomitraria* Hancock, 1907; *Rhopalina* Tinkham, 1939; *Rhynchotettix* Hancock, 1907; *Rostella* Hancock, 1913; *Spadotettix* Hancock, 1910 e *Thyrsus* Bolívar, 1887); Clinophaestini Storozhenko, 2013 (*Birmana* Brunner von Wattenwyl, 1893 e *Clinophaestus* Storozhenko, 2013); Miriatrini Cadena-Castañeda & Cardona, 2015 (composto por um único gênero encontrado na região Neotropical *Miriatra* Bolívar, 1906) e Ophiotettigini Tumbrinck & Skejo, 2017 (*Halmahera* Storozhenko, 2016; *Ophiotettix* Walker, 1871; *Paraspartolus* Günther, 1939; *Rhopalotettix* Hancock, 1910; *Spartolus* Stål, 1877; *Threciscus* Bolívar, 1887 e *Uvarovithyrsus* Storozhenko, 2016) e outros 70 gêneros (Cigliano *et al.* 2018).

Este grupo é caracterizado por apresentar antenas filiformes, com número de antenômeros variável e posicionadas abaixo da margem dos olhos compostos; ocelo mediano também posicionado abaixo dos olhos; carena fascial divergentes e formando um escutelo; lobos laterais do pronoto direcionados lateralmente e primeiro e terceiro segmentos dos tarsos posteriores com tamanho similares (Hancock 1902, Rehn 1952, Pavón-Gozalo *et al.* 2012). Porém, todas essas características não são exclusivas a essa subfamília, uma vez que os grupos que compõem Metrodorinae são muito variáveis e não possuem sinapomorfias conhecidas (Pavón-Gozalo *et al.* 2012).

Scelimeninae (Fig. 3F) é caracterizada pelo pronoto triangular e lobos laterais do pronoto com projeções que podem ser em alguns gêneros espiniformes (Tumbrinck 2014). Essa subfamília tem distribuição concentrada a Ásia e ilhas próximas à Nova Guiné com poucas exceções como *Loxilobus bantu* Rehn, 1930; *Criotettix acutipennis* Karsch, 1900 e *C. telifera* (Walker, 1871) na Africa e o gênero *Euloxilobus* Sjöstedt, 1936 na Australia (Cigliano *et al.* 2018). Esse grupo é organizado em três tribos: Criotettigini Kevan, 1966 (*Criotettix* Bolívar, 1887; *Euloxilobus* Sjöstedt, 1936; *Loxilobus* Hancock, 1904; *Paracriotettix* Liang, 2002 e *Tettitelum* Hancock, 1915), Scelimenini Bolívar, 1887 (*Amphibotettix* Hancock, 1906; *Eufalconius* Günther, 1938; *Euscelimena* Günther, 1938; *Falconius* Bolívar, 1898; *Hexocera* Hancock, 1915; *Indoscelimena* Günther, 1938; *Paragavialidium* Zheng, 1994; *Paramphibotettix* Günther, 1938; *Platygavialidium* Günther, 1938; *Scelimena* Serville, 1838; *Tagaloscelimena* Günther, 1938; *Tefrinda* Bolívar, 1906 e *Tegotettix* Hancock, 1913) e Thoradontini Kevan, 1966 (*Probolotettix*

Günther, 1939 e *Thoradonta* Hancock, 1909) e outros seis gêneros (*Bentotettix* Deng, 2016; *Bolotettix* Hancock, 1907; *Cyphotettix* Rehn, 1952; *Eucriotettix* Hebard, 1930; *Eufalconoides* Zheng, Li & Shi, 2003; *Gavialidium* Saussure, 1862; *Hebarditettix* Günther, 1938; *Syzygotettix* Günther, 1938 e *Zhengitettix* Liang, 1994) (Cigliano *et al.* 2018).

Tetriginae (Fig. 3G) é encontrada em todos os continentes (Cigliano *et al.* 2018) cuja diagnose ainda não está definida e apenas algumas características que não são exclusivas desse grupo os mantem unidos como um táxon. Esta subfamília é dividida em duas tribos que também não possuem diagnose e carecem de informações: Dinotettigini Günther, 1979; Tetrigini Rambur, 1838 e outras vinte e cinco espécies (Cigliano *et al.* 2018). Dinotettigini é um grupo com cinco gêneros restritos ao continente africano (*Afrocriotettix* Günther, 1938; *Dinotettix* Bolívar, 1905; *Ibeotettix* Rehn, 1930; *Marshallacris* Rehn, 1948 e *Pseudamphinotus* Günther, 1979) e apenas um encontrado na Asia (*Lamellitettix* Hancock, 1904) (Cigliano *et al.* 2018).

Os membros da tribo Tetrigini estão agrupados com base na forma do corpo "*Tetrix–like*" e atualmente possui as seguintes espécies: *Clinotettix* Bey-Bienko, 1933; *Coptotettix* Bolívar, 1887; *Euparatettix* Hancock, 1904; *Exothotettix* Zheng & Jiang, 1993; *Hydrotetrix* Uvarov, 1926; *Paratettix* Bolívar, 1887; *Tetrix* Latreille, 1802 e *Thibron* Rehn, 1939 (Cigliano *et al.* 2018). Na região Neotropical, temos como representantes *Clypeotettix* Hancock, 1902; *Neotettix* Hancock, 1898 e *Nomotettix* Morse, 1894 (ambos também encontrados na região Neártica); *Micronotus* Hancock, 1902; *Stenodorus* Hancock, 1906; *Ochetotettix* Morse, 1900 e alguns representantes de *Tetrix* Latreille, 1802 e *Paratettix* (Cigliano *et al.* 2018).

Tripetalocerinae (Fig. 3H) é um pequeno grupo asiático caracterizado por uma redução no número de segmentos antenas que possuem de 8–11 antenômeros amplos e providos de projeções apicais (Storozhenko 2013). Atualmente este grupo possui apenas uma tribo com dois gêneros: Tripetalocerini Bolívar, 1887 com *Tripetalocera* Westwood, 1834 e *Tripetaloceroides* Storozhenko, 2013 (Cigliano *et al.* 2018).

Entre as subfamílias de Tetrigidae, cinco ocorrem na região Neotropical: Batrachideinae, Cladonotinae, Lophotettiginae, Metrodorinae e Tetriginae (Cigliano *et al.* 2018). Historicamente, nesta região houve uma negligencia quanto à diversidade de ortópteros e, consequentemente de tetrigídeos devido às limitadas expedições e coletas direcionadas a este grupo. A partir dos trabalhos de Bolívar (1887) no qual as principais descrições supragenéricas foram desenvolvidas, apenas nos primeiros sessenta anos do século passado as pesquisas na região Neotropical se intensificaram a partir dos esforços de pesquisadores como Hancock (1900, 1902, 1907), Bruner (1910, 1920), Hebard (1933) e os trabalhos clássicos de Grant (1955, 1956, 1967, 1958) e Rehn & Grant (1958).

Após esse período, houve pouco avanço na tetridologia Neotropical até que os estudos referentes aos tetrigídeos ressurgiram a partir dos cladonotíneos coletados nas sub-regiões das Grandes Antilhas (Heads (2009); Heads *et al.* (2014); Perez-Gelabert *et al.* (1998, 1999, 2014), Perez-Gelabert (2003, 2009) e Yong (2017)) e mais recentemente, das espécies descritas no livro "*Introduccion a los saltamontes de Colombia - Orthoptera:Caelifera, Acridomorpha, Tetrigoidea & Tridactyloidea*" de Cadena-Castañeda & Cardona-Gandra (2015).

Considerando a escassez de dados sobre os grupos Neotropicais, limitados em sua maioria a estudos antigos e a diversidade presente nesta região, à proposta deste trabalho é (i) acrescentar informações sobre os representantes Neotropicais revisando e provendo novas informações para o grupo, (ii) apresentar a primeira analise cladística morfológica de um grupo de Tetrigidae e (iii) introduzir a discussão sobre o uso de genitálias para diferentes grupos de Tetrigidae.

Assim, o presente estudo foi dividido em cinco partes, as três primeiras referentes à redescrição e revisão de grupos, a quarta parte apresenta uma filogenia morfológica de Batrachideinae e a ultima parte aborda a morfologia do complexo fálico:

1. *Eomorphopus* Hancock, 1907 (Insecta: Orthoptera: Caelifera: Tetrigidae: Amorphopini): redescription of *E. granulatus* housed at Academy of Natural Sciences of Drexel University, Philadelphia and overview of the Amorphopini situation.
2. Review of the subfamily Lophotettiginae Hancock, 1909 (Insecta: Ortoptera: Caelifera: Tetrigoidea).
3. New tribes, overview and check list of Neotropical Cladonotinae (Insecta: Orthoptera: Caelifera: Tetrigidae).
4. Preliminary study on Batrachideinae (Insecta: Orthoptera: Caelifera: Tetrigidae) phylogeny based on morphology data.
5. Are the phallic complex of pygmy grasshoppers (Insecta: Orthoptera: Caelifera: Tetrigidae) useful in taxonomy? An overview of literature data.

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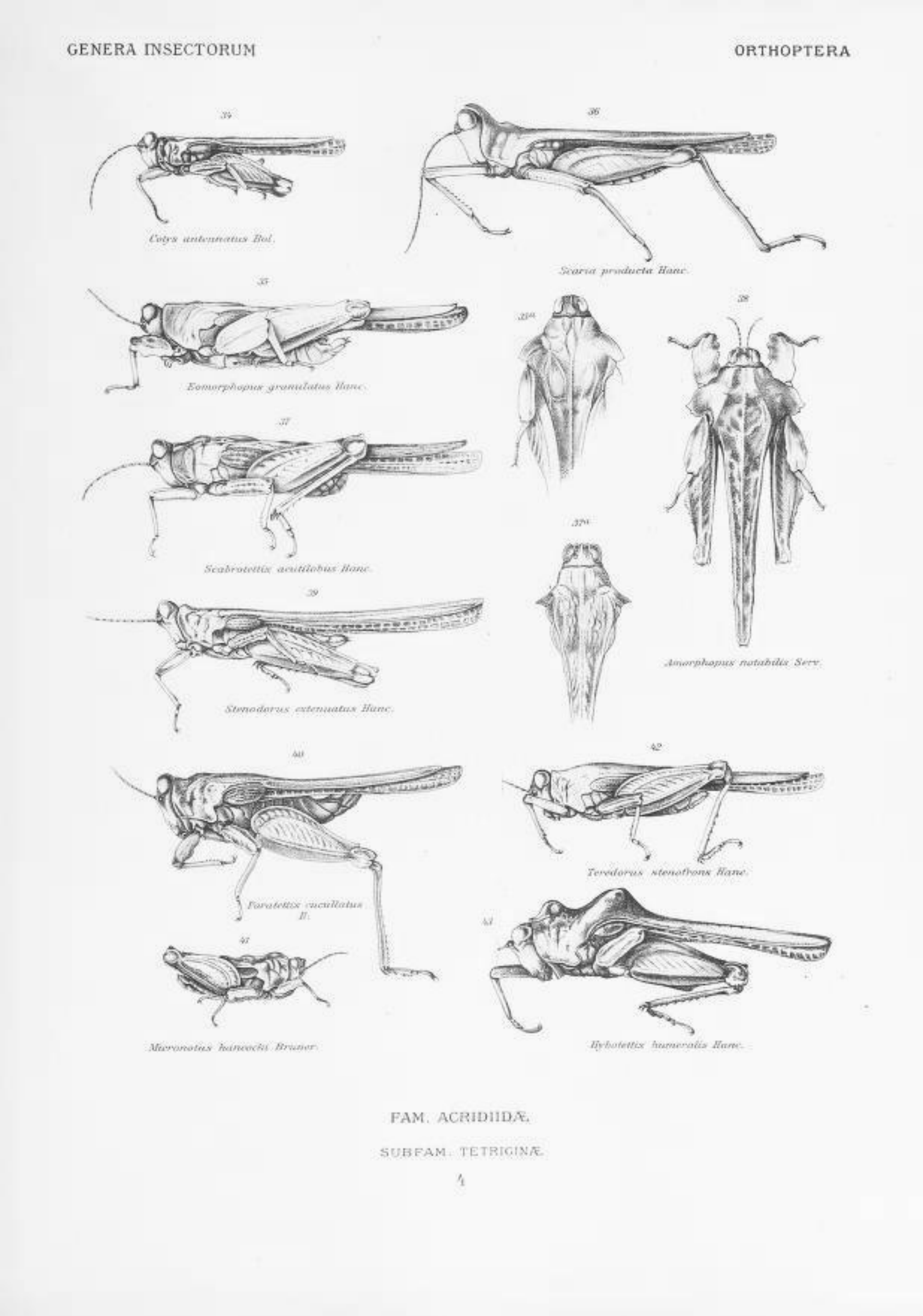
Artigo 1

Eomorphopus Hancock, 1907 (Insecta: Orthoptera: Caelifera: Tetrigidae: Metrodorinae: Amorphopini) redescription of *E. granulatus* and overview of the Amorphopini situation



Eomorphopus Hancock, 1907 (Insecta: Orthoptera: Caelifera: Tetrigidae: Metrodorinae: Amorphopini) redescription of *E. granulatus* and overview of the Amorphopini situation.

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Abstract

Eomorphopus was described by Hancock, 1907 and currently includes three species from South and Central America. The first described species was *E. purpurascens* (Olivier, 1791), followed by *E. antennatus* (Bolívar, 1887) and *E. granulatus* Hancock, 1907. Herein, we redescribe the *E. granulatus* type, housed at the Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, USA with a diagnosis, situation of each species of *Eomorphopus*, distribution data and overview of Amorphopini situation.

Key Words: Lectotype, redescription, taxonomy, tetrigids, museum

Resumo

Eomorphopus foi descrito por Hancock (1907) e atualmente incluiu três espécies da América do Sul e Central. A primeira espécie descrita foi *E. purpurascens* (Olivier, 1791), seguida de *E. antennatus* (Bolívar, 1887) e *E. granulatus* Hancock, 1907. Aqui, nós redescrevemos o tipo de *E. granulatus*, depositado na Academia de Ciências Naturais da

Drexel University (ANSP), Philadelphia, EUA com diagnose, situação de cada espécie de *Eomorphopus*, dados de ocorrência e visão geral da situação de Amorphopini.

Palavras chave: Lectótipo, redescrição, taxonomia, tetrigídeos, museu.

Introduction

Metrodorinae is a worldwide subfamily, currently composed of five tribes (Cleostratini Bolívar, 1887; Amorphopini Günther, 1939; Clinophaestini Storozhenko, 2013; Miriatrini Cadena–Castañeda & Cardona–Granda, 2015 and Ophiotettigini Tumbrinck & Skejo, 2017) and about 70 genera without placement (Cigliano *et al.* 2018). The tribe Amorphopini Günther, 1939 (*sensu* Cadena–Castañeda & Cardona–Granda (2015)) is exclusive to the New World and includes three genera: *Amorphopus* Serville, 1838 and *Eomorphopus* Hancock, 1907 in northern of South America (Cigliano *et al.* 2018) and *Platythorus* Morse, 1900 in Central America (Bruner *et al.* 1900–1909, Cigliano *et al.* 2018). Among the Amorphopini, *Eomorphopus* is morphologically similar to *Amorphopus,* but can be easily distinguished by the not enlarged forelegs (Buzzetti & Devriese 2007).

Eomorphopus was defined by Hancock (1907) and was characterized by strongly depressed body, granulose surface, oblique face, vertex truncated anteriorly, frontal costa compresso–elevated, moderately sulcated, between the antennae; pronotum anteriorly truncated and posteriorly acuminated, tegmina oval sublanceolated; fore femur strongly carinated (but not shieldlike shape as some *Amorphopus*), with the superior carinae often bi– or triundulated and inferior carina with only one lobe, middle femur clypeated and foliaceous (see Hancock 1907; Cadena–Castañeda & Cardona–Granda 2015). Such as *Amorphopus,* the genus *Eomorphopus* is distributed only for South America and includes three species: *Eomorphopus purpurascens* (Olivier, 1791), *Eomorphopus antennatus* (Bolívar, 1887) and *Eomorphopus granulatus* Hancock, 1907 (Cigliano *et al.* 2018). In the present study, we redescribe *Eomorphopus granulatus* based on the type housed at the Academy of Natural Sciences of Drexel University, (ANSP), Philadelphia (USA). Additionally, we also present information regarding the other species of *Eomorphopus* and an overview of the Amorphopini situation.

Material and Methods

The two specimens of *E. granulatus* housed at ANSP were examined. The labels information's, conservation condition and comments are given for each specimen. Types considered in good condition were those with none or few parts of the body damaged. The photographs of *habitus* and labels were taken in a photo lightbox with a Canon EOS T3i digital camera equipped with macro lens EF 100mm f/2.8 L. These photographs of morphological characteristics were obtained in four positions: dorsal, lateral (right and left) and frontal. The male genitalia was not analyzed, because the specimen is dried. Geographic occurrence data of three *Eomorphopus* species were estimated from information available in the literature (Table 1). Morphological terminology follows Devriese (1996) and Tumbrinck (2014).

Results

Family Tetrigidae Rambur, 1838
Subfamily Metrodorinae Bolívar, 1887
Tribe Amorphopini Günther, 1939
Genus *Eomorphopus* Hancock, 1907

Eomorphopus granulatus **Hancock, 1907**

Figures 1–2

Eomorphopus granulatus Hancock, 1907 (48): 38 [general description], lectotype female (ANSP) and paralectotype male designated, Plate 4, Figs. 35–35a; type-locality: "Dutch Guiana, S. America". Kirby, 1910: 22 [synonymic catalogue of Orthoptera]. Bruner, 1910 [key, new localities]. . Rehn, 1913: 82 [New localities "Suriname"] Rehn, 1916: 268 [new localities]. Rehn, 1918: 167 [new localities]. Bruner, 1919–1922: 8 [new localities]. Günther, 1939: 263 [new localities]. Liebermann, 1955: 331 [catalogue of Brazilian Orthoptera]. Otte, D. 1979(1978): 39 [catalogue of primary types at ANSP].

Type material: Lectotype female, by present designation, deposited at ANSP and labeled as follows: "*Eomorphopus granulatus* Hancock H573 [handwritten] TYPE [printed, red label]/Hancock's [printed] Type *Eomorphopus granulatus* [handwritten, white label]/Dutch Guiana [handwritten, white label]". Conservation status: Bad condition, both antennas missing; specimen glued on card and remnants of fungi on body. Paralectotype male, by present designation, deposited at ANSP and labeled as follows: "*Eomorphopus granulatus* Allotype Hancock ♂ [handwritten] PARATYPE HEBARD CLN [printed, yellow label]/Dutch Guiana [handwritten, white label]". Conservation status: Bad condition, both antennas missing; right fore and middle tarsus missing; specimen glued on card and remnants of fungi on body.

Diagnosis: This species can be distinguished from the other species of *Eomorphopus* by the following combination of characters: (i) dorsal and ventral margins of fore femur carinated and (ii) dorsal margin of fore femur triundulated.

Redescription (Female lectotype, Fig. 1): Body surface granulated. **Head.** Lateral view (Fig. 1A, B): protuberant and slightly conical eyes with a flattened base; vertex and fastigium visible between eyes; antennal groove situated between lower margin of compound eyes; frontal costa elevated. Frontal view (Fig. 1D): fastigium of vertex slightly conic; frontal costa bifurcation placed between compound eyes with narrow scutellum; fascial carinae between both superior ocelli; median ocelli placed between fascial carinae and frontal carina, but not touch o on the base by frontal carina; antennal groove situated between lower margin of compound eyes and medial ocelli. Dorsal view (Fig. 1C): vertex with distance between eyes as long as horizontal diameter of eyes; medial carina conspicuous and continuing towards frontal costa; area of fastigium to occiput granulated; occipital area visible and margin anterior of pronotum distant the eyes. **Pronotum.** Macropronotal and flattened dorso- ventrally. Lateral view (Fig. 1A, B): anterior margin of pronotum truncated and slightly elevated; median carina slightly undulated, prozonal carina and humero-apical carina visible and short, not reaching the sulci; extralateral carina inconspicuous; ventral sinus present; lateral lobe with anterior margin truncated and without spine; tegminal sinus present; length of infrascapular area shorter than length of fore tibiae; two deep sulci between prozona and humero-apical carina; paranota granulated and triangularly shaped; humero-apical carina continuous to external lateral carina and both parallel to median carina. Frontal view (Fig. 1D): lateral lobes of pronotum projected and directed sidewards. Dorsal view (Fig. 1C): dorsum granulated; prozonal carina visible and short, not reaching the sulci; median carina continuous; humero-apical carina conspicuous; anterior and posterior margin of pronotum truncated; lateral lobe directed sidewards. **Sternomentum.** Could not be checked due to it being glued on card. **Wings.** (Fig. 1A, B): tegmina and hindwings visible; tegmina oval, sublanceolated shape; hindwings dark brown and surpassing pronotum apex. **Legs.** Fore legs (Figs. 1A, B, D): fore femur flattened laterally, dorsal and ventral margins of femur carinated with three undulations in the dorsal margin and one in ventral margin; tibia as long as femur. Middle legs (Fig. 1A–C): middle fêmur shieldlike shape, flattened laterally and strongly foliaceous; dorsal and ventral margin slightly undulated; ventral margin expanded, with rounded teeth (crenated) near tibia; femur longer than tibia. Hind legs (Fig. 1A, B): dorso-external and ventro-external of femur granulated; antegenicular tooth conspicuous; dorso-external carina and ventro-external carina conspicuous; transversal ridges visible on external surface; tibia not visible and hidden behind the femur. **Abdomen.** (Fig. 1A, B): sternites not visible due to specimen glued on card; ovipositor valves short and robust, superior margin of dorsal and ventral valve with teeth. Measures (in Hancock, 1907): Total length of female body: 16,5mm; pronotum: 14,5 mm; hind femur: 7 mm.

Male (Paralectotype, Fig. 2): similar to female, except: **Head**. Frontal view (Fig. 2D): fastigium straight; **Pronotum**. Lateral view (Fig. 2A, B): humero-apical carina not continuous to external lateral carina. Measures (in Hancock, 1907): Total length of male body: 15 mm; pronotum: 13 mm; hind femur: 6 mm.

Comments on coloration of the dried specimens: In the description, Hancock (1907) indicated that body was subtly granulated and cinereous or fuscus-cinereous (ash-colored; gray tinged with blackish, see Smith (1906)). Currently this type has overall brownish-yellow and brown color.

Discussion

Amorphopini was erected as tribe status by Cadena–Castañeda & Cardona–Granda (2015) formed by three genera: *Amorphopus*, *Eomorphopus* and *Platythorus*. This new tribe was characterized by globose eyes in lateral view; body strongly flattened; fore femur carinated and mid femur strongly expanded; dorsal and ventral margin of middle femur lobed or foliaceous and frequently camouflaged with lichens or bryophytes (Cadena–Castañeda & Cardona–Granda 2015) since *Amorphopus* and *Eomorphopus* are associated to humid environments as rivers and lakes (Amédégnato & Devriese 2008).

In this tribe, *Platythorus* is easily distinguished to other Amorphopini by the lack of tegmina and wings. *Platythorus* is monotypic with only one female type, *Platythorus camurus* Morse, 1900 with occurrence from Nicaragua and Costa Rica (Bruner *et al.* 1900–1909). *Amorphopus* and *Eomorphopus* are very similar genera but, also easily separated. *Eomorphopus* has scutellum narrower than *Amorphopus*; *Amorphopus* has antennae placed much below the inferior margin of eyes; tegmina ovoid; fore femur flattened, foliaceous and clypeate, while *Eomorphopus* has antenna groove near inferior margin of eyes; tegmina sublanceolate and fore femur carinated, not clypeated and not foliaceous (see Hancock 1907, Bruner 1919–1922, Buzzetti & Devriese 2007, Cadena–Castañeda & Cardona–Granda 2015). Although these Amorphopini genera are easily distinguished among each other, the species included in each genus need revision.

For a long time, *Eomorphopus* species were described as *Amorphopus*, except for *E. purpurascens,* which was originally described as *Acrydium purpurascens* by Olivier (1791) and is still almost unknown, without photos and few morphological information's. Additionally, part of available morphological information of *E. purpurascens* is non-conservative, as the coloration used by Oliver (1791). This type of characteristics can be lost over time (*eg*. wings with purplish coloration) and the type species was not defined in the original description and the depository is still unknown. The distribution is known only for Trinidad Island (Olivier 1791) (Table 1).

Eomorphopus antennatus was described by Bolívar (1887) as *Amorphopus* and in 1907, Hancock reallocated this species in the new genus *Eomorphopus*. *E. antennatus* is very similar to *E. granulatus* but distinguished by the biundulated fore femur dorsal margin against the above triundulated fore femur dorsal margin in *E. granulatus* (Bruner 1910). *E. antennatus* has several records: Peru, Guyana, Venezuela, Ecuador, Suriname, Brazil and Trinidad Island (Table 1). Currently, the depository of primary type is unknown (Cigliano *et al.* 2018) and there is a female from Alto Amazonas in Bolívar's Tetrigoidea collection, housed at the National Museum of Natural History, Madrid, Spain (MNCN) (Paris 1993–1994). As cited by Paris (1993–1994), Bolívar (1887) studied the specimen from Bruner's collection at Vienna to describe the type of *E. antennatus* and it is necessary review this female housed at MNCN.

Eomorphopus granulatus Hancock, 1907 has records to Guyana, French Guyana, Suriname and Brazil (Table 1). *E. granulatus* is the only species of *Eomorphopus* with type species housed at the ANSP. The two specimens of museum have labels with information's as "Type" to female and "Allotype"/"Paratype" to male. As the author did not designate the holotype in the original description, we designated the female as the Lectotype and consequently, the male specimen became Paralectotype. We believe that this redescription will be able to facilitate the species recognition.

Eomorphopus, as well other species in South America exhibit a very peculiar geographical distribution (see Silva *et al.* 2017). There is a large area in the north of South

America (mainly Central Amazon Forest in Brazil) where no occurrence for this genus is known. In addition, there is only one record probably to Atlantic Forest in the Bahia state, but Günther (1939) did not provide specific information about the record place. Thus, a question arises: Why are there no *Eomorphopus* species reported to Central portion of Amazon Forest and others Atlantic Forest areas? We consider two hypotheses for that: (i) the genus does occur in these areas, but its species haven't been sampled yet, or (ii) the genus really does not occur in Central Amazon Forest and occur only in one Atlantic Forest area. Supporting the first hypothesis, the species might not have been sampled or identified due to limited zoological expeditions and taxonomic effort focusing in tiny litter insects.

Supporting the second hypothesis, *Eomorphopus* species that eventually occurred in these areas might have undergone extinction due to natural selection or anthropic pressures. For example, between August 2015 and July 2016, 6.624 km^2 of Amazonian Forest were deforested for other alternative land use (INPE 2017). Deforestation also reduced the Atlantic Forest, in the amount of 183 km^2 between 2013 and 2014 and of 291 Km^2 between 2015 and 2016 (Fundação SOS Mata Atlântica & INPE 2017).

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Table 1. Data for all records ever made and mentioned for *Eomorphopus* Hancock, 1907.

Species	Records		References
	Country	**State/Province/Department/Locality**	
Eomorphopus purpurascens (Olivier, 1791)	Trinidad Island	–	Olivier 1791
Eomorphopus antennatus (Bolívar, 1887)	Peru	–	Bolívar 1887; Günther 1939; Buzzetti & Devriese 2007; Buzzetti & Carotti (2008)
	Guyana	–	Hancock 1907
	Venezuela	–	Rehn 1916; Robert 1937
	Brazil	Mato Grosso, Chapada dos Guimarães	Bruner 1910
	Brazil	Rondônia/Porto Velho, distrito de Abunã[1]	Rehn 1916
	Suriname	–	Günther 1939; Buzzetti & Devriese 2007; Buzzetti & Carotti (2008)
	Brazil	–	Buzzetti & Devriese 2007 Buzzetti & Devriese 2007; Buzzetti & Carotti (2008)
	Trinidad Island	–	Buzzetti & Devriese 2007 Buzzetti & Devriese 2007; Buzzetti & Carotti (2008)
	Ecuador	Napo	Buzzetti & Devriese 2007
	Ecuador	Amazon Region	Buzzetti & Carotti (2008)
Eomorphopus granulatus Hancock, 1907	Guyana	–	Hancock 1907; Bruner 1910
	Brazil	Pará/Benevides and Santarém	Bruner 1910; Bruner 1919–1922
	Brazil	Pará	Rehn 1916
	Brazil	Pará/Igarapé–Açu	Rehn 1918
	Suriname	–	Rehn 1913
	Brazil	Amapá/Oucatopi Island[2]	Bruner 1919–1922
	French Guyana	Cayenne/La Mana River[3]	Bruner 1919–1922
	Suriname	–	Günther 1939
	Brazil	Bahia[4]	Günther 1939
Eomorphopus sp[5].	Colombia	Amazonas/Amacayacu National Park	Cadena–Castañeda & Cardona–Granda 2015

[1] Small city and river with the same name near to mouth of the Madeira River.

[2] Robert (1977) in a review of Tribe Leptysmini (Orthoptera: Acrididae: Leptysminae) indicated that Oucatopi Island corresponds to Ucupy Island on the Arucauá River, tributary of the Uaça River in the state of Amapá, Brazil.

[3] The La Mana river is an extensive river that runs from central French Guiana to the municipality of Mana. Information on exact sampling location is not available.

[4] Information on exactly sampling location is not available.

[5] Additional information's about *Eomophopus* especies: In Cadena–Castañeda & Cardona–Granda (2015) one species of *Eomorphopus* was not determined. The specimen was identified by Cadena–Castañeda as *Eomorphopus antennatus*.

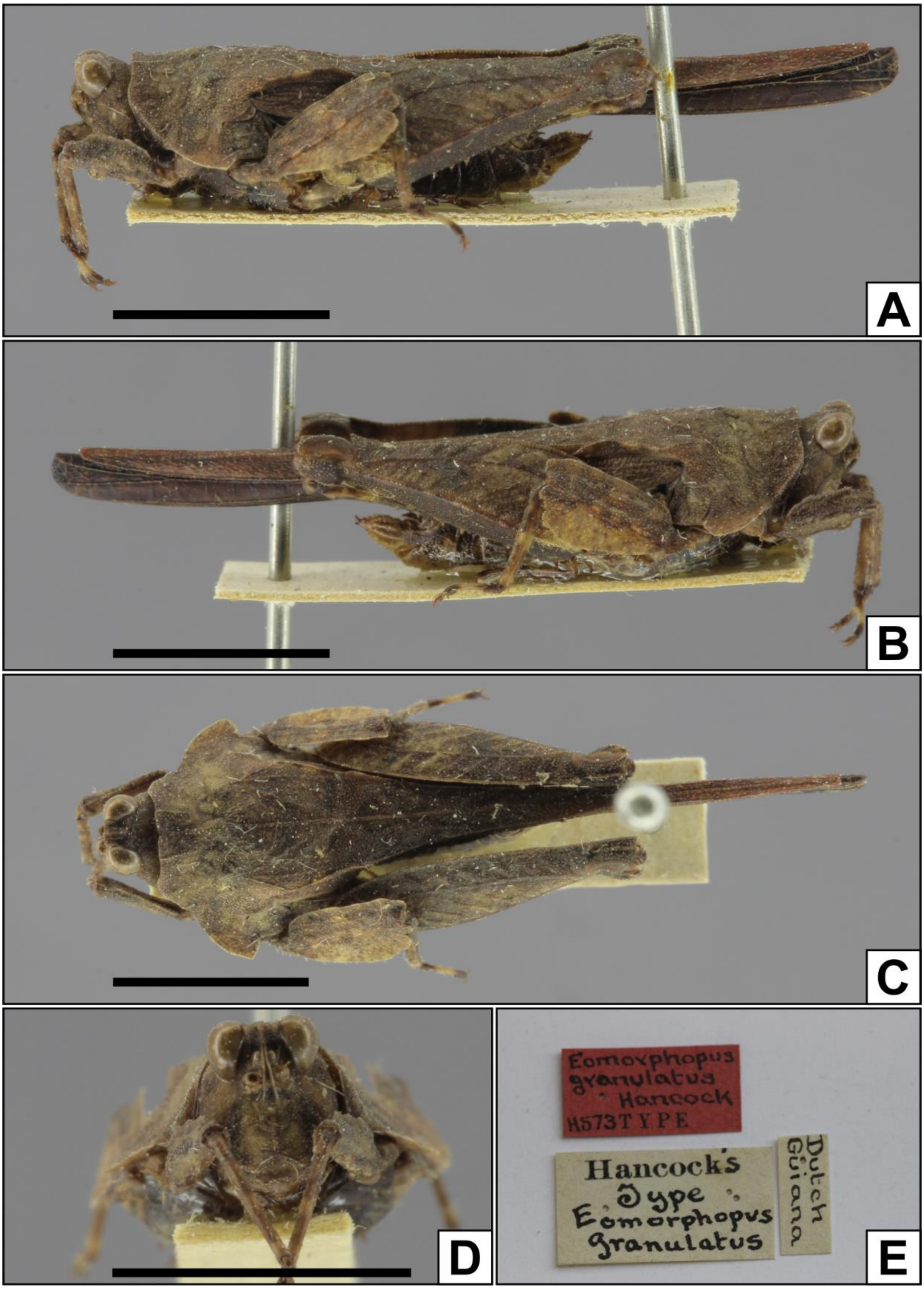


Figure 1. *Eomorphopus granulatus* Hancock, 1907 female lectotype (A) lateral left *habitus*; (B) lateral right *habitus*; (C) dorsal view; (D) head details in frontal view and (E) labels. Scale bars: 5 mm.

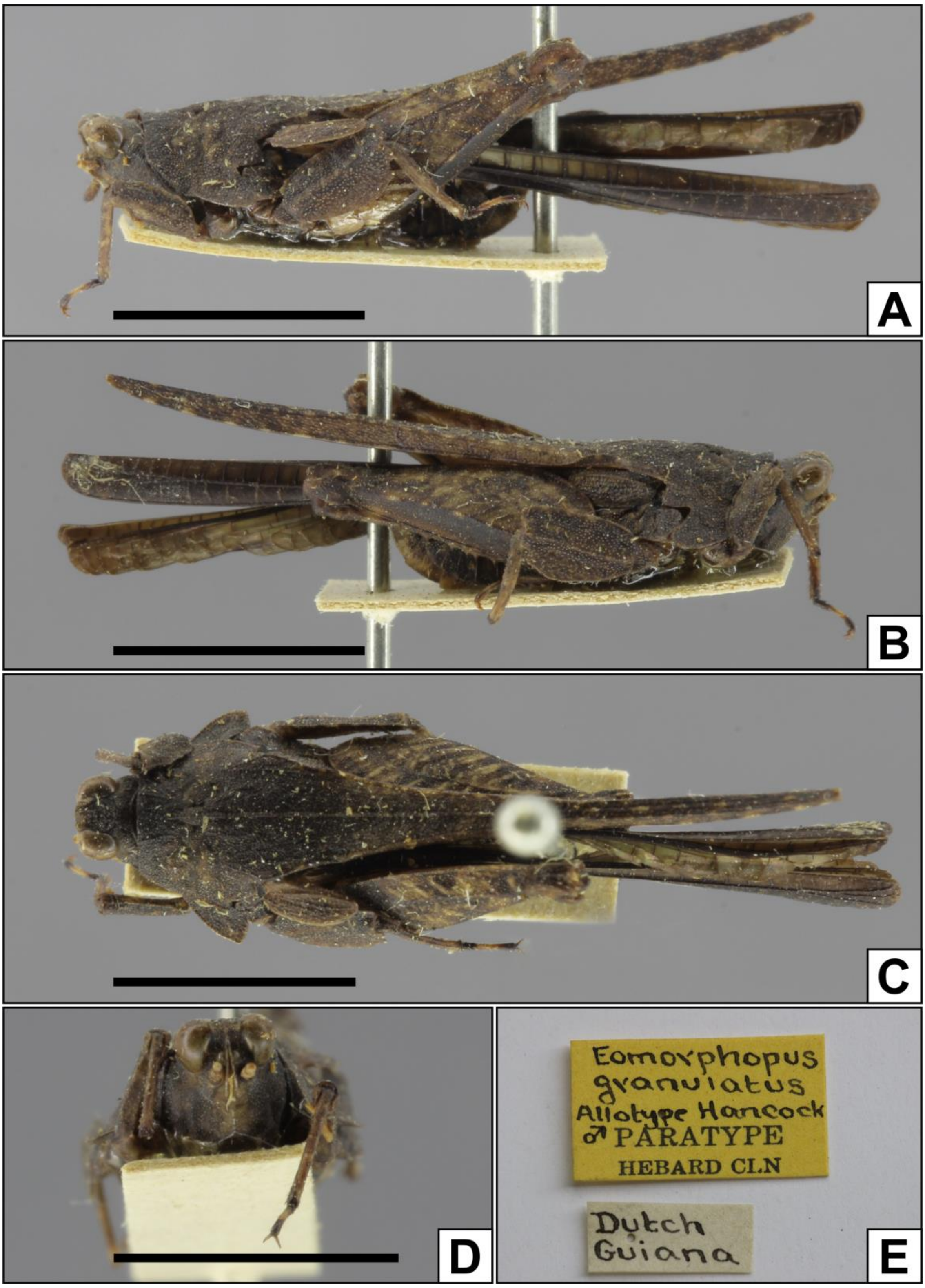
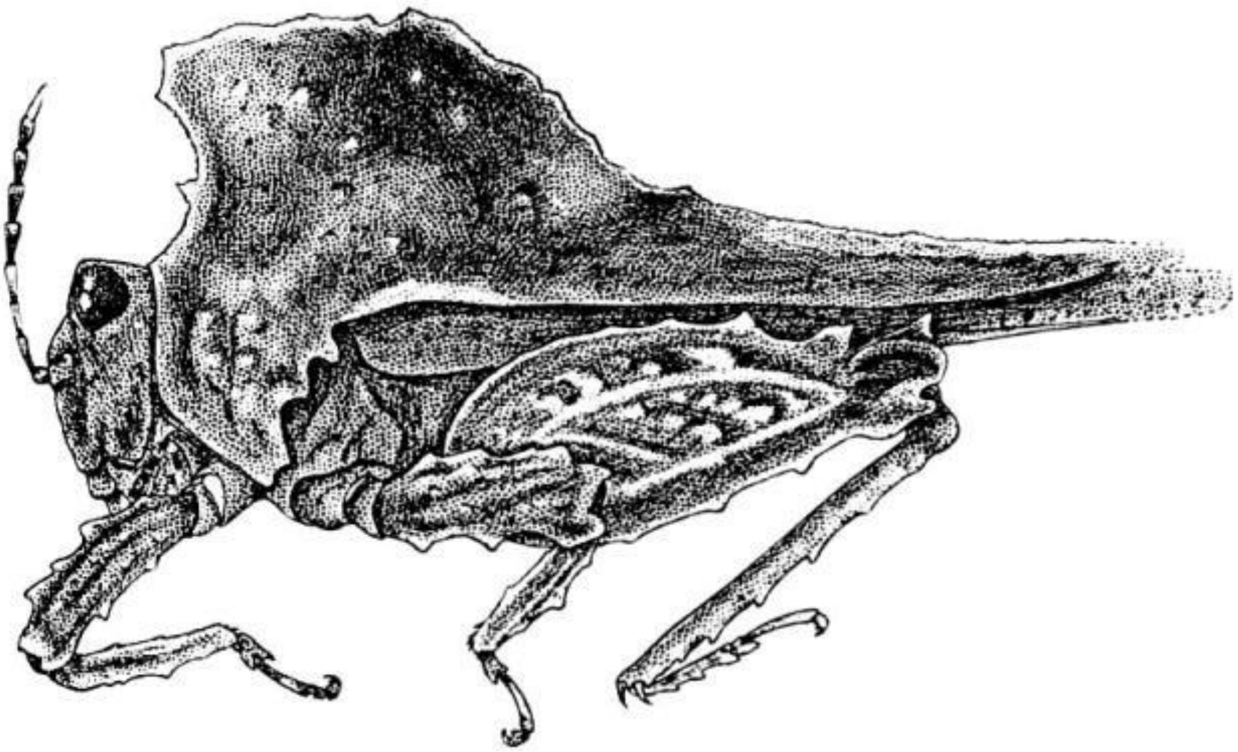


Figure 2. *Eomorphopus granulatus* Hancock, 1907 male paralectotype (A) lateral left *habitus*; (B) lateral right *habitus*; (C) dorsal view; (D) head details in frontal view and (E) labels. Scale bars: 5 mm.

Artigo 2

Review of the subfamily Lophotettiginae Hancock, 1909 (Insecta: Orthoptera: Caelifera: Tetrigidae)



Lophotettix unicristatus Hancock, 1909

Review of the subfamily Lophotettiginae Hancock, 1909 (Insecta: Orthoptera: Caelifera: Tetrigidae)

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Abstract

Lophotettiginae is peculiar small taxon of the Neotropical region characterized mainly by median carina compresso-cristated or leaf-like crest, antennae flattened laterally and expanding from the base to the apex (incrassate shape). This subfamily has only one genus known as *Lophotettix* Hancock, 1909 that presents five described species. Lophotettiginae has never been revised and there are doubts on the taxonomic status of this subfamily. Here, we reviewed the types of the five known species, highlighting morphological aspects that distinguish the species from each other and from other tetrigids. Additionally, we also provide a pictorial identification key to *Lophotettix* species. Our results indicated that Lophotettiginae is a well-defined taxon and there are no synonyms among its species.

Key words: Antennae, crested tetrigid, pictorial key, Neotropical region.

Resumo

Lophotettiginae é um pequeno e peculiar táxon da região Neotropical, caracterizado principalmente pela carena mediana cristada e comprimida ou com formato de folha, juntamente com os segmentos antenais achatados lateralmente e expandidos da base para o ápice (formato "*incrassate*"). Esta subfamília possui apenas um gênero conhecido como *Lophotettix* Hancock, 1909 e que apresenta cinco espécies descritas. Lophotettiginae nunca foi revisado e existem dúvidas quanto ao status taxonômico desta subfamília. Neste estudo revisamos os tipos das cinco espécies conhecidas e destacamos os aspectos morfológicos que distinguem as espécies entre si e das outras espécies de tetrigídeos. Adicionalmente, também apresentamos uma chave de identificação pictórica para as espécies de *Lophotettix*. Nossos resultados indicam que Lophotettiginae é um táxon bem definido e não há sinonímias entre suas espécies.

Palavras chaves: antena, tetrigídeos com crista, chave pictórica, região Neotropical.

Introduction

Lophotettiginae is a Neotropical taxon which has currently one genus and five species: *Lophotettix alticristatus* Hancock, 1909 (Brazil); *Lophotettix brevicristatus* Hancock, 1909 (Brazil); *Lophotettix hancocki* (Bruner, 1910) (Brazil); *Lophotettix unicristatus* Hancock, 1909 (Colombia, Guyana); *Lophotettix zumbadoi* Barranco, 2010 (Costa Rica) (Cigliano *et al*. 2018). This subfamily is characterized by incrassate shape of antennae segments and median carina compresso-cristated or leaf-like crest (Hancock 1909).

Although being a small group, members of this subfamily have a rather confusing and complex taxonomic history. The genus *Lophotettix* was described by Hancock (1909) on the section Lophotettigiae, with three species: *L. brevicristatus*, *L. alticristatus* and *L. unicristatus.* The latter species had been firstly described as *Nephele unicristata* Hancock, 1906. Bruner (1910) in the "*South American Tetrigids*" synopsis, attached Hancock's description of *Gladiotettix unicristata* Hancock, 1907 to his and described *Gladiotettix hancocki,* putting both *G. unicristata* and *G. hancocki* as Metrodorinae. Bruner also described a new genus of Batrachideinae named *Lophotettix*, with a single species, *Lophotettix lineatus* Bruner, 1910.

Hancock (1914), in a note named '*Some corrections in names of South American Tetriginae (Orth.)*', made some clarification and proposed changes regarding some generic name: (i) *Lophotettix* Bruner, 1910 was a generic epithet used firstly by Hancock (1909) to designate crested tetrigids, within section Lophotettigiae. Therefore Hancock (1914) transferred *Lophotettix* Bruner, 1910 to *Eutettigidea* Hancock, 1914 with the type species *Eutettigidea lineata* (Bruner, 1910) and designed *Lophotettix brevicristatus* as the type species of *Lophotettix* Hancock, 1909; (ii) *Gladiotettix* Hancock, 1907, which had three species, *G. unicristata* Hancock, 1907, *G. hancocki* Bruner, 1910 and *G. turgida* Bolívar, 1887 were modified by Hancock (1914) in that *G. unicristata and* G. *hancocki* were transferred to *Lophotettix* Bruner, 1910.

Gladiotettix (firstly named *Nephele* Bolívar, 1887) was considered synonymous to *Phelene* Bolívar, 1906 by Uvarov (1940) and Cadena-Castañeda & Cardona-Granda (2015) synonymized *Phelene* with *Chiriquia* Morse, 1900. Thus, the species *Gladiotettix turgida* Bolívar, 1887 was transferred to *Chiriquia turgida* (Bolívar, 1887) by Cadena-Castañeda & Cardona-Granda (2015).

Although plenty taxonomic changes involving the present Lophotetiginae, its species were never reviewed. Most of its species are known only by the type species or few records. Moreover, the peculiar set of morphological characters of *Lophotettix* that has gathered its five species within this subfamily is gets revision, so as to evaluate the validity of this group (as questioned by Günther (1938)). Here, we overview the five species of Lophotettiginae, discussing morphological aspects and the current classification of this group. We present photos highlighting the most important morphological characters, pictorial key to species, table of all records ever made and taxonomic comments.

Material and Methods

For an overview of *Lophotettix* we analyze the holotype of *L. hancocki* (Bruner, 1910) housed in The Academy of Natural Sciences of Drexel University (ANSP). The photographs of habitus and labels of *L. hancocki* (Bruner, 1910) were taken in a photo lightbox with a Canon EOS T3i digital camera equipped with macro lens EF 100mm f/2.8 L. To another species, we used literature and image of type specimens provided by the following museums (acronyms used in the text): Oxford University Museum of Natural History (OUM) and Museo de Insectos de la Universidad Central de Costa Rica. After data analysis, where necessary, new information has been added or highlighted. A pictorial identification key was elaborated with the aid of graphic editor, as well as the general schemes of antenna and median carina (Figs. 1, 8). The species occurrence were summarized with the information available in the literature (Table 1), including all records of known species.

Results

Family Tetrigidae Rambur, 1838

Subfamily Lophotettiginae Hancock, 1909

Lophotettigiae: Hancock, 1909
Lophotettigiae: Günther, 1938
Lophotettiginae: Steinmann, 1969.
Lophotettiginae: Otte, 1997
Lophotettiginae: Tumbrinck, 2014
Lophotettiginae: Cadena-Castañeda & Cardona-Granda, 2015

Lophotettix Hancock, 1909

Type species: *Lophotettix brevicristatus* Hancock, 1909

Etymology of *Lophotettix*: Derived from the greek λόφος (pronounced lófos): crest, ridge.

Diagnosis. Facial carinae arched, fusiform and forming broad scutellum; antennae flattened but not foliaceous, laterally expanding from the base to the apex having a incrassate shape (Fig. 1), with 11 segments (with is a distinguishable acute apical segment), the latter segment is pale; pronotum not towards the front of the head, median carina compresso-cristated or leaf-like crest (Figs. 2A, 3A, 4A, 5A, 6), in some species translucent, punctate when held against the light; first hind tarsi and third equal in length.

Composition. The subfamily has only one genus with five species: *Lophotettix alticristatus* Hancock, 1909; *L. brevicristatus* Hancock, 1909; *L. hancocki* (Bruner, 1910); *L. unicristatus* Hancock, 1909 and *L. zumbadoi* Barranco, 2010.

Lophotettix alticristatus Hancock, 1909

Figures 2 and 7A

Lophotettix alticristatus Hancock, 1909; pg. 389 [general description], female holotype (OUM); type-locality: "Brazil, South America". Günther, 1938 [crest morphology comparison]. Barranco, 2010: 23, Fig. 4 [type image].

Diagnosis: Frontal costa inconspicuous, only the bifurcation and facial carina visible (Fig. 2C); pronotum subquadrate, with denticles throughout the median carina of pronotum (Fig. 2A); anterior margin of median carina truncated, with perpendicular projection over the head, provided with three protuberances (Fig. 2A) and wavy (two conspicuous curves) (Fig. 2B, dorsal view); wings slightly longer than pronotum.

