

**JULIANA CHAMORRO RENGIFO**

**MORFOLOGIA DO FALO E TÉGMINA EM TETTIGONIOIDEA, E  
REVISÃO TAXONÔMICA DO ANTIGO GÊNERO *Agraecia*  
AUDINET-SERVILLE (ORTHOPTERA: ENSIFERA:  
TETTIGONIIDAE)**

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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Cristiano Lopes Andrade  
(Orientador)

Aos meus professores e maestros, que me ensinaram e inspiraram durante todos esses anos... porque o mundo muda com mais educação e cultura.

**Five basic principles in Science:**

Think for yourself.

Question authority, but also question yourself and your own biases and assumptions.

Test your ideas, and if the experiments fail, discard those bad ideas and move on.

Follow the evidence, and always remember:

You could be wrong -- and there's nothing wrong with that, unless you refuse to admit you were wrong.

***“Unafraid of the Dark” - Neil deGrasse Tyson***

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## RESUMO

CHAMORRO RENGIFO, Juliana, D. Sc., Universidade Federal de Viçosa, Julho de 2014. **Morfologia do falo e tégmina em Tettigonioidea, e revisão taxonômica do antigo gênero *Agraecia* Audinet-Serville (Orthoptera: Ensifera: Tettigoniidae).** Orientador: Cristiano Lopes Andrade.

*Agraecia* Audinet-Serville (Tettigoniidae: Conocephalinae: Agraeciini), o gênero-tipo de Agraeciini, compreende quinze nomes de espécies: treze usados para nomear espécies viventes, um sinônimo júnior e um fóssil. As espécies descritas de *Agraecia* são morfologicamente distintas e foram coletadas em diferentes localidades do mundo. Poucos caracteres morfológicos definem o gênero e esses, em conjunto, não são exclusivos do táxon. O objetivo desta tese é redefinir o gênero *Agraecia* com base na morfologia comparada de estruturas usadas tradicionalmente na taxonomia de Tettigonioidea e em outras estruturas que são aqui apresentadas como novidade para o estudo do grupo. Para realizar a delimitação de *Agraecia* e dos gêneros novos propostos, foi preciso realizar um estudo prévio sobre a morfologia do falo das esperanças neotropicais (Capítulo I). Adicionalmente, durante a observação das nervuras das tégminas das espécies de Tettigonioidea, notou-se que a tégmina direita possui uma fileira estridulatória vestigial, fato que não tinha sido reportado previamente nem para as espécies de Agraeciini, e com algumas exceções, nem para outros táxons da superfamília. Por tal motivo, reportou-se que a fileira direita vestigial é um componente da tégmina e é útil para o estudo taxonômico da superfamília (Capítulo II). Finalmente, delimita-se *Agraecia* (Capítulo III, manuscrito) e se propõe que somente duas espécies das previamente descritas permaneçam no gênero, *A. dorsalis* Karny e *A. punctata* Saint-Fargeau & Audinet-Serville. Designa-se um neótipo e um neoalótipo de *A. punctata*, e quatro novas espécies do gênero são descritas. Propõe-se *Bertoniella* Rehn como novo sinônimo e a nova combinação *Parasubria vittipes* (Redtenbacher) **comb. nov.** As restantes sete espécies viventes são classificadas em seis novos gêneros, a seguir: **Gen. nov. 01**, **Gen. nov. 02**, **Gen. nov. 03**, **Gen. nov. 04**, **Gen. nov. 05** e **Gen. nov. 06**. E a espécie fóssil é transferida para **Gen. nov. 07** †. Adicionalmente, quatro novas espécies de **Gen. nov. 01** são descritas. O material tipo de *Agraecia fallax* Karny, nomen dubium está perdido e o de *Agraecia festae* Griffini está atualmente indisponível para revisão, assim, essas duas espécies são tratadas como *incertae sedis*. Finalmente, discute-se sobre a morfologia, a distribuição geográfica, e sobre a biologia e a ecologia das espécies.

## ABSTRACT

CHAMORRO RENGIFO, Juliana, D. Sc., Universidade Federal de Viçosa, July 2014.  
**Morphology of the phallus and tegmina in Tettigonioidea and taxonomic revision of the old genus *Agraecia* Audinet-Serville (Orthoptera: Ensifera: Tettigoniidae).**  
Advisor: Cristiano Lopes Andrade.

*Agraecia* Audinet-Serville (Tettigoniidae: Conocephalinae: Agraeciini), the type-genus of Agraeciini, comprises fifteen species names: thirteen used for extant species, one junior synonym, and one fossil. The species are morphologically very dissimilar, and were collected and described from different localities of the world. Few morphological features define the genus *Agraecia*, and these are not unique to the taxon. The objective in this thesis is to revise and redefine the genus *Agraecia* based on morphology of structures traditionally considered in the taxonomy of Tettigonioidea, and on structures which are presented here as novelties for the study of the superfamily. To carry out the delimitation of *Agraecia* and new genera, it was necessary to conduct a preliminary study on the morphology of the phallus in Neotropical katydids (Chapter I). Additionally, during the examination of the tegminal veins of the studied species, it was noted that in the right tegmen there is a vestigial file, fact that had not been previously reported for the treated species and, with few exceptions, neither to other taxa of the superfamily. For this reason, it was elaborated a short paper reporting that the right file is an additional component of the tegmina and is useful for the taxonomic study of the superfamily (Chapter II). Finally, *Agraecia* is redelimited (Chapter III, manuscript) keeping only two of the previously described species in the genus: *A. dorsalis* Karny and *A. punctata* Saint-Fargeau & Audinet-Serville. It is designated a neotype and a neoallotype for *A. punctata*, and four new *Agraecia* species are described. *Bertoniella* Rehn, is determined as a junior synonym of *Agraecia*. The new combination *Parasubria vittipes* (Redtenbacher) **comb. nov.** is proposed. The remaining six *Agraecia* species are classified in six new genera: **Gen. nov. 01**, **Gen. nov. 02**, **Gen. nov. 03**, **Gen. nov. 04**, **Gen. nov. 05** and **Gen. nov. 06**. The fossil species is transferred to **Gen. nov. 7†**. Additionally, four new species of **Gen. nov. 01** are described. Type material of *Agraecia fallax* Karny, **nomen dobiium**, is lost and the one of *Agraecia festae* Griffini is currently unavailable for examination, thus these two species are treated as *incertae sedis*. Finally, the morphology, geographical distribution, biology and ecology of the species are discussed.

## 1. INTRODUÇÃO

Tettigonioidea está constituída por espécies fósseis classificadas em Haglotettigoniidae (Gorochov 1988) e por espécies viventes cuja classificação supragenérica tem sido instável desde a criação do táxon até a atualidade. As relações filogenéticas internas não estão bem resolvidas, e os dados morfológicos e moleculares indicam que várias das tribos e subfamílias apresentam uma origem para- e polifilética (Nickle & Naskrecki 1997; Naskrecki 2000a; Mugleston *et al.* 2013). As espécies viventes estavam incluídas dentro de uma única família, Tettigoniidae, porém uma proposta recente propôs Phaneropteridae como um grupo natural que inclui as subfamílias Phaneropterinae, Pseudophyllinae, Mecopodinae e Phyllophorinae (Heller *et al.* 2014). O restante das categorias supragenéricas não foram modificadas.

O número de espécies descritas excede sete mil, classificadas em aproximadamente mil gêneros e 19 subfamílias (Eades *et al.* 2014). A maior parte dos grupos taxonômicos ocorrem nas regiões tropicais e subtropicais (Naskrecki & Otte 1999; Naskrecki 2000b). As espécies de Tettigonioidea registradas para a América do Sul estão classificadas em duas famílias: Tettigoniidae (Conocephalinae, Hexacentrinae, Listrosclidinae, Meconematinae, e Mecopodinae) e Phaneropteridae (Phaneropterinae, Pseudophyllinae, e Tettigoniinae) (Eades *et al.* 2014).

### 1.1 Tettigonioidea, estado do conhecimento da superfamília no Brasil

No Brasil, os tettigonídeos são popularmente conhecidos como esperanças, porém esse nome vulgar se refere usualmente aos indivíduos grandes, de cor verde e com aparência de folha; caracterização que não inclui a maior parte dos tettigonídeos, diferentes desse padrão. Há registros de ocorrência de 599 espécies de esperanças, e destas, 584 foram descritas com base em indivíduos coletados no país (Eades *et al.* 2014). As espécies reportadas estão classificadas em cinco subfamílias, a saber (número de espécies entre parênteses): Phaneropterinae (287), Pseudophyllinae (150), Conocephalinae (127), Listrosclidinae (22) e Meconematinae (13) (Eades *et al.* 2014).

As primeiras espécies brasileiras conhecidas foram descritas por Linnaeus (1758; cinco espécies) e o número aumentou até a década de 80 do século XX. A partir dos anos 90, os estudos sobre as esperanças brasileiras foram escassos. Até 2005 somente uma nova espécie foi descrita (*Spinapecta alieniphaga* Naskrecki & Lopes-Andrade), e entre os anos de 2010 e 2012 dois gêneros e uma espécie foram descritos,

provenientes do material-tipo de Salvador de Toledo e Piza depositado no Museu de Entomologia da ESALQ (*Pizatettix* Chamorro-Rengifo & Braun e *Toledopizia* Chamorro-Rengifo & Braun; *Anaulacomera pizai* Cadena-Castañeda) (Chamorro-Rengifo 2014). Os estudos taxonômicos em esperanças tem se reativado recentemente com a descrição de uma tribo, um gênero e sete espécies novas de Listroscelidinae da Floresta Atlântica (Fialho *et al.* 2014).

Entre os taxonomistas brasileiros que estudaram a fauna de tettigonídeos, se destacam três pesquisadores, Salvador de Toledo e Piza, Cândido Firmino de Mello Leitão e Ângelo Moreira da Costa Lima, sendo o primeiro quem descreveu o maior número de gêneros e espécies. Após o trabalho desses autores, nenhum especialista se dedicou tanto a esse táxon no Brasil. Além do incipiente conhecimento taxonômico, pouco se sabe sobre biologia, ecologia e distribuição geográfica das espécies brasileiras (Chamorro-Rengifo 2014).

Há registros de tettigonídeos em 20 dos estados brasileiros (Eades *et al.* 2014), não existindo registros para Alagoas, Ceará, Piauí, Roraima, Sergipe e Tocantins (Chamorro-Rengifo 2014). Os estados com maior número de espécies descritas são Amazonas, Rio de Janeiro e São Paulo, o que pode estar relacionado com a presença de especialistas, como no Rio de Janeiro e em São Paulo, ou por grande número de expedições de coleta, como no caso do Amazonas (Chamorro-Rengifo & Braun 2010). Se compararmos o número de espécies descritas e tamanho do território, um país pequeno como a Costa Rica tem 89 espécies descritas, mas é 111 vezes menor que o Brasil. Assim, pode-se deduzir que o número potencial de espécies que habitam o território brasileiro deve ser muito maior do que o conhecido atualmente (Chamorro-Rengifo 2014).

## **1.2. Breve história taxonômica dos Agraeciini americanos**

Os Agraeciini são esperanças tropicais e subtropicais, que habitam principalmente florestas, encontrados no sub-bosque, vegetação herbácea (Rentz 1976), e até em habitats especializados dentro da floresta, como em líquens (Rentz & Ueshima 2012). Pouco se sabe sobre seus hábitos alimentares, porém existem registros de indivíduos se alimentando de flores (Rentz 1976), predando gastrópode terrestre e outros invertebrados (Ingrisch 1998, Leong 2011), e de galhos de árvores em decomposição (Ingrisch & Tan 2012). A maioria das espécies descritas são da região Indomalaia e muitas delas foram tratadas em trabalhos taxonômicos recentes (Rentz &

Ueshima 2012, Naskrecki & Rentz 2010, Ingrisch & Tan 2012, Ingrisch 2009, Ingrisch 1998). As faunas Americana e Africana de Agraeciini também devem ser altamente diversificadas, porém tem sido insatisfatoriamente estudadas, com poucas coletas em seus biomas.

Os limites da tribo ainda não estão muito claros, devido principalmente a vários gêneros problemáticos que ocorrem na América Central e América do Sul (Nickle & Naskrecki 1997; Naskrecki 2000a,b). Adicionalmente, há pouca informação disponível sobre as características morfológicas das espécies Neotropicais, principalmente sobre a morfologia de estruturas do pós-abdômen (cercos, paraproctos, falo) e tégminas. Atualmente, o gênero mais problemático de Agraeciini é *Agraecia* Audinet-Serville, o gênero-tipo, que agrega espécies morfológicamente muito distintas.

Redtenbacher (1891) tratou os gêneros de Conocephalinae (como “Conocephaliden”) em quatro tribos: Conocephalini, um grupo proposto anteriormente com status de família (Burmeister 1838; Thomas 1872); “Agroeciini” (=Agraeciini); “Listroscelini”; e Xiphidiini. Conocephalini agrupava gêneros que atualmente estão em Copiphorini (veja Eades *et al.* 2014). Xiphidiini é considerada um sinônimo de Conocephalini (Rehn & Hebard 1915). “Listroscelini” tem atualmente status de subfamília válida dentro de Tettigoniidae, com o nome corrigido para Listroscelidinae (ver Fialho *et al.* 2014); porém, possui uma longa história de controvérsias com Meconematinae (Fialho *et al.* 2014). Devido às inconsistências na definição dos caracteres diagnósticos das atuais tribos Agraeciini, Conocephalini e Copiphorini, existe uma sobreposição ainda não completamente resolvida de alguns gêneros problemáticos com espécies presentes na América do Sul (Nickle & Naskrecki 1997; Naskrecki 2000b).

Para compor o nome “Agroeciini”, Redtenbacher seguiu a correção injustificada de *Agraecia* por “*Agroecia*” usada previamente por Burmeister (1838). O nome correto é Agraeciini, que foi usado primeiramente por Karny (1907). Os Agraeciini de Redtenbacher (1891) incluíam espécies caracterizadas por ter a base do fastígio do vertex mais estreita e curta que o escapo antenal, e por não terem uma projeção em forma de dente na porção ventral, características que, na opinião do autor, os separava dos Conocephalini. Adicionalmente, os Agraeciini apresentam no fastígio do vertex uma carena longitudinal estendida, na superfície ventral, até o fastígio da frente; os fêmures posteriores estão armados com espinhos nos dois lados, ou somente na porção exterior; a tíbia anterior apresenta espinhos moderados; e o ovipositor é curvado para cima (Ingrisch 1998).

Originalmente, Agraeciini incluía 22 gêneros (Redtenbacher 1891), sete deles do continente Americano: *Hyperomerus* Redtenbacher, *Subria* Stål, *Eppia* Stål, *Eschatoceras* Redtenbacher, *Agraecia*, *Nannagroecia* Redtenbacher e *Cestrophorus* Redtenbacher. Posteriormente, dez gêneros americanos foram incluídos na tribo, como detalhado a seguir. *Acanthacara* Scudder foi descrito em Tettigoniidae (“Locustariae”) e tratado posteriormente como Conocephalinae (Kirby 1906) ou Copiphoridae (atualmente Copiphorini) por Bruner (1915). Atualmente, *Acanthacara* é considerado um Agraeciini (Gurney 1972). *Erechthis* Bolívar foi descrito dentro de Tettigoniidae (“Locustidae”), sinonimizado com *Subria* por Redtenbacher (1891), reestabelecido e incluído em Agraeciini por Kirby (1906). Três novos gêneros foram descritos em Conocephalinae, *Loja* Giglio-Tos, *Paralobaspis* Giglio-Tos e *Uchuca* Giglio-Tos, transferidos posteriormente para Agraeciini (Kirby 1906). *Paranelytra* Karny foi descrito diretamente em Agraeciini. *Sphyrometopa* Carl foi descrito em “Conocéphalides”, tratado posteriormente como Copiphorinae (Bruner 1915) e finalmente como Agraeciini (Rentz 1976). *Dectinomima* Caudell foi inicialmente incluído em Copiphorinae (atualmente Copiphorini) e transferido para Agraeciinae (atualmente com status de tribo; Caudell 1918). *Parasubria* Karny foi descrita como Agraeciinae e *Bertoniella* Rehn foi originalmente incluída em Tettigoniidae e depois considerado um Agraeciini (Rehn 1942). No total, os Agraeciini americanos compreendem atualmente 17 gêneros (Eades *et al.* 2014).

As espécies de Agraeciini estão distribuídas nas regiões Neotropical, Afrotropical, Indomalala e Australasiana, com um número reduzido de espécies na região Paleártica (Eades *et al.* 2014). No neotrópico, *Eppia* é o único gênero que ocorre mais ao norte da região, com registros na Costa Rica (Naskrecki 2000b). Para o Brasil estão reportados sete gêneros (número de espécies entre parênteses): *Agraecia* (7), *Eschatoceras* (3), *Nannagroecia* (1), *Paralobaspis* (1), *Parasubria* (1), *Subria* (2), e *Uchuca* (1), a maioria delas coletadas nos biomas Floresta Amazônica e Floresta Atlântica.

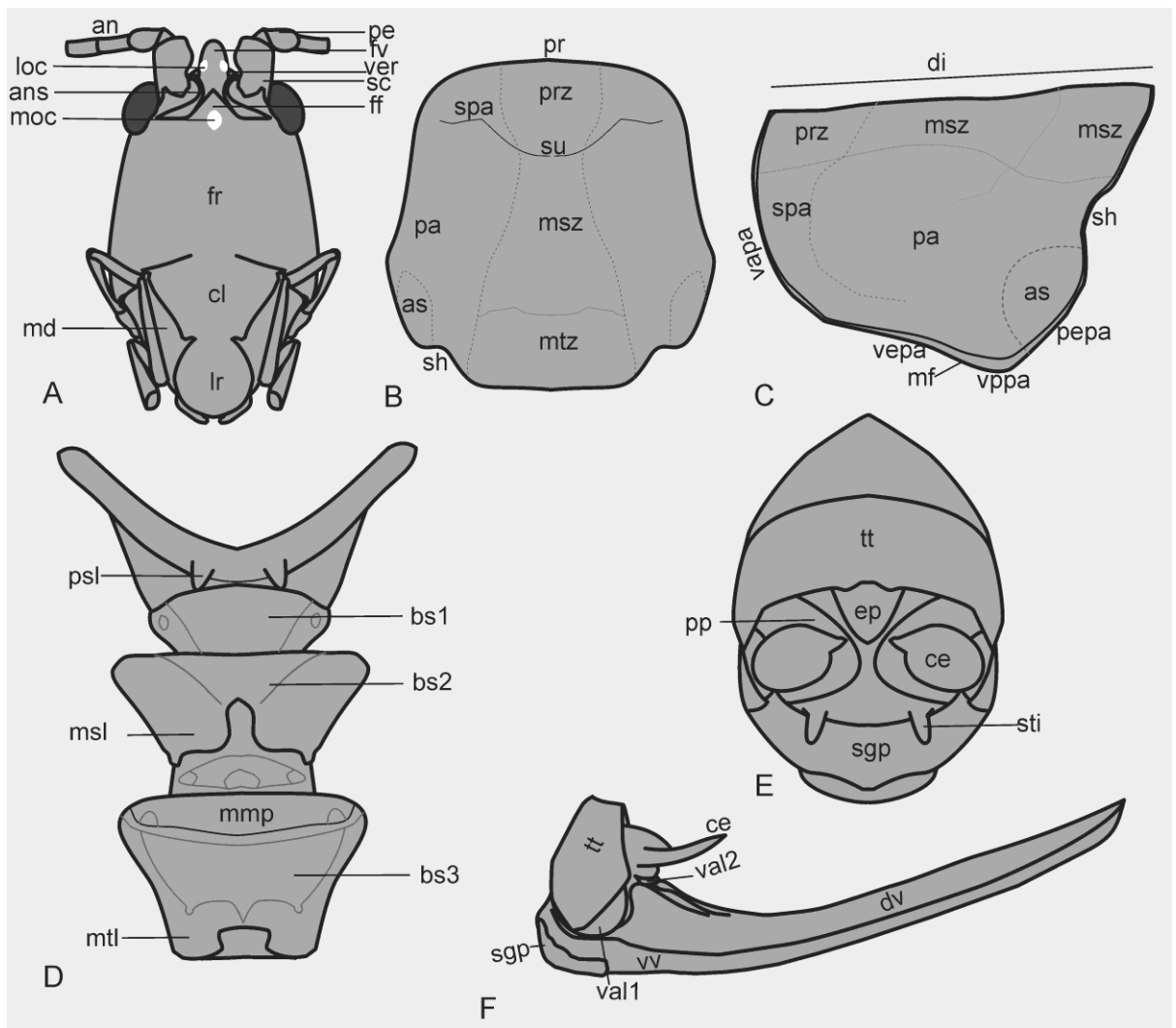
### **1.3. Problemas de classificação e relações filogenéticas em Agraeciini**

Agraeciini é considerada uma das tribos mais problemáticas e difíceis de diagnosticar dentro de Tettigoniidae (Nickle & Naskrecki 1997; Naskrecki 2000a). Como relatado anteriormente, vários dos gêneros que estão atualmente agrupados em Agraeciini não foram originalmente incluídos na tribo. Adicionalmente, uma parte dos

gêneros está classificada em quatro subtribos (número de gêneros entre parênteses): Eumegalodontina (2), Liarina (26), Oxylakina (8) and Salomonina (5). Os 57 restantes, incluindo todos os gêneros Americanos, permanecem desagrupados (Eades *et. al.* 2014). Essa condição é inconsistente e pode levar à interpretação de que todos esses 57 gêneros não-agrupados, incluindo *Agraecia*, estariam dentro da não definida subtribo “Agraeciina”.

A forma do fastígio do vertex é uma das características mais problemáticas na diagnose da tribo, em especial nos gêneros *Dectinomima*, *Eppia*, *Hyperomerus*, *Sphyrometopa* e *Uchuca*. Hebard (1927) referiu-se a *Sphyrometopa* como um gênero aberrante da tribo, pois, diferente de um Agraeciini tradicional, o fastigio é muito largo, similar ao fastigio de um Copiphorini (Rentz 1976). Por outro lado, o formato achatado do fastigio pode causar confusão e levar à identificação das espécies como pertencentes à Conocephalini (Rehn 1905). Em alguns casos, como do gênero *Eppia*, há evidências de que não seria um Agraeciini, pois os cercos do macho, o espiráculo auditivo e o fastigio são similares aos de alguns Copiphorini, como espécies de *Bucrates* e *Pyrgocorypha* Stål (Naskrecki 2000b). Porém, a maioria das comparações morfológicas, e as descrições taxonômicas dos gêneros conhecidos, não incluem caracteres robustos das tégminas e de estruturas do pós-abdômen (como o falo). Até essas estruturas serem devidamente estudadas nesses táxons, persistirão dúvidas sobre a classificação.

No único cenário filogenético disponível para Tettigoniidae, baseado em caracteres morfológicos, Agraeciini seria parafilético, apresentando reversões dentro e convergências fora do grupo (Naskrecki 2000a), tais como: (i) presença de uma dobra pleural meso- e metatorácica bem desenvolvida; (2) episterno metatorácico com uma dobra longitudinal inconspícua; (iii) fêmur frontal tão longo como a tíbia, estado que representaria uma reversão ao suposto estado ancestral da família (Naskrecki 2000a). A análise que levou a esse cenário evolutivo incluiu duas espécies provenientes da América do Sul, *Agraecia* sp. e *Subria sylvestris* Naskrecki & Morris, sete espécies de quatro gêneros da Tailândia (*Anelytra* Redtenbacher, *Lichnofugia* Ingrisch, *Mesagraecia* Ingrisch e *Nahlaksia* Ingrisch) e duas espécies da Austrália de dois gênero diferentes (a morfoespécie Gen. nov. 10 e *Scytocera* Redtenbacher). Os dois gêneros da América do sul (*Agraecia* + *Subria*) compartilhariam uma origem em comum, junto com *Mesagraecia* da Ásia Tropical. Os estudos filogenéticos baseados em dados moleculares sobre as relações de categorias superiores em Orthoptera, em especial em



**Figura 1.** Principais estruturas de Agraeiini e abreviações mencionadas ao longo do documento: ângulo ventro-posterior angle do paranota **vppa**; antena **an**; cavidade da antena **ans**; cerco **ce**; clipeo **cl**; decimo tergito **tt**; disco do pronoto **di**; dobra da margem do pronoto **mf**; epiprocto **ep**; escapo **sc**; fastígio da frente **ff**; fastígio do vértex **fv**; frons **fr**; labro **lr**; lóbulo do mesobasisterno **msl**; lóbulo do probasisterno **psl**; margem posterior do paranota **pepa**; margem ventro-anterior do paranota **vapa**; margem ventral do paranota **vepa**; metabasisterno **BS3**; metazona **mtz**; lóbulo do metabasisterno **mtl**; lóbulo do probasisterno **psl**; mesozona **msz**; lóbulo do metabasisterno **mtl**; mandíbula **md**; mesobasisterno **bs2**; metabasisterno **bs3**; ocelo lateral **loc**; ocelo médio **moc**; palpo maxilar **mp**; paranota **pa**; paraprocto **pp**; pedicelo **pe**; placa medial **mmp**; placa media do metaesterno **mmp**; placa subgenital **sgp**; probasisterno **bs1**; pronoto **pr**; sulco principal do pronoto **su**; prozona **prz**; sino humeral **sh**; sulco auditivo do pronoto **as**; sulco do paranota **spa**; stily **sti**; valva 1 **val1**; valva 2 **val2**; valva dorsal **dv**; valva ventral do ovipositor **vv**; vértex **ver**.

Tettigoniidae, incluíram diferentes sequências mitocondriais e nucleares (Flook & Rowell 1997; Flook *et al.* 1999; Jost & Shaw 2006; Rowel & Flook 1998; Zhijun *et al.* 2010; Mugleston *et al.* 2013). Somente duas das hipóteses filogenéticas incluíram dados de Agraeciini (Jost & Shaw 2006; Mugleston *et al.* 2013). Nas análises de Jost & Shaw (2006), foram incluídos dados moleculares de três morfoespécies de três gêneros diferentes, *Coptaspis* sp. (Austrália), *Eschatoceras* sp. (América do Sul) e *Austrosalomona* sp. (Austrália); os três gêneros seriam polifiléticos, agrupando com gêneros que pertencem à Copiphorini e Requenini. O estudo mais recente (Mugleston *et al.* 2013) incluiu seis gêneros de Agraeciini, *Salomona* Blanchard, *Nicsara* Walker, *Macroxiphus* Pictet, *Oxylakis* Redtenbacher provenientes da Indochina e Austrália, e *Eschatoceras* e *Sphyrometopa* da América do Sul. Segundo essa hipótese filogenética, os Agraeciini seriam um grupo polifilético, com as espécies da Indochina e Austrália em clados diferentes dos da América do Sul. *Eschatoceras* e *Sphyrometopa* também seriam parafiléticos, compartilhando origem recente com gêneros de Copiphorini (Mugleston *et al.* 2013).

#### 1.4. Breve história taxonômica do gênero *Agraecia* Audinet-Serville

A controvérsia ao redor de *Agraecia* começou desde sua descrição. Audinet-Serville (1831) derivou o nome genérico *Agraecia* baseado nas palavras gregas αγρος (agros = campo) e οικεω (oikeo = habitar). A construção correta deveria ser “*Agroecia*”, forma que foi usada posteriormente por Burmeister (1838). Porém a correção do nome original é injustificada segundo o Código de Nomenclatura Zoológica (1999), artigo 32.5.1, que cita que transliterações incorretas não são consideradas erros inadvertidos e, por isso, não devem ser corrigidas.

O gênero foi erigido baseado numa única espécie, *Agraecia punctata* (Saint-Fargeau & Audinet-Serville), que foi originalmente descrita como *Locusta punctata*, baseada em duas fêmeas desprovidas de localidade, porém, Redtenbacher (1891) cita um espécimen coletado pelo Brunner no antigo estado de Bahia, no Brasil. Posteriormente, Redtenbacher (1891) descreveu nove espécies provenientes de diferentes localidades do mundo: *A. viridipennis*, *A. subulata*, *A. nigrifrons* Redtenbacher, *A. vittata* Redtenbacher, *A. vittipes*, *A. maculata* e *A. abbreviata* da América do Sul; *A. sansibara* da África; e *A. differens* da Austrália. Todas as espécies descritas por Redtenbacher (1891) foram baseadas em indivíduos adultos, excetuando *A. vittata*, que foi baseada numa fêmea imatura. Subsequentemente, *Agraecia festae*

Griffini foi descrita do Equador (Griffini 1896), *A. dorsalis* Karny do Brasil (Karny, 1907), *A. ornata* Karny, e *A. fallax* Karny (Karny 1907, 1911) da Nova Guiné, e *A. pulchella* Hebard da Colômbia (Hebard 1927). A espécie fóssil *A. reticulata* Piton & Théobald foi descrita baseada em uma tegmina fossilizada datada do Oligoceno (Piton & Théobald 1939). Após um intervalo de 31 anos, a espécie *A. incognita* Piza foi descrita baseada em três fêmeas sem nenhuma informação de localidade (Piza 1970), e subsequentemente *A. malkini* Piza foi descrita para o Brasil (Piza 1978).

Hugel (2002) descreveu *A. cesairei* da Ilha da Martinica, incluindo a descrição do canto de chamado do macho, e a morfologia do cintilador, sendo a primeira vez que características como essas foram estudadas para uma espécie de *Agraecia*. No mesmo estudo, *A. malkini* foi sinonimizado com *A. viridipennis*, decisão controversa, baseada em espécimes coletados na Guiana Francesa (Hugel 2009). Finalmente, *Agraecia differens* foi transferida para *Secsiva* Walker (Rentz 2009) e *A. sansibara* para *Afroagraecia* Ingrisch & Hemp (Hemp 2013). Adicionalmente, foi determinado que *A. ornata* é um sinônimo de *Pseudonicsara semicrucata* (Brunner von Wattenwyl) (Ingrisch 2009) e *A. incognita* foi considerado um sinônimo de *Tettigonia viridissima* (Linnaeus, 1758) (Chamorro-Rengifo & Braun 2010).

Atualmente, *Agraecia* compreende 15 nomes de espécies, dos quais 14 estão em uso (Eades *et. al.* 2014) e um é sinônimo júnior (Hugel 2009). A diagnose de *Agraecia* está baseada em caracteres inconsistentes ou que podem ser aplicados a outros gêneros (por exemplo, “ovipositor curvado para cima”) (Audinet-Serville 1831; Redtenbacher 1891).

## **2. ESTABELECIMENTO DO PROBLEMA**

### **2.1. Problema Geral**

O gênero *Agraecia* Audinet-Serville inclui espécies distribuídas pelo mundo todo e que são morfologicamente dissimiles. Uma porção das espécies, tanto brasileiras como do resto do mundo, devem ser classificadas em gêneros diferentes.

### **2.2. Problemas específicos**

### **2.2.1. Problema I**

A atual definição morfológica do gênero *Agraecia* é insatisfatória. Além disso inclui espécies que devem ser realocadas em gêneros diferentes.

### **2.2.2. Problema II**

O falo dos insetos é uma estrutura de caráter taxonômico informativo para muitos grupos taxonômicos, porém, no caso dos tettigoniídeos, é pobremente estudado. Para resolver o problema I sobre a classificação dos *Agraecia*, faz-se necessário um estudo prévio da morfologia dos falos das esperanças.

### **2.2.3. Problema III**

Como observado em tégminas provenientes de espécies que pertencem a diversas subfamílias neotropicais de Tettigonioidea, a tégmina direita apresenta uma fileira vestigial que não está sendo usada na caracterização dos táxons. Porém, é importante reportar a presença ou ausência dessa fileira nas subfamílias de Tettigonioidea e apresentar um panorama geral desse componente no nível da superfamília.

## **3. OBJETIVOS**

### **3.1. Objetivo geral**

Revisar a classificação taxonômica das espécies do gênero *Agraecia* Audinet-Serville.

### **3.2. Objetivos específicos**

#### **3.2.1. Parte I**

Realizar um estudo morfológico comparativo do falo em Tettigonioidea que será uma das bases para a descrição e separação das espécies, e definição de gêneros de Agraeciini.

### 3.2.2. Parte II

Revisar a presença da fileira de dentes na nervura CuPb da tégmina direita nas subfamílias neotropicais. A nervura CuPb será usada como caráter na definição de táxons dentro de *Agraeciini*.

### 3.2.3. Parte III

(i) Redefinir o gênero *Agraecia* baseado na espécie-típica, e descrever os novos gêneros que serão baseados nas espécies já descritas de *Agraecia*, e/ou novas espécies;

(ii) Estudar e comparar o gênero *Agraecia* e os novos gêneros descritos, com o restante dos gêneros da tribo do continente Americano;

(iii) Realizar as modificações pertinentes referentes à nomenclatura e classificação;

(iv) Elaborar uma chave taxonômica para a identificação dos gêneros e espécies;

(vi) Elaborar mapas de distribuição dos registros das espécies de *Agraeciini*, e discutir os aspectos relevantes sobre a distribuição; e

(vii) Discutir os aspectos morfológicos relevantes para a classificação taxonômica e a sistemática dos *Agraeciini*.

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## 5. RESULTADOS

Esta tese é apresentada na forma de três capítulos, cada capítulo corresponde a cada um dos problemas expostos na seção 2 e a cada um dos objetivos específicos da seção 3. O primeiro e segundo capítulos são artigos publicados, e o terceiro corresponde a um manuscrito inédito. O capítulo III não deve ser considerado como publicação válida para fins de nomenclatura zoológica, de acordo com as normas do Código Internacional de Nomenclatura Zoológica (Cap. 3, Art. 8.2 e Art. 8.3).

**CAPÍTULO I:** Chamorro-Rengifo, J. & Lopes-Andrade, C. (2014). The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution. *Zootaxa*, 3815, 151–199.

Trabalho apresentado durante a banca de qualificação da candidata. Antes de realizar a revisão taxonômica dos *Agraecia* (Capítulo III), foi estabelecido que o falo seria usado para elaborar as diagnoses e descrições dos gêneros e espécies. Porém, sabia-se que essa estrutura era pouco usada em estudos taxonômicos sobre Tettigonioidae, e sem um

estudo comparativo da estrutura não seria possível usá-la para delimitação de gêneros e espécies de Agraeciini. Por esse motivo realizou-se um estudo detalhado do falo das esperanças neotropicais, baseado principalmente em espécies brasileiras. Padronizou-se um método para fotografar as estruturas, e para apresentar de forma esquemática a morfologia do falo e seus componentes. Como parte essencial desse trabalho, estudou-se a terminologia dos componentes, e se propôs uma nomenclatura padronizada. Demonstrou-se que somente as partes mais expostas do falo dos Tettigonioidea eram usadas para fins taxonômicos, mas que o falo é uma estrutura mais complexa, com diversos componentes, e que deve ser mais bem estudada. E considerando que o falo está sob constante pressão seletiva, é uma estrutura informativamente útil para estabelecer relações filogenéticas. Adicionalmente, o estudo detalhado da morfologia comparada dessa estrutura, em conjunto com outros componentes do pós-abdômen, é a base para a elaboração de hipóteses sobre comportamento reprodutivo e seleção sexual.

**CAPÍTULO II:** Chamorro-Rengifo, J., Braun, H. & Lopes-Andrade, C. (2014). The secret stridulatory file under the right tegmen in katydids (Orthoptera, Ensifera, Tettigonioidea). *Zootaxa*, 3821, 590–596.

Durante o estudo dos Agraeciini (Capítulo III: *Agraecia* e gêneros novos) observou-se que os machos apresentam uma fileira estridulatória vestigial na tégmina direita, porém, essa fileira não havia sido reportada nas descrições das espécies. Foi observado também que essa fileira estava presente nos machos de outras subfamílias, e que na literatura não existia informação recente sobre esse fato. Por tal motivo, antes de usar a fileira no estudo dos *Agraecia*, era importante reportar a presença desse componente para os outros táxons da superfamília. Nesse artigo, reportou-se que possuir uma fileira estridulatória na tégmina direita é um fato comum nos machos das espécies neotropicais de Tettigonioidea. Essa fileira é ausente em Pseudophyllinae, com exceção dos Pterochrozini, e algumas espécies de outras poucas tribos. Mostrou-se a existência de uma ampla variação de simetria entre a fileira direita e a esquerda, e que essa simetria, em conjunto com o nível de desenvolvimento da fileira direita, e a informação de presença ou ausência da fileira, pode ser útil para o estudo taxonômico das esperanças.

**CAPÍTULO III:** Chamorro-Rengifo, J., Braun, H. & Lopes-Andrade, C. Reassessment and splitting of the genus *Agraecia* Audinet-Serville (Orthoptera: Tettigoniidae: Conocephalinae: Agraeciini). Manuscrito original.

Através da observação de esperanças coletadas em unidades de conservação da floresta Atlântica, notou-se que o gênero *Agraecia* é um dos grupos mais problemáticos entre o material coletado, pois agrupa espécies morfologicamente dissímiles. O gênero está constituído por 15 nomes de espécies: 13 espécies viventes, um sinônimo júnior e uma espécie fóssil. Além de serem espécies muito diferentes, elas foram descritas para diversas regiões do mundo. Através desse estudo, o gênero *Agraecia* foi revisado e redefinido. Parte das espécies descritas originalmente como *Agraecia*, foram reclassificada em novos gêneros. Para elaborar as diagnoses, descrições dos gêneros e diferenciação das espécies, usaram-se estruturas tradicionalmente consideradas na taxonomia de esperanças e, adicionalmente, incluíram-se o falo (Capítulo I) e a fileira estridulatória direita (Capítulo II). Discutiu-se também aspectos relacionados à biologia e ecologia das espécies.

## CAPÍTULO I

**The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution.**

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## The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution

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### Abstract

The phallus in Tettigoniidae (katydids) is a structure informative relative to the systematics of the group. Despite this, it is often not considered in descriptions of taxa. The lack of adequate descriptions of phalli is not only a gap for systematic and morphological studies, but postpones works on the evolution of copula. Here we study the exoskeletal morphology of the phallus in katydids, its components, and revised the terminology for them. We carried out dissections for morphological comparisons, and complement the observational information with published data. We stained phalli of katydids with chlorazol black, to better contrast membranous versus sclerotized components. We demonstrate that phallic components vary at specific, generic and suprageneric levels, and that internal and external components vary in number, shape, size and position. Currently there is little comparative data to support hypotheses on the evolution of this structure, but possibly the possession of a titillator is an ancestral condition. We identify additional sclerotized components, the sclerites of the ventral fold of the dorsal lobe, which can modify the shape and function of the titillator, being also important for understanding the evolution of the phallus. Potential functional relationships based on hypothetical morphological correlations between the shape of titillator and cerci are proposed, categorized in three main groups: (i) phallus devoid of titillator and cerci simple, (ii) titillator with bifurcated or paired sclerites, and cerci adapted for grasping, and (iii) titillator with single process and/or sclerite and cerci simple, sometimes with a pointed tip. Two explanations for these hypothetical morphological correlations and morphological variation are proposed: first, species with similar structures at the postabdomen would share similar copulatory behaviour, and second, more than one selective pressure would have acted over the structures of the postabdomen.

**Key words:** apodemes, chlorazol black, copula, ejaculatory vesicles, functional morphology, genital lobes, male genitalia, postabdomen

### Introduction

Currently there are more than 7,000 described species of Tettigoniidae (katydids) in 19 subfamilies (Eades *et al.* 2014). The family has been recognized as monophyletic, but its internal relationships are yet unsolved and some subfamilies and tribes have been considered paraphyletic or polyphyletic in phylogenetic analyses (*e.g.* Naskrecki 2000; Jost & Shaw 2006; Mugleston *et al.* 2013). The number of species in the family has continuously grown. For instance in 2013 approximately 120 new species were described (after a search on Eades *et al.* 2014). And additionally to the unsolved phylogeny, the taxonomic positioning of several taxa are frequently discussed in literature (*e.g.* *Arachnoscelis* Karny, included in either Meconematinae or Listroscelidinae).

Descriptions of new Tettigoniidae species are based mostly on external morphological features, but sometimes acoustic (*e.g.* Morris *et al.* 1989; Walker *et al.* 2003; Montealegre-Z. *et al.* 2011), karyotypic (*e.g.* Rentz *et al.* 2007; Rentz *et al.* 2009; Rentz *et al.* 2010; Hemp *et al.* 2010a) or molecular data (*e.g.* Hemp *et al.* 2010b) are also

provided. Morphological and acoustical information are the most recurrent in studies on boundaries between katydid species. The phallus is described in few studies (e.g. Emsley 1970; Bowen-Jones 1994; Shi *et al.* 2008). Among 90 taxonomic papers on Tettigoniidae arbitrarily chosen and evaluated by us, only 43 included information on phallus morphology (Appendix 1). Studies that provide acoustic data usually do not describe the phallus (e.g. Braun *et al.* 2009; Hemp *et al.* 2010a; Montealegre-Z. *et al.* 2011). However, the calling song may not be important in the mating behaviour of some species. For instance, males of *Anonconotus* Camerano (Tettigoniinae) do not produce calling songs but silently stalk females (Vahed & Carron 2008). In species of *Eupholidoptera* Maran (Tettigoniinae), both genital and acoustical data were studied and it was noticed that male calling songs are relatively invariable, suggesting that, at least in Tettigoniinae, morphological divergence of phalli may occur prior to acoustical differentiation (Çiplak *et al.* 2009). And yet the song is less important in brachypterous species, as in Tabariini species (Braun *et al.* 2009). Furthermore, external features which are traditionally useful in morphological differentiation in most katydids should be treated with caution in others, as in the case of the “walking leaves” (Pterochroziini). The tegmina of walking leaves can exhibit a wide intraspecific variation of shape and coloration (Xiberras & Ducaud 2004), which have led to numbers of synonyms (e.g. in *Pterochroza ocellata* (Linné)). Additionally, cerci are similar between species of this tribe, therefore, not very useful for diagnoses. And as verified in literature, the phallus in species of this tribe bears sclerotized components (see results) and can thus provide significant systematic information, but it has been barely explored.

Authors who studied the phallus of katydids proposed different interpretations and terminologies for structural components. Chopard (1920, 1949) studied the male postabdomen (Phasgonuridae, Chopard 1920; Tettigonioidae, Chopard 1949) and distinguished two morphological regions, the perianal and the genital region. According to this author, the perianal region comprises the tenth tergite, the supraanal plate, the paraprocts (anal valves) and the cerci. The genital region consists of the subgenital plate, the styli, the genital valves and the “titillators”, the latter also called epiphallus. This author succinctly defined the phallus as a vestibule configured by valves where the “titillators” are located. Walker (1922) based his interpretation on species belonging to Tettigoniinae and Conocephalinae (sensu Eades *et al.* 2014), but apparently specimens of Phaneropterinae and Meconematinae were also examined. The phallus was described as a pouch which bears the opening of the ejaculatory duct and the “titillators” (called “parameres”) arising from the lobes. The pouch would function as a spermatophore sac. Walker’s (1922) description of the phallus included a dorsal membranous fold called “pseudosternite”, a ventral lobe, a dorsal and a ventral cavity. According to him, the dorsal membranous fold would be equivalent to the pseudosternite of Rhabdophoridae. Later, Snodgrass (1937) examined specimens of Phaneropterinae, Conocephalinae and Tettigoniinae (following classification in Eades *et al.* 2014), and provided a much more detailed description and interpretation of the phallus. Several components of the structure, not considered in previous studies, were pointed out and named. The phallus was defined as a chamber with three lobes (dorsal, ventral and lateral) and also with a dorsal and a ventral cavity. Ander’s (1956, 1970) proposal did not include a description specific for Tettigoniidae, and the drawings were of the phallus of a Rhabdophoridae. This interpretation was diametrically different to that of previous authors, the phallus being defined as an ensemble of membranous lobes and their derivatives, the main lobes being often divided into secondary lobes, and the paired “titillators” arising from the upper side of the dorsal lobe. The author did not list the Tettigoniidae species he examined. Gorochov (1995) disclosed a variety of divergent phalli (Gorochov 1995: figs 663–697) of species belonging to several Tettigoniidae genera, but without revealing their details. Desutter-Grandcolas (2003), more concerned with homologies among ensiferan subgroups, pointed out that the male genitalia of Tettigoniidae would be characterized by the presence of a pair of eversible “titillators”, which arise from an overdeveloped epiphallus. The structures named “epi-ectophallic invagination” and “ectophallic dorsal lobe” by her are not as widely occurring in Tettigoniidae as in other Ensifera. It is important to note that most, if not all, authors who recognized the “titillators” considered that they were paired structures.

Postabdominal structures close to the phallus, such as the cerci (Mcpeek *et al.* 2009) and adjacent ventral sclerites, can be involved in copulation and so they are usually called “non-genital contact structures” (Eberhard 2010), discerning them from the phallus itself. In fact, the non-genital contact structures are characterized by elaborated, often species-specific forms (Eberhard 2010; Mcpeek *et al.* 2008; Mcpeek *et al.* 2009). The mechanical function of these non-genital structures is usually to grasp (Eberhard 1985, 2004) or stimulate (Sirot 2003; Helversen & Helversen 1991) the female during copula. Actually, a change in shape of a non-genital contact structure could affect the performance in copula, being possibly a prezygotic hybridization barrier. Changes in

copulatory behaviour accompanied by morphological differentiation was observed in two species of predatory Saginae, *Saga campbelli* Uvarov and *Saga natoliae* Serville. In the former species, male cerci bear an internal padding, and during copula male bends his abdomen inward (see image in Kaltenbach 1990: fig. 3) until clasping the end of the female's abdomen with his cerci. In *S. natoliae*, male cerci are devoid of internal padding, so male clasps the basal portion of the ovipositor with his mandibles during the entire copula (Kaltenbach 1990: fig. 2). As in the latter example, cerci that are adapted for grasping help holding female during copula, while lobes of the phallus and "titillators" are in intimate contact with female genitalia (Kaltenbach 1990; Duijm *et al.* 1983), allowing the spermatophore transfer. Only one author explicitly proposed a hypothetical morphological correlation between cerci and "titillators" (Ingrisch 1998). This author hypothesized that in the Oriental Agraeciini, in which species have membranous phallus, the cerci can carry modified structures that replace the stimulatory function of "titillators". As with the phallus, the structures of the postabdomen are usually poorly described, postponing the proposition of hypotheses on their evolution and function during copula. An example is the shape of the paraprocts, that in groups as *Agraecia* Serville, or the South American Listroscelidinae, are comparatively modified and they fit with the cerci or the subgenital plate, forming a kind of lock (pers. obs.); but the form of the paraprocts, as well as other postabdominal structures, are usually unsatisfactorily described. Different types of copula of katydids have been described (*e.g.* Alexander & Otte 1967; Duijm *et al.* 1983; Kaltenbach 1990; Morris 1980; De Souza *et al.* 2011; Helversen & Helversen 1991). However, the morphology and evolution of the postabdomen in relation to the copula has not been discussed.

Considering the phallus is an important diagnostic feature in most insect taxa and very important for taxonomic decisions (*e.g.* Antunes-Carvalho & Lopes-Andrade 2013; Chamorro-Rengifo & Lopes-Andrade 2009; Ingrisch 2009; Oliveira *et al.* 2013), we studied the morphology of this structure and discuss the implications of its use in taxonomic and systematic studies of katydids. We provide a comparative morphological approach on the phallus and contrast our own observations with interpretations and terminologies proposed by previous authors. We give emphasis to the definition and characterization of the titillator, which is considered by us to be a complex of components. As the titillator has been observed and registered in many subfamilies of katydids, we trace its presence over two phylogenetic hypotheses. However, as we will show, the lack of detailed information on the structure prevents a clear idea about its evolution, but allows the development of questions that can be the focus of future studies. Finally, we point out hypothetical morphological correlations of titillator, as we redefine here, and cerci that are repeated in different taxa, which may be a clue of possible functional relationships between these structures. This study was conducted with the main objective of making a claim for the phallus to be described in detail in taxonomic works on katydids as well as the other structures of the postabdomen.

## Material and methods

**Terminology and morphology of the phallus.** We searched the literature for morphological and taxonomic studies describing or showing phalli of Tettigoniidae species. On this basis, we provide a compilation of terms and abbreviations proposed by Chopard (1920, 1949), Walker (1922), Snodgrass (1937) and Ander (1956, slightly modified in 1970). We summarize equivalence of terms for each component of the phallus (Table 1), and provide diagrams for the morphological interpretation used by us in this study (Fig. 1) and by each of the abovementioned authors (Figs 2–5). The diagrams were inspired by Snodgrass (1937: 63, fig. 22C). None of the authors identified and named all phallic components, and the terminologies used by them partially complement each other. We considered Snodgrass's (1937) terminology the most complete. However, a few abbreviations used by him are meaningless, for example the "h" and "e" lack a corresponding name. While we broadly corroborate his propositions, we use new abbreviations which are suggestive of the full names. A bauplan and template for description of phallic morphology is defined based on *Conocephalus* sp. 1 (Conocephalinae) (Figs 1, 6–9). The phallus of this species was chosen as a model because it exemplifies one of the most complex morphological patterns among the studied species, considering the amount of components. Moreover, this genus has a worldwide distribution, so it can be easily studied and verified. We also describe the variation of the components of the phallus (Figs 6–71), and the presence of microstructures (Figs 72–94) on it.

**Terminology and abbreviations used here.** The word "structure" used as here refers to the entire phallus, including internal and external components. "Components" refers to each of the major elements that compose the

phallus, as membranes, ducts, folds, lobes, processes, microstructures, sclerites and apodemes. The term “lobe” is applied for large membranous folds, such as the dorsal lobe or the ventral lobe, and the term “fold” is applied to small membranous folds or subfolds of them, referring also to both inwardly and outwardly directed folds, *e.g.* the dorsal fold of the dorsal lobe. “Microstructures” refer to minute spines, protuberances, sclerotizations in high-relief or any other repeated minute element on external components. From now on, abbreviations or terms cited between quotation marks refer to those proposed or used by previous authors but not adopted here. Abbreviations given in bold-face print in the text are adopted here. Abbreviations in lower-case letters denote membranous or formative components, such as lobes or processes; upper-case letters are used for sclerites. We also distinguish between the titillatory process(es) (**ti**) and the titillator sclerite(s) (**TS**). This is important because processes and sclerites can be co-extensive but are not always (as the sclerites may extend away from the process). Furthermore, processes and sclerites can undergo transformations independently. In the literature on Tettigoniidae, there are no such distinctions. Previous authors referred to “titillators” because they considered there were always two structures. Also, they have not recognized the components of these “structures”. From now on in the text, the term titillator refers to the entire structure or complex as we define here. When between quotations, it refers to definitions used by previous authors. For easy reading, part of the names will be used along the text together with the abbreviations (*e.g.* lobes **vl**), instead of single abbreviations, and this will be used again in the text when necessary. Abbreviations alone will be used when the component is repeated several times in the same paragraph. Complete explanation for each name is provided in results. The abbreviations adopted by us for external and internal components are listed separately, below, in alphabetical order.

#### External components of the phallus

<b>df</b>	dorsal fold
<b>dc</b>	dorsal cavity
<b>ddl</b>	dorsal fold(s) of dorsal lobe(s)
<b>dl</b>	dorsal lobe(s)
<b>ldl</b>	lateral folds of dorsal lobe
<b>lw.vl</b>	lower folds of ventral lobe
<b>ti</b>	titillatory process(es)
<b>TS</b>	titillator’s sclerite(s)
<b>up.vl</b>	upper folds of ventral lobe
<b>vl</b>	ventral lobe

#### Internal components of the phallus

<b>ap</b>	anterophallic apodemes
<b>AP</b>	sclerites of apodemes
<b>ec</b>	endophallic cavity
<b>ejd</b>	ejaculatory duct
<b>ejv</b>	ejaculatory vesicles
<b>ES</b>	ejaculatory duct’s sclerites
<b>fdl</b>	fore fold of dorsal lobe
<b>vdl</b>	ventral fold(s) of dorsal lobe
<b>VS</b>	sclerite(s) of ventral fold of dorsal lobe

**Field collection, identification and depository.** All examined specimens were collected in Brazil (Appendix 2). The majority of them were preserved in ethanol, except for a dried preserved male of *Cerberodon viridis* Perty borrowed from the Museu Nacional do Rio de Janeiro (MNRJ; Rio de Janeiro, RJ, Brazil). Approximately 40 adult individuals were dissected. A few dissected phalli were not adequate for detailed examination, because parts were lost during dissection. The 32 phalli reliable for examination belong to 32 species (Appendix 2). Except for the single katydid from MNRJ, the other specimens are deposited in Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera da Universidade Federal de Viçosa (CELC; Viçosa, MG, Brazil).

We identified specimens to the finest possible taxonomic level, and for genera and suprageneric taxa we consider the recent changes in the classification of Neotropical Tettigoniidae (Cadena-Castañeda 2012; Chamorro-Rengifo & Braun 2010). Several recognized genera and species are new and will be treated in separate works. *Spinapecta alieniphaga* Naskrecki & Lopes-Andrade was collected in the type locality and is the unique Polyancistrini known from Brazil (Naskrecki & Lopes-Andrade 2005). For unidentified species we provide the genus and number them consecutively (e.g. *Conocephalus* sp.1, *Conocephalus* sp.2). Undescribed genera are numbered consecutively (Gen.1 sp., Gen.2 sp.) as they appear in Appendix 2. Although identifications such as “Gen. sp.” are not useful for taxonomic purposes, we consider them sufficient in the context of the present work. The examined species belong to five subfamilies of Tettigoniidae: Conocephalinae, Listrosclidinae, Meconematinae, Phaneropterinae and Pseudophyllinae. Numerically, it is a small subset of the 19 subfamilies recognized by Eades *et al.* (2014), but they represent the major tettigoniid clades.

**Dissection and photography.** Specimens were dissected, examined and photographed using a Zeiss Discovery V8 Stereomicroscope. After dissection, each phallus was left for 48h in 10% aqueous solution of KOH and then washed with 1% acetic acid for five minutes. We removed muscles, fat and other attached elements, and then stained them with a solution of 85% Chlorazol Black diluted in alcohol. This staining technique was adapted from Carayon (1969). Staining membranous components of phalli highlights by contrast with sclerotized elements and eases recognition of membranous folds and lobes. Extracted and stained phalli were kept in vials with 70% alcohol. For digital photographs, each phallus was submerged in water (Chamorro-Rengifo & Lopes-Andrade 2009). Final images were the result of stacking 30–50 photographs in different focus using AxioVision 4.8 digital image processing software of Zeiss Company. Position of phalli shown in plates can be slightly different, because they did not take exactly the same orientation in the water. But their aspects are sufficiently similar to allow comparisons.

We elaborated drawings and diagrams of phalli and cerci in CorelDraw X5. The images are shown in a logical order. The first plate (Figs 1–5) compares interpretations and terminologies used here and the proposed by previous authors. The subsequent plates are arranged to show one model species for each subfamily and, then, images of the remaining examined phalli of the respective subfamily organized in taxonomic order (see Appendix 2). We elaborated diagrams of phalli exposing their components located in different positions (or depths), treated here as “layers”. To emphasize the outermost layers, items are drawn in continuous bold lines, and items below in dashed lines. Edges of membranous and sclerotized components devoid of membranes are in black line, and edges of portions or entire sclerotized components that are contiguous to membranes are in light grey. Components coloured in light grey are membranous and in dark grey, sclerotized. The drawing of each phallus shows half of the dorsal view at left and half of the ventral view at right, each delimited by a thin vertical line. An exemplar phallus of each examined subfamily was chosen to be drawn and disclosed in components, shown in individual plates (Conocephalinae, Figs 6–9; Listrosclidinae, Figs 22–25; Meconematinae, Figs 30–33; Phaneropterinae, Figs 34–37; Pseudophyllinae, Figs 44–47). We provide only photographs of ventral and dorsal views of the remaining phalli.

**Evolutionary scenarios for the titillator.** Based on the insufficient information on phallus morphology in Tettigoniidae (see also Appendix 3), proposing evolutionary scenarios for the phallus in Tettigoniidae is by now an arduous task. Most of the components of the phallus were not described by authors and, when available, information is usually about conspicuous exposed components, such as the titillator. Nonetheless, we contrasted the available information on the morphology of the titillator at subfamily level with two published phylogenetic hypotheses for Tettigoniidae. The objective of this exercise is to show how the lack of information on the characteristics of the components of the phallus, here mostly of the titillator, prevent the elaboration of a clear idea of their evolution. On the other hand, this exercise will raise questions that can be the focus of future research studies.

The first hypothesis (Fig. 95), based on morphological features, but not on a formal analysis of characters (Nickle & Naskrecki 1997), was elaborated by Gorochoy (1988). We modified tree topology proposed by him according to the suggestions of Gwynne & Morris (2002), following commentaries and conclusions on the relationships of Austrosaginae and Zaprochilinae by Rentz (1993) and of Lipotactinae by Ingrisch (1995). The second hypothesis (Fig. 96) was proposed by Jost & Shaw (2006) based on molecular data. Phylogenetic hypotheses proposed by Rowell & Flook (1998), Flook *et al.* (1999) and Zhou *et al.* (2010) were also checked but disregarded here because of the low number of representatives of each subfamily. The most recent phylogenetic

hypothesis based on molecular data (Mugleston *et al.* 2013) was also dismissed in this exercise only because it is difficult to reconcile the terminal taxa and taxonomic classification used in the analyses of the tree. We clarify that the selection of the topologies does not represent our agreement with the phylogenetic relationships between the terminal groups or with any topology in particular, because that is not the goal. They were chosen because they facilitated the completion of this exercise.

In order to evaluate whether the titillator is common to several Tettigoniidae lineages, we traced two traits over the available phylogenetic hypotheses (Appendix 3). These traits cannot be called characters at this moment, and they are not necessarily homologous in these lineages. The first trait (I) is absence (0) or presence (1) of a titillator. The second trait (II) is whether the titillator is formed by paired (0) or single (1) components. A paired titillator has two processes **ti**, or two **ti** with sclerites **TS**. A single titillator is the one that has a single process **ti** with conspicuous microstructures, or a **ti** with a single sclerite **TS**, one **ti** with bifurcated **TS**, or one **TS** with bifurcated apical portion.

**Hypothetical morphological correlations between titillator and cerci.** As explained in introduction, male cerci can be functionally important during copula, therefore they can be modified or possess secondary structures. The titillate cerci may be important to stimulate female, while cerci adapted for grasping can keep clinging male to the female during copula. In the other hand, when the phallus is devoid of titillator, secondary structures on cerci can exert the stimulatory function. In the latter case, copulatory behaviour is expected to change to ensure receipt of sperm by the female, for example by producing larger spermatophilax. Also, depending on the copulatory behaviour, the necessity for grasping or stimulating female can be low and, therefore, constitute a weak evolutionary pressure on postabdominal components.

For these reasons we propose some hypothetical morphological correlations between titillator and cerci, which can denote functional relationships. Based on our previous observations, we compared the morphology of the phallus of each species with its respective cerci (Figs 97–128). In order to complement our observations, we evaluated 90 papers for information on the morphology of the phallus and cerci (Appendix 1). When information on cerci and titillator were not complete, images of these components were searched in Orthoptera Species File Version 5.0/5.0 (Eades *et al.* 2014). We observed whether the phallus had titillator or not; when the phallus had titillator, whether it has paired or bifurcated, or single components. These components were mainly process(es) **ti** with microstructures and sclerite(s) **TS**. We observed whether cerci were simple (not angulated, devoid of spines or secondary components), simple but with a pointed tip, or cerci that we presume are adapted for grasping (curved or angulated cerci resembling hooks, or with secondary components such as inner spines). The correlations proposed here are based on functionality and general appearance, and we cannot state at this moment whether or not these structures evolved together.

## Results

### Description and terminology of tettigoniid phallus

Below we provide definitions and explanations for the components we observed in the phallus. The interpretation of the phallus and nomenclature proposed by us and previous authors are confronted in Figs 1–5 and Table 1.

**External components of the phallus. df.** A transverse outwardly directed membranous fold, which is devoid of sclerites and microstructures. This is the dorsalmost membranous component of the phallus (Fig. 1). It is attached to the ventromesal portion of the tergite IX and part of the reduced tergite X. Chopard (1920) didn't recognize this component (Fig. 2). Walker (1922) recognized that the phallus is covered by the "pseudosternite" ("pst") (Fig. 3), which is a sclerotized plate in Rhaphidophoridae, but in Tettigoniidae it is only a membranous fold. Additionally, lateral ramifications of this membranous fold were called "rami of pseudosternite" ("ra"), and the tip of each ramus was called "endoapophysis" ("end") (Walker 1922: plate IV, figs 30–31). The two apodemes **ap** (which would be similar to "end") are located at the ventralmost portion of the phallus, on the membrane that forms the lobe **vl**, not over the fold **df**, so that the **ap** would not be an extension of the "pst", at least in Tettigoniidae. As it was characterized by Walker (1922) "sometimes the endapophyses may be separated from the pseudosternite and are present in many forms (Tettigoniidae) in which the latter has disappeared". It is doubtful whether it was a mistake of the author to recognize the position of this "end" on the **df**; however, his drawings suggest that this

“end” would be the **ap** (Walker 1922: 24, fig. 4b). Nonetheless, the “end” would be functionally similar to the **ap** “for attachment of muscles concerned in the movements of the penis” (Walker 1922). Snodgrass (1937) identified this portion as the anterior margin (as “e”) of the cavity **dc** (Fig. 4). Ander (1956) also recognized the “pseudosternite” (as “ps.s”) in Rhabdiphoridae, but the homologous component in Tettigoniidae was not indicated.

**dc.** Cavity between the fold **df** and the lobe **dl**. Chopard (1920) and Walker (1922) didn’t name the **dc**. Snodgrass (1937) called it cavity **dc**, which was also identified by Ander (1956; as “d.cav”). However, Ander (1970) renamed it as “titillators cavity” (“cav”).

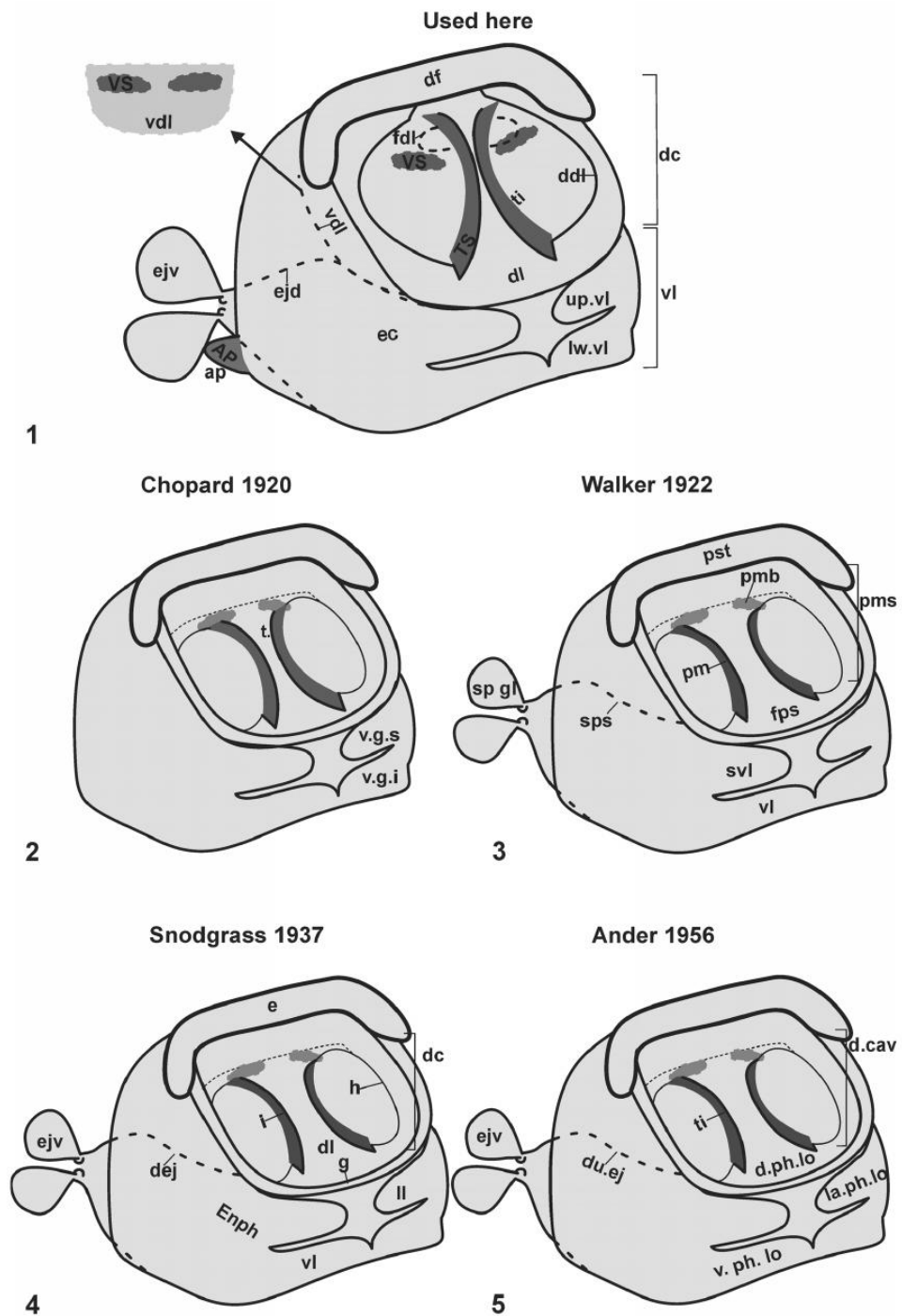
**ddl.** A fold at the middle of the lobe **dl**. This fold is raised over the lobe **dl** together with the sclerite(s) **TS**. It would correspond to the fold identified by Snodgrass (1937) as the membranous lobe or fold on floor of the cavity **dc** of the phallus (“h”).

**dl.** Medially fused dorsal lobe which forms the entire dorsal part of the phallus. The **dl** is usually the largest lobe of the phallus and extends backward. It is characterized by its rough texture and presence of conspicuous sclerotized microstructures of different types, and other components such as the process(es) **ti** and the sclerite(s) **TS**. Sclerotization degree of the cuticle of **dl** is variable. The sclerite(s) **TS** are the most widely recognized components associated with the **dl**. The **dl** can also comprise the folds **ddl**, **ldl** and the **vd**, the process(es) **ti**, and the sclerite(s) **VS**. Chopard (1920) identified it as the lobe where “titillators” are located, but he didn’t name it. Walker (1922) called it “paramere sac” (“pms”), where “parameres” (“pm”) and “base of parameres” (“pmb”) are located. The dorsalmost portion of this “paramere sac” was called “floor of the paramere sac” (“fps”). Snodgrass (1937) called it **dl**. Additionally he identified the lateral margin of the cavity **dc** (“f”), the posterior margin of the **dl** (“g”) and the membranous fold on floor of the **dc** (“h”). Ander (1956) defined this fold as a dorsal pair of lobes (“d.ph.lo”).

**ldl.** Fold on each lateral portion of the lobe **dl**. But not all **dl** have lateral lobes. Snodgrass (1937) identified the lateral folds (“ll”) in some of his drawings, but sometimes it was described as being located on the lobe **vl** (Snodgrass 1937: 66–67, figs 24B and 25D). As used here, the **ldl** are always on the lobe **dl**.

**lw.vl.** These are the lowermost subfolds of the lobe **vl**. Chopard (1920) identified them as lower genital valves (“valve génitale inférieure”, “v.g.i”). Walker (1922) identified them as “ventral lobe” (“vl”), different from the “subventral lobe” (“svl”). The **lw.vl** would be equivalent to the “ventral fold of the phallus” (“vf”) or “ventral lobe” (“vl”) in Snodgrass (1937). And Ander (1956) described it as a pair of “ventral lobes” (“v.ph.lo”).

**ti** and **TS**. For us, the titillator is a complex of components of the lobe **dl**, and the minimum criteria we used to recognize the titillator was the presence of at least one process **ti** with microstructures. If there were a process but devoid of microstructures, we would not consider it to be a titillator, because such a simple process would not have stimulatory function during copula. Based on our observations, we believe that the aggregation and fusion of microstructures forms the observed sclerites **TS**. The process(es) **ti** and the sclerite(s) **TS** are modifications of part of the middle region of the cuticle of the lobe **dl**. The process(es) **ti** is the marked and inflated membranous region where the **TS** can be formed. The sclerite **TS** is usually projected outward. Traditionally, the sclerites(s) **TS** or process(es) **ti** have been identified as being “titillators” by authors. The phallus can bear process(es) **ti** and/or not and, when present, **ti** and/or sclerite(s) **TS** can be single or paired components (Appendix 3). If the phallus bears titillator, they are usually in a dorsal position, on the lobe **dl**, or secondarily adopting a ventral position (see variation of phallic components). We distinguish between the process(es) **ti**, and the sclerites(s) **TS**, because both components can evolve independently, for example the form of **ti** and its position could be identified as homologous between species of a single genus or tribe, but the form of the **TS** can be variable between species. The process(es) **ti** can accompany the sclerite(s) **TS** in its full length, but the **TS** can also be partially free (see variation below). “Titillators” was the name used by Chopard (1920), described as being part of the epiphallus. Walker (1922) called them “parameres” (“pm”), “main process” or “ectoparameres”, these “ectoparameres” would exactly correspond to the here sclerites(s) **TS**. He also used the word “titillators”, but stated to prefer “parameres”. The base or innermost portion of the “parameres” was called “base of parameres” (“pmb”) or “endoparamere” by Walker (1922). This “pmb” can refer to the basalmost portion of the sclerite(s) **TS** or to the sclerite(s) **VS**, because the **VS** is sometimes indiscernible from the base of **TS** and can be interpreted as a single component. Snodgrass (1937) characterized the titillator as a pair of “sclerotized bars” (“i”), and Ander (1956) considered it as “basal sclerotized bands” or “distinct sclerites”.



**FIGURES 1–5.** Diagrams of the dorsolateral oblique view of the phallus of *Conocephalus* sp.1. Each diagram shows one morphological interpretation of the phallus. 1. Interpretation used in the present study, with an additional diagram showing the fold **vdl** and the sclerites **VS**; margins of fold **vdl** in dotted line indicating cutting edges. This phallus is devoid of fold **ldl** and sclerite **ES**. In the diagrams, the duct **ejd** and the vesicles **ejv** are displaced to a more lateral position, but in fact those components are in a more anterior position as shown in the subsequent images. Previous propositions of: 2. Chopard (1920). 3. Walker (1922). 4. Snodgrass (1937). 5. Ander (1956). Terminology and abbreviations used here are listed in methods, and the respective ones of the previous authors are shown in Table 1.

**TABLE 1.** Names and abbreviations assigned by previous authors and by us to components of the phallus. Hyphens indicate cases in which no name was proposed by a previous author for the respective component treated in the present work.

Abbreviations used here	CHOPARD 1920	WALKER 1922	SNODGRASS 1937	ANDER 1956, 1970
<b>df</b>	-	pseudosternite ("pst") ramus ("ra") endoapophysis ("end")	anterior margin of dorsal cavity of the phallus ("e")	pseudosternite ("ps.s")
<b>ap</b>	-	endoapophysis ("end")?	-	-
<b>AP</b>	-	-	-	-
<b>dc</b>	-	-	dorsal cavity ( <b>dc</b> )	dorsal cavity ("d.cav") titillator cavity ("cav")
-	-	paramere sac ("pms")	dorsal lobe ( <b>dl</b> )	dorsal lobe ("d.ph.lo")
-	-	floor of the paramere sac ("fps")	-	-
-	-	-	lateral margin of dorsal cavity of the phallus ("f")	-
-	-	-	posterior margin of dorsal lobe of the phallus ("g")	-
<b>ddl</b>	-	-	membranous lobe or fold on floor of the dorsal cavity of phallus ("h")	-
<b>fdl</b>	-	-	-	-
<b>ldl</b>	-	-	lateral lobe ("ll")	-
<b>VS</b>	-	base of paramere, endoparamere ("pmb")	-	-
<b>dl</b>	<b>ti, TS, ti+TS, or ti+TS+VS (when fused to TS)</b>	paramere, or its main process; the ectoparamere ("pm")	a pair of sclerotized bars ("i")	titillators
	titillators or epiphallus	base of paramere, endoparamere ("pmb")	-	-
<b>vdl</b>	-	-	-	-
<b>ejd</b>	-	spermatophore sac ("sps")	ductus ejaculatorius ("dej")	ejaculatory duct ("du. ej")
<b>ejv</b>	-	lateral glandular pouch ("sp gl")	vesicle of the ejaculatory duct ( <b>ejv</b> )	ejaculatory vesicles ( <b>ejv</b> )
<b>ec</b>	-	-	endophallic cavity ("Enph")	endophallic cavity
<b>vl</b>	valve genital ("v.g")	-	lateral lobe ("ll") ventral lobe ("vl") ventral fold ("vf").	-
	<b>lw.vl</b>	valve genital inferior ("v.g.i")	ventral lobe ("vl")	ventral lobes ("v.ph.lo")
	<b>up.vl</b>	valve genital superior ("v.g.s")	subventral lobe ("svl").	lateral lobes ("la.ph.lo")

**up.vl.** These are two pair and upper subfolds of the lobe **vl**. The upper lobes can be derived or be a ventral continuation of the fold **ldl**. Chopard (1920) called them higher genital valve (“valve génitale supérieure”, “v.g.s”). Walker (1922) called them “subventral lobes” (“svl”). In some of Snodgrass (1937) drawings it can be equivalent to the fold **ldl** (“ll”). Ander (1956) identified them as lateral lobes (“la.ph.lo”).

**vl.** The last and ventralmost membranous lobe of the phallus, a continuation of the fold **df** that is laterally folded and ventrally extended forming this component. The fold is evident when the phallus is observed from the lateral view. The **vl** can be folded several times, with folds inside folds, which are completely visible when the structure is seen from below or above. Mostly the lobe **vl** is subfolded in two upper folds **up.vl** and two lower lobes **lw.vl**, but the number of lobes can be infrequently different (see section of variation). It was called “genital valves” by Chopard (1920) and described as being divided into higher genital valve (“valve génitale supérieure”, “v.g.s”) and lower genital valve (“valve génitale inférieure”, “v.g.i”). For Walker (1922) this component would be equivalent to the “ventral lobe” (“vl”) plus the “subventral lobe” (“svl”). In Snodgrass (1937) this component would be the “ventral lobe” (“vl”) plus the “lateral lobe” (“ll”) and the “ventral fold of the phallus” (“vf”). In Ander (1956) it is equivalent to the “ventral” (“v.ph.lo”) plus the “lateral lobes” (“la.ph.lo”).

**Internal components of the phallus. ap.** Two processes on each side of the ventralmost portion of the phallus on the membrane that forms the lobe **vl**. It is an extension or modification of the membrane, but differentiated because it is rougher than the remaining membranous portion. It can be a conspicuous extension, or difficult to be recognized when it is short. It can be a sclerotized component, and the degree of sclerotization is variable. When it is completely sclerotized it forms the sclerite **AP**. The **ap** can be equivalent to the “endoapophysis” (“end”) identified by Walker (1922), as was discussed above, and it would be directly attached to the ventral retractor muscles (Snodgrass 1937, “rpv”).

**ec.** Cavity formed between the inner walls of lobe **dl** and **vl**, which is continued anteriorly with the ejaculatory duct (Snodgrass 1937). Chopard (1920) didn’t name this cavity. Walker (1922) only identified the “gonopore” (“gp”) which is the external opening of the **ec**, and Snodgrass (1937) called it **ec** (as “Enph”). Ander (1956) also identified this component, but none abbreviation was proposed.

**ejd.** A saclike membranous component at the anterior portion of the phallus. The **ejd** is attached to the fold **vdI** dorsally, and to the folds of the lobe **vl** ventrally. Its opening is located mostly between the subfolds of the **vl**, **lw.vl** and **up.vl**. In few phalli there is a sclerotization on the laterals of the **ejd**, forming the sclerite **ES**. Walker (1922) called it “spermatophore sac” (“sps”); Snodgrass (1937), “ductus ejaculatorius” (“dej”); and Ander (1956), “ejaculatory duct” (“du.ej”).

**ejv.** A pair of oval or rounded membranous components attached on each side of the duct **ejd**. Walker (1922) identified them as lateral glandular pouches (“sp gl”). Snodgrass (1937) called them “vesicles of the ejaculatory duct”, and Ander (1956) called them “ejaculatory vesicles”, both using the same abbreviation (**ejv**).

**fdI.** Secondary swollen fold inwardly directed, usually between the lobe **dl** and the folds **vdI**. When the phallus bears separated sclerites **TS**, the fold **fdI** is located between them.

**vdI.** A membranous extension of the lobe **dl**, which is developed ventrally, below the **dl**, and can be directly attached to the duct **ejd**. It can be an entire lobe, or folded in two subfolds. This fold can be simple or bear sclerotized components or microstructures; when it is highly sclerotized, it forms the sclerite(s) **VS**. It is usually very difficult to locate the **vdI**, and it is most conspicuous in phalli of Pseudophyllinae and Conocephalinae. In Phaneropterinae, it can be a simple fold.

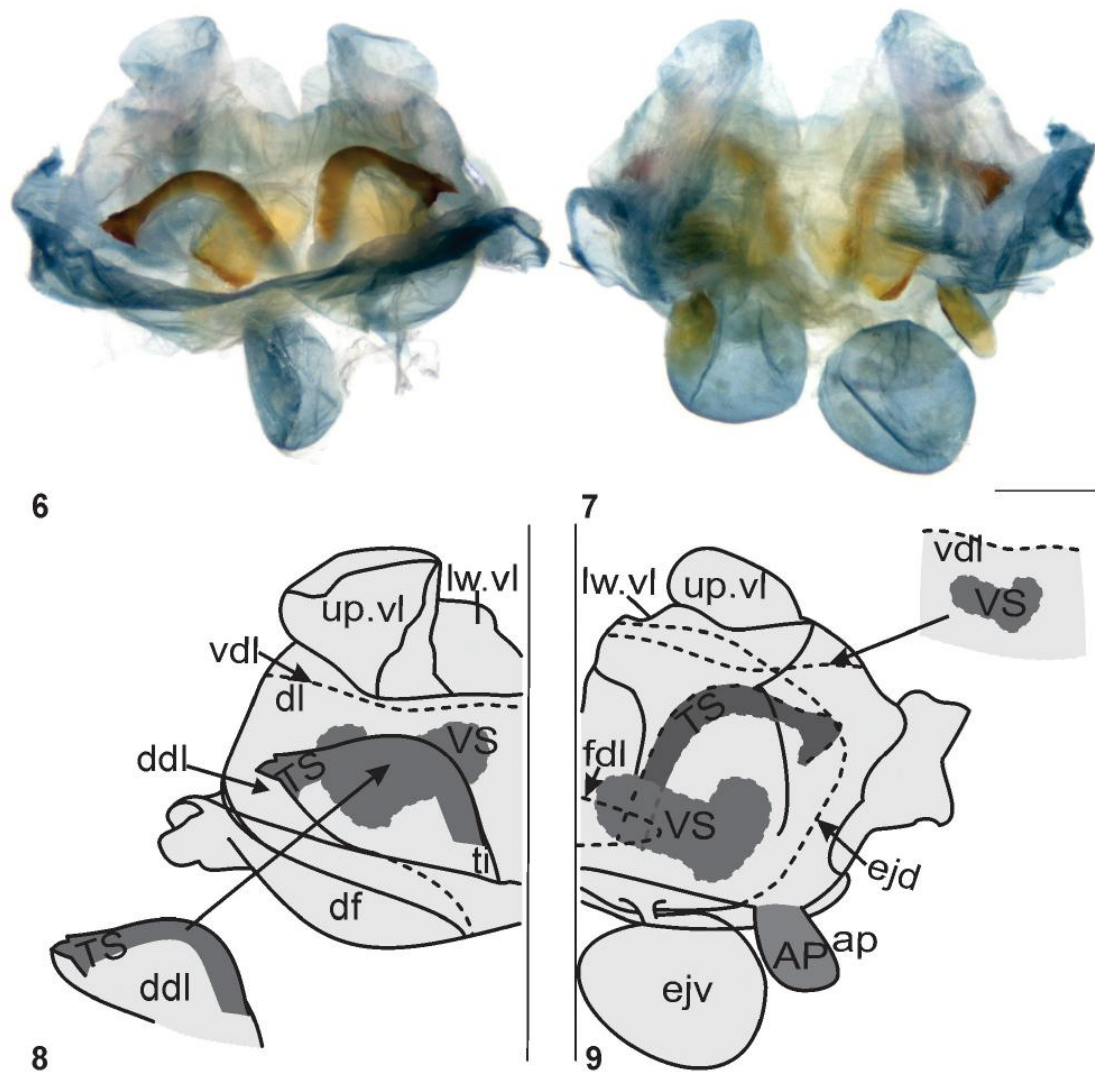
**VS.** Sclerotized component(s) observed in some phalli. It is a modification of the fold **vdI**. Possibly, Walker (1922) identified this inner sclerite(s) as “base of paramere” (“pmb”) or “endoparamere”. This component(s) can be separated from sclerite(s) **TS**, but sometimes it can be in touch or even completely fused with **TS**. Here we propose that **TS** and **VS** are distinct components mainly because each one is developed in separated folds of the lobe **dl** (except for when they are fused). For taxa with both sclerite(s) **TS** and **VS**, we hypothesize that the ancestral condition is separated **TS** and **VS**, and the derived condition is fused **TS** and **VS**.

### **Bauplan of external and internal components of the phallus**

(Figs 1, 6–9)

The phallus of katydids is usually a membranous structure with various folds. It is considered a pouch or a sac by

previous authors because the basic form of this structure is composed by a membrane which is folded, forming mostly one dorsal and one ventral cover, and the lateral portions are closed. In some cases, the membranous lobes **dl** and **vl** bear folds inside folds. Cavities are formed by folds and invaginations of the membrane, thus they are located between the lobes. Number and shape of lobes, sclerites, and cavities vary between taxa, but it is not our aim to describe quantity or quality of variation at the different taxonomic levels, because we only have a subsample of the total variation, geographically restricted. In future, more data will be obtained as more information on the phallus morphology is compiled in taxonomic descriptions. Membranous components of the phallus as the lobe **vl**, fold **fdl** and vesicles **ejv** are originally inflated, but after the treatment with KOH they deflate. Although muscles are important components of phalli (Eades 2000) they were not examined in this occasion. But it is important to point out that muscles are attached to sclerotized components at the inner anteriorportion of phalli, to the sclerotized components on the lobe **dl**, and to the apodemes **ap**. The bauplan described here includes all the basic components that a tettigoniid phallus could bear. However, it is important to emphasize that position, quantity and form of the components vary between taxa. Exemplification of morphological variation is treated below. The bauplan we describe is based on the phallus of *Conocephalus* sp.1 (Figs 1, 6–9).



**FIGURES 6–9.** Phallus of *Conocephalus* sp.1 (Conocephalinae, Conocephalini). 6. Image of dorsal view. 7. Image of ventral view. 8. Diagram of the left half of dorsal view, and detail showing the lobe **ddl** and one sclerite **TS**. 9. Diagram of the right half of ventral view, and detail showing the lobe **vdl** and one sclerite **VS**. Scale bar: 1.00 mm.

The following description considers the phallic components from the dorsalmost to the ventralmost portion: The fold **df** is a fine and smooth membranous portion folded outwardly. The **df** is folded at the fore portion and continues posteriorly with the lobe **dl**. The **dl** is wrinkled, with striations. The cavity **dc** is located between the fold **df** and the lobe **dl**. On the basal portion of **dl**, there are two processes **ti** which are separated from each other from the base, and each **ti** then continues posteriorly until the sclerites **TS** are formed. On the **dl** there are also two secondary folds, the **ddl**, which are laterally raised because the outer and curved margin of the sclerites **TS** are full attached on the membrane, and put pressure over these regions. Below the lobe **dl** there is the fold **vdl**, which is derived directly from the ventral surface of the **dl**. On the fold **vdl** there are two separated sclerites **VS**. At the inner anterior portion, between **TS**, there is the fold **fdl**. The duct **ejd** is attached to the ventral surface of the fold **vdl**, and to the folds of the lobe **vl**. There are two vesicles **ejv**, one at each lateral side of the duct **ejd**. The latest and ventralmost membranous fold is the continuation of the **df**, that is laterally folded and ventrally extended forming the lobe **vl**. The **vl** is folded at the midline forming two folds **up.vl** and two folds **lw.vl**. At the anterior margin of the lobe **vl**, on each side, there is one apodema **ap** with one oval sclerite **AP**.

### Variation of phallic components

(Figs 6–71)

Phalli of Tettigoniidae are most similar between species of the same genus, in comparison to species belonging to different genera or suprageneric taxa. Despite these differences being much evident, morphological characteristics of the phallus have been rarely used as diagnostic features. An example of intrageneric variation is shown for three *Conocephalus* spp. (Figs 6–9, 14–17). Below we provide information for the most remarkable cases of morphological variation based only on the phalli dissected by us. We emphasize that it is a subsample of the whole variation existing in the family.

External components such as lobe **dl**, fold **ddl**, processes **ti**, sclerites **TS** and **VS**, fold **vdl**, and lobe **vl** can be single (e.g. lobe **dl** in *Eriolus* sp., Fig. 18, and in *Phlugis ocraceovittata* Piza, Figs 30, 32; fold **vdl** in *Conocephalus* sp.1, Fig. 8; lobe **vl** in *Teleutias* sp., Fig. 70, and in *Gen.9* sp., Fig. 89) or paired (e.g. lobes **dl** in *Schedocentrus* sp., Fig. 48; folds **ddl** in *Conocephalus* sp.1, Figs 6, 8; folds **vdl** in *Schedocentrus* sp., Figs 48, 49). One phallus has mixed single and paired components, and not exclusively single or exclusively paired components. The position of the phallic components can vary, so they can be displaced both vertically and horizontally, and even comparatively reversed. In detail, components can vary as follows:

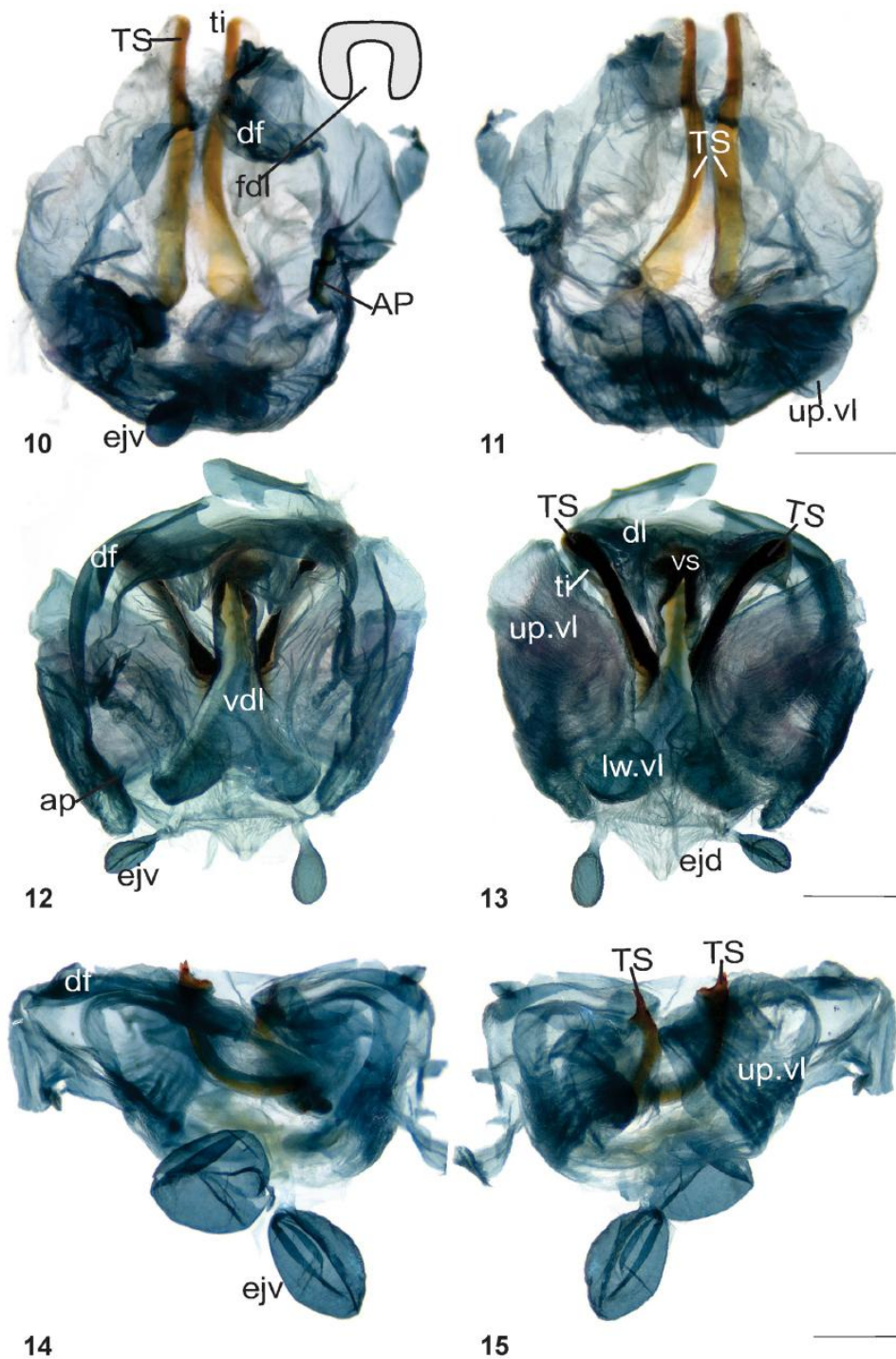
The fold **df** can be short as in *Neoconocephalus* sp.1 (Figs 20, 21), or large, covering part of the dorsal portion along the phallus, as in *Gen.3* sp. (Fig. 38).

The apodemes **ap** were not observed in all phalli and this may be due to errors during the dissections, because they are the anteriormost components and can be easily cut. The position, form and size of the sclerites **AP** varies. The ones we observed are as large as the apodemes **ap** (e.g. sclerites **AP** in *Conocephalus* sp.1, Fig. 7), small and at the middle of the **ap** (e.g. *Cerberodon viridis* Perty Figs 23, 25) or the apodeme **ap** barely sclerotized without a defined sclerite **AP** (e.g. *Gen.4* sp., Fig. 41). The **AP** can have an arch shape and be located in the basal portion of the apodeme **ap**, which apparently gives to the **ap** a structural reinforcement (*Gongrocnemis* sp., Fig. 63). The **ap** also vary in shape and size.

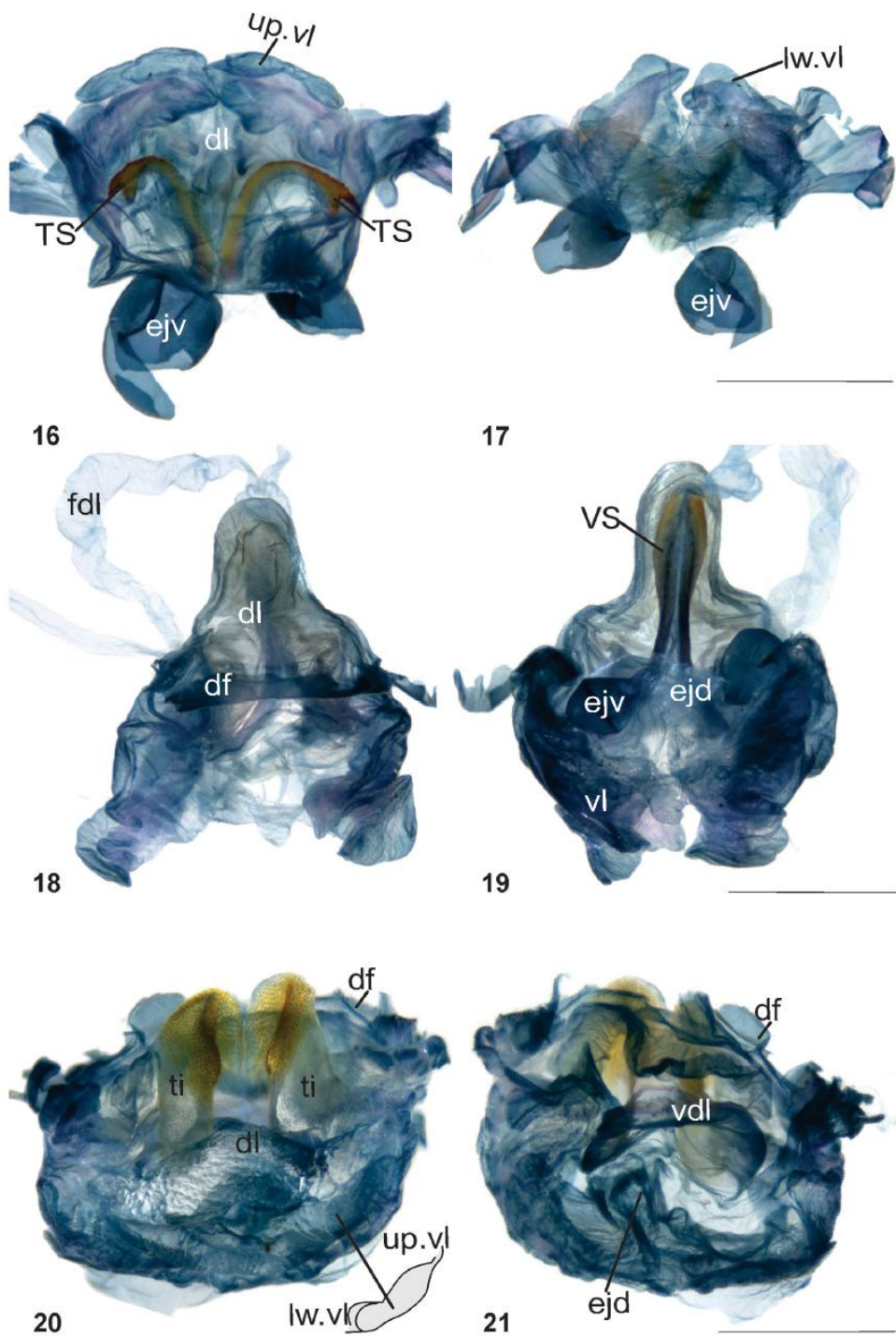
The cavity **dc** can be conspicuous and well defined as in *Conocephalus* sp.1 (Fig. 6) and *C. viridis* (Fig. 22), simply a shallow cavity as *S. alieniphaga* (Fig. 64), or inverted in a ventral position as in *Eriolus* sp. (Fig. 18).

The lobe **dl** can be large as in *Conocephalus* sp.1 (Figs 6, 8) and *C. viridis* (Figs 22, 24); or comparatively less developed as in *Gen.8* sp. (Fig. 54), the latter being possibly a consequence of the overdevelopment of the process **ti**. It can be reduced as in *Teleutias* sp. (Fig. 70), a stretched lobe without secondary folds (*Gen.3* sp., Fig. 38), folded at the midline (*Schedocentrus* sp., Fig. 48) or with lateral folds **ldl** (*Gen.1* sp., Fig. 26). The level of sclerotization of the cuticle of the entire lobe varies, being moderately sclerotized when microstructures are present, mostly in the area of the process **ti** (see below), or thoroughly rough as in *P. ocraceovittata* (Fig. 30), the roughness being evident because the lobe **dl**, specifically where the process **ti** is, it is not stained as in the other phalli.

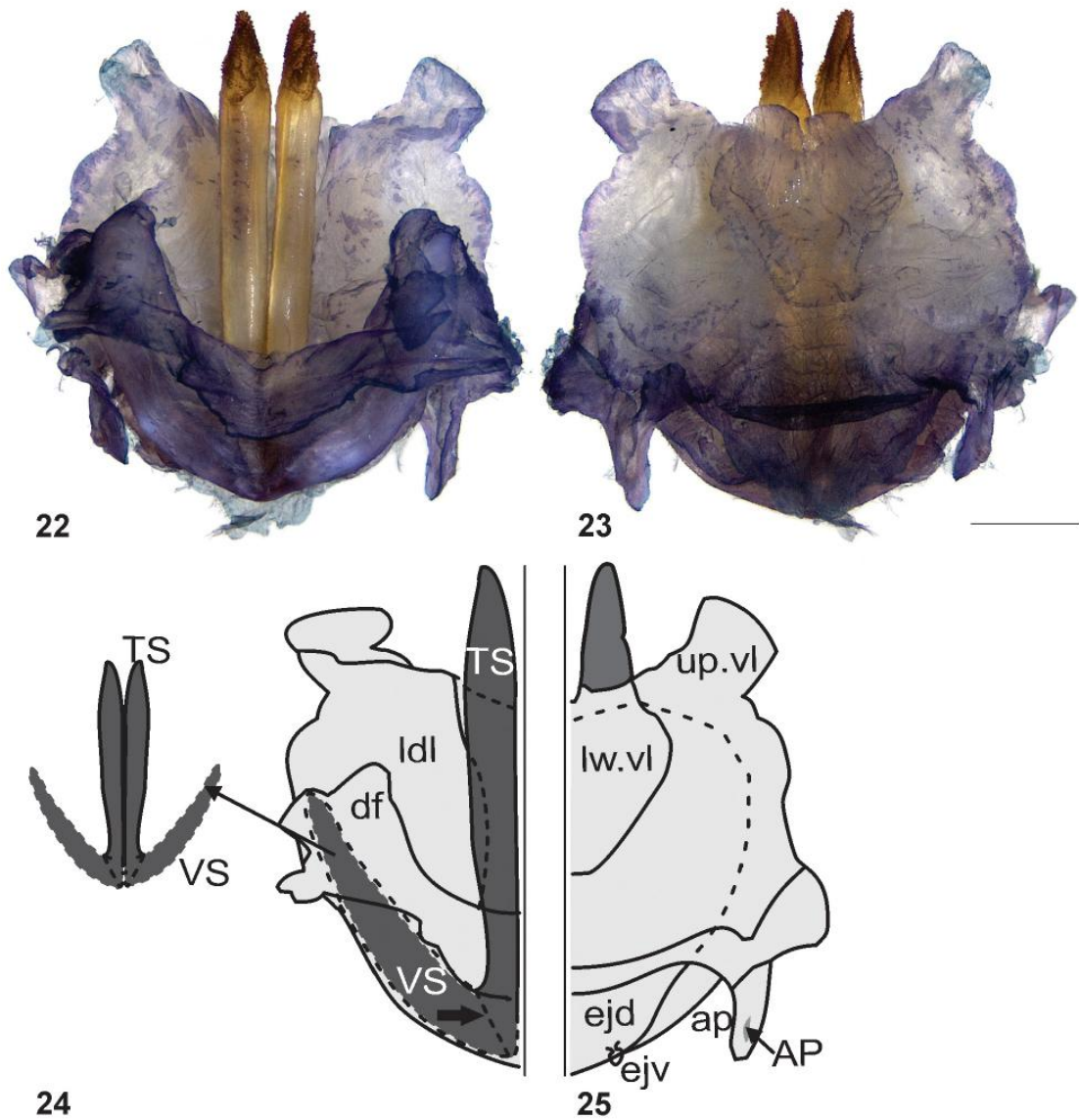
The shape of duct **ejd** has little variation. It is usually completely membranous, but can bear sclerotized components as the lateral sclerites **ES** in *Acanthodis* sp. (Figs 58–59).