Redescription (Female holotype, Fig. 2): Body surface rugose. **Head**. Lateral view (Fig. 2A): head and compound eyes inserted below median carina crest; protuberant and globose eyes with straight base; vertex and fastigium not visible between eyes; antennal groove situated below margin of compound eyes; facial carinae arched. Frontal view (Fig. 2C): fastigium of vertex straight; front hirsute; eyes laterally arranged on the head but not pedunculated; frontal costa inconspicuous, only the bifurcation and facial carina visible; two superior ocelli between facial carina; medial ocellus involved by facial carinae; antennal grooves placed beside facial carinae; antennae shaped as compressed segments laterally expanding from the base to the apex; left antennae missing; apex of each antennal segments with a lighter color than the remaining antenna; scapus and pedicel with small tubercles; maxillary palpi having the two last articles flattened and hirsutes. Dorsal view (Fig. 2B): vertex between eyes wider than eyes in horizontal and vertical diameter; supraocular lobe conspicuous; rectangularly shaped head. **Pronotum**. Macropronotal, rugose, subquadrate, erose, having irregular teeth and emarginations, with denticles throughout the median carina of pronotum. Lateral view (Fig. 2A): anterior margin of median carina truncated, with perpendicular projection over the head, provided with three protuberances; median carina crest begins to decline after surpassing the apex of tegmina and then becomes thinner; prozonal carina and extralateral carina inconspicuous; ventral sinus and tegminal sinus present; lateral lobe almost truncated and slightly laterally directed; infrascapular area narrow, thin and shorter than fore tibiae; wings slightly longer than pronotum. Frontal view (Fig. 2C): lateral lobes of pronotum slightly projected and directed sidewards. Dorsal view (Fig. 2B): median carina continuous and strongly elevated, with crested wavy (two conspicuous curves) (Fig. 7A), lateral lobe almost truncated. **Sternomentum**. Inconspicuous. **Wings**. (Fig. 2A): tegmina and wings visible; wing longer than pronotum; tegmina ovoid and elongated with rounded apex; tegmina with slightly marked venation . **Legs.** Hirsute. Fore legs (Fig. 2A,B): dorsal and ventral margins of femur with undulated carinae; tibias with two crests on dorsal margin. Middle legs (Fig. 2A,B): left leg missing; dorsal and ventral margins of femur with undulated carina, with a dorso-apical blunt spine; tibiae with two crests on the dorsal margin. Hind legs: both hind legs missing in the type. **Abdomen.** (Fig. 2A): eight sternites visible, ovipositor valves short, superior margin of dorsal and ventral valve with small teeth.

Sampling data (Hancock, 1909): "One specimen from Brazil, South America, collected by Bates; W.W. Saunders' collection, presented by Mrs. F.W. Hope to the University Museum, Oxford."

Original coloration description: "Darker almost black body, (…) antennae black and pale annulate at the joints, (…) the middle tibiae pale annulate at the middle and margins little compresso-tuberculate; apical half of tarsi black."

Current coloration: Similar to the original description but with fore and middle tibiae and second tarsus with brown markings.

Comments: This species is based on a single female specimen and the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotype.

***Lophotettix brevicristatus* Hancock, 1909**

Figures 3 and 7B

Lophotettix brevicristatus Hancock, 1909; pg. 388 [general description], female holotype (OUM); type-locality: "Brazil, South America". Günther, 1938 [crest morphology comparison]. Steinmann, 1969 [list of species]. Barranco, 2010, Fig.2 [holotype image].

Diagnosis: Frontal costa conspicuous with bifurcation and facial carina visible (Fig. 3C); pronotum rounded, directed forwards, anterior margin of median carina concave before the crest, few small denticles throughout the median carina of pronotum (Fig. 3A) (less than in *L. alticristatus*); median carina almost straight and with two small ripples (Fig. 3B, dorsal view); femur robust and with lappets throughout on dorsal, ventral and external margins (Fig. 3A,B).

Redescription (Female holotype, Fig. 3): Body surface rugose. **Head**. Lateral view (Fig. 3A): head and compound eyes inserted below median carina crest; protuberant and globose eyes with straight base; vertex and fastigium not visible between eyes; antennal groove situated below margin of compound eyes; facial carinae arched. Frontal view (Fig. 3C): fastigium of vertex straight; eyes laterally arranged on the head, but not pedunculated; costa frontal conspicuous, the bifurcation and facial carina visible; both superior ocelli between facial carinae; antennal grooves placed beside facial carinae; antennae shaped as compressed segments, laterally expanding from the base to the apex; right antennae missing. Dorsal view (Fig. 3B): vertex between eyes wider than eyes in horizontal and vertical diameter; supraocular lobe conspicuous; rectangularly shaped head. **Pronotum**. Macropronotal, rugose, rounded and projected forwards with few small denticles throughout the median carina. Lateral view (Fig. 3A): anterior margin of median carina, rounded, concave before the crest with few small denticles throughout the median carina of pronotum; median carina crest projection begins to decline after surpassing apex of tegmina and then becomes thinner; prozonal carina and extralateral carina inconspicuous; ventral sinus and tegminal sinus present; lateral lobe triangular, with rounded apex directed laterally; infrascapular area narrow, thin and shorter than fore tibiae; wings shorter than pronotum. Frontal view (Fig. 3C): lateral lobes of pronotum projected and directed sidewards. Dorsal view (Fig. 3B): median carina continuous and elevated, with crest almost straight and with two small ripples (Fig. 7B), lateral lobes with pointed and rounded expansion. **Sternomentum**. Inconspicuous. **Wings**. (Fig. 3A): tegmina and wings visible; wing shorter than pronotum; tegmina ovoid and elongated, slightly thinner than *L. alticristatus* and with rounded apex; tegmina with slightly marked venation and punctated. **Legs.** Fore legs (Fig. 3A,B): dorsal and ventral margin of femur with undulated carinae, tarsi missing. Middle legs (Fig. 3A,B): dorsal and ventral margins of femur with undulated carinae with a dorso-apical blunt spine; right tarsus missing. Hind legs (Figs. 3A-B): femur robust and with lappets throughout, on dorsal, ventral and external margins; antegenicular tooth robust. **Abdomen.** Not visible on the type, completely covered by the pronotum (dorsal view) and hind femur (lateral view).

Sampling data (Hancock, 1909): "One example from Brazil, South America, in the University Museum, Oxford."

Original coloration description: "(…) the body strongly rugose, ferruginous; antennae (…) the last articles pale yellow".

Current coloration: Similar to the original description but body darker.

Comments: This species is based on a single female specimen and the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotypy.

***Lophotettix hancocki* (Bruner, 1910)**

Figures 4 and 7C

Lophotettix hancocki (Bruner, 1910); pg. 102 [general description of *Gladiotettix hancocki*], male holotype (ANSP); type-locality: “Brazil, Pará”. Hancock, 1914 [*Gladiotettix hancocki* is synonymous to *Lophotettix unicristatus*]. Günther, 1938 [*Lophotettix hancocki* potential synonym of *L. unicristatus*]. Liebermann, 1955 [first list of grasshopper species of Brazil]. Grant, 1957 [Lecotype designation]. Steinmann, 1969 [list of species]. Barranco, 2010 [taxonomic comments].

Diagnosis: Facial carina and conspicuous frontal costa bifurcation visible (Fig. 4C); pronotum subquadrate, many small denticles throughout the median carina of pronotum (Fig. 4A); anterior margin of median carina truncated and crest slightly arched, provide with two protuberances (Fig. 4A); crest almost straight, with only one curve (Fig. 4B, dorsal view); femur robust and with small lappets throughout on its dorsal margin (Fig. 4A).

Redescription (Male holotype, Fig. 4): Body surface rugose and crest punctuated. **Head**. Lateral view (Fig. 4A): head and compound eyes inserted below median carina crest; protuberant and globose eyes with straight base; vertex and fastigium not visible between eyes; antennal groove situated below margin of compound eyes; facial carinae arched. Frontal view (Fig. 4C): fastigium of vertex straight; eyes laterally arranged on the head but not pedunculated; frontal costa conspicuous, the bifurcation and facial carina visible; both superior ocelli between facial carinae; antennal grooves placed beside facial carinae; both antennae missing. Dorsal view (Fig. 4B): vertex between eyes wider than eyes in horizontal and vertical diameter; supraocular lobe conspicuous; rectangularly shaped head. **Pronotum**. Macropronotal, rugose, subquadrate, erose, having irregular teeth and emarginations, many small denticles throughout the median carina of pronotum. Lateral view (Fig. 4A): anterior margin of pronotum truncated and crest slightly arched, provided with two tubercle protuberances; median carina crest projection begins to decline after surpassing apex of tegmina and then becomes thinner; prozonal carina and extralateral carina inconspicuous; ventral sinus and tegminal sinus present; lateral lobe rounded and slightly directed laterally; infrascapular area narrow, thin and shorter than fore tibiae;

wings slightly longer than pronotum. Frontal view (Fig. 4C): lateral lobes of pronotum slightly projected and directed sidewards. Dorsal view (Fig. 4B): median carina continuous and strongly elevated, straight, with only one curve (Fig. 7C), lateral lobes with rounded tip and small expansion. **Sternomentum**. Inconspicuous. **Wings**. (Fig. 4A): tegmina and wings visible; wing longer than pronotum; tegmina ovoid and elongated, slightly thinner than *L. alticristatus* and *L. unicristatus*, with rounded apex; tegmina without venation, but with small punctuations. **Legs.** Fore legs (Fig. 4A, B): dorsal and ventral margins of femur with undulated carinae, right leg missing. Middle legs (Figs. 4A-B): dorsal and ventral margins of femur with undulated carinae with a dorso-apical blunt spine. Hind legs (Fig. 4A, B): femur robust and with small lappets throughout, on its dorsal margin. **Abdomen.** Not visible on the type, completely covered by the pronotum (dorsal view) and hind femur (lateral view).

Sampling data (Bruner (1910)): “The type and only specimen of the present species comes from Pará, Brazil, where it was taken during the month of July by H.H Smith”.

Original coloration description: “General color dark fuscous, with the apical half of the pronotum and hind femora tinged ferruginous”.

Current coloration: The same of original description.

Comments: Although Grant (1957) has designated a lectotype for *L. hancocki*, the specimen deposited in the ANSP should be considered a holotype, since Bruner (1910) refers to the specimen as "type" in the original publication (see article 73.1.1 of the ICZN).

Lophotettix unicristatus Hancock, 1909

Figures 5 and 7D

Lophotettix unicristatus Hancock, 1909; pg. 390 [general note about the specimen sampled in Colombia], female holotype (OUM). Bruner, 1910 [annexed description of male from Guiana written by Hancock]. Hancock, 1914 [*Gladiotettix unicristatus* is synonymous to *Lophotettix unicristatus*]. Hebard, 1923 [recorded specimen]. Günther, 1938 [potential synonym of *L. hancocki*]. Barranco, 2010, Fig. 3 [holotype image]. Cuespán, Westerduijn

& Cadena-Castañeda, 2014 [recorded specimen]. Cadena-Castañeda & Cardona-Granda, 2015 [recorded specimen].

Diagnosis: Facial carina and conspicuous frontal costa bifurcation visible (Fig. 5C); pronotum slightly subquadrate (Fig. 5A); anterior margin of median carina concave, provide with one protuberance, slightly hook-like over the head (Fig. 5A); median carina continuous, with three curves (Fig. 5B, dorsal view); infrascapular area broader than *L. hancocki*; femur robust and with small lappets throughout on dorsal and external margins.

Redescription (Female holotype, Fig. 5): Body surface rugose. **Head**. Lateral view (Fig. 5A): head and compound eyes inserted below the median carina crest; protuberant and globose eyes with straight base; vertex and fastigium not visible between eyes; antennal groove situated below the margin of compound eyes; facial carinae arched. Frontal view (Fig. 5C): fastigium of vertex straight; eyes laterally arranged on the head but not pedunculated; frontal costa conspicuous, the bifurcation and facial carina visible; both superior ocelli between facial carinae; antennal grooves placed beside the facial carinae; both antennae missing. Dorsal view (Fig. 5B): vertex between eyes wider than eyes in horizontal and vertical diameter; supraocular lobe inconspicuous; rectangularly shaped head. **Pronotum**. Macropronotal, rugose, pronotum slightly subquadrate. Lateral view (Fig. 5A): anterior margin of median carina concave, provide with one protuberance, slightly hook-like over the head; median carina crest projection begins to decline after surpassing apex of tegmina and then becomes thinner; prozonal carina and extralateral carina inconspicuous; ventral sinus and tegminal sinus present; lateral lobe almost truncated with a pointed protuberance and slightly directed laterally; infrascapular area broader than *L. hancocki* and shorter than fore tibiae; wings slightly shorter than pronotum. Frontal view (Fig. 5C): lateral lobes of pronotum slightly projected and directed sidewards. Dorsal view (Fig. 5B): median carina continuous and strongly elevated, with three curves (Fig. 7D); lateral lobes with pointed protuberance. **Sternomentum**. Inconspicuous. **Wings**. (Fig. 5A): tegmina and wings visible; wing shorter than pronotum; tegmina ovoid and elongated, with rounded apex; tegmina without venation but with small punctuations. **Legs.** Fore legs (Fig. 5A, B): dorsal margin and ventral margin of femur with undulated carinae. Middle legs (Fig. 5A, B): dorsal margin and ventral margin of femur with undulated carinae and without dorso-apical blunt spine. Hind legs (Fig. 5A, B): femur robust and with small lappets throughout, on its dorsal margin and external pagina of femur, right tarsi missing; antegenicular tooth robust. **Abdomen.** Not visible on the type, completely covered by the pronotum.

Sampling data (on Hancock (1909)): "One specimen collected by Bates in Colombia, South America; from the W.W. Saunders's collection, presented by Mrs. F.W. Hope to the University Museum, Oxford."

Original coloration description: "(…) color fusco-ferruginous, legs somewhat interspersed with lighter ferruginous, apical half of the tarsal articles fuscous."

Current coloration: Similar to the original description but body darker.

Comments: This species is based on a single female specimen and the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotypy.

Lophotettix zumbadoi Barranco, 2010

Figures 6 and 7E

Lophotettix zumbadoi Barranco, 2010 (22) (Museo de Insectos de la Universidad Central de Costa Rica) [general description], holotype female; type-locality: "Central America, Costa Rica, Reserva Biológica Alberto Manuel Brenes, San Ramón, Alajuela".

Additional information in description (Female Holotype, Fig. 6): Facial carina and conspicuous frontal costa bifurcation visible; infrascapular area narrow, femurs robust and with small lappets throughout dorsal and external margins; median carina (dorsal view) continuous and strongly elevated, with one curve and a pointed protuberance (Fig. 7E).

Comparative notes. The most recently described species *L. zumbadoi* shares with *L. brevicristatus* the rounded shape of pronotum and can be easily distinguished by the direction of pronotum which in *L. zumbadoi* has the median carina crest directed backwards and *L. brevicristatus* has the median carina crest directed forwards (Fig. 8). *L. alticristatus*, *L. hancocki* and *L. unicristatus* have a crest directed forwards and can also be distinguished from *L. zumbadoi* and *L. brevicristatus* by the almost subquadrate shape of the pronotum crest (Fig. 8). All these species also have different shapes of pronotum median carina in dorsal view (Fig. 7).

Discussion

Taxonomic considerations on Lophotettiginae

Hancock (1909) described this subfamily as a taxon similar to Tripetalocerinae and probably the most important character used to hypothesize this relation, was the similarity in the shape of the antennal segments. Günther (1938) questioned the establishment of the section Lophotettiginae based on the shape of antennae, since there are other taxa which also have a very similar form of antennae, as *Ophiotettix* Walker, 1871 and *Andriana* Rehn, 1929.

Ophiotettix recently was placed in Metrodorinae, but with more refined studies, this genus can be a different group outside Metrodorinae, because this taxon is not related to the *Metrodora*-genera group in South America (Tumbrinck & Skejo 2017). This particular case is complex, since Metrodorinae is difficult to distinguish from other subfamilies, because there is a set of diagnostic morphological characters and none of them are exclusive to the Metrodorinae. Thus, it is considered that the characters used to diagnose Metrodorinae are homoplastic (Pavón-Gozalo *et al.* 2012).

Examples of homoplasy are common in tetrigids (*e.g.* horn-like protuberance in some tetrigids, see Rehn (1938) and Silva *et al.* 2017) and although a robust cladistic analysis is not yet available, Lophotettiginae species share many characters that support this group. The combination of antennae with 11 segments (distinguishing them from Metrodorinae, Tripetalocerinae, *Ophiotettix* and *Andriana* (see Rehn 1929)), flattened, but not foliaceous antennal segments (also distinguishing them from Tripetalocerinae), laterally expanding from the base to the apex (incrassate shape) and pronotum median carina elevated over the head, but not surpassing the front of the head (distinguishing them from leaf-like Neotropical cladonotines) make this group unique and robust, until cladistic or morphological analyses confirm or question it.

Taxonomic considerations on *Lophotettix* species

Basically everything that is known about this genus comes from the data about species types that do not have a designated type series. Therefore, establishing and describing intraspecific morphological variations is not possible. Because of these restrictions, it was necessary to conduct this study with only type species, which also led to limitations due to the state of preservation of the specimens (some characters were not available or visible) leading to a limitation in the handling to guarantee the integrity of the material.

These restrictions may cause serious troubles in some taxonomic groups, but in *Lophotettix*, the available data revealed that the species within the group appear homogeneous as well as easily distinguishable. The mainly character that distinguishes the species from each other is the shape of the pronotum in lateral view, revealing two pronotum shapes used as first step in the pictorial key: species with almost square shape (*L. alticristatus*, *L. hancocki* and *L. unicristatus*) and those with rounded shape (*L. brevicristatus* and *L. zumbadoi*) (Fig. 8). There are also differences between each species in the shape of median carina of pronotum in dorsal view (Fig. 7).

Despite the species of *Lophotettix* being easily distinguished, Günther (1938) suggested the possible synonymy between *L. hancocki* and *L. unicristatus.* About these two type species, a male and a female respectively, there are no data on the exact location where they were sampled, only the countries and the state (Brazil, Pará from *L. hancocki* and Guyana, Demerara region from *L. unicristatus*). We were able to observe the following morphological differences between these species: in *L. hancocki* the pronotum has many small denticles throughout the median carina; anterior margin of median carina truncated and crest slightly arched, provide with two protuberances, projection over the head while in *L. unicristatus* the anterior margin of median carina is concave, provide with one protuberance, slightly hook-like over the head.

We conclude that: (i) *L. hancocki* and *L. unicristatus* cannot be considered synonymous. This conclusion is based in the available data, since there are morphological differences between them that we could not considered as intraspecific variation (the type species are not of the same sex and, it is not possible to define if these differences are dimorphism); and (ii) there are morphological characters that support Lophotettiginae as a distinct taxon from Metrodorinae or other Neotropical tetrigid subfamilies. Additional specimens would aid enormously to the knowledge of this group, allowing the identification of more variation among Lophotettiginae species.

Acknowledgements

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Weintraub and Daniel Otte for allowing access to type material of Orthoptera deposited at the Academy of Natural Sciences of Drexel University (ANSP). The photographs of *L. hancocki* holotype was taken during the execution of the project: "*The Neotropical Tetrigidae (Caelifera: Tetrigoidea) deposited in the Academy of Natural Sciences of Drexel University, Philadelphia, USA*" financed by The Orthopterists' Society. We would like to thank Pablo Barranco for provide essential data for this manuscript.

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Table 1. Data for all records ever made for the genus *Lophotettix* Hancock, 1909.

Species	**Sex**	**Type depository**	**Type Locality**	**Other localities**	**References**
Lophotettix alticristatus Hancock, 1909	F	OUM	Brazil	-	Hancock (1909)
Lophotettix brevicristatus Hancock, 1909	F	OUM	Brazil	-	Hancock (1909)
Lophotettix hancocki (Bruner, 1910)	M	ANSP	Brazil, Pará	-	Bruner (1910)
Lophotettix unicristatus Hancock, 1909	F	OUM	Guyana	Colombia, Peru	Hancock (1909), Bruner (1910), Hebard, (1923), Huamán Cuespán et al. (2014) and Cadena-Castañeda & Cardona-Granda (2015)
Lophotettix zumbadoi Barranco, 2010	F	Museo de Insectos de la Universidad Central de Costa Rica	Costa Rica	-	Barranco (2010)

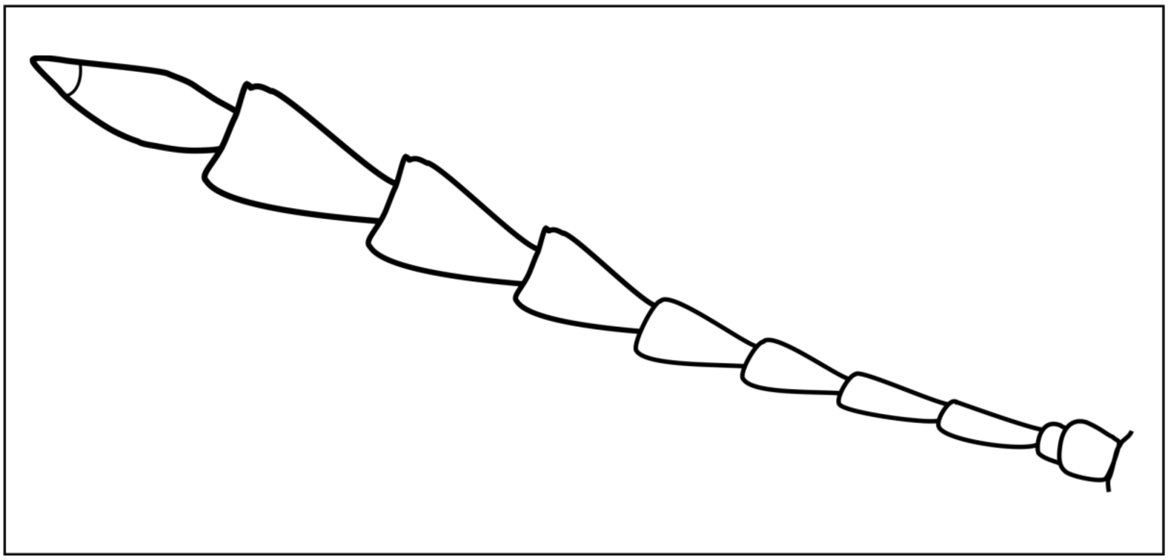


Figure 1. General scheme of antennal segment morphology present in *Lophotettix* species, highlighting the incrassate shape and the apical last segment.

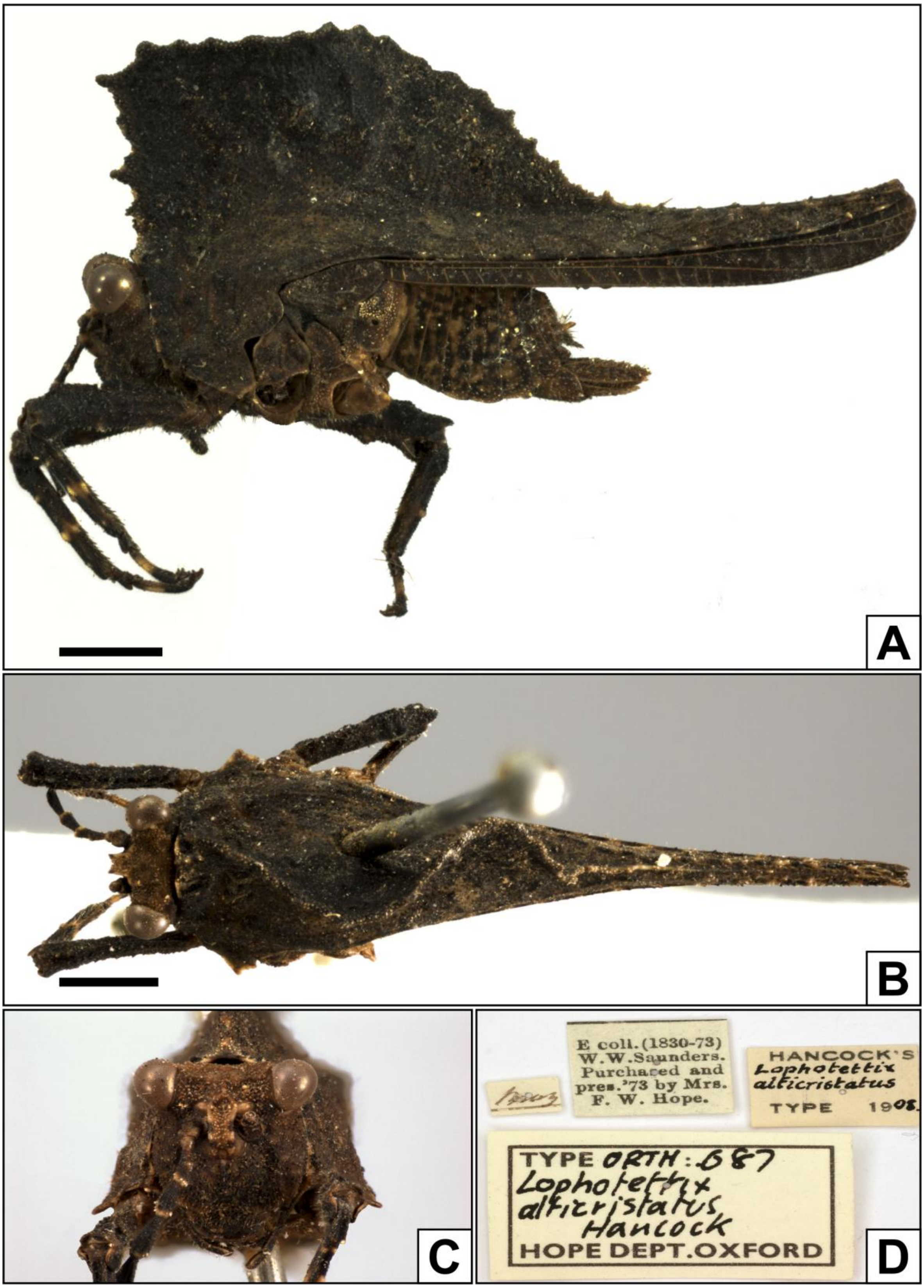


Figure 2. *Lophotettix alticristatus* Hancock, 1909 female holotype (A) *habitus* in left lateral view, (B) *habitus* in dorsal view, (C) frontal view and (D) labels. Scale bar = 2 mm. Photo of type: Museum of Oxford University/James Hogan, photo of label: Josef Tumbrinck.

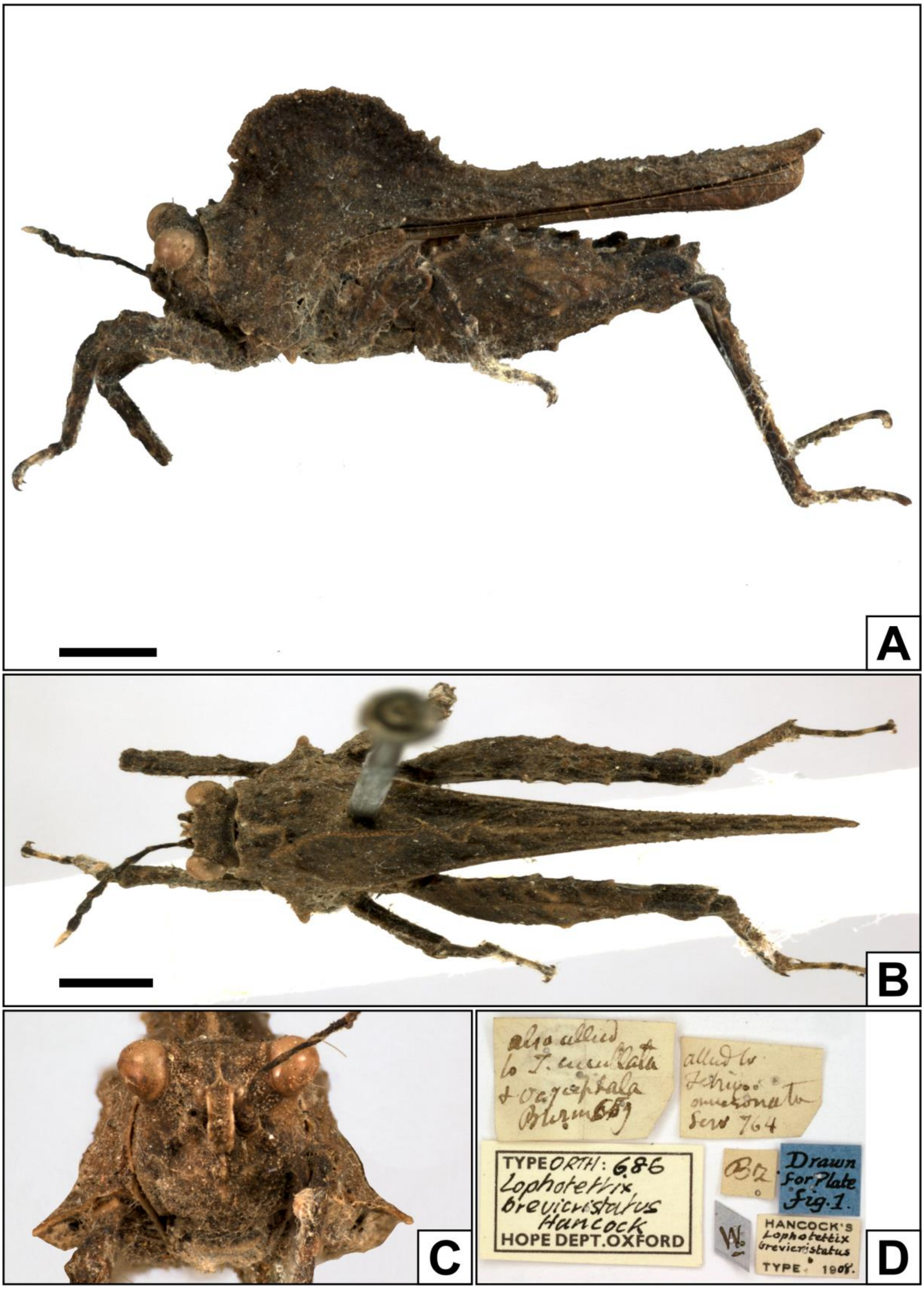


Figure 3. *Lophotettix brevicristatus* Hancock, 1909 Hancock, 1909 female holotype (A) *habitus* in left lateral view, (B) *habitus* in dorsal view, (C) frontal view and (D) labels. Scale bar = 2 mm. Photo of type: Museum of Oxford University/James Hogan, photo of label: Josef Tumbrinck.

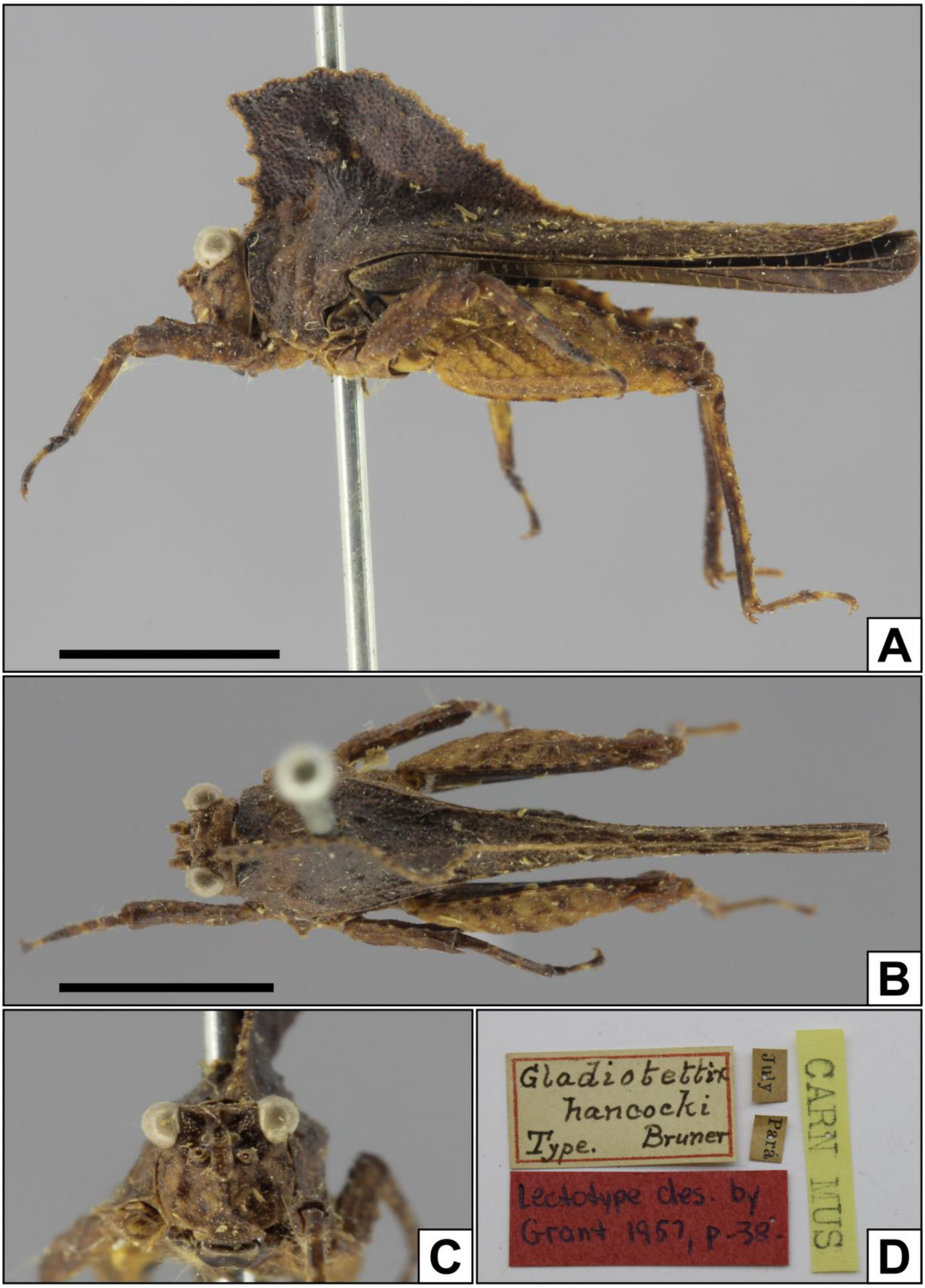


Figure 4. *Lophotettix hancocki* (Bruner, 1910) male holotype. (A) *habitus* in left lateral view, (B) *habitus* in dorsal view, (C) frontal view and (D) labels. Scale bar = 5 mm.

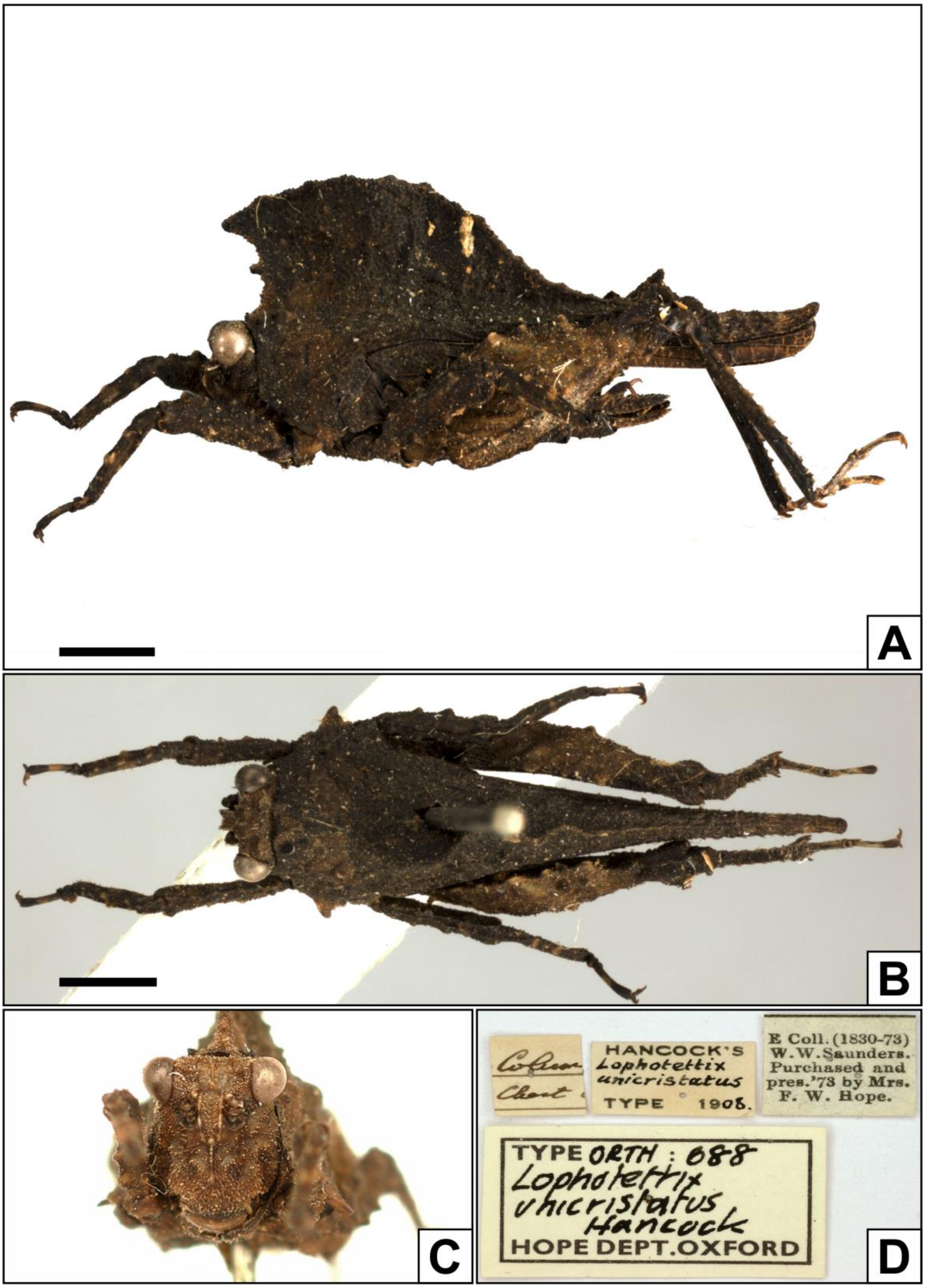


Figure 5. *Lophotettix unicristatus* Hancock, 1909 female holotype. (A) *habitus* in left lateral view, (B) *habitus* in dorsal view, (C) frontal view and (D) labels. Scale bar = 1 mm. Photo of type: Museum of Oxford University/James Hogan, photo of label and dorsal view: Josef Tumbrinck.

Figure 6. *Lophotettix zumbadoi* Barranco, 2010 right lateral view of holotype. Photo of type: Pablo Barranco.

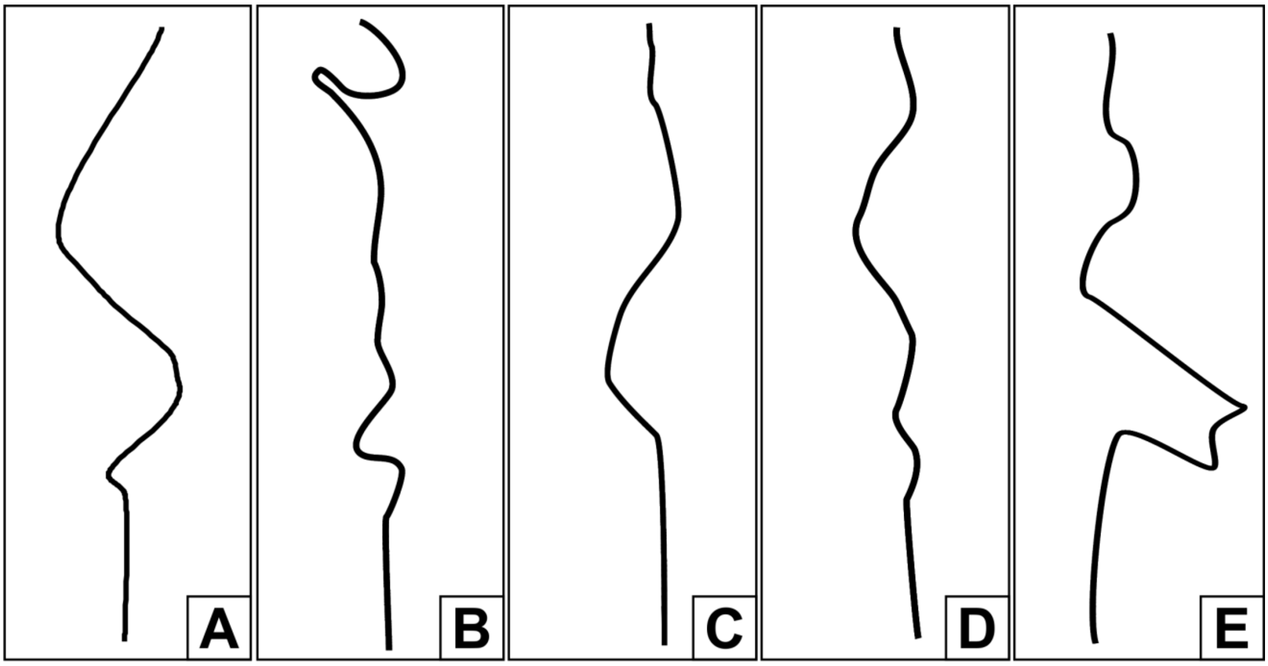


Figure 7. General scheme of median carina of pronotum crest in dorsal view. (A) *L. alticristatus*, (B) *L. brevicristatus*, (C) *L. hancocki*, (D) *L. unicristatus* and (E) *L. zumbadoi*.

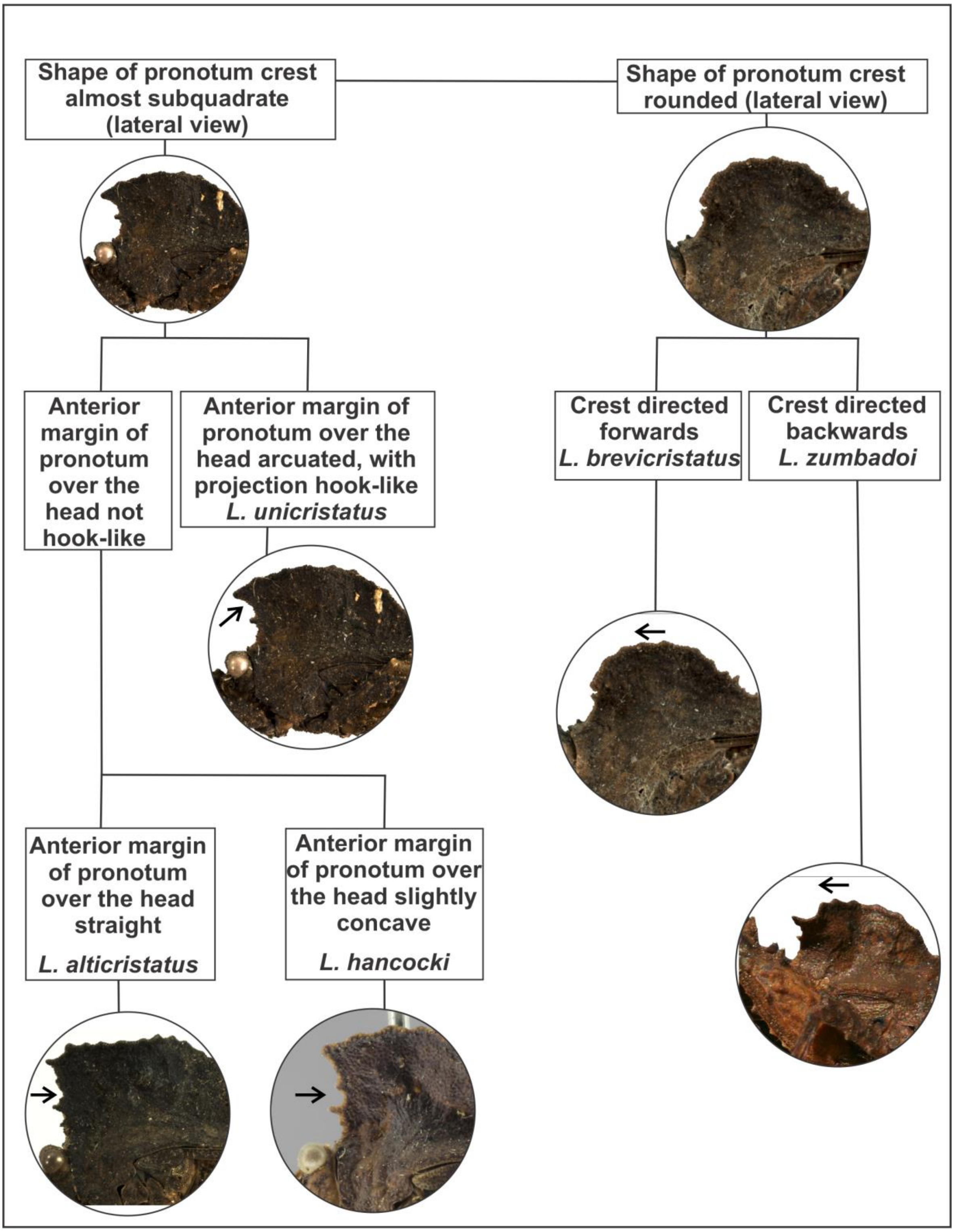
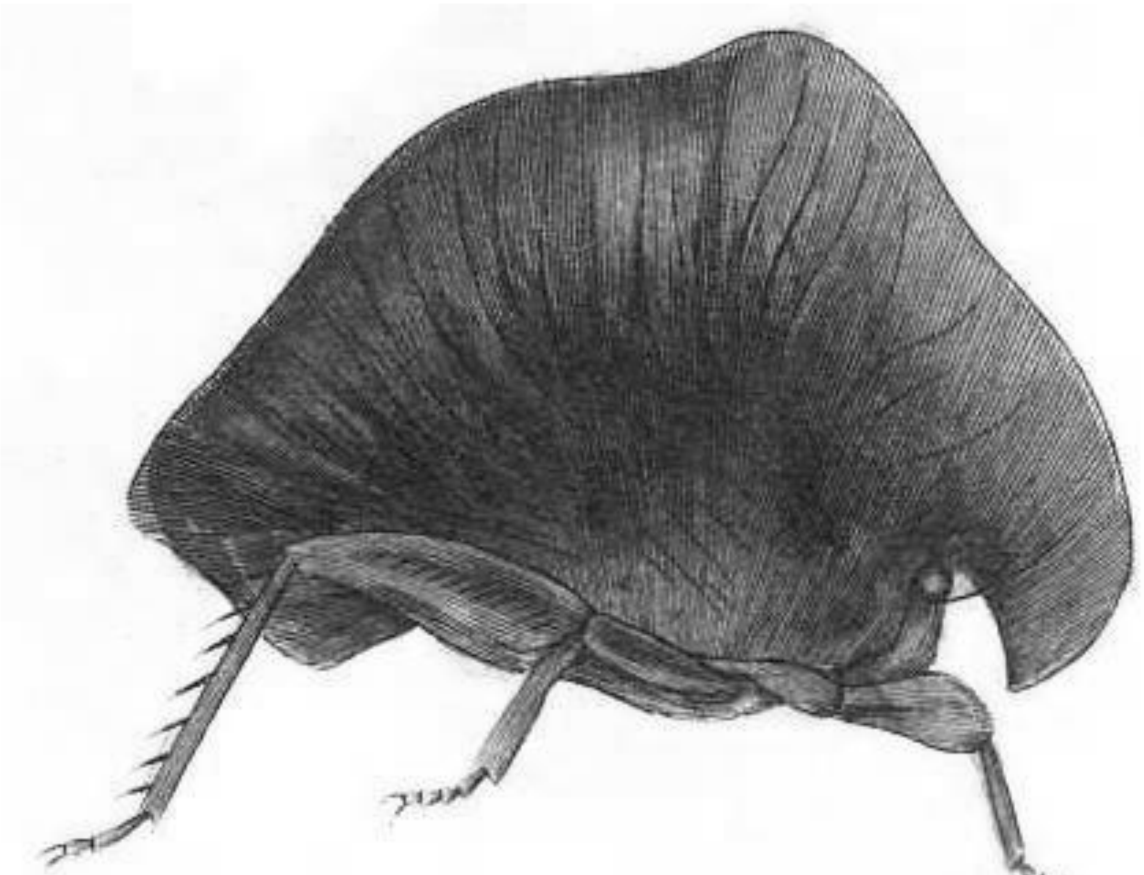


Figure 8. Pictorial key to species of *Lophotettix*. Arrows in *L. brevicristatus* and *L. zumbadoi* indicate pronotum direction; in *L. unicristatus* the arrow points to the hook-like shape of the pronotum and in *L. alticristatus* and *L. hancocki* the arrow points to the shape of the anterior margin of the pronotum over the head.