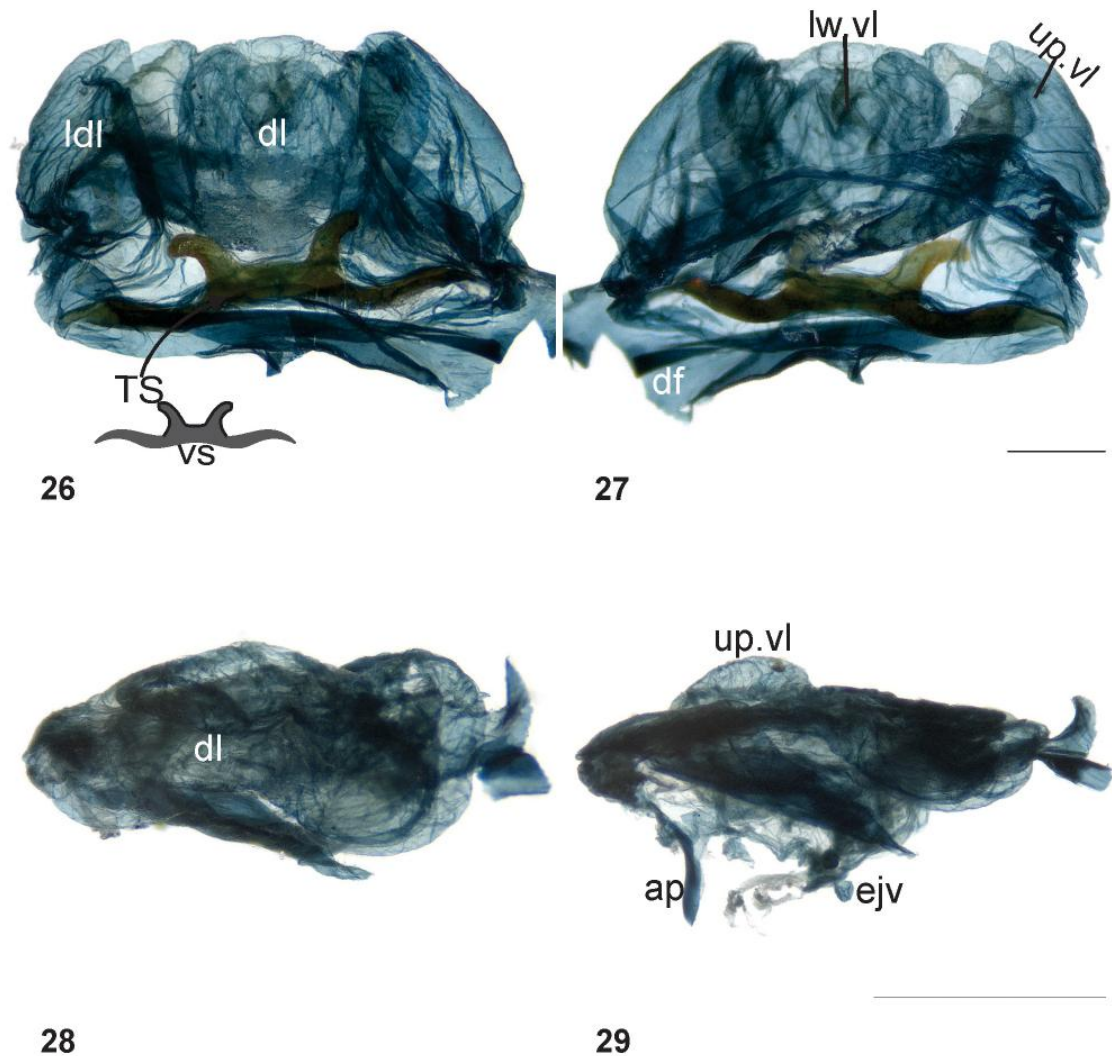
**FIGURES 10–15.** Images of phalli of Conocephalinae species, showing examined Agraeciini (10–13) and Conocephalini (14–15). 10–11. *Eschatoceras* sp., dorsal (10) and ventral (11) views, with a diagram showing the fold *fdl* in 10. 12–13. *Uchuca ferreirai* (Piza), dorsal (12) and ventral (13) views. 14–15. *Conocephalus* sp.2, dorsal (14) and ventral views (15). Scale bars: 1.00 mm.



**FIGURES 16–21.** Images of phalli of Conocephalinae species, showing examined Conocephalini (16–17) and Copiphorini (18–21). 16–17. *Conocephalus* sp.3, dorsal (16) and ventral (17) views. 18–19. *Eriolus* sp., dorsal (18) and ventral (19) views, respectively. 20–21. *Neoconocephalus* sp.1., posterior (20) and ventral (21) views, with a diagram showing portions of the ventral lobes **up.vl** and **lw.vl** in 20. Scale bars: 1.00 mm.



**FIGURES 22–25.** Phallus of *Cerberodon viridis* Perty (Listrosclidinae, incertae sedis). 22. Image of dorsal view. 23. Image of ventral view. 24. Diagram of the left half of dorsal view, and detail showing the two sclerites TS and two sclerites VS, all four sclerites are unfused, the boundaries between them are indicated by the black dotted line. 25. Diagram of the right half of ventral view. Scale bar: 1.00 mm.

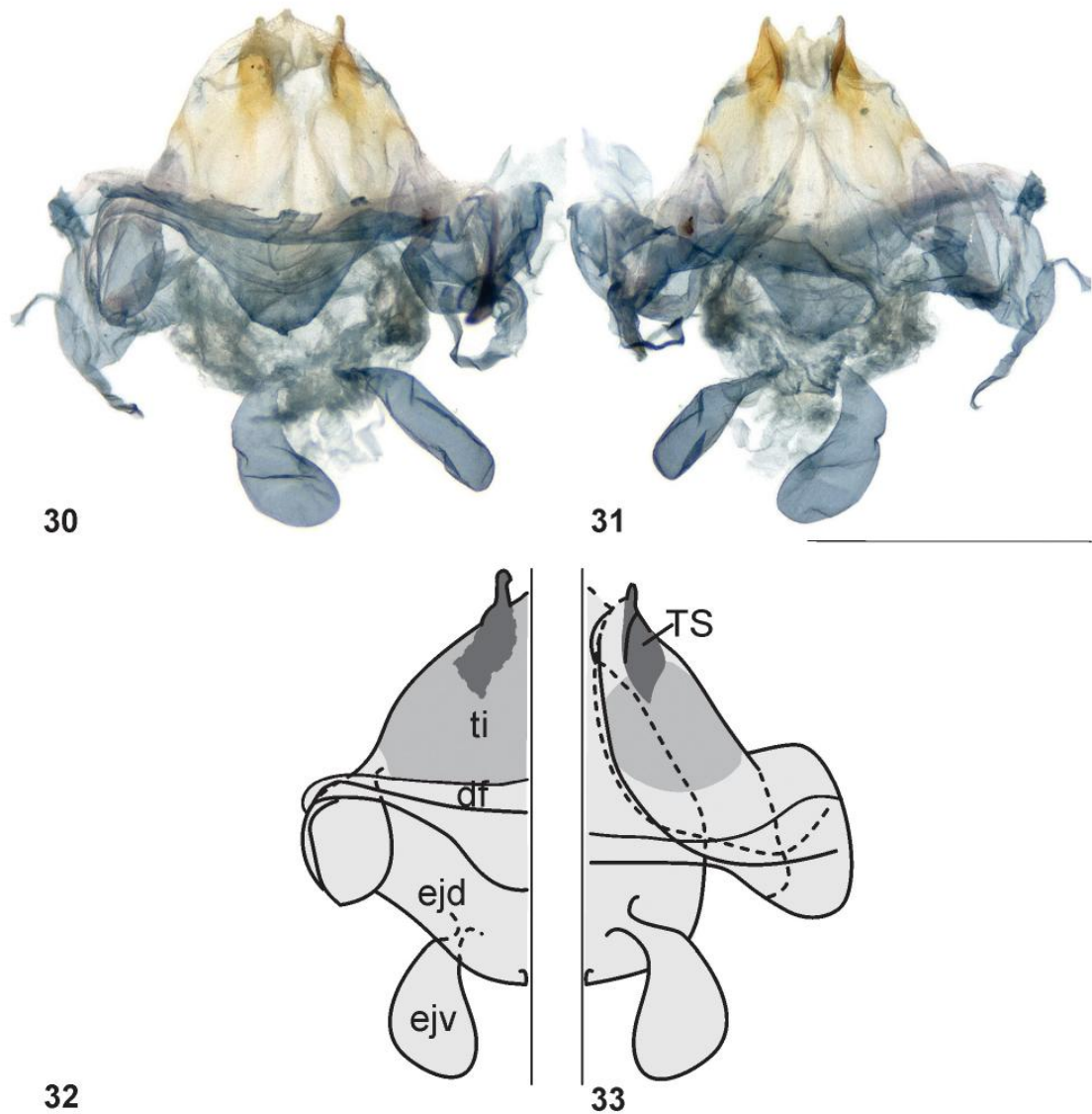


**FIGURES 26–29.** Images of phalli of *Listroscolidinae* species, *incertae sedis*. 26–27. Gen.1 sp., dorsal (26) and ventral (27) views, with a diagram showing fused sclerites **TS** and **VS** in 26. 28–29. Gen.2 sp., posterior (28) and ventral (29) views. Scale bars: 1.00 mm.

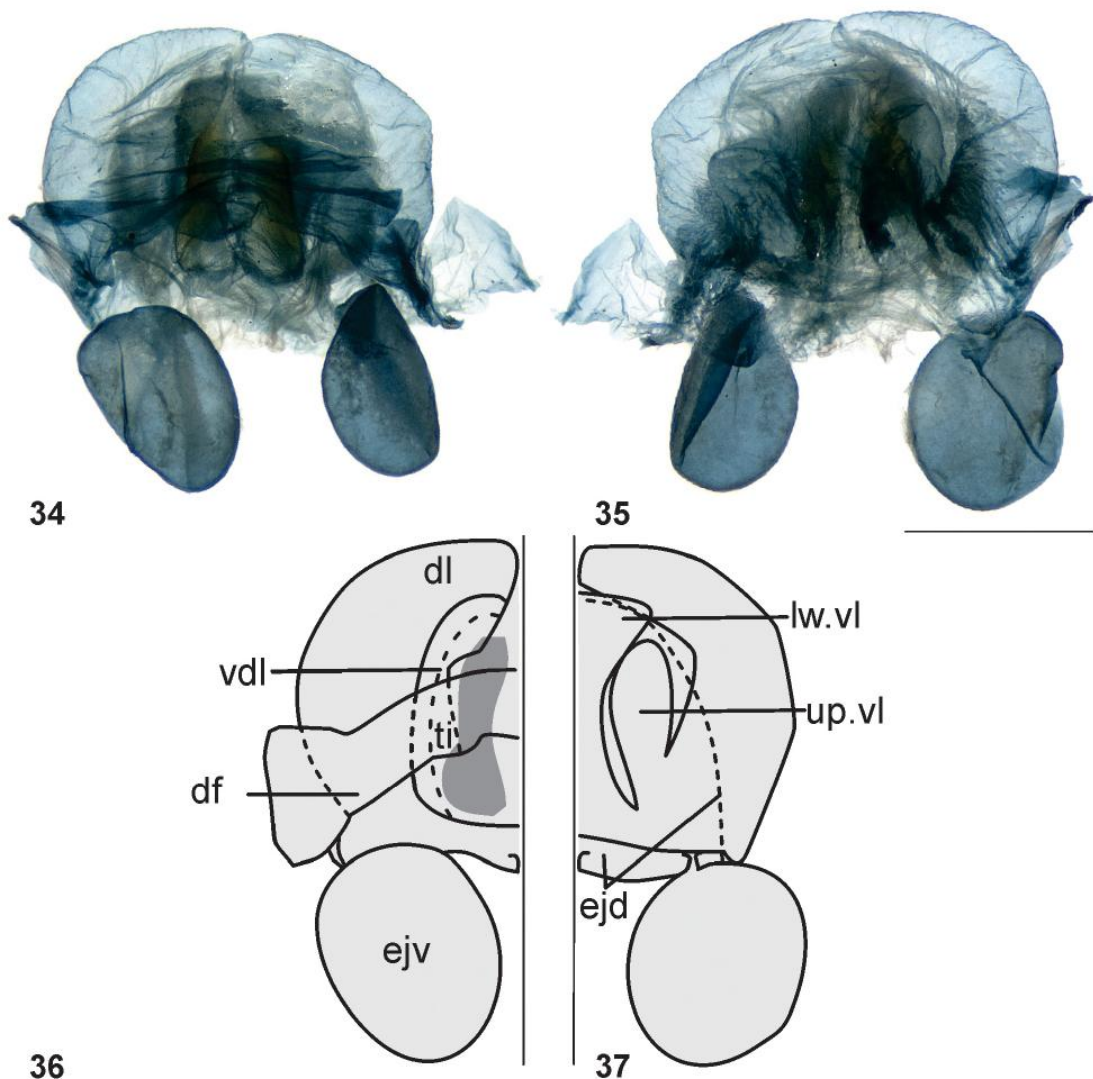
The vesicles **ejv** vary in size and form, but that seems not to be correlated to the size of the phallus. The smallest **ejv** were observed in Gen.2 sp. (Fig. 29), but the smallest in proportion to the size of the phallus are those of *Uchuca ferreirai* (Piza) (Figs 12–13), *Porphyromma* sp. (Fig. 67) and *P. ocellata* (Figs 68, 69). The largest in proportion to the size of the phallus are those of *Conocephalus* sp.1 (Figs 7, 9) and *Anaulacomera* sp. (Figs 34–37).

The process(es) **ti** and sclerite(s) **TS** can be completely absent (Gen.2 sp., Fig. 28). When they are present, **ti** and **TS** can be a single component (*Leptotettix crassiceri* Piza, Fig. 56; Gen.9 sp., Fig. 60, 61; *Gongrocnemis* sp., Fig. 62), a single component bifurcated close to its apex (*Porphyromma* sp., Fig. 66, 92), an enlarged longitudinal base with two free projections (Gen.1. sp., Fig. 26), or paired components (*Eschatoceras* sp., Fig. 13; *C. viridis*, Figs 22, 24, *Anaulacomera* sp. Fig. 80). The sclerite **TS** can also be asymmetric (Gen.9 sp., Fig. 60) or symmetric (most of the examined species; e.g. *Conocephalus* sp.1, Figs 6, 8). The degree of sclerotization of process **ti** also varies, being slightly sclerotized as in *Neoconocephalus* sp.1 (Fig. 20) and *L. crassiceri* (Fig. 56) or only covered by microstructures as in *Neoconocephalus* sp.2. (Fig 75). The base of the process **ti** or sclerite **TS** can be at an

anterior position on the lobe **dl** (*Leptotettix* sp., Figs 44, 46 and *Gnathoclitia vorax* (Stoll), Figs 50–51), or displaced at a more posterior position (*U. ferreirai*, Fig. 13). The sclerite(s) **TS** can extend along the lateral length of the lobe **dl** (*Conocephalus* sp.1, Figs 6, 8), attached to the **dl** until the median portion of the **dl** (*Gongrocnemis* sp., Fig. 62) or only at the anterior portion (*Gen.1* sp., Fig. 26). The sclerite(s) **TS** and the process(es) **ti** vary in their orientation, being usually rearwardly oriented (*G. vorax*, Fig. 60 and *Leptotettix* sp., Figs 44, 46), and in these cases the sclerites can exceed the length of phallic lobes, leaving their tips exposed. They can be anterior-upwardly oriented (*Neoconocephalus* sp.1, Fig. 20), upwardly oriented (*C. viridis*, Figs 22, 24; *Gen.1* sp., Fig. 26), or downwardly displaced. The latter case is possibly due to the downward displacement of the fold **vdl**, being the lobe **vl** wrapped by the lobe **dl** (*P. ocraceovittata*, Figs 31, 33). The sclerite(s) **TS** vary in size, and the largest **TS** we observed were in *C. viridis* (Figs 22–25) with 4.48 mm of length and 0.50 mm of width.

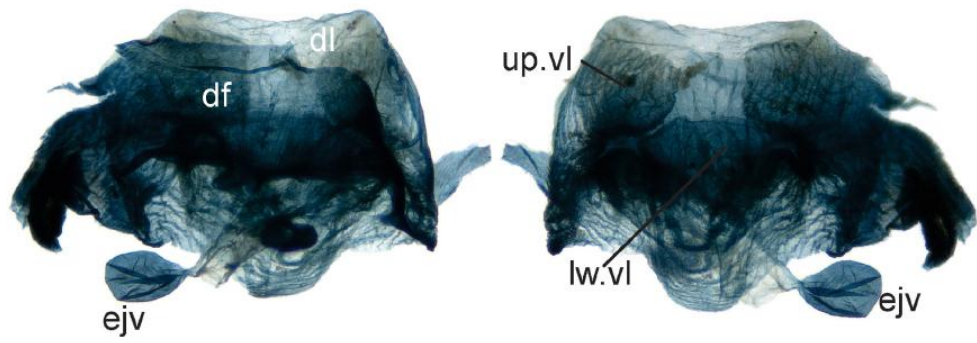


**FIGURES 30–33.** Phallus of *Phlugis ocraceovittata* Piza (Meconematinae, Phlugidini). 30–31. Images of dorsal (30) and ventral (31) views. 32. Diagram of the left half of dorsal view. 33. Diagram of the right half of ventral view. Scale bar: 1.00 mm.



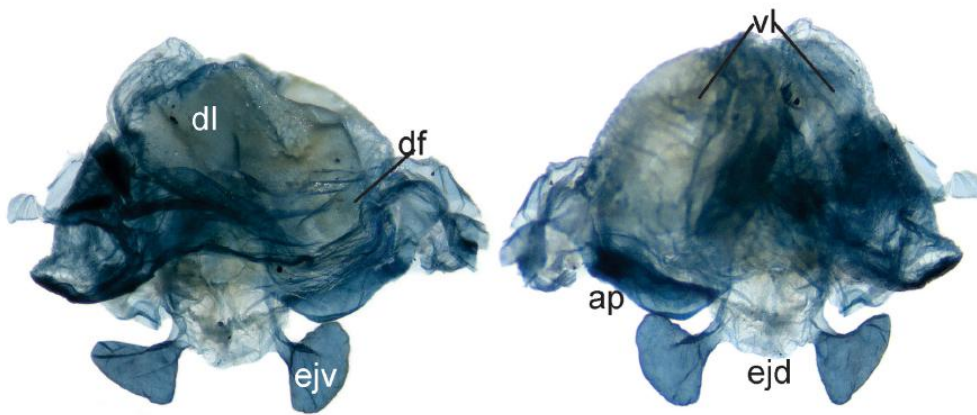
**FIGURES 34–37.** Phallus of *Anaulacomera* sp. (Phaneropterinae, Viadanini). 34–35. Images of dorsal (34) and ventral (35) views, respectively. 36. Diagram of the left half of dorsal view. 37. Diagram of the right half of ventral view. Scale bar: 1.00 mm.

The fold **vdl** can be hidden under de lobe **dl** (*Conocephalus* sp.1, Figs 6, 8) or exposed dorsally (*U. ferreirai*, Fig. 13, 73). In some species, the fold **vdl** bear sclerite(s) **VS**, which can be two spaced sclerites hidden below the lobe **dl** (*Conocephalus* sp.1, Figs 6–9); or an exposed sclerotization (*U. ferreirai*, Fig. 13), in which this sclerite is displaced to a more posterior position, forming a kind of pathway. The sclerite(s) **VS** can also be modified into two longitudinal bars close together at the midline, forming a bridge (*C. viridis*, Fig. 24); in this case, the bridge is displaced to a more anterior position and remains in contact with sclerites **TS**, possibly providing mechanical support to their movement. Sclerite(s) **VS** and fold **vdl** can be fused with process(es) **ti** and lobe **dl**, resulting in a single piece (Gen.1 sp., Figs 26, 77), possibly a step in the transformation series beyond separated sclerites **VS** and **TS** (*C. viridis*, Fig. 24). Also, **TS** and **VS** can be fused forming a single component, which can be easily recognized as separated components because there are conspicuous boundaries between them (*Gongrocnemis* sp., Figs 62, 90). The sclerite(s) **VS** can be inside process **ti**, being an inner support (Fig. 86) for this kind of elongated **ti**.



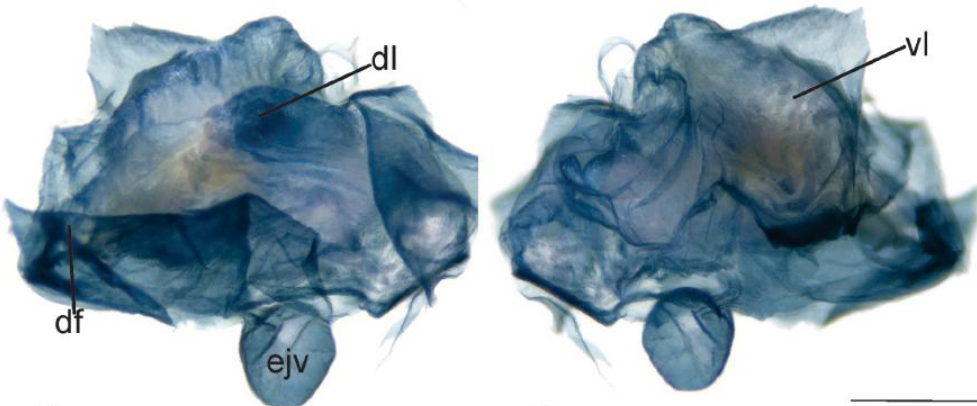
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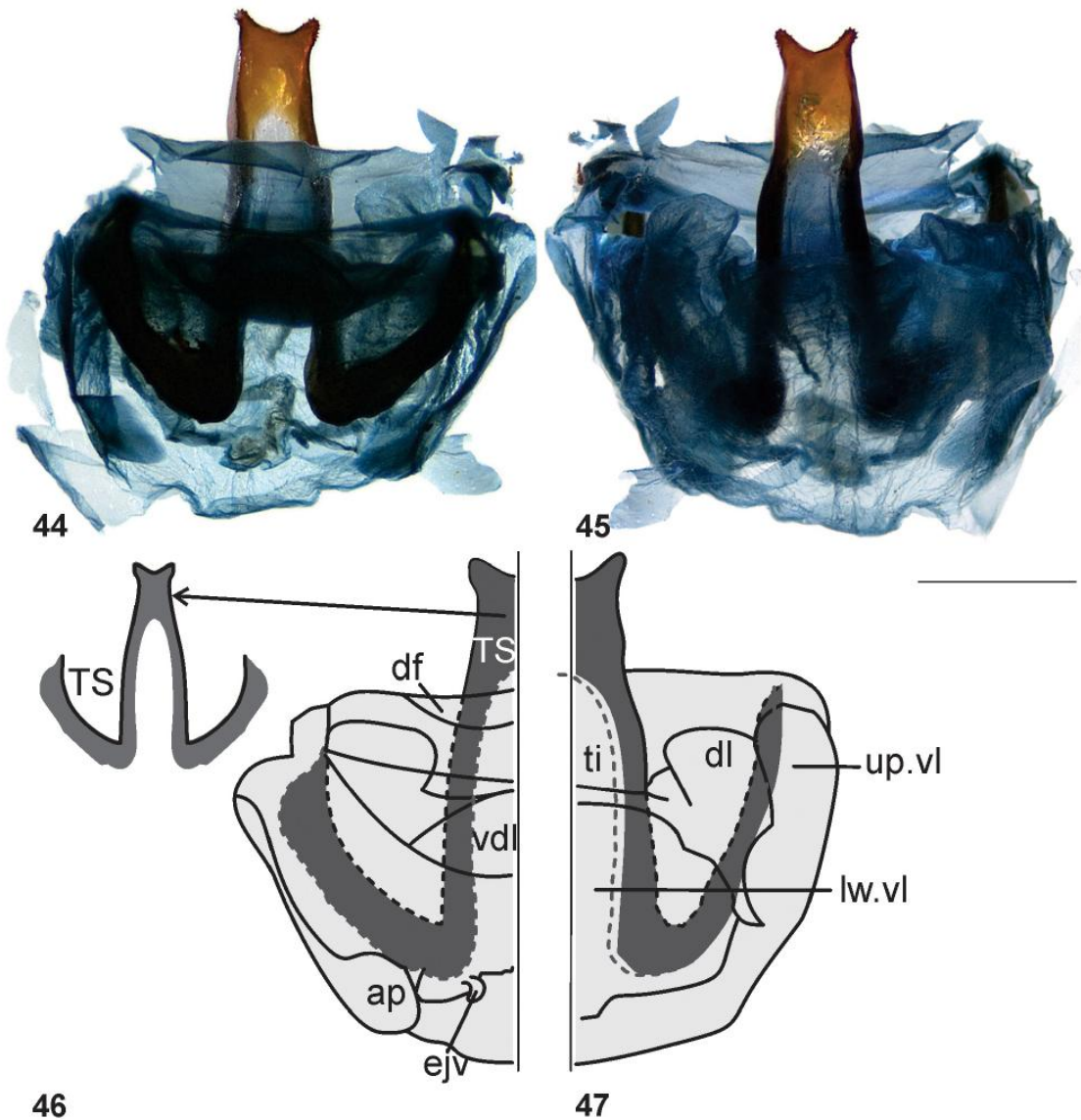
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**FIGURES 38–43.** Images of phalli of Phaneropterinae species, incertae sedis. 38–39. Gen.3 sp., dorsal (38) and ventral (39) views. 40–41. Gen.4 sp., dorsal (40) and ventral (41) views, respectively. 42–43. Gen.5 sp., dorsal (42) and ventral (43) views. Scale bars: 1.00 mm.

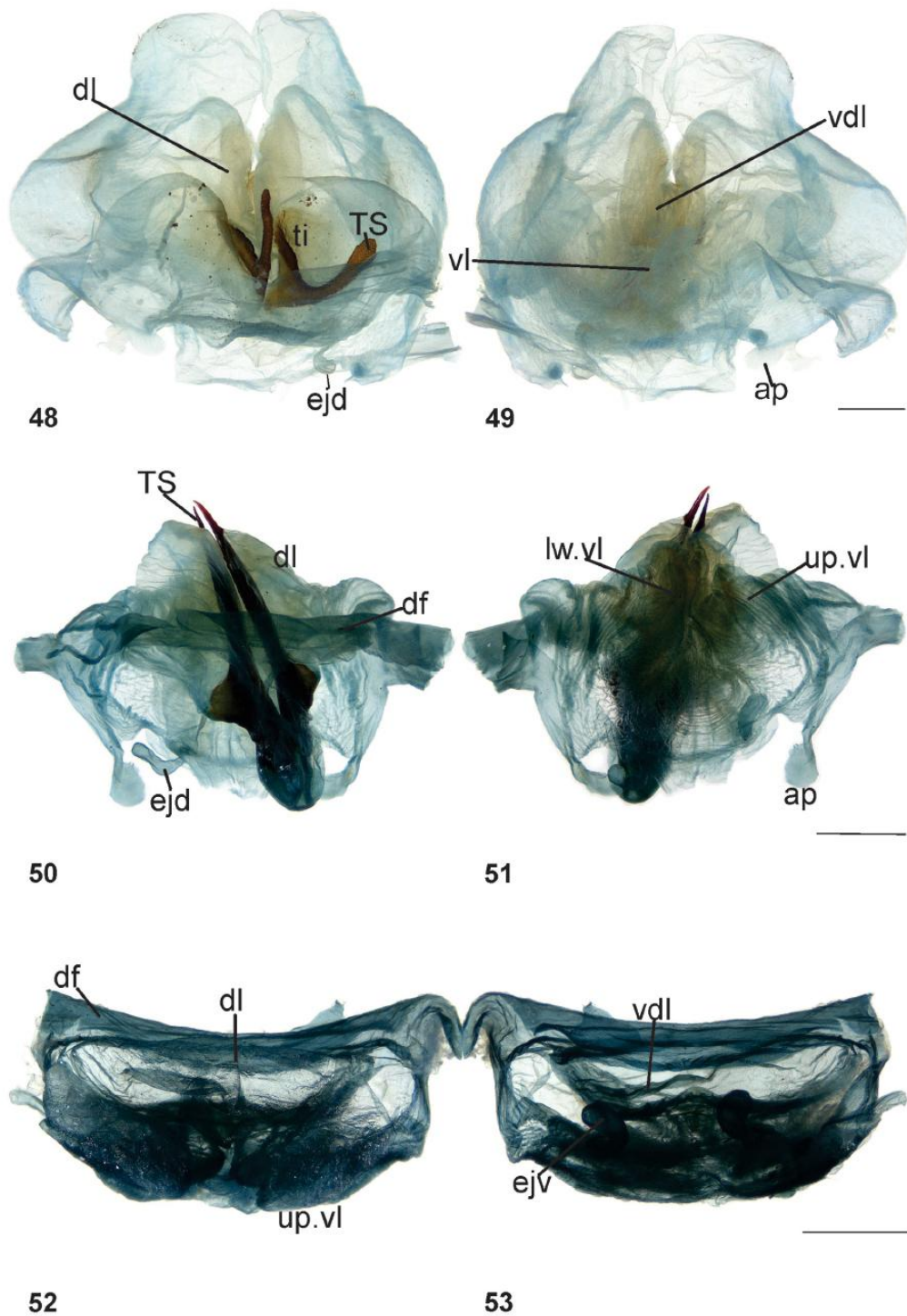


**FIGURES 44–47.** Phallus of *Leptotettix* sp. (Pseudophyllinae, Leptotettigini). 44–45. Images of dorsal (44) and ventral (45) views, respectively. 46. Diagram of the left half of dorsal view, and detail showing the entire sclerite TS. 47. Diagram of the right half of ventral view. Scale bar: 1.00 mm.

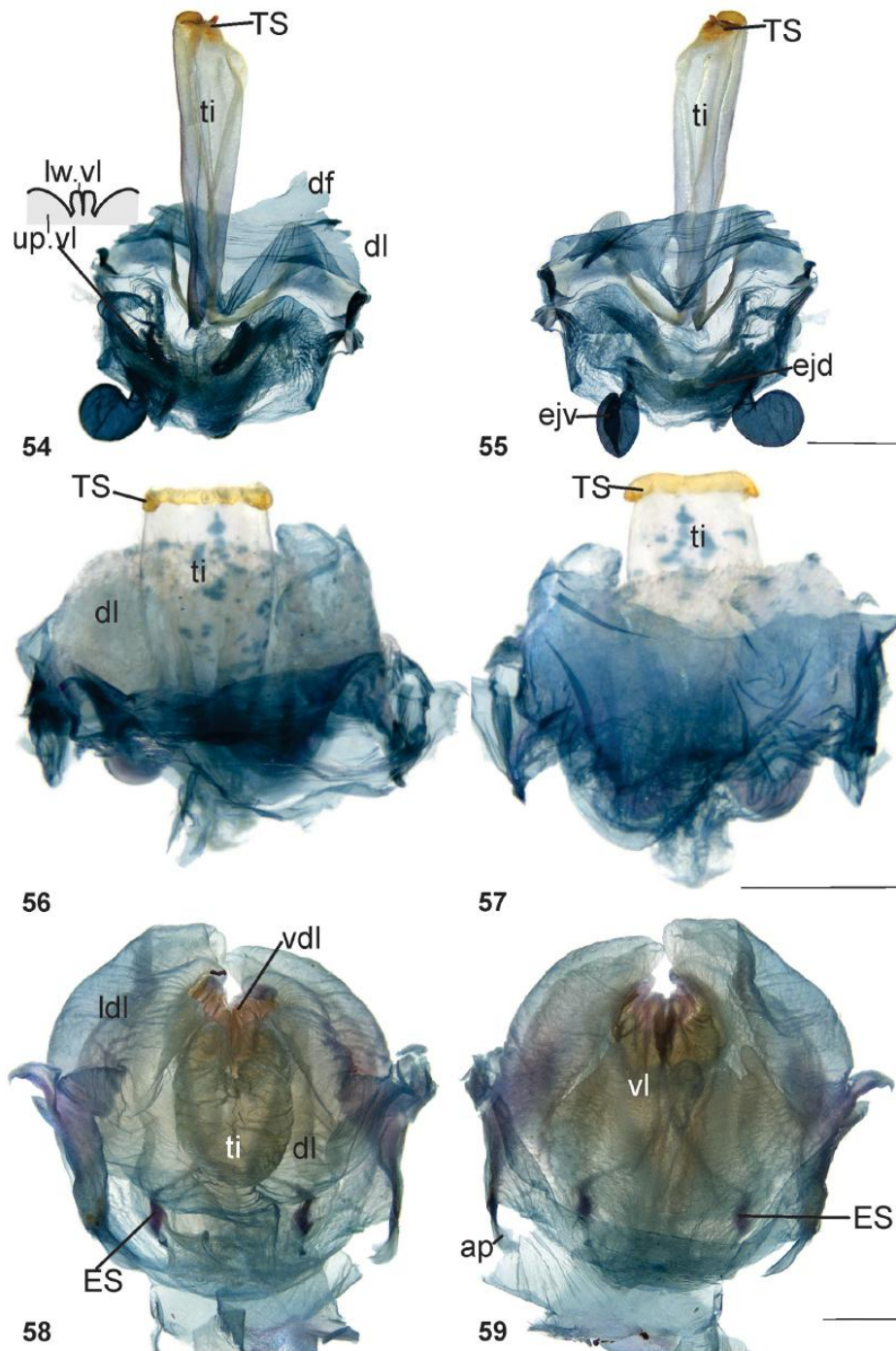
The lobe **vl** can be composed by barely developed lobes (*Neoconocephalus* sp.1, Fig. 20; Gen.8 sp., Fig. 54) or by larger lobes (*Schedocentrus* sp., Figs 48–49). The **vl** can be folded once forming two folds **up.vl** and two folds **lw.vl** (*Eschatoceras* sp., Fig. 11; Gen.1 sp., Fig. 27 *Conocephalus* sp.3, Fig. 17) or two **up.vl** and one **lw.vl** (*Anaulacomera* sp., Figs 35, 37).

The position of the components can be inverted. The fold **vdl** can be displaced vertically to a ventralmost position, laying the duct **ejd** above the fold **vdl** as in *U. ferreirai* (Fig. 12); in this phallus, **vdl** and sclerite **VS** form a pathway through which the **ejd** opens. And as was described above, the processes **ti** and sclerites **TS** can be in a reversed position (*P. ocraceovittata* (Figs 30–33), *Eriolus* sp. (Figs 18–19, 74).

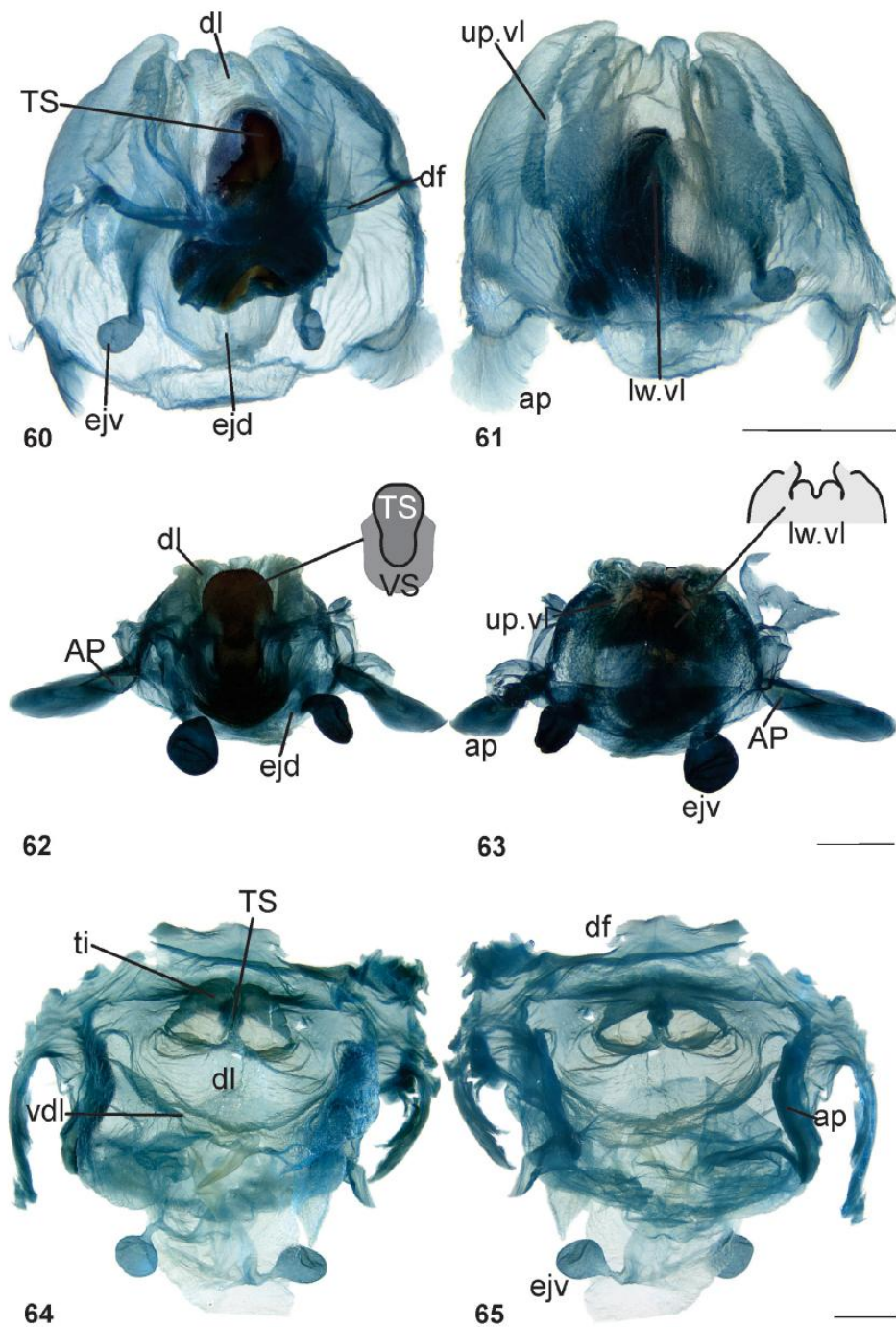
A remarkable morphology was observed in Gen.5 sp. (Figs 42–43), in which only one side of the phallus is developed, turning it into a completely asymmetric structure.



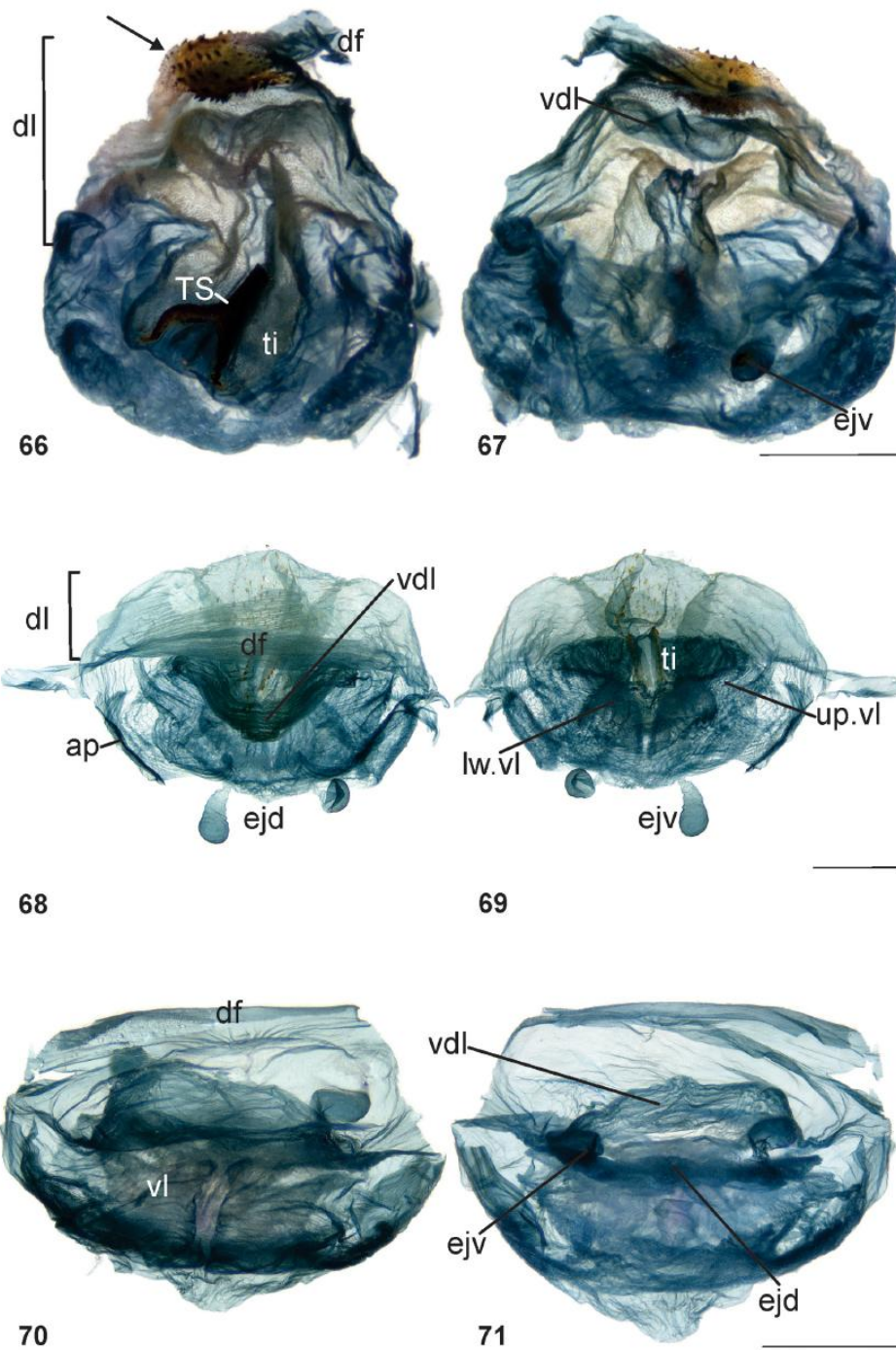
**FIGURES 48–53.** Images of phalli of Pseudophyllinae species, showing examined Cocconotini (48–49), Eucoconotini (50–51) and Leptotettigini (52–53). 48–49. *Schedocentrus* sp., dorsal (48) and ventral (49) views. 50–51. *Gnathoclitia vorax* (Stoll), dorsal (50) and ventral (51) views. 52–53. Gen.7 sp., dorsal (52) and ventral (53) views, respectively. Scale bars: 1.00 mm.



**FIGURES 54–59.** Images of phalli of Pseudophyllinae species, showing examined Leptotettigini (54–57) and Pleminiini (58–59). 54–55. Gen.8 sp., dorsal (54) and ventral (55) views, respectively, with a diagram showing portions of the ventral lobes *lw.vl* and *up.vl* in 54. 56–57. *Leptotettix crassicerci* Piza, dorsal (56) and ventral (57) views, respectively. 58–59. *Acanthodis* sp., dorsal (58) and ventral (59) views, respectively. Scale bars: 1.00 mm.



**FIGURES 60–65.** Images of phalli of Pseudophyllinae species, showing examined Pleminiini (60–63) and Polyancistrini (64–65). 60–61. *Gen.9* sp., dorsal (60) and ventral (61) views. 62–63. *Gongrocnemis* sp., dorsal (62) and ventral (63) views, with one diagram showing the sclerite **TS** and the **VS** (62) and another showing portion of the ventral lobe **lw.vl** (63). 64–65. *Spinapecta alieniphaga* Naskrecki & Lopes-Andrade, dorsal (64) and ventral (65) views, respectively; single sclerite **TS** hidden between the two processes **ti**. Scale bars: 1.00 mm.

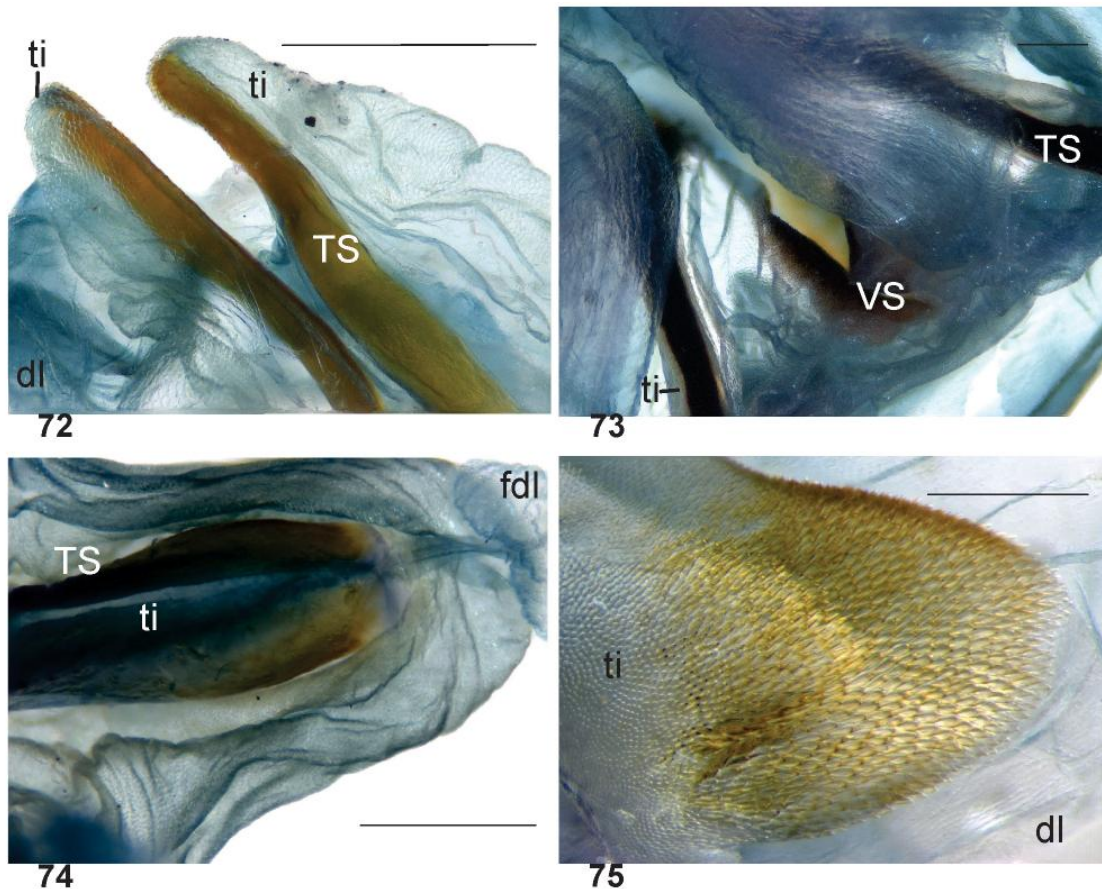


**FIGURES 66–71.** Images of phalli of Pseudophyllinae species, showing examined Pterochrozini. 66–67. *Porphyromma* sp., dorsal (66) and ventral (67) views; the arrow indicates a secondary portion over the **dl** with conspicuous spines, that are not part of the sclerite **TS**, and we have not determined whether this portion is part of the process **ti** or an additional component on the **dl**. 68–69. *Pterochroza ocellata* (Linnaeus), dorsal (68) and posterior (69) views. 70–71. *Teleutias* sp., posterior (70) and anterior (71) views. Scale bars: 1.00 mm.

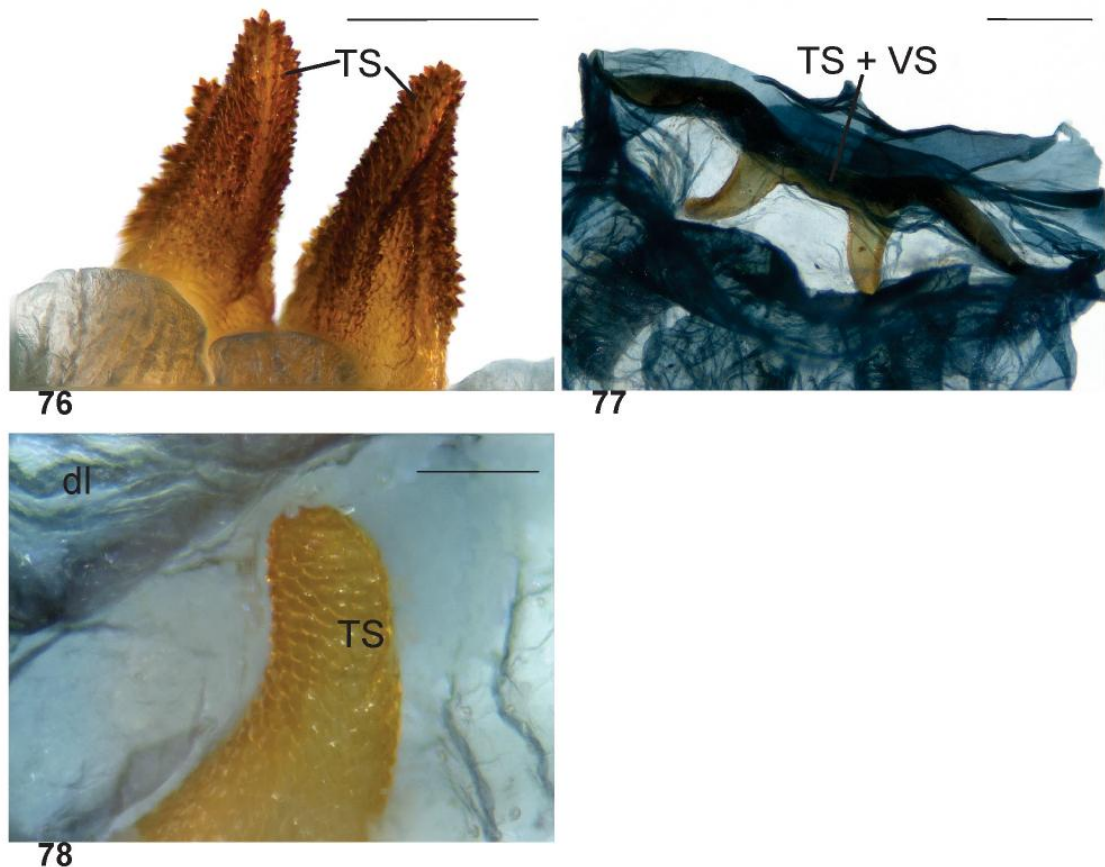
### Microstructures on the phalli

(Figs 72–94)

We observed several microstructures on the phalli. All species are devoid of conspicuous microstructures on the fold **df**. The lobe **dl** bears several types of microstructures, especially around the process(es) **ti** and sclerite(s) **TS**. The lobe **dl** is usually a wrinkled membrane (Gen. sp.9, Fig. 89). The **dl** can bear groups of microspines (*Porphyromma* sp., Fig. 91; *P. ocellata*, Fig. 94), sclerotized scale-like microstructures (*Eschatoceras* sp., Fig. 72; *Machima* sp., Fig. 79; Gen.7 sp., Fig. 84; *Porphyromma* sp., Fig. 92), or punctures with bristles (*Schedocentrus* sp., Fig. 83; *P. ocellata*, Fig. 94). The lobe **dl** can be crested because of the folding of the membrane as in *Gongrocnemis* sp. (Figs 62). The sclerites **TS** can be smooth (*Conocephalus* spp., Figs 6, 15, 16; *U. ferreirai*, Fig. 73), with few punctures bearing bristles (*Leptotettix* sp., Fig. 87), and conspicuously sclerotized with scale-like microstructures or thin spines (Gen.1 sp., Fig. 78; *Schedocentrus* sp., Fig. 83; *Gongrocnemis* sp., Fig. 90). The **TS** and process **ti** can bear simple spines or tubercles at apex (*C. viridis*, Fig. 76; *Leptotettix* sp., Fig. 88; Gen.8 sp., Fig. 85; Gen.9 sp., Fig. 89); or at base (*Porphyromma* sp., Fig. 93). The process(es) **ti** can bear microspines or scales (*Neoconocephalus* sp.2, Fig. 75, *Anaulacomera* sp. Fig. 81). In the most simple case, the titillator can be formed only by processes **ti** covered with stout spines (*P. ocellata* sp., Fig. 94).



**FIGURES 72–75.** Components and microstructures in phalli of Conocephalinae species, showing examined Agraeciini (72–73) and Copiphorini (74–75). 72. *Eschatoceras* sp., showing part of sclerites **TS**, processes **ti**, and lobe **dl**. 73. *Uchuca ferreirai* (Piza), showing bridge formed by sclerites **VS**, part of sclerites **TS**, and part of only one of the processes **ti**. 74. *Eriolus* sp., showing part of inverted sclerites **TS**, process **ti**, and fold **fdl**. 75. *Neoconocephalus* sp.2, showing part of process **ti** with lots of microstructures, and lobe **dl**. Scale bars: 0.50 mm.



**FIGURES 76–78.** Components and microstructures in phalli of Listrosclidinae species. 76. *Cerberodon viridis* Perty, showing apices of sclerites TS. 77. Gen.1 sp., showing inner view of fused sclerites TS+VS. 78. Gen.1. sp., showing part of lobe dl and part of one of the sclerites TS with its microstructures. Scale bars: 0.50 mm (76–77), 0.10 mm (78).

### Evolutionary scenarios for the titillator

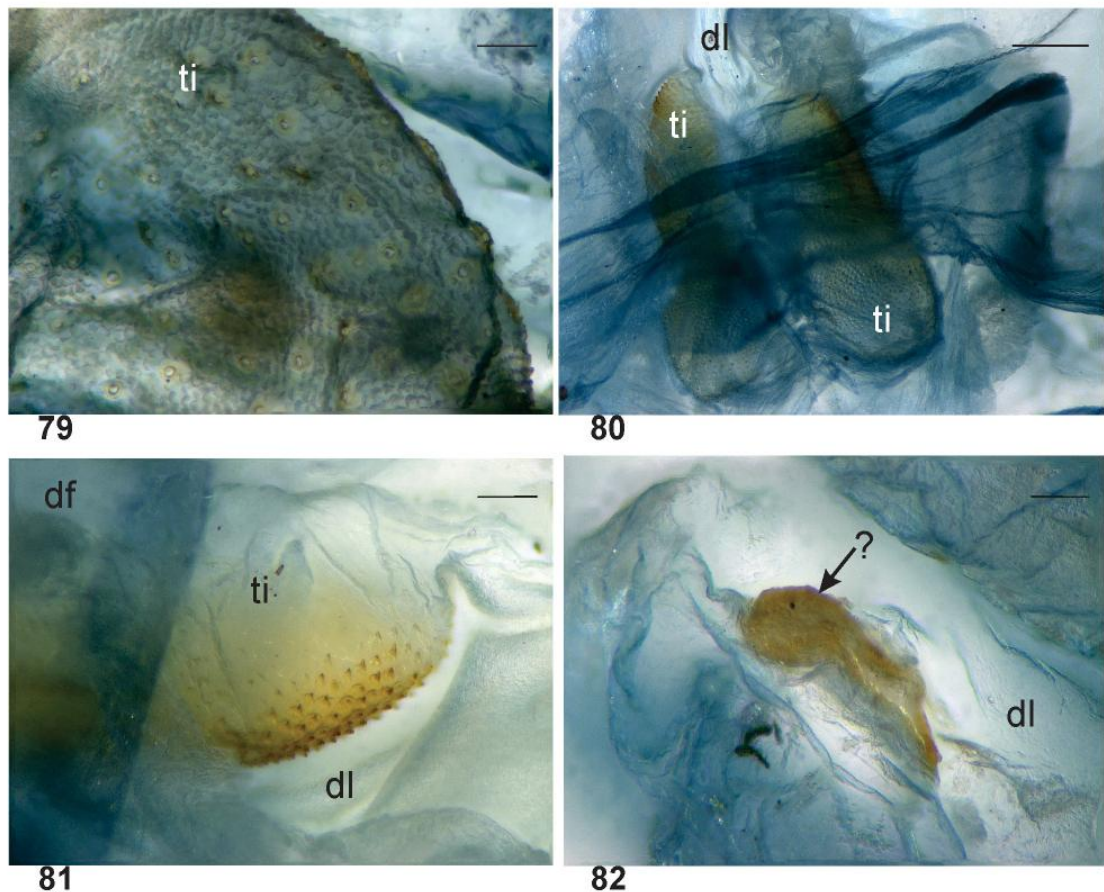
(Figs 95–96)

None of the available phylogenetic hypotheses for Tettigoniidae includes the 19 living subfamilies recognized by Eades *et al.* (2014). And it is also essential to note that besides lacking important terminal groups, the trees show controversies such as a polyphyletic Listrosclidinae (Naskrecki 2000, Jost & Shaw 2006). The proposal by Gorochov (1988), with the modifications suggested by Gwynne & Morris (2002), is the only topology that includes the largest number of subfamilies. On each clade of the trees (Figs 95, 96), when the titillator (trait I: 1) is present in at least one of the terminal groups (subfamilies), and at the same clade there are subfamilies devoid of titillator, we assume that the titillator is present in the most recent common ancestor and that the absences represent independent losses of this structure. Tracing the titillator on Gorochov's tree (Fig. 95), we suggest it is possibly an ancestral feature that was lost independently several times. The same conclusion is possible tracing the trait I (absence (0) or presence (1) of a titillator) in Jost & Shaw (2006) tree (Fig. 96).

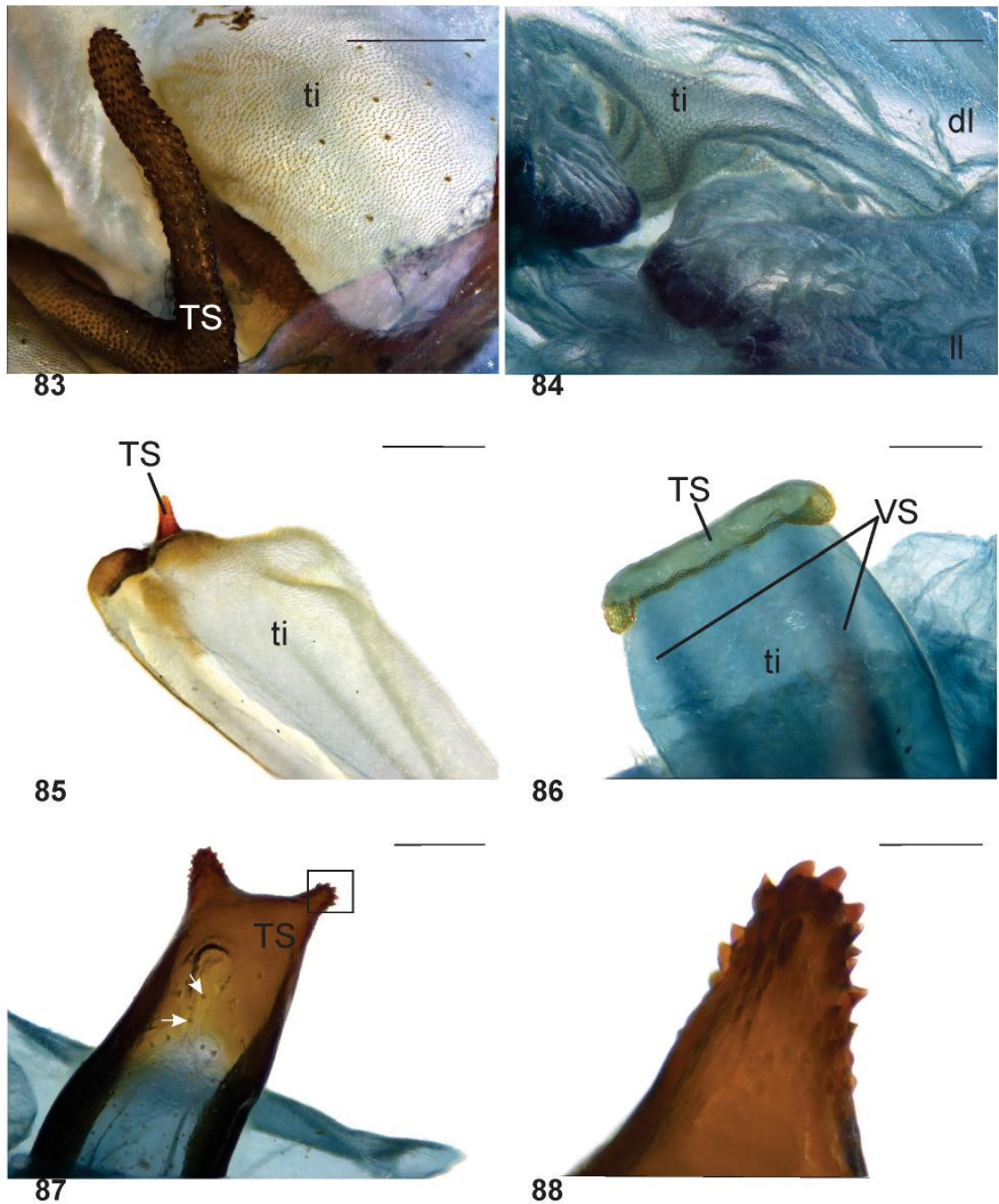
Species without titillator (trait I: 0) belong to the clades Phyllophorinae + Mecopodinae and Zaprochilinae + Phasmodinae. In both clades, titillator was possibly lost in the most recent common ancestor. And an independent loss has possibly occurred in Lipotactinae. Species bearing titillator (trait I: 1) belong to Conocephalinae, Hetrodinae, Tettigoniinae, Bradyporinae and Austrosaginae. Subfamilies in which there are species bearing titillator but with independent losses inside them are Phaneropterinae, Pseudophyllinae, Listrosclidinae,

Meconematinae and possibly Hexacentrinae (incomplete information; see Gorochov 2007). There are gaps of information on the titillator of Acridoxeninae (not included in the trees), Saginae, Tympanophorinae and Microtettigoniinae.

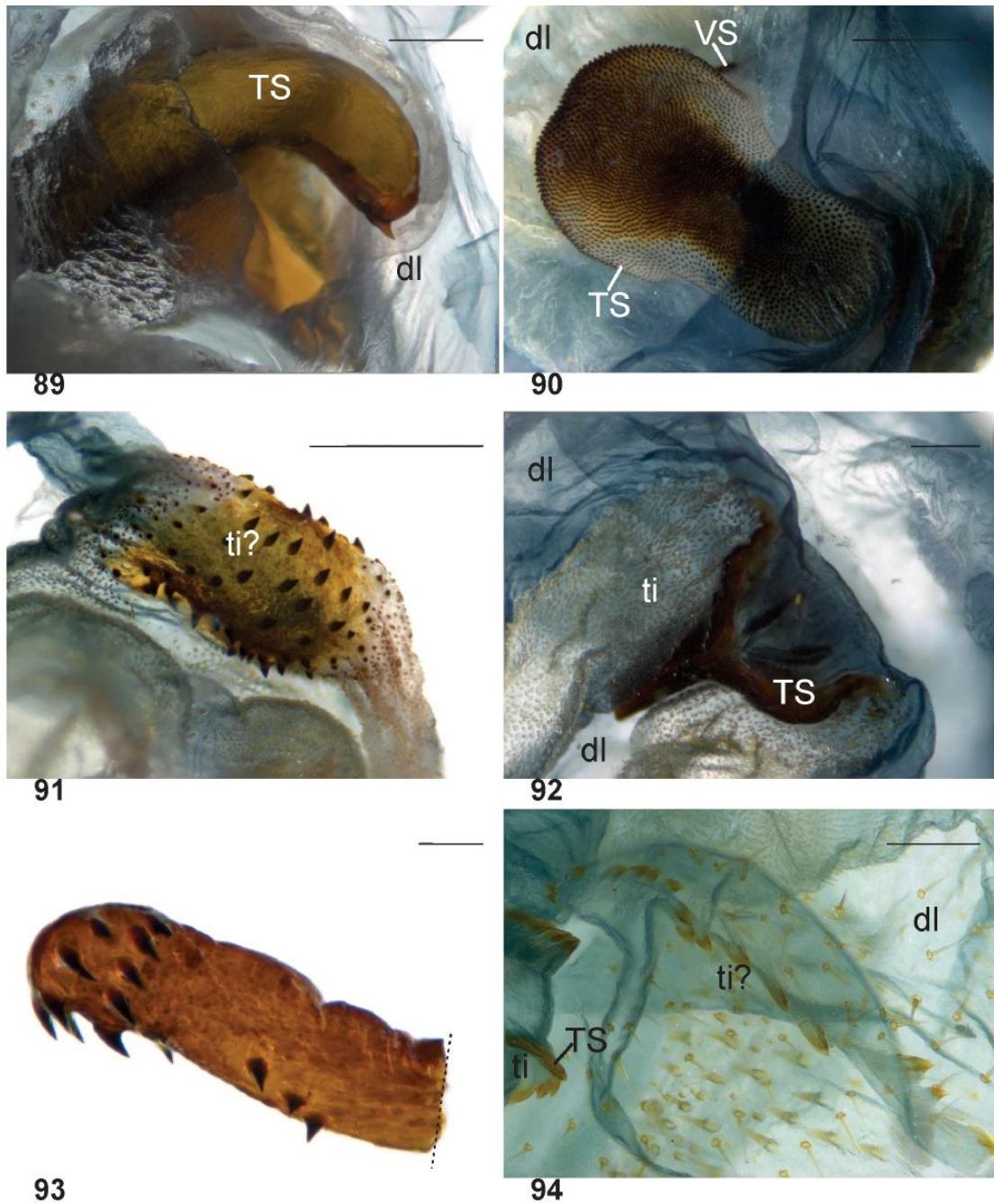
When a titillator is present, it can be formed by single or paired components, as detailed above. Subfamilies bearing species with titillator of either single or paired components are Phaneropterinae, Pseudophyllinae, Tettigoniinae, Listrosclidinae and Meconematinae. Available information on Conocephalinae and Hetrodinae suggest their species bear titillator with paired components. Species of Bradyporinae are reported to bear a titillator with single components, the same occurring in Austrosaginae and Hexacentrinae. It is very premature to suppose whether a hypothetical ancestor of Tettigoniidae would have had a titillator of single or paired components (process(es) **ti** and sclerite(s) **TS**).



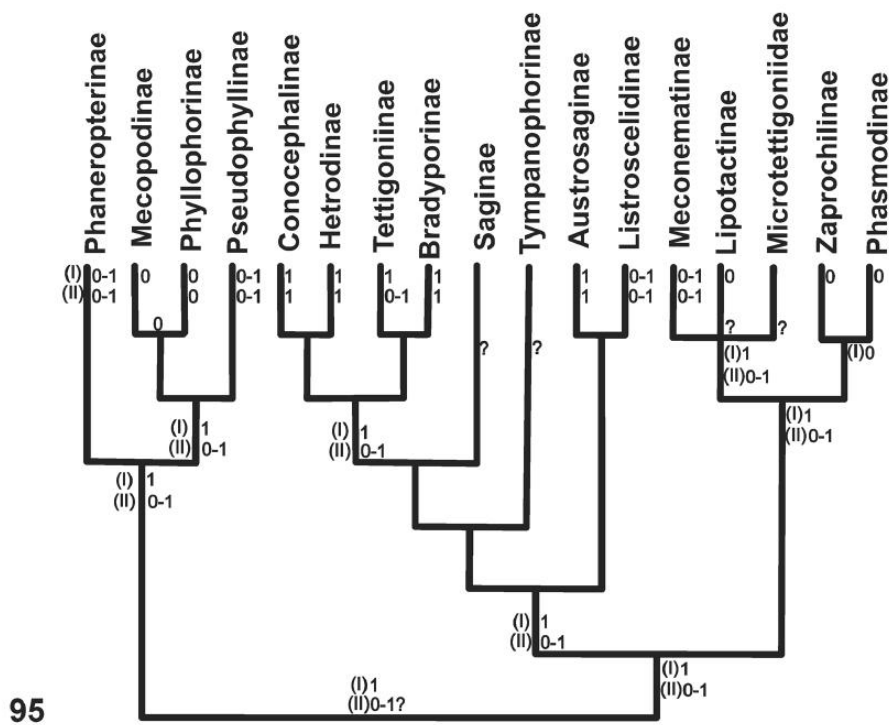
**FIGURES 79–82.** Components and microstructures in phalli of Phaneropterinae species, showing examined Dysoniini (79) and Viadanini (80–82). 79. *Machima* sp., showing microstructures on process **ti**. 80–81. *Anaulacomera* sp., showing part of lobe **dl** and processes **ti** (80), part of fold **df** and lobe **dl**, and microstructures on **ti** (81). 82. Gen.6 sp., showing amorphous sclerotization on lobe **dl**. Scale bars: 0.05 mm (79, 81–82), 0.20 mm (80).



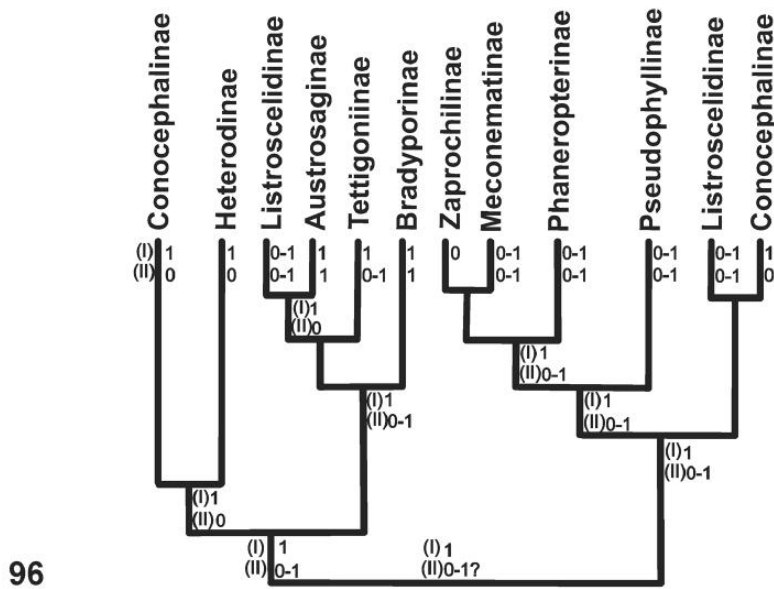
**FIGURES 83–88.** Components and microstructures in phalli of Pseudophyllinae species, showing examined Coconotini (83) and Leptotettigini (84–88). 83. *Schedocentrus* sp., microstructures on sclerites TS and process ti. 84. Gen.7 sp., showing part of fold Idl and microstructures on process ti. 85. Gen.8 sp., apex of the single process ti, and apical sclerite TS. 86. *Leptotettix crassicerci* Piza, showing apex of the single process ti, the apical sclerite TS and the sclerites VS inside the process ti. 87–88. *Leptotettix* sp., showing part of sclerite TS with arrows indicating pores; the square indicates the apical portion of TS showed in Fig. 88 (87) and apicalmost projection of TS with spine-like microstructures (88). Scale bars: 0.50 mm (83, 85), 0.20 mm (84, 86), 0.40 mm (87), 0.10 mm (88).



**FIGURES 89–94.** Components and microstructures in phalli of Pseudophyllinae species, showing examined Pleminiini (89–90) and Pterochrozini (91–94). 89. *Gen.9* sp, showing part of lobe **dl** and the asymmetrical single sclerite **TS**. 90. *Gongrocnemis* sp., showing single sclerite **TS** and **VS** and part of lobe **dl**. 91–93. *Porphyromma* sp. showing spine-like microstructures on the upper portion of lobe **dl**, possibly a continuation of the process **ti** showed in Figs 91 and 66, indicated as **ti?** (91), part of sclerite **TS** and process **ti** (92), and broken basal portion of sclerite **TS** (93). 94. *Pterochroza ocellata* (Linnaeus) showing part of **ti** with spiny **TS**, and microstructures on lobe **dl**, that possibly are part of an overdeveloped process **ti**. Scale bars: 0.20 mm (89, 92, 94), 0.50 mm (90, 91), 0.10 mm (93).



95



96

**FIGURES 95–96.** Traits related to the tillator traced over two available phylogenetic hypotheses. 95. Tree from Gorochov (1988) based on morphological features, with addition of Austrosaginae and Zaprochilinae (Rentz 1993) and Lipotactinae (Ingrisch 1995) as suggested by Gwynne *et al.* (2002). 96. Tree from Jost & Shaw (2006) based on molecular data. First trait (I) and the states without (0) and with tillator (1), second trait (II) and the states tillator formed by paired (0) or single (1) components. See Material and Methods for further explanations. See Appendix 3 for available information on these traits in the literature and the present work.

**Hypothetical morphological correlations between shape of cerci and titillator in related and unrelated taxa**  
(Figs 97–128)

Since our preliminary dissections, morphological correlations between the shape of cerci and the shape or absence of a titillator, mainly of the sclerite(s) TS, were observed. Our observations were complemented with literature data (Appendix 1). Of the 90 inspected papers, only 43 included information on phalli in species' descriptions. Among these 43 articles, 36 included information on phalli for all species, and seven only for some. We observed three main patterns of hypothetical morphological correlations that are described below. We consider these morphological correlations as functionally different during copula. At this very moment, the main issue to emphasize is that these morphological correlations occur in different subfamilies, and reinforce that morphological patterns of cerci and titillator do not necessarily correspond to homologies. Therefore, they could have evolved independently in these taxa. Not all the evaluated species fit in the three most common cases of morphological correlations, and these exceptions are also listed at the end.

*First hypothetical morphological correlation*

Males with simple cerci (not angulated, without spines or secondary components) and phallus devoid of sclerite TS. Such combination occurs in the following taxa:

**Listrosclidinae. Incertae sedis.** Gen.2 sp. (Figs 28–29, 107).

**Meconematinae. Aprophyliini.** *Pseudosaga maraisi* Naskrecki. **Meconematini.** *Xiphidiopsis* Redtenbacher: *X. amnicola* Gorochov; *X. platycerca* Bey-Bienko. *Xizicus fascipes* (Bey-Bienko). **Incertae sedis.** *Exoteratura kerinci* (Gorochov), with the distal part of the phallus bearing a pair of pubescent and weakly sclerotized areas. *Grigoriora* Gorochov; *G. beybienkoi* Gorochov; *G. beybienkoi* Gorochov.

**Phaneropterinae. Ducetiini.** *Ducetia borealis* Gorochov & Kang; *Prohimerta sichuanensis* Gorochov & Kang. **Incertae sedis.** Gen.3 sp. (Figs 38–39, 112); Gen.4 sp. (Figs 40–41, 113); Gen.5 sp. (Figs 42–43, 114). **Phyllopterae group.** *Itarissa* sp. (Fig. 110). **Steirodontini.** *Stilpnochlora acanthonotum* Nickle; *Stilpnochlora quadrata* (Scudder); *Stilpnochlora azteca* (Saussure,); *Stilpnochlora thoracica* (Serville).

**Phyllophorinae.** *Phyllophorella queenslandica* Rentz, Su & Ueshima; *Siliquofera grandis* (Blanchard), in which cerci are comparatively longer.

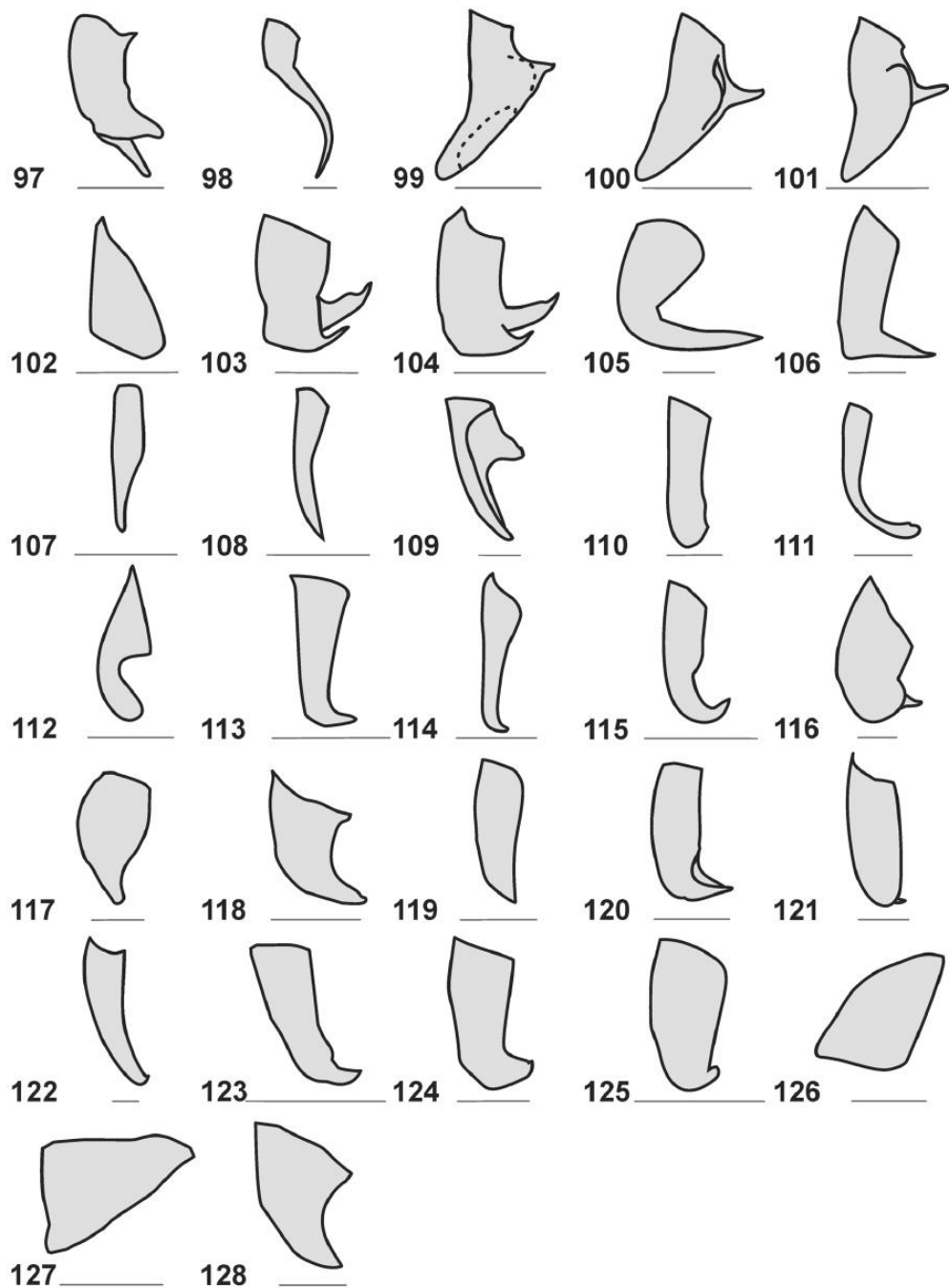
**Pseudophyllinae. Polyancistrini.** *S. alieniphaga* (Figs 64–65, 125). **Teleutiini.** *Chibchella nigrospecula* Montealegre-Z. & Morris; *Stetharasa exarmata* Montealegre-Z. & Morris. *Teleutias* sp. (Figs 70–71, 128). **Pleminiini.** *Acanthodis* sp. (Figs 58–59, 122).

**Zaprochilinae.** *Kawanaphila* Rentz. *Zaprochilus* Caudell.

*Second hypothetical morphological correlation*

Males with curved or angulated cerci resembling hooks, or cerci with secondary components such as inner spines, usually accompanied by sclerite(s) TS. The sclerite(s) TS can be two longitudinal sclerotized bars, an entire TS with a bifurcated apex or a transversal bridge with two free projections. Such combination occurs in:

**Conocephalinae. Agraeciini.** *Agraecia*, all species. *Anelytra* Redtenbacher: *A. compressa* Shi & Qiu; *A. jinghonga* Shi & Qiu; *A. spinia* Shi & Qiu. *Anthracites nakanaiensis* Naskrecki & Rentz; *Dectinomima* Caudell, all species. *Eschatoceras* sp. (Figs 10–11, 97). *Gonatacanthus gahavisuka* Naskrecki & Rentz; *Ingrischia macrocephala* Naskrecki & Rentz. *Microsalomona* Karny, all species. *Pandanagraecia* Naskrecki & Rentz, all species. *Philmontis* Willemse: *P. lobatus* Naskrecki & Rentz; *P. nigrofasciatus* Willemse; *Pseudonicsara fascifrons* Naskrecki & Rentz; *Salomona richardsi* Naskrecki & Rentz; *Scytocera smaragdifrons* Naskrecki & Rentz; *Spinisternum castaneipictus* Willemse; *Sphyrometopa* Carl, all species. *Trichophallus tricuspis* Naskrecki & Rentz; *Uchuca* Giglio-Tos, possibly all species. *U. ferreirai* (Figs 12–13, 98). **Conocephalini.** *Conocephalus*, possibly all species. *Conocephalus* sp.1 (Figs 6–9, 99–101). **Copiphorini.** *Borinquenula* Walker & Gurney, all species. *Neoconocephalus* Karny, possibly all species, *Neoconocephalus* spp. (Figs 20–21, 103–104). *Panacanthus* Walker, possibly all species.



**FIGURES 97–128.** Drawing silhouettes of cerci of examined male specimens (Figs 6–71). See Appendix 2 for suprageneric classification. 97. *Eschatoceras* sp. 98. *Uchuca ferreirai* (Piza). 99. *Conocephalus* sp.1. 100. *Conocephalus* sp.2. 101. *Conocephalus* sp.3. 102. *Eriolus* sp. 103. *Neoconocephalus* sp.1. 104. *Neoconocephalus* sp.2. 105. *Cerberodon viridis* Perty. 106. Gen.1 sp. 107. Gen.2 sp. 108. *Phlugis ocraceovittata* Piza. 109. *Machima* sp. 110. *Itarissa* sp. 111. *Anaulacomera* sp. 112. Gen.3 sp. 113. Gen.4 sp. 114. Gen.5 sp. 115. Gen.6 sp. 116. *Schedocentrus* sp. 117. *Gnathoclitia vorax* (Stoll). 118. Gen.7 sp. 119. Gen.8 sp. 120. *Leptotettix crassicerci* Piza. 121. *Leptotettix* sp. 122. *Acanthodis* sp. 123. Gen.9 sp., 124. *Gongrocnemis* sp. 125. *Spinapecta alieniphaga* Naskrecki & Lopes-Andrade. 126. *Porphyromma* sp. 127. *Pterochroza ocellata* (Linnaeus). 128. *Teleutias* sp. Scale bars: 1.00 mm.

**Bradyporinae. Ehippigerini.** *Ehippiger ehippiger* (Fiebig). *Bradyporus* Charpentier, possibly all species.

**Listroscolidinae. Terpandrini.** *Neobarrettia* Rehn: *N. hakippah* Cohn; *N. sinaloae* (Rehn & Hebard). **Incertae sedis.** *C. viridis* (Figs 22–25, 105). *Listroscolis* Serville all species. *Monocerophora* Walker, possibly all species. Gen.1 sp. (Figs 26–27, 106).

**Meconematinae. Meconematini.** *Decma* Gorochov: *D. elefani* Gorochov; *D. thai* Gorochov. *Kuzicus* Gorochov, apparently all species. *Pseudokuzicus tamdao* Gorochov, in which the single **ti** is bifurcated at apex. *Teratura darevskyi* Gorochov, with cerci similar to those of *Xiphidiopsis* but bearing sclerites **TS**.

**Phaneropterinae. Ducetiini.** *Abaxisotima multipunctata* (Kang & Yang). *Paraducetia paracruciata* Gorochov & Kang. **Incertae sedis.** *Brinckiella* Chopard, *Paraxantia* Liu & Kang. *Stylomolpa angustipennis* Karny. **Mirollini.** *Mirollia rostellum* Gorochov. **Odonturini.** *Cohnia andeana* (Hebard). **Viadanini.** *Anaulacomera* sp. (Figs 34–37, 111).

**Tettigoniinae. Drymadusini.** *Atlanticus testaceus* (Scudder). *Delodusa humeralis* (Uvarov); *Exodrymadusa inornata* (Uvarov), a monospecific genus. *Leptodusa harzi* (Karabag). *Mixodusa* Stolyarov, possibly all species. *Novadrymadusa* Dermirsoy, Salman & Sevgili, two species included in the genus. *Phytodrymadusa* Ramme, possibly all species. *Scotodrymadusa philbyi* (Uvarov). **Glyphonotini.** *Cyrtophyllicus chlorum* Hebard. **Nedubini.** *Aglaothorax* Caudell: *A. diminutiva* (Rentz & Birchim *A. morsei* (Caudell). *Neduba* Walker: *N. castanea* (Scudder); *N. macneilli* Rentz & Birchim; *N. sierranus* (Rehn & Hebard). **Platycleidini.** *Anterastes* Brunner von Wattenwyl, all species. *Clinopleura* Scudder, all species. *Decorana buxtoni* (Uvarov). *Decticita* Hebard, all species. *Eremopedes* Scudder: *E. cryptoptera* (Rehn & Hebard); *E. scudderi* Cockerell. *Idiostatus hermannii* (Thomas); *Inyodectes pallidus* Rentz & Birchim; *Pediodytes nigromarginatus* (Caudell); *Steiroxys strepens* Fulton. **Pholidopterini.** *Eupholidoptera* Maran. *Parapholidoptera* Maran, all species. **Tettigoniini.** *Ateloplus notatus* Scudder. *Capnobotes* Scudder: *C. arizonensis* (Rehn); *C. occidentalis* (Thomas); *C. attenuatus* Rentz & Birchim; *C. unodontus* Rentz & Birchim; *C. granti* Rentz & Birchim. *Idionotus* Scudder, possibly all species.

**Pseudophyllinae. Cocconotini.** *Schedocentrus* sp. (Figs 48–49, 116). **Teleutiini.** *Teleutias*: *T. fasciatus* Brunner von Wattenwyl; *T. akraonos* Montealegre-Z. & Morris.

#### *Third hypothetical morphological correlation*

Simple cerci and a single sclerite **TS** or a single enlarged process **ti**. In most cases, the tip of **TS** or **ti** remains exposed beyond the abdominal apex. Such combination occurs in:

**Phaneropterinae. Holochlorini.** *Stictophaula* Hebard: *S. armata* Ingrisch; *S. spinosolaminata* (Brunner von Wattenwyl). **Incertae sedis.** *Tamdaopteron major* Gorochov, with the tip of cerci curved outward, apparently not adapted for lateral grasping of females.

**Pseudophyllinae. Eucocconotini.** *Panoploscelis specularis* Beier. **Leptotettigini.** *L. crassicerci* (Figs 56–57, 120); *Leptotettix* sp. (Figs 44–47, 121); Gen.8 sp. (Figs 54–55, 119). **Pleminiini.** Gen.9 sp. (Figs 60–61, 123); *Gongrocnemis* sp. (Figs 62–63, 124).

#### *Variations to the proposed hypothetical morphological correlations*

**Copiphorini.** *Eriolus* sp. with two sclerites **TS** in an inverted position and simple cerci (Figs 19, 102). **Meconematinae.** *P. ocraceovittata*, with inverted sclerites **TS** but cerci simple (Fig. 108). **Phaneropterinae. Dysoniini.** *Machima* sp. (Fig. 109), which has almost entirely membranous phallus in combination with cerci that are apparently adapted to hook. **Incertae sedis.** Gen.6 sp. with membranous phallus, excepting for the sclerotization on lobe **dl** (Fig. 82) and cerci slightly curved (Fig. 115). **Pseudophyllinae. Eucocconotini.** *G. vorax* (Figs 50–51, 117), which bears two enlarged sclerites **TS**, but cerci in *Gnathoclita* species are not adapted for grasping (De Souza *et al.* 2011). The **TS** in this species are very different from those of other species bearing paired sclerites **TS**, because their apices exceed the length of the phallus. **Leptotettigini.** Gen.7 sp. (Figs 52–53, 118),

without sclerites **TS** but with curved cerci. **Pterochrozini**. In *Porphyromma* sp. the phallus bears a sclerite **TS** with divided apex (Fig. 66), not projected over the lobe **dl**, and cerci are not adapted for grasping (Fig. 126). *Porphyromma ocellata* and *P. ocellata* have simple cerci as in most Pterochrozini (Figs 126, 127), and the phallus bears spiny microstructures throughout the surface of the lobe **dl** (Figs 68–69).

## Discussion

**On the interpretations of the phallus and terminology.** From the first interpretations of the male genitalia's morphology of Tettigoniidae until now, the word “genitalia” was used with different means in descriptions. The term “genitalia” has been used to describe the last abdominal tergite (e.g. Zeuner 1940), or the subgenital plate and cerci together (e.g. Hemp 2001; Montealegre-Z. *et al.* 2011). Other authors distinguished between an “external” and an “internal” genitalia. In those cases, the external genitalia includes the tenth abdominal tergite, epiproct, paraprocts, subgenital plate and cerci (e.g. Ingrisch 1998; Nickle 1983), and the internal genitalia, also called “phallus” (e.g. Ingrisch 1998) or “penis” (Walker 1922), refers to the membranes and sclerotized components around the gonopore. The word “terminalia” is used as a synonym of abdominal apex and postabdomen, and comprises all the abovementioned structures (e.g. Liu & Kang 2009; Montealegre-Z. & Morris 1999). However, most of the descriptions that include characteristics of the “genitalia” unusually include description of the phallus.

Morphological interpretations of the phallus in Tettigoniidae proposed by later authors (Chopard 1920; Walker 1922; Snodgrass 1937; Ander 1956) are essentially quite similar. Differences are on number of lobes and folds, names and abbreviations (Figs 25, Table 1). The interpretations can be seen as partially complementary, as each author took into account components not observed by others. They are all, indeed, gross interpretations of the phallus' components, and usually are based on just one or a few species. For instance, although Snodgrass's interpretation was very detailed (e.g. for *Conocephalus* sp.), it was not taken into account the association of the sclerite(s) **VS** to **TS** (Figs 6–9) and the existence of all folds of membranes described here.

Despite being possible to establish the equivalence between the various names given to components (Table 1), some terms shall no longer be used in descriptions of phallus of katydid, to avoid confusion and misinterpretations. The term “paramere” used by Walker (1922) in reference to the named here sclerite(s) **TS** is incorrect. The parameres in insects are “the outer pair of phallomeres that develop into male copulatory appendages; sometimes synonymized with gonapophyses” (Maggenti *et al.* 2005). The word “epiphallus” has been used with different meanings. For instance, Chopard (1920) used it as a synonym of titillator (**ti**+**TS**?), and Desutter-Grandcolas (2003) identified it as the whole overdeveloped membranous portion of the phallus. The titillator (e.g. **ti**+**TS**, or **ti**+**TS**+**VS**) has been also called “concealed sclerotized genitalia complex” and “sclerite of the phallus” (Liu & Kang 2009), or “median sclerite of the genitalia” (Gorochov 2004). The term “titillators” is widely used in the literature since Chopard (1920), and we also prefer this term over others, although we use it in the singular, referring to the complex as a whole (and not referring exclusively to its sclerotized and exposed components, the sclerite(s) **TS**). Titillator is referred here to the complex of process(es) **ti** and sclerotized components developed on the lobe **dl**, sometimes with single or paired sclerite(s) **TS** and, in a few cases, with sclerites **VS** fused to **TS**. Although titillator is a term that denotes functionality and not position or form, the comparison of its components, as explicated here, can allow the proposition of homologies. A few terms for the different parts of the sclerite(s) **TS** were proposed by Çiplak *et al.* (2009, see figs 4A–4B of them), but this terminology shall be expanded to apply to the various configurations of **TS** shown by us. As verified in literature, there was no terminological consensus for the names and abbreviations used for components of the phallus. Unification of the terminology is a first step to facilitating the proposition of homologies and hypotheses on the evolution of the phallus in Tettigoniidae. Despite recent attempts to establish homologies at the suborder level (Desutter-Grandcolas 2003), even for Tettigoniidae the homologies are not fully understood.

**The phallus as a feature used in taxonomic and phylogenetic studies.** Despite the phallus in insects being characterized by a rapid evolution with great phylogenetic signal (Eberhard 2010; Song 2009), the phallus of Tettigoniidae was included in few phylogenetic studies (Rentz & Colless 1990; Çiplak 2000; Çiplak 2004; Montealegre-Z. & Morris 2004). It is a fact that the phallus in Tettigoniidae varies between species, as confirmed here. However, most previous literature data have clearly demonstrated such variation only for the sclerite(s) **TS** (e.g. Appendix 1), and few detailed information on the membranous portions and cavities is available. Some

features of the sclerite(s) **TS** are shared by all or part of the species of a genus, and details of these variations can be used as characters (Çiplak 2000). However it shall be noted that the number of spines or microstructures on the sclerites(s) **TS** and around it may be asymmetric (Çiplak *et al.* 2009). Although the variety of microstructures on the entire structure are remarkable, few descriptions include details of them and usually only for sclerite(s) **TS** (*e.g.* Liu & Kang 2009). All external and internal components of the phallus in katydids vary, enabling their use as diagnostic features at specific and supraspecific levels, being also informative for phylogenetic studies.

A simple change in position or development of one component can modify the shape and position of others. Despite these apparently linked morphological changes, it is known that the phallic components, with different functions, can evolve independently from each other (Huber *et al.* 2005; Song & Wenzel 2008). Membranous lobes are usually not shown or described, and most available figures in literature show only dorsal and lateral views of part of the phallus. For example, the number of folds of the lobe **vl** can be used as a diagnostic feature. A modification of the lobe **vl** from being two folds **up.vl** plus two folds **lw.vl**, or a **vl** with two **up.vl** and only one **lw.vl** would be a drastic evolutionary change. Components located at the proximal portion of the phallus, which are not traditionally described, can be used as diagnostic features or phylogenetic characters, as the cases of the apodemes **ap**, as well as the vesicles **ejv**, and also the position of the duct **ejd**. Among the evaluated published figures of phalli of katydids, none include the most inner proximal components, except for the ones in Márquez (1963: figs 34–36), which shows the vesicles **ejv**. And photographs of the entire phallus, for detailing sclerotized components, are included in Ingrisch (2009). The fold **fdl** can vary in shape and depth, which would be important during copula because it would have different capacities of outward expansion of sclerites(s) **TS** or process(es) **ti** or of sclerite(s) **VS**; the **fdl** shape could influence on the contact with the female genital chamber, what would make this a component that changes rapidly, and provide useful information on the evolution of the phallus.

Here we expose a subsample of the morphological diversity of katydids' phalli, mostly observable only after being dissected. It would be almost impossible to perceive differences in the position of the components without extractions and staining of phalli. Staining and stacking photography techniques were applied here to improve image quality. However, the configuration of the phallus makes difficult the recognition of each component, even after staining. The use of staining and photographs is important for evidencing outline of the phallus and to distinguish between sclerotized and membranous components, but it is also essential to make drawings for showing details and interpretations. Other techniques have been used for documenting morphology of the phallus, such as confocal laser scanning microscopy and 3-D reconstruction (Klaus *et al.* 2003), X-ray synchrotron microtomography (Perreau & Tafforeau 2011) and fluorescence from different stains (Lee *et al.* 2009), among others. But staining and photographing is one of the easiest and cheapest. In the near future, the treatment of the phallus with lactic acid solution shall be experimented; this technique seems to maintain the natural inflated shape of membranous components (Scudder & Schwartz 2012), contrary to the caustic effect of the KOH as used here. We consider that it is essential the standardization of a minimum method to provide information on katydids' phalli, with images and drawings that allow in a future the proposition of hypotheses on the evolution of katydids that also includes data on phallic components.