Artigo 3

New tribes, overview and check list of Neotropical Cladonotinae (Insecta: Orthoptera: Caelifera: Tetrigidae)



Choriphyllum sagrai Serville, 1838

New tribes, overview and check list of Neotropical Cladonotinae (Insecta: Orthoptera: Caelifera: Tetrigidae)

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Abstract

Cladonotinae is a peculiar tetrigid taxon characterized by significantly widened fascial carina on their frontal costa. This group has currently a doubtful taxonomic status, since there is only this characteristic shared by its members. Here we showed that Neotropical Cladonotinae share more characteristics, which strengthen its taxonomical status. We revised the species reported to the Neotropical region, highlighting the morphology of the species housed at several museums. From these observations, we found twenty-eight species, being three fossil in ambar resin from Miocene and twenty-six live species. Thus, we have done the following taxonomic proposals: *Dasyleurotettix* Rehn, 1904 was allocated to Tetriginae; one new combination was proposed from *Metrodora undulata* Cadena-Castañeda & Cardona, 2015 to *Cota undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.** and the two new tribes were proposed: Chorophyllini **n. trib.** and Mucrotettigini **n. trib.** Additionally, we provided keys of genus and species. All taxonomic modifications aimed to ameliorate the taxonomy of the group, so as to serve as a basis for future cladistics analyses.

Key words: Classification, Greater Antillean sub-region, Neotropical region, tetrigids.

Resumo

Cladonotinae é um peculiar táxon de tetrigídeos caracterizados pelo alargamento significativo da carena fascial da costa frontal. Este grupo atualmente apresenta posição taxonômica duvidosa, pois há apenas essa característica compartilhada por seus membros. Aqui mostramos que os Cladonotinae neotropicais compartilham mais características, o que reforça seu status taxonômico. Revisamos a situação das espécies registradas para a região Neotropical, destacando a morfologia das espécies depositadas em vários museus. A partir dessas observações encontramos vinte e oito espécies, sendo três fosseis em âmbar do Mioceno e vinte e seis espécies viventes. Assim, fizemos as seguintes propostas taxonômicas: *Dasyleurotettix* Rehn, 1904 foi transferido para Tetriginae; uma nova combinação foi proposta na qual *Metrodora undulata* Cadena-Castañeda & Cardona, 2015 passa a ser denominada *Cota undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.** e duas novas tribos foram propostas: Chorophyllini **n. trib**. e Mucrotettigini **n. trib**. Adicionalmente, nós apresentamos chaves taxonômicas para gêneros e espécies. Todas as modificações taxonômicas visaram aprimorar a taxonomia do grupo, de forma a servir de base para futuras análises cladísticas.

Palavras-chaves: Classificação, Subregião das Grandes Antilhas, região Neotropical, tetrigídeos.

Resumen

Cladonotinae es un grupo peculiar de tetrígidos, que se caracteriza por presentar una carina significativamente ensanchada en la costa frontal. Actualmente, este grupo tiene un estatus taxonómico dudoso, ya que solo hay una característica que los une. Sin embargo, los Cladonotinae neotropicales comparten más características, lo que fortalece su estatus taxonómico. Revisamos las especies reportadas para la región Neotropical, destacando la morfología de las especies depositadas en varios museos. A partir distas observaciones encontramos veintiocho especies, tres fósiles en ambar del Mioceno y veintiséis especies vivas. Así, hicimos las siguientes propuestas taxonómicas: *Dasyleurotettix* Rehn, 1904 se transfirió a Tetriginae; se propone una nueva combinación de *Metrodora undulata* Cadena-Castañeda & Cardona, 2015 a *Cota undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.**, y se proponen dos nuevas tribus: Chrophyllini **n. trib.** y Mucrotettigini **n. trib.** Además, presentamos claves de género y especie. Todas las modificaciones taxonómicas aquí realizadas tienen como objetivo, un mejor entendimiento de la taxonomía, morfología y nomenclatura, además de ser un aporte preliminar para futuros análisis cladísticos.

Palabras clave: Clasificación, Antillas Mayores, región Neotropical, tetrígidos.

Introduction

Cladonotinae Bolívar, 1887 is formed by one unique tribe, Xerophyllini Günther, 1979 and other 61 genera without placement. The type genus is *Cladonotus* Saussure, 1862 and the type species is *C. humbertianus* Saussure, 1862 from Sri Lanka (Cigliano *et al*. 2018). This subfamily was defined for the first time by Bolívar (1887) as a section named *Cladonotae* encompassing all species characterized uniquely by significantly widened fascial carina of the frontal costa and the consequently broadened scutellum (broader than the scapus) (see Tumbrinck 2014). However, the term *Cladonotinae* was used for the first time by Hancock (1902).

As in most taxa of Tetrigidae, with few exceptions, the relationship between the species of Cladonotinae remain unknown (see Devriese 1999 and Tumbrinck 2014), and for the most part of this subfamily, there is no deeper morphological analysis or revision. This subfamily has a doubtful taxonomic status, as far as it was suggested to be polyphyletic (Skejo & Bertner 2017).

The cladonotine's species are distributed on Australian, Ethiopian, Oriental and Neotropical regions (Cigliano *et al*. 2018) and for the latter region, there are several cladonotines that are still poorly known, with many species recorded to one or few localities. On this region, with the exception of leaf-mimic species, there are a lot of taxa found in some localities of the Greater Antillean sub-region (Cuba, Jamaica and Hispaniola – formed by Haiti, Dominican Republic and Puerto Rico (see bioregions of Morrone 2014) characterized by coarsely granulose integument, presence of fastigial horns or tubercles (also named carinula transversal of vertex) and no foliaceous pronotal crests of median carina (see Heads *et al*. 2014). The South America taxa have a lower diversity of cladonotines represented so far by only two genera (*Cota* Bolívar, 1887and *Eleleus* Bolívar, 1887).

In the present study, we overview the Neotropical species of Cladonotinae deposited at several museums, discussing morphological aspects and the current classification of this group. As a result, we present two new tribes, keys of genus and species and a proposal of taxonomic alterations and comments. Additionally, we provide a check list of species and photos highlighting the most important morphological characters.

Material and Methods

Overview of the groups present in the Neotropical region and their depository

The type species of The Academy of Natural Sciences of Drexel University (ANSP) were analyzed. Additionally, we also used literature and image data provide for curator from specimens housed in the following museums or collections (acronyms used in the text); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); Colección de Artrópodos y otros Invertebrados, Universidad Distrital Francisco José de Caldas, Bogotá, Colombia (CAUD); Florida State Collection of Arthropods, Gainesville, USA (FSCA); Illinois Natural History Survey, Champaign, USA (INHS); Naturhistorisches Museum Wien, Vienna, Austria (NMW); Muséum d'histoire naturelle de la Ville de Genève, Genève, Switzerland (MHNG); Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN); Museum of Evolution Uppsala University, Uppsala, Sweden (UZIU) and The Natural History Museum, London, UK (BMNH). The type, locality and held data are summarized in the Table 1. After the data analysis, when necessary, new information has been added or highlighted.

Key of Neotropical Cladonotinae

Based on morphologic and literature data, we provide an identification key for species and for all Neotropical genera. For biogeographical regionalization we followed Morrone's classification (2014 and 2015).

Results

Twenty-nine taxa were recorded for the Neotropical region, with three fossils found in amber resin from Early Miocene period and twenty-six live species. The Neotropical cladonotine's were reported to Brazil, Cuba, Dominican Republic, Jamaica, Haiti and Peru (Cigliano *et al.* 2018) (Tab. 1), added to an unidentified Cladonotinae juvenile specimen for Puerto Rico (not included in Table 1, see Perez-Gelabert & Yong 2014). Here, we proposed two new tribes to include the Neotropical genera.

Chorophyllini Cadena-Castañeda & Silva n. trib.

Diagnosis: Body flattened laterally, fascial carinae almost straight or arcuated (lateral view); antennal groove situated below lower margin of compound eyes; pronotum crest high, leaf-like, with variable shape of edge; marked by leaf-like veins and granulose; anterior margin of the pronotum extending over the head with rounded or almost truncated shape; posterior margin of pronotum rounded, with truncated or bifid shape, covering the apex of the abdomen; lateral lobes directed downwards, close to the body; broad infrascapular area; tegmina and wing absent; fore and middle femur undulated, hind femur robust, flattened laterally or with dorsal margin excavated on distal portion.

Included genera: *Choriphyllum* Serville, 1838 and *Phyllotettix* Hancock, 1902.

Distribution: Cuba, Jamaica and Bahamas.

Remarks: Chorophyllini **n. trib.** is distinguished from Xerophyllini Günther, 1979 (the unique tribe established for Cladonotinae until this moment) by the absence of spiny protuberances in the face and/or body; middle femur not flattened or foliaceous, without lappets and with tegmina and wings absent.

Choriphyllum Serville, 1838

Type species: *Choriphyllum sagrai* Serville, 1938

Emended Diagnosis. Head and compound eyes inserted below the pronotum disc; pronotum largely compressed; crest highly elevated, foliaceous, rounded-angulate or with general shape variable; anterior margin of pronotum over the head anteriorly rounded and posteriorly truncate or slightly concave (*C. plagiatum*) (Fig.1), covering the abdomen; infrascapular area visible and broad; tegmina and wings absent; fore and middle legs margin undulated; hind femur flattened laterally (*C. plagiatum* and *C. saussurei*) (Fig.2-5) or robust; hind femur compressed and first article of hind tarsi longer than third.

Comments: Serville (1938), in the original description of *Choriphyllum,* did not provide the description and diagnoses separately. Afterwards, Hancock (1902, 1907) studied the genus, but also provides only the "Characteristics". Thus, the first diagnosis to genus was proposed by Perez-Gelabert & Otte (1999).

Choriphyllum (Cuba, Bahamas and Jamaica) and *Phyllotettix* (Jamaica) are allied leaf-mimics tetrigids (Heads 2014) that share several morphological characteristics. For some time, species of *Choriphyllum* were considered as *Phyllotettix* and vice-versa (see

Hancock (1902)). However, Hancock (1907) assigns this to a compiling error from his 1902 data. *Choriphyllum* is a genus with four species: *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999 from Bahamas; *Choriphyllum plagiatum* Walker, 1871 from Jamaica; *Choriphyllum sagrai* Serville, 1838 and *Choriphyllum saussurei* Bolívar, 1887 from Cuba (Cigliano *et al.* 2018).

Choriphyllum plagiatum Walker, 1871

Diagnosis. Body surface granulated; antennae longer than length of hind femur; antennal groove situated below lower margin of compound eyes; eyes globose with flattened dorsal base; fascial carinae arcuate; interocular width of vertex between eyes (dorsal view) is wider than vertical width of one compound eye; anterior margin of pronotum rounded, slightly arcuated and with subtriagulated shape over the head; middle part of median carina protruding, giving the pronotum a leaf-like triangular shape with posterior part slightly concave; pronotum ornamented with black spots of different size and without definite shape; pronotum with parallel radiating veins and a lot of small granules on the foliaceous part of pronotum; lateral lobes being directed downwards, close to the body.

Comments. Walker (1871) only provided general description of *C. plagiatum*. Afterwards, Hancock (1902) presented the species as *Phyllonotus plagiatum*, but Hancock (1907) corrected the name justifying a compilation error. In this two publications Hancock do not provide the diagnosis and description separately. The original description was based on one female from Jamaica but there is a male specimen housed at BMNH with labels indicated that it's from a series. As a consequence, or Walker confused the sex or this is not the original specimen. Whereas terminalia is partially covered, probably Walker confused the sex of the specimen. Additionally, the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotypy.

Choriphyllum saussurei Bolívar, 1887

Diagnosis. Body surface granulated; antennae shorter than length of hind femur; antennal groove situated below lower margin of compound eyes; eyes globose with flattened dorsal base; fascial carinae arcuate; interocular width of vertex between eyes (dorsal view) is wider than vertical width one compound eye; anterior margin of pronotum rounded, slightly arcuated and with subtriagulated shape over the head; pronotum leaf-like with crest uniformly elevated up to the middle of the body, from the middle to the end of the body, the median carina is undulated, posteriorly partly truncated; pronotum with parallel radiating veins highlighted only on the small foliaceous part; lateral lobes being directed downwards, close to the body.

Comments. *C. saussurei* and *C. sagrai* are poorly known, few specimens were recorded and the latter species was not found in MHNG (John Hollier, *personal observation*). There is a scarce data about *C. sagrai* and we designated this species as *nomen dubium* status. There are two females syntypes of *C. saussurei* designed by Paris (1994), housed at the MHNG (Fig. 2). Bolívar (1887) only provided general description of *C. saussurei*. Afterwards, Hancock (1902) presented the species as *Phyllonotus saussurei*, but Hancock (1907) corrected the name justifying a compilation error. In this two publications Hancock do not provide the diagnosis and description separately.

Choriphyllum bahamensis Perez-Gelabert & Otte, 1999

Emended Diagnosis. Body surface granulated; pronotum leaf-like with crest uniformly elevated throughout its length, without undulations, slightly higher at its midpoint; antennae shorter than length of hind femur; antennal groove situated below lower margin of compound eyes; eyes globose with flattened dorsal base; fascial carinae arcuate; interocular width of vertex between eyes (dorsal view) from above is wider than vertical width a compound eye; median carina anteriorly rounded, arcuated, with hook-like shape over the head and posteriorly truncated; pronotum ornamented with small black spots; pronotum with radiating veins throughout the pronotum, but more densely concentrated on the foliaceous part of pronotum; lateral lobes being directed downwards, close to the body.

Comments. *C. bahamensis* was the last species described and in the original description, the author provides a type series composed by holotype, allotype and one paratype. However, the material housed at the museum (Table 1) labeled as *C. bahamensis* included only the holotype and two paratypes (one male and one female) (Figs. 3-5).

Key to species of *Choriphyllum* Servile (adapted of Perez-Gelabert & Otte 1999 and Gundlach 1891)

1. Posterior part of median carina slightly concave..…*Choriphyllum plagiatum* (Fig. 1A)
1'. Posterior part of median carina truncated ………..……………………..………... 2
2. Median carina (general shape of pronotum) with crest uniformly elevated throughout its length, without undulations ……..............…….. *Choriphyllum bahamensis* (Figs. 3A, 5A)
2'. Median carina (general shape of pronotum) with crest not uniformly elevated throughout it length, with undulations …………..…...……………...…………………… 3
3. Undulations evident only on the median to posterior part of median carina ……………………………………………….………….... *Choriphyllum saussurei* (Fig. 2)
3'. Undulations evident perpendicular to the head ……..............................… ………………...*Choriphyllum sagrai* (based on Serville's (1838: plate 8, fig. 5 – drawing).

Phyllotettix Hancock, 1902

Type species: *Phyllotettix compressus* (Thunberg, 1815)

Diagnosis. Body strongly compressed with surface finely rugose; head and compound eyes inserted below pronotum disc; antennal groove situated below margin of compound eyes; facial carinae placed between antennal groove; scutellum distinctly rounded and wider. Pronotum with radiating veins; crest highly elevated, with edge undulated or almost straight; anterior margin of pronotum elevated overhead, covering dorsally the head with a truncated projection or almost rounded extending down almost to the vertex portion; margin posterior of pronotum not truncated; infrascapular area visible and broad. Tegmina and wings absent. Fore femur undulated, middle femur elongated; hind femur robust, with dorsal margin excavated on distal portion (Fig. 6-7).

Comments. *Phyllotettix* has three species: *Phyllotettix compressus* (Thunberg, 1815), *Phyllotettix foliatus* (Hancock, 1902) and *Phyllotettix rhombeus* (Felton, 1765). *P. foliatus* is the species described more recently. Otte (1978) listed the primary type housed at the ANSP, but this specimen was not found for us.

Phyllotettix compressus (Thunberg, 1815)

Diagnosis. Body surface finely rugose, pronotum leaf-like with crest elevated with median protuberance backwards; antennae shorter than hind femur; antennal groove situated below lower margin of compound eyes; eyes globose with flattened dorsal base; fascial carinae arcuate; intraocular width of vertex between eyes from above wider than vertical width of one compound eye; median carina anteriorly almost truncated and posteriorly bifid; median carina with edge almost straight; pronotum without parallel radiating veins; lateral lobes being directed downwards, close to the body; fore and middle femur undulated; dorsal margin of hind femur slightly excavated on the distal portion (Fig. 6).

Comments. *P. compressus* male specimen is housed at the UZIU and the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotypy. Thunberg (1815) only provided general description of *P. compressus* and here we provided a diagnosis from this species.

Phyllotettix rhombeus (Felton, 1765).

Diagnosis. Body surface finely rugose, pronotum leaf-like with crest elevated with median undulated protuberance backwards; antennal groove situated below lower margin of compound eyes; eyes globose with flattened dorsal base; intra-ocular width of vertex between eyes from above is wider than vertical width of compound eye; median carina anteriorly undulated and subtriangulate, posteriorly undulated and rounded; pronotum with parallel radiating veins of higher caliber and small veins with smaller caliber throughout pronotum; lateral lobes being directed downwards, close to the body; fore and middle femur undulated; dorsal margin of hind femur excavated on distal portion (Fig. 7).

Comments. *P. rhombeus* (Fig. 7) was mentioned in the early studies as cicada and *Membracis* (Hemiptera, Auchenorrhyncha) by Felton (1765), Linnaeus (1767) and Fabricius (1775), until Westwood (1837) allocated this taxon to a genus of Orthoptera (Cigliano *et al.* 2018). This species did not have a diagnosis and the author did not designate the holotype in the original description. However, following the article 73.1.2 of ICZN that specimen is the holotype fixed by monotypy.

Mucrotettigini Cadena-Castañeda & Silva n. trib.

Diagnosis: Body not flattened laterally, rugose and granulose integument; fascial carinae arcuated (lateral view); fastigium prominent above eyes (lateral view); antennal groove situated below lower margin of compound eyes; pronotum short, brachypronotal, slightly surpassing abdomen; median carina continuous; posterior margin of pronotum with diverse shapes, being truncated in the most cases, with peculiar forms; lateral lobes directed downwards, close to the body (only in *Armasius* there is a spine and the lateral lobe of pronotum is projected sidewards); broad infrascapular area, extending towards to posterior margin of pronotum in lateral view; tegmina and wing absent (the unique exception is fossil of *Electrotettix attenboroughi*† Heads & Thomas, 2014 with tegmina and rudimentary hind wings (Heads *et al.* 2014)); fore and middle femur undulated, hind femur robust.

Included genera: *Antillotettix* Perez-Gelabert, 2003; *Baeotettix* Heads (2009); *Electrotettix* Heads & Thomas, 2014; *Armasius* Perez-Gelabert & Yong, 2014; *Bahorucotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubanotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubonotus* Perez-Gelabert, Hierro & Otte, 1998; *Eleleus* Bolívar, 1887; *Haitianotettix* Perez-Gelabert, Hierro & Otte, 1998; *Hottettix* Perez-Gelabert, Hierro & Otte, 1998; *Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998; *Sierratettix* Perez-Gelabert, Hierro & Otte, 1998; *Tiburonotus* Perez-Gelabert, Hierro & Otte, 1998 and *Truncotettix* Perez-Gelabert, Hierro & Otte, 1998.

Distribution: Cuba, Dominican Republic, Jamaica, Haiti, Puerto Rico and Brazil.

Remarks: Mucrotettigini **n. trib.** is distinguished from Chorophyllini **n. trib.** and some Xerophyllini due the absence of high and foliaceous crest on pronotum. It distinguishes itself from Xerophyllini also by the same characters cited in the comparison of Chorophyllini **n. trib**.

Antillotettix Perez-Gelabert, 2003

The genus *Antillotettix* has two taxa from Dominican Republic: a live species *Antillotettix nanus* Perez-Gelabert, 2003 and the fossil *Antillotettix electrum*† Heads, 2009 (Cigliano *et al*. 2018). This genus is distinguish from the other cladonotines by very small body size (4 to 7 mm); rounded body shape; integument coarsely granulose; antennae 10-segmented; fascial carinae not widely bifurcated; anterior margin of pronotum tectate, elevated only slightly above the head and pronotum extending over half to 3⁄4 of the abdomen (Perez-Gelabert 2003).

A. electrum is distinguished from *A. nanus* by antennae almost twice longer than fore femur, body less granulose, pronotum diminute and smaller humeral sinus (Heads 2009). Both *A. nanus* and *A. electrum* have posterior margin of pronotum with slight medial notch (op. cit).

Baeotettix† **Heads (2009)**

This taxon is a monotypic fossil with an uncommon morphology of the pronotum and frontal costa. *Baeotettix lottiae*† Heads, 2009 has the posterior margin of pronotum serrate and is unique among Neotropical Cladonotinae species with fascial carinae bilobate (Heads 2009). This taxon was found in the Dominican Republic (Heads 2009; Cigliano *et al*. 2018).

Electrotettix † **Heads & Thomas, 2014**

Electrotettix† also has a unique species, *Electrotettix attenboroughi*† Heads & Thomas, 2014. It is distinguished from other Cladonotinae by the presence of tegmina and rudimentary hind wings (Heads *et al.* 2014), since the recent Neotropical cladonotines have no wings. This species was also found in the Dominican Republic (Heads *et al.* 2014; Cigliano *et al*. 2018).

Armasius **Perez-Gelabert & Yong, 2014**

Regarding only the live taxa, *Armasius* is the most recent record of cladonotines from the Neotropical region. It was found in Cuba (Perez-Gelabert & Yong 2014, Cigliano *et al*. 2018). *Armasius iberianus* Perez-Gelabert & Yong, 2014 is the unique species in the genus, which has the characteristic among Neotropical Cladonotinae, of lateral lobe of pronotum modified with sharp projection, with triangular shape (male) (Yong 2017) or forming a spine (female) (Perez-Gelabert & Yong 2014).

Bahorucotettix **Perez-Gelabert, Hierro & Otte, 1998**

Bahorucotettix was also found in Dominican Republic. It has a single species, *Bahorucotettix larimar* Perez-Gelabert, Hierro & Otte, 1998. This genus is distinguished from the other cladonotines by low pronotum, not much produced over the vertex, blunt ended and almost covering the whole abdomen (Pérez-Gelabert *et al*. 1998). The depository of the type is uncertain. We analyze the ANSP collection and consult the FSC curator (Kyle Schnepp, *personal observation*) and then confirm that the type is not housed in these two collections.

Cubanotettix Perez-Gelabert, Hierro & Otte, 1998

This taxon has only one known species, *Cubanotettix turquinensis* Perez-Gelabert, Hierro & Otte, 1998 from Cuba. It is distinguished from the other Cladonotinae by antennae with 10-11 segments, eyes lower than level of vertex, not so wide scutellum of fascial carinae and a pronotum shorter than the abdomen (Pérez-Gelabert *et al.* 1998) (Fig. 8A-D). The holotype was sampled on "16-21 vi 1936" in an area with "3.000-6.000 ft" altitude. However, the holotype label has different data: it was sampled on "June 18-20, 1936" in an area with "4.500-6.000 ft" altitude. This last information refers the data of the seven paratypes mentioned by the original author (Fig. 8E).

Cubonotus Perez-Gelabert, Hierro & Otte, 1998

This genus is also monotypic, with the single species *Cubonotus altinotatus* Perez-Gelabert, Hierro & Otte, 1998 from Cuba. This taxon is characterized by pronotum anteriorly tectiform, median carina laterally compressed and elevated, but not foliaceous, flattened spines projected laterally in hind femur, posterior margin of pronotum slightly pointed (Pérez-Gelabert *et al.* 1998) and posterior margin of pronotum truncated in dorsal view (Fig. 9C).

Eleleus Bolívar, 1887

Type species: *Eleleus curtus* Bolívar, 1887.

Diagnosis (new information and adjustments using data of Hancock (1907) and Bolívar (1887))**.** Body almost smooth; fastigium visible between eyes; frontal costa placed between compound eyes with wide scutellum, fascial carinae elevated; eyes globose with flattened dorsal base; vertex lower than median carina of pronotum; both superior ocelli placed between fascial carinae. Pronotum slightly rugose, brachypronotal; anterior margin of pronotum curved; median carina elevated but not foliaceous nor flattened; ventral sinus present; posterior margin of pronotum rounded; sternomentum conspicuous. Fore and middle femur undulated with sulcation on the dorsal margin; hind femur broad, entire, with femoral spine very prominent; first and third articles of hind tarsi subequal in length.

Ovipositor valves short and slender, margin of dorsal and ventral valves with teeth (Fig. 10).

Comments. This genus is known only to Brazil and has a single known species, *Eleleus curtus* Bolívar, 1887. In the original description, only general characteristics were provided. This species was also examined by Hancock (1907) which added new information, but did not provide a diagnosis separately. The only specimen known of the type series is a syntype designed by Paris (1994), housed at the NMW Vienna Museum (Paris 1994, Cigliano *et al.* 2018) (Fig. 10). Regarding this specimen, on ventral view there is a longitudinal suture on the subgenital plate (Fig. 10D).

***Haitianotettix* Perez-Gelabert, Hierro & Otte, 1998**

Perez-Gelabert *et al.* (1998) described this genus with two species: *Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998 and *Haitianotettix monstruosus* Perez-Gelabert, Hierro & Otte, 1998. These species were described based on nine males of *H. tuberculatus* and a single female of *H. monstruosus* (Pérez-Gelabert 2009). However, new specimens from expeditions to the Hispaniola Mountains were sampled and a female of *Haitianotettix* was found from the same region of the *H. tuberculatus*. The analysis of this female indicated that this specimen shared morphological similarities with *H. monstruosus*, so Perez-Gelabert (2009) synonymized *H. monstruosus* with *H. tuberculatus*.

H. tuberculatus differs from the cladonotines by its tuberculate surface, vertex with transversal carinula between the eyes, pronotum elevated only anteriorly, covering half of the abdomen, and hind femur with two tooth-like projections on median external area (Pérez-Gelabert 2009) (Fig. 11).

***Hottettix* Perez-Gelabert, Hierro & Otte, 1998**

This genus has only a single species, *Hottettix haitianus* Perez-Gelabert, Hierro & Otte, 1998 from Haiti (Fig. 12). It differs from all other cladonotines in having the posterior margin of pronotum 'U' shaped (Pérez-Gelabert *et al.* 1998) (Fig. 12C).

***Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998**

Mucrotettix has two species, from the Dominican Republic: *Mucrotettix gibbosus* Perez-Gelabert, Hierro & Otte, 1998 (Fig. 13) and *Mucrotettix spinifer* Perez-Gelabert, Hierro & Otte, 1998 (Fig. 14). *Mucrotettix* is morphologically similar to *Truncotettix*, but can be distinguish from it by the sharply pointed posterior margin of pronotum, body slightly larger, antennae 14-segmented, pronotum less tectiform with anterior margin not produced over vertex (Pérez-Gelabert *et al*. 1998) (Figs. 13, 14). These two species can be distinguished by some characteristics. *M. gibbosus* has a wider scutellum (Fig. 13D), rounded lateral lobes of pronotum (Fig. 13A), fore and middle legs without spines or projections (Fig. 13A-D), while *M. spinifer* has a narrower scutellum (Fig. 14C), lateral lobes of pronotum truncated (Fig. 14A) and fore and middle legs with spines or projections (Fig. 14A-C) (Pérez-Gelabert *et al.* 1998).

Sierratettix **Perez-Gelabert, Hierro & Otte, 1998**

This taxon has only one species, from the Dominican Republic: *Sierratettix carinatus* Perez-Gelabert, Hierro & Otte, 1998 (Fig. 15). Its main distinguishing character, in relation to the other Neotropical cladonotines, is the anterior margin of pronotum slightly hook-like over the head, in dorsal view (Pérez-Gelabert *et al.* 1998) (more protruding than *Eleleus*) (Fig. 15A: arrow).

Tiburonotus **Perez-Gelabert, Hierro & Otte, 1998**

This genus has only one species, *Tiburonotus peninsularis* Perez-Gelabert, Hierro & Otte, 1998, from Haiti (Fig. 16). This genus can be distinguished by elevated pronotum, only anteriorly increased, with its posterior margin slightly concave in dorsal view (Fig. 16C) (Pérez-Gelabert *et al.* 1998).

Truncotettix **Perez-Gelabert, Hierro & Otte, 1998**

Perez-Gelabert *et al.* (1998) described this genus with two species: *Truncotettix fronterizus* Perez-Gelabert, Hierro & Otte, 1998 (Fig. 17) and *Truncotettix interruptus* Perez-Gelabert, Hierro & Otte, 1998 (Fig. 18), both from Dominican Republic. This genus has very small body size among Neotropical cladonotines, having antennae 12-segmented, pronotum tectiform with anterior margin slightly produced over vertex, in dorsal view (Pérez-Gelabert *et al.* 1998) (Figs. 17, 18). The two species are very similar, but can be distinguished by posterior margin of pronotum, notch in *T. fronterizus* (Fig. 17C) and slightly truncated in *T. interruptus* (Fig. 18C).

Ungrouped taxa

***Cota* Bolívar, 1887**

Type species: *Cota saxosa* Bolívar, 1887.

Diagnosis. Body surface granulated with spine-like tubercles over the tegument; head and compound eyes inserted slightly below pronotal disc; face oblique; fastigium visible between eyes; antennal groove situated much bellow lower margin of compound eyes, eyes globose with flattened dorsal base; vertex lower than median carina of pronotum; fascial carinae elevated; fastigium of vertex protruding as a horn-like structure (lateral view) and carinula transversal to vertex, between the eyes, with cusp shape surpassing dorsal margin of the eyes, forming small horns in frontal view (referred by Hancock (1907) and Bolívar (1887) as tricuspidate form) in *C. saxosa*; interocular width of vertex between eyes, in dorsal view, wider than vertical width one compound eye. Pronotum granulated with spine-like tubercles, anteriorly truncated or rounded, median carina conspicuous, continuous with protuberances; lateral lobes being directed sidewards; median carina continuous, with two strongly elevated cusps. Tegmina and wings absent. Fore and middle femur with lappets and protuberances, *saxose* (with various lumps and teeth on femora, giving a stone-like appearance); hind femur with lappets, genicular teeth conspicuous; the first and third articles of posterior tarsi with subequal length.

Comments. This genus is found in South America and has three species: *Cota bispina* (Saussure, 1861) from Brazil; *Cota saxosa* Bolívar, 1887 and *Cota strumosa* Bolívar, 1887 from Peru (Cigliano *et al.* 2018). *Cota* has characteristics which in do not allow it to be classified in Chorophyllini **n. trib.** or Mucrotettigini **n. trib.** as spiny protuberances in the face and body and femurs with lappets. We maintain it within the subfamily Cladonotinae, until future cladistic analysis can clarify its classification. Bolívar (1887) only provided general description of *Cota*. Later, Hancock (1907) also does not provide the diagnosis and description separately.

Cota bispina (Saussure, 1861)

C. bispina is an old Cladonotinae described to South America and poorly known. There is one male in the collection of the MHNG, but this specimen needs to be analyzed since the type material is unknown (Hollier 2013). As we were not able to examine the type specimen of the species concerned, because it was not found in the collection of the

MHNG, and there is scarce data on this species, we designated this species with *nomen dubium* status.

Cota saxosa Bolívar, 1887

Diagnosis. Head with carinula transversal to vertex, between the eyes, with cusp shape surpassing dorsal margin of the eyes, forming small horns in frontal view with a tricuspidate form; anterior margin of pronotum and first cusp rounded, lateral lobe of pronotum directed sidewards with tricuspid shape, fore and middle femur with undulated carina, lappets and protuberances saxose (similar to 'stones') (Fig. 19).

Comments. There is a syntype designed by Paris (1994) and housed at the NMW (Fig. 19).

Cota strumosa Bolívar, 1887

Diagnosis. Anterior margin of pronotum truncated and first cusp rounded, lateral lobe of pronotum directed sidewards and subquadrate, fore and middle femur less protruding than *C. saxosa*.

Comments. There is a lectotype designed by Paris (1994) and housed at the MNCN (Fig. 20).

Regarding the species of this group, we noted that *Metrodora undulata* Cadena-Castañeda & Cardona, 2015, from Colombia, is not a member of *Metrodora* Bolívar, 1887, but represents a species of *Cota.* The holotype of *M. undulata* has head and pronotal morphology corresponding to members of *Cota.* Thus, the new combination *Cota undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.** should be used when referring to this specimen. This species is very close to *C. saxosa* and can be distinguished from *C. saxosa* by horn-like structure more rounded and lateral lobes of pronotum directed sidewards and subquadrate (Fig. 21).

Key to species of *Cota* Bolívar, 1887 (adapted from Bruner 1910 and Cadena-Castañeda & Cardona 2015).

1. First cusp on pronotum rounded or subquadrate ..……………….……………..…… 2

1'. First cusp on pronotum with other shape …………………………..……………..... 4

2. First cusp on pronotum subquadrate and lateral lobe of pronotum rounded at apex .... *C. strumosa* (Fig. 20)

2'. First cusp on pronotum rounded and lateral lobe of pronotum with other shape …..…. 3

3. Lateral lobe of pronotum with tricuspid shape …………….……….. *C. saxosa* (Fig. 19)

3'. Lateral lobe of pronotum subquadrate …….. ………….......…. *C. undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.** (Fig. 21)

4. First cusp on pronotum spiniform ……………………….......................... *C. bispina.*

Dasyleurotettix Rehn, 1904

Dasyleurotettix has widespread distribution, found on Neotropical and Ethiopian regions (see Cigliano *et al.* 2018). This genus has five species: *Dasyleurotettix affinis* (Bruner, 1920) (Argentina); *Dasyleurotettix infaustus* (Walker, 1871) (Southern Africa); *Dasyleurotettix lobulatus* (Stål, 1861) (Brazil); *Dasyleurotettix miserabilis* (Blanchard, 1851) (Chile) and *Dasyleurotettix sublaevis* (Bolívar, 1912) (West-Central Tropical Africa) (Cigliano *et al.* 2018). The type species of *Dasyleurotettix* is *D. infaustus* (Walker, 1871) and this taxon does not have fascial carina of the frontal costa as widened as *Cladonotus* or the similar taxa indicated by Rehn (1904), *Diotarus* Stål, 1877 and *Trachytettix* Stål, 1876.

Rehn (1907) wrote that after examining the types of *Dasyleurotettix*, he was convinced that this taxon should be a Tetriginae member. This genus has head, pronotum and leg morphology rather different from other cladonotines members. Thus, we proposed transfer *Dasyleurotettix* to the subfamily Tetriginae.

Key to Neotropical Cladonotines extant genera

1. Body laterally compressed with foliaceous pronotum ……….. Chorophyllini **n. trib.** 2

1'. Body not laterally compressed without a foliaceous pronotum ....…………………….. ……………………………………………………Mucrotettigini **n. trib.** (and *Cota*).3

2. Hind femur with continuous dorsal margin …………………..... *Choriphyllum* (Figs. 1-5)

2'. Hind femur with dorsal margin excavated on distal portion …………………………….. ……….……………….……..…………………..…………………… *Phyllotettix* (Figs. 6, 7)

3. Lateral lobe of pronotum directed sidewards, flattened and with spine …………………..

……………………………………..……………………………......................... *Armasius*

3’. Lateral lobe of pronotum directed downward and continuous with body ………………………………………………………………………………..….……… 4

4. Posterior margin of pronotum sharply pointed ………………………………..……...… 5

4’. Posterior margin of pronotum not sharply pointed …………..………………...……… 6

5. Pronotum slightly tapering towards the posterior margin of pronotum, with arrow shaped apex ………………………………………………………………... *Cubanotettix* (Fig. 8)

5’. Pronotum tapering towards the posterior margin of pronotum and abruptly sharpening up as a spine ………………………….......................... *Mucrotettix* (Figs. 13C, 14B)

6. Posterior margin of pronotum ‘U’ shaped ……………….…..…… *Hottettix* (Fig. 12C)

6’. Posterior margin of pronotum not ‘U’ shaped ………………….…….……….……… 7

7. Posterior margin of pronotum rounded ………………..………..……. *Bahorucotettix*

7’. Posterior margin of pronotum not rounded ……………………….……………..……... 8

8. Posterior part of pronotum slightly tapering from the base towards the end, with truncated apex …………………………………………………….... *Cubonotus* (Fig. 9C)

8’. Posterior part of pronotum tapering from the base towards the end, without truncated apex …………………………………………………………...…..………………… 9

9. Posterior margin of pronotum slightly turning upward ………..... *Tiburonotus* (Fig. 16)

9’. Posterior margin of pronotum does not not turn upwards ……………..………… 10

10. Anterior margin of pronotum slightly hook-like over the head …………………..…………………………………………..…….. *Sierratettix* (Fig. 15)

10’. Anterior margin of pronotum rounded or angular …..…………………..…………. 11

11. Hind legs with at least two denticles (lappets) in dorsal view ……………......…... 12

11’. Hind legs without denticles (lappets) in dorsal view …………………….....…….. 13

12. Pronotum not covering the whole abdomen, with only one elevation (cusp) on the pronotum in lateral view …………………………….………… *Haitianotettix* (Fig. 11)

12’. Pronotum covering the whole abdomen, with two elevations (cusps) on the pronotum in lateral view ……………………………………………..……….… *Cota* (Figs. 19-21)

13. Pronotum elevated (not foliaceous) with infrascapular area evident and humero-apical carina continuous with internal lateral carina ………………..…...……..... *Eleleus* (Fig. 10)

13’. Pronotum elevated (not foliaceous) with infrascapular area evident, without humero-apical carina continuous with internal lateral carina …..……... *Truncotettix* (Figs. 17-18).

Discussion

Since the establishment of the basis for the present Cladonotinae taxonomy by Bolívar (1887), little suprageneric information was added to this taxon. Although the characteristics that unify the cladonotines of some regions of the Great Antillean sub-region are evident (see Heads 2014) as well as Xerophyllini (see Devriese 1999), the remaining groups of Cladonotinae need revision. There are few researchers working on this group and the most part of the recent data about these taxa in Neotropical region come from the studies of only few researchers: Heads, regarding fossil (Heads 2009, Heads *et al.* 2014) and Bolívar (1887), Perez-Gelabert and co-workers (1998, 1999, 2014), Perez-Gelabert (2003, 2009) and Yong (2017) for extant Cladonotinae.

The Neotropical cladonotines species occur basically in two areas: (i) South America, in which the tetrigid fauna is formed mainly by Batrachideinae, Metrodorinae and other less representative subfamilies, as Tetriginae, Lophotettiginae and Cladonotinae (only two genera) (see Perez-Gelabert 1998; Heads 2009; Cigliano *et al.* 2018) and (ii) some localities of the Greater Antillean sub-region. The Antillean cladonotines represent more than 75% of the total tetrigid species known from the West Indies (Heads 2009) and many groups are likely to be discovered in this region.

This huge diversity in the Greater Antillean sub-region resulted from the dynamic geological history, ecological complexity and evolution of these islands, which probably produced numerous vicariance events and consequent allopatric speciation for these wingless taxa with limited dispersion ability (Pérez-Gelabert *et al.* 1998, 1999; Heads 2009, 2014). All these islands landmasses had a complex history of drift, submergence and land bridge formation (Iturralde-Vinent and MacPhee 1996) that may have directed vicariance and dispersion of taxa during one or more geological episodes, as it probably occurred with *Choriphyllum* (Perez-Gelabert & Otte 1999). All these facts also have made the morphology of this restricted group unique among the cladonotines.

In this study we have proposed some taxonomic alterations and presented information on the morphology of cladonotines, among which we highlight the following:

(i) Regarding the new tribes proposal, our suggestions increase the Cladonotinae tribes to three. The two new tribes, Chorophyllini **n. trib.** and Mucrotettigini **n. trib.**, gathered all Neotropical species of Cladonotinae, with exception of *Cota* that did not have the characters needed.

(ii) We highlighted an unusual morphological characteristic, among tetrigids, that distinguishes *Eleleus*: the longitudinal suture on the subgenital plate. Chopard (1920) was the first researcher who noticed that the terminalia region of tetrigids was totally different from other grasshoppers. He noted that the male subgenital plate is divided transversally on two parts with the apical part flexible, forming a triangular projection. In *Eleleus,* the female has a longitudinal suture on the subgenital plate. This longitudinal suture was also noted in female of *Tripetalocera ferruginea* Westwood, 1834 and male of *Tripetaloceroides tonkinensis* (Günther, 1938) (see Storozhenko (2013: drawings)).

(iii) The genus *Cota*, as most tetrigids needs to be reviewed, particularly referring its cladistics position, regarding the ongoing discussion about the taxa with the presence of a horn developed from fastigium, frontal costa or scutellum (see Silva *et al.* 2017). The prolonged horn occurs in different evolutionary groups and, thus, is not a useful character in Tetrigidae suprageneric taxonomy (Silva *et al.* 2017). However, among taxa with horn in the Neotropical region, *Cota* shares with *Metrodora* Bolívar, 1887 other characteristics, as the elevated cusp on the pronotum, and the lateral lobe of pronotum directed sidewards.

Some *Metrodora* have, also, the fascial carina of frontal costa widened. We regard *Cota bispina* as *nomen dubium,* since the type is not available and the diagnostic characters are insufficient (see Mones (1989)). Similar situation occurs with some other Orthoptera species such as the Tetigonioidea: *Tympanophyllum (Anaprion) semivitreum* (Serville, 1838) and *Bliastonotus specularis* (Fabricius, 1775) (Cigliano *et al.* 2018).

(iv)We are according with the proposal of Rehn (1907) that suggested the allocation of *Dasyleurotettix* in Tetriginae. In this study we reinforced the repositioning of the *Dasyleurotettix* based mainly on morphological differences in the head, pronotum and legs with other Cladonotinae members.

We were able to provide complete morphological information from the specimens housed on museums and collections, essential for species with scarce field data. As several studies about the relevance of biological collections (*eg*. Allmon 1994; Rocha *et al*. 2014), our data endorse the overwhelming importance of collections. For tetrigids, the biological collection permit to preserve information for rare species and with historical value, species found in inaccessible geographic areas, or whose habitats have not been preserved.

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Table 1. Checklist of Neotropical species of Cladonotinae with type, locality and depository.

Species	Type	Locality	Depository
Fossil species			
Antillotettix electrum Heads, 2009	Holotype	Dominican Republic	American Museum of Natural History(AMNH)
Baeotettix lottiae Heads, 2009	Holotype	Dominican Republic	American Museum of Natural History (AMNH)
Electrotettix attenboroughi Heads & Thomas, 2014	Holotype	Dominican Republic	Illinois Natural History Survey (INHS)
Live species			
Antillotettix nanus Perez-Gelabert, 2003	Holotype	Dominican Republic	Carnegie Museum of Natural History (CMNH)
Armasius iberianus Perez-Gelabert & Yong, 2014	Holotype	Cuba	Museo Nacional de Historia Natural, La Habana
Bahorucotettix larimar Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	It was not found in Florida State Collection of Arthropods (FSCA)
Choriphyllum bahamensis Perez-Gelabert & Otte, 1999	Holotype	Bahamas	Florida State Collection of Arthropods (FSCA)
Choriphyllum plagiatum Walker, 1871	Holotype	Jamaica	The Natural History Museum, London (BMNH)
Choriphyllum sagrai Serville, 1838	*nomen dubium*	Cuba	It was not found in Muséum d'histoire naturelle de la Ville de Genève (MHNG)
Choriphyllum saussurei Bolívar, 1887	Syntype	Cuba	Muséum d'histoire naturelle de la Ville de Genève (MHNG)
Cota bispina (Saussure, 1861)	*nomen dubium*	Brazil	-
Cota saxosa Bolívar, 1887	Syntype	Peru	Naturhistorisches Museum Wien (NMW)
Cota strumosa Bolívar, 1887	Lectotype	Peru	Museo Nacional de Ciencias Naturales, (MNCN)
Cota undulata (Cadena-Castañeda & Cardona, 2015) **n. comb.**	Holotype	Colombia	Colección de Artrópodos y otros Invertebrados, Universidad Distrital Francisco José de Caldas (CAUD)
Cubanotettix turquinensis Perez-Gelabert, Hierro & Otte, 1998	Holotype	Cuba	The Academy of Natural Sciences of Drexel University (ANSP)
Cubonotus altinotatus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Cuba	The Academy of Natural Sciences of Drexel University (ANSP)
Eleleus curtus Bolívar, 1887	Syntype	Brazil	Naturhistorisches Museum Wien (NMW)

Table 1. Continued.

Species	Type	Locality	Depository
Live species			
Haitianotettix tuberculatus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	Carnegie Museum of Natural History (CMNH)
Hottettix haitianus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Haiti	The Academy of Natural Sciences of Drexel University (ANSP)
Mucrotettix gibbosus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	The Academy of Natural Sciences of Drexel University (ANSP)
Mucrotettix spinifer Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	The Academy of Natural Sciences of Drexel University (ANSP)
Phyllotettix compressus (Thunberg, 1815)	Holotype	Jamaica	Museum of Evolution Uppsala University (UZIU)
Phyllotettix foliatus (Hancock, 1902)	Holotype	Jamaica	It was not found in The Academy of Natural Sciences of Drexel University (ANSP)
Phyllotettix rhombeus (Linnaeus, 1767)	Holotype	Jamaica	The Natural History Museum, London (BMNH)
Sierratettix carinatus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	The Academy of Natural Sciences of Drexel University (ANSP)
Tiburonotus peninsularis Perez-Gelabert, Hierro & Otte, 1998	Holotype	Haiti	The Academy of Natural Sciences of Drexel University (ANSP)
Truncotettix fronterizus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	The Academy of Natural Sciences of Drexel University (ANSP)
Truncotettix interruptus Perez-Gelabert, Hierro & Otte, 1998	Holotype	Dominican Republic	The Academy of Natural Sciences of Drexel University (ANSP)

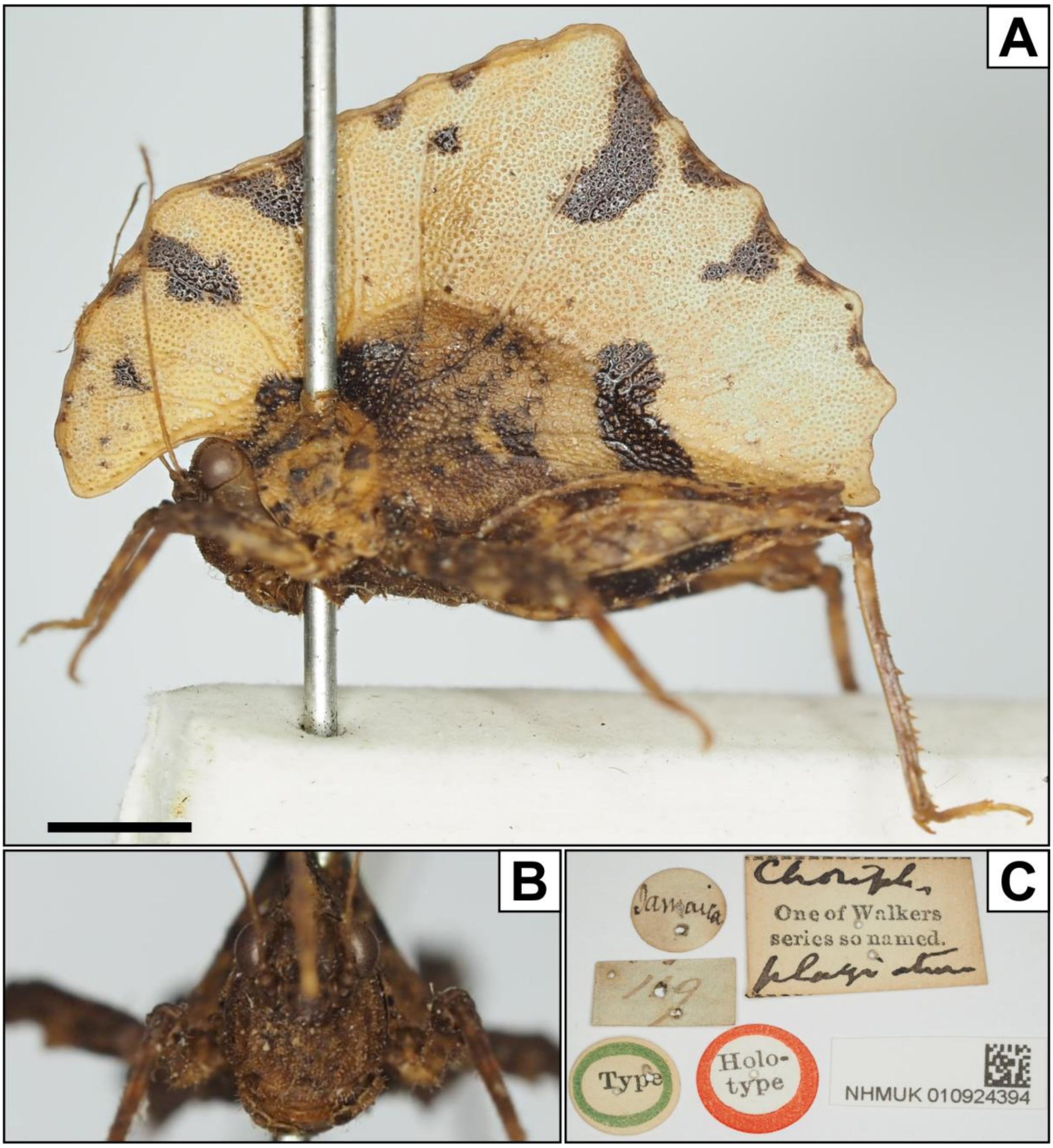


FIGURE 1. *Choriphyllum plagiatum* Walker, 1871 Holotype male. (A) *habitus* left lateral view, (B) frontal view and (C) labels. Photos: Josef Tumbrinck (BMNH).

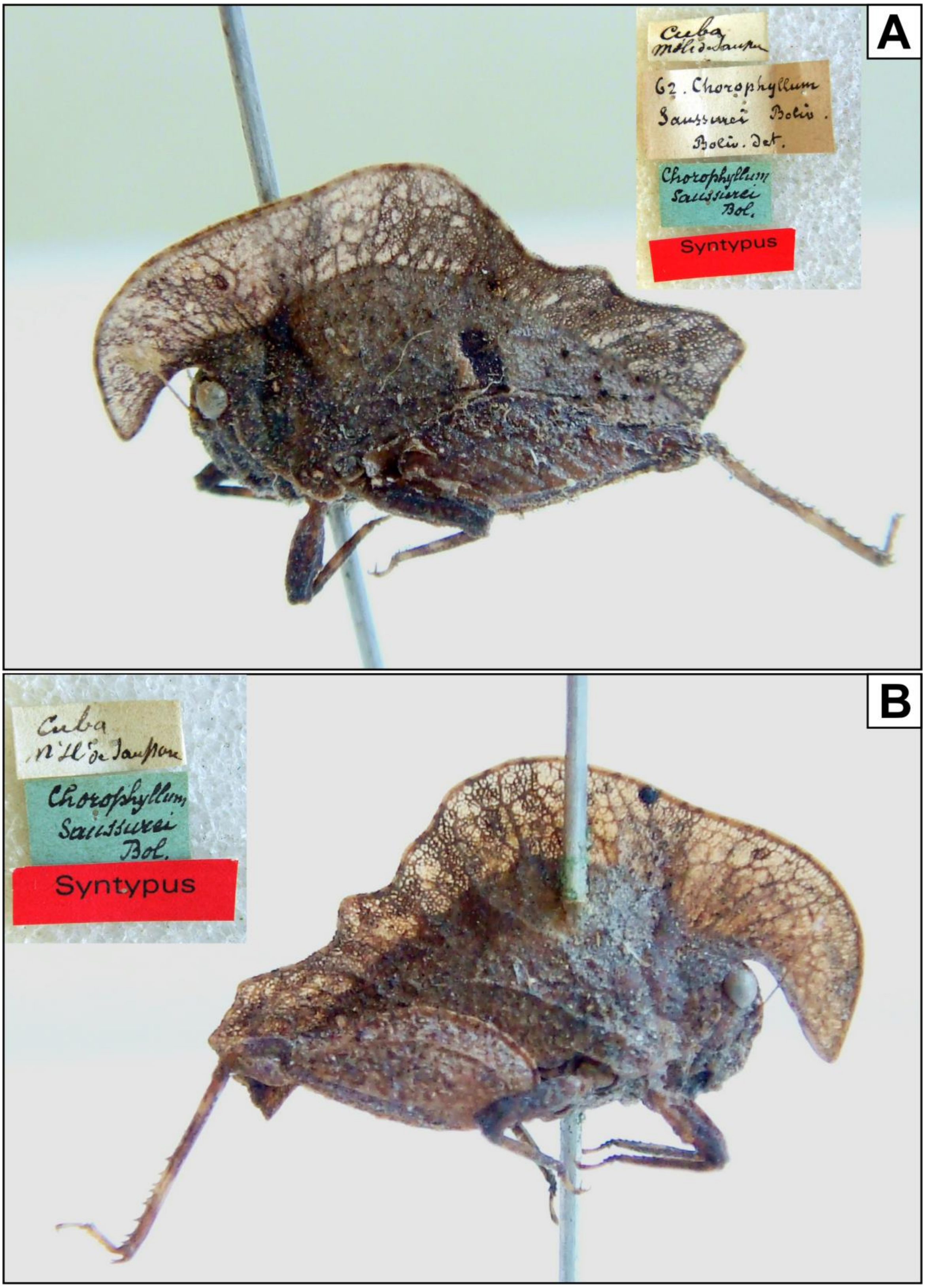


FIGURE 2. *Choriphyllum saussurei* Bolívar, 1887 Syntypes female. (A) *habitus* left lateral view with labels and (B) *habitus* right lateral view with labels. Photos: John Hollier (MHNG).

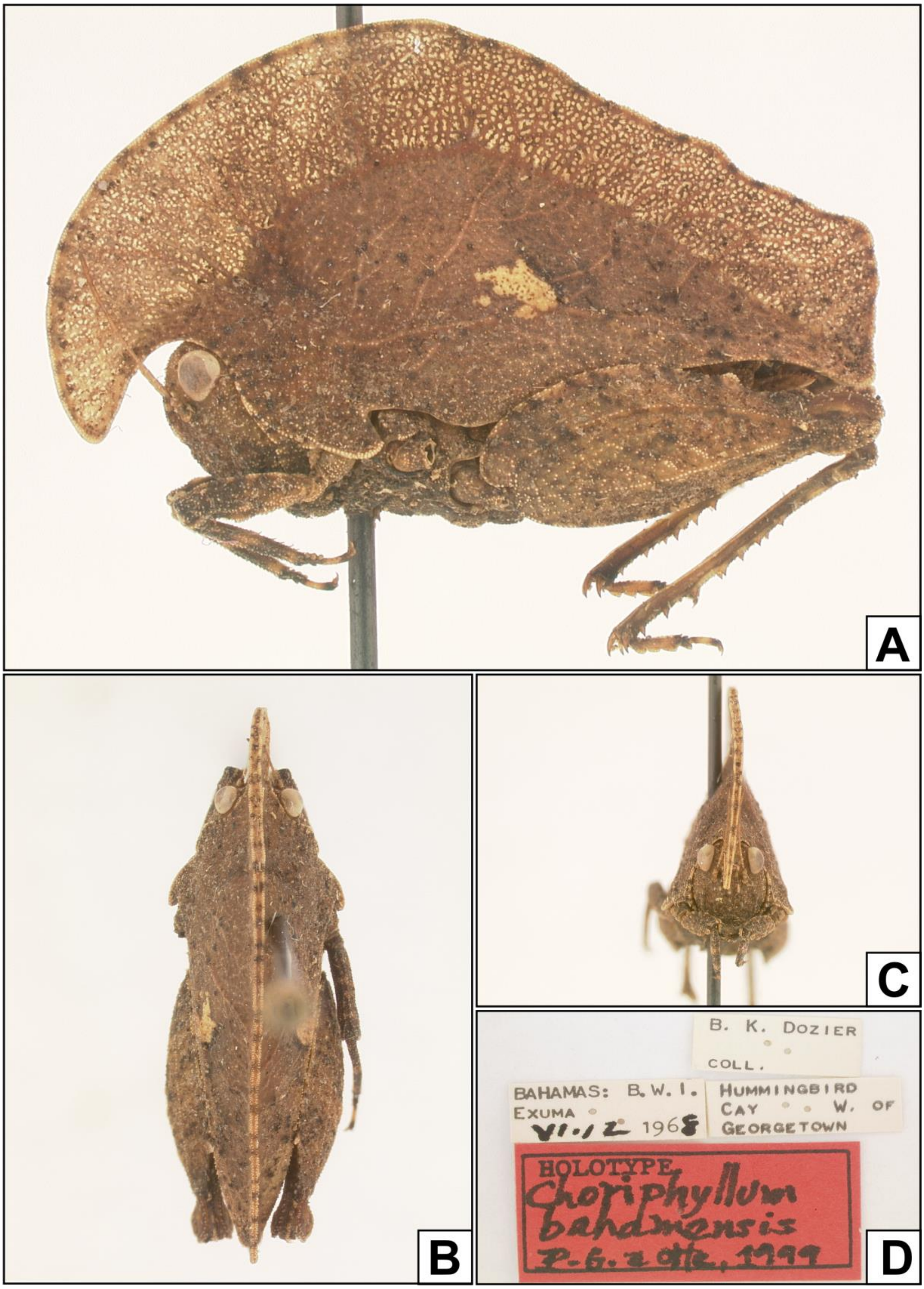


FIGURE 3. *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999 Holotype female. (A) *habitus* left lateral view (B) *habitus* dorsal view, (C) frontal view and (D) labels. Photos: Kyle E. Schnepp (FSCA).

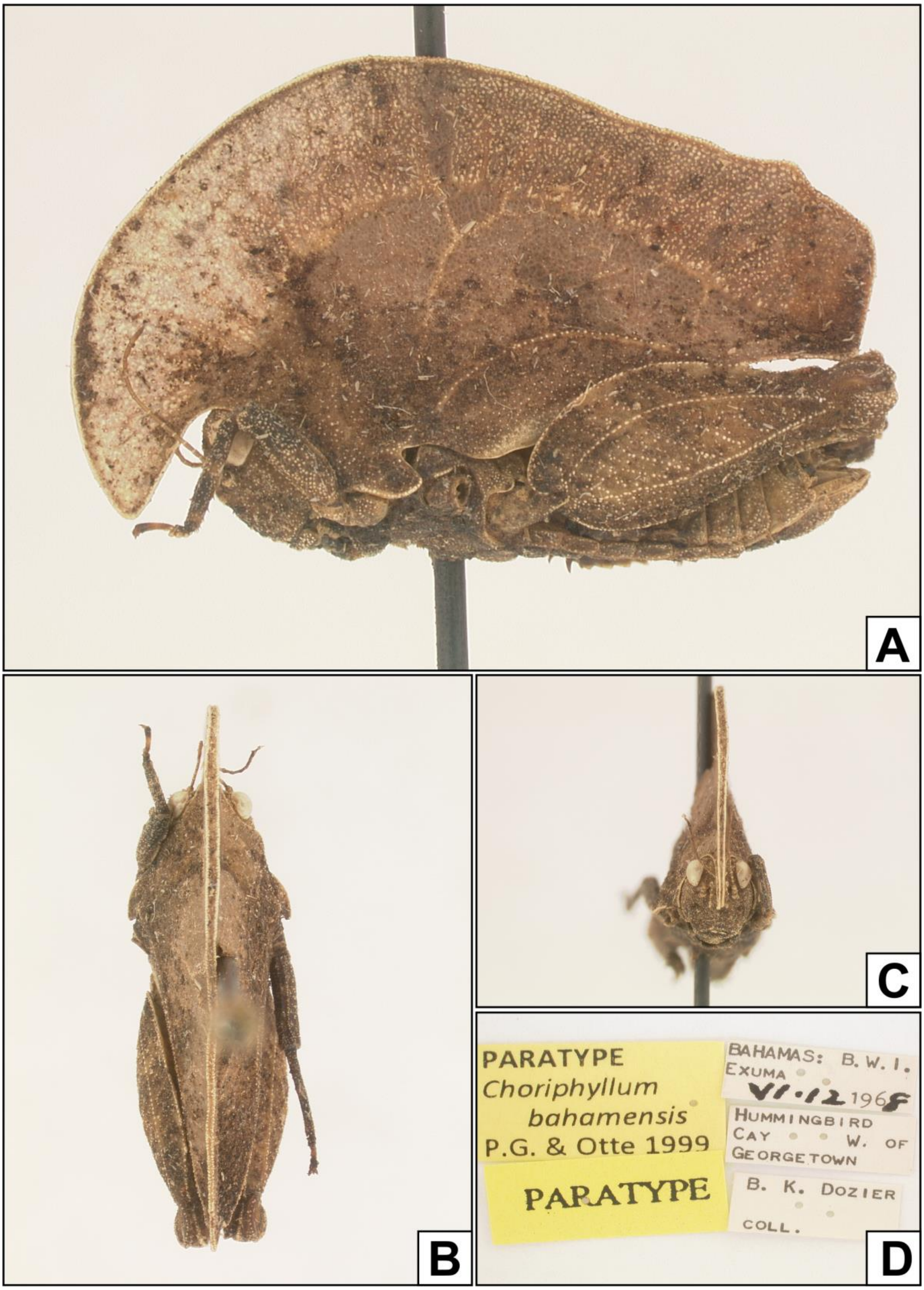


FIGURE 4. *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999 Paratype male. (A) *habitus* left lateral view, (B) *habitus* dorsal view, (C) frontal view and (D) labels. Photos: Kyle E. Schnepp (FSCA).

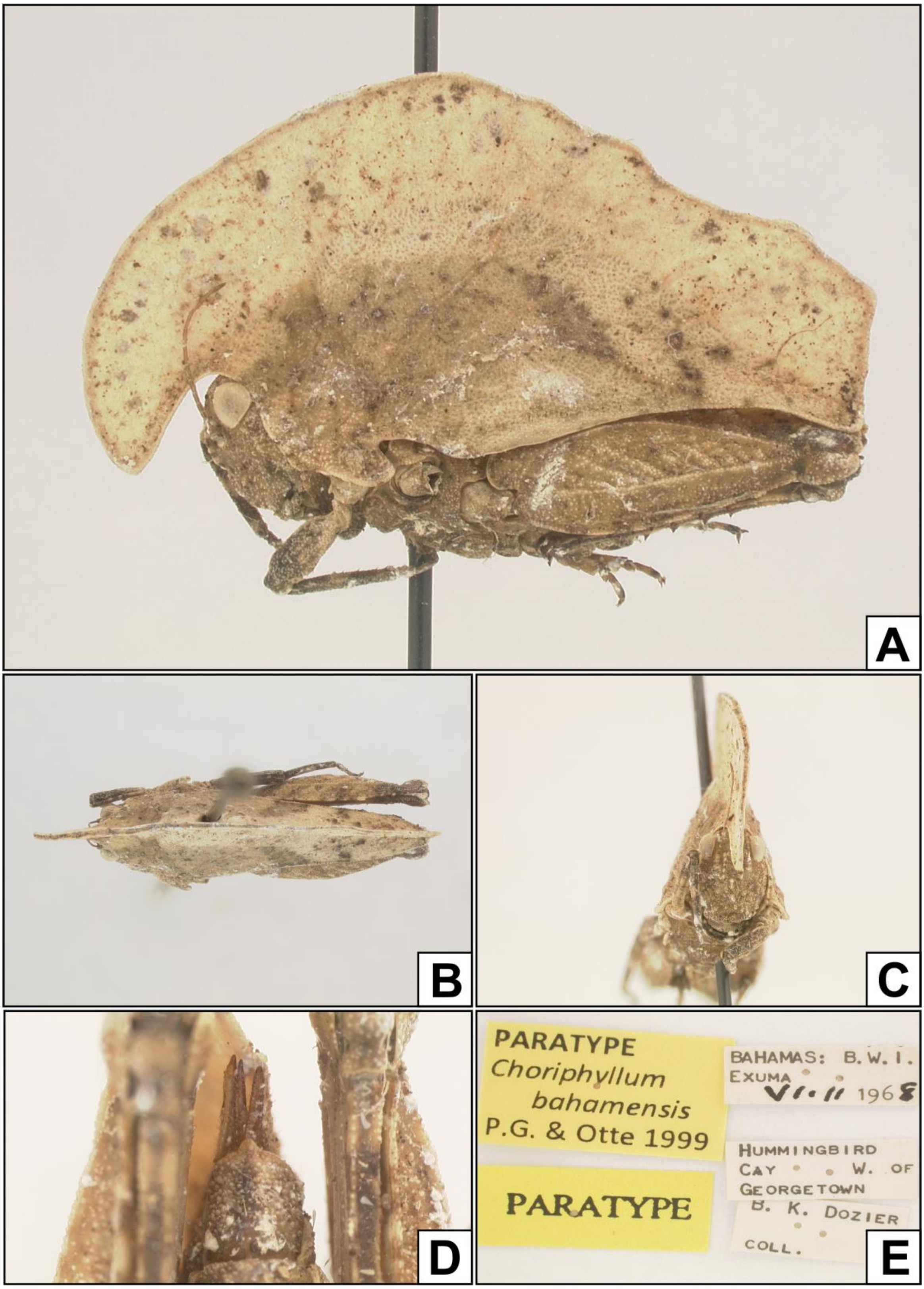


FIGURE 5. *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999 Paratype female. (A) *habitus* left lateral view, (B) *habitus* dorsal view, (C) frontal view and (D) terminalia ventral view and (E) labels. Photos: Kyle E. Schnepp (FSCA).

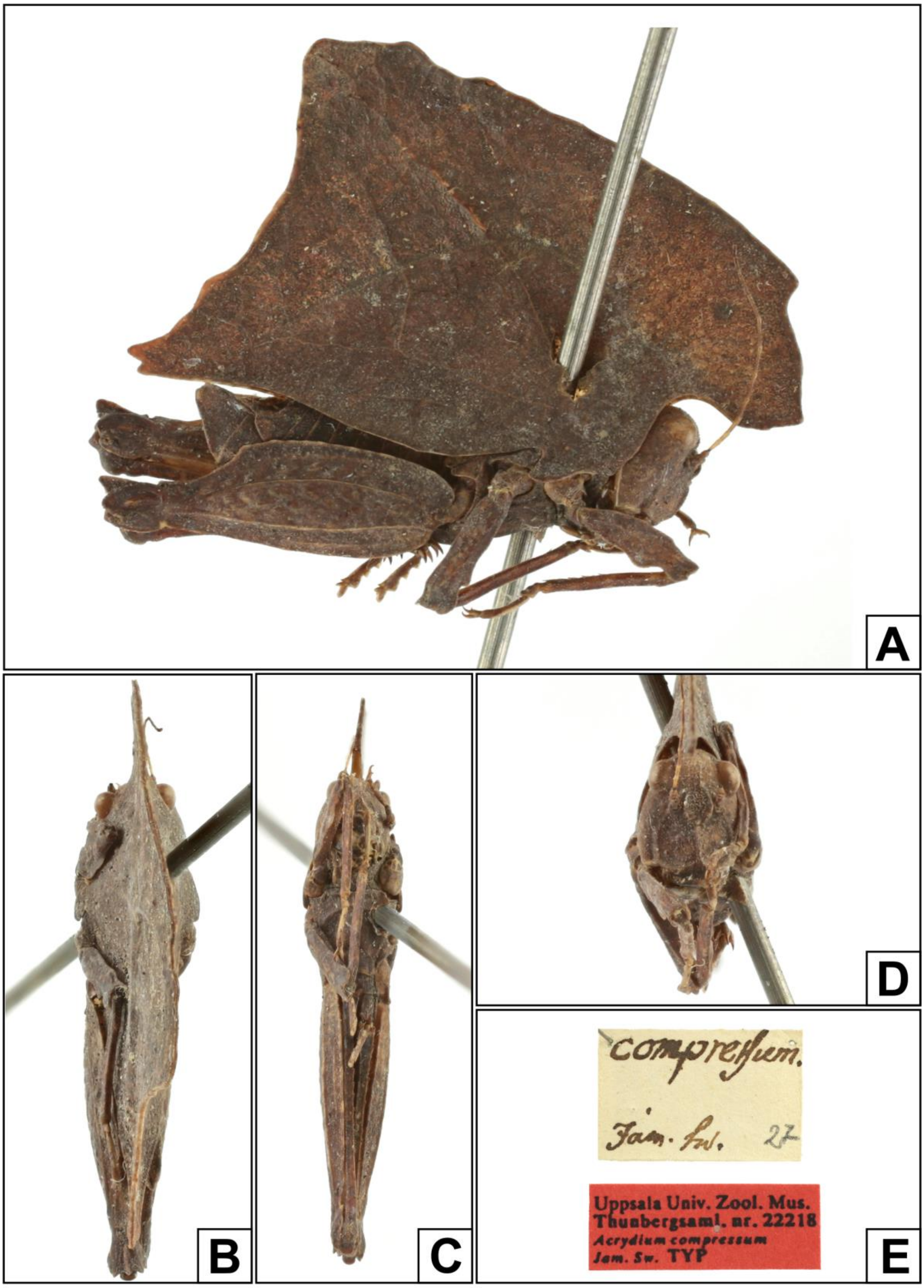


FIGURE 6. *Phyllotettix compressus* (Thunberg, 1815) Holotype male. (A) *habitus* right, (B) *habitus* dorsal view, (C) *habitus* ventral view, (D) frontal view and (E) labels. Photos: Hans Mejlon (UZIU).

FIGURE 7. *Phyllotettix rhombeus* (Felton, 1765) Holotype female. (A) habitus left lateral view and (B) hind leg and labels. Arrow indicating the dorsal margin excavated on distal portion. Photos: Josef Tumbrinck (BMNH).

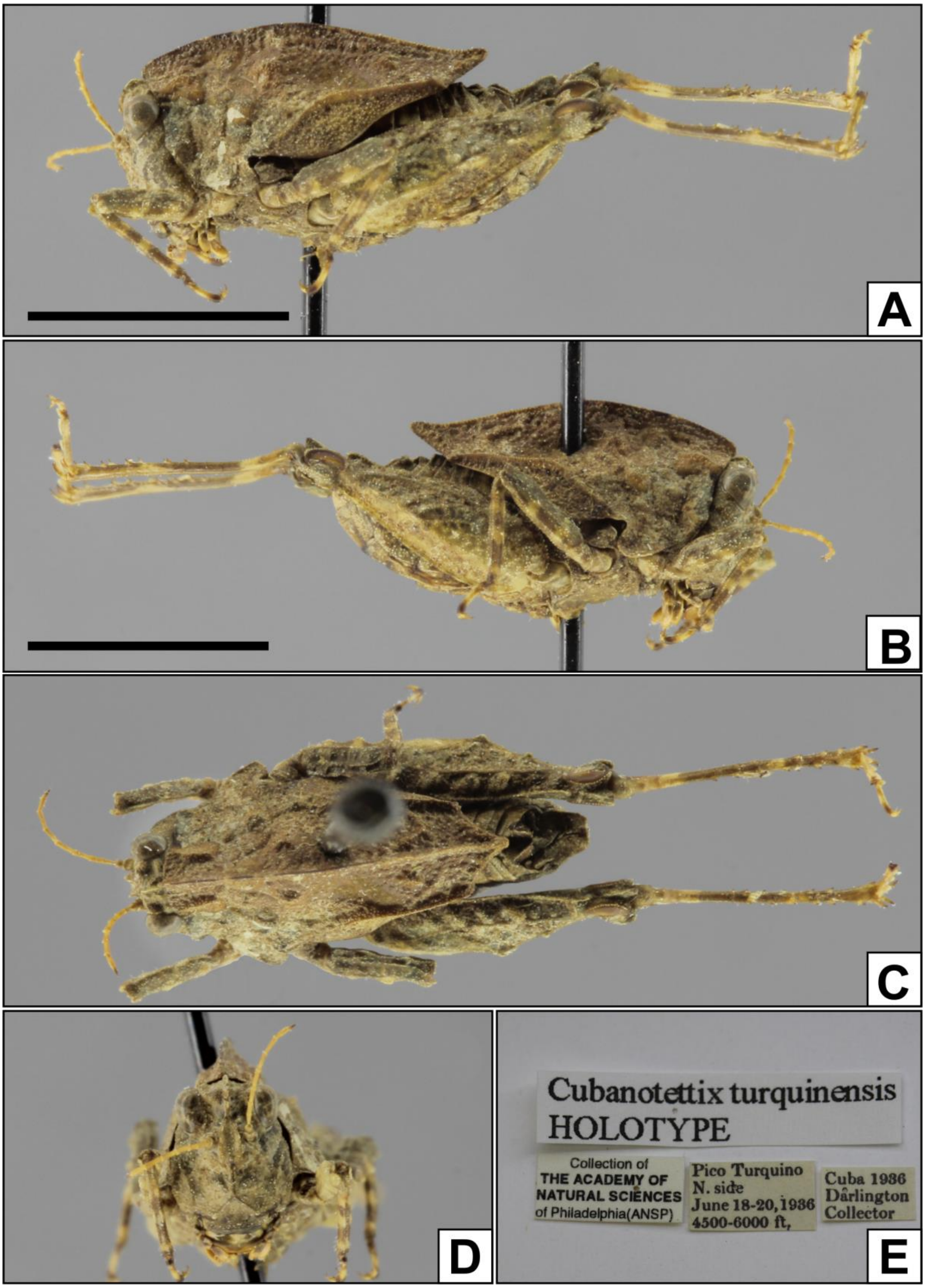


FIGURE 8. *Cubanotettix turquinensis* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, (D) frontal view and (E) labels. Scale bar = 0,5 cm.

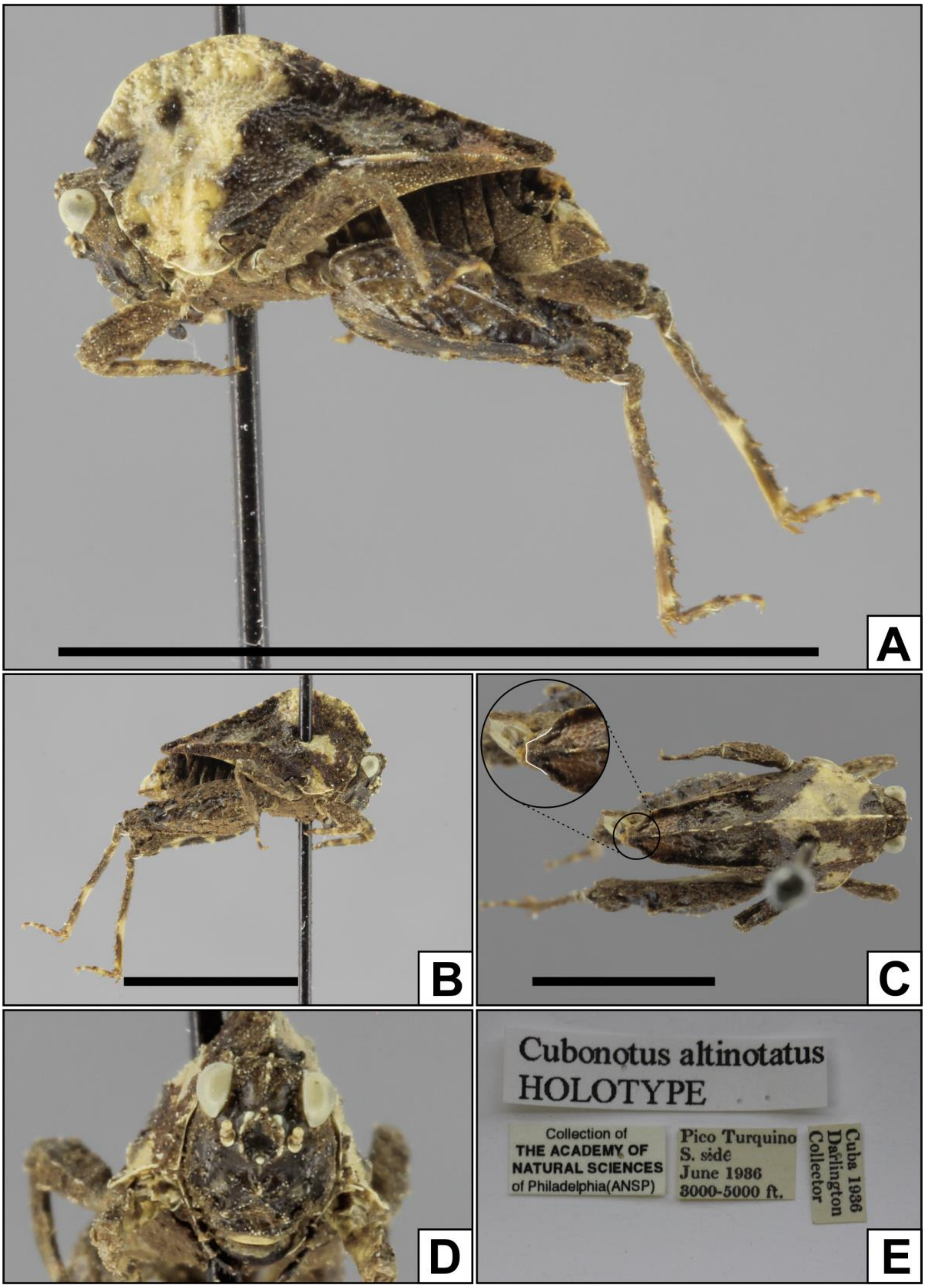


FIGURE 9. *Cubonotus altinotatus* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, highlight the shape of posterior margin of pronotum (outlined in white color), (D) frontal view and (E) labels. Scale bar = 0,5 cm.

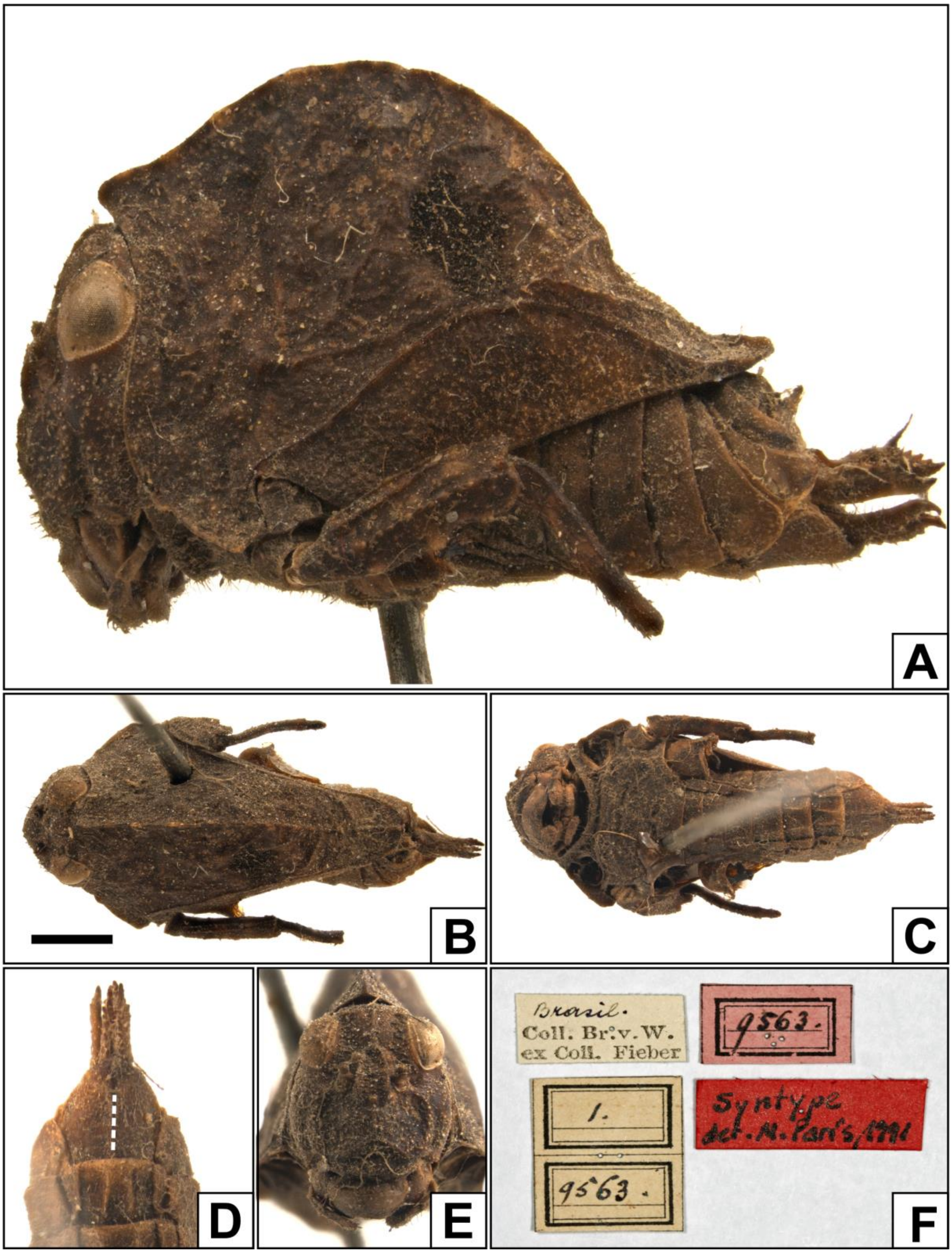


FIGURE 10. *Eleleus curtus* Bolívar, 1887 Syntype female. (A) *habitus* left lateral view, (B) *habitus* dorsal view, (C) *habitus* ventral view, (D) ventral view of subgenital plate highlight a longitudinal suture, (E) frontal view and (F) labels. Scale bar = 2mm. © *by Natural History Museum Vienna, NOaS Image Collection / H. Bruckner; published with permission*.

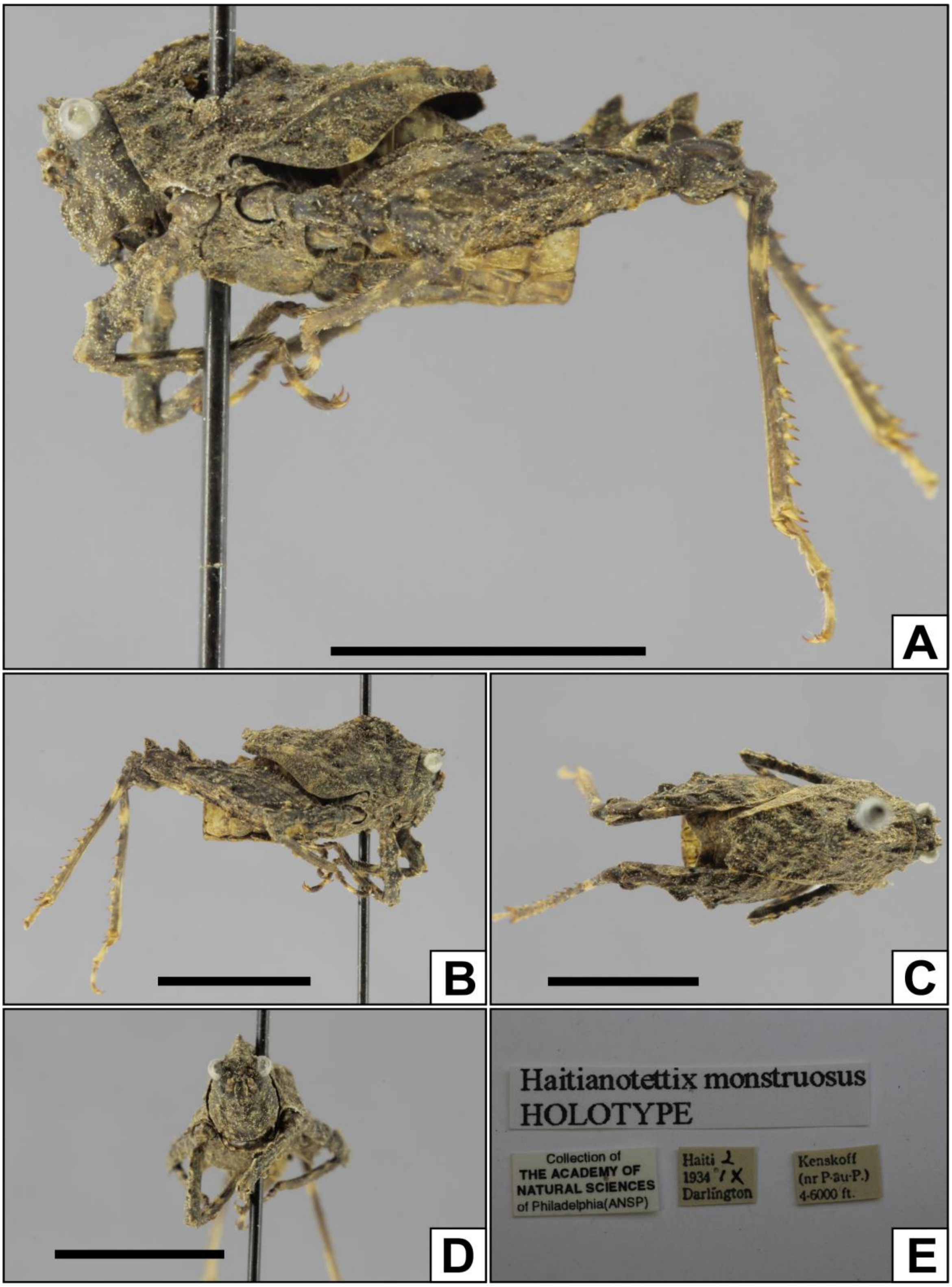


FIGURE 11. *Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998 Holotype of *Haitianotettix monstruosus* Perez-Gelabert, Hierro & Otte, 1998. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view (D) frontal view and (E) labels. Scale bar = 0,5 cm.

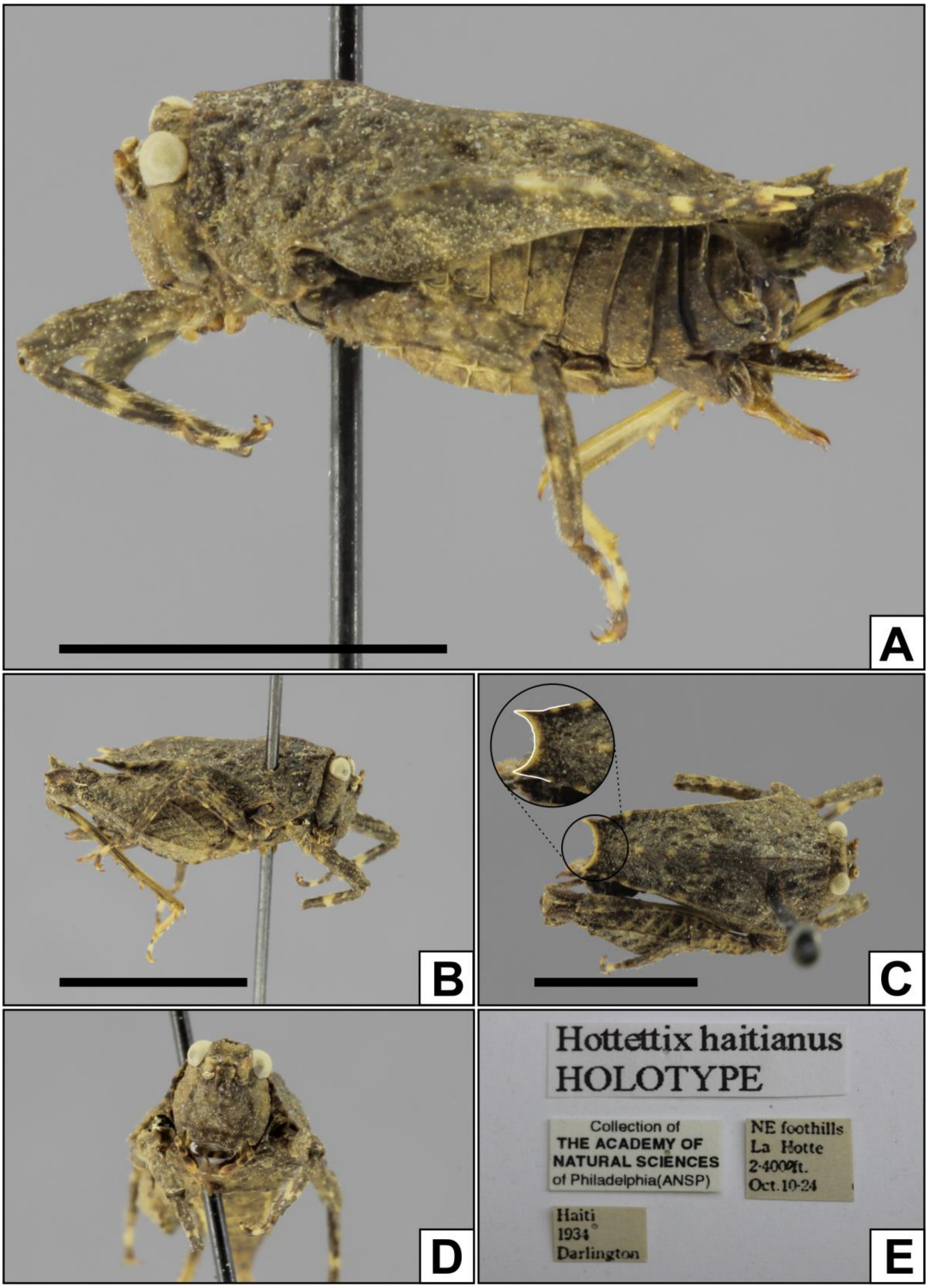
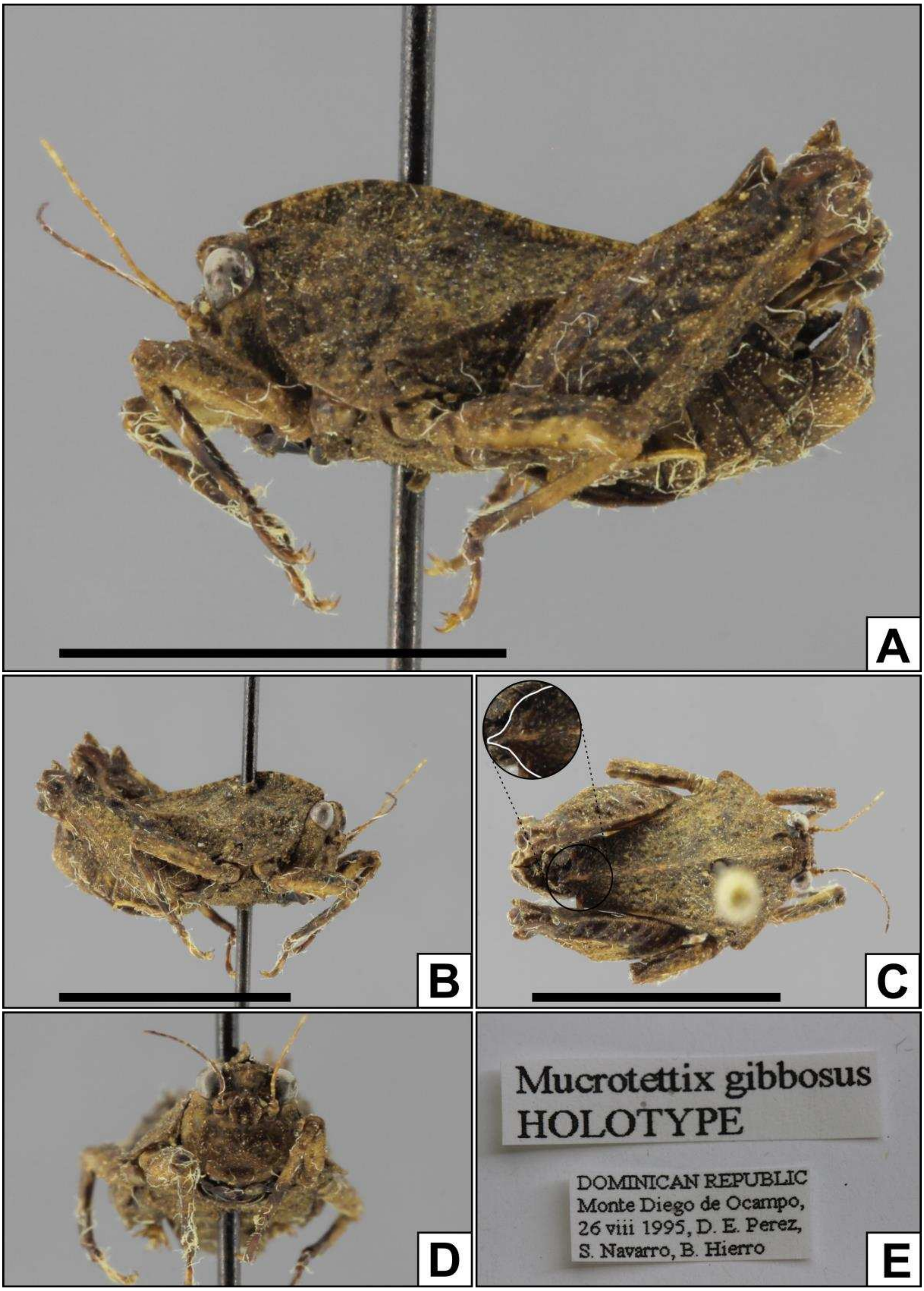


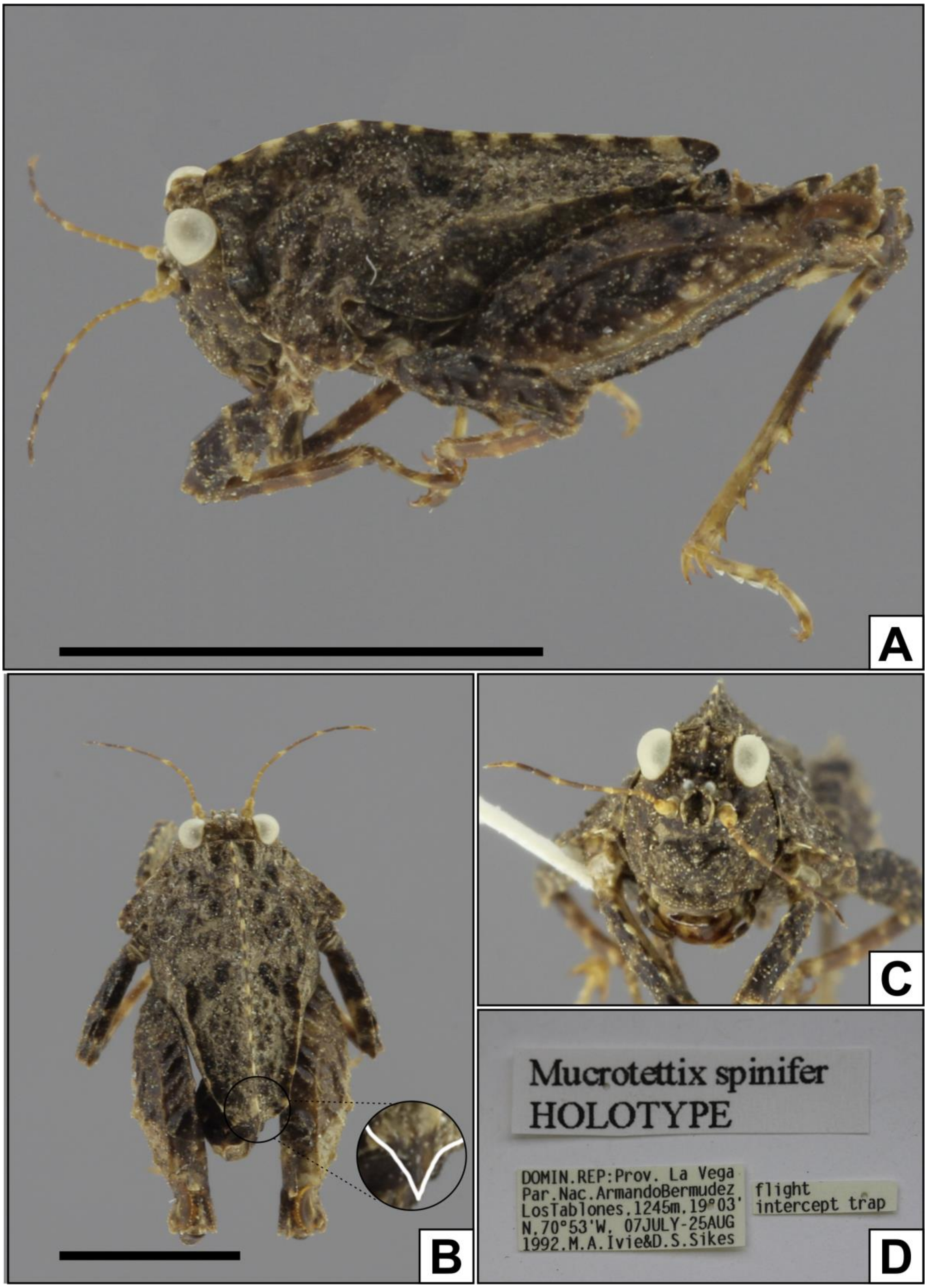
FIGURE 12. *Hottettix haitianus* Perez-Gelabert, Hierro & Otte, 1998 Holotype female. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, highlight the shape of posterior margin of pronotum (outlined in white color), (D) frontal view and (E) labels. Scale bar = 0,5 cm.