**Sclerites of the phallus and hypotheses on their evolution and function.** Descriptions of the phallus of katydids usually mention a pair of eversible sclerites, the “titillators” (see above), notably in the most recent study on phalli of Ensifera (Desutter-Grandcolas 2003). However, the characterization of “titillators” uniquely as a paired structure, as used by previous authors, is incorrect, because in several cases, as demonstrated here, there can be only one sclerite **TS** (Figs 54–56, 62) or the sclerite **TS** can be at an intermediate state of division (or at an intermediate state of fusion, but we cannot take conclusions on the polarity of this character at the moment). Moreover, the phallus can be devoid of sclerotized structures. Here we suggest that variable conspicuous sclerotized structures, called sclerites **TS**, are formed from the middle of the lobe **dl**, and the shape, number and size of these sclerotized structures depend on the form, extension and degree of cuticle sclerotization. The potential formation of microstructures and increasing sclerotization of the cuticle of lobe **dl** can be common to most, if not all, Tettigoniidae, and that can be an ancestral condition. We point out issues to be evaluated in futures studies on this matter: (i) Clarify whether the titillator evolved once among katydids, or if its development happened through independent events. If there was a single event, then there were losses in independent lineages. We consider that our observations (see the contrasted evolutionary scenarios, Figs 95–96) sustain that bearing a titillator can be an ancestral condition, possibly an apomorphy of the family. For complex structures, multiple losses may explain the observed distribution of the character in a group more plausibly than multiple acquisitions (Béthoux 2012).

However, in the case of the titillator, more data is necessary to consolidate our proposition; (ii) Clarify whether or not the distinct components of the titillator, as we described here, are homologous; (iii) What are the possible selective pressures for single or paired sclerite(s) TS?; (iv) Are there differences in copula between species with and without titillator (e.g. Vahed *et al.* 2011)?; (v) Is the function performed by paired sclerites TS the same as those made by single TS? Remarkable microstructures on sclerites(s) TS were observed, and we do not know their functions during copula. The variety of shapes of sclerites(s) TS is so extraordinary that we cannot consider a priori they all have the same function, or even the same origin. This idea about the uncertainty of the origin of sclerotized structures on the phallus, and the possible homologies of titillator at the subfamily level were also discussed by Ingrish (1995). Further, the existence of additional sclerotized components, the sclerite(s) VS, which can affect the morphology and function of the titillator, is another matter to be evaluated. The sclerite(s) VS can alter the functionality and provide mechanical support to sclerites(s) TS, and also can cause mechanical pressure on the duct **ejd**. The sclerites(s) VS can also be fused to TS, forming a single component. It can even hypothetically play the role of a titillator, thus it is important to identify whether exposed sclerotized components of the phallus are part of a true titillator (developed on the lobe **dl**) or are sclerites(s) VS.

**Morphology of structures of the postabdomen and possible relationships to mating behaviour.** Mating behaviour of some katydid species have been recorded in detail (De souza *et al.* 2011; Duijm *et al.* 1983; Helversen & Helversen 1991; Kaltenbach 1990; Morris 1980; Petit *et al.* 2007; Vahed & Carron 2008). The primary interest was on the variation of the spermatophore in relation to the mating behaviour characteristics, e.g. the duration of the copula (Vahed 1997; Vahed 2007; Vahed *et al.* 2011), or on characteristics of the song influencing female choice (De Souza *et al.* 2011; Gwynne 1982). But only for few species, such as *Ephippiger* spp. (Duijm *et al.* 1983), *Metaplastes ornatus* (Ramme) (Helversen & Helversen 1991) and *Saga* spp. (Kaltenbach 1990) there are available information describing how structures of the postabdomen work during copula. Males of *M. ornatus* carry out mechanical sperm removal, using the keel of the subgenital plate to remove sperm of previous copulations, which demonstrates the importance of external structures for sperm competition (Helversen & Helversen 1991). Males can grasp females with their cerci during copula (Lehmann & Lehmann 2008; Rentz 1972), and there can even be a morphological relationship between shape of male cerci and pockets of the female subgenital plate, allowing a mechanical coupling during copula (Rentz 1972). Grasping by male cerci can control the duration of copula prior to spermatophore transfer (Vahed 1997; Vahed *et al.* 2011), and males can even force females to copulate by using their cerci (Vahed & Carron 2008). Specific adaptations for hooking with cerci can evolve, but shape of cerci and their performance and function during copula have not been documented for most described species. Grasping can be performed by several external structures with species-specific morphology (Eberhard 1985, 2004). We assume that cerci presumably adapted for grasping are angulated or bear spines at the inner portion or both, and species with paired sclerites TS usually bear cerci adapted for grasping. In the contrary way, not all species with cerci adapted for grasping bear TS. The shape of cerci and sclerites(s) TS together may vary between species of a genus (e.g. Appendix 1) and most notably between species of different genera. Examples of transition of this morphological correlation can be found inside higher taxonomical ranks. In Ducitiini, for instance, *Ducetia* Stål species bear simple cerci and no sclerite TS, and in *Abaxisotima* spp. the cerci are curved with pointed tips and the phallus bears TS (Gorochov & Kang 2002). About the functionality of sclerites(s) TS and cerci, it is known that TS move rhythmically within the female's genital chamber (e.g. Boldyrev 1928; Duijm *et al.* 1983; Gerhardt 1913, 1914; Hartley & Warne 1984; Vahed 1997). These movements, together with a long copula, would require mechanical support by cerci that are adapted for grasping. Therefore, sclerites(s) TS would not function as anchors. It was already proposed that sclerite(s) TS were for grasping (Edvardsson & Canal 2006; Vahed *et al.* 2011). But if the main function of cerci were to hook female, the titillator and its components, including sclerite(s) TS, would have other functions, as female stimulation. In species with cerci not adapted for grasping, others structures may perform that function. For instance, some species bear specialized paraprocts with hooks or teeth, so they can replace cerci as the grasping apparatus during copula (Ander 1956), or grasping together with the cerci (e.g. *Agraecia* spp. and South American Listrosclidinae, pers. obs.) or, in the extreme case of *S. natoliae*, with the mandibles. In species devoid of titillator, cerci can bear large processes, or there are projections on the last tergite, which can function as stimulatory structures (e.g. species of *Xiphidiopsis* and *Xizicus* Gorochov; Ingrisch 1998).

Finally, we propose two explanations to the morphological correlations, and possible functional relationships, between cerci and titillator. First, species with similar structures on the postabdomen can perform similar

behaviours during copula. Similar cerci and titillator occurring in species that belong to unrelated genera would be the result of convergence due to similar copulatory behaviour. In such cases, there could be associations between morphological complexity and mating patterns across species (Hosken & Stockley 2004; Eberhard 2010). Recent data reinforcing the existence of morphological correlations and convergent functionality show that copula is much longer in species with titillator than in those without, and species with more complex titillator transfer larger spermatophores and more rapidly than those with simpler titillator (Vahed *et al.* 2011). It could also be expected that species bearing cerci for grasping would have prolonged copulation (Alexander & Otte 1967; Vahed 1997). And a correlation between prolonged copulation and small size of spermatophylax has been detected, supporting the hypothesis that large spermatophylax functions to prevent females from eating sperm (Vahed 1997). In Tettigoniidae, the presence of a spermatophylax seems to be an ancestral condition (Gwynne 1990, 1995). Therefore, the spermatophylax would have been secondarily lost in species with prolonged copulation (possible species with cerci adapted for grasping) (Vahed 1997). The second explanation is that more than one mechanism of sexual selection is acting on the postabdomen in Tettigoniidae (Arnqvst 1997; Arnqvist & Nilsson 2000; Eberhard 2006; Hosken & Stockley 2004), because the behaviour of species can be more complex and diversified than the morphology of the phallus and other contact courtship devices (Eberhard 2011). In this case, the phallus can act as a copula courtship device to ensure female acceptance of the ejaculate (Eberhard 1985), and certain characteristics of the titillator would be preferred by females, leading to cryptic selection (Hosken & Stockley 2004). On the other hand, as the titillator constitutes an intromittent organ, and in some species it bears spiny microstructures or projections, certain types of titillator could allow sperm competition by sperm removal behaviour, similar to the sperm removal performed by the subgenital plate in *M. ornatus* (Helversen & Helversen 1991). Some of the extraordinary spiny structures of the titillator could also damage the membranous genitalia of females, decreasing their reproductive success by impeding successful subsequent copulations. On the grasping function of cerci, it is known that they can sink into the female cuticle and leave visible wounds after mating (Chopard 1951). In these cases, the main mechanism would be sexual conflict (Çiplak *et al.* 2009; Hosken & Stockley 2004).

## Conclusions

The phallus in Tettigoniidae, as in other insects, is a structure that undergoes rapid evolutionary changes and, therefore, is quite informative for understanding the evolution of the family. Its morphology is understood only when the entire structure is dissected, revealing the inner components, as was carried out here. The use of simple techniques, as staining and photographing, facilitates the display of components. Standardization of terminology for the description of the postabdomen, especially for the phallus and its components, is the first step to allow the formulation of homologies and hypotheses on its evolution. The observed great morphological variation of the phallus can be explained by sexual selection. But evolutionary pathways will be understood only after acquiring a considerable amount of new data on the morphology of components of the phallus and their mechanical function during copula.

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**APPENDIX 1.** List of the 90 taxonomic papers on Tettigoniidae evaluated by us. We indicate whether a paper provides information on the phallus (Yes), does not include any information (No) or information on the phallus are provided for part of the studied species (Part). The list is organized in alphabetical order following the name of authors.

Author	Year	Title	Information on the phallus
Bader, A.K. & Massa, B.	2001	Tettigoniidae (Orthoptera) from Jordan with description of new species and redescription of less known species. <i>Journal of Orthoptera Research</i> , 10, 25–37.	Yes
Bolívar, I. & Bolívar, C.	1942	Estudio de dos nuevas <i>Pterophylla</i> mexicanas (Orthoptera: Tettigoniidae: Pseudophyllinae). <i>Revista de la Sociedad Mexicana de Historia Natural</i> , 3, 87–101.	No
Bowen-Jones, E.	1994	A description of <i>Arachnoscelis feroxnotha</i> sp. nov. (Tettigoniidae: Listroselidinae) from southwest Costa Rica. <i>Journal of Orthoptera Research</i> , 2, 47–48.	No
Bowen-Jones, E.	2000	Description of two new species of Tettigoniidae from Corcovado National Park, Costa Rica: <i>Rossophyllum maculosum</i> Phaneropterinae and <i>Idiarthron cerosum</i> Pseudophyllinae. <i>Journal of Orthoptera Research</i> , 9, 21–25.	No
Braun, H.	2011	A brief revision of brachypterous Phaneropterinae of the tropical Andes (Orthoptera, Tettigoniidae, Odonturini). <i>Zootaxa</i> , 2991, 35–43.	No
Braun, H., Chamorro-Rengifo, J. & Morris, G.K.	2009	Curious katydids from the Andes of Colombia and Ecuador: three new species, a new genus and acoustic baffles. <i>Journal of Orthoptera Research</i> , 18, 225–235.	No
Buzzetti, F.M.	2008	A new species of <i>Incanotus</i> Beier from Ecuador (Orthoptera: Tettigoniidae: Pseudophyllinae). <i>Entomotropica</i> , 23, 37–41.	No
Buzzetti, F.M., Fontana, P. & Carotti, G.	2010	Bioacoustic of Bioacoustic of <i>Cohnia andeana</i> (Hebard, 1924) comb. nov. (Insecta: Orthoptera: Tettigoniidae). <i>Zootaxa</i> , 2661, 59–68.	Yes
Cadena-Castañeda, O. & Braun, H.	2011	A new brachypterous genus of Platyphyllini (Orthoptera, Tettigoniidae, Pseudophyllinae) from Colombia. <i>Zootaxa</i> , 2763, 34–38.	No
Çiplak, B.	2000	Systematics and phylogeny of <i>Parapholidoptera</i> (Orthoptera: Tettigoniidae: Tettigoniinae). <i>Systematic Entomology</i> , 25, 411–436.	Yes
Çiplak, B.	2004	Systematics, phylogeny and biogeography of <i>Anerastes</i> (Orthoptera, Tettigoniidae, Tettigoniinae): evolution within a refugium. <i>Zoologica Scripta</i> , 33, 19–44.	Yes
Çiplak, B., Heller, K.-G. & Willemse, F.M.H.	2009	Review of the genus Review of the genus <i>Eupholidoptera</i> (Orthoptera, Tettigoniidae): different genitalia, uniform song. <i>Zootaxa</i> , 2156, 1–77.	Yes
Cohn, T.	1965	The arid-land katydids of the N. American genus <i>Neobarrettia</i> : their systematics and a reconstruction of their history. <i>Miscellaneous Publications Museum of Zoology University of Michigan</i> , 126, 1–179.	Part
Da Costa Lima, A.M. & Guitton, N.	1960	Gênero <i>Dysonia</i> (Orth. Tettig. Phaneropteridae) Parte I. <i>Anais da Academia Brasileira de Ciências</i> , 32, 399–418.	No
Da Costa Lima, A.M. & Guitton, N.	1961	Gênero <i>Dysonia</i> (Orth. Tettig. Phaneropteridae) Parte II Conclusão. <i>Anais da Academia Brasileira de Ciências</i> , 33, 69–89.	No
Demirsoy, A., Salman, S. & Sevgili, H.	2002	<i>Novadrymadusa</i> , a new genus of bushcricket with a new species and notes on related genera (Orthoptera: Tettigoniidae). <i>Journal of Orthoptera Research</i> , 11, 175–183.	Yes

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APPENDIX 1. (Continued)

Author	Year	Title	Information on the phallus
Dias, P., Rafael, J.A. & Naskrecki, P.	2012	A Taxonomic Revision of the Neotropical Genus <i>Aegimia</i> Stål, 1874 (Orthoptera, Tettigoniidae, Phaneropterinae). <i>Journal of Orthoptera Research</i> , 21, 109–132.	Part
Emsley, M.G.	1970	A revision of the steirodontine katydids (Orthoptera: Tettigoniidae: Phaneropterinae: Steirodontini). <i>Proceedings of the Academy of Natural Sciences</i> , Philadelphia, 122, 125–248.	No
Glenn, Jr.	1991	A systematic revision of <i>Enyaliopsis</i> Karsh 1887 (Orthoptera, Tettigoniidae, Hetrodinae). <i>Transactions of the American Entomological Society</i> , 117, 67–102.	Yes
Gorochov, A.V.	1998	New and little known Meconematinae of the tribes Meconematini and Phlugidini (Orthoptera, Tettigoniidae). <i>Zoosystematica Rossica</i> , 7, 101–131.	Part
Gorochov, A.V.	2002	A new subgenus and two new species of <i>Xizicus</i> (Orthoptera: Tettigoniidae: Meconematinae). <i>Zoosystematica Rossica</i> 10, 256.	No
Gorochov, A.V.	2002	A new subgenus of <i>Leptotera</i> for a new species from Sumatra (Orthoptera: Tettigoniidae: Meconematinae). <i>Zoosystematica Rossica</i> , 10, 280.	Yes
Gorochov, A.V.	2003	A new species of <i>Prohimerta</i> from Vietnam (Orthoptera: Tettigoniidae: Phaneropterinae). <i>Zoosystematica Rossica</i> , 11, 304.	No
Gorochov, A.V.	2003	A new species and a new subspecies of <i>Stictophaula</i> from Java (Orthoptera: Tettigoniidae: Phaneropterinae). <i>Zoosystematica Rossica</i> , 11, 372.	Yes
Gorochov, A.V.	2003	A new species of <i>Mirollia</i> Stål from Philippines (Orthoptera: Tettigoniidae: Phaneropterinae). <i>Zoosystematica Rossica</i> , 12, 28.	Yes
Gorochov, A.V.	2004	A new subgenus and two new species of <i>Decma</i> (Orthoptera: Tettigoniidae: Meconematinae). <i>Zoosystematica Rossica</i> , 13, 28.	Yes
Gorochov, A.V.	2005	New species of the tribe Phisidini from Indonesia (Orthoptera: Tettigoniidae: Meconematinae). <i>Zoosystematica Rossica</i> , 13, 243.	No
Gorochov, A.V.	2005	New taxa of Tettigoniidae (Orthoptera) from Vietnam. <i>Far Eastern Entomologist</i> , 148, 1–12.	Yes
Gorochov, A.V.	2006	A new katydid genus of unclear systematic position from Ecuador (Orthoptera: Tettigoniidae). <i>Zoosystematica Rossica</i> , 15, 47–50.	Yes
Gorochov, A.V.	2007	Notes on taxonomy of the subfamily Hexacentrinae with descriptions of some taxa (Orthoptera: Tettigoniidae). <i>Zoosystematica Rossica</i> , 16, 209–214.	Part
Gorochov, A.V. & Kang, L.E.	2002	Review of the Chinese species of Ducetiini (Orthoptera: Tettigoniidae: Phaneropterinae). <i>Insect Systematics and Evolution</i> , 33, 337–360.	Part
Gorochov, A.V. & Llorente, V.	2004	Remarks on the genus <i>Megalotheca</i> and new species of <i>Conocephalus</i> (Orthoptera, Tettigoniidae). <i>Memorie della Società Entomologica Italiana</i> , 82, 397–402.	Yes
Gurney, A.B.	1950[1951]	On <i>Dicranostomus</i> a remarkable Peruvian genus of katydids; and notes on other insects having elongate mandibles (Orthoptera Tettigoniidae). <i>Annals of the Entomological Society of America</i> , 43, 546–554.	No
Gurney, A.B. & Liebermann, J.	1975	A new species of shield-backed katydid from Cerro Aconcagua, Argentina, with notes on other species and their habitats (Orthoptera, Tettigoniidae, Decticinae). <i>Journal of the Washington Academy of Sciences</i> , 65, 102–107.	No

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APPENDIX 1. (Continued)

Author	Year	Title	Information on the phallus
Hemp, C.	2001	<i>Aerotegmina</i> , a new genus of African Listrosclidinae (Orthoptera: Tettigoniidae, Listrosclidinae, Hexacentrini). <i>Journal of Orthoptera Research</i> , 10, 121–128.	No
Hemp, C.	2001	Two new species of <i>Amytta</i> Karsch (Orthoptera: Meconematinae) from East Africa (Tanzania, Mt. Kilimanjaro). <i>Journal of Orthoptera Research</i> , 10, 129–134.	No
Hemp, C., Heller, K-G., Kehl, S., Warchalowska-Śliwa, E., Wägele, W.J. & Hemp, A.	2010	The Phlesirtes complex (Orthoptera, Tettigoniidae, Conocephalinae, Conocephalini) reviewed: integrating morphological, molecular, chromosomal and bioacoustic data. <i>Systematic Entomology</i> , 35, 554–580.	No
Hugel, S.	2009	Un nouvel <i>Agraecia</i> de Martinique et présence de <i>Agraecia viridipennis</i> en Guyane française. <i>Bulletin de la Société Entomologique de France</i> , 114, 129–140.	Yes
Ingrisch, S.	1995	Revision of the Lipotactinae, a new subfamily of Tettigonioidae (Ensifera). <i>Entomologica Scandinavica</i> , 26, 273–320.	Yes
Ingrisch, S.	1998	Monograph of the Oriental Agraeciini (Insecta, Ensifera, Tettigoniidae): Taxonomic revision, phylogeny, biogeography, stridulation, and development. <i>Courier Forschungsinstitut Senckenberg</i> , 206, 1–391.	Yes
Ingrisch, S.	2009	Revision of the genus <i>Pseudonicsara</i> Karny, 1912 (Orthoptera: Tettigoniidae: Conocephalinae: Agraeciini) - Revision of the Indo-Australian Conocephalinae, part 2. <i>Zootaxa</i> , 2185, 1–122.	Yes
Ito, G. & Mohamed, M.	2004	Description of a new phaneropterine species, <i>Stylomolpa montana</i> (Orthoptera: Tettigoniidae) from Sabah, Borneo. <i>Journal of Orthoptera Research</i> , 13, 19–20.	Yes
Kastner, A.	1932	Die Meconeminae des Stettiner Museums (Orthoptera). <i>Stettiner Entomologische Zeitung</i> , 93, 163–182.	No
Liu, C-X. & Kang, L.	2009	A new genus, <i>Paraxantia</i> gen. nov., with descriptions of four new species (Orthoptera: Tettigoniidae: Phaneropterinae) from China. <i>Zootaxa</i> , 2031, 36–52.	Yes
Marquez, C.	1958[1957]	Tres especies nuevas de phaneropterinae de Mexico (Orthoptera, Tettigoniidae). <i>Anales del Instituto de Biología</i> , Universidad Nacional Autónoma de México, Serie Zoología, 28, 289–300.	No
Marquez, C.	1963	Estudio morfológico de tres especies de <i>Stilpnochlora</i> (Orthoptera, Tettigoniidae). <i>Anales del Instituto de Biología</i> , Universidad Nacional Autónoma de México, Serie Zoología, 34, 275–283.	Yes
Montealegre-Z., F., Guerra, P.A. & Morris, G.K.	2003	<i>Panoploscelis specularis</i> (Orthoptera: Tettigoniidae: Pseudophyllinae): extraordinary female sound generator, male description, male protest and calling signals. <i>Journal of Orthoptera Research</i> , 12, 173–181.	Yes
Montealegre-Z., F. & Morris, G.K.	1999	Songs and systematics of some tettigoniidae from Colombia and Ecuador, part I. Pseudophyllinae (Orthoptera). <i>Journal of Orthoptera Research</i> , 8, 163–236.	Part
Montealegre-Z., F. & Morris, G.K.	2003	<i>Uchuca</i> Giglio-Tos, <i>Dectinomima</i> Caudell and their Allies (Orthoptera: Tettigoniidae: Conocephalinae). <i>Transactions of the American Entomological Society</i> , 129, 503–537.	Yes
Montealegre-Z., F. & Morris, G.K.	2004	The spiny devil katydids, <i>Panacanthus</i> Walker (Orthoptera: Tettigoniidae): an evolutionary study of acoustic behaviour and morphological traits. <i>Systematic Entomology</i> , 29, 21–57.	Yes

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## APPENDIX 1. (Continued)

Author	Year	Title	Information on the phallus
Montealegre-Z., F., Morris, G.K., Sarria-S.F. & Mason, A.C.	2011	Quality calls: phylogeny and biogeography of a new genus of neotropical katydid (Orthoptera: Tettigoniidae) with ultra pure-tone ultrasonics. <i>Systematics and Biodiversity</i> , 9, 77–94.	No
Montealegre-Z., F. & Potles, M.	2010	Resonant sound production in <i>Copiphora gorgonensis</i> (Tettigoniidae: Copiphorini), an endemic species from Parque Nacional Natural Gorgona, Colombia. <i>Journal of Orthoptera Research</i> , 19, 347–355.	No
Morris, G. & Beier, M.	1982	Song structure and description of some Costa Rican katydids (Orthoptera: Tettigoniidae). <i>Transactions of the American Entomological Society</i> , 108, 287–314.	No
Morris, G.K., Klimas, D.E. & Nickle, D.A.	1989	Acoustic Signals and Systematics of False-Leaf Katydid from Ecuador (Orthoptera, Tettigoniidae, Pseudophyllinae). <i>Transactions of the American Entomological Society</i> , 114, 215–263.	No
Naskrecki, P.	2003	A new species of <i>Pseudosaga</i> (Orthoptera: Tettigoniidae: Mecopodinae) from Brandberg Massif, Namibia. <i>Journal of Orthoptera Research</i> , 12, 105–109.	Yes
Naskrecki, P. & Bazelet, C.A.	2009	A species radiation among South African flightless spring katydids (Orthoptera: Tettigoniidae: Phaneropterinae: Brinckiella Chopard). <i>Zootaxa</i> , 2056, 46–62.	Yes
Naskrecki, P. & Rentz, D.C.F.	2010	Studies in the orthopteran fauna of Melanesia: New katydids of the tribe Agraeciini from Papua New Guinea. <i>Zootaxa</i> , 2664, 1–35.	Yes
Nickle, D.	1966	A New Species of <i>Montezumina</i> with the Description of the Male of <i>M. bradleyi</i> Heb. (Orthoptera: Tettigoniidae: Phaneropterinae). <i>Entomological News</i> , 77, 159–165.	No
Nickle, D.	1967	The Neotropical Katydid Genus <i>Raggophyllum</i> (Orthoptera; Tettigoniidae; Phaneropterinae). <i>Entomological News</i> , 78, 7–12.	No
Nickle, D.	1983	A new species of pseudophylline katydid from Cocos island, Costa Rica. <i>Entomological News</i> , 94, 1–6.	No
Nickle, D.	1985	A new steirodont katydid from colombia (Orthoptera: Tettigoniidae). <i>Entomological News</i> , 96, 11–15.	Yes
Nickle, D.	2001	Descriptions of the male of <i>Acantheremus granulatus</i> Saussure and Pictet and a new species from Peru (Orthoptera: Tettigoniidae). <i>Journal of Orthoptera Research</i> , 10, 135–139.	No
Nickle, D.	2001	New Species of the Neotropical Genus <i>Daedalellus</i> Uvarov (Orthoptera: Tettigoniidae: Copiphorinae). <i>Transactions of the American Entomological Society</i> , 127, 173–187.	No
Nickle, D.	2002	New species of katydids of neotropical genera <i>Arachnoscelis</i> and <i>Phlugiola</i> . <i>Journal of Orthoptera Research</i> , 11, 125–133.	No
Nickle, D.	2003	New neotropical species of the genus <i>Phlugis</i> (Orthoptera: Tettigoniidae: Meconematinae). <i>Journal of Orthoptera Research</i> , 12, 37–56.	No
Nickle, D.	2005	Additional notes on the genus <i>Phlugis</i> with the description of two new arboreal species from Costa Rica. <i>Journal of Orthoptera Research</i> , 14, 57–62.	No
Nickle, D.	2007	<i>Graminofolium</i> Nickle: a new genus of katydid with two species from northern South America. <i>Journal of Orthoptera Research</i> , 16, 97–102.	No

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APPENDIX 1. (Continued)

Author	Year	Title	Information on the phallus
Oudman, L., Duijimm, M. & Landman, W.	1990	Morphological and Allozyme Variation in the <i>Ephippiger</i> <i>Ephippiger</i> Complex (Orthoptera, Tettigoniioidea). <i>Netherlands Journal of Zoology</i> , 40, 454–483.	Yes
Rentz, D.C.F.	1975	Two new katydids of the genus <i>Melanonotus</i> from Costa Rica with comments on their life history strategies (Tettigoniidae: Pseudophyllinae). <i>Entomological News</i> , 86, 129–140.	No
Rentz, D.C.F.	1976	Systematics, behavior & bionomics of costa Rican Katydids of the genus <i>Sphyrometopa</i> (Orthoptera: Tettigoniidae: Agroecinae). <i>Entomological News</i> , 87, 189–202.	Yes
Rentz, D.C.F.	1993	The Austrosaginae, Zaprochilinae and Phasmodinae. A Monograph of the Tettigoniidae of Australia. CSIRO, Melbourne, 386 pp.	Yes
Rentz, D.C.F.	2010	A guide to the Katydids of Australia. CSIRO, Melbourne, 224 pp.	Yes
Rentz, D.C.F. & Birchim, J.D.	1968	Revisionary studies in the nearctic Decticinae. <i>Memoirs of the Pacific Coast Entomological Society</i> , 3, 1–173.	Yes
Rentz, D.C.F. & Colless, D.H.	1990	A classification of the shield-backed katydids (Tettigoniinae) of the world. In: Bailey, W.J. & Rentz, D.C.F. (Eds), <i>Tettigoniidae: Biology, Systematics and Evolution</i> . Springer – Verlag, Berlin, pp. 352–377.	Yes
Rentz, D.C.F., Su, Y.N. & Ueshima, N.	2009	Studies in Australian Tettigoniidae: The Phyllophorinae (Orthoptera: Tettigoniidae; Phyllophorinae). <i>Zootaxa</i> , 2075, 55–68.	Yes
Sevgili, H.	2001	A new bushcricket species and notes on some less known species of the genus <i>Poecilimon</i> Fischer, 1853 from Turkey (Orthoptera, Phaneropterinae). <i>Journal of Orthoptera Research</i> , 10, 15–24.	No
Shi, F.-M. & Li, R.-L.	2009	A review of the genus <i>Lipotactes</i> Brunner v. W., 1898 (Orthoptera, Tettigoniidae, Lipotactinae) from China. <i>Zootaxa</i> , 2152, 36–42.	No
Shao-Li, M., Yuan, H. & Fu-Ming, S.	2009	Review of the genus <i>Kuzicus</i> Gorochov, 1993 (Orthoptera: Tettigoniidae: Meconematinae) from China. <i>Zootaxa</i> , 2137, 35–42.	Part
Shi, F.-M., Mao, S.-L. & Ou, X.-H.	2008	A revision of the genus <i>Conanalus</i> Tinkham, 1943 (Orthoptera: Tettigoniidae). <i>Zootaxa</i> , 1949, 30–36.	No
Shi, F.-M. & Qiu, M.	2009	Remarks on the Chinese species of the genus <i>Anelytra</i> Redtenbacher, 1891 (Orthoptera, Conocephalinae). <i>Zootaxa</i> , 2280, 53–62.	Yes
Ünal, M.	2008	The Cyprian genus <i>Exodrymadusa</i> Karabab (Orthoptera: Tettigoniidae). <i>Zootaxa</i> , 1934, 40–46.	Yes
Ünal, M.	2009	<i>Spinisternum castaneipictus</i> Willemse, 1966 (Orthoptera: Tettigoniidae: Conocephalinae) from Papua New Guinea, with description of the male and remarks on the relationship. <i>Zootaxa</i> , 2065, 61–68.	Yes
Ünal, M.	2011	Taxonomic review of the subfamily Bradyporinae (Orthoptera: Tettigoniidae; Bradyporini; Ephippigerini) of Turkey, with description of new species and the relationship of the taxa. <i>Zootaxa</i> , 2899, 1–42.	Yes
Walker, T.J.	2004	The uhleri group of the genus <i>Amblycorypha</i> (Orthoptera: Tettigoniidae): extraordinarily complex songs and new species. <i>Journal of Orthoptera Research</i> , 13, 169–183.	No
Walker, T.J., Forrest, T.G. & Spooner, J.D.	2003	The rotundifolia complex of the genus <i>Amblycorypha</i> (Orthoptera: Tettigoniidae): songs reveal new species. <i>Annals of the Entomological Society of America</i> , 96, 433–447.	No

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APPENDIX 1. (Continued)

Author	Year	Title	Information on the phallus
Walker, T.J. & Gurney, A.B.	1972	Systematics and acoustic behavior of <i>Borinquenula</i> , a new genus of brachypterous coneheaded katydids endemic to Puerto Rico (Orthoptera, Tettigoniidae, Copiphorinae). <i>Annals of the Entomological Society of America</i> , 65, 460–474.	Yes
Walker, T.J. & Whitesell, J.J.	1978	New species of conehead from Florida Everglades (Orthoptera: Tettigoniidae: <i>Neoconocephalus</i> ). <i>Entomological News</i> , 89, 27–32.	No
Walker, T.J., Whitesell, J.J. & Richard, A.	1973	The Robust Conehead: Two Widespread Sibling Species (Orthoptera: Tettigoniidae: <i>Neoconocephalus</i> “robustus”). <i>Ohio Journal of Science</i> , 73, 321–330.	No
Xiberras, S. & Ducaud, P.	2004	Sauterelles-feuilles de Guyane. Révision du genre <i>Pterochroza</i> . (Orthoptères Tettigoniidae). <i>Lambillionea</i> , 104, 1–38.	Yes
Zeuner, F.E.	1940	<i>Phlugiolopsis henryi</i> n.g., n.sp., a new Tettigoniid, and other Saltatoria (Orthop.) from the Royal Botanic Gardens, Kew. <i>Journal of the Society for British Entomology</i> , 2, 77–84.	No

**APPENDIX 2.** List of dissected male specimens, arranged taxonomically. All specimens were collected at localities in Brazil, in the following states (the respective abbreviation between parentheses): Amazonas (AM), Bahia (BA), Minas Gerais (MG), Mato Grosso (MT), Rio de Janeiro (RJ), Santa Catarina (SC), São Paulo (SP). The column “Figures” lists numbers for figures of the phallus or microstructure corresponding to the species cited in the text.

Subfamily	Tribe	Genus	Epithet	Locality	Figures
Conocephalinae					
	Agraeciini	<i>Eschatoceras</i>	sp.	Manaus, AM	10, 11, 72, 97
		<i>Uchuca</i>	<i>ferreirai</i>	Manaus, AM	12, 13, 73, 98
	Conocephalini	<i>Conocephalus</i>	sp.1	Texeiras, MG	6–9, 99
		<i>Conocephalus</i>	sp.2	Salesópolis, SP	14, 15, 100
		<i>Conocephalus</i>	sp.3	Texeiras, MG	16, 17, 101
	Copiphorini	<i>Eriolus</i>	sp.	Manaus, AM	18, 19, 74, 102
		<i>Neococephalus</i>	sp.1	Manaus, AM	20, 21, 103
		<i>Neococephalus</i>	sp.2	Viçosa, MG	75, 104
Listrosclidinae					
	Incertae sedis	<i>Cerberodon</i>	<i>viridis</i>	Nova Friburgo, RJ	22–25, 76, 105
		Gen.1	sp.	Manaus, AM	26, 27, 77, 78, 106
		Gen.2	sp.	Prado, BA	28, 29, 107
Meconematinae					
	Phlugidini	<i>Phlugis</i>	<i>ocraceovittata</i>	Viçosa, MG	30–33, 108
Phaneropterinae					
	Dysoniini	<i>Machima</i>	sp.	Salesópolis, SP	79, 109
	Phyllopterae group	<i>Itarissa</i>	sp.	Manaus, AM	110
	Viadanini	<i>Anaulacomera</i>	sp.	Manaus, AM	34–37, 80, 81, 111
	Incertae sedis	Gen.3	sp.	Joinville, SC	38, 39, 112
		Gen.4	sp.	Prado, BA	40, 41, 113
		Gen.5	sp.	Salesópolis, SP	42, 43, 114
		Gen.6	sp.	Manaus, AM	82, 115
Pseudophyllinae					
	Cocconotini	<i>Schedocentrus</i>	sp.	Manaus, AM	48, 49, 83, 116
	Eucocconotini	<i>Gnathoclita</i>	<i>vorax</i>	Aripuanã, MT	50, 51, 117
	Leptotettigini	Gen.7	sp.	Manaus, AM	52, 53, 84, 118
	Leptotettigini	Gen.8	sp.	Manaus, AM	54, 55, 85, 119
	Leptotettigini	<i>Leptotettix</i>	<i>crassicerci</i>	Manaus, AM	56, 57, 86, 120
	Leptotettigini	<i>Leptotettix</i>	sp.	Manaus, AM	44–47, 87, 88, 121
	Pleminiini	<i>Acanthodis</i>	sp.	Manaus, AM	58, 59, 122
	Pleminiini	Gen.9	sp.	Manaus, AM	60, 61, 89, 123
	Pleminiini	<i>Gongrocnemis</i>	sp.	Manaus, AM	62, 63, 90, 124
	Polyancistrini	<i>Spinapecta</i>	<i>alieniphaga</i>	Grão Mogol, MG	64, 65, 125
	Pterochrozini	<i>Porphyromma</i>	sp.	Manaus, AM	66, 67, 91–93, 126
	Pterochrozini	<i>Pterochroza</i>	<i>ocellata</i>	Manaus, AM	68, 69, 94, 127
	Teleutiini	<i>Teleutias</i>	sp.	Manaus, AM	70, 71, 128

**APPENDIX 3.** Available information on the titillator for subfamilies of Tettigoniidae. The classification follows Eades *et al.* (2014). The column “Taxa” indicates the taxa examined in the present work and the corresponding section citing them, or taxa cited in works of previous authors. In the latter case, the respective citation is indicated in the column “References” and the respective reference listed in Appendix 1. The first trait (I) is the absence (0) or presence (1) of a titillator. The second trait (II) is whether the titillator is formed by paired (0) or single (1) components. See Material and Methods for further explanation. In several cases, no information was available (?).

Subfamily	Taxa	I	II	References
<b>Acridoxeninae</b>		?	?	
<b>Austrosaginae</b>	<i>Hemisaga</i> Saussure	1	1	Rentz (2010)
<b>Bradyporinae</b>	Species cited in text Bradyporini and Ehippigerini	1	1	Ünal (2011)
<b>Conocephalinae</b>	Species cited in text	1	0	
<b>Hetrodinae</b>	<i>Enyaliopsis</i> spp.	1	0	Glenn (1991)
<b>Hexacentrinae</b>	<i>Ecuaneduba</i> Gorochov	0-1	1	Gorochov (2006) Gorochov (2007)
<b>Lipotactinae</b>	<i>Mortoniellus</i> Griffini <i>Lipotactes</i> Brunner von Wattenwyl <i>Windbalea viride</i> Rentz	0	-	Ingrish (1995)
<b>Listroscelidinae</b>	Species cited in text	0-1	0-1	
<b>Meconematinae</b>	Species cited in text	0-1	0-1	
<b>Mecopodinae</b>	<i>Pseudosaga</i> Brancsik	0		Naskrecki 2003
<b>Microtettigoniidae</b>		?	?	
<b>Phaneropterinae</b>	Species cited in text	0-1	0-1	
<b>Phasmodinae</b>	<i>Phasmodes</i> Westwood	0	-	Rentz (1993)
<b>Phylloporinae</b>	Species cited in text	0	-	
<b>Pseudophyllinae</b>	Species cited in text	0-1	0-1	
<b>Saginae</b>		?	?	
<b>Tettigoniinae</b>	Species cited in text	1	0-1	
<b>Tympanophorinae</b>		?	?	
<b>Zaprochilinae</b>	<i>Kawanaphila</i> Rentz <i>Zaprochilus</i> Caudell <i>Windbalea</i> Rentz	0	-	Rentz (1993)

## CAPÍTULO II

### **The secret stridulatory file under the right tegmen in katydids (Orthoptera, Ensifera, Tettigonioidea)**

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<http://dx.doi.org/10.11646/zootaxa.3821.5.7>  
<http://zoobank.org/urn:lsid:zoobank.org:pub:DE57217C-04EC-4BC0-8E1D-1B29BD240BDC>

## The secret stridulatory file under the right tegmen in katydids (Orthoptera, Ensifera, Tettigoniodea)

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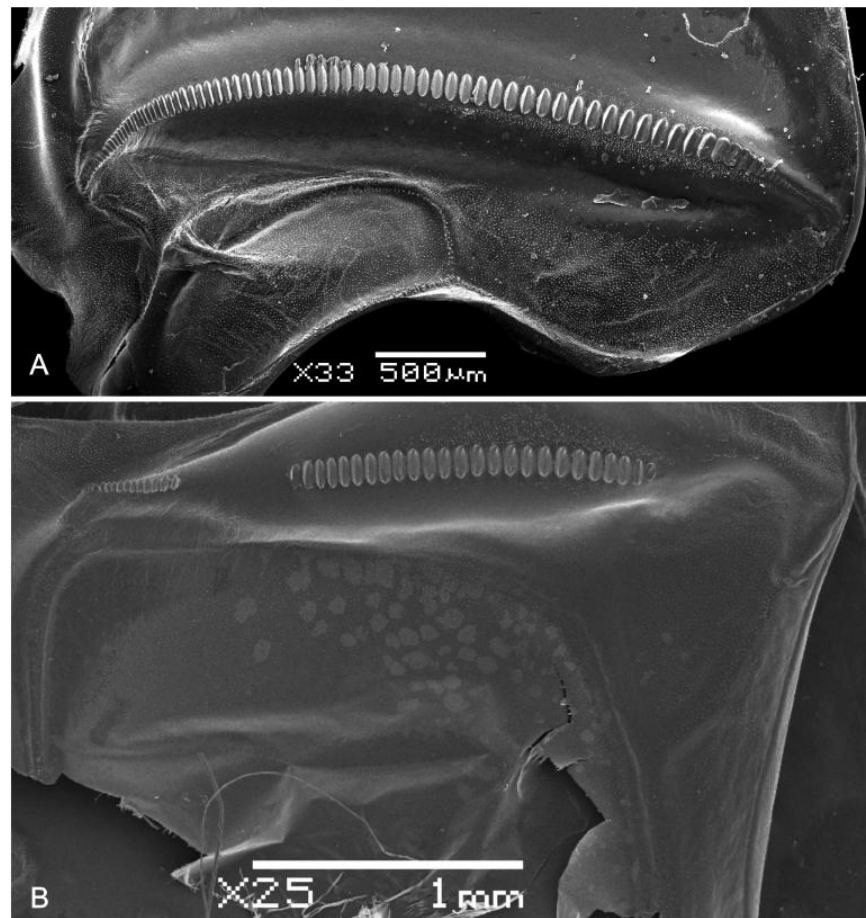
Males of most species of crickets and katydids produce species-specific calling songs to attract conspecific females. The typical stridulatory apparatus of the Ensifera consists of a file-and-scraper system in the basal dorsal region of the forewings (tegmina): the file on the underside of the cubital vein of one tegmen is composed of a series of lamelliform teeth and is run against the sclerotized scraper at the edge of the other tegmen. The region directly distal of the cubital vein is often thin and glassy and serves to amplify and spread the sound. In stridulating crickets the tegmina are quite symmetrical with both the left and the right one containing a file, which is considered the ancestral condition (Béthoux 2012). Most of these crickets adopted a right-over-left wing overlap and use only the right file. The few extant species of the ancient group Hagloidea have bilaterally symmetrical tegmina, both with functional files, and individual males can change the overlap (Morris & Gwynne 1978). Katydids are distinguished by a left-over-right wing overlap, with a stridulatory file on the underside of the left tegmen, and a scraper on the right one, which usually is also equipped with a mirror as resonating structure.

During taxonomic studies in Brazilian Agraeciini (JCR & CLA) and the study of the peculiar stridulatory apparatus of *Xiphelimum amplipennis* found at the Argentine side of the Iguazú Falls (Cataratas do Iguazú) (HB & co-authors), we were surprised to find fairly well-developed files also on the underside of the stridulatory area of the right tegmen. We then examined more specimens from Colombia and Brazil (verified or collected by JCR) as well as from Ecuador and Argentina (collection HB), and noticed that a file on the ventral side of the right tegmen is more common than we expected.

While the first draft of our paper had in the title “the untold history of the stridulatory files in katydids”, we found several studies documenting files on the right tegmen. In the apparently first correct description of the mechanism of sound production in Ensifera (Landois 1867) are already mentioned two species of Tettigoniidae with right files of somewhat fewer teeth than in the functional left one. A study on the stridulatory apparatus of katydids (Graber 1872) reports right files for one species of each Conocephalinae and Bradyporinae (or Ehippigerinae depending on classification), three species of Phaneropterinae, and two additional species of Tettigoniinae. And for still another species of Tettigoniinae is reported a right file (Petrunkevitch & Guaita 1901). Another study reports a right file for two additional species of Phaneropterinae with fewer and smaller teeth than on the functional file, and also includes illustrations of the non-functional file and individual teeth (Regen 1903). That male katydids have a rudimentary file on the right tegmen is actually considered as normal condition (Roy-Noel 1954). Measurements on numerous specimens of ten species show that the right file is always shorter than the left one, is always composed of fewer teeth, and that the tooth density is about equal, with sometimes being a little lower or even a little higher (Stärk 1958). For one male of Pseudophyllinae was also found a right file (Klee 1961). However, in another species of that subfamily the right file is totally absent, while a right file is also found in one species of Phlugidini (Meconematinae) (Leroy 1969). Among 27 species of Phaneropterinae are reported two species without right file: *Phaneroptera sparsa* and *Zeumeria melanopeza* from Africa (Leroy 1970). Of another species of this subfamily, *Ectomoptera nepicauda*, was recently described the extraordinarily derived and completely asymmetrical stridulatory apparatus of the male, where the stridulatory area of the left tegmen is

reduced to the file, and in the right one consists only of the mirror (Heller & Hemp 2014). Interestingly, there is still a vestigial right file, which under the stereomicroscope is hardly discernible in the anterior wall of the mirror (K.-G. Heller, personal communication, 2014).

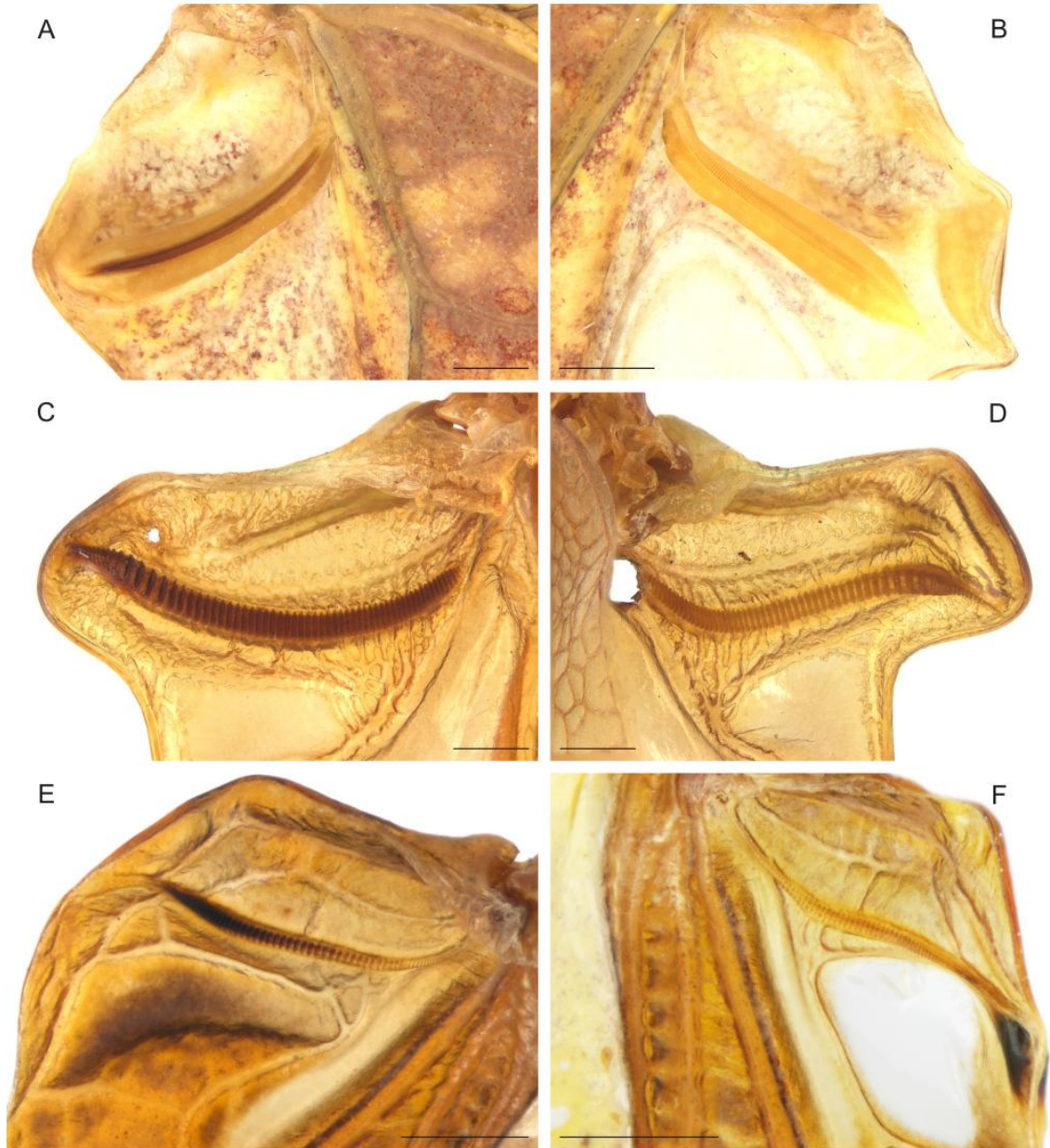
Very rarely there occur male individuals with right-over-left wing overlap (Stärk 1958). In experiments with forced right-tegmen overlap the animals try to correct the overlap immediately, sometimes needing several attempts and producing short and damped sounds (Klee 1961). Interestingly, in two species of *Neduba* (Tettigoniinae), whose males do have right files, right-over-left overlap seems to be quite common, and manual manipulation of the tegmina of freshly killed specimens results in a similar sound with either overlap (Morris *et al.* 1975). That the right file could be used for stridulation has also been suggested for *Megatympanon speculatum* (Listroscolidinae, Figs 2C, D), where the male has symmetrically developed stridulatory areas on left and right tegmina, with mirrors, scrapers and files (Rentz 2001). G.K. Morris (personal communication, 2013) reported a curious observation for a member of the Conocephalinae: "I once encountered an *Orchelimum* whose stridulation was strangely low-intensity, though he moved his forewings to and fro, buzzing and ticking in an apparently proper manner. When I came to look closely the overlap was seen to be reversed and he was rubbing the left forewing edge up and down his right forewing's vestigial file".