Mucrotettix gibbosus
HOLOTYPE

DOMINICAN REPUBLIC
Monte Diego de Ocampo,
26 viii 1995, D. E. Perez,
S. Navarro, B. Hierro

FIGURE 13. *Mucrotettix gibbosus* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, highlight the shape of posterior margin of pronotum (outlined in white color), (D) frontal view and (E) labels. Scale bar = 0,5 cm.



Mucrotettix spinifer
HOLOTYPE

DOMIN.REP:Prov. La Vega
Par.Nac.ArmandoBermudez
LosTablones.1245m.19°03'
N.70°53'W. 07JULY-25AUG
1992.M.A.Ivie&D.S.Sikes

flight
intercept trap

FIGURE 14. *Mucrotettix spinifer* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* dorsal view, highlight the shape of posterior margin of pronotum (outlined in white color); (C) frontal view and (D). Scale bar = 0,5 cm.

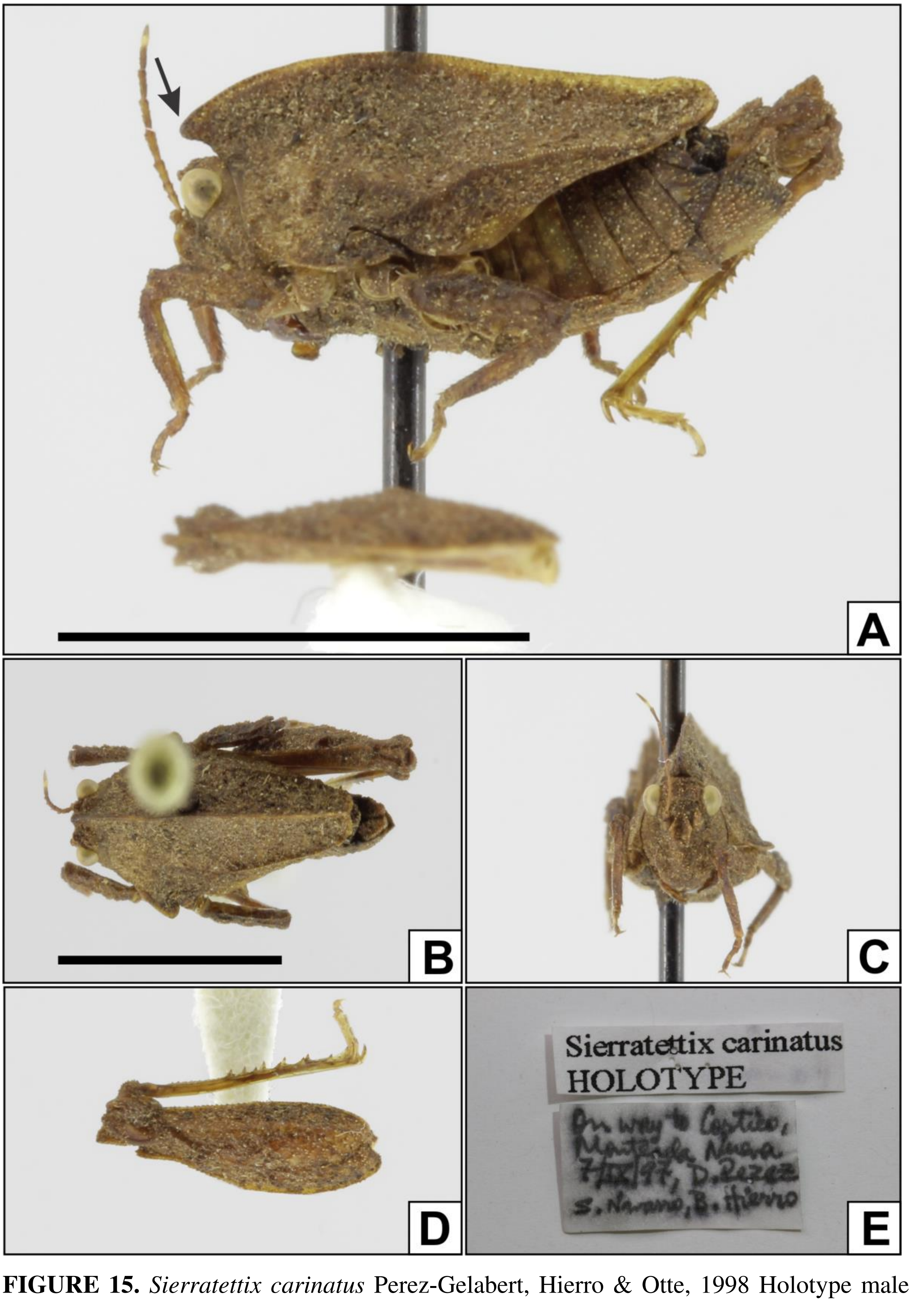


FIGURE 15. *Sierratettix carinatus* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, arrow pointing the anterior margin of pronotum slightly hook-like over the head, (B) *habitus* dorsal view, (C) frontal view, (D) hind femur glued on triangle and (E) labels. Scale bar = 0,5 cm.

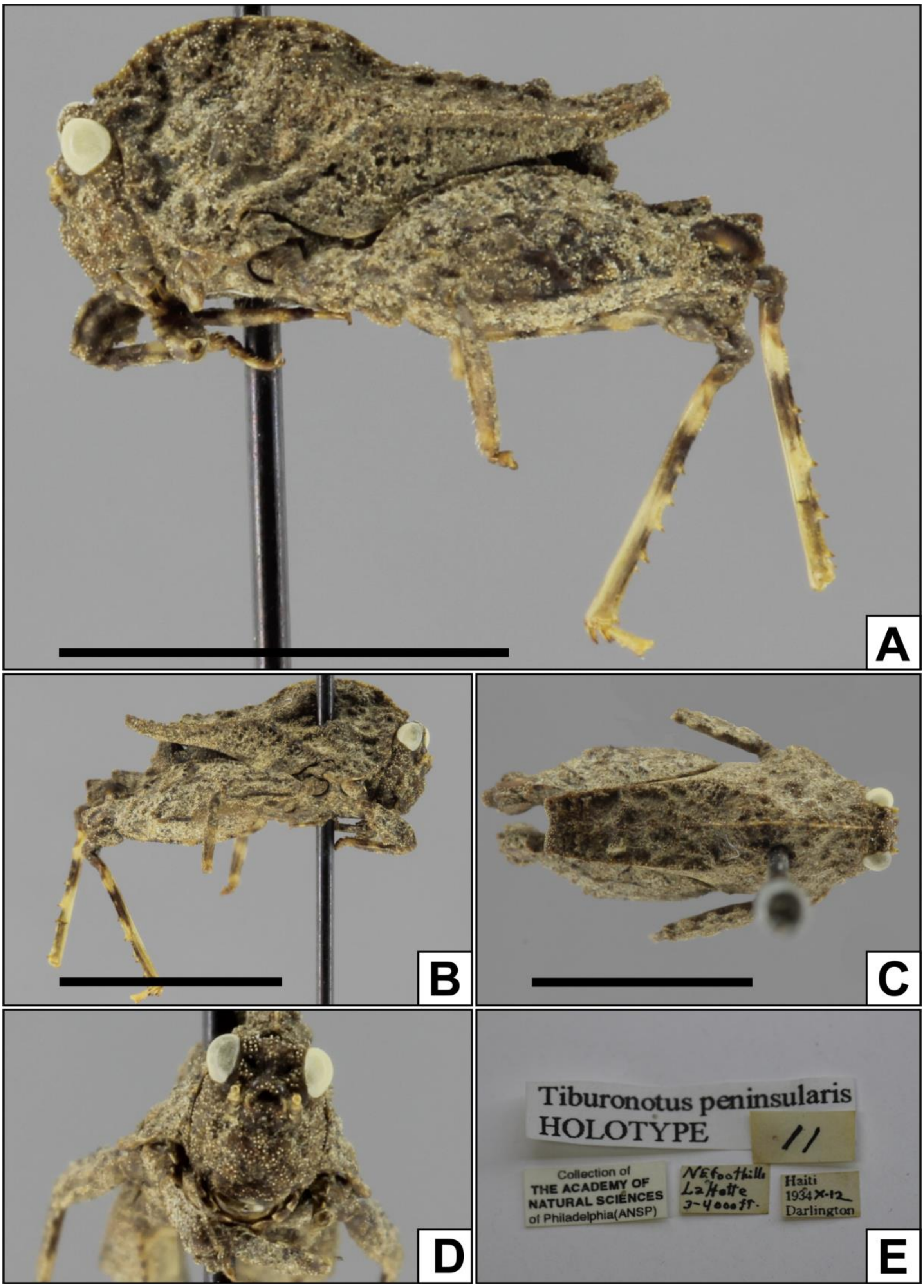
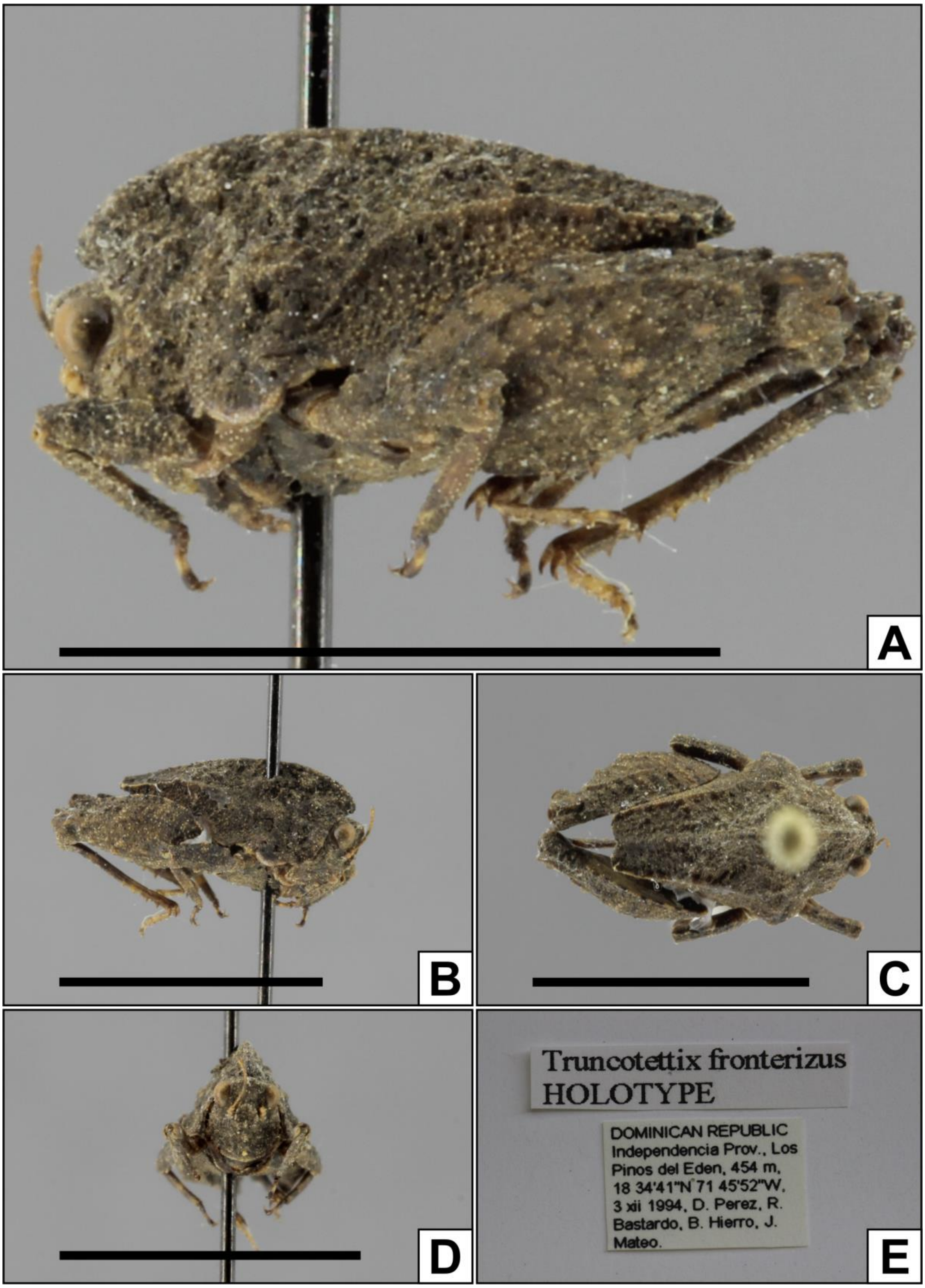


FIGURE 16. *Tiburonotus peninsularis* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, (D) frontal view and (E) labels. Scale bar = 0,5 cm.



Truncotettix fronterizus
HOLOTYPE

DOMINICAN REPUBLIC
Independencia Prov., Los
Pinos del Eden, 454 m,
18 34'41"N 71 45'52"W,
3 xii 1994, D. Perez, R.
Bastardo, B. Hierro, J.
Mateo.

FIGURE 17. *Truncotettix fronterizus* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* right lateral view, (C) *habitus* dorsal view, (D) frontal view and (E) labels. Scale bar = 0,5 cm.

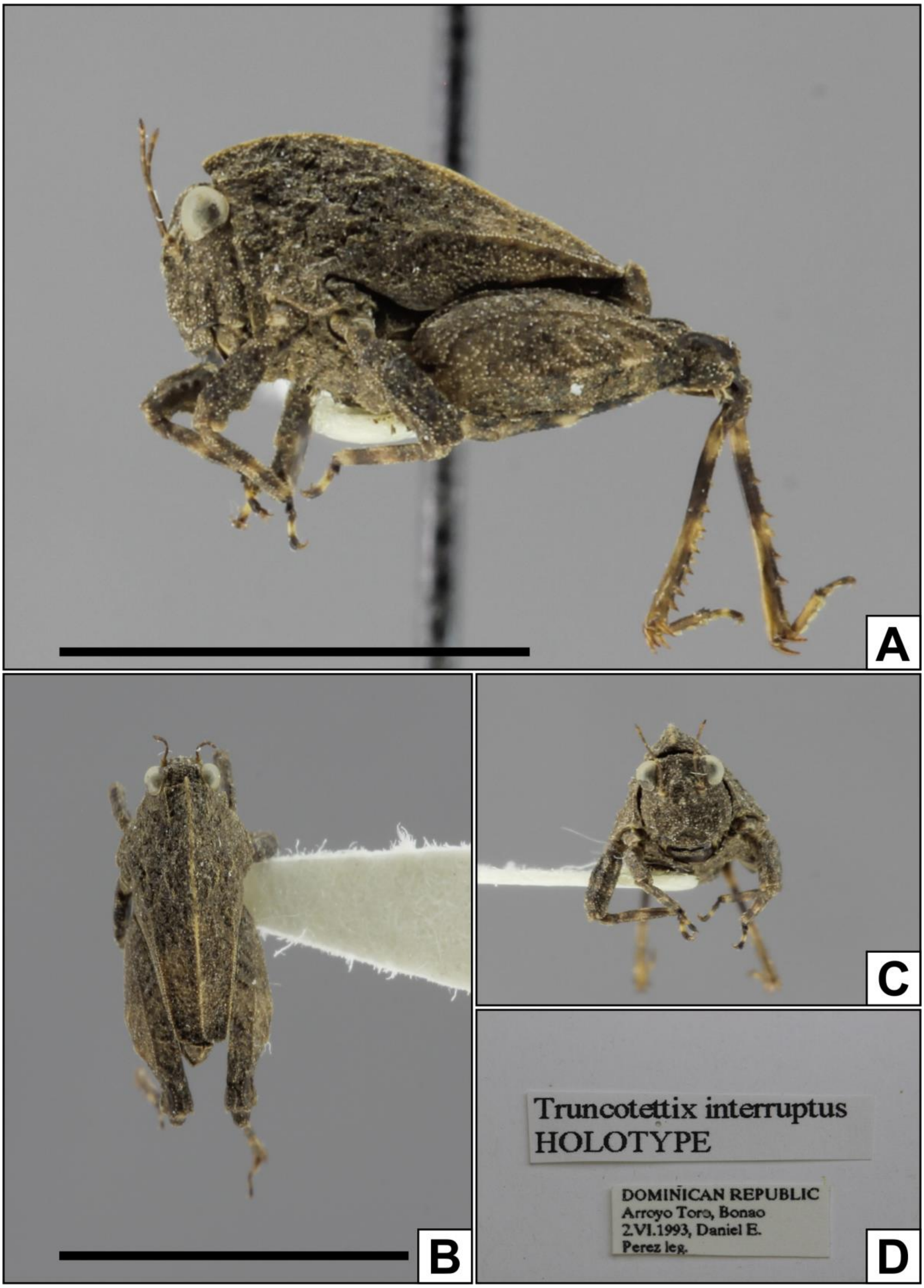


FIGURE 18. *Truncotettix interruptus* Perez-Gelabert, Hierro & Otte, 1998 Holotype male. (A) *habitus* left lateral view, (B) *habitus* dorsal view, (C) frontal view and (D) labels. Scale bar = 0,5 cm.

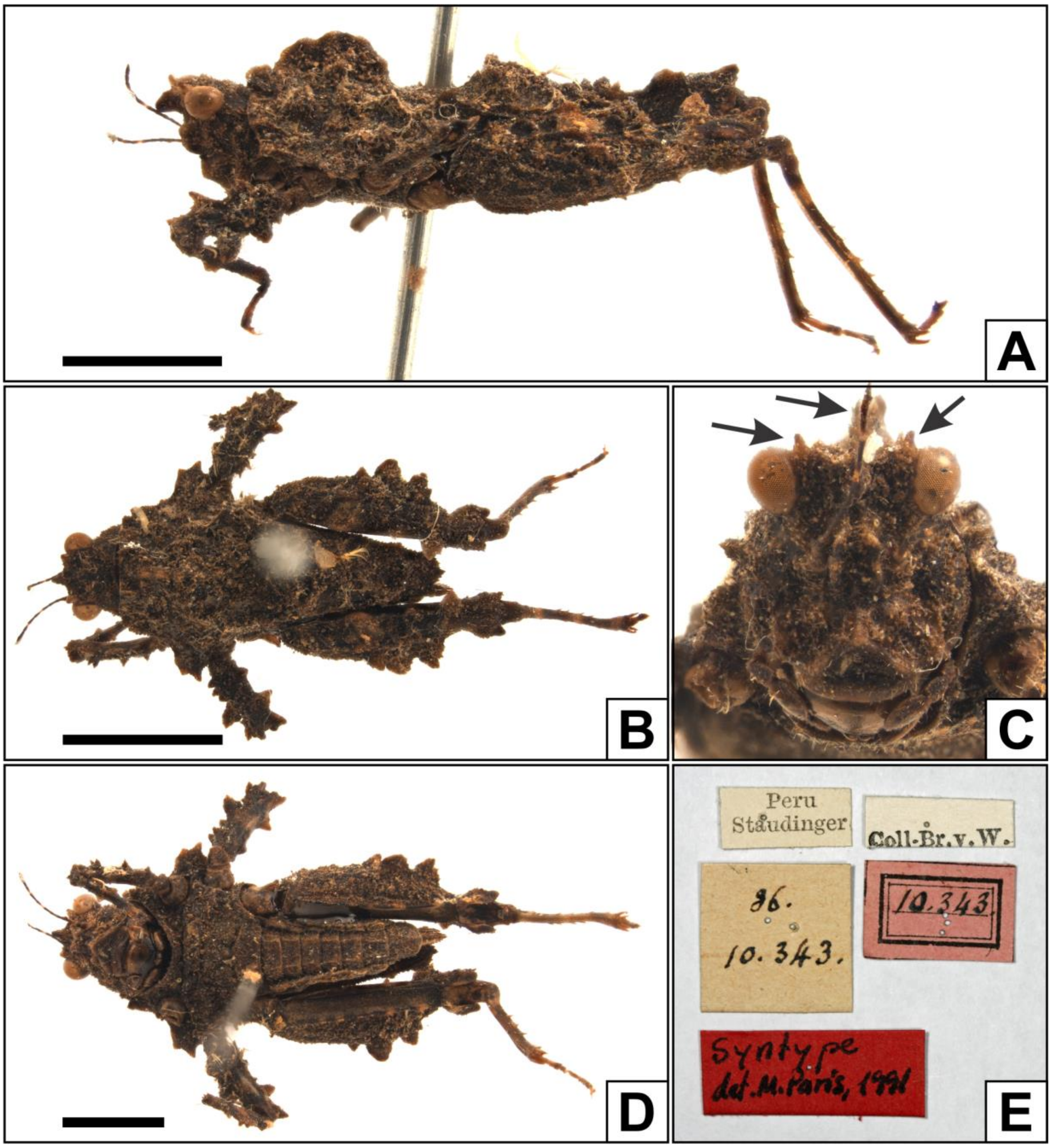


FIGURE 19. *Cota saxosa* Bolívar, 1887 Syntype female. (A) *habitus* left lateral view, (B) *habitus* dorsal view, (C) *habitus* ventral view, (D) frontal view with arrows pointing the Hancock's and Bolívar's tricuspidate form and (E) labels. Scale bar = 2 mm. © *by Natural History Museum Vienna, NOaS Image Collection / H. Bruckner; published with permission.*

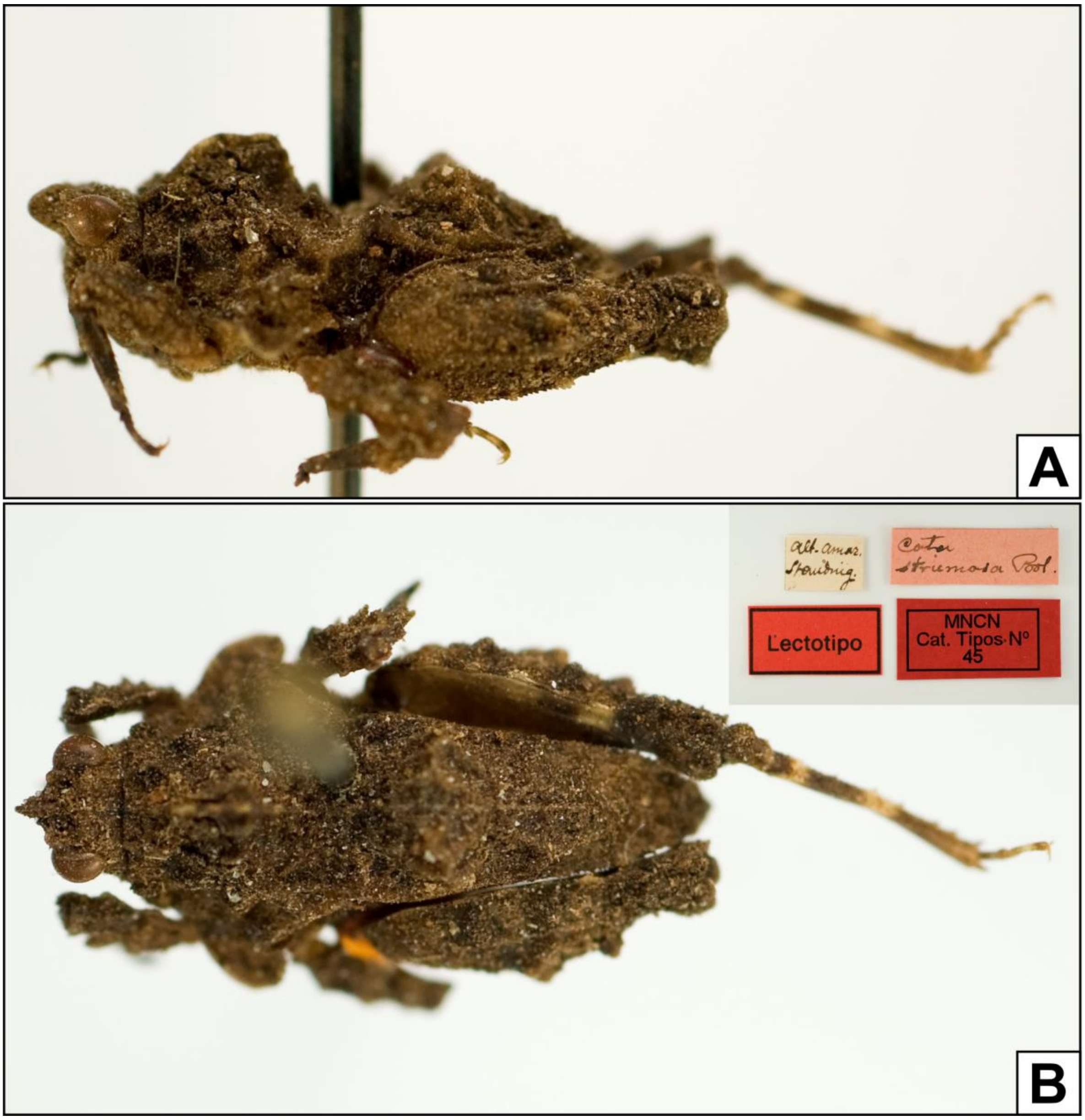
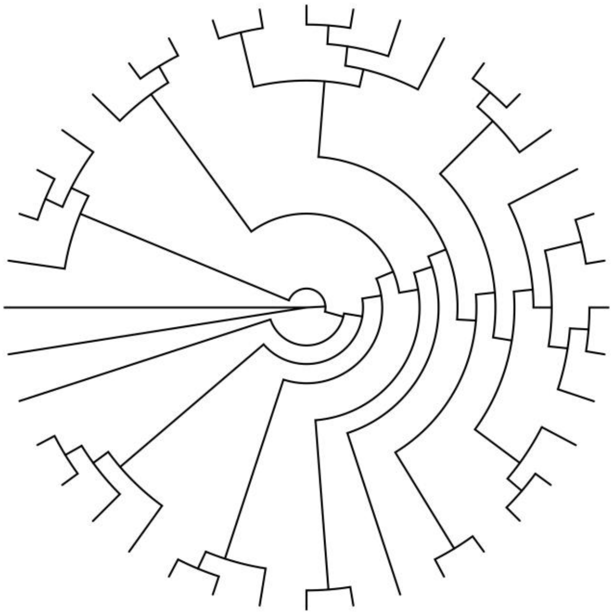


FIGURE 20. *Cota strumosa* Bolívar, 1887; Lectotype male. (A) *habitus* left lateral view and (B) *habitus* dorsal view with labels. Photos: Josip Skejo (MNCN).

FIGURE 21. *Cota undulata* (Cadena-Castañeda & Cardona, 2015) **n. comb.** to *Metrodora undulata* Cadena-Castañeda & Cardona, 2015 Holotype male. *Habitus* left lateral view. Photo: Oscar J. Cadena-Castañeda (CAUD).

Artigo 4

Preliminary study on Batrachideinae (Insecta: Orthoptera: Caelifera: Tetrigidae) phylogeny based on morphology data



Preliminary study on Batrachideinae (Insecta: Orthoptera: Caelifera: Tetrigoidea: Tetrigidae) phylogenetic based on morphology data

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Abstract

Batrachideinae is pantropical distribution subfamily whose diversity is expressive in the Neotropical region. Despite being easily distinguished from other taxa of tetrigids and being an expressive taxa, poorly is known about the relationships among the genera and the phylogeny of this family has never been proposed using modern cladistics methods. In this study, we present the first phylogenetic analysis of Batrachideinae based on 28 taxa and 71 morphological characters. The analyses of the resulting data matrix supported the monophyly of Batrachideinae with two districts clades and a new combination *Scaria verutum* (Grant, 1956) **n. comb.** was proposed. This proposal is the first step towards building the evolution history of Batrachideinae.

Key Words: Diversity, tetrigids, Neotropical region.

Resumo

Batrachideinae é uma subfamília com distribuição pantropical cuja diversidade é expressiva na região Neotropical. Apesar de ser facilmente distinto dos demais tetrigídeos e ser um grupo expressivo, pouco se sabe sobre as relações entre os gêneros e nunca foi proposta uma filogenia baseada em métodos cladísticos. Neste estudo, apresentamos a primeira analise filogenética de Batrachideinae baseada em 28 táxons e 71 caracteres morfológicos. A análise da matriz de dados resultante sustentou a monofilia de Batrachideinae com dois distintos clados e uma nova combinação foi proposta *Scaria verutum* (Grant, 1956) **n. comb.** Esta proposta é o primeiro passo para construir a história da evolução de Batrachideinae.

Palavras-chave: Diversidade, tetrigídeos, região Neotropical.

Introduction

The Batrachideinae Bolívar, 1887 is composed of species easily distinguish from other tetrigids subfamilies by the presence of anterior femur usually sulcate above in at least part of femoral length and median femur always distinctly sulcate above for entire lengths (Rehn & Grant 1958, 1961, Grant 1962); usually with an internal dorso-apical spine on middle femur; female spermatheca with two diverticula, the dorsal one longer and usually with an apical development (expansion, or Y-shaped structure) and the ventral one simple or slightly expanded (Grant 1962, 1966). They have a body generally square shaped, robust and a high number of antennal segments (usually more than 20) (Rehn & Grant 1958).

This group was described by Bolivar (1887) on the "*Essai sur les Acridiens de la tribu des Tettigidae*" as "*Section Batrachideae*" and from this first publication, several authors were adding species and genera to this taxon as Bruner *et al.* (1900-1909); Hancock (1902), Bruner (1910), Sjöstedt (1921) and Günther (1936) even the most deeply studies done by Grant (1955, 1956, 1962, 1966) and Rehn & Grant (1958, 1961) which in reviewed and described several species from different localities on the world. The last two genera descriptions were made by Steinmann (1973) regarding *Vilma* and after forty years, the latter genus *Wiemersiella* described by Tumbrinck (2014).

In these one hundred and twenty-seven years of taxonomic history, the diversity of Batrachideinae it showed is unique among the tetrigids. In the Neartic region, there are *Paxilla* Bolívar, 1887 and some members of *Tettigidea* Scudder, 1862; in the Neotropical region there are significant diversity (Rehn & Grant 1961) represented by *Batrachidea* Serville, 1838; *Cranotettix* Grant, 1955; *Eutettigidea* Hancock, 1914; *Halmatettix* Hancock, 1909; *Lophoscirtus* Bruner, 1910; *Paurotarsus* Hancock, 1900; *Plectronotus* Morse, 1900; *Puiggaria* Bolívar, 1887; *Rehnidium* Grant, 1956; *Scaria* Bolívar, 1887 and *Tettigidea*. In Africa continent, there are only two known genera: *Ascetotettix* Grant, 1956 and *Phloeonotus* Bolívar, 1887 and in Asia, Australia and Pacific region there are *Bufonides* Bolívar, 1898; *Palaioscaria* Günther, 1936; *Saussurella* Bolívar, 1887; *Vingselina* Sjöstedt, 1921; *Vilma* Steinmann, 1973 and *Wiemersiella* Tumbrinck, 2014 (Cigliano *et al*. 2018).

The disjunctive distribution essentially pantropical of Batrachideinae suggests that this group is an old taxa (Rehn & Grant 1961) and little is known about the relations among the members of this group. There has never been a modern phylogenetic analysis to Tetrigidae, only some suprageneric taxonomic proposals were indicated by Kevan (1982) and Rowell & Flook (1998).

According with them, Batrachideinae is the most well defined tetrigid group and this cohesive taxon has exclusives characteristics in which stimulated proposal for this group to become a family of Tetrigidae. Kevan (1982) from the morphological characteristics as antennal segments, fore femur crest and pronotum shape, had suggested that the subfamily Batrachideinae is taxa distinct of the other tetrigids, which in the name would be Batrachideidae. Rowell & Flook (1998) indicated the similar results from molecular data (18S rRNA). However, there is no agreement about this question.

Grant (1955,1956a,b; 1966) indicated that some genera are related based on morphological characters and in his unpublished thesis (Grant 1962), reviewing several studies regarding the Batrachideinae, he hypothesized the possible relationship between geographically distant taxa, particularly the Neotropical and Neartic taxa as *Tettigidea*, *Batrachidea*, *Paurotarsus*, *Paxilla* and *Rehnidium* which in form one related complex; *Cranotettix* and *Pletronotus* also appear to be related; one species of *Rehnidium* is related to *Scaria* and *Paxilla* is considered closely related to *Tettigidea*.

According with Grant (1962), there was no clear definition for each Batrachideinae genera since this definition is harder to limit than the determination of species and it is possible to observe easily this affirmation since some characteristics used to define a specific genera also are shared with different taxa. The scarcity in diagnostic characteristics, the polymorphism between specimens of same species present in the Neartic and Neotropical groups (see Grant 1955a,b 1956) and the limited representativeness of sampled specimens makes harder the establish relationship among the known species.

Thus, in this study we present the first cladistic hypothesis of Batrachideinae to describe the relationships among the genera of different bioregions. We also provide a discussion about the morphological characters to establish a basis for future studies on the evolution of batrachideines.

Material and Methods

Taxon sampling

Our study included 28 terminals (two outgroups and twenty-six ingroup taxa) (Figs. 1-4), for outgroup taxa we included two Neotropical species: *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999 (Cladonotinae) (Fig. 2B) and *Lophotettix hancocki* (Bruner, 1910) (Lophotettiginae) (Fig. 2A) (Table1). The ingroup taxa comprised one species of each genus: *Ascetotettix capensis* (Günther, 1956) (Fig. 4A); *Batrachidea vesca* Grant, 1956 (Fig. 2C); *Bufonides antennatus* Bolívar, 1898 (Fig. 4B); *Cranotettix* alpha Grant, 1955 (Fig. 2D); *Eutettigidea lineata* (Bruner, 1910) (Fig. 2E); *Halmatettix furcatus* Grant, 1955 (Fig. 2F); *Lophoscirtus gracilis* (Bruner, 1900) (Fig. 2G); *Palaioscaria calosoma* (Günther, 1934) (Fig. 4C); *Paxilla obesa* (Scudder, 1877) (Fig.2H); *Plectronotus excavatus* Grant, 1955 (Fig.3A); *Phloeonotus humilis* (Gerstaecker, 1869) (Fig. 4E); *Puiggaria antennata* Bolívar, 1887 (Fig. 1); *Saussurella cornuta* (Haan, 1843) (Fig. 4D); *Vingselina crassa Sjöstedt*, 1921 (Fig. 4F) and *Wiemersiella highlandensis* Tumbrinck, 2014 (Fig. 4G) (Table 1). The remaining genus, *Vilma* was not included because this species was not available at the time of the study.

For other four genera we used more than one species with the purpose of prospect the relations within these genera: (i) *Paurotarsus ruficornis* (Walker, 1871) (Fig. 2J) and *Paurotarsus insolitus abbreviatus* Grant, 1955 (Fig. 2I); (ii) *Scaria fasciata* Hancock, 1907 (Fig. 3G) and *Scaria producta* Hancock, 1907 (Fig. 3H) and its relative genus (iii) *Rehnidium* with *Rehnidium mendosum* Grant, 1956 (Fig. 3B); *Rehnidium necopinum* Grant, 1956 (Fig. 3C); *Rehnidium omnivagum* Grant, 1956 (Fig. 3D); *Rehnidium perexiguum* Grant, 1956 (Fig. 3E); *Rehnidium verutum* Grant, 1956 (Fig. 3F) and the Neotropical (iv) *Tettigidea scudderi* Bolívar, 1887 (Fig. 3J) with the Neartic *Tettigidea prorsa* Scudder, 1877 (Fig. 3I) (Table 1).

The studied materials can be found at the following institutions: Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), British Museum of Natural

History (BMNH),California Academy of Sciences (CAS), Florida State Collection of Arthropods (FSCA), Lyman Entomological Museum and Research Laboratory (LEMQ), Museum für Naturkunde Berlin (MNB), Museo Civico di Storia Naturale "Giacomo Doria" (MCSN), Muséum National d'histoire naturelle (MNHN), Naturhistorisches Museum Wien (NMW), Naturhistoriska Riksmuseet Stockholm (NHRS), University of Michigan Museum of Zoology (UMMZ Ann Arbor) and Hope Entomological Collections, University Museum of Natural History Oxford (UMO) (Table 1).

Character sampling and terminology

We consulted Grant (1955, 1956a,b; 1962, 1966) and Rehn & Grant (1958, 1961) to get characters that had been traditionally used in the batrachideines taxonomy. After this analysis, 71 morphological characters of head, pronotum, wings, tegmina and legs were sampled (Appendix 1-2). Though coloration in tetrigids is known to be variable in some taxa and is sometimes affected by local environmental conditions, the body coloration characters used here were invariable at the intraspecific level and appear to be heritable. The phallic complex was not included because was not possible made dissection procedure on the specimens. Also some characters regarding the terminalia were not sampled due the delicate condition of the types studied and the limited manipulation of these materials

Types imaging data

We photographed the type material deposited at the Academy of Natural Sciences, Philadelphia, USA (ANSP). External morphological characteristics were photographed with a Canon EOS T3i digital camera equipped with macro lens EF 100mm f/2.8 L in a photo lightbox. The other type species not housed at ANSP had the details photos provide by curators of collections (Table 1).

Cladistic analysis

Morphological characters used and their states are listed (Appendix 1) and the data matrix is presented in Appendix 3. Nonapplicable data were recorded as '–' and missing data as '?'. All characters were considered of equal weight and the multi-state characters were treated without particular order. We searched for the most parsimonious trees in TNT (Goloboff *et al.* 2003). The analysis were ran though "New Technology search" and for an independent analysis using a combination of 'sectorial search', 'drift', 'tree fusing' (Goloboff 1999) and 'ratchet' (Nixon 1999). The 'Random seed' indicated was 10 and the option ‘Collapse trees after search’ was flagged. Support for individual nodes was assessed by calculation of absolute Bremer (Br) support (Bremer 1994) and bootstrap support (Bs) (10.000 replicates) for the equally weighted analysis. Winclada (Nixon 2002) was used to map the characters and plot the tree.

Results and Discussion

Phylogenetic analysis: Batrachideinae is monophyletic taxa

The analysis resulted in seven most parsimonious trees of 301 steps with a consistency index (CI) of 0,35 and retention index (RI) of 0,54 indicating numerous homoplastic events (Fig. 5).The Bremer (Br) and the Bootstrap (Bs) are shown in the branches of the consensus tree (Fig. 6). Bremer Support was recapitulated from 70.792 trees with 0 cuts.

We recovered the Batrachideinae as a monophyletic group (Fig. 5), the clade including these members is supported by a 100% Bootstrap and Bremer values (Fig. 6) and also is supported by six synapomorphies: (i) lower margin of antennal grooves near the lower margin of the compound eye (17:1); (ii) first portion of median carinae slightly arcuate (26:1); (iii) fore femur dorsal and ventral margin almost straight (54:0); (iv) fore femur with paralell crest of the lateral margin (59:1) (Fig. 1); (v) middle femur dorsal and ventral margin almost straight (60:0) and (vi) middle femur with paralell crest of the lateral margin (62:1) (Fig. 1). Also two homoplasies supported this group: (i) apex of lateral lobe of pronotum shape almost squared (nearly 90º) (42:1) and (ii) pronotum apex rounded (47:0).

Relationships among Batrachideinae genera

The present study represents the first modern cladistic analysis of Tetrigidae which in Batrachideinae was strongly recovered as a monophyletic group. In our results, *H.furcatus*, *P.obesa* and *T. prorsa* diverged early and the remaining species were grouped into two main clades (Figs. 5-6).

Halmatettix is found in Peru, Bolivia and southeastern Brazil and currently has five species, *Halmatettix allardi* Grant, 1955; *Halmatettix cristinotus* Hancock, 1909; *Halmatettix major* Grant, 1955; *Halmatettix sordidus* Grant, 1955 and *H. furcatus* (Fig. 2F). This genus was considered by Grant (1962) as a taxon with “bizarre morphology”. This situation prevented him from establishing any idea of relationship with other taxa of Batrachideinae. However in our results, *Halmatettix* was recoverd as a sister-group of all species of Batrachideinae studied (Fig. 6).

Paxilla (Fig. 2H) is an endemic taxon from southeastern United States (Rehn & Grant 1961, Grant 1962) and is related with the Neartic *Tettigidea* species, as *T. prorsa* (Fig. 3I) but is easily distinguished from *Tettigidea* mainly by the fusiform shaped of body (Rehn & Grant 1961). *Tettigidea* is the biggest group of Batrachideinae, currently with forty one species and some subspecies described (Cigliano *et al*. 2018). *Tettigidea* has a wide distribution, from North America on the southern Canada to South America on northern Argentina (Rehn & Grant 1961, Cigliano *et al*. 2018). The morphology aspect of these species also varies widely as the distribution of this group, since the species of *Tettigidea* may present brachypronotal or macropronotal forms in a same species and also have species showing neotenic condition (Rehn & Grant 1961).

Tettigidea never been reviewed and as indicated by Grant (1962), probably with detailed studies this genus may be segmented into other small groups which in more closely related species will form distinct groups of species. In our analysis, this affirmation was observed from the relationship of the two *Tettigidea* species in relation the other batrachideines.

Our results divide Batrachideinae into two main clades, clade A and B (Figs. 5- 6). The clade A consists of the following species: *P.humilis* (Fig. 4E) from Ethiopian bioregion; *S.cornuta* (Fig. 4D) from Oriental bioregion; *W. highlandensis* (Fig. 4G), *B. antennatus* (Fig. 4B) and *V. crassa* (Fig. 4F) from Australian bioregion; *A. capensis* (Fig. 4A) from Ethiopian bioregion; *C. alpha* (Fig. 2D) and *P. excavates* (Fig. 3A) from Neotropical region, more specifically both found in Panamá (Figs. 5-6). This clade is supported by one synapomorphy, the projection slightly tapering towards the anterior margin of pronotum, but not hook-like, over the head (27:5) and seven homoplasies: (i) general coloration body with the same tones on the whole body excepting the macula and/or other highlighted part of body (2:1); (ii) vertex lower than median carina of pronotum anteriorly (3:2); (iii) facial carinae parallel, not touching each other (9:4); (iv) posterior part of frontal costa (before the bifurcation) not visible or small (15:1); (v) medial carina of the vertex inconspicuous (22:0); (vi) anterior margin of the pronotum projection produced over the head beyond the fastigium (29:0) and (vii) macula or cicatrix present (50:1).

In this clade, there is *Phloeonotus* that currently has three species: *P. humilis*, *P. masaiensis* Grant, 1956 and *P. planus* Podgornaya, 1982 (Cigliano *et al*. 2018). This genus was considered by Grant (1956b) closely related to *Halmatettix*, sharing several morphological details as shape of vertex, length of antennae, a tendency of reduction or loss of tegmina among other. Also are easily distinguished by the form of anterior margin of pronotum. Likewise, Grant (1956b) indicated that *Phloeonotus* also which seem to be allied with *Ascetotettix* and *Saussurella*, being this hypothesis closer to our results (Figs. 5-6).

Saussurella has eleven species: *S. acuticornis* Zheng, 1998; *S. borneensis* Hancock, 1912; *S. brachycornis* Deng, 2016; *S. cornuta* (Haan, 1843); *S. curticornu* Hancock, 1912; *S. decurva* Brunner von Wattenwyl, 1893; *S. indica* Hancock, 1912; *S. inelevata* Podgornaya, 1992; *S. javanica* Bolívar, 1898. *S. longiptera* (Yin, 1984) and *S. xizangensis* Zheng, Lin & Shi, 2013 (Cigliano *et al.* 2018). According Grant (1962, 1966) *Saussurella* has the relationships difficult to determine and in our results, this taxon is sister- group of two small clades into clade A (Figs. 5-6).

The small clade A1, consists of the three species: *W. highlandensis*, *B. antennatus* and *V. crassa* . This clade is supported by two homoplasies: fascial carina not touching or completely enveloping the medial ocellus on the base (11:0) and ventral sinus absent (40:2) (Fig. 5). In this clade, *W. highlandensis* was recovered as sister-group of *B. antennatus* and *V. crassa* which in are related by two homoplasies: the antennal grooves placed below the lower margin of the compound eye (17:0) and fore femur apical spine present (58:1) (Fig. 5).

Among the species of clade A1, The genus *Bufonides* currently has tree species: *Bufonides antennatus* Bolívar, 1898; *Bufonides sellatus* Hinton, 1940 and *Bufonides uvarovi* Hinton, 1940 (Cigliano *et al.*, 2018). Based on *B. antennatus* species, Hancock (1907) described a new section Bufonidae (or Bufonidinae), including only *Bufonides*. This genus is determined by broadly rounded and strongly convex pronotum, median carina absent, anterior border of the pronotum extended in a horn above the head and tegminal and ventral sinuses absent (see Hinton 1940; Tumbrinck, 2014).

Recently Tumbrinck (2014) designated this taxon from Cladonotinae due to their widened scutellum. However, the widened scutellum is not exclusive to Cladonotinae and Tumbrinck & Skejo (2017) based on comparative morphological data, suggested placed *Bufonides* into Batrachideinae.

The clade A2 consists of the three species: *A. capensis*, *P. excavates* and *C. alpha* supported by one synapomorpy: eyes globose and slight narrow with a flattened dorsal base (20:1) (Fig. 5). This clade exhibits a peculiar biogeographical pattern with in *A. capensis* occurs in Ethiopian region (South Africa) and *C. alpha* + *P. excavates* occur in Central America (both in Panamá). According Grant (1956b), *A. capensis* is slightly similar to *Cranotettix* but is easily distinguished by the shape of posterior margin of pronotum. *Plectronotus* is a small genus with two species: *P. excavates* and *Plectronotus scaber* Morse, 1900. Both are known only in central Costa Rica and northern Panama (Grant 1955b; Grant 1962; Cigliano *et al*. 2018).

In our results, *Plectronotus* was recovered as sister-group of *Cranotettix* in which is a monotype taxon and as mentioned by Grant (1955, 1962) is allied with *Plectronotus* (Figs. 5-6). This clade is supported by seven homoplasies: (i) Body coloration more or less the same tones on the whole body (2:0); (ii) frontal costa and fastigium not protruding or exceeding the level of dorsal margin of eyes (6:0); (15:0) posterior part of frontal costa visible (15:0); (iv) pronotum flattened laterally (25:0); (v) anterior margin of the pronotum hook-like, as a spine over the head (27:4) and (vi) anterior margin of the pronotum sharply cristate, high and thin (28:1); (vii) fore femur thin in relation to tibia (55:1) (Fig. 5). Both genera are endemic to Central America and are easily distinguished by the first portion of median carinae of pronotum with 'hump' and femurs dorsal and ventral margin with undulated carinae in *Plectronotus.*

The clade B consists of the following species: *P. insolitus abreviatus* and *P. ruficornis* ; *T. scudderi*; *E. lineata*; *L. gracilis*; *B. vesca*; *P. antennata*; all *Rehnidium* species: *R. mendosum*, *R. perexiguum*, *R. necopinum*, *R. omnivagum* and *R. verutum*; *S. fasciata*, *S. producta* and *P. serena* (Figs. 5-6). This clade is supported by two synapomorphies: pronotum flattened dorso- ventrally (25:2), median carina flatted dorsally (36:3) and one homoplasy: hind femur 3-3.5 times longer than broad (64:1) (Fig. 5).

Among the taxa of clade B, the two species of *Paurotarsus* was shown to be the sister-group of the clade (Figs. 5-6). There are only two species on this genus: *Paurotarsus ruficornis* (Walker, 1871) and *Paurotarsus insolitus* Rehn, 1916 with three subspecies *Paurotarsus insolitus abbreviatus* Grant, 1955; *Paurotarsus insolitus extremus* Grant, 1955 and *Paurotarsus insolitus insolitus* Rehn, 1916 (Grant 1955a, Cigliano *el al.* 2018) with wide distribution on Peru, Bolivia, Brazil, the Guianas, Trinidad, northern Colombia and southern Panama (Grant 1962). *Paurotarsus* is a sympatric genus (Grant 1955a) and is easily distinguishable from other batrachideines by the robust body and a large size (Grant 1962). In our results, this genus also has one synapomorphy: the "V" inverted shape of fascial carinae (9:6). Regarding the second *Tettigidea* species here included, *T. scudderi* confirmed the probably subdivisions inside the genus *Tettigidea*.

Eutettigidea and *Lophoscirtus* were grouped forming a small pectinate clade (Fig. 6). *Eutettigidea* has only one species, which in is poorly understood. About *E. lineata*, Grant (1956) affirmed that this taxon is most closely related to *Tettigidea*. In our results, *E. lineata* is related with *L. gracilis*. *Lophoscirtus* has a unique species and only four specimens known (Grant 1956, 1962; Cigliano *et al*. 2018) found in northeastern Argentina and southern Uruguay (Grant 1962). The head of *Lophoscirtus* with the frontal costa protrusive, almost horn-like (8:1) and the antennal groves placed between the compound eyes (17:2) are an exclusive characteristic among the Batrachideinae (Fig. 6).

In the clade B, there are *Rehnidium*, *Batrachidea*, *Puiggaria*, *Scaria* which in were considered by Grant (1962) as complex of species. Allied with *Scaria*, also there is *Palaioscaria*, the unique species non Neotropical present in this clade that share several characters to the genus *Scaria* (Fig. 5). In our results, the complex *Rehnidium*, *Batrachidea*, *Puiggaria* does not fall apart in a consensus tree, forming a pectinate clade (Fig. 6), but for future studies, the phylogenetic relationships of the species could likely be resolved.

Rehnidium is a small group with five species: *Rehnidium mendosum* Grant, 1956; *Rehnidium necopinum* Grant, 1956; *Rehnidium omnivagum* Grant, 1956; *Rehnidium perexiguum* Grant, 1956 and *Rehnidium verutum* Grant, 1956 (Grant 1956, 1962; Cigliano *et al*. 2018). All of them based on few specimens, poorly sampled and overlooked.

Batrachidea is a South America genus with five species: *Batrachidea flavonotata* Bolívar, 1887; *Batrachidea inermis* Hebard, 1923; *Batrachidea macella* Grant, 1956; *Batrachidea mucronata* (Saint-Fargeau & Serville, 1825) and *Batrachidea vesca*. The latter species is a small species of genus which in Grant (1956) indicated that it was closely related to *Scaria*, slightly less to *Rehnidium* and *Tettigidea*. *Puiggaria* Bolívar, 1887 has a unique species, *P. antennata* found only in Brazil (Grant 1956; Cigliano *et al*. 2018). Bruner (1910) indicated that this genus is related with *Batrachidea* and *Scaria* and Grant (1956) considered *Puiggaria* remotely related to others Batrachideinae due the fascial carinae widely divergent.

The pectinate clade formed by *Rehnidium*, *Batrachidea*, *Puiggaria* in our results was grouped to *Scaria, R. verutum* a and *P. serena* (Fig. 6). The three latter species were united by six homoplasies: (i) body slender (0:2); (ii) pronotum length shorter than wings (45:0) and with (iii) approximately 1/3 of total pronotal length extending beyond the limits of the abdomen; (iv) macropterus (53:1); (v) fore femur thin in relation to tibia (55:1) and (vi) femur and tibia almost equally thin (56:1) (Fig. 5).

Regarding *Scaria*, our study confirmed the affirmation of Grant (1962) in which *R. verutum* resembling morphologically with a *Scaria*. *R. verutum* also was recovered as sister-group of *Scaria* and *Palaioscaria.* Thus, according with the morphological similarities, the new combination *Scaria verutum* (Grant, 1956) **n. comb.** should be used when referring to this specimen. Our results also indicated similar results of Grant (1962) hypothesis which in *Palaioscaria* has an apparent resemblance to the South American genus *Scaria* but this relationship needs to be morphologically assessed more depth.

Morphological comments of some Batrachideinae

The relation among the taxa presented here are very similar to the morphological suggestion of kinship presented by Grant (1955, 1956a,b; 1962, 1966) and Rehn & Grant (1958, 1961). Although being a cohesive group, many characteristics in batrachideine have several states, which indicates the immense diversity of morphological characteristics present in this analysis (Appendix 1- 2), as the body shape, all possible forms of the facial carinae and anterior margin of the pronotum shape. Rehn & Grant (1958) shown that the Batrachideinae may always be distinguished by the presence of crest on the middle femur and, usually, of a similar crest on the fore femur although this latter character is sometimes obsolete in Neotropical genera. According Grant (1962), due the diversity present in Batrachideinae, the only constant morphological characteristic present in all batrachideines is the sulcate median femora and the bi-diverticulate character of the female spermatheca.

Spermatheca of Tetriginae and Batrachideinae species were firstly studied by Slifer (1943) and she indicated two kind of spermatheca, one for each subfamily. From this study, Grant (1962) also showed the peculiar shape of batrachideines spermatheca and indicated the spermathecal diverticula are characters of high utility in separating genera and species. Grant (1962) assumed that two diverticula in a spermatheca is a basal character since this condition is unique among tetrigid which corroborates that batrachideines are an ancient group. However, this aspect needs to be analyzed, since the data about the morphology of female structures are overlooked and poorly understood. The spermatecal data were not available to this study since this analysis was conducted on type species and it was not recommended to handle or cause modifications to the specimens.

Among all species known of Batrachideinae and all aspects concerning it taxonomy, the delimitation of genera is considerably the most difficult features in this group (Grant 1962). Thus, among the taxa here analyzed, *Tettigidea* is the group with several morphological variations and needs a deep revision. Our results indicated that *T. prorsa* and *T. scudderi* presented distinct positions in the tree and this probably occurs due the divergent morphological aspects in species of *Tettigidea*.

As *T.prorsa*, there are several species of *Tettigidea* that not share the the pronotum flattened dorso- ventrally (*eg*. *Tettigidea annulipes* Bruner, 1910; *Tettigidea paratecta* Rehn, 1913; *Tettigidea pulchella* Rehn, 1904; *Tettigidea steinbachi* Bruner, 1920 among other) or species without anterior margin of the pronotum rounded and slightly protruding but with hook-like margin (*eg*. *Tettigidea acuta* Morse, 1895; *Tettigidea chapadensis* Bruner, 1910; *Tettigidea corrugata* Bruner, 1910; *Tettigidea costalis* Bruner, 1910; *Tettigidea hancocki* Bruner, 1910 among other). Probably, due to this variation of characteristics in *Tettigidea*, Grant (1962) indicated the possible complex between *Tettigidea* - *Rehnidium* – *Batrachidea*. Thus, *Tettigidea* must be deep reviewed to show the affinities which the genus with other taxa.

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FIGURE 1. Lateral view of *Puiggaria antennata* Bolívar, 1887 with arrows highlighting the crest presents in the fore and middle femurs. Scale bar: 5 mm.

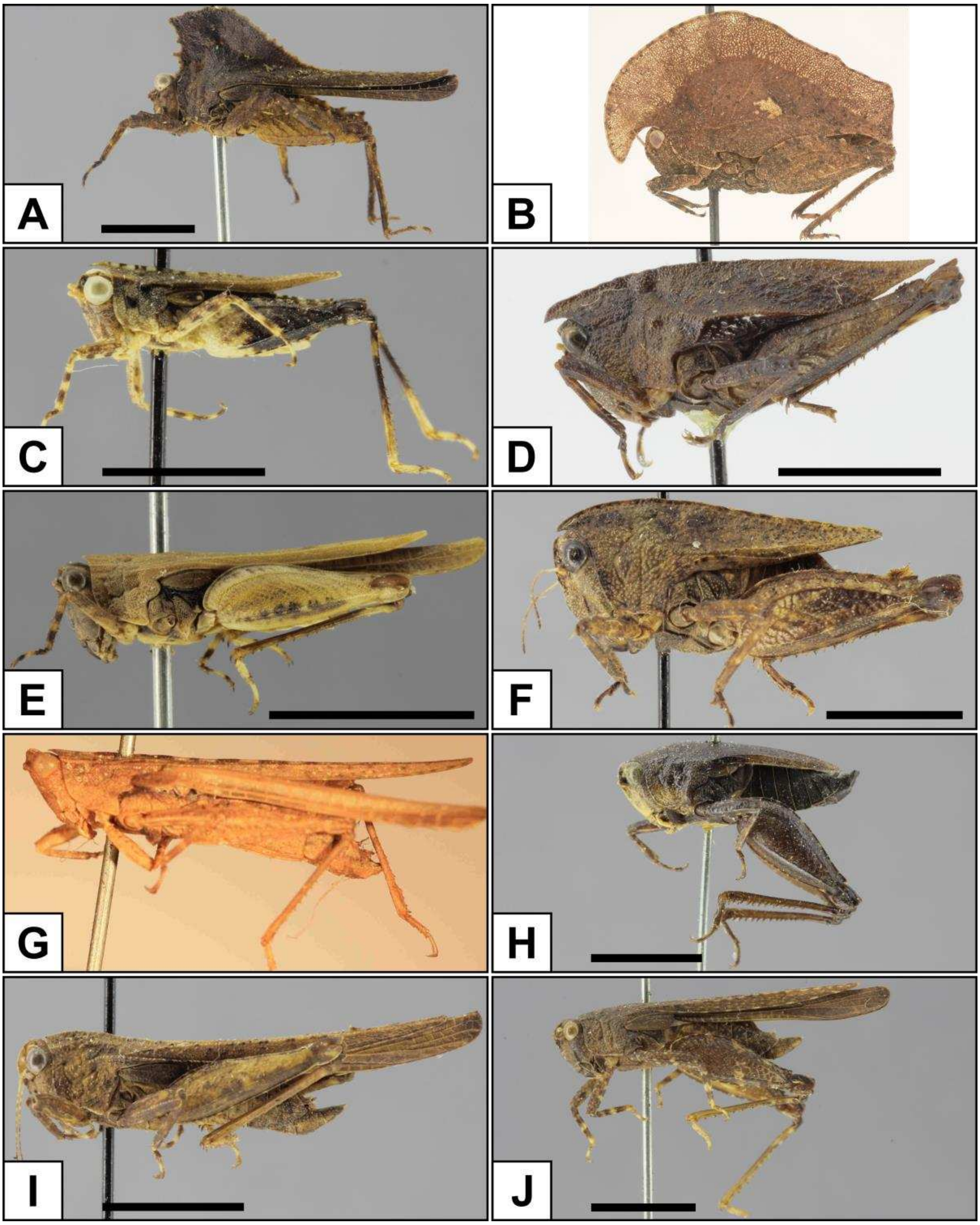


FIGURE 2. Neartic and Neotropical taxa of Bratrachideinae (lateral view): (A) *Lophotettix hancocki* (Bruner, 1910); (B) *Choriphyllum bahamensis* Perez-Gelabert & Otte, 1999; (C) *Batrachidea vesca* Grant, 1956; (D) *Cranotettix alpha* Grant, 1955; (E) *Eutettigidea lineata* (Bruner, 1910); (F) *Halmatettix furcatus* Grant, 1955; (G) *Lophoscirtus gracilis* (Bruner, 1900); (H) *Paxilla obesa* (Scudder, 1877); (I) *Paurotarsus insolitus abbreviatus* Grant, 1955 and (J) *Paurotarsus ruficornis* (Walker, 1871). Scale bar: 5 mm.

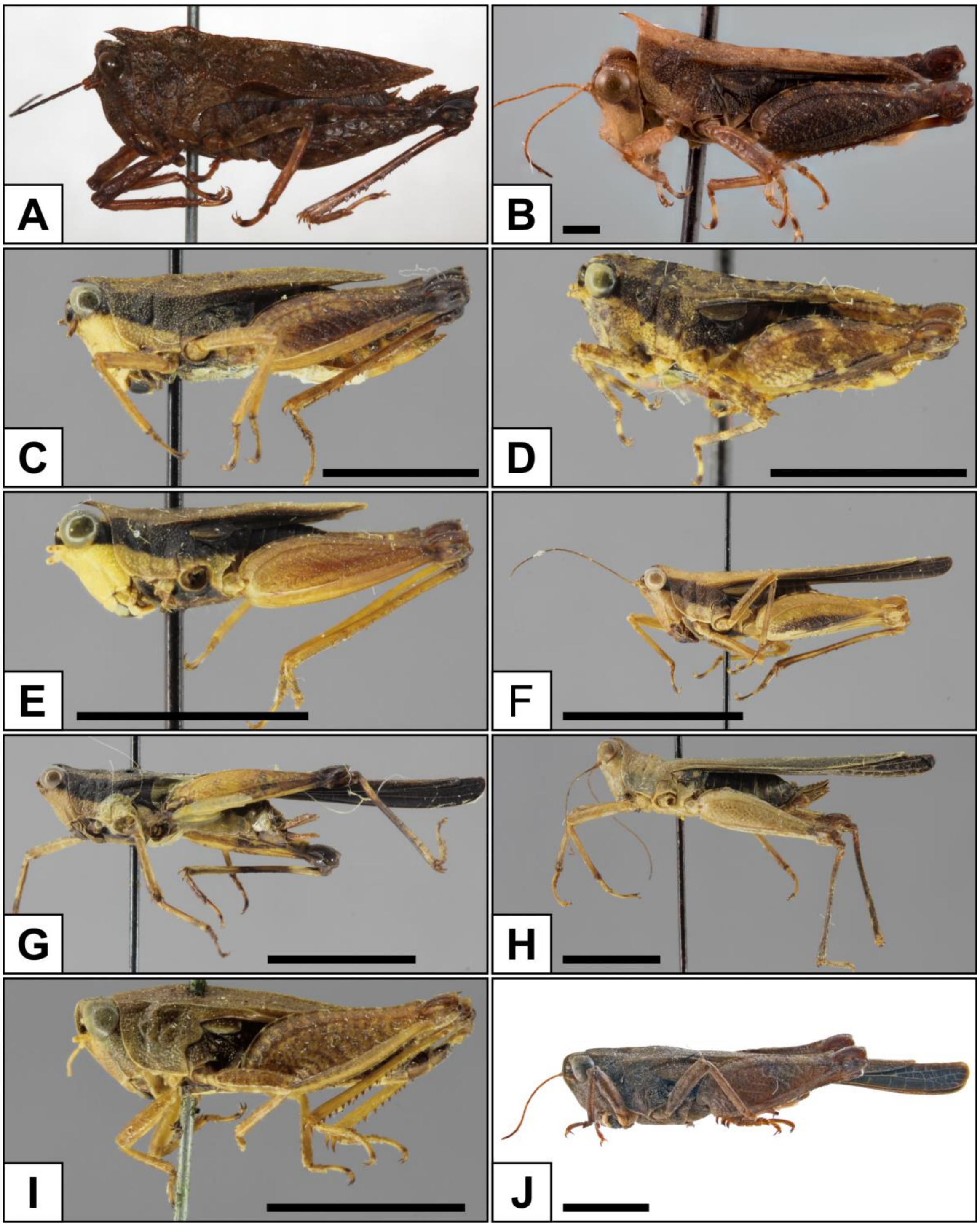


FIGURE 3. Neartic and Neotropical taxa of Bratrachideinae (lateral view): (A) *Plectronotus excavatus* Grant, 1955; (B) *Rehnidium mendosum* Grant, 1956; (C) *Rehnidium necopinum* Grant, 1956; (D) *Rehnidium omnivagum* Grant, 1956; (E) *Rehnidium perexiguum* Grant, 1956; (F) *Scaria verutum* (Grant, 1956) **n. comb.**; (G) *Scaria fasciata* Hancock, 1907; (H) *Scaria producta* Hancock, 1907; (I) *Tettigidea prorsa* Scudder, 1877 and (J) *Tettigidea scudderi* Bolívar, 1887. Scale bar: 5 mm.

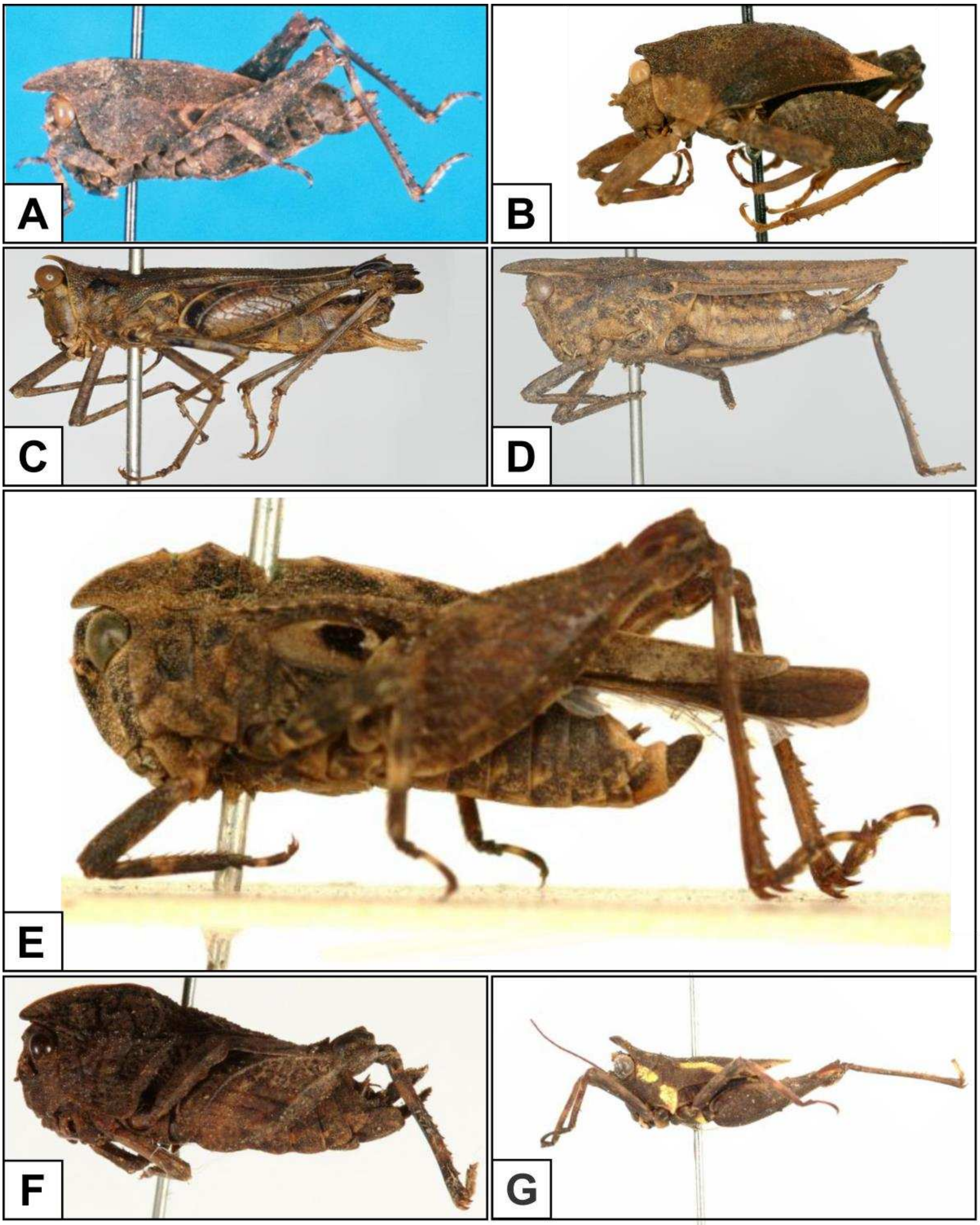


FIGURE 4. Asian, Australian and Ethiopian (lateral view): (A) *Ascetotettix capensis* (Günther, 1956); (B) *Bufonides antennatus* Bolívar, 1898; (C) *Palaioscaria serena* Günther, 1938; (D) *Saussurella cornuta* (Haan, 1843); (E) *Phloeonotus humilis* (Gerstaecker, 1869) holotype of *Phloeonotus sinuatus* Hancock, 1907; (F) *Vingselina crassa* Sjöstedt, 1921 and (G) *Wiemersiella highlandensis* Tumbrinck, 2014.

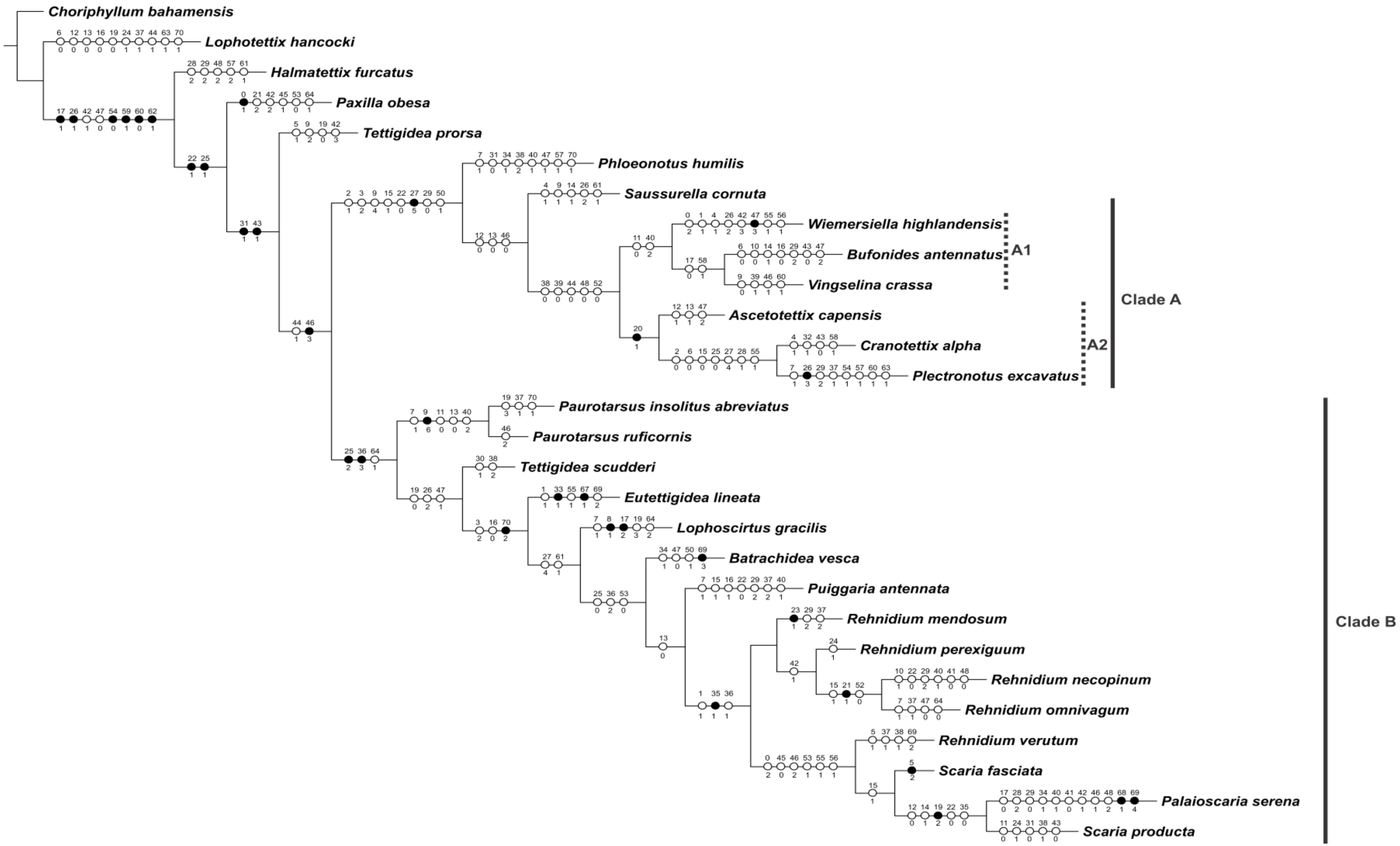


FIGURE 5. Most parsimonious tree of the Batrachideinae (length 301, consistency index = 0.35, retention index = 0.54) resulting from the cladistic analysis of the morphological character dataset. Black circles indicate unique changes, and white circles indicate homoplasies.

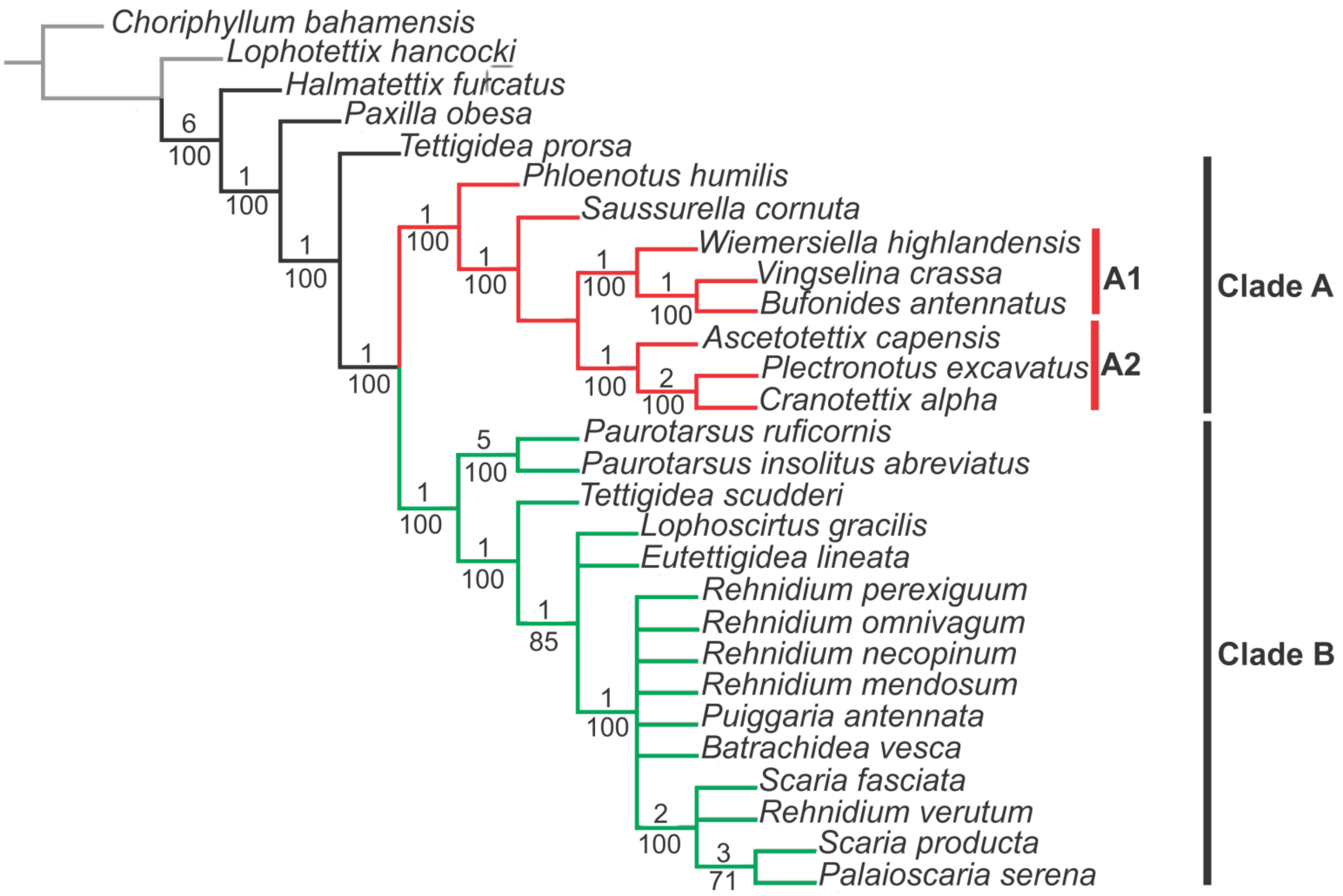


FIGURE 6. Consensus tree from New Technology search. The numbers above are Bremer support and numbers below are bootstrap support.

TABLE 1. Specimen information of outgroups and ingroups taxa.

Species	**Sex**	**Type**	**Country**	**Museum or Collection**	**Additional information**
Ascetotettix capensis (Günther, 1956)	Female	Paratype	South Africa	Museum für Naturkunde Berlin (MNB)	Grant (1956b)
Bufonides antennatus Bolívar, 1898	Male	Lectotype	Papua New Guinea	Museo Civico di Storia Naturale "Giacomo Doria" (MCSN)	Hinton (1940)
Cranotettix alpha Grant, 1955	Female	Holotype	Panamá	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1955b)
Choriphyllum bahamensis Perez-Gelabert & Otte, 1999	Male	Holotype	Bahamas	Florida State Collection of Arthropods (FSCA)	Perez-Gelabert & Otte (1999)
Batrachidea vesca Grant, 1956	Male	Holotype	Bolivia	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
Eutettigidea lineata (Bruner, 1910)	Female	Lectotype	Brazil	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
Halmatettix furcatus Grant, 1955	Female	Holotype	Peru	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1955b)
Lophoscirtus gracilis (Bruner, 1900)	Male	Allotype	Uruguay	Muséum national d'histoire naturelle (MNHN)	Grant (1956)
Lophotettix hancocki (Bruner, 1910)	Male	Lectotype	Brazil	The Academy of Natural Sciences of Drexel University (ANSP)	Bruner (1910)
Palaioscaria serena Günther, 1938	Female	Holotype	New Guinea	British Museum of Natural History (BMNH)	Grant (1966)
Paurotarsus insolitus abbreviatus Grant, 1955	Male	Holotype	Trinidad	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1955a)
Paurotarsus ruficornis (Walker, 1871)	Male	Holotype of *Paurotarsus amazonus* Hancock, 1900	Brazil	The Academy of Natural Sciences of Drexel University (ANSP)	Hancock (1900)
Paxilla obesa (Scudder, 1877)	Male	Lectotype	United State of America	The Academy of Natural Sciences of Drexel University (ANSP)	Rehn & Grant (1958)
Phloeonotus humilis (Gerstaecker, 1869)	Male	Holotype of *Phloeonotus sinuatus* Hancock, 1907	South Africa	Hope Entomological Collections, University Museum of Natural History Oxford (UMO)	Grant (1956b)

TABLE 1. Continued.

Species	Sex	Type	Country	Museum or Collection	Additional information
Plectronotus excavatus Grant, 1955	Female	Holotype	Panamá	Museum of Evolution Uppsala University (UZIU)	Grant (1955b)
Puiggaria antennata Bolívar, 1887	Male	Allotype	Brazil	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956)
Rehnidium mendosum Grant, 1956	Male	Holotype	Peru	California Academy of Sciences (CAS)	Grant (1956a)
Rehnidium necopinum Grant, 1956	Female	Holotype	Peru	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
Rehnidium omnivagum Grant, 1956	Female	Holotype	Brazil	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
Rehnidium perexiguum Grant, 1956	Male	Holotype	Ecuador	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
Rehnidium verutum Grant, 1956	Female	Holotype	Peru	The Academy of Natural Sciences of Drexel University (ANSP)	Grant (1956a)
*Saussurella cornuta (*Haan, 1843)	Female	Neotype	Malesia	Naturhistorisches Museum Wien (NMW)	Grant (1966)
Scaria fasciata Hancock, 1907	Female	Holotype	Ecuador	The Academy of Natural Sciences of Drexel University (ANSP)	Hancock (1907)
Scaria producta Hancock, 1907	Female	Holotype	Peru	The Academy of Natural Sciences of Drexel University (ANSP)	Hancock (1907)
Tettigidea prorsa Scudder, 1877	Male	Lectotype	United State of America	The Academy of Natural Sciences of Drexel University (ANSP)	Rehn & Grant (1958)
Tettigidea scudderi Bolívar, 1887	Female	Syntype	Peru	Naturhistorisches Museum Wien (NMW)	Paris (1993-1994)
Wiemersiella highlandensis Tumbrinck, 2014	Male	Holotype	Papua New Guinea	Lyman Entomological Museum and Research Laboratory (LEMQ)	Tumbrinck. (2014b)
Vingselina crassa Sjöstedt, 1921	Female	Holotype	Australia	Naturhistoriska Riksmuseet Stockholm (NHRS)	Rehn (1952)

APPENDIX 1. List of characters and states used in the phylogenetic analysis of Neartic and Neotropical Batrachideinae. CI and RI values are shown for each character, and those characters without these values are characterized as uninformative (UNINF). (All figures given here are in Appendix 2).

Body6

0. General shape of the body: (0) Robust (Fig .A1), (1) Fusiform (Fig. A2) and (2) Slender (Fig. A3). CI= 0.66, RI=0.75

1. Integument: (0) Rugose (Fig. A2) and (1) Slight rugose (Fig. A3). CI= 0.33, RI=0.77.

2. General coloration: (0) More or less the same tones on the whole body (Fig. A1) and (1) Same tones on the whole body excepting the macula and/or other highlighted part of body (Fig. A3). CI= 0.20, RI=0.66

Head

3. Head position: (0) Vertex extremely low than median carina of pronotum (Fig. A4), (1) Vertex almost on the level of the median carina anteriorly (Fig. A5) and (2) Vertex lower than median carina of pronotum anteriorly (Fig. A6). CI=0.50, RI=0.60

4. Fastigium as a projection of a head anteriorly to the vertex (lateral view): (0) Inconspicuous (Fig. A7) and (1) Conspicuous (Fig. A8). CI=0.33, RI=0. We followed the definition of Snodgrass (1993) and Torre-Bueno (1989) in which defined the fastigium as an anterior projection of vertex.

5. Frontal costa bifurcation (frontal view): (0) Above paired superior ocellus (Fig. A9), (1) Below paired superior ocellus and (2) On the same level (Fig. A10). CI=0.66, RI=0. We followed the definition of Albrecht (1953), who defined frontal costa as fontal median region delimited by facial carinae.

6. Frontal costa and fastigium (lateral view): (0) Not protruding or exceeding the level of dorsal margin of eyes (Fig. A11) and (1) Protruding in the same level or exceeding the level of dorsal margin of eyes (Fig. A4). CI=0.20, RI=0.66

7. Frontal costa bifurcation (frontal view): (0) Between the compound eyes (Fig.A12) and (1) Almost on the level of fastigium (Fig. A13). CI=0.16, RI=0.16

8. Frontal costa (lateral view): (0) Not prominent and (1) Protrusive, almost horn-like (Fig. 14). UNINF. Only in *Lophoscirtus gracilis*.

9. Facial carinae shape (frontal view): (0) Broad, (1) Fusiform (Fig. A15), (2) Parallel and touching each other (Fig. A16), (3) Parallel and almost touching each other (Fig. A17), (4) Parallel and not touching each other (Fig. A12), (5) Furcated (Fig. A18) and (6) “V” inverted (Fig. A19). CI=0.42, RI=0.27

10. Fascial carinae crest height (lateral view): (0) Less than scapus and (1) Bigger than scapus. CI=0.20, RI=0.60.

11. Fascial carina (frontal view): (0) Not touch or completely enveloping the medial ocellus on the base (Fig. A19) and (1) Involving the medial ocellus on the base (Fig. A15). CI=0.25, RI=0.50

12. Fascial carina (lateral view): (0) Protruding only in the lower half of the eyes (Fig. 11) and (1) Not protruding or slightly protruding on throughout the carenae (Fig. A5). CI=0.25, RI=0.62

13. Fascial carina (lateral view): (0) Pronouncedly arcuate (Fig. A11) and (1) Almost plane, straight (Fig.A7). CI=0.20, RI=0.55

14. Costa frontal (frontal view): (0) Touching or almost touching the fastigial region (Fig. A17) and (1) Not touching the fastigial region. CI=0.33, RI=0.33

15. Posterior part of frontal costa (before the bifurcation) (frontal view): (0)Visible (Fig.A18) and (1) Not visible or small (Fig.A15). CI=0.20, RI=0.60

16. Vertex (lateral view): (0) Lower than dorsal surface of eyes (Fig. A6) and (1) Vertex above dorsal surface of eyes (Fig.A5). CI=0.25, RI=0.72

17. Position of the antennal grooves (frontal view): (0) Below the lower margin of the compound eye (Fig. A20), (1) Lower margin of antennal grooves near the lower margin of the compound eye (Fig. A21) and (2) Between the compound eyes. CI=0.50, RI=0.50

18. Number of the antennal segments: (0) 20 or less than 20 and (1) Between 21-24. CI=1.0, RI=1.0

19. Shape of top of head (frontal view): (0) Plane or truncated, (1) Domed, (2) Convex and (3) Triangular. CI=0.42, RI=0.50

20. Eyes shape (lateral view): (0) Globose and wide with a flattened dorsal base (Fig.A6) and (1) Globose and slight narrow with a flattened dorsal base (Fig. A22). CI=1.0, RI=1.0

21. Interocular horizontal width of vertex between the eyes (dorsal view): (0) Wider than horizontal width a compound eye, (1) The same horizontal width as a compound eye and (2) Narrower than horizontal width of compound eye. CI=0.50, RI=0.71

22. Medial carina of the vertex (dorsal view): (0) Inconspicuous and (1) Conspicuous (Fig. A23). CI=0.20, RI=0.66

23. Secondary carina of the vertex (dorsal view): (0) Inconspicuous and (1) Conspicuous (Fig. A23). UNINF.

24. Occipital area (dorsal view): (0) Not visible and margin anterior of pronotum touching (or almost) the eyes (Fig. A24) and (1) Visible and margin anterior of pronotum distant the eyes (Fig. A25). CI=0.33, RI=0

Pronotum

25. General shape of the pronotum (lateral view): (0) Flattened laterally (Fig.A3), (1) Slight flattened laterally (Fig.A2) and (2) Flattened dorso- ventrally (Fig.27). CI=0.50, RI=0.81

26. Pronotum first portion of median carinae (lateral view): (0) Leaf-like (Fig.A28), (1) Slightly arcuate (Fig.A2), (2) Not arcuate (Fig.A27) and (3) In lateral aspect undulate, with a 'hump' (Fig.A29). CI=0.60, RI=0.80

27. Anterior margin of the pronotum (lateral and dorsal view) (near the occipital region): (0) Completely covered over the head (Fig.A4), (1) Almost straight (Fig.A30), (2) Rounded (Fig.A31), (3) Rounded and slightly protruding (concave) between prozonal carina (Fig.A23); (4) Hook-like, as a spine over the head (Fig.A24) and (5) Projection slightly tapering towards the anterior margin of pronotum, but not hook-like, over the head (Fig. A26). CI=0.71, RI=0.77

28. Anterior margin of the pronotum (lateral view): (0) Not hook-like (Fig.A31); (1) Hook-like, sharply cristate, high and thin (Fig.A7) and (2) Hook-like, moderately cristate, low (Fig.A32). CI=0.40, RI=0.75

29. Anterior margin of the pronotum projection (lateral view): (0) Produced over the head beyond the fastigium (Fig.A4), (1) Produced over the head before the fastigial region (Fig.A31) and (2) Produced over the head, on the fastigium (Fig.A32). CI=0.22, RI=0.41

30. Anterior margin of pronotum (lateral view): (0) Almost straight margin (Fig.A32) and (1) Very arcuate (curved in the form of a bow, bow-like) (Fig.A33). CI=0.25, RI=0

31. Prozonal carinae: (0) Inconspicuous (Fig.A2) and (1) Conspicuous (Fig.A7). CI=0.33, RI=0.60

32. Longitudinal sulci on the side of pronotum (lateral view): (0) Present (Fig.A3) and (1) Absent (Fig.A34). CI=0.50, RI=0

33. Parallel deep sulcus on the side of pronotum (lateral view): (0) Absent and (1) Present (Fig.A35). UNINF.

34. Paranota (lateral view): (0) Without black small marks/spots and (1) With black small marks/spots (Fig.A7). CI=0.33, RI=0

35. Lateral darkish perpendicular band from eyes to pronotum, separating the lateral lobe of pronotum region into a whitish band: (0) Absent and (1) Present (Fig.6). CI=0.50, RI=0.80

36. Median carina: (0) Foliaceous (Fig. A28), (1) Cristate (pronotum slightly elevated over the head and slightly flatted laterally) (Fig. A8), (2) Extremely cristate (with crest high and thin, but not foliaceous) (Fig. A2) and (3) Flatted dorsally (Fig. A27). CI=0.60, RI=0.71

37. Infrascapular area: (0) Longer than middle femur, (1) Shorter than middle femur and (2) As longer as middle femur. CI=0.28, RI=0

38. Infrascapular area: (0) Broader area (Fig. A29), (1) Very thin, almost non-existent (Fig. A28), (2) Narrow with smooth and shiny throughout area (Fig. A36) and (4) Narrow and thin (Fig. A27). CI=0.30, RI=0.41

39. Internal lateral carina: (0) Absent and (1) Present (Fig. A3). CI=0.33, RI=0.50

40. Ventral sinus: (0) Present and well defined (Fig. A28), (1) Present, but not well defined (Fig. A2) and (2) Absent (Fig. 37). CI=0.25, RI=0.33

41. Tegminal sinus: (0) Absent (Fig. A34) and (1) Present (Fig. A27). CI=0.16, RI=0.37

42. Apex of lateral lobe of pronotum shape (lateral view): (0) Projection squared (Fig. A28), (1) Almost squared (nearly 90º) (Fig. A5), (2) With rounded projection, almost "U" shaped (Fig. A29) and (3) Almost sharped projection, "V" shaped (Fig. A1). CI=0.30, RI=0.46

43. Humero- apical carina: (0) Absent and (1) Present (Fig. A7). CI=0.25, RI=0.50

44. Pronotum length: (0) Brachpronotal and (1) Macropronotal. CI=0.16, RI=0.58

45. Pronotum length: (0) Shorter than wings and (1) Longer than wings. CI=0.20, RI=0.33

46. Pronotum length: (0) Exceeding few centimeters of the abdomen (Fig. A38), (1) Not exceeding the limits of abdomen (Fig. A2), (2) Approximately 1/3 of total pronotal length extending beyond the limits of the abdomen (Fig. A28), (3) Approximately 1/4 or more of total pronotal length extending the limits of the abdomen (Fig. A27). CI=0.25, RI=0.30

47. Pronotum apex (dorsal view): (0) Rounded, (1) Truncate, (2) Notched and (3) Sharped. CI=0.30, RI=0.46

48. Tegmina: (0) Absent, (1) Present and (2) Cryptic (Fig. A39). CI=0.40, RI=0.62

49. Tegmina shape: (0) Ovoid with rounded apex (Fig. 40) and (1) Other shape. UNINF.

50. Macula or cicatrix: (0) Absent (Fig. A40) and (1) Present (Fig. A41). CI=0.25, RI=25

51. Macula or cicatrix shape: (0) Small and circular (Fig. A42), (1) Large and oval (Fig. A41) and (2) Large and circular (Fig. A43). 2UNINF.

52. Wings: (0) Inconspicuous/absent and (1) Conspicuous/present. CI=0.20, RI=0.55

53. Wings length: (0) Brachypterous and (1) Macropterus. CI=0.33, RI=0.50

Legs

54. Fore femur dorsal and ventral margin: (0) Almost straight (continuous carinae) (Fig. A3) and (1) With undulated carinae (Fig. A28). CI=0.50, RI=0.50

55. Fore femur: (0) Robust in relation to tibia and (1) Thin in relation to tibia. CI=0.25, RI=0.57

56. Femur and tibia: (0) Fore femur more robust than tibia and (1) Both almost equally thin. CI=0.50, RI=0.75

57. Fore femur length: (0) Bigger than fore tibia, (1) Almost the same size and (2) Smaller then fore tibia. CI=0.25, RI=0.33

58. Fore femur apical spine: (0) Absent and (1) Present (Fig. A44). CI=0.50, RI=0.50

59. Fore femur paralell crest of the lateral margin: (0) Absent and (1) Present (Fig. A35). CI=1.0, RI=1.0

60. Middle femur dorsal and ventral margin: (0) Almost straight (continuous carinae) (Fig. A3) and (1) With undulated carinae (Fig. A29). CI=0.33, RI=0.33

61. Middle femur apical spine: (0) Absent and (1) Present (Fig. A3). CI=0.33, RI=0.83

62. Middle femur paralell crest of the lateral margin: (0) Inconspicuous and (1) Conspicuous (Fig. A3). CI=1.0, RI=1.0

63. Hind femur dorsal and ventral margin: (0) Almost straight (continuous carinae) (Fig. A3) and (1) With undulated carinae and/or lappets (Fig. A28). CI=0.50, RI=0

64. Hind femur: (0) 2-2.9 times longer than broad, (1) 3-3.5 times longer than broad and (2) 3.6-4 times longer than broad. CI=0.25, RI=0.40

65. Hind femur dorso-external carina: (0) Present and (1) Absent. UNINF.

66. Hind femur ventro-external carina: (0) Present and (1) Absent. UNINF.

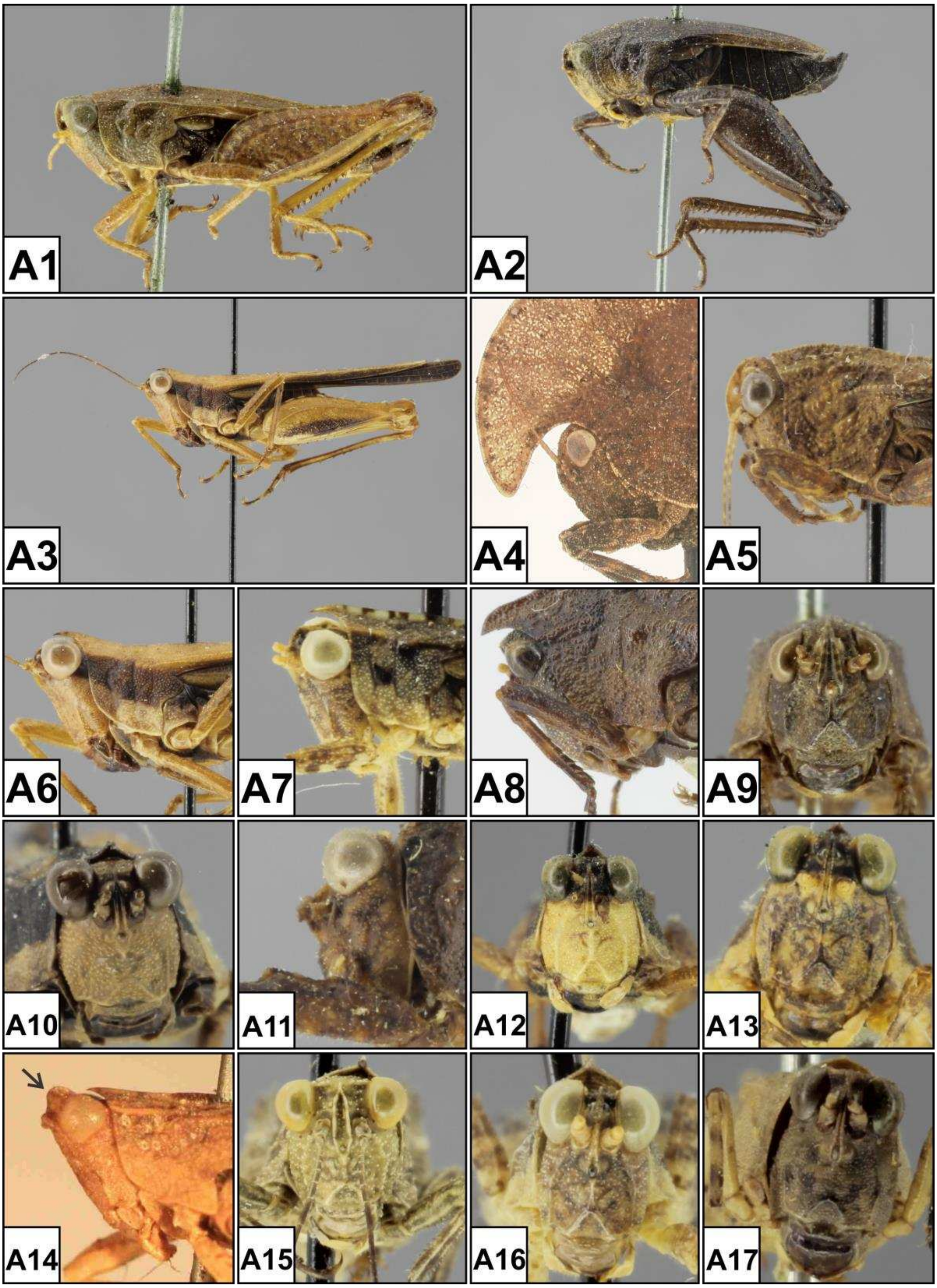
67. Hind femur median external area: (0) Well marked transversal ridge and (1)Absent transversal ridge. UNINF.