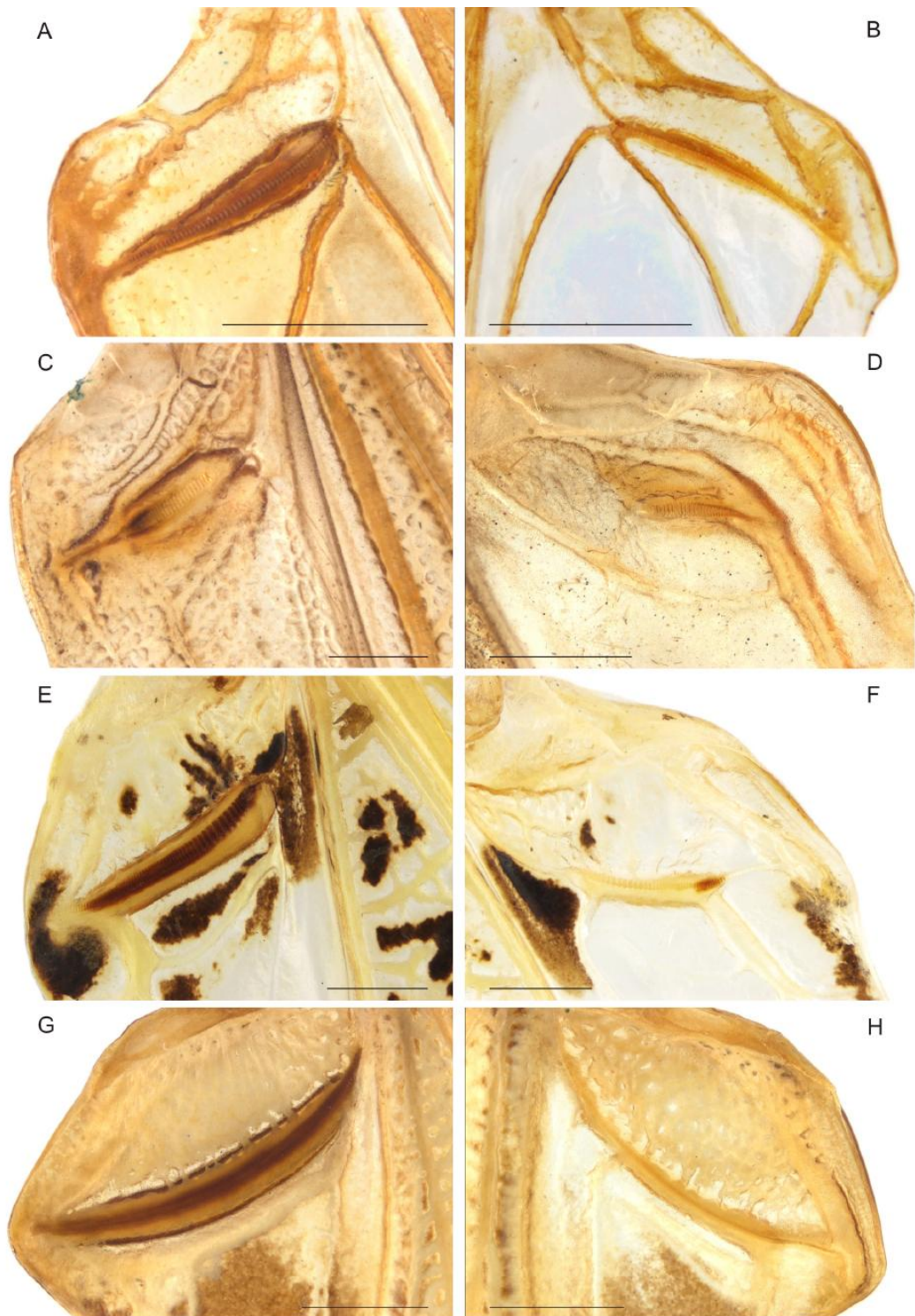
**FIGURE 1.** Scanning electron micrographs of left and right files of *Xiphelimum amplipennis* (Conocephalini). (A) left file. (B) right file. The gap in the right file is an anomaly, in other examined males of this species it is continuous.

Our survey adds 36 species to the 52 of which we found the presence or absence of right files reported in the literature, extending the scope with Hexacentrinae to eight subfamilies. Not counting in the apterous Tabariini (Mecopodinae), representatives of all the other seven subfamilies present in South America are included (Table 1). Only within the Pseudophyllinae we found species without right file. The left and right files of the other species

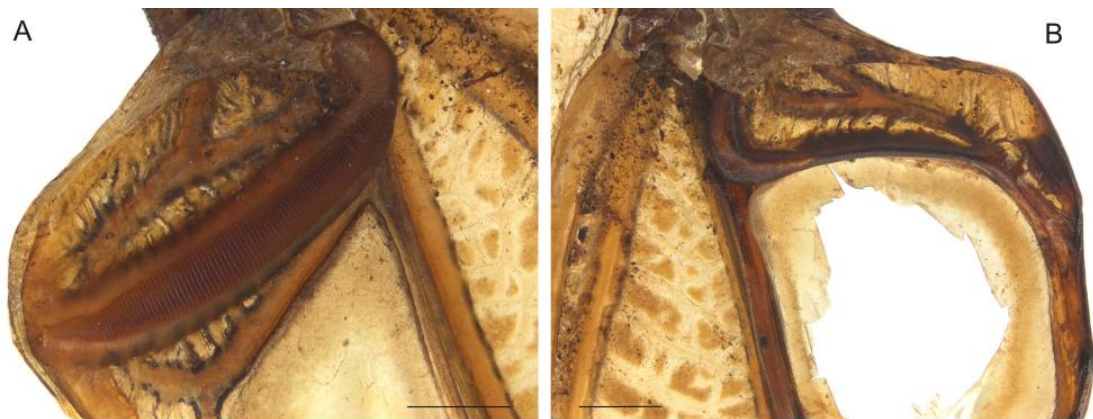
differ in the degree of symmetry. In a particular species the teeth of the right file are always less sclerotized, it is shorter and usually consists of fewer teeth compared to the left file (Figs 1A, B). There are some species with almost symmetrical left and right files, similar in shape, width and length (Figs 2A, B). In other species both files are somewhat less similar in shape and length and the right one is moderately less sclerotized (Figs 2C–F). And there are species with a more reduced and vestigial right file, which it is shorter, narrower and much less sclerotized than the left one (Figs 3A–H).



**FIGURE 2.** Fairly symmetrical left and right files. Left column showing left functional file. Right column showing right non-functional file. Number of teeth on left and right file in parenthesis. (A–B) Pseudophyllinae (Pterochrozini): *Porphyromma* sp. nov. (133, 122). (C–F) Listroscelidinae: (C–D) *Megatympanon speculatum* (63, 60); (E–F) *Listroscelis* sp. nov. (63, 44). (G–H) Phaneropterinae: Gen. et sp. nov. (220, 173). Scale bars = 1.00 mm.



**FIGURE 3.** More asymmetrical left and right files. Left column showing left functional file. Right column showing right reduced or vestigial file. Number of teeth on left and right file in parenthesis. (A–D) Conocephalinae: (A–B) *Conocephalus ochroteus* (54, 42); (C–D) *Neoconocephalus* sp. 1. (60, 30). (E–H) Phaneropterinae: (E–F) *Machima phyllacantha* (59, 43); (G–H) Gen. et sp. nov. Scale bars = 1.00 mm.



**FIGURE 4.** Cubital veins of left and right tegmina in a species belonging to “true” Pseudophyllinae: *Gnathoclita vorax*. (A) Stridulatory file of left tegmen with 109 teeth; (B) cubital vein of right tegmen smooth, devoid of teeth. Scale bars = 1.00 mm.

**TABLE 1.** List of examined species, following the current classification (Eades *et al.*), and including the countries where the specimens were collected. Right file greatly reduced indicated by \*, and right file absent by \*\*.

Subfamily	Tribe	Species	Country	
Conocephalinae	Agraeciini	<i>Agraecia pulchella</i>	Colombia	
		<i>Agraecia punctata</i>	Brazil	
		<i>Agraecia vittipes</i>	Argentina	
		<i>Eppia truncatipennis</i>	Colombia	
	Conocephalini	<i>Conocephalus ochrotelus</i>	Brazil	
		<i>Conocephalus longipes</i>	Argentina	
		<i>Xiphelimum amplipennis</i>	Argentina	
	Copiphorini	<i>Neoconocephalus</i> sp. 1	Brazil	
		<i>Neoconocephalus</i> sp. 2	Argentina	
	Hexacentrinae	Ecuanedubini	<i>Ecuaneduba aequatorialis</i>	Ecuador
Listrosclidinae	Terpandrini	<i>Megatympanon speculatum</i>	Brazil	
	Listrosclidini	<i>Listrosclis</i> sp. nov.	Brazil	
	Insertae sedis	<i>Monocerophora longispina</i>	Brazil	
Meconematinae	Phlugidini	<i>Phlugis ocraceovittata</i>	Brazil	
Phaneropterinae	Dysoniini	<i>Machima phyllacantha</i>	Brazil	
		<i>Dysonia</i> sp. nov.	Ecuador	
		<i>Dissonulichien</i> sp. nov.	Ecuador	
	Viadanini	<i>Anaulacomera</i> sp. nov.	Ecuador	
		<i>Viadana</i> sp.	Ecuador	
	Insertae sedis	<i>Philophyllia venosa</i>	Brazil	
		Gen. et sp. nov.	Brazil	
		<i>Scaphura elegans</i>	Argentina	
	Pseudophyllinae	Cocconotini	<i>Schedocentrus</i> cf. <i>viridinervosus</i> *	Ecuador
			<i>Mystron</i> sp. nov.**	Ecuador
Eucoconotini		<i>Gnathoclita vorax</i> (Stoll)**	Brazil	
		<i>Ottotettix smaragdopoda</i> **	Ecuador	
Leptotettigini		<i>Leptotettix voluptarius distinctus</i> *	Ecuador	
Platyphyllini		<i>Triencentrus</i> sp. nov.**	Ecuador	
Pleminiini		<i>Dasyscelus normalis</i> **	Argentina	

.....continued on the next page

**TABLE 1.** (Continued)

Subfamily	Tribe	Species	Country
		<i>Gongrocnemis</i> sp. nov.**	Ecuador
		Gen. et sp. nov. *	Ecuador
	Pterochrozini	<i>Porphyromma</i> sp. nov.	Brazil
		<i>Typophyllum egregium</i>	Ecuador
		<i>Typophyllum inflatum</i>	Argentina
		<i>Typophyllum</i> sp. nov.	Ecuador
	Teleutiini	<i>Pemba cochleata**</i>	Ecuador
Tettigoniinae	Nedubini	<i>Platydecticus</i> cf. <i>angustifrons</i>	Argentina

Among the Pseudophyllinae we found files on the right tegmina in six species out of 14 (Table 1). Only in the four species of the Pterochrozini it is equally well developed as in members of the other subfamilies, but this tribe should probably be separated from the Pseudophyllinae, because it seems to be a sister lineage of all other Tettigoniidae (Mugleston *et al.* 2013). In one species of *Schedocentrus* the right tegmen has on the basal portion of the cubital vein 16 very small teeth (corresponding to the basal end of the left file with altogether more than 100 teeth), the remainder of the vein being completely smooth. A very curious male, which seems to represent an undescribed genus of Pleminiini, also shows a peculiar condition of the right tegmen: It is lacking the typical mirror and there are 25 teeth on the basal half of the cubital vein, only 10 of them relatively well-developed. For the Brazilian *Thliboscelus hypericifolius* (Pterophyllini) is reported a right file with 46 teeth in contrast to 78 on the functional file (Klee 1961, as *Th. camellifolius*, *sensu* Serville). The African *Pantecphylus helleri* (Pantecphyllini) has a right file on the distal portion of the cubital vein that is much shorter than the left file, while several Phyllomimini do not have any traces of a right file (K.-G. Heller, personal communication, 2014). This is also the case for the remaining species we examined: the ventral surface of the cubital vein of the right tegmen is perfectly smooth (Fig. 4B). So the common condition in Pseudophyllinae seems to be the complete reduction of the right file.

The aim of this note is to provide some new qualitative data for several subfamilies (detailed measurements can be found in Stärk 1958, Klee 1961, Leroy 1969 & 1970), and in particular highlight the frequency of a vestigial or not-so-vestigial right file among male katydids, which seems to be largely overlooked in recent literature. It might be a useful character to include in morphological and phylogenetic studies in katydids, and perhaps the mechanisms that lead to the observed variety in development of the right file could be elucidated. It might be worthwhile to look under the right tegmen, which in pinned male specimens is rarely extended, and document the development or absence of stridulatory teeth.

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### **CAPÍTULO III**

#### **Reassessment and splitting of the genus *Agraecia* Audinet-Serville (Orthoptera: Tettigoniidae: Conocephalinae: Agraeciini)**

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Manuscrito original.

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<sup>1</sup> Este manuscrito não deve ser considerado como publicação válida para fins nomenclaturais, de acordo com as normas do Código Internacional de Nomenclatura Zoológica (Cap. 3, Art. 8.2 e Art. 8.3).

## Abstract

*Agraecia* Audinet-Serville, the type-genus of Agraeciini, comprises fifteen species names: thirteen used for extant species, one junior synonym, and one fossil. The species are morphologically very dissimilar, and were collected and described from different localities of the world. We carried out a reassessment of the genus based on new collected material from Brazil and specimens from scientific collections. We re-delimit *Agraecia*, keeping only two of the previously described species in the genus: *A. dorsalis* Karny and *A. punctata* Saint-Fargeau & Audinet-Serville. We designate a neotype and a neoallotype for *A. punctata* and describe four new *Agraecia* species. We propose *Bertoniella* Rehn, as a junior synonym of *Agraecia*. The new combination *Parasubria vittipes* (Redtenbacher) **comb. nov.** is proposed. We classify the remaining six *Agraecia* species in six new genera: **Gen. nov. 1**, **Gen. nov. 2**, **Gen. nov. 3**, **Gen. nov. 4**, **Gen. nov. 5**, **Gen. nov. 6**, and we transfer the fossil *Agraecia* species to **Gen.7. nov.†**. We also describe four new species of **Gen. nov. 1**. Type material of *Agraecia fallax* Karny **nomen dubium** is lost and the one of *Agraecia festae* Griffini is currently unavailable for examination, thus these two species are treated as *incertae sedis*, but in our opinion they do not belong to *Agraecia* and shall be transferred to new genera in the future. A key to the genera is provided, as well as a key to species *Agraecia* and **Gen. nov. 1**. We discuss the morphology of features not considered in previous studies on the fauna of the American katydids, as the stridulatory file of the right tegmen, microstructures on the ventral surface of the tegmina, and morphology of postabdominal sclerites, especially of the phallus. The calling songs of *Parasubria vittipes* (Redtenbacher) **comb. nov.** and **Gen. nov. 4 pulchella** (Hebard) **comb. nov.** are described. We show that species of South American Agraeciini seem to have restricted geographic distribution and are frequently found in bromeliads.

## Introduction

Agraeciini are katydids that occur mainly in tropical and subtropical forests, on herbaceous vegetation and in the understory (Rentz 1976, Braun 2002), also in the canopy (Rentz *et al.* 2012), grassland and eucalyptus woodland (Naskrecki and Rentz 2010), fern and bamboo thickets of landslides (Braun 2008), and specialized forest microhabitats as on lichens (Rentz *et al.* 2012). Little is known about their feeding habits, there are records for feeding on flowers (Rentz 1976), dead wood (Ingrisch and Tan 2012) and even preying on a land snail (Leong 2011). Most species are described from the Indomalayan and Australasian regions, as their katydid faunas were focus of major revisionary works (Ingrisch 1998, Ingrisch 2008, Ingrisch 2009, Naskrecki and Rentz 2010, Rentz *et al.* 2010, Rentz *et al.* 2012). The American and African faunas are possibly well diversified, but they were unsatisfactorily studied and their biomes insufficiently explored. The taxonomic limits of the tribe are barely defined (Nickle and Naskrecki 1997, Naskrecki 2002a) and several of the problematic genera occur in Central and South America. Additionally, there is little available information on important morphological characteristics of Neotropical species, mainly on the morphology of postabdominal structures (cerci, paraprocts, phallus) and tegmina. The most nebulous genus of Agraeciini is the nominotypical *Agraecia* Audinet-Serville, 1831, an aggregate of not very closely related species that urge a taxonomic revision.

The controversy around *Agraecia* begun with its description. The author derived the generic name *Agraecia* based on the Greek words *αγρος* (agros = field) and *οικεω* (oikeo = to inhabit). The correct formation would be “*Agroecia*”, a form first used by Burmeister (1838). However the original spelling did not use -oe-, but an old -ae- ligature, as substantiated by Audinet-Serville's approximately homonymous French name “Agrécie” and difference to a clear o-e ligature in *Chæradodis* in the same work (see also Walker and Gurney 1972). According to the ICZN (article 32.5.1), incorrect latinization is not to be considered an inadvertent error and therefore must not be emended. The genus was erected for the sole species *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825), type-species by monotypy, originally described as *Locusta punctata* based on two females collected from Brazil; latter Redtenbacher (1891) cites a specimen collected by Brunner from the south of the old state of Bahia, in Brazil. Then, Redtenbacher (1891) described nine species from different localities in the world: *A. abbreviata*, *A. maculata*, *A. nigrifrons*, *A. subulata*, *A. viridipennis*, *A. vittata*, and *A. vittipes* from South America; *A. sansibara* from Africa; and *A. differens* from Australia.

All these species were described from adult specimens, except for *A. vittata*, which was based on an immature female. Subsequently, *Agraecia festae* Griffini, 1896 was described from Ecuador, *A. dorsalis* Karny, 1907 from Brazil, *A. ornata* Karny, 1907 and *A. fallax* Karny, 1911 from New Guinea, and *A. pulchella* Hebard, 1927 from Colombia. The fossil species *A. reticulata* Piton & Théobald, 1939 was described from on fossilized tegmen dated from the Oligocene. Then after 31 years without descriptions of *Agraecia*, *A. incognita* Piza, 1970 was described based on one male and three females supposedly lacking locality data (the type specimens actually to have labels with localities); and subsequently *A. malkini* Piza, 1978 was described from Brazil. Hugel (2002) described *A. cesairei* from the island of Martinique, including description of its calling song and morphology of the titillator, this being the first time such information was provided for *Agraecia* species. In the same work, *A. malkini* Piza was synonymized with *A. viridipennis* based on specimens collected in the French Guiana (Hugel 2009). Finally, *Agraecia differens* was transferred to *Secsiva* Walker, 1869 (Rentz 2009) and *A. sansibara* to *Afroagraecia* Ingrisch & Hemp, 2013 (Hemp 2013). It was also recognized that *A. ornata* is actually a synonym of *Pseudonicsara semicrucata* (Brunner von Wattenwyl, 1898) (Ingrisch 2009) and *A. incognita* a synonym of *Tettigonia viridissima* (Linnaeus, 1758) (Chamorro-Rengifo and Braun 2010).

Before our revision *Agraecia* comprised 15 proposed species names, of which 14 are currently in use (Eades *et. al.*) and one is a junior synonym (Hugel 2009). The diagnosis of *Agraecia* (Audinet-Serville 1831, Redtenbacher 1891) is based on characters that are inconsistent or apply to taxa outside the genus (for instance, “ovipositor curved upward”).

During examination of specimens from Brazil and Colombia we noted that *Agraecia* currently includes species that cannot be assigned to this genus. In this work, we revise *Agraecia* and propose a new diagnosis for it in a very restricted sense, retaining only *A. punctata* and *A. dorsalis*. The remaining 12 names are transferred to existing or new genera, or left as *incertae sedis*.

## **Materials and Methods**

### **Field collection**

Katydidids were collected from November 2011 to January 2012 in conservation units and reserves in the Southeast Brazilian Atlantic Forest. Fifteen areas were surveyed in the states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro. Individuals belonging to Agraeciini were collected in thirteen of the visited localities. The complete names of the conservation units are listed below in the section on terminology. As most katydidids, Agraeciini are active at night, thus we searched for specimens between 19 pm and 1 am, by active capturing with the aid of flashlights for at least three consecutive nights in each CU. We captured specimens with transparent polyethylene vials of 500 ml with lid and photographed them alive. Specimens were killed using acetate, dried and kept individually. Each katydidid received a label with a collection code. The code is composed by a consecutive number, the first part of the name of the subfamily, in all cases “Cono”, and the final name of the locality.

All the individuals of *Parasubria vittipes* **comb. nov.** and one male of **Gen. nov.** *1 maculata* **comb. nov.** were collected in February 2011 in Parque Nacional Iguazú, Argentina.

### **Examination and dissections**

Collected katydidids were morphotyped and the information of each one was standardized and systematized in a spreadsheet. Additionally to the collected specimens, we received material loaned by museums (see list below). Most specimens are kept dry, except for specimens from the collections of “Coleção de Insetos do Departamento de Zoologia do Instituto de Biociências de Botucatu (IBI)” and from “Museu de Zoologia da Universidade de São Paulo (MZUSP)”, which are kept in alcohol.

Specimens were pinned and examined under a Zeiss Stemi DV4 stereomicroscope. Only a few specimens of each morphotype were pinned. Tegmina and postabdominal components were dissected to be better observed and photographed. In case there were few available specimens of a morphotype, we dissected only one male. Left and right tegmina of males were extracted and kept in glass slides. Male cerci and paraprocts were extracted and kept dried in plastic vials. Phalli were dissected and left for 48h in 10% aqueous solution of KOH and then washed with 1% acetic acid for five minutes. Muscles, fat and other attached elements were removed, and then stained with a solution of 85% Chlorazol Black diluted in alcohol (Carayon 1969). Phalli are kept in plastic vials with 70% alcohol. Dissected components have the same collection code as whole preserved specimens.

Measurements of the largest components of the body were taken using graph paper. Measurements and counting parts of minute structures were made using the Zeiss AxioVision 4.8 software measure tools. Number of spines of femora, on inner and outer margins of the left and right legs were counted. It is provided the range of the variation found in holotype and allotype, and in males and females of the whole type series or specimens examined. Measurements of previously described species are included and indicated in the text. Old specimens kept in alcohol were not measured because they were usually very inflated.

The size of the proesternal spines were described in comparison to the length of fore coxa (Ingrisch 1998).

A complete list of abbreviations for measurements and counting parts is provided below.

### **Description of *Agraecia*, new genera and species**

The genus *Agraecia* was delimited based on the original description and new collected material. The species that do not belong to the genus were reclassified in new genera. For each genus a diagnosis and a complete description were elaborated. A diagnostic description is provided for each species. Descriptions of new species are based on the holotype, and redescriptions are mostly based on newly collected material, original descriptions and images are available in Orthoptera Species File (Eades *et al.*), and in the catalog of type species of the MNHN – the Muséum National d'Histoire naturel ([science.mnhn.fr/institution/mnhn/search](http://science.mnhn.fr/institution/mnhn/search)).

A taxonomic key for all treated genera is provided, as well as separate keys to species in genera with more than one species (*Agraecia* and **Gen. nov. 1**).

### **Current species in the genus *Agraecia***

*Agraecia* currently includes fourteen species names, corresponding to thirteen extant and one fossil species from different localities of the world (see introduction). After each species is mentioned the country where it was registered for the first time.

*Agraecia* Audinet-Serville, 1831

*A. abbreviata* Redtenbacher, 1891, Brazil

*A. cesairei* Hugel, 2009, French Guiana

*A. dorsalis* Karny, 1907, Brazil

*A. fallax* Karny, 1911, New Guinea

*A. festae* Griffini, 1896, Panama  
*A. maculata* Redtenbacher, 1891, Brazil  
*A. nigrifrons* Redtenbacher, 1891, Brazil  
*A. pulchella* Hebard, 1927, Colombia  
*A. punctata* (Saint-Fargeau & Audinet-Serville, 1825), Brazil. Type species  
*A. reticulata* Piton & Théobald, 1939, fossil species, France  
*A. subulata* Redtenbacher, 1891, Brazil  
*A. viridipennis* Redtenbacher, 1891, Brazil  
*A. malkini* Piza, 1978, Brazil  
*A. vittata* Redtenbacher, 1891, Colombia  
*A. vittipes* Redtenbacher, 1891, Brazil

### **Photographing, drawings and plates**

Photos of body parts were taken under a Zeiss Discovery V8 stereomicroscope. Images were stacked with Zeiss AxioVision 4.8, and then edited in Photoshop CS6. Tegmina, cerci and paraprocts were photographed over a glass slide above a white background. Phalli were photographed submerged in a petri dish with water. Whole specimens were photographed with a Nikon D90 equipped with the lens AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED. Images of *Parasubria vittipes* (Redtenbacher, 1891) **comb. nov.**, were obtained separately in the Museo de la Plata in Argentina (Figs 23, 24A,B, 25). Diagrams of body parts or specific structures were elaborated with a free image editor. Diagrams of phalli follows the same pattern as in Chamorro-Rengifo & Lopes-Andrade (2014), as follows: sclerotized and not completely sclerotized components that are not contiguous with membranes are outlined in black, and portions or entire sclerotized components that are contiguous with membranes are outlined in light grey; membranous components are represented by light grey areas, sclerotized ones by dark grey. The drawing of each phallus shows half of the dorsal view at left and half of the ventral view at right, both delimited by a thin vertical line.

### **Geographic distribution and maps**

For most specimens collected in the Brazilian Atlantic Forest, the geographical coordinates were taken in field with an eTrex Vista–Garmin GPS. For the remaining specimens or data from literature, coordinates were obtained from electronic gazetteers and databases. Maps were elaborated in the freeware Diva-Gis 7.5, with shapes of administrative division and altitude.

## Acoustic data

The sound recording equipment used **Gen. nov. 4 pulchella comb. nov.** in its natural habitat in Colombia several years ago unfortunately was not documented. The sample frequency must have been 44 kHz. The carrier frequency spectrum does not seem to be cut off, but it cannot be excluded that the song contains ultrasound components. *Parasubria vittipes comb. nov.* was recorded with an Ultrasound Detector D1000X (Pettersson Elektronik) at 200 kHz sample frequency. Males were recorded in the field as well as accommodated in a cubic gauze cage with 30 cm edge length. Sound analysis was done with SASLab Pro (Avisoft Bioacoustics). Voucher recordings will going to be available in Orthoptera Species File Online.

## Terminology, abbreviations and labels

Terminology and abbreviations of body parts are mostly based on literature (Naskrecki 2000a, pg. 273, Table IV; and Ingrisch 2009). To facilitate reading the text abbreviations will be used accompanied by part of the name; abbreviations alone are used only in figures.

For tegmina, terminology and abbreviations of veins are based on Béthoux (2012) and Béthoux and Nel (2001). For components of the phallus, the terminology is based on Chamorro-Rengifo and Lopes-Andrade (2014).

Abbreviations for body parts, measured or counted components are as follows: TL, total body length; FF, length of fore femur; FT, length of fore tibia; HF, length of hind femur; HT, length of hind tibia; PL, pronotal length at midline; TegL, maximum tegmina length; SL, length of the stridulatory file; NT, number of teeth in the stridulatory file; minT, minimum tooth length; maxT, maximum tooth length; OL, length of the ovipositor. For number of spines on femora: sFF, for fore legs, sMF, for mid legs; and sHF, for hind legs.

Most of the specimens were collected in the following national parks or reserves from the Brazilian Atlantic Forest: Reserva Biológica (ReBio) de Sooretama; Floresta Nacional (FLONA) do Rio Preto; Parque Estadual (P. E.) da Serra do Brigadeiro; Parque Estadual do Rio Doce (PERD); Parque Nacional (P. N.) de Itatiaia; P. N. do Caparaó; P. N. do Descobrimento; P. N. do Pau Brasil; P. N. da Serra dos Órgãos;

Estação Biológica Santa Lúcia (EBSL); Reserva Particular do Patrimônio Natural (RPPN) Bacchus; RPPN Serra Bonita; RPPN Serra do Teimoso; RPPN Sítio do Zaca.

Specimens were collected in the following Brazilian states: Bahia (BA); Espírito Santo (ES); Minas Gerais (MG); Rio de Janeiro (RJ); and São Paulo (SP). State abbreviations are used only in sections on examined specimens and in figure legends.

Specimens have been deposited in or belong to the following institutional collections (with acronyms used in this paper):

<b>ANSP</b>	Entomology collection of The Academy of Natural Sciences of Drexel University (Philadelphia, USA)
<b>CEIOC</b>	Coleção Entomológica do Instituto Oswaldo Cruz (Rio de Janeiro, RJ, Brazil)
<b>CELC</b>	Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera, Universidade Federal de Viçosa (Viçosa, MG, Brazil)
<b>ESALQ</b>	Museu de Entomologia da Escola Superior de Agricultura “Luiz de Queiroz” (Piracicaba, SP, Brazil)
<b>IBB</b>	Coleção de Insetos do Departamento de Zoologia do Instituto de Biociências de Botucatu, Universidade Estadual Paulista (Botucatu, SP, Brazil)
<b>MLP</b>	Museo de La Plata (La Plata, Argentina)
<b>NMW</b>	Naturhistorisches Museum Wien (Wien, Austria)
<b>MNHN</b>	Muséum national d'histoire naturelle (Paris)
<b>MNRJ</b>	Museu Nacional do Rio de Janeiro (Rio de Janeiro, RJ, Brazil)
<b>MZUSP</b>	Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil)
<b>MUSENUV</b>	Museo de Entomologia de la Universidad del Valle (Cali, Valle del Cauca, Colombia)

All specimens collected recently in Brazil have a label printed on white paper with locality information, and another label with a collection code. Each specimen of the type series received an additional label containing species name, authors and its status in the type series (holotype, allotype, neotype, or neoallotype). Holotypes are labeled with red labels and paratypes (including allotypes) with blue labels. Specimens from other museums kept in alcohol have labels of parchment paper.

## Results

List of genera and species (including synonyms):

*Agraecia* Audinet-Serville, 1831

*Bertoniella* Rehn, 1911 **syn. nov.**

*Guaranina* Pirán, 1942 **syn.**

*A. punctata* (Saint-Fargeau & Audinet-Serville, 1825)

*A. dorsalis* Karny, 1907

*A. agraecioides* (Rehn, 1911) **comb. nov.**

*Bertoniella agraecioides* Rehn, 1911

*Agraecia* **sp. nov. 1**

*Agraecia* **sp. nov. 2**

*Agraecia* **sp. nov. 3**

*Agraecia* **sp. nov. 4**

*Parasubria* Karny, 1911

*P. vittipes* (Redtenbacher, 1891) **comb. nov.**

*Agraecia vittipes* Redtenbacher, 1891

*P. ziczac* Karny, 1911 **syn. nov.**

**Gen. nov. 1**

**Gen. nov. 1** *maculata* (Redtenbacher, 1891) **comb. nov.**

*Agraecia maculata* Redtenbacher, 1891

**Gen. nov. 1** *subulata* (Redtenbacher, 1891) **comb. nov.**

*Agraecia subulata* Redtenbacher, 1891

**Gen. nov. 1** **sp. nov. 1**

**Gen. nov. 1** **sp. nov. 2**

**Gen. nov. 1** **sp. nov. 3**

**Gen. nov. 1** **sp. nov. 4**

**Gen. nov. 2**

**Gen. nov. 2** *nigrifrons* (Redtenbacher, 1891) **comb. nov.**

*Agraecia nigrifrons* Redtenbacher, 1891

**Gen. nov. 3**

**Gen. nov. 3** *abbreviata* (Redtenbacher, 1891) **comb. nov.**

*Agraecia abbreviata* Redtenbacher, 1891

**Gen. nov. 4**

**Gen. nov. 4** *pulchella* (Hebard, 1927) **comb. nov.**

*Agraecia pulchella* Hebard, 1927

**Gen. nov. 4** *vittata* (Redtenbacher, 1891) **comb. nov.**

*Agraecia vittata* Redtenbacher, 1891

**Gen. nov. 5**

**Gen. nov. 5** *cesairei* (Hugel, 2009) **comb. nov.**

*Agraecia cesairei* Hugel, 2009

**Gen. nov. 6**

**Gen. nov. 6** *viridipennis* (Redtenbacher, 1891) **comb. nov.**

*Agraecia viridipennis* (Redtenbacher, 1891)

*Agraecia malkini* Piza, 1978 syn.

**Gen. nov. 7†**

**Gen. nov. 7** *reticulata*† (Piton & Théobald, 1939) **comb. nov.**

*Agraecia reticulata*† Piton & Théobald, 1939

***Incertae sedis***

*Agraecia fallax* Karny, 1911, **nomen dubium**

*Agraecia festae* Griffini, 1896

**Identification key for Agraeciini genera treated in the present work.**

This key does not include the fossil **Gen. nov. 6†**.

1. Female tergite X strongly prolonged behind into two strong projections. Apex of ovipositor blunt... **Gen. nov. 4**
- 1'. Female tergite X short and devoid of projections. Apex of ovipositor acute (Fig. 1D)...(2)
- 2(1'). Male cerci very long and slender, devoid of projections or ramifications... **Gen. nov. 5**
- 2'. Male cerci short, robust, or long with projections (Fig. 7)...(3)
3. Median ocellus very large, as large as an eye. Male cerci very long, cylindrical and with lateral projections. Ventral valves of ovipositor, with two tiny spine-like projections at the basal portion... **Gen. nov. 6**
- 3'(2). Median ocellus small, much smaller than an eye (Fig. 1A). Male cerci short, sometimes cylindrical, but devoid of lateral projections (Fig. 7). Ventral valves of ovipositor devoid of spiny projections... (4)
- 4(3'). Male tergite X very large and flat, covering almost completely paraprocts and cerci, apical portion strongly emarginated (Fig. 25A,B)... **Parasubria**
- 4'. Male tergite X short, prolonged behind, leaving paraprocts and ceci exposed, apical portion with a small incision (Fig. 7)...(5)
- 5(4'). Male cerci conspicuously hook-like, devoid of apical projections (Fig. 8). Paraprocts comprised by a plate and a lateral projection (Fig. 9)... **Agraecia Audinet-Serville, sensu novo.**
- 5'. Male cerci comparatively more delicate, cylindrical, with thin apical projections (Figs 32, 43A,D, 43E). Paraprocts simple, triangular or boot-like (Figs 32, 43D, 43G)...(6)
- 6(5') Apical portion of sclerites **TS** of phallus straight, free from dorsal lobe (Figs 11E, 44A,B)... **Gen. nov. 2**
- 6'. Apical portion of sclerites **TS** rounded and attached to dorsal lobe (Figs 11B,D, 34, 35, 44C)...(7)

- 7(6'). Eyes and median ocellus greenish (Fig. 28A). Tegmina with vein **M+CuA** thin, extended until less than the posterior portion of the mirror (Fig. 3C). Paraprocts triangular, simple (Fig. 32)...**Gen. nov. 1**
- 7'. Eyes and median ocellus brownish (Fig. 46A). Tegmina with vein **M+CuA** very short, extended until the stridulatory file (Fig. 3E). Paraprocts boot-like (Fig. 43G)...**Gen. nov. 3**

## Descriptions

*Agraecia sensu novo* and the new genera described here differ from *Acanthacara* Scudder, *Cestrophorus* Redtenbacher and *Erechthis* Bolívar in the shape of the fastigium verticis, which is much longer than the scape and has a pointed apex. In *Dectinomima* Caudell, *Eppia* Stål, *Hyperomerus* Redtenbacher, *Sphyrometopa* Carl, *Uchuca* Giglio-Tos, the fastigium verticis is blunt and wide. In *Paralobaspis* Giglio-Tos the fastigium verticis is shorter than the scapus and sharply pointed. In *Eschatoceras* Redtenbacher the scapus bears a protruding blunt projection at the apical inner margin. In *Loja* Giglio-Tos, the tergite X is not elongated caudally. In *Nannagroecia* Redtenbacher the posterior margin of the paranota is continuous to the dorsal margin of the pronotal disc and the sinus humeralis is completely absent, the ovipositor is sickle-shaped, with the apical margin strongly curved upward. In *Paranelytra* Karny the tegmina are greatly reduced. And in *Subria* Stål the male cerci are armed with one or two apical spines.

### *Agraecia* Audinet-Serville, 1831

(Figs 1, 2A, 3A, 4, 5, 7A, 8–11A, 12–15A, 16–22)

*Bertoniella* Rehn, 1911: 255, **syn. nov.**

*Guaranina* Pirán, 1942: 4, **syn. by Renh 1942**

**Type species by original monotypy.** *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825): 342

**Diagnosis.** This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis thinner and shorter than scapus (Fig. 1A). Tegmina with vein **M+CuA** thick, a little shorter than the posterior portion of the mirror (Fig. 3A). Male postabdomen with posterior portion of tergite X moderately prolonged caudally into two delicate lobes (Fig. 7A); cercus robust (Fig. 8), hook-like, with a pronounced tip; paraprocts consisting of a disc and an elongated upward projection (Fig. 9); subgenital plate with a V-shaped emargination at apex (Fig. 10A); titillator with sclerites **TS+VS** completely attached to the lobe **dl**, sclerites **TS** mostly smooth, or with small spinymicrostructures on the apical portion (Fig. 11A); process of the titillator **ti** consisting of dense and grouped sclerotized microstructures at the dorsum and sides of lobe **dl**. Female postabdomen with tergite X straight; subgenital plate trapezoidal and with two projections forming a U-shaped emargination (Fig. 10B).

**Redescription.** (Male and female similar, except for sexual features). Head more or less conical, hypognathous (Fig. 1A). Vertex of head normal, not dorsally protruding. Antennae long, filiform, longer than body. Scapus about twice as long and wide as pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular (Fig. 1A), about as long as or slightly shorter than scapus (0.80–1.20 mm), narrower than scapus and with a blunt apex, projecting straight between scapus and pedicellus; dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of the head (Fig. 1A), weakly protruding. Face longer than wide. Fastigium frontis triangular (Fig. 1A), not distinctly protruding. Frons flat and smooth, devoid of dots or wrinkles. Integument of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Frontal ocellus usually well defined (Fig. 1A), comparatively small; lateral ocelli occupying lateral portion of fastigium verticis near at the base. Pronotum mostly smooth; disc broadly rounded into paranota and caudally elongated (Fig. 1B,C); in lateral profile dorsal contour totally flat. Metazona produced caudally, in some species extending over the stridulatory region. Pronotal disc slightly widened from pro- to metazona; anterior margin concave; posterior margin strongly curved backward; principal transverse sulcus deep, curved, continuous at midline; devoid of second transverse sulcus; metazona without traces of longitudinal keel. Humeral sinus hardly indicated. Paranota longer than high (Fig. 1C); with a sulcus prolonged onto the metazona of the disc; ventral margin straight and oblique; ventro-caudal angle obtuse; caudal margin convex, straight. Anterior portion of mesopleurum with a vertical and thick carina. Thoracic auditory spiracle oval, in lateral view conceal

by the auditory swelling of the paranota, a bit higher than half the height of paranota and free from pronotum; marginal bristles dense; posterior edge of spiracle with a small, finger-like projection. Prosternum armed with a pair of spines (Fig. 2A); each spine as long as the inner portion of the forecoxa. Meso- and metabasisternal lobes trapezoidal and erected (Fig. 2A), in particular the metabasisternal lobes; lateral margins strongly concave; inner margins concave, both separated at the base; mesobasisternal lobes with each posterior angle bearing a strong tubercle-like projection. Metasternal medial plate with one delicate tubercle at each lateral portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coriaceous (Fig. 3A), with multiple secondary veins and cells; length of tegmina variable, usually elongated and slender, surpassing apices of hind femora, or shorter and broad. For coxae dorsally with a spine-like projection; mid- and hind coxae with a strong tubercle-like projection on the posterior ventral margin. Mid coxae without small dorsal spine. Fore femora armed ventrally with 2–3 spines ventrally on inner margins, mid femora with 2–4 spines on outer ventral margin, and hind femora with 0–3 on inner margin and 6–9 on outer margin. Inner genicular lobes of fore- and mid femora armed with an acute and tiny spine; inner and outer lobes of hind femora armed with one acute and strong spine. Fore tibiae square in cross section, dorsally rounded, ventrally angular. Fore- and mid tibiae armed with spines on both margins but only ventrally; spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibiae armed on all four dorsal and ventral margins; apex of hind tibia with a ventral pair and a dorsal pair of movable spurs. Tympanal region weakly swollen; tympanal slits on fore tibiae very narrow, facing forward, with a pair of small, elongated pits below and close to each tympanal slit. Dorsal surface of abdominal tergites smooth, unmodified.

**Male.** Tegmina with costal margin basally and apically distinctly concave and mid portion straight or slightly sinuate; anal margin with basal portion distinctly concave and mid portion straight; apex rounded. Pre-costal region usually narrowing toward apex, sometimes wide along the entire length (Fig. 17). Vein **RP** ramified into two subveins or devoid of them; vein **MA** with two to four subveins. Cubital region of tegmen short, usually extending to less than half the length of the tegmen, but can be unusually extended to more than half the length of the tegmen; with dense network of veinlets. Veins **M+CuA** twice as broad as **MA**. Vein **Cu1** weakly marked. Region between vein **CuPa** and the mirror mostly membranous, devoid of pigmentation. Vein **CuPb** of left tegmen irregular (Fig. 4), very narrow at left and right portion, mid portion wider; maximum width of vein 0.24 to 0.37 mm. Stridulatory file 1.59 to 1.76 mm long,

with 116 to 213 teeth; length of the smallest teeth 0.03 mm to 0.04 mm, and of the largest ones 0.08 mm to 0.11 mm; teeth lamelliform, homogenously arranged on the file; usually few teeth dispersed at the distal end of the file (right end in ventral view). Vein **CuPb** of right tegmen much narrower than the left one (Fig. 5); length 0.45 to 1.26 mm; vein at the middle considerably wider than teeth (0.08 to 0.26 mm); number of teeth 84 to 143. Left mirror region fairly large, almost reaching the anal margin of the tegmen; vein parallel to **CuPb** straight and slightly oblique; the other mirror-region-delimiting veins forming semi-circle; portion close to anal margin pigmented. Right mirror oval; completely transparent. Stridulatory region ventrally with dense small spine-like microstructures (Fig. 6A). Tergite IX with lateral portions a bit wider than the remaining tergites. Tergite X subquadrate (Fig. 7A), with lateral portions as long as tergite IX. Posterior portion of tergite X, cerci and subgenital plate with dense and short bristles. Epiproct large and triangular, with a longitudinal fold at midline of the basal portion. Cerci with the entire integument bearing tubercles and bristles (Fig. 8), but with smooth apex; integument of posterior ventral portion finer than the remaining structure, forming an excavation without or a few scattered tubercles. Paraprocts comparatively modified (Fig. 9), consisting of a large disc which is directly attached to each cercus, and a free, upcurved and elongated projection; the latter projection usually with an acute apex; portion close to each cercus with a small finger-like process; when cerci and paraprocts are close (Fig. 7A), the paraprocts fit under the cerci. Subgenital plate usually with a pair of short styli (Fig. 10A), usually oriented inward, rarely longer and parallel (Fig. 10K); disc with an apical V-shaped emargination. Phallus with processes of titillator consisting of dense spine-like and strongly sclerotized microstructures over lateral portions of lobe **dl** (Fig. 11A), the form of these grouped microstructures varies between species. In some species there are secondary portions with microstructures, mostly scattered. Sclerites **TS** completely attached to lobe **dl**; each **TS** is close to each group of microstructures on **dl**; sometimes **TS** is hidden under the group of microstructures; **TS** with the outer margin characteristically rounded, this portion fits under the group of microstructures. The **TS** is expanded inwardly toward the lobe **vdl**, and each **TS** is fused with each sclerite **VS**. Both sclerites **TS+VS** are widely separated at midline. The fold **fdl** is usually laterally elongated. The vesicles **ejv** are oval and small; the apodemes **ap** are usually defined by a membranous thicker portion, but sometimes there is an elongated sclerite **AP**. The lobe **vl** is formed by two folds, an upper and a lower pair; the apex of each fold ending in an acute tip.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular, large. Paraprocts triangular with a dorsally expanded concave tip, surrounding the epiproct. Cerci simple (Fig. 1D), short, cylindrical and acuminate. Subgenital plate with basal portion wider than apical portion (Fig. 10B); the plate usually consisting of two regions, one joined directly to the abdomen, and an outer and second one projected over the first region; both regions vary in shape between species. Ovipositor concave (Fig. 1D), shorter than hind femur, upcurved; dorsal valve about three times as wide as ventral one, somewhat expanded at middle; apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Males and females of a particular species bear the same coloration pattern. General coloration yellowish with dark brownish regions and markings (Fig. 14). The following components are dark brownish: sclerites of antennal scrobes, scapus and pedicellus; cutting edges of mandibles. Femora and tibiae with blackish markings close to the apices and at tympanal region. Tip of cercus and tip of projection of paraprocts reddish. Coloration is conserved in dead specimens.

**Distribution.** *Agraecia* has a wider distribution if compared with other South American Agraeciini (Fig. 15A). Species of *Agraecia* are distributed from southern Brazil to Paraguay and northern Argentina. Nevertheless, the species have restricted distributions. *Agraecia punctata* (mentioned above with **Gen. nov. 2 nigrifrons comb. nov.**) occurs only at the south of Bahia. *Agraecia sp. nov. 2* was collected only on the north of the state of Espírito Santo. *Agraecia dorsalis* and the rare *Agraecia sp. nov. 4* were collected only in the ReBio Sooretama, showing they have the same restricted distribution as *Monocerophora* sp. and *Listroscelis sooretama* Fialho *et al.* (see Fialho *et al.* 2014). *Agraecia watopotami sp. nov.* was found only in the middle east of Minas Gerais, with distribution similar to that of **Gen. nov. 1 sp.3 nov.** and *Listroscelis carinata* Karny. *Agraecia sp. nov. 3* inhabits the south of Rio de Janeiro state, occurring together with **Gen. nov. 1 maculata comb. nov.**, **Gen. nov. 3 abbreviata comb. nov.**, and the listroscelidines *Listroscelis itatiaia* Fialho *et al.* and *Monocerophora spinosa* (Karny). *Agraecia agraecioides comb. nov.* has a wider distribution, through all the three Paraná Provinces (*sensu* Morrone 2014).

**Included species.** *Agraecia* comprises the following species: *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825), *Agraecia dorsalis* Karny, 1907, *Agraecia agraecioides* (Rehn, 1911) **comb. nov.**, *Agraecia sp. nov. 1*, *Agraecia sp. nov. 2*, *Agraecia sp. nov. 3*, and *Agraecia sp. nov. 4*. The species differ in pattern of dark

brownish markings on legs, size, shape and venation of the tegmina, shape of male cerci and paraprocts, subgenital plate of male and female, and in the components of the phallus.

**Excluded species.** *Agraecia maculata* Redtenbacher, 1891, *Agraecia subulata* Redtenbacher, 1891, *Agraecia nigrifrons* Redtenbacher, 1891, *Agraecia abbreviata* Redtenbacher, 1891, *Agraecia pulchella* Hebard, 1927, *Agraecia vittata* Redtenbacher, 1891, *Agraecia cesairei* Hugel, 2009, *Agraecia viridipennis* (Redtenbacher, 1891), *Agraecia vittipes* Redtenbacher, 1891, *Agraecia reticulata*† Piton & Théobald, 1939.

**Incertae sedis.** The following two species remain in *Agraecia*; however they need to be assigned to different genera: *Agraecia fallax* Karny, 1911, **nomen dubium** and *Agraecia festae* Griffini, 1896.

**Notes.** *Bertoniella* Rehn, 1911 **syn. nov.** of *Agraecia*. When Rehn (1911) erected *Bertoniella*, the genus was compared with *Lobaspis* Redtenbacher, 1891, *Gonatacanthus* Karny, 1907, *Anthracites* Redtenbacher, 1891, *Paralobaspis* Gigliot-Tos, 1898, *Nannagroecia* Redtenbacher, 1891, and *Alphopteryx* Walker, 1869 (currently *Veria* Walker, 1869). *Bertoniella* was not compared with *Agraecia*. Posteriorly, Pirán (1942) described *Guaranina*, which was synonymized with *Bertoniella* by Rehn (1942). Pirán (1942) compared *Guaranina* only with *Xiphelimum* Caudell, 1906. The defining features of both *Bertoniella* and *Guaranina* correspond to those of *Agraecia sensu novo*.