68. Antegenicular tooth: (0) Present and (1) Absent. UNINF.

69. Coloration (different of the body) on the hind femur: (0) Absent, (1) Two transversal bands (Fig. A45), (2) A parallel bands on ventro-external carina; (3) Color not in a band position, half lighter and half darker and (4) Some points with coloration. CI=0.60, RI=0

70. Comparison of length of first and third tarsal segments of hind leg: (0) First tarsal segment longer than third, (1) First segment as long as third (almost equal) and (2) First tarsal segment shorter than third. CI=0.40, RI=0.66

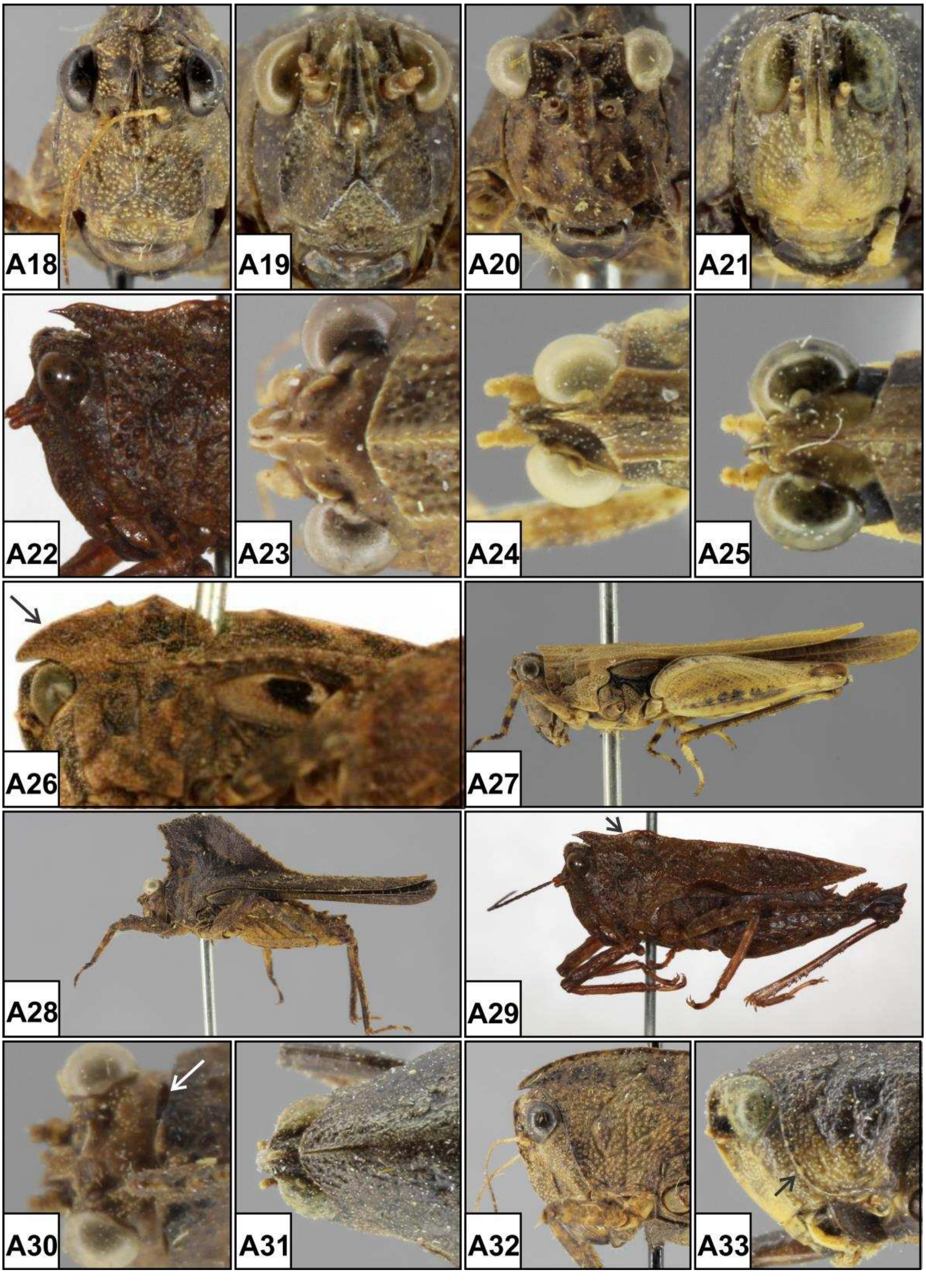
APPENDIX 2. Morphological characters used in the phylogenetic analysis.



Some morphological characters used in the phylogenetic analysis: (A1) *T. prorsa* in lateral view; (A2) *P. obesa* in lateral view; (A3) *S.verutum* (Grant, 1956) **comb. n** in lateral view; (A4) *C. bahamensis* head, pronotum and fore legs in lateral view; (A5) *P. insolitus abbreviatus* head, pronotum and fore legs in lateral view; (A6) *S.verutum* (Grant, 1956)

comb. n. head and pronotum in lateral view; (A7) *B. vesca* head, pronotum and fore legs in lateral view; (A8) *C. alpha* head, pronotum and fore legs in lateral view; (A9) *P. ruficornis* frontal view; (A10) *S. fasciata* frontal view; (A11) *L. hancocki* head, pronotum and fore femur in lateral view; (A12) *R. necopinum* frontal view; (A13) *R. omnivagum* frontal view; (A14) *L. gracilis* head and pronotum in lateral view with arrow highlighting the costa frontal prominent; (A15) *P. antennata* frontal view; (A16) *B. vesca* frontal view; (A17) *E. lineata* frontal view.

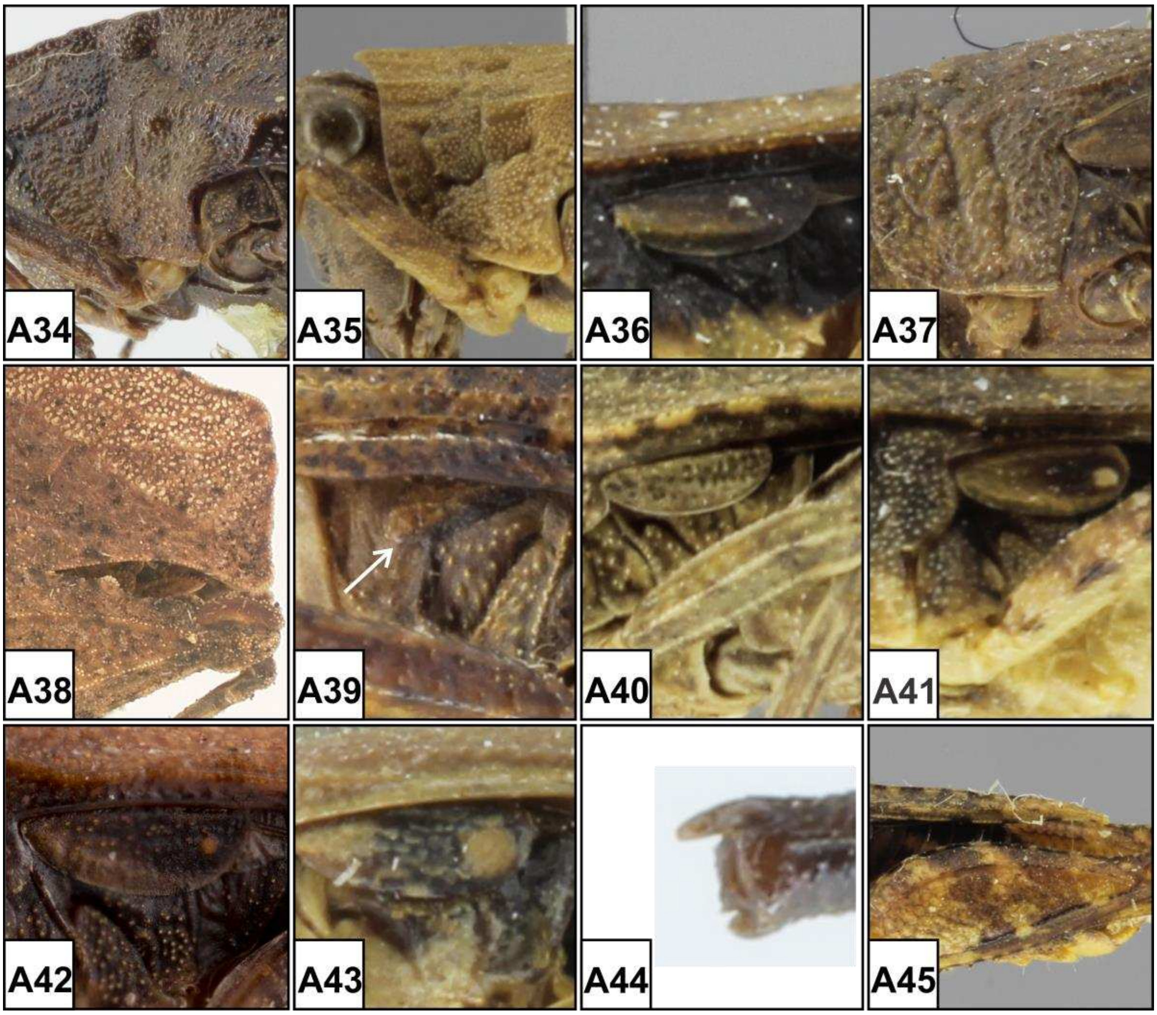
APPENDIX 2. (Continued)



Some morphological characters used in the phylogenetic analysis: (A18) *H. furcatus* frontal view; (A19) *P. ruficornis* frontal view; (A20) *L. hancocki* frontal view; (A21) *P. obesa* frontal view; (A22) *P.excavatus* head and pronotum lateral view; (A23) *P. insolitus abbreviatus* head in dorsal view; (A24) *B. vesca* head in dorsal view; (A25) *R. perexiguum* head in dorsal view; (A26) *P. humilis* pronotum details; (A27) *E. lineata* lateral view;

(A28) *L. hancocki* lateral view; (A29) *P.excavatus* lateral view with arrow highlighting the ‘hump’; (A30) *L. hancocki* head in dorsal view with arrow highlighting the anterior margin of the pronotum almost straight; (A31) *P. obesa* head and pronotum part in dorsal view; (A32) *H. furcatus* head, pronotum and fore leg in dorsal view; (A33) *P. obesa* head and pronotum in lateral view with arrow highlighting the very arcuate shape of the anterior margin of pronotum.

APPENDIX 2. (Continued)



Some morphological characters used in the phylogenetic analysis: (A34) *C. alpha* pronotum in lateral view; (A35) *E. lineata* pronotum with parallel deep sulcus on the side of pronotum in lateral view; (A36) *R. perexiguum* infrascapular area and tegmina; (A37) *P. ruficornis* lateral part of pronotum; (A38) *C. bahamensis* ending of abdomen; (A39) *H. furcatus* criptic tegmina indicated by the arrow; (A40) *P. antennata* tegmina; (A41) *B. vesca* tegmina; (A42) *R. mendosum* tegmina; (A43) *S. producta* tegmina; (A44) *C.alpha* spine on fore femur and (A45) *R. omnivagum* hind femur.

APPENDIX 3. Matrix data.

	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
Choriphyllum bahamensis	0	0	0	0	0	0	1	?	0	0	0	0	1	1	?	?	1	0	0	1	0	0	0	0	0	0
Lophotettix hancocki	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	?	0	0	0	0	0	1	0
Ascetotettix capensis	0	0	1	2	0	0	1	0	0	4	1	1	1	1	0	1	1	1	?	1	1	0	0	0	0	1
Batrachidea vesca	0	0	1	2	0	0	0	0	0	2	1	1	1	1	0	0	0	1	?	0	0	2	1	0	0	0
Bufonides antennatus	0	0	-	2	0	0	0	0	0	4	0	0	0	0	1	1	0	0	?	0	0	?	0	0	0	1
Cranotettix alpha	0	0	0	2	1	0	0	0	0	4	1	1	0	0	0	0	1	1	?	?	1	0	0	0	0	0
Eutettigidea lineata	0	1	0	2	0	0	1	0	0	3	0	1	1	1	0	0	0	1	?	0	0	0	1	0	0	2
Lophoscirtus gracilis	0	0	0	2	0	0	1	1	1	3	-	-	1	1	0	0	0	2	?	3	0	0	1	0	0	2
Halmatettix furcatus	0	0	0	2	0	0	1	0	0	5	1	1	1	1	0	0	1	1	0	?	0	0	0	0	0	0
Palaioscaria serena	2	1	1	2	0	0	0	0	0	4	0	1	0	0	1	1	0	0	?	2	0	2	0	0	0	0
Paurotarsus insolitus abreviatus	0	0	0	1	0	0	1	1	0	6	1	0	1	0	0	0	1	1	1	3	0	0	1	0	0	2
Paurotarsus ruficornis	0	0	0	1	0	0	1	1	0	6	1	0	1	0	0	0	1	1	?	1	0	0	1	0	0	2
Paxilla obesa	1	0	0	1	0	0	1	0	0	3	1	1	1	1	0	0	1	1	?	1	0	2	1	0	0	1
Phloeonotus humilis	0	0	1	2	0	0	1	1	0	4	1	1	1	1	0	1	1	1	?	1	0	0	0	0	0	1
Plectronotus excavatus	0	0	0	2	0	0	0	1	0	4	1	1	0	0	0	0	1	1	?	1	1	?	?	?	0	0
Puiggaria antennata	0	0	0	2	0	0	1	1	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0
Rehnidium mendosum	0	1	1	2	0	0	0	0	0	4	0	1	1	0	0	0	0	1	?	0	0	?	1	1	?	0
Rehnidium necopinum	0	1	1	2	0	0	0	0	0	4	1	1	1	0	0	1	0	1	?	0	0	1	0	?	0	0
Rehnidium omnivagum	0	1	1	2	0	0	0	1	0	4	0	1	1	0	0	1	?	1	?	0	0	1	1	0	0	0
Rehnidium perexiguum	0	1	1	2	0	0	0	0	0	3	0	1	1	0	0	0	0	1	?	0	0	2	1	0	1	0
Rehnidium verutum	2	1	1	2	0	1	0	0	0	2	0	1	1	0	0	0	0	1	?	0	0	2	1	0	0	0
Scaria fasciata	2	1	1	2	0	2	0	0	0	3	0	1	1	0	0	1	0	1	?	0	0	2	1	0	0	0
Scaria producta	2	1	1	2	0	0	0	0	0	4	0	0	0	0	1	1	0	1	1	2	0	2	0	0	1	0
Tettigidea scudderi	0	0	0	1	0	0	1	0	0	3	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0	2
Tettigidea prorsa	0	0	0	1	0	1	1	0	0	2	1	1	1	1	0	0	1	1	?	0	0	0	1	0	0	1
Saussurella cornuta	0	0	1	2	1	0	1	0	0	1	1	1	0	0	1	1	1	1	?	1	0	0	0	0	0	1
Vingselina crassa	0	0	0	2	0	0	1	0	0	0	1	0	0	0	0	1	1	0	?	?	0	0	0	0	0	1
Wiemersiella highlandensis	2	1	1	2	1	0	1	0	0	4	1	0	0	0	?	?	1	1	?	?	0	0	0	0	0	1

APPENDIX 3. **Continued**

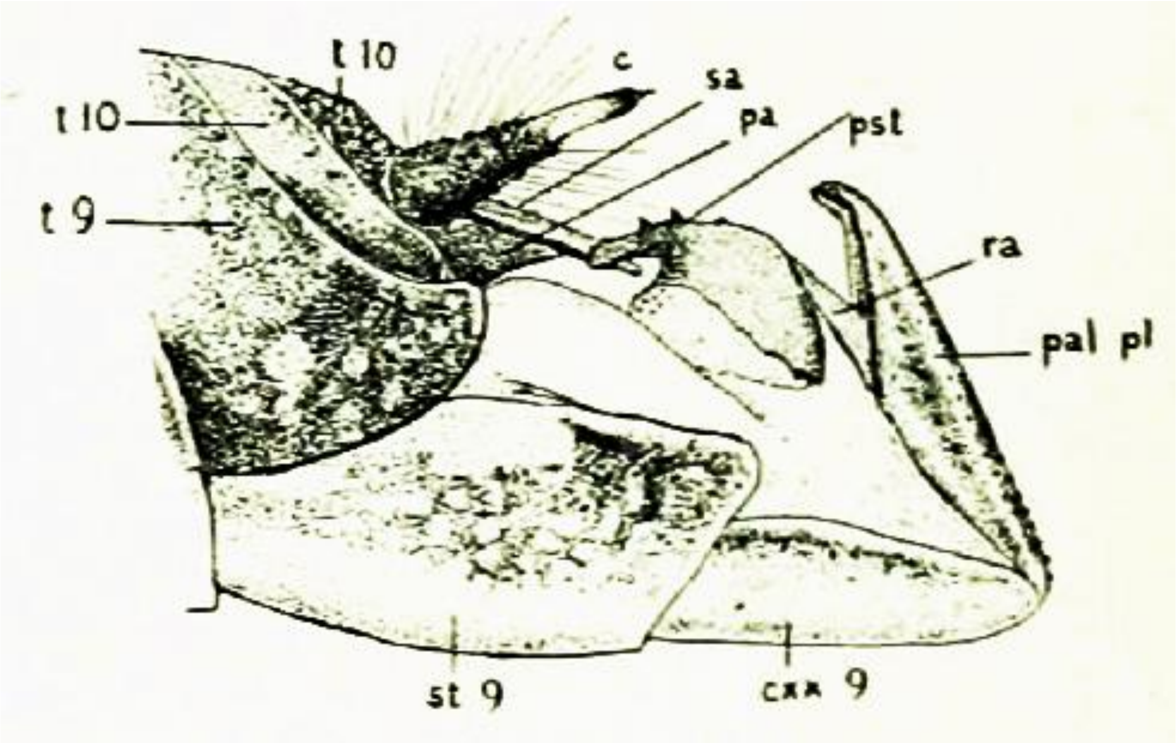
	26	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**
Choriphyllum bahamensis	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	0	-	-	-
Lophotettix hancocki	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	2	1	1	0	0	-
Ascetotettix capensis	1	5	0	0	0	1	?	0	0	0	1	0	0	?	0	0	0	1	0	-	1	2	0	-	-	-
Batrachidea vesca	2	4	1	1	0	1	0	0	1	0	2	0	3	1	0	1	2	1	0	1	0	0	1	0	1	1
Bufonides antennatus	1	5	0	2	0	?	0	0	0	-	1	0	0	0	2	0	1	0	0	-	0	2	0	-	-	-
Cranotettix alpha	1	4	1	0	0	1	1	0	0	0	1	0	0	0	0	0	2	0	0	-	0	0	0	-	-	-
Eutettigidea lineata	2	3	0	1	0	1	0	1	0	0	3	0	3	1	0	1	2	1	1	1	3	1	1	0	0	-
Lophoscirtus gracilis	2	4	2	1	0	1	-	0	0	0	3	-	-	1	0	1	2	1	1	0	3	1	1	0	?	-
Halmatettix furcatus	1	4	2	2	0	0	0	0	0	0	2	0	3	1	1	0	1	0	0	-	1	0	2	0	0	-
Palaioscaria serena	2	4	2	0	0	1	0	0	1	0	1	0	3	1	1	0	1	1	1	0	1	2	2	0	0	-
Paurotarsus insolitus abreviatus	1	3	0	1	?	1	0	0	0	0	3	1	3	1	2	1	1	1	1	0	3	0	1	?	0	-
Paurotarsus ruficornis	1	3	0	1	0	1	0	0	0	0	3	0	3	1	2	1	1	1	1	0	2	0	1	0	0	-
Paxilla obesa	1	2	0	1	1	0	0	0	0	0	1	0	3	1	1	1	2	0	0	1	1	0	1	0	0	-
Phloeonotus humilis	1	5	0	0	0	0	0	0	1	0	1	0	2	1	1	1	1	1	1	0	3	1	1	0	1	1
Plectronotus excavatus	3	4	1	2	0	1	0	0	0	0	1	1	0	0	0	0	2	1	0	-	1	?	0	-	-	-
Puiggaria antennata	2	4	1	2	0	1	0	0	0	0	2	2	3	1	1	1	2	1	0	1	1	1	1	0	0	-
Rehnidium mendosum	2	4	1	2	0	1	0	0	0	1	1	2	2	1	0	1	2	1	0	1	1	1	1	0	0	0
Rehnidium necopinum	2	4	1	2	0	1	0	0	0	1	1	0	3	1	1	0	1	1	1	-	1	1	0	-	-	-
Rehnidium omnivagum	2	4	1	1	0	1	0	0	0	1	1	1	1	1	0	1	1	1	1	?	1	0	1	0	0	-
Rehnidium perexiguum	2	4	1	1	0	1	0	0	0	1	1	0	2	1	0	1	1	1	1	1	1	1	1	0	0	-
Rehnidium verutum	2	4	1	1	0	1	0	0	0	1	1	1	1	1	0	1	2	1	1	0	2	2	1	0	0	-
Scaria fasciata	2	4	1	1	0	1	0	0	0	1	1	0	3	1	0	1	-	1	1	0	2	1	1	0	1	1
Scaria producta	2	4	1	1	0	0	0	0	0	0	1	-	1	1	0	1	2	0	1	0	2	2	1	0	1	2
Tettigidea scudderi	2	3	0	1	1	1	0	0	0	0	3	?	2	1	0	1	3	1	1	0	3	1	1	0	0	-
Tettigidea prorsa	1	3	0	1	1	1	0	0	0	0	1	?	3	1	0	1	3	1	0	?	1	0	1	0	0	-
Saussurella cornuta	2	5	0	0	0	1	0	0	0	0	1	0	3	1	0	1	1	1	1	1	0	0	1	0	1	1
Vingselina crassa	1	5	0	0	0	1	0	0	0	0	1	0	0	1	2	0	1	1	0	-	1	0	0	-	-	-
Wiemersiella highlandensis	2	5	0	0	0	1	0	0	0	0	1	0	0	0	2	1	3	1	0	-	0	3	0	-	-	-

APPENDIX 3. **Continued**

	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Choriphyllum bahamensis	0	-	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lophotettix hancocki	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1
Ascetotettix capensis	0	-	0	0	0	0	0	1	0	0	1	0	1	0	0	?	0	0	0
Batrachidea vesca	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	3	2
Bufonides antennatus	0	-	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Cranotettix alpha	0	-	0	1	0	0	1	1	0	0	1	0	2	0	0	0	0	0	?
Eutettigidea lineata	1	1	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	2	2
Lophoscirtus gracilis	1	1	0	0	0	?	0	1	0	1	1	0	2	0	0	?	?	0	?
Halmatettix furcatus	0	-	0	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0
Palaioscaria serena	1	1	0	1	1	2	0	1	0	1	1	0	1	0	0	0	1	4	1
Paurotarsus insolitus abreviatus	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1
Paurotarsus ruficornis	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Paxilla obesa	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Phloeonotus humilis	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1
Plectronotus excavatus	0	-	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0
Puiggaria antennata	1	0	0	0	0	2	0	1	0	1	1	0	1	0	0	0	0	0	2
Rehnidium mendosum	1	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	?
Rehnidium necopinum	0	-	0	0	0	2	0	1	0	1	1	0	1	0	0	0	0	2	2
Rehnidium omnivagum	0	-	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	?	?
Rehnidium perexiguum	1	0	0	?	?	?	?	?	0	1	1	0	1	0	0	0	0	0	2
Rehnidium verutum	1	1	0	1	1	1	0	1	0	1	1	0	1	0	0	0	0	2	2
Scaria fasciata	1	1	0	1	1	2	0	1	0	1	1	0	1	0	0	0	0	0	2
Scaria producta	1	1	0	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	?
Tettigidea scudderi	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Tettigidea prorsa	0	-	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Saussurella cornuta	1	1	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	0	?
Vingselina crassa	-	-	0	0	0	?	1	1	1	0	1	0	0	0	0	0	0	0	?
Wiemersiella highlandensis	0	-	0	1	1	0	0	1	0	0	1	0	2	0	0	0	0	0	

Artigo 5

Are the phallic complex of pygmy grasshoppers (Insecta: Orthoptera: Caelifera: Tetrigidae) useful in taxonomy? An overview of literature data



Are the phallic complex of pygmy grasshoppers (Insecta: Orthoptera: Caelifera: Tetrigidae) useful in taxonomy? An overview of literature data

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Abstract

The genital organs of Orthoptera have been used for decades to distinguish species and supra-generic taxa, but for tetrigids these morphological characters data are overlooked and poorly understood. A literature review research was conducted from all the references about the phallic complex in Tetrigidae found in descriptions and general morphological studies to answer the following question: Are the phallic complex of pygmy grasshoppers useful in taxonomy? And if the answer was positive, why this information is not used in species descriptions? Encouragingly, we found thirteen studies that cited or described the genital organs, but there is no standardization of the terms or comparison of the morphological data between species. Even so, these results provided morphological data that indicated the potential use of genital organs of tetrigids as complement in description of the species and tool to distinguish taxa, as it occurs in other groups of Orthoptera. From the comparison between the terms adopted by all the authors, we propose a standard nomenclature to be used in subsequent studies.

Key words: morphology, phallic organ, terminalia, tetrigids.

Resumo

Os órgãos genitais dos Orthoptera têm sido usados nas últimas décadas para distinguir espécies e táxons supra genéricos, mas para tetrigídeos esses dados morfológicos são ignorados e pouco entendidos. Uma pesquisa de revisão de literatura foi realizada a partir de todas as referências ao complexo fálico em Tetrigidae encontradas em descrições e estudos morfológicos para responder a seguinte questão: O complexo fálico de tetrigídeos é útil na taxonomia do grupo? E se a resposta foi positiva, por que essa informação não é usada nas descrições de espécies? De forma encorajadora, encontramos treze estudos que citaram ou descreveram os órgãos genitais sem uma padronização dos termos ou comparação dos dados morfológicos entre os táxons. Ainda assim, estes resultados forneceram dados morfológicos que indicaram o potencial uso de órgãos genitais de tetrigídeos como complemento à descrição de espécies e ferramenta para distinguir táxons, como ocorre em outros grupos de Orthoptera. A partir da comparação entre os termos utilizados por todos os autores, nós propomos uma nomenclatura padrão para ser utilizada em estudos futuros.

Palavras-chave: morfologia, órgão fálico, terminalia, tetrigídeos.

Introduction

The Family Tetrigidae (often referred to in the vernacular name as *pygmy locusts, pygmy grasshoppers; pygmy unicorns; pygmy giraffhoppers; grouse locusts; dornschrecken*) are widely distributed over the world (Hancock 1902), excluding deserts, New Zealand (Rehn 1952, Tumbrinck 2014) and Arctic and Antarctic regions (Cigliano et al. 2018). They are characterized by the affinity for wet environments and usually live close to water, lichens, decomposing soil and leaf litter (Hancock 1902, Nabour 1929), being more active in warmer weather (Ragge 1965) and feeding aquatic algae (Amédégnato & Devriese 2008), lichens and moss (Nabour 1929). Several species are limno-terrestrial and some species are swimmers, able to dive underwater (Amédégnato & Devriese 2008).

Tetrigids are small orthopterans, whose morphology is one of the most peculiar among orthopterous. The pronotum is prolonged, covering part or the whole abdomen (Fig. 1); prosternum specialized in a collar–like around the mouthparts (sternomentum) (Fig. 2A-B); elytra shortened and laterally arranged in the body (Fig. 2C), wings developed and anal area with expansion (there are some species without one or both characters);

tympanal organ absent; anterior and middle tarsis with two segments and hind tarsis with three segments (Fig. 2E); arolia absent (Hancock 1902, Dirsh 1961); male genital organs composed by two layers (Amédgnato 1976) with organs membranous and concealed under paired chitinous plates (Flook & Rowell 1997) (Fig. 2D) and it is directed to the anterior ends of the body (Dirsh 1961); cerci short and unsegmented (Rentz 1991) and egg as wine-bottle-shaped, cylindrical with acutely pointed extremity, such as horn of the egg (Hancock 1902, Nabour 1929, Hartley 1962).

Orthoptera taxonomists spend their lifetimes studying species from morphological characters, mainly male genitalia for species-level analysis. Different taxonomists and morphologists as Walker (1922), Snodgrass (1935), Robert (1941), Dirsh (1956, 1961), Kevan et al. (1973), Amédégnato (1976), Eades (2000), Song & Mariño-Pérez (2013) among other, described patterns of species-specificity of the male genitalia and then, worked with descriptions from suprageneric groups until species level.

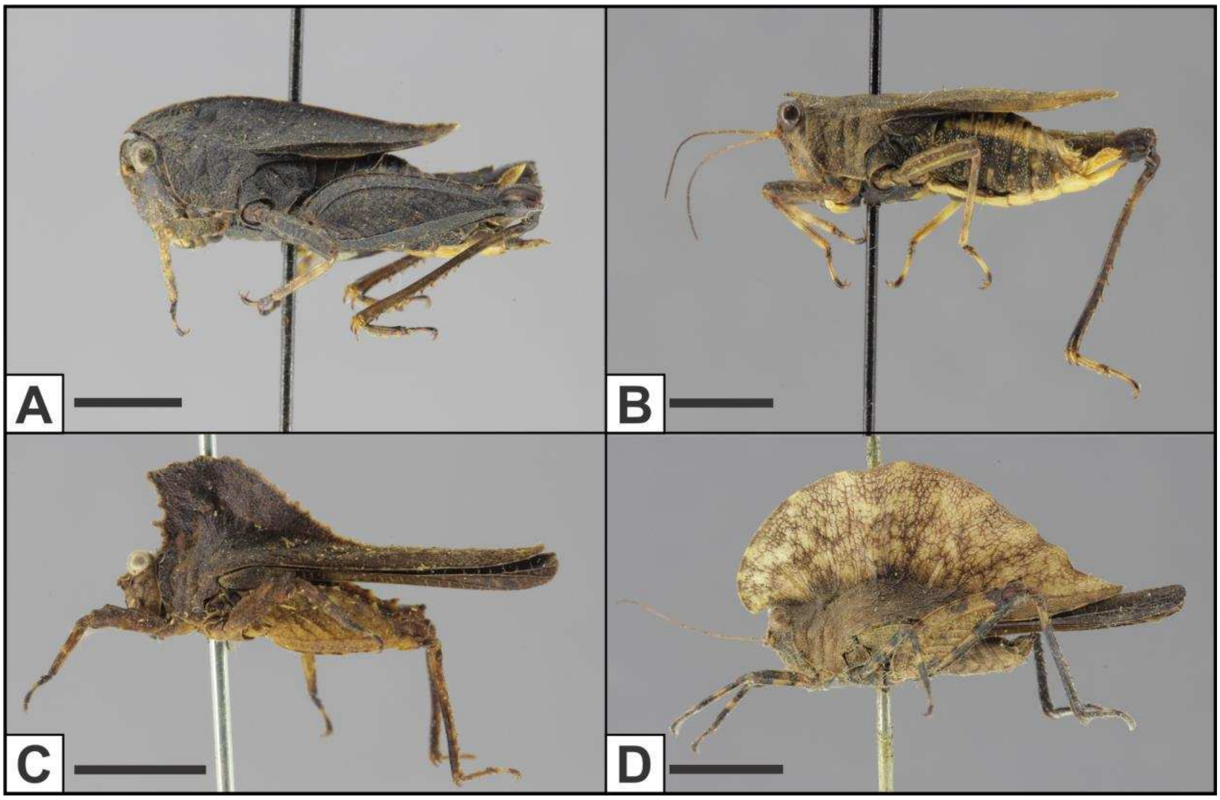

Figure 1. Examples of pronotum length (vista lateral): (A) *Halmatettix sordidus* Grant, 1955 covering part of abdomen and (B) *Batrachidea inermis* Hebard, 1923, (C) *Lophotettix hancocki* (Bruner, 1910) and (D) *Paraphyllum antennatum* Hancock, 1913 covering the whole abdomen. Scar bar: 0,5 cm.

However, currently for Tetrigidae only external characters are often used to distinguish species. This is a problem since this family has a complex taxonomic history including several synonyms (Rehn & Grant 1961, Lehmann et al. 2017); a huge polymorphism (same population have macropronotal and brachypronotal forms, *eg*. *Tetrix subulata* (Linnaeus, 1758) and *Nomotettix* Morse, 1894 (Rehn & Grant 1955)); wings polymorphism (Steenman et al. 2013, 2015); polychromatism (Nabours 1929, Rehn 1952, Rehn & Grant 1961) and misidentified nymphs and adults (Tae-Woo & Kim 2004, Skejo et al. 2018). Also, there are species with morphological characters of neotenic species as *Neotettix* Hancock, 1898 (Rehn & Grant 1957) and some *Tettigidea S*cudder, 1862 (Rehn & Grant 1958); species in which were verified variations between the shape of lateral lobes of pronotum, apex of posterior angle and pronotum length in individuals of the same population (e.g. *Thoradonta varispina* Zha & Sheng, 2016 (Zha et al. 2016)) and several examples of morphological evolution convergence (Rehn 1938, Silva *et al*. 2017).

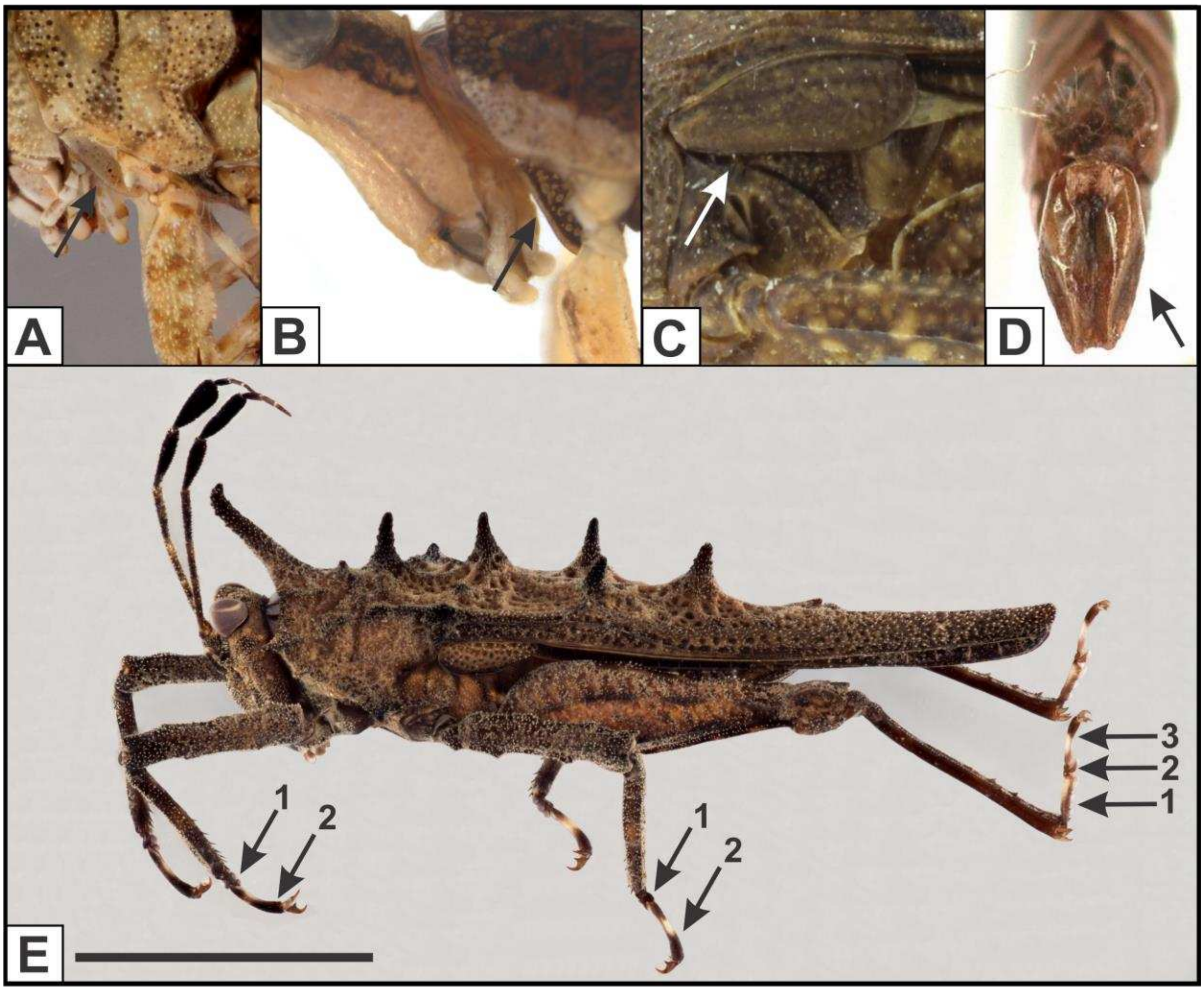

Figure 2. Some diagnostic characters of Tetrigidae: prosternum specialized in a collar–like around the mouthparts (sternomentum) in (A) *Paratettix mexicanus* (Saussure, 1861) and (B)

Metopomystrum muriciense Silva & Skejo, 2017 (both indicated by the arrow); tegmina laterally arranged in the body in (C) *Paurotarsus ruficornis* (Walker, 1871) (indicated by the arrow); male genital organs in (D) *Ophiotettix roesleri* Tumbrinck & Skejo, 2017 (pallial plates indicated by the arrow) (photo Josef Tumbrinck) and tarsal formula 2-2-3 in (E) *Discotettix belzebuth* (Serville, 1838). Scale bar: 0,5 cm.

All these examples point toward the necessity to use multiple characters to improve the determination of species. The genital organs are not used in the description of Tetrigidae species since the genitalia is considered a poorly specialized structure (Podgornaya 2003). Thus, the objective of this study is figure out if the genital organs are really simplified structure, with a limited use as taxonomic characters, or if they could be used to improve the descriptions, phylogenetic and taxonomic studies of the Tetrigidae from review of the literature regarding this tetrigids' genital organs.

Material and Methods

Terminology and morphology of genital organs

We searched the literature for morphological and taxonomic studies describing or showing genital organs of tetrigids. A systematic review of studies related to genital organs of tetrigids was carried out and searches were performed in bibliographic databases and researching in the morphology and taxonomy papers of Orthoptera.

The term "genital organ" used here refers to entire external organs used during the copula and this term also was used to describe the general structures of terminalia when the previous author did not indicate a term for some or all of the genital structures. On this basis, we provide a comparative list of terms proposed by each author and indicated the terms and abbreviations used by us in this study (Table 1) and a complete explanation for each name is provided in results and discussion topic 'Male external genital organs: update to morphological terminology'. The most of the studies cited here are very old and when necessary, the names of the species have been updated.

Schematic drawings and dissections

We redraw the figures from the previous studies exactly as in the original images, indicating comparatively the structures mentioned by each author through the colors of each structure according to our interpretation (since, for each author, the same structure will have a different name and with the coloration would be possible to compare the cited structures even with different nomenclatures). Some structures were not mentioned by authors (without specific term) and they were redrawn with the colors corresponding to topological morphological structures. The terms and abbreviations used by us in this study (Table 1) also were indicated in each redraw with the colors scheme to facilitate the interpretation of structures.

To exemplify the results of the literature review, three species have been dissected and the genitals cleaned by treating them with a KOH solution at room temperature. After being dissected and cleaned in KOH, the phallic complex were stained with Chlorazol Black-E, as biological stain that fixed to the insects cuticle for optimal contrasting (Carayon, 1969; Martínez, 2002) following the Pecci-Maddalena & Lopes-Andrade (2017) protocol. This sequence of procedures guarantees a better observation of the non-visible characters inside the genital organ and membranes.

Results and Discussion

Male external morphological structures according previous authors (with the original terms used by each author)

The grasshoppers' genital organs, since the beginning of the 20th century have been used systematically in the taxonomy of the acridids. Likewise, the tetrigids' male genital organs are known and have been studied since the 1920s but, in the most part of taxonomic studies, they have not been used in the description of species or in the definition of supraspecific groups. We found thirteen studies that mentioned the genital organs without a standardization of the terms or comparison of the morphological data between species. The terms used by the most part of authors to describe the tetrigids morphology of genital organs are derived of acridids terminology.

Chopard (1920) was one of the first's taxonomists in remarked comparatively male and female genitalia of orthopteroids. In 1920, in the '*Recherches sur la conformation et le dévelopement des demiers segments abdominaux chez les Orthopteres*', using some species as *Tetrix bipunctata* (Linnaeus, 1758) (Fig. 3A); *Criotettix miliarius* Hancock, 1904 (Fig. 3B); *Paratettix meridionalis* (Rambur, 1838) (Fig. 3C); *Afrocriotettix nigellus* (Bolívar, 1887) (Fig. 3D) and *Pterotettix andrei* Bolívar, 1887 (Fig. 3E), he verified that terminalia region of tetrigids were totally different of other grasshoppers.

According to Chopard (1920), the subgenital plate is divided in two parts, with the apical part flexible, forming a triangular projection, and the penis is completely welded in the subgenital plate. The genital organs are composed by two large valves that fit into the apical part of subgenital plate. They are separated by deep median sulci, limited on each side by a chitinous piece. These structures (valves, chitinous pieces and median sulci) on terminalia formed the genital pieces (Fig. 3) (Tab.1).

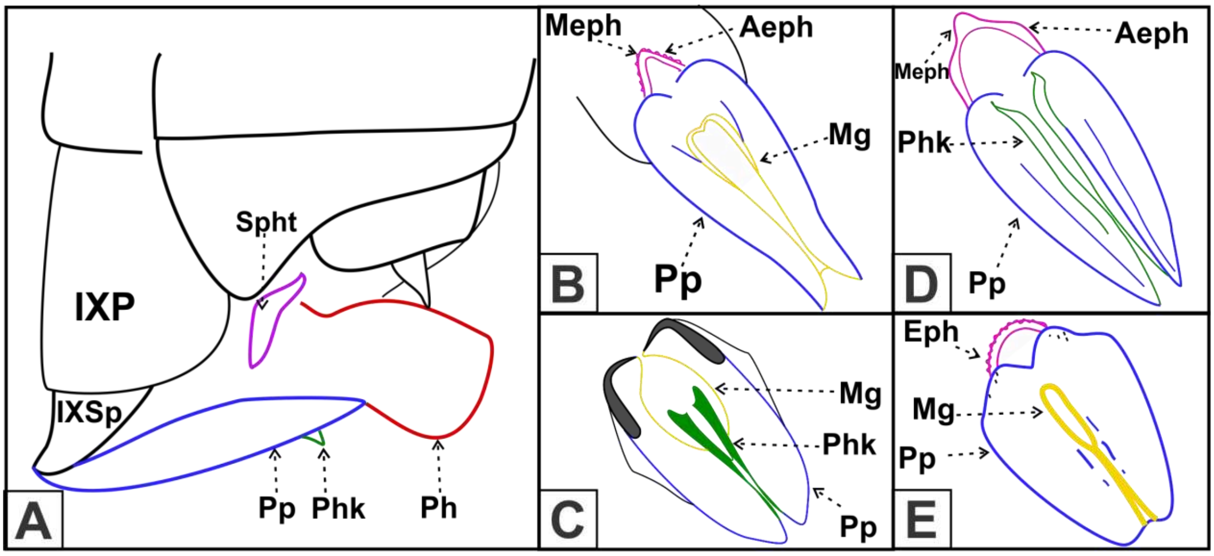

Figure 3. Terminalia in male terminalia in dorsal-lateral view of (A) *Tetrix bipunctata* (Linnaeus, 1758); male terminalia in dorsal view of (B) *Criotettix miliarius* Hancock, 1904; (C) *Paratettix meridionalis* (Rambur, 1838); (D) *Afrocriotettix nigellus* (Bolívar, 1887) and (E) *Pterotettix andrei* Bolívar, 1887. The drawings are adapted from Chopard (1920) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Eph: epiphallus; Meph: median process of epiphallus; Mg: medial groove; Ph: phallic organ; Phk: pallial hooks; Pp: pallial plates; Spht: sclerites of phallotreme; IXP: 9th sternum proximal part and IXSP: subgenital plate.

Walker (1922), in a more comprehensive study of the morphology of numerous ortopteroids, also indicated that tetrigids genital organs are unlike from the other grasshoppers. He named the intromittent organ as a penis and indicated for the first time the presence of *pallium* in tetrigids (a membrane from the margin of subgenital plate covering the retracted phallus in Caelifera, see Schuh 1989) and the morphological differences in genital organs between three species: *Tettigidea lateralis lateralis* (Say, 1824) (Fig. 4A-B), *Tetrix subulata* (Linnaeus, 1758) (Fig. 4C) and *Paratettix cucullatus* (Burmeister, 1838) (not represented in Walker's drawings in original work).

Walker (1922) observed that the *pallium* is more hardened than other Caelifera and it dorsal surface is covered by a pair of plates (pallial plates) separated by a median groove or median suture (Fig. 4B-C) (Tab.1). In *T. subulata* and *P.cucullatus,* there are two slender rods between the pallial plates which ends in a pair of small hooks (pallial hooks) (Fig. 4C), absent in *T. lateralis lateralis*. Walker also indicated a structure named pseudosternite (as a structure equivalent to epiphallus of other grasshoppers) with V-shaped arms and recurved apex with a group of spines (median process). Behind and between the arms of the pseudosternite, there are two slender plates named rami, around the opening of the genital cavity (named gonopore) (Fig. 4A-B). According to Walker, the gonopore is wide, membranous, near the ends of ejaculatory duct and has a dilatation which represents the spermatophore sac. There are no rami and the pseudosternite is more slender with a reduced median process in *T. subulata* and *P.cucullatus* (Fig. 4C).

Harman (1925), in a paper about reproductive system of *Apotettix eurycephalus* Hancock, 1902 (currently classified as *Paratettix toltecus* (Saussure, 1861)), explained more simply the genital organs parts (Fig. 4D-E). In her work, the genital organs are named penis or sac-like intromittent organ and the chitinous collar is equivalent to the Walker's pseudosternite (Tab.1).

Snodgrass (1935) in '*The abdominal Mechanisms of a Grasshopper*' agreed with Walker in the fact of genital organs of tetrigids have not a simple structure but with morphology contrasting with other grasshoppers. For *Tettigidea lateralis* (Say, 1824) he named the intermittent organ as phallic organ and described as a structure placed on the floor of genital chamber and covered by pallial valve (Fig. 4F). The dorsal part of *pallium* forms the valves which is has two elongate plates (pallial valves) and as indicated by previous authors, between each plate, there is structure that separates them, which can be the median membranous line (Fig. 4G) or bars terminating anteriorly in upcurved hooks (he did not schematize that) (Tab.1). According Snodgrass, *T. lateralis* has phallic organ with a median process armed with small spines; the gonopore is an ejaculatory duct that opens anteriorly and during the copulation, occurs the eversion of endophallic sac (Fig. 4H).

Hinton (1940), in a revision of *Bufonides* Bolívar, 1898 made schematics of what he called "genitalia and associated sclerites" for *Bufonides antennatus* Bolívar, 1898 and *Bufonides uvarovi* Hinton, 1940, without mentioning names for the genital structures (Fig. 5).

Carpentier (1942) in the '*Les Acrydium (Orthoptera) de Belgium*' described the morphological aspects of *Tetrix subulata* (Linnaeus, 1758) from a drawing with open parts of genital organs. Carpentier indicated in the legend of his figure only the penis and the pallial valves, but showed more structures like Walker's pseudosternite and pallial hooks (Fig. 6A) (Tab.1).

Widdows & Wick (1959), from the data of *Tetrix arenosa angusta* (Hancock, 1896), reviewed all nomenclature from internal and external morphologic structures used up to that time in tetrigids. The membranous genital organ was named intromittent organ because, according to the authors, did not have the characteristics of penis or phallus organs. The intromittent organ is continuous with ejaculatory duct and practically impossible to delimit the boundary between these both (Fig.6B).

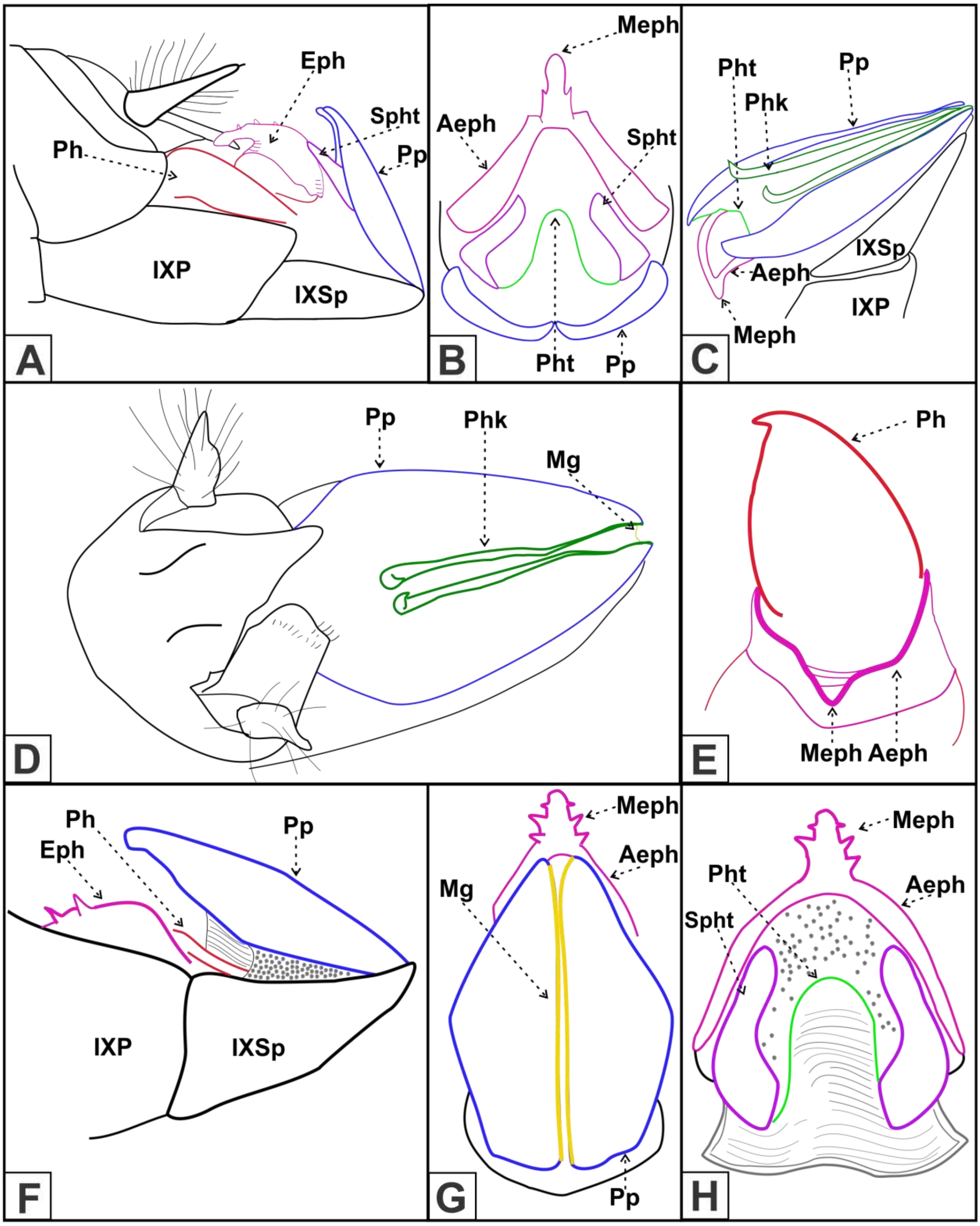

Figure 4. Terminalia in lateral view of (A) *Tettigidea lateralis lateralis* (Say, 1824) and (B) dorsal view of genital organs; (C) dorso- lateral view of *Tetrix subulata* (Linnaeus, 1758) terminalia; terminalia in dorsal view of (D) *Paratettix toltecus* (Saussure, 1861) and (E) the everted phallic organ; terminalia in lateral in lateral view of (F) *Tettigidea lateralis* (Say, 1824) and dorsal view (G) highlighting the pallial plates; (H) terminalia of *Tettigidea lateralis* (Say, 1824) without pallial plates. The drawings are adapted from Walker (1922), Harman (1925) and Snodgrass (1935) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of

epiphallus; Eph: epiphallus; Meph: median process of epiphallus; Mg: medial groove; Ph: phallic organ; Phk: pallial hooks; Pht: phallotreme; Pp: pallial plates; Spht: sclerites of phallotreme; IXP: 9th sternum proximal part and IXSP: subgenital plate.

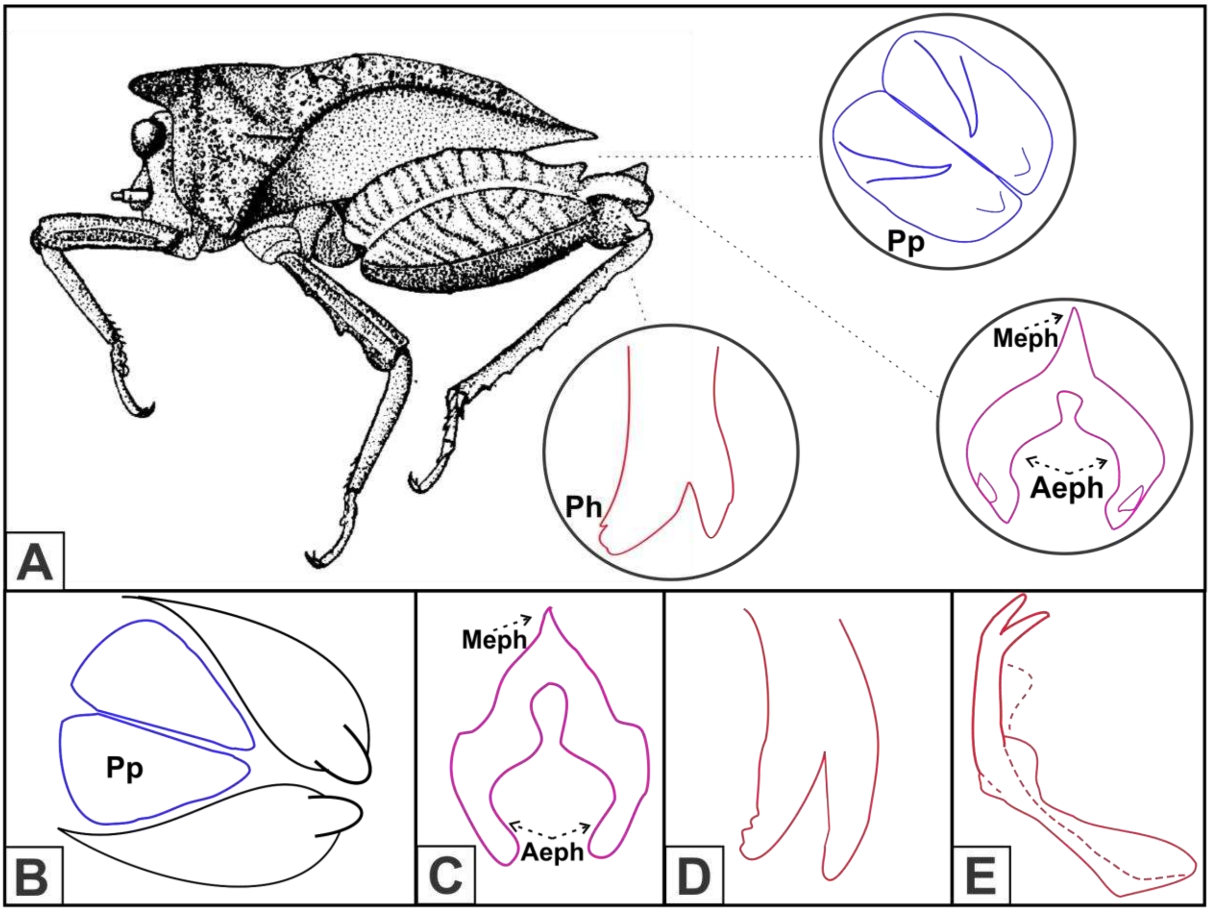

Figure 5. Phallic complex of (A) *Bufonides sellatus* Hinton, 1940 highlighting the pallial plates, epiphallus and phallic organ and *Bufonides antennatus* Bolívar, 1898 with terminalia in dorsal view (B), (C) epiphallus and (D-E) phallic organ. The drawings are adapted from Hinton (1940) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Meph: median process of epiphallus; Ph: phallic organ Pp: pallial plates.

According to the authors, the pallial complex is formed by three parts: pallial valves, pallial hook and pallial membrane. The pallial valves is formed by two plates which covered the opening of intromittent organ and near on the chitinous colar. This sclerite is U-shaped and at the moment when the intromittent organ is exposed, the chitinous collar is placed in the base of this organ.

Farrow (1964), in a simple study on the development of the genital organs of *Tetrix subulata*, indicated that the pallial hooks started developing from the fourth instar nymphs in this species. In the schematic drawing of *T. subulata*, the author indicated the presence of intromittent organ, chitinous collar, pallial valves and pallial hooks with sclerotized bands similar to Snodgrass's bars (Fig. 6C) (Tab.1).

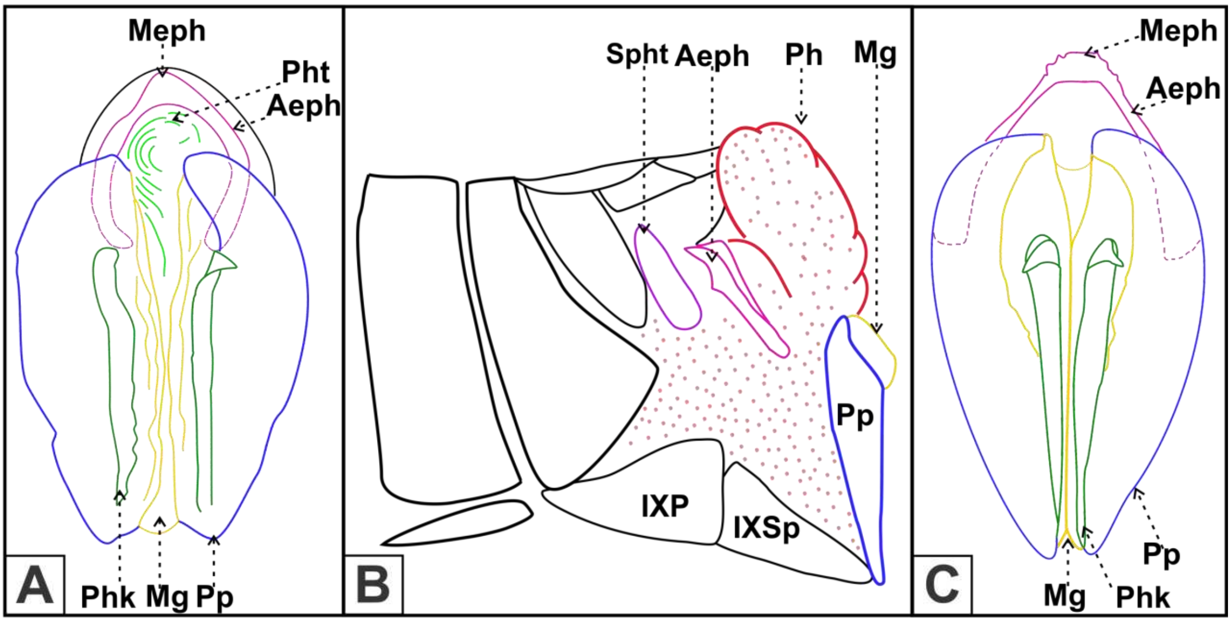

Figure 6. Terminalia dorsal view of (A) *Tetrix subulata* (Linnaeus, 1758); lateral view of (B) *Tetrix arenosa angusta* (Hancock, 1896) and dorsal view of (C) *T. subulata*. The drawings are adapted from Carpentier (1942), Widdows & Wick (1959) and Farrow (1964) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Meph: median process of epiphallus; Mg: medial groove; Ph: phallic organ; Phk: pallial hooks; Pht: phallotreme; Pp: pallial plates; Spht: sclerites of phallotreme; IXP: 9th sternum proximal part and IXSP: subgenital plate.

Harz (1975) in an extensive work on the fauna of Orthoptera in Europe, used the term phallic complex to indicate all structures lied above the subgenital plate, including the penis (Fig. 7A) (Tab.1). He gave a special attention to the epiphallus, term used to the U-shaped sclerite. He indicated that this structure is different to several species of *Tetrix* (Fig. 7B-E).

Nadig (1991), in a paper about the zoogeographic data of *Tetrix transsylvanica* (Bazyluk & Kis, 1960), also used the term phallic complex (Fig. 8A) as Harz (1975) with the same characteristics, highlighting the epiphallus (Fig. 8B) (Tab.1).

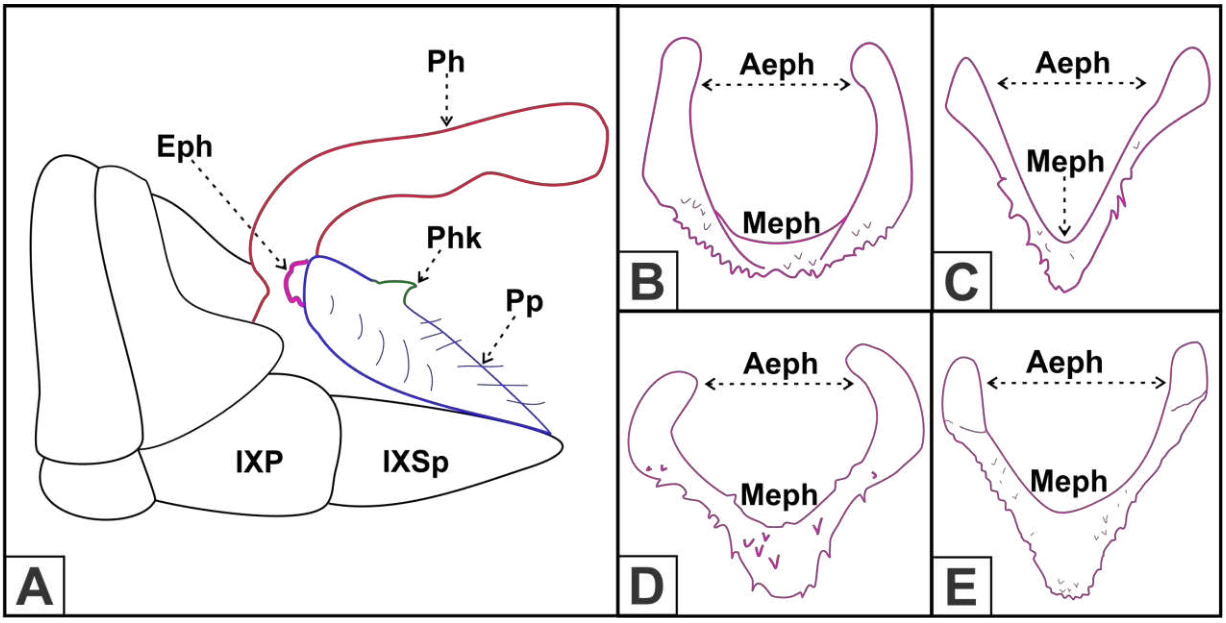

Figure 7. Terminalia in lateral view with phallic organ everted of (A) *T. subulata* and epiphallus on different species of *Tetrix* Latreille, 1802. The drawings are adapted from Harz (1975) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Eph: epiphallus; Meph: median process of epiphallus; Ph: phallic organ; Pp: pallial plates; IXP: 9th sternum proximal part and IXSP: subgenital plate.

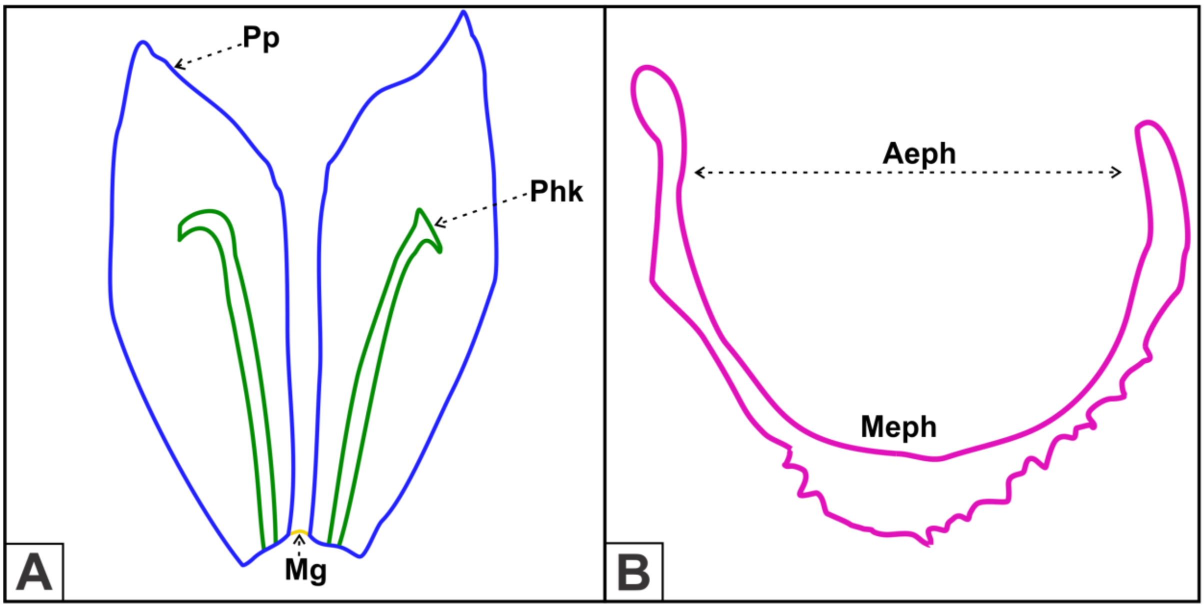

Figure 8. *Tetrix transsylvanica* (Bazyluk & Kis, 1960) terminalia in dorsal view (A) and epiphallus'(B). The drawings are adapted from Nadig (1991) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Meph: median process of epiphallus; Mg: medial groove; Phk: pallial hooks; Pp: pallial plates.

Hendrik Devriese (1996), in a review of tetrigids morphology endorsed the assertion of Amédgnato (1976) in which the genital organs are formed by two layers, but he did not mention the name of these layers. In his drawings he included a scheme of genital organs (Fig. 9A), the position of organs when is everted penis (Fig. 9B), the 'arcus' without the U-shaped and the ejaculatory duct. His study was the first in indicated the position of the parts during the genital organs eversion (Fig. 9) (Tab.1).

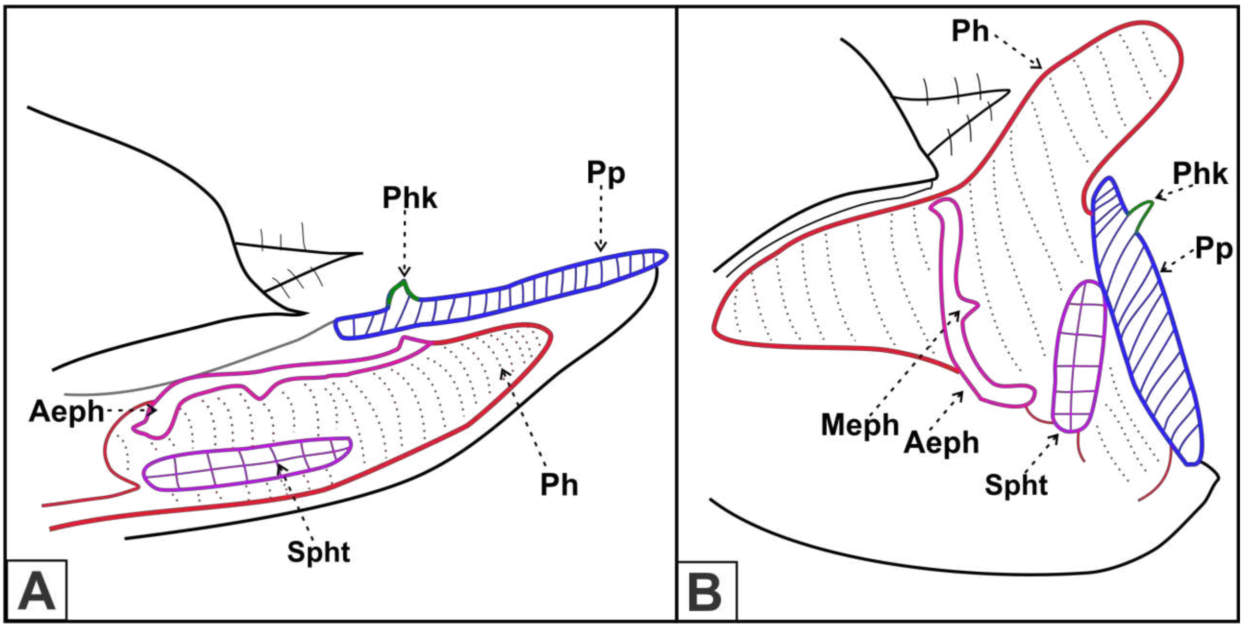

Figure 9. Terminalia in lateral view of *Tetrix tuerki* (Krauss, 1876) (A) highlighting the genital phallic complex and (B) the position of the same organs when the phallic organ is everted. The drawings are adapted from Devriese (1996) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Meph: median process of epiphallus; Ph: phallic organ; Phk: pallial hooks; Pp: pallial plates; Spht: sclerites of phallotreme.

The most recent researches have been made by **LI. Podgornaya (2002, 2003)** that broadens the discussion from the data of *Saussurella* Bolíva, 1887. In 2002 study, there are a general description of genital organs of *Tetrix subulata*, *Tettigidea lateralis* and *Saussurella cornuta* (Haan, 1843). In 2003, was indicated an important morphological discrepancy of *Saussurella cornuta* (Haan, 1843) and *Saussurella inelevata* Podgornaya, 1992 in contrast to the tetrigids species studied earlier in Podgnornaya's papers. In these latter species, the sclerotized plate of *pallium* form only one plate, combined anteriorly and separated only by a median longitudinal depression (Fig. 10E) while in the species known hitherto, *pallium* forms two separate plates.

This paper also has schemes of genital organs of *Tetrix subulata* and *Tettigidea lateralis*. **Podgornaya (2003)** uses terms for morphological structures different from those used in your previous work and also indicated that morphological differences may separate *Saussurella* on a different group of Batrachideinae. (Fig. 10) (Tab.1).

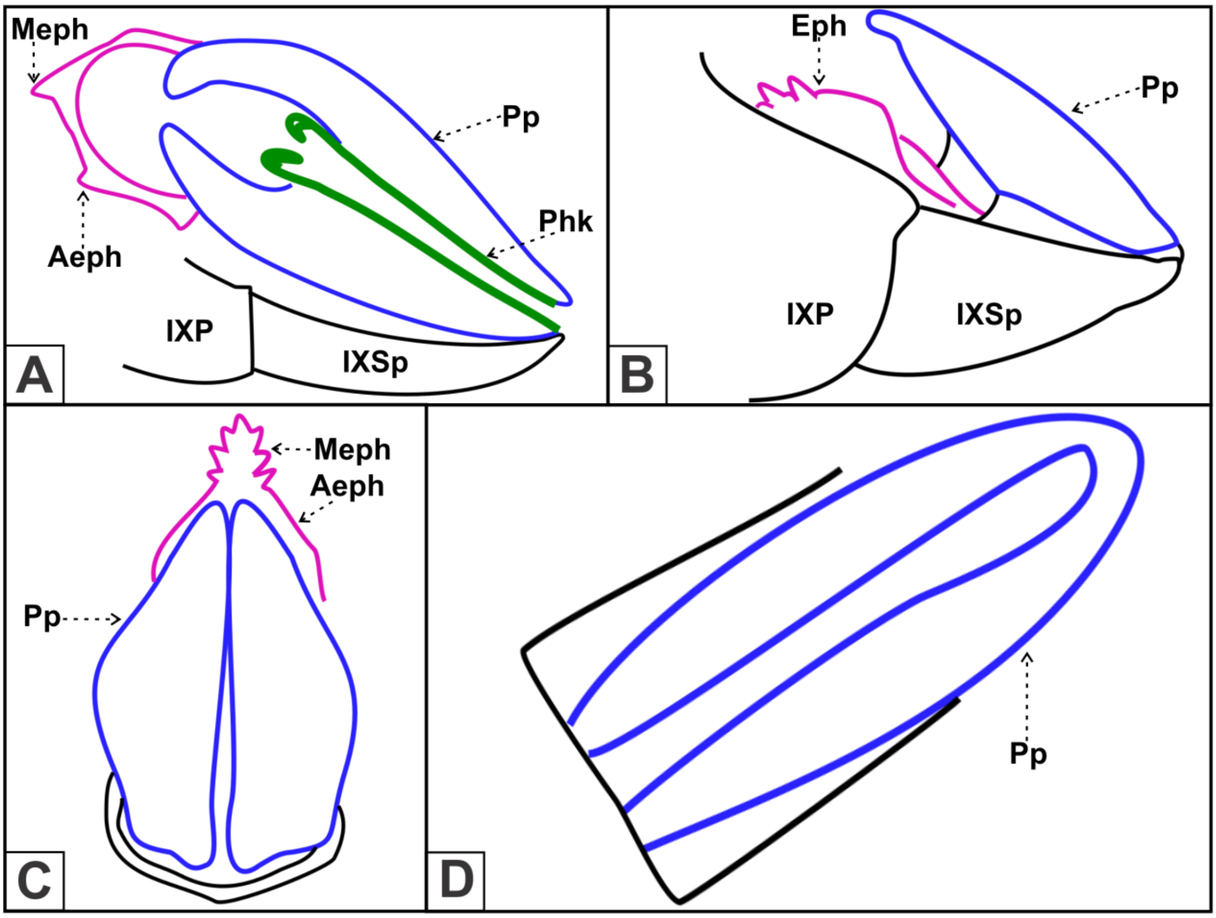

Figure 10. Terminalia dorsal view of (A) *T.subulata*; terminalia lateral view (B) and dorsal view of *T. lateralis* and dorsal view highlighting the pallial plates of (D) *Saussurella cornuta* (Haan, 1843). The drawings are adapted from Podgornaya (2002, 2003) with the correspondent terminology of structures and color in Table 1. Legends. Aeph: arms of epiphallus; Eph: epiphallus; Meph: median process of epiphallus; Pp: pallial plates; Phk: pallial hooks; Spht: sclerites of phallotreme; IXP: 9th sternum proximal part and IXSP: subgenital plate.

Male external genital organs: update to morphological terminology

The terminologies proposed by each author have been based on the interpretations of few species and several terms had already been used into previous literature of acridids (see Robert 1941, Dirsh 1956, Tuxen 1956, Kevan et al. 1973, Amédégnato 1976, Song & Mariño-Pérez 2013, Woller & Song 2017). Here, the terminology was derived, combined or modified on the basis of precision of definition or appropriateness for tetrigids morphology.

For grasshopper's non-tetrigids, Dirsh (1956) used 'phallic complex' to comprising the genital organs and the epiphallus. Kevan et al. (1969) used the same term as a synonymous of phallic organ or phallus but without epiphallus (Tab.1). Regarding tetrigids, Chopard (1920) pointed all parts placed on terminalia as 'Genital piece' (Tab.1); Harz (1975) and Nadig (1991) used the term 'phallic complex' to designate Chopard's structures, all of them placed on terminalia (Tab.1). Here, we consider the term **phallic complex** in tetrigids as genital organs related to copulation, forming by pallial structures, endophallic and epiphallic layers.

As has been noted by authors in the past, the genital organs of the Tetrigidae are a relatively complex, specialized organ and considerable differentiation has now been found among the specimens on literature. The study of Neotropical acridids from Amédégnato (1976) regarding the origin and development of genital organs placed on the terminalia (the terminal abdominal segments and their parts modified to form the genital segments, see Schuh et al. (1989)), deduced that the male genitalia of tetrigids would be formed by two concentric layers: the endophallic and epiphallic, being the ectophallic absent. The ectophallic layer or ectophallus is structure which among the various attributions, may be related to support for phallic complex, being an attachment points for muscles (Woller & Song, 2017). Possibly, this structure is not present in tetrigids since the phallic complex is anchored in the ninth abdominal sternum (Fig. 11C-D).

Podgornaya (2003) considered that the tetrigid male genitalia was a simple structure lies on the tip of subgenital plate and covered dorsally with the *pallium,* but our results indicated other important structures placed in the tetrigids terminalia in which is attached the genital organs: the ninth abdominal sternum. This segment is divided into two parts: a proximal (**IXP**) (Fig. 11) and a distal part, also called as the **subgenital plate** (**IXSp**) (Fig. 11), more flexible as designed by Walker (1922) and Snodgrass (1935) (Fig. 11). Unlike Podgornaya (2003) hypothesis, we found that above the IXP is attached the genital organs.

Covering the dorsal surface of the IXP and IXSp, there is the *pallium* which constitutes the **pallial plates** (**Pp**) (Fig. 11), terminology proposed by Walker (1922) (Tab.1) with only one continuous plate with a unique division (particular case of *Saussurella*) (Fig. 10E) or two distinct plates, both connecting on the apex of IXSp by membrane (Fig. 11A-B). The *pallium* is common in other grasshoppers, characterized as structure in a continuation of the ectophallic membrane, connecting the genital organs with posterior parts of the subgenital plate (see Kevan et al. 1973). However, there is no ectophallic membrane in tetrigids and the *pallium* is a plate continuous with the IXSp, which partly covers the genital organs (Fig. 11). The **pallial plates** (**Pp**) are sclerotized and covered the genital organs in the retracted state (Fig. 11A-B).

In some tetrigids, there are **pallial hooks** (**phk**) on the **pallial plates** (terminology proposed by Walker (1922) followed by Widdows & Wick (1959) and Farrow (1964)) (Tab.1) as two continuous slender bars with hooks in a distal part of **pallial plates**. Between the **pallial hooks**, there is a **median groove** (**Mg**) (Fig. 11A-B) (terminology proposed by Walker (1922) and also used by Podgornaya (2002)) (Tab.1) as an entire filiform median membranous line (Fig. 4G, 11B) or a filiform membrane with the distal part expanded (Fig. 3, 6C).

The endophallic layer or endophallus containing several structures as apodemes, gonopore processes, valves of aedeagus, phallotreme, arch of aedeagus (see Roberts 1941; Kevan et al., 1969; Woller & Song, 2017) and also for these structures, there are several different terms used in tetrigids which had been used to the similar morphological structures in other grasshoppers. Here, the membranous organ usually called intromittent organ (Harman, 1925; Widdows & Wick, 1959; Farrow, 1964), penis (Chopard, 1920; Walker, 1922; Harman, 1925; Carpentier, 1942; Harz, 1975; Nadig, 1991; Devriese, 1996) or aedeagus (Podgornaya, 2003) in tetrigids is named **phallic organ** (**Ph**) (Fig. 11C-F), as mentioned by Snodgrass (1935) and Podgornaya (2002) (Tab.1).

Other researchers have also used this term as Dirsh (1956) meaning the organ concerned by ecto- and endophallus and Kevan et al. (1969) as phallic complex (for him, formed by epiphallus + ectophallus + endophallus) without the epiphallus. Thus, we propose that **phallic organ** in Tetrigidae would be the intromittent organ forming by the endophallic layer, as was indicated by Amédégnato (1976) and the **phallic complex** would be this structure, the pallial structures and epiphallic layers. The **phallic organ** has sclerotized portions, as indicated in the drawing of Hinton (1940) (Fig. 5) and different levels of sclerotization were also noted in species of *Tettigidea* sp. (Fig. 11C-D) and *Tettigidea lateralis lateralis* (Say, 1824) (Fig. 11E-F).

The epiphallus in grasshoppers is usually a sclerotized structure situated on the dorsal surface of ectophallus (Kevan et al. 1969) with different functions during copulation as the sensory receptors, structural support for muscle attachment site, hook onto and pull down female subgenital plate to gain access to vulva and pushed into female lophi receptacles to keep her subgenital plate pulled down for aedeagus insertion through her vulva (Woller & Song, 2017). According to Walker (1922) this structure in tetrigids is an external phallic plate, named *pseudosternite* and corresponds to the epiphallus of acridids.

Here, this structure is also named **epiphallus** (**Eph**) (Fig. 11) because is placed dorsally to **phallic organ** and above the ninth sternum of tetrigids while in the other grasshoppers, is above the ectophallus. The **epiphallus** is in tetrigids a sclerotized structure V- or U-shaped, dorsally to the **phallic organ**. It is composed by two arms placed dorso-anteriorly to the phallic organ (**arms of epiphallus** (**Aeph**)) and may have a **median process of ephiphallus** (**Meph**) (Fig. 11). The median process and the arms may be narrow or broad and can have projections as little spines, only on a portion or in entire structure (Figs. 4B, G-H; F; 6A, C; 7; 8).

Other structure mentioned by previous authors to describe the tetrigids morphology of genital organs was named gonopore (Tab. 1), which is defined as short passage connecting the ventral part of the spermathophore sac with the ejaculatory sac (Kevan et al. 1973). In tetrigids, we found a structure which corresponds to the **phallotreme** (**Pht**) (Fig. 11B), the opening through which in the **phallic organ** is everted. Among the **arms of epiphallus** (**Aeph**) and circumvention the **phallotreme**, there are two lateral plates which in Walker (1922) named as ‘rami’ and Podgornaya (2002, 2003) termed as ‘plane plates’ and ‘plates strengthening posterior part of aedeagus’ respectively (Tab. 1). Here, the nomenclature used for these plates are **sclerite of phallotreme** (**Spht**) (Figs. 4B,H; 9; 11A-D,F) since these structures are located laterally the opening of **phallotreme**.

<u>According the literature information, are the Phallic Complex and Genital Organs useful in taxonomy? Yes</u>

The terminalia and the phallic complex have presenting different degrees of complexity and all authors cited in this present study indicated or described morphological structures associated with tetrigids genitalia without deeply comparisons between species. Podgornaya (2003) affirmed that the possible reason to genitalia of tetrigids have not been used in taxonomic studies is the simplified structure found in this taxa. However, the previous studies about the genital morphology of tetrigids shown a variation of forms which are more easily noted in two structures: the phallic organ and epiphallus. The phallic organ has sclerotized portions as indicated by Hinton (1940) and the specimens here dissected, there is sclerotization placed inside the phallic organ (Fig. 11C-F). *Tettigidea* sp. (Fig. 11C-D) has a cylindrical internal sclerotization in which it was not necessary to apply coloration to better visualize the internal morphology of this organ and in the *Tettigidea lateralis lateralis* (Fig. 11E-F) were stained with Chlorazol Black-E since the sclerotization is reduced.

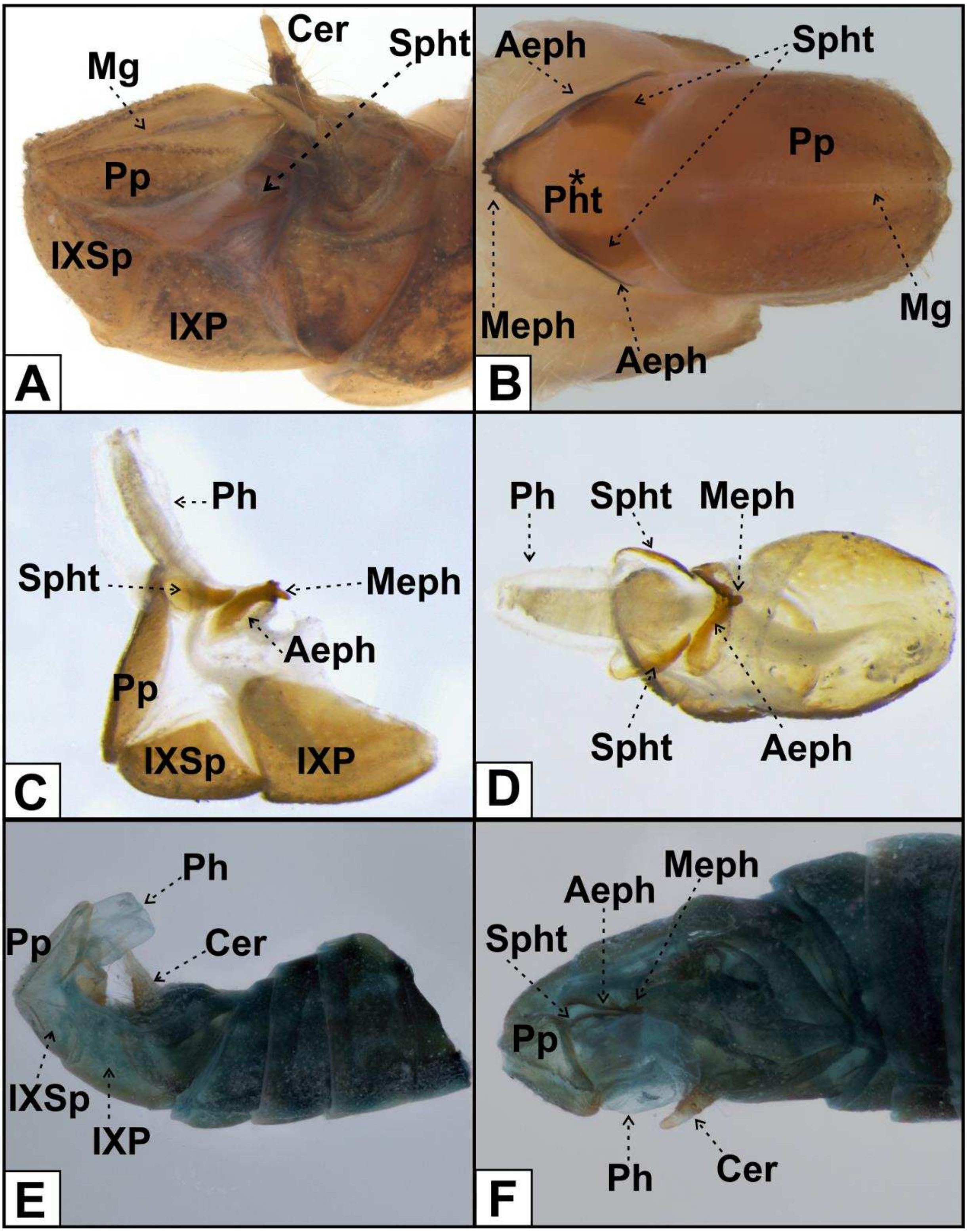

Figure 11. Terminalia structures of *Halmatettix* sp. with phallic organ not everted (A) in lateral and (B) dorsal view; position of phallic complex structures with phallic organ everted in *Tettigidea* sp.

(C) in lateral and (D) dorsal view and *Tettigidea lateralis lateralis* (E) in lateral and (F) dorsal-lateral view. Legends. Aeph: arms of epiphallus; Cer: cercus; Meph: median process of epiphallus; Mg: medial groove; Ph: phallic organ; Pht: phallotreme; Pp: pallial plates; Spht: sclerites of phallotreme; IXP: 9th sternum proximal part and IXSP: subgenital plate.

Although apparently without this objective, Hinton (1940) and Harz (1975) indicated through their drawings significant differences between the ephiphallus to base comparisons of species of *Bufonides* and *Tetrix*. The epiphallus shape, angulation of arms, ornamentation of median process and surface of this structure presents morphological differences that allowed used this structure as a taxonomic character to compare different species. Nadig (1991) also indicated in his drawings that for the species *Tetrix transsylvanica*, the arms of epiphallus are neither symmetrical nor bilaterally similar.

The data of Harz (1975) and Nadig (1991) as well contradict Podgornaya's (2003) statement in which the structure of genitalia could not be taxonomically used for the subfamily Tetriginae because the uniformity in the genital morphology of this group. Precisely in this subfamily, the drawings indicated that there are genital structures that can add information and facilitate the distinction of species. The pallial plates are also informative structures, presenting unique differences to the *Saussurela* genus. Podgornaya (2003) indicated that the pallial plates in this group is continuous, separated only by a single depression.

A similar situation on theoretical construction of the study of tetrigids genital organs happened with other grasshoppers, and starting from this study the evidence from the shape of the phallic organs and complex phallic data should be investigated in detail in order to facilitate the complement of these data on the conventional classification of tetrigids.

Can other terminalia structures be used to distinguish species? Yes

In addition to the phallic complex, the terminalia region has structures that also have historically been neglected in the taxonomy of tetrigids. With rare exceptions such as the studies made by Grant (1955, 1956, 1966), structures such as the subgenital plate, epiproctrus and cerci are not included in the descriptions of the species nor are they considered taxonomic characteristics. Thus, here we indicate that in a series of species of *Scaria*, that the subgenital plate of the most recent species described for South America (Fig. 12) add information that improve the description of species.

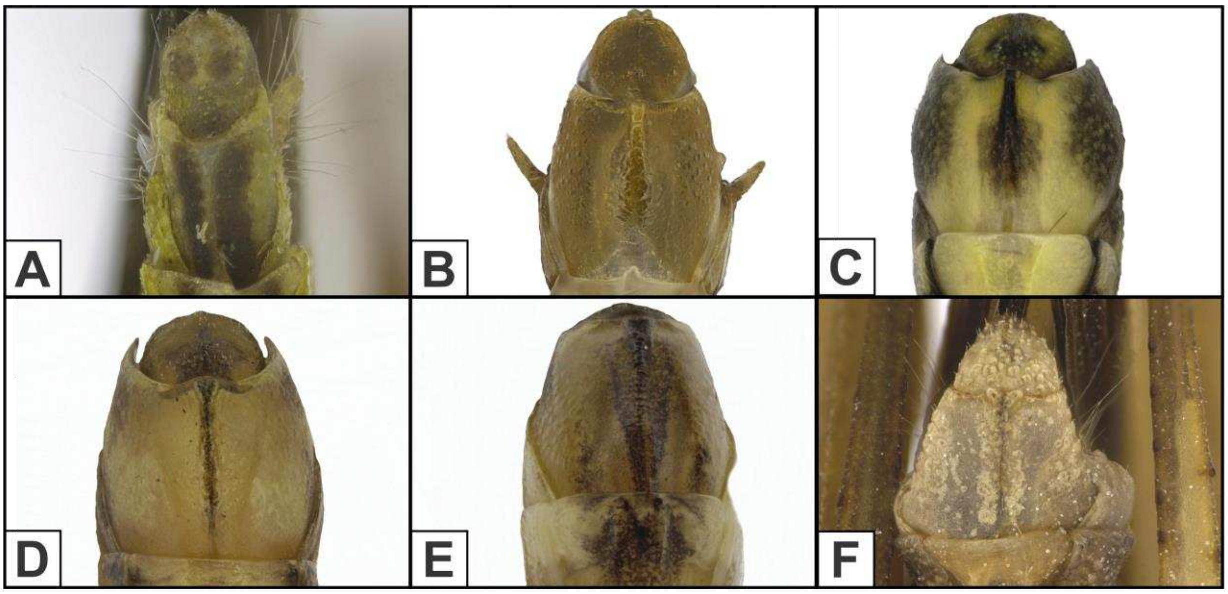

Figure 12. 9th sternum proximal part and subgenital plates in ventral view shape of (A) *Scaria laeta* sp.1; (B) *Scaria ferruginea* Hancock, 1909; (C) *Scaria granti* sp.2; (D) *Scaria jonasi* sp.3; (E) *Scaria rafaeli* sp.4 and (F) *Scaria hamata* (De Geer, 1773).

Next steps and recommendations

More studies are needed to improve the understanding of the phallic complex functions, origin and evolution in Tetrigidae. For this purpose, we should sample more specimens as maximum as possible and conserve some of them in alcohol to genitalia extraction because genitalia of fresh material are easier to work than in dry material. In specimens dried, the phallic organ collapses or the specimen is empty on the inside, due to the action of collembolans and small insects.

From correctly preserved specimens for morphological studies, the next step is to verify the variation of the sclerotizations of the phallic organ, epiphallus among species and supra-generic levels besides comparing with the other structures of the terminalia. Thus, with this information we can indicate in the future a possible Bauplan of external components of the genital organs in tetrigids and insert in the taxonomic description of this taxon, data referring to the phallic complex.

Acknowledgements

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Table 1. Comparison of terminologies of Tetrigidae genital organs (based on the comparison of morphological positions structures cited by each author in the original texts and figures).

Structures Colors	**Chopard (1920)**	**Walker (1922)**	**Harman (1925)**	**Snodgrass (1935)**	**Carpentier (1942)**	**Widdows & Wick (1959)**	**Farrow (1964)**	**Harz, (1975)**	**Nadig (1991)**	**Devriese (1996)**	**Podgornaya (2002)**	**Podgornaya (2003)**	**Terms and abbreviations used here**
-	Genital pieces (Valvas + Chitinous pieces+ median sulci)	-	-	-	-	-	-	Complex Phallic	Complex Phallic	-	-	-	-
Red	Penis	Penis	Penis or sac-like intromittent organ	Phallic organ with median process armed with small spines	Penis	Intromittent organ	Intromittent organ	Penis	Penis	Penis	Phallus or Phallic organ	Eadeagus	**Phallic organ (Ph)**
Blue	Valvas (part of genital pieces)	Pallial plates	-	Pallial valves	Pallial valves	Pallial valves (part of pallial complex)	Pallial valves	-	-	Pallial valves	Sclerotized plate of pallium	Valves of pallium	**Pallial plates (Pp)**
Green	Chitinous piece (part of genital pieces)	Pallial hooks	Ridge of chitin with a small hook	Bars terminating anteriorly in upcurved hooks	-	Pallial hook (part of pallial complex)	Pallial hook (with sclerotized bands)	-	-	-	Two slender rods, with a pair of small hooks	Hooks between valves of pallium	**Pallial hooks (Phk)**

Table 1. Continued

Structures Colors	Chopard (1920)	Walker (1922)	Harman (1925)	Snodgrass (1935)	Carpentier (1942)	Widdows & Wick (1959)	Farrow (1964)	Harz, (1975)	Nadig (1991)	Devriese (1996)	Podgornaya (2002)	Podgornaya (2003)	Terms and abbreviations used here
Orange	Median sulci (part of genital pieces)	Median suture or Median Groove	Groove	Median membranous line	-	Pallial membrane (part of pallial complex)	Pallial membrane	-	-	-	Median Groove or Median membranous suture	Narrow membranous strip	**Median groove (Mg)**
Pink	-	Pseudosternite v-shaped (ephiphallus)	Chitinous collar	-	-	Chitinous collar	Chitinous collar	Epiphallus	Epiphallus	Arcus	Sclerites of phallus	Sclerites of aedeagus	**Epiphallus (Eph)**
Pink	-	Median process (spines in pseudosternite)	-	This character is not mentioned separated.	-	-	-	-	-	-	-	-	**Median process of epiphallus (Meph)**
Purple	-	Rami	-	-	-	-	-	-	-	-	Plane plates	Plates strengthening posterior part of aedeagus	**Sclerite of phallotreme (Spht)**
Light green	-	Gonopore (genital opening)	-	Gonopore (ejaculatory duct opens anteriorly)	Gonopore	-	-	-	-	-	-	Gonopore	-

Legend. "-" when the structure is not mentioned by authors.

CONCLUSÕES GERAIS

Nossos resultados reforçaram a afirmativa de que os tetrigídeos são um grupo que apresenta lacunas nos mais diversos aspectos relacionados à descrição, identificação, classificação, amostragem e morfologia entre os Caelifera. Apesar de serem um grupo representativo em diversidade, principalmente na região Neotropical, muitos táxons além dos aqui abordados, necessitam ser revistos sistematicamente. Assim, as revisões apresentadas neste trabalho tiveram como objetivo fornecer uma nova releitura, mais ampla e minuciosa de detalhes taxonômicos que até então não haviam sido incluídos ou destacados nos táxons aqui estudados. A partir dessas novas e/ou reorganizadas informações, a sistematização desses dados ampara e enriquece a definição dos grupos e consequentemente, leva à diminuição de problemas e hesitações taxonômicas.

Como indicado em nossos resultados, Lophotettiginae e Batrachideinae são as subfamílias que possuem a delimitação mais clara dentre os tetrigídeos até o presente momento. Lophotettiginae, com apenas um gênero e cinco espécies conhecidas, apresenta um conjunto de características que os distinguem facilmente dos demais tetrigídeos, enquanto Batrachideinae, em toda sua diversidade, se consolida como um grupo monofilético que ainda precisa ter alguns de seus táxons revisados.

Para alcançar esse refinamento taxonômico, novas informações, já utilizadas em outros táxons de Caelifera devem ser incorporadas à definição dos grupos. Uma vez que a delimitação de organismos se baseia tradicionalmente em caracteres morfológicos diagnósticos, a inclusão de dados referentes à terminalia e mais especificamente, ao complexo fálico é um caminho conhecido e seguro, que como indicado nos nossos resultados, deve ser incorporado aos trabalhos morfológicos e taxonômicos de tetrigídeos.