#### **Identification key to the species of *Agraecia* Audinet-Serville, 1831, *sensu novo***

1. Femora with blackish marks at the base and all genicular lobes (Fig. 18)...***A. agraecioides* (Rehn) comb. nov.**
- 1'. Femora without blackish marks (Fig. 1)...(2)
- 2(1'). Male subgenital plate with long and parallel styli (Fig. 10K)...***Agraecia* sp. nov.**
- 4
- 2'. Male subgenital plate with short styli, oriented inward (Fig. 10A)...(4)

- 4(2'). Male tegmina 27.00–28.00 mm long; paraprocts with disc large and rounded (Fig. 9A). Female subgenital plate with ventral region narrow, the two apically projecting portions touching each other at midline (Fig. 10B)...***A. punctata* (Saint-Fargeau & Audinet-Serville)**
- 4'. Male tegmina 24.00–26.00 mm long; paraprocts with disc large, or short and rounded, or semitriangular. Female subgenital plate with ventral region wide, the two apically projecting portions not touching at midline...(5)
- 5(4'). Male tegmina about 24.00 mm. Phallus with microstructures of the titillator process forming two symmetric oval transversal groups (Fig. 12B)... ***A. dorsalis* Karny**
- 5'. Male tegmina 25.00–26.00 mm; microstructures of the titillator process forming two asymmetric amorphous groups...(6)
- 6(5'). Cerci with dorsal portion weakly protruding (Fig. 8D); paraprocts with disc short and triangular (Fig. 9D). Phallus with groups of microstructures of the titillator process conspicuously asymmetrical (Fig. 12D)...***Agraecia* sp. nov. 1**
- 6'. Cerci with dorsal portion protruding; paraprocts with disc large and more rounded. Phallus with groups of microstructures of the titillator process just slightly asymmetrical ...(7)
- 7(6'). Cerci shortened, with tip curved upward (Fig. 8E)...***Agraecia* sp. nov. 2**
- 7'. Cerci elongated, with tip curved downward (Fig. 8F)...***Agraecia* sp. nov. 3**

***Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825)**

(Figs 1, 2A, 3A, 4, 5, 7A, 8A, 9A, 10A,B, 11A, 12A, 14A, 15A)

*Locusta punctata* Saint-Fargeau & Audinet-Serville, 1825: 342.

*Agraecia punctata* (Saint-Fargeau & Audinet-Serville), Audinet-Serville, 1831: 153.

**Neotype male**, here designed (CELC), labeled \Brasil, BA, Porto Seguro, P.N. do Pau Brasil, 4–6, I, 2012, J. Chamorro *leg.* [printed on white paper] \ 15-Cono-Pau [printed on white paper] \ *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825)

[handwritten on blue paper]\. TL 25.00; PL 8.00; TegL 28.00; FF 7.00; FT 8.00; HF 18.00; HT 19.00; sFF 2; sMF 4; sHF inner 2; sHF outer 8.

**Neotype female**, here designed (CELC), labeled \Brasil, BA, Porto Seguro, P.N. do Pau Brasil, 4–6, I, 2012, J. Chamorro *leg.* [printed on white paper] \ 6-Cono-Pau [printed on white paper] \ *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825) [handwritten on blue paper]\. TL 35.00; PL 8.00; TegL 32.00; FF 8.00; FT 9.00; HF 18.00; HT 20.00; sFF 3; sMF 4; sHF inner 2; sHF outer 7.

See below comments on unspecified primary type.

**Diagnostic redescription.** This species can be distinguished from the remaining *Agraecia* species by the following combination of features. **Male.** Pronotum with posterior portion short (Fig. 1B), leaving the stridulatory region of the tegmina exposed. Tegmina elongated and slender (Fig. 3A). Pre-costal region narrowing toward apex; vein **Ri** devoid of ramifications; vein **Rs** with three subveins; vein **MA** with more than two subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4A, with 213 teeth. Cerci comparatively elongated (Fig. 8A); dorsal portion weakly protruding; ventral subapical portion finer, dorsally and ventrally; apex strongly curved downward. Paraprocts with projection as long as disc (Fig. 9A); projection uniformly curved upward. Subgenital plate narrowing gradually toward apex (Fig. 10A); apical emargination cutting of about one-third the length of the plate; styli short, one-eighth the length of the plate, oriented inward. Titillator with processes of **ti** slightly asymmetric (Fig. 12A); dorsal region on **dl** with a secondary group of microstructures at midline; sclerite **VS** broad, expanded over a large portion of the lobe **vdl**.

**Female.** Subgenital plate with basal portion laterally elongated (Fig. 10B); mid portion of the plate projected, protruding over the basal portion; this mid portion is narrower than the basal one; projections of the apical portion oriented inward, touching at midline; emargination between projections less than one-third the length of the plate.

**Variation.** Measurements of males (n = 5): TL 24.00–29.00; PL 8.00; TegL 27.00–28.00; FF 7.00–9.00; FT 8.00–9.00; HF 16.00–19.00; HT 16.00–19.00. Measurements of females (n = 7): TL 28.00–35.00; PL 8.00–9.00; TegL 32.00–36.00; FF 8.00–10.00; FT 9.00–10.00; HF 18.00–22.00; HT 20.00–21.00; OL 15.00–17.00. Spines of male and female (n = 13): sFF 2–3; sMF 3–4; sHF inner 0–3; sHF outer 6–9. The only available measurement for the female holotype is the body length, of “II lignes”, corresponding to about 25.00 mm. Some specimens are darker than others.

**Distribution.** This species possibly inhabits in the costal portion of the state of Bahia in Brazil. It is currently registered in the P. N. do Pau Brasil and P. N. do Descobrimento. Female holotype was also collected in Bahia (Fig. 15A).

**Specimens examined.** Nineteen specimens (CELC) labeled \Brasil, BA, Porto Seguro, P.N. do Pau Brasil, 4–6, I, 2012, J. Chamorro *leg.* [printed on white paper] \ *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825) [printed on white paper], and additionally labeled as follows: seven adult males \4\, \12\, \24\, \27\, \31\, \32\, \33\, and labeled \-Cono-Pau [printed on white paper]; eight adult females \3\, \5\, \7\, \9\, \10\, \16\, \23\, \30\, and labeled /-Cono-Pau [printed on white paper]; four immature females \13\, \14\, \17\, \25\, and labeled /-Cono-Pau [printed on white paper]. Twenty-five specimens (CELC) labeled \Brasil, BA, Prado, P.N. do Descobrimento, 13–15, I, 2012, J. Chamorro *leg.* [printed on white paper] \ *Agraecia punctata* (Saint-Fargeau & Audinet-Serville, 1825) [printed on white paper], and additionally labeled as follows: twelve adult males \5\, \8\, \20\, \21\, \24\, \25\, \28\, \30\, \31\, \36\, \38\, \40\, and labeled \-Cono-Des [printed on white paper]; twelve adult females \1\, \4\, \6\, \7\, \17\, \18\, \19\, \22\, \23\, \27\, \29\, \35\, and labeled \-Cono-Des [printed on white paper]; one immature female \33-Cono-Des [printed on white paper].

**Comments.** *Agraecia punctata* was described based on one female. The identity of the female holotype is doubtful and the information available in the description (see Audinet-Serville 1838[1839]) is insufficient for the accurate identification of this species. Additionally there are no detailed measurements of the specimen. The only available schematic drawing (Audinet-Serville 1838[1839]) is not sufficient to distinguish several species of the Agraeciini genera. However there are one female and one male deposited in the NMW identified as *A. punctata*. Images of these specimens are available in OSF (taken by Holger Braun). Both specimens were identified by Audinet-Serville and were collected in Bahia, Brazil. As some of the specimens collected by us in the same region are similar to the specimens identified by Audinet-Serville, our opinion is that they do belong to *A. punctata*.

### ***Agraecia dorsalis* Karny, 1907**

(Figs 4B, 5B, 8B, 9B, 10C, 12B, 15A, 16, 17A)

**Holotype** (male, NMW) labeled \Minas Geraës Brasil 1897 ex coll. Fruhstorfer [typewritten on green paper] \ 22.096 [handwritten on red paper] \ determ. Karny *Agraecia dorsalis* m. [type- and handwritten on white paper] \ Holotype TYPUS [handwritten on red paper].

**Diagnostic redescription.** (Male only, based on new collected material). This species can be distinguished from the remaining *Agraecia* species by the following combination of features: Pronotum with posterior portion short (Fig. 16B), covering partially the stridulatory region. Tegmina elongated and slender (Fig. 17A). Pre-costal region narrowing toward apex; vein **Ri** devoid of ramifications; vein **Rs** with three subveins; vein **MA** with three subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4B, with 188 teeth. Cerci comparatively elongated (Fig. 8B); dorsal portion weakly protruding; ventral subapical portion finer dorsally than ventrally; last portion downward projected only at last apex. Paraprocts with projection longer than the disc (Fig. 9B); projection curved upward only at apical portion. Subgenital plate narrowing gradually toward apex (Fig. 10C); apical emargination cutting about of one-third the length of the plate; styli short, one-eighth the length of the plate, oriented inward. Titillator with processes **ti** symmetric (Fig. 12B); dorsal portion at midline of lobe **dl** with a group of microstructures; sclerites **VS** broad, expanded almost at the entire lobe **vdl**.

**Variation.** Measurements of males (n = 2, including holotype): TL 21.00–24.00; PL 7.50–8.00; TegL 24.00–25.00; FF 7.00; FT 7.00; HF 14.00–16.00; HT 15.00. Spines of male (n = 1): sFF 2; sMF 3; sHF inner 2; sHF outer 7.

**Distribution.** This species was originally registered from Minas Gerais (Karny 1907). *Agraecia dorsalis* was collected in ReBio de Sooretama, in the state of Espírito Santo, Brazil (Fig. 15A).

**Specimens examined.** One adult male (CELC) labeled \Brasil, ES, Sooretama, ReBio de Sooretama, 29, XI to 2, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ *Agraecia dorsalis* Karny, 1907 [printed on white paper] \ 38-Cono-Sooretama [printed on white paper].

**Comments.** Instead of *A. dorsalis* was originally registered for Minas Gerais, the specimen collected in Espírito Santo have the same appearance as the holotype. Additionally, males of this species are the smaller of the genus (with exception of *A. agraeciodes*); measurements of males and data from holotype (Karny 1907) are similar.

Several females were collected in ReBio Sooretama, but as there is a second and new species in the same locality, *Agraecia* **sp. nov. 4**, there is insufficient information for determine which female correspond to which species.

***Agraecia agraeioides* (Rehn, 1911) comb. nov.**

(Figs 4C, 5C, 8C, 9C, 10D,E, 12C, 14B–D, 15A, 18)

*Bertoniella agraeioides* Rehn, 1911 syn.: 255.

*Guaranina daguerrei* Pirán, 1942 syn.: 4.

**Holotype male** (ANSP): Puerto Bertoni, Paraguay – November, 1909 (A. de Winkelried Bertoni.), Type No. 5176.

**Diagnostic redescription** (based on new collected material). This species can be distinguished from the remaining *Agraecia* species by the following combination of features. **Male**. Pronotum with posterior portion covering almost the entire stridulatory region (Fig. 18B). Tegmina comparatively broader and more rounded (Fig. 17B). Pre-costal region narrower only at the apex; vein **Ri** devoid of ramifications; vein **Rs** with two subveins; vein **MA** with two subveins. Cubital region of each tegmen elongated, extending beyond the half of the tegmen length. Left stridulatory file as shown in Fig. 4C; with about of 116 teeth. Cerci comparatively elongated; dorsal portion weakly protruding (Fig. 8C); with subapical portion finer dorsally; apical portion only strongly downward curved. Paraprocts with projection as long as disc (Fig. 9C); projection uniformly upward curved. Subgenital plate with basal portion about twice wider than apical portion (Fig. 10D); apical emargination cutting about of one-third the length of the plate, styli short, about of one-fifth the length of the plate, oriented inward. Titillator with processes **ti** symmetric (Fig. 12C); lobe **dl** devoid of additional areas with a group of microstructures; sclerites **VS** comparatively shorter, extending only on a short portion of the lobe **vdl**.

**Female**. Subgenital plate devoid of differentiated regions (Fig. 10E); apical projections backward oriented, separated at midline, forming an U-shaped emargination of about of one-third the length of the plate.

**Coloration**. Femora with a blackish spot at the apical portions; tibiae with a blackish spot at the basal and apical portions.

**Variation.** Measurements of males (n = 10, including holotype): TL 22.50–28.00; PL 8.00–9.20; TegL 13.50–18.00; FF 6.00–8.00; FT 6.00–9.00; HF 12.00–13.00; HT 12.00–16.00. Measurements of females (n = 9, including female of the original description): TL 26.00–29.00; PL 8.00–9.00; TegL 16.00–26.00; FF 8.00–9.00; FT 9.00; HF 16.20–20.00; HT 17.00–20.00; OL 12.00–15.00.

Spines of males and females (n = 16): sFF 2–3; sMF 3–4; sHF inner 0–3; sHF outer 6–9.

Some females collected in RPPN sítio do Zaca, and females from collection of MZUSP are smaller and bear reduced tegmina. In RPPN sítio do Zaca four adult females were captured, of them, one female is similar to the typical females of this species (code 2-Cono-Zaca, Fig. 18D); by contrast three females are smaller and bear reduced tegmina (Fig. 18E) and slightly different subgenital plate. No male was collected. Measurements of these females with reduced tegmina are showed separately: Measurements of short winged females (n = 4): TL 21.00–25.00; PL 7.00–8.00; TegL 10.00–11.00; FF 7.00; FT 7.00–8.00; HF 14.00–16.00; HT 12.00–15.00; OL 11.00.

Spines of females with short wings (n = 4): sFF 2–3; sMF 2–3; sHF inner 1–2; sHF outer 6–7.

**Distribution.** This species is distributed from Pará at the North of Brazil to Paraguay and North of Argentina (Fig. 15A). Additionally to the examined specimens, *A. agraeioides* **comb. nov.** was registered from Posadas, in Argentina (Pirán 1942).

**Specimens examined.** Three adult males (CELC) \Brasil, MG, Alto Caparaó, P.N. do Caparaó, 23–26, XI, 2011, J. Chamorro *leg.* [printed on white paper] \ *Agraeicia agraeioides* (Rehn, 1911) **comb. nov.** [printed on white paper], with the codes: \2\, \3\, \4\ and labeled \Cono-Caparaó [printed on white paper]. One male adult (CELC) \Brasil, MG, Alto Caparaó, P.N. do Caparaó, 4–8, II, 2012, V. Fialho [printed on with paper] \ *Agraeicia agraeioides* (Rehn, 1911) **comb. nov.** [printed on white paper], and labeled \32-Cono-Caparao [printed on white paper]. Fourteen specimens (CELC) labeled \Brasil, MG, Timoteo, PERD, 9–12, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ *Agraeicia agraeioides* (Rehn, 1911) **comb. nov.** [printed on white paper], and additionally labeled as follows: five adult males \15\, \27\, \28\, \29\, \30\, and labeled \Cono-PERD [printed on white paper]; nine adult females \5\, \6\, \8\, \12\, \21\, \31\, \32\, \33\, \34\, and labeled \Cono-PERD [printed on white paper]. Four adult females (CELC) labeled \Brasil, MG, Ipatinga, RPPN Sítio do Zaca, 5–9, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ *Agraeicia agraeioides* (Rehn, 1911) **comb. nov.** [printed on white paper], with codes: \2\, \4\, \20\, \24\, and labeled \Cono-

Zaca [handwritten on white paper]\. One adult female (IBB) \Brasil, SP, Salesópolis, Est. Biol. de Boracéia, 20–27.iv.2011 F.A.G. Mello, col. [printed on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\, and additionally labeled \TETTIGO/BO/L16IH [printed on white paper]\. Two adult males (CEIOC) labeled \PALMEIRAS, ESTADO DO RIO, S. LOPES, 7-1-39 [typewritten on brownish paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [printed on white paper]\. \Brasil – São Paulo, Juquiá – Fonte Tapir, 400 mts. 3.XI.1941, Trav. & trav.Fo. [typewritten on whitish paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [printed on white paper]\. Two adult females (CEIOC) labeled \Itatiaia, E. do Rio-Brasil, J.F. Zikan, 18-I-48 [type- and handwritten on white paper] \ Coleção J.F. Zikan [typewritten on whitish paper] \ 018-1-48 [handwritten on white paper]\. \Calado-Rio Doce, Minas 12 a 15. 11. 39, Martins e Lopes [typewritten on brownish paper] \ 4606 [typewritten on brownish paper] \ *Agraecia punctata* (servile, 1825), Costa Lima det. [typewritten on brownish paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [printed on white paper]\. One adult male (MZUSP) labeled \ Agraeidae sp., Brasil (PA) Ceu Zul, Creta de Lourdes, 26-viii-2000 // A. olebz-Akio [handwritten on white paper] \ Coleção Alejo Mesa [printed on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\. One adult male and two adult females (MZUSP) labeled \BR: MG: Botelhos, Córrego da Onça, 21°40'80"s / 46°22'09"S W, Malaise – mata. 20-XI-28. XII. 2006., Amorin, Falaschi & Oliveira [handwritten on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\. Three adult females (MZUSP) labeled \BR: MG: Botelho, Corrego da Onça, 21°40'90"S 46°22'05" W, malaise – mata 20.XI.2006, Amorin, Falaschi & Oliveira col. Biota-Fapesp. [handwritten on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\. One adult female (MZUSP) labeled \Tanhaem (Cidade Sta Julia), SP – 28.XII.1978, L. R. Fontes & P. S. Terra col., Restinga pouco úmida, a 800 m da praia [handwritten on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\. One adult female (MZUSP) labeled \Piedade S g R Preto, S. Paulo, 20-vii-965, L. lata col [handwritten on white paper] \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\. One adult female (MZUSP) labeled \Brasil: SP, P.E. Jacupiranga, Núcleo Cédro (656 m), 245747.0S 482500.0W, 27.i-02.ii.2006, E. Aguiar & MG Esteres col. \ *Agraecia agraeoides* (Rehn, 1911) **comb. nov.** [handwritten on white paper]\.

**Comments.** Individuals are very scarce in field and inhabit wetter and best preserved areas within the forest. They are very fast and difficult to collect.

***Agraecia* sp. nov. 1**

(Figs 4D, 5D, 8D, 9D, 10F, 12D, 15A)

**Holotype male** (CELC) labeled \Brasil, MG, Timoteo, PERD, 9–12, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 22-Cono-PERD [printed on white paper] \ *Agraecia* sp. nov. 1 [handwritten on red paper]. TL 26.00; PL 8.00; TegL 26.00; FF 8.000; FT 7.00; HF 19.00; HT 16.00; sFF 2; sMF 4; sHF inner 1; sHF outer 6.

**Diagnostic description.** This species can be distinguished from the remaining *Agraecia* species by the following combination of features. Pronotum with posterior short, leaving the stridulatory region partially exposed. Tegmina elongated and slender (Fig. 17C). Pre-costal region narrowing toward apex; vein **Ri** devoid of ramifications; vein **Rs** with two or three subveins; vein **MA** with more than two subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4D, with 143 teeth. Cerci comparatively elongated (Fig. 8D); dorsal portion weakly protruding; ventral subapical portion finer dorsally than ventrally; apical portion only with tip downward curved. Paraprocts with projection about of three times longer than the disc (Fig. 9D); projection upward curved only at apex. Subgenital plate narrowing gradually toward apex (Fig. 10F); apical emargination cutting about of one-third the length of the plate; styli short, one-eighth the length of the plate, oriented inward. Titillator with processes **ti** asymmetric (Fig. 12D); dorsal portion of lobe **dl** at midline with a group of microstructures; sclerite **VS** short, expanded only on a partial portion of the lobe **vdl**.

Female unknown.

**Distribution.** This species is registered by the first time from the PERD in Minas Gerais, Brazil (Fig. 15A).

***Agraecia* sp. nov. 2**

(Figs 4E, 5E, 8E, 9E, 10G,H, 13E, 14E, 15A, 17D, 20)

**Holotype male** (CELC) labeled \Brasil, ES, Flona do Rio Preto, 02–05, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 13-Cono-Riopreto [printed on white

paper] *Agraecia* **sp. nov. 2** [handwritten on red paper]\. TL 25.00; PL 8.00; TegL 25.00; FF 7.00; FT 8.00; HF 19.00; HT 19.00; sFF 2; sMF 3; sHF inner 2; sHF outer 7.

**Allotype female** (CELC) labeled \Brasil, ES, Flona do Rio Preto, 02–05, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 14-Cono-Riopreto [printed on white paper] \ *Agraecia* **sp. nov. 2** [handwritten on blue paper]\. TL 25.00; PL 9.00; TegL 35.00; FF 9.00; FT 10.00; HF 21.00; HT 21.00; OL 15.00; sFF 2; sMF 3; sHF inner 2; sHF outer 6.

**Diagnostic description.** This species can be distinguished from the remaining *Agraecia* species by the following combination of features. **Male.** Pronotum with posterior portion short (Fig. 20B), leaving the stridulatory region exposed. Tegmina elongated and slender (Fig. 17D). Pre-costal region narrowing toward apex; vein **Ri** devoid of ramifications; vein **Rs** with three subveins; vein **MA** with two or more than two subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4E, with 190 teeth. Cerci comparatively shorter (Fig. 8E); dorsal portion weakly protruding; ventral subapical portion finer dorsally and ventrally; apex upward curved. Paraprocts with projection as long as disc (Fig. 9E); projection uniformly curved upward. Subgenital plate sharply narrowing towards the apex (Fig. 10G); apical emargination cutting more than one-third the length of the plate; styli short, slightly shorter than one-ninth the length of the plate, oriented inward. Titillator with processes **ti** asymmetric (Fig. 13E); dorsal lobe **dl** at midline with a group of microstructures; Sclerite **VS** broad, expanded on a large portion of the lobe **vdl**.

**Female.** Subgenital plate with an elongated basal region (Fig. 10H); mid portion of the plate slightly projected ventrally; this mid portion comparatively broad; projections at the apical portion separated, forming an U-shaped emargination cutting less than one-third the length of the plate.

**Variation.** Measurements of males ( $n = 2$ , including holotype): TL 24.00–25.00; PL 8.00; TegL 25.00–26.00; FF 7.00; FT 7.00–8.00; HF 16.00–19.00; HT 17.00–19.00. Measurements of females ( $n = 4$ , including allotype): TL 25.00–29.00; PL 8.00–9.00; TegL 34.00–36.00; FF 9.00; FT 8.00–1.00; HF 19.00–21.00; HT 20.00–21.00; OL 14.00–17.00. Spines on male and female ( $n = 6$ ): sFF 2; sMF 2–4; sHF inner 1–3; sHF outer 6–7.

**Distribution.** This species is registered by the first time in Flona do Rio Preto in Espirito Santo, Brazil (Fig. 15A).

**Additional type series. Six Paratypes.** All specimens were collected at single locality and labeled as follows: \Brasil, ES, Flona do Rio Preto, 02–05, XII, 2011, J.

Chamorro *leg.* [printed on white paper]\, additionally labeled \ *Agraecia sp. nov. 2* [handwritten on blue paper]\. Two males with codes \8\, \12\; four females \4\, \7\, \9\, \10\, and labeled \-Cono-RioPreto [printed on white paper]\.

### ***Agraecia sp. nov. 3***

(Figs 4F, 5F, 8F, 9F, 10I,J, 13F, 14F, 15A, 17E, 21)

**Holotype male** (CELC) labeled \Brasil, RJ, Itatiaia, P.N. de Itatiaia, 7–13, XI, 2011, J. Chamorro *leg.* [printed on white paper] \ 15-Cono-Itatiaia [printed on white paper] \ *Agraecia sp. nov. 3* [handwritten on red paper]\. TL 27.00; PL 8.00; TegL 26.00; FF 8.00; FT 7.00; HF 16.00; HT 16.00; sFF 3; sMF 3; sHF inner 2; sHF outer 6.

**Allotype female** (CELC) labeled \ Brasil, RJ, Itatiaia, P.N. de Itatiaia, 7–13, XI, 2011, J. Chamorro *leg.* [printed on white paper] \ 3-Cono-Itatiaia [printed on white paper] \ *Agraecia sp. nov. 3* [handwritten on blue paper]\. TL 29.00; PL 9.00; TegL 36.00; FF 8.00; FT 9.00; HF 20.00; HT 20.00; OL 17.00; sFF 2; sMF 3; sHF inner 1; sHF outer 7.

**Diagnostic description.** This species can be distinguished from the remaining *Agraecia* species by the following combination of features. **Male.** Pronotum with posterior portion short (Fig. 21B), leaving the stridulatory region partially exposed. Tegmina elongated and slender (Fig. 17E). Pre-costal region narrowing toward apex; vein **Ri** devoid of ramifications; **Rs** with two or three subveins; **MA** with two or more than two subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4F, with 123 teeth. Cerci elongated (Fig. 8F); dorsal portion strongly protruding; ventral subapical portion thick; apical portion only strongly downward curved at apex. Paraprocts with projection shorter than the disc (Fig. 9F); projection only with apical portion upward curved. Subgenital plate narrowing gradually toward apex (Fig. 10I); discal apical emargination cutting of about less than one-half the length of the plate; styli short, of about less than one-fifth the length of the plate, oriented inward. Titillator with processes of **ti** asymmetric (Fig. 13F); dorsal portion of lobe **dl** at midline with group of microstructures; sclerite **VS** broad, expanded on a large portion of the lobe **vdl**.

**Female.** Subgenital plate with basal region short (Fig. 10J); mid portion of the plate projected, protruding over the basal region; this mid portion comparatively

broader; projections of the apical portion backward oriented, separated at midline; an U-shaped emargination between projections of about one-third the length of the plate.

**Distribution.** This species is registered in the state of Rio de Janeiro, Brazil (Fig. 15A).

**Variation.** Measurements of females (n = 3): TL 28.00–35.00; PL 8.00–9.50; TegL 35.00–38.00; FF 9.00–10.00; FT 9.00–10.00; HF 20.00–21.00; HT 20.00–21.00; OL 17.00–20.00.

Spines of females (n = 3) sFF 2–3; sMF 3; sHF inner 1–2; sHF outer 7–8.

**Additional type series.** **One Paratype female** (CEIOC) labeled \RIO DE JANEIRO, GAVEA, BRASIL, J. JURBERG, 1-1963 [type- and handwritten on white paper] \ *Agraecia* **sp. nov. 3** [handwritten on blue paper] \ **One Paratype female** (MNRJ) labeled \Represa RIO GRANDE, Guanabara, Brasil, 16/30 Setembro 1960, F. M. Oliveira [printed and handwritten on brownish paper] \ COLEÇÃO CAMPOS SEABRA [printed on brown paper] \ *Agraecia* **sp. nov. 3** [handwritten on blue paper] \

#### ***Agraecia* sp. nov. 4**

(Figs 4G, 5G, 8G, 9G, 10K, 13G, 15A, 22)

**Holotype male** (CELC) labeled \ Brasil, ES, Sooretama, ReBio de Sooretama, 29, XI to 2, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 1-Cono-Sooretama [printed on white paper] \ *Agraecia* **sp. nov. 4** [handwritten on red paper] \ TL 26.00; PL 8.00; TegL 25.00; FF 8.00; FT 8.00; sFF 2–3; sMF 3 (no hindlegs).

**Diagnostic description.** This species can be distinguished from the remaining *Agraecia* species by the following combination of features. **Male.** Pronotum with posterior portion short (Fig. 22B), leaving the stridulatory region partially exposed. Tegmina elongated and slender (Fig. 17F). Pre-costal region narrowing toward apex; vein **Ri** with two ramifications; vein **Rs** with two subveins; vein **MA** with more than two subveins. Cubital region of each tegmen comparatively shorter. Left stridulatory file as shown in Fig. 4G, with 120 teeth. Cerci comparatively elongated (Fig. 8G); dorsal portion strongly protruding (Fig. 8GC); ventral subapical portion finer dorsally and ventrally; preapical and apical portion downward curved. Paraprocts as long as the disc (Fig. 9G); projection curved upward only at the apex. Subgenital plate more elongated than in the remaining species (Fig. 10K); basal portion broader than the apical one; apical emargination cutting less of one-fifth the length of the plate; styli

comparatively longer, about of more than half of the length of the plate, backward oriented. Titillator with processes **ti** slightly asymmetric (Fig. 13C); lobe **dl** devoid of secondary areas with microstructures; sclerite **VS** narrow, extending on a short portion of the lobe **vdl**.

**Variation.** Measurements (n = 2, including holotype). TL 25.00–26.00; PL 7.00–8.00; TegL 25.00–26.00; FF 7.00–8.00; FT 8.00; HF 16.00; HT 17.00.

Spines of males (n = 2, holotype lacking hindlegs): sFF 2–3; sMF 3; sHF inner 1; sHF outer 6.

**Distribution.** This new species is registered by the first time only from the ReBio de Sooretama in Espirito Santo, Brazil (Fig. 15A).

**Additional type series. Three Paratypes** (CELC), one adult male and two immature males labeled \ *Agraecia* **sp. nov.** 4 [handwritten on blue paper] \ and respectively labeled \39\, \4\, \11\, and labeled \Cono-Sooretama [printed on white paper]\.

**Comments.** Several females were collected in ReBio Sooretama, but as there is a second species in the same locality, *Agraecia dorsalis* Karny, 1907, there is not enough information for determine which female correspond to which species.

### ***Parasubria* Karny, 1911**

(Figs 2B, 3B, 15B, 23, 24A,B, 25, 26A,B, 27A)

**Type species.** *Parasubria ziczac* Karny, 1911

**Diagnosis.** This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis as long as and as broad as scapus (Fig. 23A). Tegmina with vein **M+CuA** a bit thick than vein **M**, extends beyond the posterior margin of the mirror (Fig. 3B). Male postabdomen with posterior portion of tergite X strongly prolonged behind into two lobes (Fig. 25A,B); paraprocts sickle-shaped (Fig. 25A); cerci elongated (Fig. 25A,B), cylindrical and curved, with apical projections; subgenital plate with a shallow U-shaped emargination at apex (Fig. 26A); titillator with sclerites **TS+VS** attached to the lobe **dl** (Fig. 25C,D), excepting for the tip of **VS**; sclerites **TS** mostly smooth, excepting for the small spiny-microstructures on the apical portion; processes of the titillator **ti** consisting of dense and grouped sclerotized microstructures at the dorsum and sides of lobe **dl**. Female postabdomen with tergite X

straight; subgenital plate elongated and with two projections forming an U-shaped emargination (Fig. 26B).

**Description.** (Male and female similar, except for sexual features. Head more or less conical, hypognathous (Fig. 23A). Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus about twice as long and wide as pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular (Fig. 23A), about as long and broad as the scapus and with a blunt apex, projected straight between scapus and pedicellus;

dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to the size of head (Fig. 23A), weakly protruding. Face longer than wide. Fastigium frontis triangular (Fig. 23A), not distinctly protruding. Frons flat and smooth, devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium usually well defined (Fig. 23A), comparatively small; each lateral ocellus defined over each lateral portion of fastigium verticis, close to its base. Pronotum mostly smooth (Fig. 23B,C); disc broadly rounded into paranota and posterior portion shouldered; metazona produced caudad, but leaving the tegminal tympanum exposed. Pronotal disc slightly widened from pro- to metazona; anterior margin concave at its anteriormost portion; posterior margin straight; principal transverse sulcus deep, curved, discontinuous at midline; devoid of second transverse sulcus; metazona without traces of longitudinal keel. Humeral sinus weakly indicated. Paranota wider than deep (Fig. 23C); with a sulcus prolonged to the metazona on disc; ventral margin obliquely curved; ventro-caudal angle obtuse; caudal margin curved. Anterior portion of mesopleurum with a vertical and thick carina. Thoracic auditory spiracle oval, hidden under the auditory swelling, as long as half the length of paranota and free from pronotum; marginal trichobotria dense; posterior edge of spiracle with a small, finger-like projection. Prosternum unarmed or with a tiny pair of tubercles (Fig. 2B). Meso- and metabasisternal lobes trapezoidal (Fig. 2B), slightly projected downward; lateral margins of metabasisternal lobes semi-triangular, angulated, mesobasisternal lobes concave; inner margins concave, both separated at the base; meso- and metabasisternal lobes devoid of projections on each posterior portion. Metasternal medial plate smooth. Wings in both sexes fully developed (macropterous species). Tegmina coriaceous (Fig. 3B), with multiple secondary veins and cells; length of tegmina variable, as long as or shorter than the abdomen. Pro coxae with an elongated, strong and forwardly curved spine-like projection dorsally; mid and hind

coxae with a tiny tubercle-like projection on each posterior portion, ventrally. Mid coxae devoid of small spine on basal portion dorsally. Fore femora armed with spines (2) ventrally only on inner margins, mid femora with spines (2–3) on outer margins, and hind femora on both margins (inner, 1–2; outer 4). Only inner and outer genicular lobes of hind femora armed with one spine. Fore- and mid tibiae armed with spines on both margins but only ventrally; spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibiae armed on all four dorsal and ventral margins; apex of each hind tibia with one pair dorsally and one pair ventrally of movable spurs. Tympanal region weakly swollen; each tympanal slit on fore tibiae very narrow, facing forward, with a pair of small, elongated pits below and close to each tympanal slit. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with costal margin with basal and apical portion distinctly concave and mid portion straight or slightly sinuate (Fig. 3B); anal margin with basal portion distinctly concave and mid portion straight, apical portion curved toward posterior margin; posterior margin outwardly concave. Pre-costal region usually wide at the entire length. Vein **RP** ramified into two subveins; vein **MA** with two subveins. Cubital region of each tegmen than half the length of the tegmen with dense network of veinlets. Veins **M+CuA** twice as broad as **MA**. Vein **Cu1** weakly marked. Region between vein **CuPa** and the mirror mostly membranous, very pigmented. Vein **CuPb** of left tegmen mostly straight (Fig. 24A), uniform, with margins slightly concave; maximum width of vein 0.24 to 0.37 mm. Stridulatory file 1.59 to 1.76 mm long, with 116 to 213 teeth; length of the smallest teeth 0.03 mm to 0.04 mm, and of the largest ones 0.08 mm to 0.11 mm; teeth lamelliform, homogeneously arranged on the file; usually few teeth dispersed at the right portion of the file. Vein **CuPb** of right tegmen much narrower than the left one (Fig. 24B); length 0.45 to 1.26 mm; vein at the middle wider than teeth (0.08 to 0.26 mm); number of teeth 84. Left mirror rectangular, comparatively larger, away from the anal margin and very pigmented. Right mirror rectangular; completely membranous. Stridulatory region devoid of spiny-like microstructures ventrally; but sometimes with microstructures on dorsal portion. Tergite IX with lateral portions a bit wider than the remaining tergites. Tergite X with reduced lateral portions (Fig. 23C). Posterior portion of tergite X, cerci and subgenital plate with dense short bristles. Epiproct large and triangular, as long as paraprocts, devoid of longitudinal fold at midline of the basal portion. Cerci with the entire tegmen bearing strong tubercles and bristles, excepting for the apical projections (Fig. 25A,B). Paraprocts simple (Fig. 25A), consisting only of a short plate sickle-shaped; portion

close to each cercus with a small finger-like projection; Subgenital plate with a pair of short styli (Fig. 26A), outwardly oriented; disc with an apical wide and shallow U-shaped emargination. Phallus devoid of processes of titillator as spiny-like microstructures over each lateral portion of lobe **dl** (Fig. 25C,D), Sclerites **TS** completely attached to lobe **dl**, excepting for the apex. The **TS** is expanded inwardly toward the lobe **vdl**, and each **TS** is fused with each sclerite **VS**. Both sclerites **TS+VS** are widely separated from each other at midline. The fold **fdl** is usually laterally elongated. The vesicles **ejv** are oval and comparatively large; the apodemes **ap** are with a sickle-shaped sclerite **AP**. The lobe **vl** is formed by two folds, two upper, and two lower pairs; the apex of each lobe ending in an acute tip.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular, large. Paraprocts very thin. Cerci simple (Fig. 23D), short, cylindrical and acuminate. Subgenital plate (Fig. 26B) elongated, with a deep U-shaped emargination. Ovipositor semi-straight, shorter than hind femur (Fig. 23D), upcurved; dorsal valve about two times as wide as ventral one; apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Males and females of the same species bear the same coloration pattern. General coloration dark brownish with blackish marks.

**Distribution.** Species of *Parasubria* are distributed from southeastern Brazil to northern Argentina (Fig. 15B). *Parasubria ziczac* Karny, 1911 was first time collected in Santa Catarina, south Brazil at the middle of the distribution of *Parasubria vittipes* (Redtenbacher, 1891) **comb. nov.**

*Parasubria* comprises the following species: *Parasubria ziczac* Karny, 1911 and *Parasubria vittipes* (Redtenbacher, 1891) **comb. nov.**

Drawing of female in Karny (1912) *Parasubria ziczac* Karny seems to bear shorter tegmina than in female syntype of *Parasubria vittipes* (Redtenbacher, 1891) **comb. nov.** As there is not enough information to confirm whether the two species are different, or the same species, the two names are considered as valid names.

***Parasubria vittipes* (Redtenbacher, 1891) comb. nov.**

(Figs 2B, 3B, 15B, 23, 24A,B, 25, 26A,B, 27A)

**Syntype** (male, MNW) labeled \Coll. Br. v. W. Theresopolis Michaelis [type- and handwritten on white paper] \ det Redtenbacher Agroecia vittipes [type- and handwritten on white paper] \ 17.602 [handwritten on white paper]\.

**Diagnostic description.** (based on new collected material). General features as in the description of the genus. **Male.** Tegmina with left stridulatory file as shown in Fig. 24A. Cerci and paraprocts as shown in Fig. 25A. Subgenital plate semi-rounded (Fig. 26A); apical emargination cutting only at the most apical portion; styli short, about of one-quarter the length of the plate, outward oriented. Phallus as shown in Fig. 25C,D.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular, large. Paraprocts triangular. Cerci simple (Fig. 23D), short, cylindrical and acuminate. Subgenital elongated, narrowing from basal to apical portion, apical emargination about one-third the length of the plate. Ovipositor shorter than hind femur (Fig. 23D), upcurved dorsal valve about three times as wide as ventral one, its width decreasing toward apex; ventral valve with constant width over the entire length; apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** General coloration dark brownish with blackish marks. The following structures or areas are blackish: front of fastigium verticis, subgena, mandibles, sclerites of the antennal scrobes, a longitudinal stripe on sides of pronotal disc, region between **M+CuA** and mirror, meso- and metasternum, a narrow stripe on each sub basal portion of tibia, a elongated stripe on external portion of hind femora, a spot on dorso-external portion of fore coxae, marks between the mesepimeron and metapisternum, female with a mark on the external basal portion of the ovipositor. Ovipositor reddish.

**Calling song.** Males call very continuously at night, and the song is quite conspicuous to the unaided ear over short distances (Fig. 27A). The repetition rate is fairly constant with about 4.5 calls per second at 27°C in the natural habitat. Individual calls consist of two pulses, where the first and less intense one probably corresponds to the opening stroke of the tegmina, and the second one to the more powerful closing stroke, so that one call would also be one syllable. The pulses are quick zip sounds, consisting of rapidly decaying impulses corresponding to tooth-scraper impacts. The spectrum is the same for both pulses and is remarkably broad, with peaks around 10 and 20 kHz, and considerable energy in the ultrasound above 35 kHz and up to almost 80 kHz.

**Distribution.** This species possibly inhabits in the costal portion of the state of Rio de Janeiro in Brazil to north Argentina (Fig. 15B). It is currently registered in Teresopolis (type locality, Redtenbacher (1891)) and in Iguazú falls.

**Variation.** Measurements of males (n = 3, including holotype): TL 25.00–28.00; PL 7.00; TegL 15.00–16.00; FF 7.00; FT 7.00; HF15.50; HT 14.50. Spines of male (n = 1): sFF 2; sMF 2–3; sHF inner 1–2; sHF outer 4.

**Specimens examined.** Three adult males (MLP), each one respectively labeled \MLP-OR-3098\, \MLP-OR-3099\ and additionally labeled \Sendero Macuco, 18.02.2011, leg. H. Braun\, and \MLP-OR-3100\, additionally labeled \al lado de la pasarela en el área de las cataratas, 17.02.2011, leg. Dardo Marti\. One female (MLP) labeled \MLP-OR-3097\ Sendero Macuco, 18.02.2011, leg. H. Braun\.

### **Gen. nov. 1**

(Figs 2C, 3C, 7B, 11B, 15C, 26C,D, 28–41)

**Type species.** **Gen. nov. 1** *maculata* (Redtenbacher, 1891) **comb. nov.**

**Diagnosis.** This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis as broad as and longer than scapus (Fig. 28A). Tegmina with vein **M+CuA** thin (Fig. 3C), extended until less than the posterior portion of the mirror. Male postabdomen with posterior portion of tergite X strongly prolonged behind in two lobes (Fig. 7B); paraprocts simple (Fig. 32), semi-triangular; cerci fine (Fig. 32), elongated and cylindrical, with two finger-like projections at the apex; subgenital plate with a shallow and V-shaped emargination (Fig. 33A); phallus with sclerite **TS+VS** completely attached to the lobe **dl** (Fig. 11B); process of the titillator **ti** consisting of scattered sclerotized microstructures on laterals of lobe **dl**. Female postabdomen with tergite X straight; subgenital plate trapezoidal (Fig. 33B), sometimes emarginate.

**Description.** (Male and female similar, except for sexual features). Head more or less conical, hypognathous (Fig. 28A). Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus little longer and two times wider than pedicellus; apex straight, devoid of protruding projections. Fastigium verticis conical (Fig. 28A), longer than scapus (1.33–2.77 mm), basal portion as broad as scapus, and with a blunt apex; projected straight between scapus and pedicellus,

curved only at the tip; dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of head (Fig. 28A), weakly protruding. Face longer than wide. Fastigium frontis triangular (Fig. 28A), not distinctly protruding. Frons flat and smooth, devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium usually well defined, comparatively small; each lateral ocellus defined over each lateral portion of fastigium verticis, close to its base. Pronotum with tegumen punctate (Fig. 28B,C), more densely punctate on disc; with disc broadly rounded into paranota and posterior area shouldered; in profile with dorsal line and in transverse section straight, devoid of elevated or protruding zones. Metazona slightly produced caudad, leaving the mirror exposed. Pronotal disc with metazona wider than pro- and the metazona. Anterior margin concave; posterior margin mostly straight; principal transverse sulcus deep, curved, discontinuous at midline; devoid of second transverse sulcus; metazona without traces of longitudinal keel. Humeral sinus hardly indicated. Paranota wider than deep (Fig. 28C); with a sulcus which is prolonged to the pronotal disc at metazona; ventral margin obliquely truncate, ventro-caudal angle obtuse, caudal margin concave. Anterior portion of mesopleurum with a vertical and thick carina. Thoracic auditory spiracle oval, hidden under the auditory swelling, a bit longer than half the length of paranota and free from pronotum, marginal trichobotria dense; posterior edge of spiracle with a small finger-like projection. Prosternum armed with a pair of spines (Fig. 2C); each spine as long as the inner portion of the forecoxa. Meso- and metabasisternal lobes trapezoidal (Fig. 2C), projected downward, most strongly projected the mesobasisternal ones; lateral margins strongly concave; inner margins concave, both separated at the base. Posterior angle of mesobasisternal lobes with a strong tubercle-like projection. Posterior angle of metabasisternal lobes with a small protuberance. Metasternal medial plate with one strong tubercle at each lateral posterior portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coriaceous (Fig. 3C), with multiple secondary veins and cells; length of tegmina usually elongated and slender, surpassing apices of hind femora. Pro coxae with an elongated, strong and forwardly curved projection spine-like, dorsally; mid- and hind coxae with a tubercle-like projection on posterior margin, ventrally. Mid coxae devoid of small spine on basal portion dorsally. Fore femora armed ventrally only on inner margin (2–3 spines), midfemora on outer margin (2–4), and hindfemora on both margins (inner, 0–3; outer 5–8). Genicular lobes of fore- and midfemora armed with an acute and tiny spine only in inner lobe, and hind lobes armed on inner and outer lobe. Fore tibiae with four

angles, two rounded dorsally and two angular ventrally. Fore- and mid tibiae with spines on both margins but only ventrally, spines about of  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibia armed on all four dorsal and ventral margins; apex of hind tibiae with one pair dorsally and two pair ventrally of movable spurs. Tympanal region weakly swollen; each tympanal slit on Fore tibiae very narrow, facing forward; with pair of small, elongated pits below and close to each tympanal slit. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with costal margin with basal portion very concave (Fig. 3C), mid portion straight, and apical portion concave toward the posterior margin; anal margin concave; posterior margin outwardly concave. Pre-costal region usually narrowing toward apex. Vein **RP** ramified into two to four subveins; vein **MA** with more than four subveins. Cubital region of each tegmen short, usually extending to less than half the length of the tegmen; with dense network of veinlets. Vein **M+CuA** missing or very narrow, as wide as vein **MA**. Vein **Cu1** marked. Region between the **CuPa** vein and the mirror pigmented. Vein **CuPb** of left tegmen mostly straight (Fig. 30), uniform, with margins slightly concave at apex; maximum width of vein 0.38 to 0.71 mm. Stridulatory file 2.15 mm to 2.72 mm long; with 50 to 199 teeth; length of the smallest teeth 0.02 mm to 0.04 mm, and of the largest ones 0.09 mm to 0.20 mm; teeth lamelliform, homogeneously arranged on the file. Vein **CuPb** of right tegmen much narrower than the left one (Fig. 31); length 1.17 to 1.39 mm; vein at the middle as wide as the teeth (0.07 to 0.12 mm), number of teeth 30 to 108. Left mirror cup-shaped; comparatively shorter, away from of the costal margin of the tegmen; anterior margin oblique, partially pigmented. Right mirror oval; completely membranous. Stridulatory region with dense small spiny-like microstructures ventrally. Tergite IX with lateral portions a bit wider than the remaining tergites. Tergite X subquadrate, with lateral portions as wide as tergite IX (Fig. 7B). Posterior portion of tergite X, cerci and subgenital plate with dense bristles. Epiproct large, triangular, hidden under paraprocts. Cerci slender and elongated (Fig. 32), cylindrical, tip with fingers-like projections; the entire surface mostly bearing strong tubercles and bristles. Paraprocts sub-triangular (Fig. 32); smooth; portion near to each cercus with a small finger-like projection. Subgenital plate (Fig. 33A) usually with a pair of short stily usually backward oriented; disc with a weak apical U-shaped emargination. Phallus with process of titillator consisting of scattered spiny microstructures on dorsal and each lateral portion of lobe **dl** (Figs 34, 35). Sclerites **TS** completely attached to lobe **dl**; with a rounded projection on basal portion, with spiny-like microstructures. The **TS** is expanded inwardly toward the

lobe **vdl**, and fused with the sclerite **VS**. Both sclerites **TS+VS** are widely separated from each other at midline. The fold **fdl** is usually elongated. The vesicles **ejv** oval; the apodemes **ap** semicircular, usually defined by a membranous portion thicker, but sometimes there is an elongated **AP**. The lobe **vl** is formed by two folds, two upper, and two lower pair; the apex of each lobe ending in an acute tip.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular. Paraprocts triangular; as long as epiproct. Cerci simple (Fig. 28D), short, cylindrical and acuminate. Subgenital plate mostly trapezoidal (Fig. 33B); apical portion with two projections that configures usually an U-shaped emargination. Ovipositor concave, shorter than hind femur (Fig. 28D), upcurved; dorsal valve about three times as wide as ventral one, somewhat expanded midlength, apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Male and female with the same pattern of coloration. General coloration consisting of dark brownish with darker areas and blackish marks. A brownish darker stripe on pronotal disc. A blackish spot at each apical portion of tibiae and below the tympanal openings. A shallow mark on each basal portion of tibiae. Mandibles mostly blackish. Color pattern between species is very similar. Alive specimens with eyes and middle ocelus greenish (Fig. 36), after dead, change to brownish. Coloration of nymphs mostly reddish (Fig. 36E).

The species of **Gen. nov. 1** differ on the length of fastigium vertices, the form of the tegmina (Fig. 29), form of the stridulatory file and number of teeth (Fig. 30), form of cerci and paraprocts (Fig. 32), and form of the phallus (Figs 34, 35).

**Distribution.** **Gen. nov. 1** has a wider distribution if compared with other South American *Agraeciini* (Fig. 15C). This genus is distributed from the south of Bahia to the north of Argentina. **Gen. nov. 1 sp. nov. 3** was found only in the middle east of Minas Gerais, with similar distribution to that of *Agraecia sp. nov. 1* and *Listroscelis carinata* Karny. **Gen. nov. 1 maculata sp. nov.** inhabits the south of Rio de Janeiro state, occurring together with *Agraecia sp. nov. 3*, **Gen. nov. 3 abbreviata comb. nov.**, and the listroscelidines *Listroscelis itatiaia* Fialho *et al.* and *Monocerophora spinosa* (Karny). And at the south there is **Gen. nov. 1 sp.2 nov.**, with distribution similar to those of the *Agraeciini* *Parasubria vittipes comb. nov.*, and the listroscelidines *Megatympanon speculatum* Piza and *Cerberodon viridis* Perty.

**Gen. nov. 1** comprises the following species: **Gen. nov. 1 maculata** (Redtenbacher, 1891) **comb. nov.**, **Gen. nov. 1 subulata** (Redtenbacher, 1891) **comb.**

**nov., Gen. nov. 1 sp. nov. 1, Gen. nov. 1 sp. nov. 2, Gen.1. nov sp. nov. 3, and Gen. nov. sp. nov 4.**

**Identification key to the species of Gen. nov. 1**

1. Fastigium verticis elongated, about of or more than 2.00 mm...(2)
- 1'. Fastigium verticis short, less than 2.00 mm...(4)
  
- 2(1). Fastigium verticis very elongated about of 2.77 mm...**Gen. nov. 1 sp. nov. 2**
- 2'. Fastigium verticis less than 2.50 mm...(3)
  
- 3(2'). Fastigium verticis about of 2.31 mm; left stridulatory file with about of 50 teeth...**Gen. nov. 1 subulata (Redtenbacher) comb. nov.**
- 3'. Fastigium verticis about of 2.05 mm; left stridulatory file with about of 128 teeth  
**Gen. nov. 1 sp. nov. 1**
  
- 4(1'). Left stridulatory file with about of 135 teeth... **Gen. nov. 1 maculata (Redtenbacher) comb. nov.**
- 4'. Left stridulatory file with about of 173–176 teeth...(5)
  
- 5(4'). Male subgenital plate (Fig. 33I) wide, square; with lateral portions laterally elongated. Microstructures of process of titillator (Fig. 35C) comparatively scattered, barely sclerotized; fold **fdl** comparatively shorter...**Gen. nov. 1 sp. nov. 3**
- 5'. Male subgenital plate (Fig. 33K) large, rectangular; with lateral portions comparatively short. Microstructures of process of titillator (Fig. 35E) comparatively dense, strongly sclerotized; fold **fdl** very large...**Gen. nov. 1 sp. nov. 2**

**Gen. nov. 1 maculata (Redtenbacher, 1891) comb. nov.**

(Figs 2C, 3C, 11B, 15C, 28, 30A, 31A, 32A, 33A,B, 34A,B, 36A)

*Agraecia maculata* Redtenbacher, 1891: 455.

Unspecified female syntypes. See comments below.

**Diagnostic redescription** (based on new collected material). This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis (Fig. 28A) about of 1.35 mm. **Male.** Tegmina slender (Fig. 29A); costal and anal margin mostly straight; anal margin barely curved inward; vein Rs ramified in two subveins. Left stridulatory file as shown in Fig. 30A, with 135 teeth. Cerci and paraprocts as shown in Fig. 32A. Subgenital plate mostly elongated (Fig. 33A), rectangular; devoid of apical emargination; apical margin mostly straight. Titillator with apical portion of sclerites **TS** oval (Fig. 34A), protruding, with little spiny-like microstructures; inner portion of sclerite **TS+VS** deep inwardly projected toward the lobe **vdl**.

**Female.** Subgenital plate transversal rectangular (Fig. 33B); apical portion narrower; with a V-shaped emargination cutting about one-quarter the length of the plate.

**Distribution.** This species is registered from Rio de Janeiro, Brazil and north of Argentina (Fig. 15C).

This species was registered from Paraguay (Rehn 1907), and Argentina, (Rehn 1913) however the identification of the individuals is dubious, and these registers are not included in the map.

**Variation.** Measurements of males (n = 4): TL 27.00–31.00; PL 7.00; TegL 31.00–34.00; FF 7.00–8.00; FT 8.00–9.00; HF 17.00–19.00; HT 17.00–19.00. Measurements of females (n = 8, including type specimen data): TL 30.00–35.00; PL 7.00–8.00; TegL 33.00–42.00; FF 8.00–9.00; FT 8.00–9.00; HF 18.00–22.00; HT 19.00–21.00; OL 16.00–18.00.

Spines of males and females (n = 9): sFF 2; sMF 2–3; sHF inner 0–2; sHF outer 6–7.

**Specimens examined.** Eighteen specimens (CELC) labeled \Brasil, RJ, Itatiaia, P.N. Itatiaia. 7–13, XI, 2011 J. Chamorro leg. [printed on white paper] \ **Gen. nov. 1 maculata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\\. Four adult males with the respective codes \1\, \5\, \11\, and labeled \-1-Cono-Itatiaia [printed on white paper]\\. Six immature males with codes \6\, \12\, \13\, \21\, \23\, and labeled \-25-Cono-Itatiaia [printed on white paper]\\. and eight adult females with codes \2\, \4\, \8\, \2\, \9\, \10\, \2\, \16\, \18\, and labeled \-19-Cono-Itatiaia [printed on white paper]\\. One adult female (CEIOC) labeled \Itatiaia E. do Rio Brasil, J.F. Zikan [typewritten on white paper] \ Coleção J. F. Zikan [typewritten on white paper] \ 13-1-35 [handwritten on

yellowish paper] \ 51 [handwritten on yellow paper] \ **Gen. nov. 1** *maculata* (Redtenbacher, 1891) **comb. nov.** [printed on white paper]. One adult female (MZUSP) labeled \BRASIL: RJ Reserva Biol da Tingá, 22°34'27"S 43°26'10"W, Armadilha Malaise – trilha 5-8 iii.2002, STP. Amaranto & eq. col. [handwritten on white paper]\ Orthoptera “Ensifera” Tettigoniidae [handwritten on white paper] \ **Gen. nov. 1** *maculata* (Redtenbacher, 1891) **comb. nov.** [handwritten on white paper].

**Comments.** There are doubts about the identity of the type material and quantity of specimens used to describe this species. Redtenbacher (1891) cited a female collected in Terezopolis (RJ), and provide measurements apparently for only one individual. However it was cited other collectors and collections (Coll. Brunner, coll. Dohrn, coll. Schulthess-Rechberg, Mus. Genf, Mus. Hamburg). There is a female syntype deposited in Muséum d’histoire naturelle de Genève (Hollier 2012).

This is the only species of *Agraecia* (*sensu* Redtenbacher) for which the author provided drawings (Redtenbacher 1891, Taf. IV, fig. 63).

This is the first time the male is described. There is a male in MNV identified as *A. maculata* labeled \Coll. Br.v.W., St. Paul, Standinger \ Coll. Br.v.W, *Agraecia maculata* \ 21.603. This specimen is not cited in the original description, but have similar labels as the remaining Redtenbacher’s type material. Possibly this material was subsequently added to the collection.

**Gen. nov. 1** *subulata* (Redtenbacher, 1891) **comb. nov.**  
(Figs 15C, 29A, 30B, 31B, 32B, 33C,D, 34C,D, 36B, 37)

*Agraecia subulata* Redtenbacher, 1891: 453.

Unspecified male and female syntypes.

**Diagnostic description** (based on new collected material). This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis about of 2.31 mm (Fig. 37A). **Male.** Tegmina robust (Fig. 39A); costal and anal margins broaden at mid portion; vein **Rs** ramified into three subveins. Left stridulatory file as shown in Fig. 30B, with 50 teeth. Cerci and paraprocts as shown in Fig. 32B. Subgenital plate mostly elongated (Fig. 33C), rectangular; barely concave-shaped emarginated. Titillator with apical portion of sclerite

**TS** oval (Fig. 34C), protuding, with little spiny-like microstructures; inner portion of sclerite **TS+VS** shortly inward projected toward the lobe **vdl**.

**Female.** Subgenital plate trapezoidal (Fig. 33D); apical portion narrower; with an U-shaped emargination cutting about one-quarter the length of the plate.

**Variation.** Measurements of males (n = 5, including type material data): TL 25.00–30.00; PL 7.00–8.00; TegL 27.00–31.00; FF 8.00; FT 8.00–9.00; HF 15.00–18.00; HT 16.00–18.00. Measurements of females (n = 5, including type material data): TL 25.00–28.00; PL 7.70–8.00; TegL 27.70–30.00; FF 8.00–9.00; FT 8.00–9.00; HF 16.40–19.00; HT 18.00; OL 13.00–14.00. Spines on male and female (n = 8): sFF 2; sMF 2–3; sHF inner 0–2; sHF outer 5–6.

**Distribution.** This species is here registered only in the P.E. Serra do Brigadeiro (Fig. 15C).

The information in the original descriptions referes only to Brazil as a locality type. Two specimens deposited in MNW were collected in Espírito Santo, however, this locality was no cited in the original description.

**Specimens examined.** Fourteen specimens (CELC) labeled \Brasil, MG, Araponga, P.E. Serra do Brigadeiro, 12–15, XII, 2011, J. Chamorro *leg.* [handwritten on white paper] \ **Gen. nov. 1** *subulata* (Redtenbacher, 1891) **comb. nov.** [printed on white paper] \. Four adult males with the respective codes \2\, \4\, \5\, \15\, and labeled \-Cono-Brigadeiro\; two immature males \3\, \6\, and labeled \-Cono-Brigadeiro\; four adult females \1\, \18\, \21\, \22\, and labeled \-Cono-Brigadeiro\; and four immature females \7\, \8\, \10\, \20\, and labeled \-Cono-Brigadeiro [printed on white paper] \. One adult female (MZUSP) labelled \Fervedouro, MG, PE. Serra do Brigadeiro, 21-24.iii.05, [Exp. Opiliedógia, cachaça, Uai!], M.B. da Silva, H.v. Xamaguti, A.A. Nogueira col. [handwritten white paper] \ **Gen. nov. 1** *subulata* (Redtenbacher, 1891) **comb. nov.** [handwritten white paper] \.

**Comments.** This species was described based on syntypes. In the original descriptions it is provided measurements of two specimens, one male and one female. In the MNW there are three specimens identified as syntypes.

**Gen. nov. 1 sp. nov. 1**

(Figs 15C, 29C, 30D, 31D, 32D, 33G,D, 35A,B, 36D,E, 39)

**Holotype male** (CELC) labeled \Brasil, ES, ReBio de Sooretama, 29, XI to 2, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 2-Cono-Sooretama [printed on white paper] \ **Gen. nov. 1 sp.1 nov.** [handwritten on red paper]\. TL 23.00; PL 6.00; TegL 35.00; FF 7.00; FT 7.00; HF 18.00; HT 18.00; sFF 2; sMF 3; sHF inner 2; sHF outer 6.

**Allotype female** (CELC) labeled \Brasil, ES, ReBio de Sooretama, 29, XI to 2, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 37-Cono-Sooretama [printed on white paper] \

**Gen. nov. 1 sp. nov. 1** [handwritten on blue paper]\.

**Diagnostic description.** This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis about of 2.05 mm (Fig. 39A). **Male.** Tegmina slender (Fig. 29C); costal and anal margin mostly straight; cubital margin barely curved inward; vein **Rs** ramified in three subveins. Left stridulatory file as shown in Fig. 30D, with 128 teeth. Cerci and paraprocts as shown in Fig. 32D. Subgenital plate elongated (Fig. 33G), trapezoidal, widening from base to apex; barely concave-shaped emarginated. Titillator with apical portion of sclerite **TS** larger (Fig. 35A), with little spiny-like microstructures; inner portion of sclerite **TS+VS** largely inward projected toward the lobe **vdl**.

**Female.** Subgenital plate transversal rectangular (Fig. 33H); with basal portion as wide as apical portion; apical margins obliques.

**Distribution.** This species was collected in ReBio de Sooretama and Estação Biológica Santa Lúcia in the state of Espírito Santo, Brazil (Fig. 15C).

**Variation.** Measurements of males (n = 5, including holotype): TL 23.00–28.00; PL 6.00–7.00; TegL 31.00–35.00; FF 7.00–8.00; FT 7.00–8.00; HF 18.00–19.00; HT 18.00. Measurements of females (n = 4, including allotype): TL 26.00–30.00; PL 7.00; TegL 37.00; FF 8.00; FT 8.00–9.00; HF 19.00–20.00; HT 19.00–21.00; OL 12.00–14.00.

Spines of males and females (n = 9): sFF 2; sMF 2–3; sHF inner 1–2; sHF outer 6–7.

**Additional type series. Fourteen Paratypes** (CELC) labeled \Brasil, ES, ReBio de Sooretama, 29, XI to 2, XII, 2011, J. Chamorro *leg.* [printed on white paper] \. Four adult males with codes \2\, \13\, \16\, \21\; three immature males \14\, \32\, \34\; three adult females \3\, \5\, \8\, and four immature females \12\, \17\, \23\, \28\ \-Cono-Sooretama [printed on white paper]\, additionally labeled \**Gen. nov. 1 sp. nov. 1** [handwritten on blue paper]\. **Two Paratypes** (CELC) labeled \Brasil, ES, RPPN Santa Lucia, 26, XI to 29, XI, 2011, J. Chamorro *leg.* [printed on white paper]\. One adult

male with code \1-Conoce-Sta. Lúcia\, and additionally labeled \Gen. nov. 1 sp. nov. 1 [handwritten on blue paper]. One immature female with code 2-Conoce-Sta.Lucia\

**Gen. nov. 1 sp. nov. 2**

(Figs 15C, 29B, 30C, 31C, 32C, 33EF, 34E,F, 36C, 38)

**Holotype female** (CELC) labeled \Brasil, RJ, Terezópolis, P.N. Serra dos Órgãos, 13–16, XI, 2011 J. Chamorro *leg.* [printed on white paper] \ 2-Cono-Órgãos [printed on white paper] \ **Gen. nov. 1 sp.2 nov.** [handwritten on red paper]\. TL 37.00; PL 8.00; TegL 33.00; FF 10.00; FT 10.00; HF 21.00; HT 20.00; sFF 2; sMF 3; sHF inner 1–2; sHF outer 6.

**Allotype female** (CEIOC) labeled \Petropolis, Tq. E. do Rio, Brasil, H. S. Lopes, 2.69 \ **Gen. nov. 1 sp.2 nov.** [handwritten on blue paper]\. TL: 35.00; PL 8.00; TegL 35; FF 9.00; FT 9.00; HF 20.00; HT 21; OV 20.00; sFF 2–3; sMF 3; sHF inner 3–4; sHF outer 6–7.

**Diagnostic description.** This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis about of 2.77 mm (Fig. 38A). **Male.** Tegmina slender (Fig. 29B); costal margin mostly straight; cubital margin barely curved inward; vein **Rs** ramified in three subveins. Left stridulatory file as shown in Fig. 30C, with 199 teeth. Cerci and paraprocts as shown in Fig. 32C. Subgenital plate with basal portion wider than apical portion (Fig. 33E); apical portion with a short and wide V-shape emargination. Titillator with apical portion of sclerites **TS** oval (Fig. 34E), protruding with little spiny-like microstructures on inner portion; inner portion of sclerite **TS+VS** deeply inward projected toward the lobe **vdI**.

**Female.** Subgenital plate transversal rectangular (Fig. 33F), with apical margin with projected configuring a V-shaped emargination cutting about of one-quarter de length of the plate.

**Distribution.** This species is distributed from the states of Rio de Janeiro to São Paulo, in Brazil (Fig. 15C).

**Additional type series. Twelve Paratypes** (CELC), four immature males and two immature females labeled \Brasil, RJ, Nova Friburgo, RPPN Bachus [printed on white paper] \ **Gen. nov. 1 sp. nov. 2** [handwritten on blue paper]\, and respectively labeled \9\, \12\, \17\, \25\, \13\, \20\, and labeled \-Cono-Bachus\. **One male Paratype**

(MZUSP) labeled \BRASIL SP, Salesópolis, Estação Biológica de Boracéia, 23°39'14"S, 45° 53'25"O, 24-28.iii.2011, Expedição MZUSP/FFCLRP Col. \ **Gen. nov. 1 sp. nov. 2** [handwritten on white paper]\. **One male and one female Paratypes** (MZUSP) labeled \SALESÓPOLIS, EST-BIOL. DE BORACÉIA, 24-30.i.1979, L.R. FONTES & P.S. TERRA col [handwritten on white paper]\ **Gen. nov. 1 sp. nov. 2** [handwritten on white paper]\. **One female Paratype** (MZUSP) labeled \BRASIL. SP. Ubatuba, Pq Est Serra do Mar, Núcleo Picinguaba, Malaise [printed on white paper, damaged label] \ **Gen. nov. 1 sp. nov. 2** [handwritten on white paper]\. **One female Paratype** (MZUSP) labeled \Est. Bio/ Boracéia, SP, 2.III.976, L.R. Fontes col., Tettigoniidae: dentro de Bromélia \ **Gen. nov. 1 sp. nov. 2** [handwritten on white paper]. **One female Paratype** (MZUSP) labeled \BRASIL: SP. Salesópolis, Est.Biol. Boracéia, 01-29 iii.2002, S.A. Casari, I.B. Franscini, Fit. 3, Loet. [handwritten on white paper] \ Tettigonidae “Conocephalinae” Flávio M.O. det. [handwritten on white paper] \ ORTHOPTERA \ **Gen. nov. 1 sp. nov. 2** [handwritten on white paper]\.

### **Gen. nov. 1 sp. nov. 3**

(Figs 15C, 29C, 30E, 31E, 32E, 33I,J, 35C,D, 36F, 40)

**Holotype male** (CELC) labeled \Brasil, MG, Timoteo, PERD, 9–12, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 3-Cono-PERD [printed on white paper] \ **Gen. nov. 1 sp. nov. 3** [handwritten on red paper]\. TL 27.00; PL 6.00; TegL 32.00; FF 7.00; FT 8.00; HF 17.00; HT 17.00; sFF 2; sMF 3; sHF inner 2; sHF outer 7.

**Allotype female** (CELC) labeled \Brasil, MG, Timoteo, PERD, 9–12, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ 1-Cono-PERD [printed on white paper] \ **Gen. nov. 1 sp. nov. 3** [handwritten on blue paper]\. TL 30.00; PL 7.00; TegL 34.00; FF 8.00; FT 8.00; HF 19.00; HT 19.00; OL 14.00; sFF 2; sMF 3; sHF inner 1; sHF outer 6.

**Diagnostic description.** This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis about of 1.32 mm (Fig. 40A). **Male.** Tegmina slender (Fig. 29C); costal and anal margins mostly straight; anal margin barely curved inward; vein **Rs** ramified in three subveins. Left stridulatory file as shown in Fig. 30E, with 173 teeth. Cerci and paraprocts as shown in Fig. 32E. Subgenital plate squared (Fig. 33I); with a wide V-shape emargination. Titillator with apical portion of sclerites **TS** no protruding (Fig.

35C), with little spiny-like microstructures; inner portion of sclerites **TS+VS** deeply inward projected toward the lobe **vdI**.

**Female.** Subgenital plate transversal trapezoidal (Fig. 33I); with basal portion wider than apical portion; apical margin concave.

**Distribution.** This species was collected in PERD in the state of Minas Gerais, Brazil (Fig. 15C).

**Variation.** Measurements of males (n = 6, including holotype): TL 25.00–27.00; PL 6.00–7.00; TegL 31.00–33.00; FF 7.00–8.00; FT 8.00; HF 17.00–18.00; HT 17.00–18.00. Measurements of females (n = 3, including allotype): TL 27.00–30.00; PL 7.00–8.00; TegL 32.00–34.00; FF 8.00–9.00; FT 8.00–9.00; HF 19.00–21.00; HT 19.00–21.00; OL 14.00. Spines on male and female (n = 9): sFF 2–3; sMF 3–4; sHF inner 1–3; sHF outer 6–8.

**Additional type series. Eight Paratypes** (CELC) labeled \Brasil, MG, Timoteo, PERD, 9–12, XII, 2011, J. Chamorro *leg.* [printed on white paper] \ **Gen. nov. 1 sp. nov. 3** [handwritten on blue paper]. Five adult males with the respective codes \2\, \4\, \7\, \9\, \24\, three adult females \10\, \11\, \26\, and labeled \Cono-PERD [printed on white paper].

#### **Gen. nov. 1 sp. nov. 4**

(Figs 15C, 29D, 30F, 31F, 32F, 33K, 35E,F, 41)

**Holotype male** (CELC) labeled \Brasil, BA, Porto Seguro, P.N. do Pau Brasil, 4–6, I, 2012, J. Chamorro *leg.* [printed on white paper] \ 28-Cono-Pau [printed on white paper] \ **Gen. nov. 1 sp. nov. 4** [handwritten on red paper]. TL 27.00; PL 7.00; TegL 26.00; FF 7.00; FT 8.00; HF 18.00; HT 17.00; sFF 2; sMF 3; sHF inner 1; sHF outer 7.

**Diagnostic description.** This species can be distinguished from the remaining **Gen. nov. 1** species by the following combination of features. Length of fastigium verticis about of 1.33 mm (Fig. 41A). **Male.** Tegmina elongated (Fig. 29D); costal and anal margins mostly straight; anal margin barely curved inward; vein **Rs** ramified in three subveins. Left stridulatory file as shown in Fig. 30F, with 176 teeth. Cerci and paraprocts as shown in Fig. 32F. Subgenital plate elongated (Fig. 33K); basal portion wider than apical portion; apical portion with a short V-shape emargination. Titillator with apical portion of sclerites **TS** no protruding (Fig. 35E), with little spiny-like

microstructures; inner portion of sclerites **TS+VS** deeply inward projected toward lobe **vdI**.

Female unknown.

**Distribution.** This species was only registered from P.N. do Pau Brasil in the state of Bahia, Brazil (Fig. 15C).

## **Gen. nov. 2**

(Figs 2D, 3D, 6B, 7C, 11C, 15B, 24C,D, 26C,D, 42, 43A–D, 44A,B, 45)

**Type species. Gen. nov. 2 *nigrifrons* (Redtenbacher, 1891) comb. nov.**

**Diagnosis.** This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis as wide as and shorter than scapus (Fig. 42A). Tegmina with vein **M+CuA** long (Fig. 3D), as long as the posterior portion of mirror. Male postabdomen with posterior portion of tergite X moderately prolonged behind into two delicate lobes (Fig. 7C); cerci fine (Fig. 43A–D), elongated and cylindrical, with one delicate projections at the apex; paraprocts simple (Fig. 43A–C), semi-triangular; subgenital plate with a shallow emargination (Fig. 26C); phallus with apical portion of sclerite **TS** free from lobe **dl** (Figs 11C, 44A), sclerite **TS** smooth; laterals of lobe **dl** with few but dense sclerotized microstructures (**ti**). Female postabdomen with tergite X straight; subgenital plate semicircular (Fig. 26D), devoid of emargination.

**Description.** (Male and female morphologically similar, but can be dimorphic in relation to the coloration, and sexual features). Head more or less conical, hypognathous (Fig. 42). Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus two times longer and wider than pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular (Fig. 42); about as long (1.56 mm) as or slightly longer than scapus, slightly narrower than scapus (1.01 mm), and with a blunt apex; projected straight between scapus and pedicellus, dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of head (Fig. 42), weakly protruding. Face longer than wide. Fastigium frontis triangular, not distinctly protruding. Frons flat and weakly punctate. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium well defined (Fig. 42), comparatively large; each lateral ocellus defined over each lateral portion of fastigium verticis, close to the base. Pronotum punctate (Fig. 42B,C);

with disc broadly rounded into paranota and posterior area shouldered; in profile with dorsal line and in transverse section straight, without higher or protruding zones. Pronotum in profile with dorsal line and in transverse section straight, without elevated or protruding zones. Metazona weakly produced caudad, leaving the stridulatory region completely exposed. Pro- and mesozona narrower than metazona. Anterior margin concave; posterior margin mostly straight or slightly backward curved; principal transverse sulcus deep, curved, continuous at midline; devoid of second transversal sulcus; metazona without traces of longitudinal keel, but with a longitudinal sulcus. Humeral sinus weakly indicated. Paranota wider than deep (Fig. 42C); ventral margin oblique; ventro-caudal angle obtuse; caudal margin rounded. Anterior portion of mesopleurum with a vertical and thin carina. Thoracic auditory spiracle oval, hidden under the auditory swelling, longer than half the length of the paranota and free from pronotum; marginal trichobotria dispersed; posterior edge of spiracle with a small, finger-like projection. Prosternum armed with two strong spines (Fig. 2D); each spine shorter than the inner portion of the forecoxa. Meso- and metabasisternal lobes trapezoidal (Fig. 2D), projected downward, most strongly projected the mesobasisternal ones; lateral margins strongly concave; inner margins concave; inner margins separate at the base. Posterior angle of mesobasisternal lobes with a strong tubercle-like projection. Posterior angle of metabasisternal lobes with a tubercle-like projection. Metasternal medial plate with one strong tubercle at each lateral portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coriaceous (Fig. 3D), with multiple secondary veins and cells; tegmina as long as or longer than postabdomen. Pro coxae with an elongated, strong and forwardly curved projection spine-like dorsally; mid- and hind coxae with a strong tubercle-like projection on posterior portion, ventrally. Mid coxae devoid of small spine on basal portion dorsally. Fore femora armed ventrally only on inner margin (2–3 spines), midfemora on outer margin (3–5), and hindfemora on both margins (inner, 0–2; outer 5–9). Genicular lobes of Fore femora with the tip acute, like a spine, the inner lobe acuter than the outer one. Inner genicular lobes of the midfemora with the tip acute, outer ones obtuse. Both inner and outer genicular lobes of the hindfemora similar, with acute tip. Fore tibiae with four angles, two rounded dorsally and two angular ventrally. Fore- and mid tibiae armed with spines on both margins but only ventrally, spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibia armed on all four dorsal and ventral margins; apex of hind tibia with one pair dorsally and two pair ventrally of movable spurs. Tympanal region weakly swollen; each tympanal slit on Fore tibiae very narrow, facing forward;

with pair of small, elongated pits below and close to each tympanal slit. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with costal margin with basal margin concave (Fig. 3D), mid portion straight; anal margin mostly concave; posterior margin outwardly concave. Pre-costal region curved narrowing toward apex. Vein **RP** ramified into three subveins; vein **MA** with more than four subveins. Cubital region of each tegmen, extending to less than half the length of the tegmen; with dense network of veinlets. Vein **M+CuA** large, as long as the posterior margin of mirror. Vein **Cu1** weakly marked. Region between the **CuPa** vein and the mirror mostly membranous, with scarce pigmentation. Vein **CuPb** of left tegmen mostly straight (Fig. 24C), uniform, with margins slightly concave; maximum width of vein 0.52 mm. Stridulatory file 2.23 mm long, with 118 teeth; length of the smallest teeth 0.03 mm, and of the largest ones of 0.13 mm; teeth lamelliform, homogeneously arranged over the file. Vein **CuPb** of right tegmen much narrower than the left one (Fig. 24D); length 1.16 mm; vein width as wide as teeth (0.05); number of teeth 67. Left mirror cup-shaped; comparatively shorter, away from the anal margin; anterior margin straight, slightly oblique, partially pigmented. Right mirror oval; completely membranous. Stridulatory region ventrally, with dense small spiny-like microstructures. Tergite IX with lateral portions a bit wider than the remaining tergites. Tergite X semioval (Fig. 7C), with lateral portions as wide as tergite IX. Posterior portion of tergite X, cerci and subgenital plate with dense bristles. Epiproct elongated and triangular, devoid of longitudinal fold. Cerci with the entire tegmen bearing strong tubercles and bristles (Fig. 43A–D). Paraprocts comparatively simple and subtriangular (Fig. 43A–D), with a protruding tubercle-like protuberance close to each cercus, smooth; when paraprocts are close, both paraprocts can overlap on each other. Subgenital plate with a pair of short stily (Fig. 26C), weakly oriented inward; disc with an apical U-shaped emargination. Phallus with dense and slightly sclerotized microstructures (**ti**) over lateral portion of lobe **dl** (Figs 11C, 44A–B). Sclerites **TS** partially attached to lobe **dl**, basal and mid portion attached to membranes, but apical portion free. Each **TS** is expanded inwardly toward the lobe **vdl**, and the **TS** is joined with the sclerite **VS**. Sclerites **TS** are widely separated at apical portion, but **TS+VS** are close at basal portion on midline. The fold **fdl** is large and elongated. The vesicles **ejv** oval; the apodemes **ap** elongated, defined by a thicker membranous portion. The **vl** is formed by two folds, two upper, and two lower pair; the apex of each upper lobe is acute.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular, twice longer than paraproct. Paraprocts triangular, with apex little rounded and protruding. Cerci simple (Fig. 42B), short, cylindrical and acuminate. Subgenital plate semirounded (Fig. 26D), devoid of apical emargination. Ovipositor concave (Fig. 42B), shorter than hind femur, upcurved; dorsal valve about three times as wide as ventral one, somewhat expanded midlength, apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Based on the only known species, there is sexual dimorphism related to the coloration (Fig. 42).

**Distribution.** **Gen. nov. 2 *nigrifrons* comb. nov.** has a short geographic distribution range, the species being registered only on the southern portion of Bahia (Fig. 15B), which is similar to the distribution of *Agraecia punctata* and the listroscelidine *Monocerophora minax* Walker, *Listroscelis magnomaculata* Fialho *et al.*, *Listroscelis cohni* Fialho *et al.*, and *Hamayulus rufomaculatus* Fialho *et al.* None of those species are found at the more southern portion of Brazil.

This new genus comprises only **Gen. nov. 2 *nigrifrons* (Redtenbacher, 1891) comb. nov.**

**Gen. nov. 2 *nigrifrons* (Redtenbacher, 1891) comb. nov.**

(Figs 2D, 3D, 6B, 7C, 11C, 15B, 24C,D, 26C,D, 42, 43A–D, 44A,B, 45)

*Agraecia nigrifrons* Redtenbacher, 1891: 453.

**Holotype male** (NMW) labeled \Coll. Br. v. W. Bahia Thorey? [type- and handwritten on white paper] \ 4876 [handwritten on white paper] \ det. Redtenb. *Agraecia nigrifrons* [type- and handwritten on white paper] \ HOLOTYPE TYPES [handwritten on red paper].

**Diagnostic description** (based on new collected material). General features as in the description of the genus. **Male.** Tegmina with left stridulatory file as shown in Fig. 24C. Cerci as shown in Fig. 43A–D. Paraprocts as shown in Fig. 43A–D. Subgenital plate mostly elongated and rectangular (Fig. 26C); apical emargination cutting of about one-sixth the length of the plate; styli short, of about less than one-nine the length of the plate, backward oriented. Titillator with processes **ti** asymmetric as shown in Fig. 44A.

**Female.** Subgenital plate with basal region short (Fig. 26D); mid portion of the plate projected, protruding over the basal region; this mid portion comparatively broader; projections of the apical portion backward oriented, separated at midline; an U-shaped emargination between projections of about one-third the length of the plate.

**Coloration.** Male and female mostly dark brownish (Fig. 42), with defined blackish spots and blackish shadow areas. Female darker than male. With blackish marks on: ventral portion of scapus; ventral portion of fastigium verticis; frons and sclerites of antennal sockets; a mark on central portion of face; two marks on each corner of the clypeus and one on the midline at the base; mandibles; lateral margins of pronotum; a short stripe on mezosone at midline; cells of tegmina; mirror and stridulatory file; femora with a mark on apical portion; tibiae with a spot at apical and basal portion; tympanal area and below the tympanal openings. Whitish areas at the dorsal portion of head; and spines of the femurs, but with tip brownish. Alive specimens with eyes greenish (Fig. 45), median ocellus whitish, palpes light yellowish, spines of femora whitish, sternites and ovipositor reddish.

**Variation.** The blackish mark on the face of males can be only at the central region or extending more laterally.

**Distribution.** This species is present in the south of the state of Bahia, Brazil, with records from RPPN Serra Bonita, RPPN Serra do Teimoso and P.N. do Pau Brasil (Fig. 15B).

**Specimens examined.** Twenty-three specimens (CELC) labeled \Brasil, BA, Camac an, RPPN Serra Bonita, 10–12, I, 2012, J. Chamorro *leg.* [printed on white paper] \ **Gen. nov. 2 nigrifrons** [printed on white paper], and additionally labeled as follows: eleven adult males \16\, \17\, \21\, \26\, \27\, \31\, \35\, \41\, \45\, \46\, \51\, and labeled \-Cono-Bonita [printed on white paper]; eleven adult females \1\, \2\, \5\, \13\, \14\, \18\, \20\, \24\, \34\, \37\, \39\, and labeled \-Cono-Bonita [printed on white paper]; one immature male \-50-Cono-Bonita [printed on white paper]. Three specimens (CELC) labeled \Brasil, BA, Jussari, RPPN Serra do Teimoso, 7–9, I, 2012, J. Chamorro *leg.* [printed on white paper] \, two adult females and one immature female respectively labeled \2\, \10\, \16\, and labeled \-Cono-Teimoso [printed on white paper]. Two specimens (CELC) labeled \Brasil, BA, Porto Seguro, P.N. do Pau Brasil, 4–6, I, 2012, J. Chamorro *leg.* [printed on white paper] \ one male and one female respectively \8\, \35\ and labeled \-Cono-Pau [printed on white paper].

**Comments.** This is the first time the female is described. Also this is the first records of exactly locality.

**Gen. nov. 3**

(Figs 2E, 3E, 6C, 7D, 11D, 15B, 24E,F, 26E,F, 43EG, 44CD, 46)

**Type species. Gen. nov. 3 *abbreviata* (Redtenbacher, 1891) comb. nov.**

**Diagnosis.** This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis as wide as and little longer than scapus (Fig. 46A). Tegmina with vein **M+CuA** very short (Fig. 3E), extended until the stridulatory file. Male postabdomen with posterior portion of tergite X moderately prolonged behind into two delicate lobes (Fig. 7D); cerci oval and robust with two opposite small finger-like projections; paraprocts comprising a robust and big boot-shaped region which is exposed dorsally (Fig. 43E,G), and two smaller valves which are hidden anteriorly; subgenital plate with a deep V-shape emargination (Fig. 26E); phallus with sclerite **TS+VS** completely attached to lobe **dl** (Figs 11D, 44C,D); anterior portion of **TS** protruding over the dorsal lobe with little scale-like microstructures; anterior portion of lobe **dl** with dense sclerotized microstructures (**ti**). Female postabdomen with tergite X straight; subgenital plate trapezoidal (Fig. 26F), may be weakly emarginated.

**Description.** (Male and female similar, except for sexual features). Head more or less conical, hypognathous (Fig. 46A). Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus little longer and two times wider than pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular, about as wide (1.61 mm) the scapus (Fig. 46A), and with a blunt apex; projected straight between scapus and pedicellus, dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of head (Fig. 46A), weakly protruding. Face longer than wide. Fastigium frontis triangular (Fig. 46A), not distinctly protruding. Frons flat and smooth (Fig. 46A), devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium well defined (Fig. 46A), comparatively large; each lateral ocellus defined over each lateral portion of fastigium verticis, close to its base. Pronotum mostly smooth (Fig. 46A,C); with disc broadly rounded into paranota and posterior area shouldered; in profile with dorsal line and in transverse section straight, without higher or protruding zones. Metazona produced caudad, covering only the basal portion of the stridulatory region. Pronotal disc with the same width along the entire length; anterior margin concave; posterior margin backward concave; principal transverse sulcus deep,

curved, discontinuous at midline; devoid of second transverse sulcus; metazona without traces of longitudinal keel. Humeral sinus weakly indicated. Paranota wider than deep (Fig. 46C); with a sulcus which is prolonged to the pronotal disc at the metazona; ventral margin obliquely truncate, ventro-caudal angle obtuse; caudal margin concave. Anterior portion of mesopleurum with a vertical and thick carina. Thoracic auditory spiracle oval, hidden under the auditory swelling, a bit longer than half the length of paranota and free from pronotum; marginal trichobotria dense; posterior edge of spiracle with a small, finger-like projection. Prosternum armed with a pair of spines (Fig. 2E); each spine as long as the inner portion of the forecoxa. Meso- and metabasisternal lobes trapezoidal (Fig. 2E), projected downward, most strongly projected the mesobasisternal ones; lateral margins strongly concave; inner margins concave; inner margins separate at the base. Posterior angle of mesobasisternal lobes with a strong spine-like projection. Posterior angle of metabasisternal lobes with a robust tubercle-like projection. Metasternal medial plate with one strong tubercle at each lateral portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coraceous (Fig. 3E), with multiple secondary veins and cells; tegmina as long as or longer than postabdomen. Pro coxae with an elongated, strong and forwardly curved projection spine-like dorsally; mid- and hind coxae with a strong tubercle-like projection on posterior portion, ventrally. Mid coxae devoid of small spine on basal portion dorsally. Fore femora armed with spines (2–3) ventrally only on inner margin; midfemora with spines on outer margin (3); and hindfemora on both margins (inner, 0–3; outer 6–7). Genicular lobes of fore- and midfemora armed with a delicate little spine on inner margin, and an acute and strong spine on outer margin; inner and outer genicular lobes of hindfemora with one acute spine-like projection. Fore tibiae with four angles, two rounded dorsally and two angular ventrally. Fore tibiae with four angles, two rounded dorsally and two angular ventrally. Fore- and mid tibiae armed with spines on both margins but only ventrally; spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibiae armed on all four dorsal and ventral margins; apex of hind tibiae with one pair dorsally and two pair ventrally of movable spurs. Tympanal region weakly swollen; each tympanal slit on Fore tibiae very narrow, facing forward; with pair of small, elongated pits below and close to each tympanal slit. Abdomen. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with costal margin concave (Fig. 3E); anal margin mostly straight; posterior margin outwardly concave. Pre-costal region curved narrowing toward apex. Vein **RP** ramified into two subveins; vein **MA** with four to five subveins.

Cubital region of each tegmen short, extending to less than half the length of the tegmen; with dense network of veinlets. Vein **M+CuA** missing. Vein **Cu1** weakly marked. Region between the vein **CuPa** and the mirror mostly membranous, with scarce pigmentation. Vein **CuPb** of left tegmen mostly straight (Fig. 24E), uniform, with margins slightly concave; maximum width of vein 0.52 mm. Stridulatory file 2.23 mm long, with 167 teeth; length of the smallest teeth 0.03 mm, and of the largest ones 0.13 mm; teeth lamelliform, homogenously arranged over the file. Vein **CuPb** of right tegmen much narrower than the left one (Fig. 24F); length 1.44 mm; vein width as wide as teeth (0.06 mm); number of teeth 87. Left mirror cup-shaped; comparatively short; away from the anal margin; anterior margin oblique, very pigmented. Right mirror oval; completely membranous. Stridulatory region with dense small spiny-like microstructures ventrally. Tergite IX with lateral portions a bit wider than the remaining tergites. Tergite X subquadrate, with lateral portion as wide as tergite IX (Fig. 7D). Posterior portion of tergite X, cerci and subgenital plate with dense bristles. Epiproct short and triangular, with a longitudinal fold at midline on the entire length. Cerci with the entire tegmen bearing strong tubercles and bristles (Fig. 43E–G). Paraprocts comparatively modified (Fig. 43E–G), comprising a robust and big portion boot-shaped which is exposed dorsally, and two smaller valves which are hidden anteriorly; portion close to each cercus with a small finger-like projection; when paraprocts are close (Fig. 7D), both paraprocts can overlap on each other. Subgenital plate with a pair of short and oval stily outward oriented (Fig. 26E); disc with an apical V-shaped emargination. Phallus with dense spiny microstructures on the anterior region over the lobe **dl** (Figs 11D, 44C,D). Sclerites **TS** completely attached to lobe **dl**; with a strong and rounded projection on basal portion, with scale-like microstructures. The **TS** is expanded inwardly toward the lobe **vdl**, and the **TS** is joined with the sclerite **VS**. Both sclerites (**TS+VS**) are widely separated from each other at midline. The fold **fdl** is large and oval. The vesicles **ejv** are oval and small; the apodemes **ap** are oval and barely sclerotized. The lobe **vl** is large, comprising two folds, two upper, and two lower pairs; apparently the apex of each lobe have rounded tips.

**Female.** Tergite X divided at midline, straight, devoid of projections. Epiproct triangular, large. Cerci simple (Fig. 46B), short, cylindrical and acuminate. Paraprocts triangular. Subgenital plate trapezoidal (Fig. 26F). Ovipositor concave (Fig. 46B), shorter than hind femur, upcurved; dorsal valve about four times as wide as ventral one, its width decreasing toward apex; ventral valve with constant width over the entire

length; apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Checked specimens are completely dark brownish (Fig. 46), all of them are old, from museums.

**Gen. nov. 3** comprises only the species **Gen. nov. 3** *abbreviata* (Redtenbacher, 1891) **comb. nov.**

**Gen. nov. 3** *abbreviata* (Redtenbacher, 1891) **comb. nov.**

(Figs 2E, 3E, 6C, 7D, 11D, 15B, 24E,F, 26E,F, 43EG, 44CD, 46)

*Agraecia abbreviata* Redtenbacher, 1891: 456.

**Holotype female** (NMW) labeled \Coll. Br. v. W. Brasilien [typewritten on white paper] \ Coll. Br. v. W. Agraecia abbreviate [type- and handwritten on white paper] \ 1101 [handwritten on white paper] \ HOLCITPE TYPUS [handwritten on red paper].

**Diagnostic description** (based on new collected material). General features as in the description of the genus. **Male.** Tegmina with left stridulatory file as shown in Fig. 24E. Cerci and paraprocts as shown in Fig. 43 E,G. Subgenital plate with a square shape (Fig. 26E); apical emargination cutting of about one-third the length of the plate; styli short, about of one-sixth the length of the plate, outward oriented. Phallus as shown in Figs 11D, 44C,D.

**Female.** Subgenital plate trapezoidal (Fig. 26F) with two fine lateral projections which forms a shallow but large emargination.

**Coloration.** Specimens are homogenously dark brownish (Fig. 46), devoid of a distinctive stripe on pronotal disc. Specimens are old, but some of them remain a dark mark on the tympanal region, as pointed in original description (Redtenbacher 1891).

**Distribution.** The Female holotype was collected in Brazil (Redtenbacher 1891), but the accurate type locality is unknown. There is an additional register of a male collected in RJ (Bruner 1915); however there is no information about the accurate locality of this specimen. All examined specimens are from the Parque Ecológico Chico Mendes in Rio de Janeiro (Fig. 15B).

**Variation.** Measurements of males (n = 4): TL 26.00–30.00; PL 8.00–9.00; TegL 19–22; FF 7.00; FT 8.00; HF 16.00–17.00; HT 16–18. Measurements of females (n = 3): TL 25.000–33.00; PL 8.00–9.00; TegL 18.00–20.00; FF 8.00–9.00; FT 8.00–9.00; HF 18.00–20.00; HT 19.00; OL 13–14.

Spines of male and female (n = 7): sFF 2–3; sMF 3–4; sHF inner 0–3; sHF outer 6–7.

**Specimens examined.** Four males (MNRJ) labeled \Exc. 289. Lagoinha das Taxas (mata) G.B. 29.v.1966. N.Santos e Fa fil Piedade cols. [printed and handwritten on brownish paper] \ **Gen. nov. 3 abbreviata**, **comb. nov.** [printed on white paper]\. \Exc 265. col 3. L. Taxas (zona umbriufila) G. B. 5.ix.965. N. Dias dos Santos [printed and handwritten on brown paper] \ M.N. N. R-6 [printed and handwritten on brown paper] \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\. \Exc. 265. Col. 3. L. Taxas (Zona umbrofila) G. B. 5.ix.965. Dias dos Santos. \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\. Lg. das Tachas IX – 961 J.C.M. C. col. [handwritten on white paper] \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\. Three females (MNRJ) labeled \Exc. 265. Col 3. L. Taxas (zona Umbrofila) G.B. 5.ix.965 [printed and handwritten on brownish paper] \ M.N. N. R-6. [printed and handwritten on brown paper] \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\. \Exc. 265. Col 3. L. Taxas (zona Umbrofila) G.B. 5.ix.965 [printed and handwritten on brown paper] \ M.N. N. R-6. [printed and handwritten on brown paper] \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\. \Exc. 289. Lagoinha das Taxas (mata) G. B. 29.v.1966. N. Santos e Feie.fil. Pidade cols. [handwritten on white paper] \ **Gen. nov. 3 abbreviata** (Redtenbacher, 1891) **comb. nov.** [printed on white paper]\.

**Comments.** Additionally to the female holotype there is a male identified by Redtenbacher in 1931 deposited in the MNW (see images in OSF). In variation section it is not included holotype data, because total length (TL) is much lesser than the checked specimens, however other measures coincide (TL 22.50; PL 7.90; TegL 20.30; HF 19.5; OL 13.00; sFF 2–3; sMF 3–4; sHF inner 2; sHF outer 7 (Redtenbacher 1891)).

#### **Gen. nov. 4**

(Figs 3F, 11E, 24G,H, 26G,H, 27B, 43H–L, 44E,F, 47, 48)

**Type species. Gen. nov. 4 pulchella** (Hebard, 1927) **comb. nov.**

**Diagnosis.** Species of this new genus share the following combination of features: fastigium verticis thinner and shorter than scapus, apex rounded, tegmina with vein **M+CuA** longer than the mirror (Fig. 3F). Male postabdomen with, posterior portion of tergite X strongly prolonged behind in two protruding lobes which forms an U-shaped emargination; cerci elongated and very robust (Fig. 43J) with a strong finger-like projection on outer portion and a strong and spine-like projection on inner portion; paraprocts comprising a simple shell-like plate (Fig. 43I); subgenital plate with an short V-shape emargination (Fig. 26G); titillator with sclerite **TS+VS** fused and completely attached to lobe **dl** (Figs 11E, 44E); lateral portions of lobe **dl** with minute microstructures (**ti**). Female postabdomen with tergite X strongly prolonged behind in two strong projections; subgenital mostly squared with two projections forming a broad U-shaped emargination (Fig. 26H).

**Description.** (Male and female similar, except for sexual features). Head more or less conical, hypognathous. Vertex of head normal, not dorsally protruding. Antennae long, filiform, hypognathous. Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus longer than pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular, slightly shorter than scapus; narrower than scapus; apex rounded; projected straight between scapus and pedicellus; dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of head, weakly protruding. Face longer than wide. Fastigium frontis semitriangular not distinctly protruding. Frons flat and smooth, devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium well defined, comparatively small; each lateral ocellus defined over each lateral portion of fastigium verticis, nearest to the apice. Tegumen of pronotum smooth. Pronotum mostly smooth; with disc broadly rounded into paranota and posterior area shouldered; in profile with dorsal line and in transverse section straight, without higher or protruding zones. Metazone produced caudad but leading the tegminal stridulatory region expose. Pronotal disc with the same width along the entire length. Anterior margin concave; posterior margin backward concave; principal transverse sulcus deep, curved, continuous; metazona without traces of longitudinal keel. Humeral sinus weakly indicated. Paranota wider than deep; ventral margin oblique, slightly curved, ventro-caudal angle obtuse, rounded; caudal margin obliquely truncate. Thoracic auditory spiracle oval, hidden under the auditory swelling, a bit longer than half the length of paranota and free from pronotum; marginal trichobotria sparse; posterior edge of spiracle devoid of finger-like projection, instead

of that with a protruding region. Prosternum armed with a pair of spines; each spine longer than the inner portion of the forecoxa. Meso- and metabasisternal lobes trapezoidal, projected downward, most strongly projected the mesobasisternal ones; lateral margins concave; inner margins concave, both separated at the base. Each posterior angle of mesobasisternal lobes with one strong tubercle-like projection. Metasternal medial plate with one tubercle at each lateral portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coraceous with multiple secondary veins and cells (Fig. 3F); longer than postabdomen. Fore coxae with an elongated, strong and forwardly curved projection spine-like dorsally; mid- and hind coxae with a small rounded projection on apical portion, ventrally. Fore femora armed with spines (2–4) ventrally only on inner margin, midfemora armed on inner (2) and outer margin (4–5), and hindfemora on both margins (inner, 3–4; outer 5–6). Fore genicular lobes with an acute pointed tip at inner margin, but not as acute as the remaining. Midgenicular lobes armed with an acute spine only at the inner margin; hindgenicular lobes with inner and outer one armed with one acute. Fore- and mid tibiae armed with spines on both margins but only ventrally; spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibiae armed on all four dorsal and ventral margins; apex of each hind tibia e with one pair dorsally and two pairs of movable spurs ventrally. Tympanal region weakly swollen; each tympanal slit on Fore tibiae very narrow, facing forward, with pair of small, rounded pits bellow each tympanal slit. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with costal margin concave (Fig. 3F); anal margin mostly straight; posterior margin outwardly concave. Pre-costal region straight, narrowing toward apex. Vein **RP** devoid of subveins; vein **MA** with ramified into three subveins. Cubital region of each tegmen large, extending more than half the length of the tegmen. Vein **Cu1** weakly marked. Region between the vein **CuPa** and the mirror mostly pigmented. Vein **CuPb** of left tegmen slightly curved, uniform (Fig. 24G), with margins slightly concave; maximum width of vein 0.51 mm. Stridulatory file 2.54 mm long, with 133 teeth; length of the smallest teeth 0.04 mm and of the largest ones 0.13mm, teeth lamelliform, homogenously arranged over the file. Vein **CuPb** of right tegmen much narrower than the left one (Fig. 24H); length 1.81 mm; vein width as wide as teeth (0.10 mm); number of teeth 97. Left mirror rectangular, comparatively larger, away from the anal margin and very pigmented. Right mirror oval; completely membranous. Stridulatory region with scattered and few small spiny-like microstructures ventrally, most of them on vein **M+CuA**. Tergite X as wide as the

remaining (Fig. 43H,I); elongated behind covering epiproct and paraprocts; tegumen smooth and shining, with dense bristles at mid portion. Epiproct short and triangular; covered by dense tubercles and bristles; gross bristles at apical margins. Cerci robusts (Fig. 43J–L), bearing small tubercles and long bristles dorsally and ventrally at basal region, with strong projections apically, smooth and a semitriangular projection dorsally. Paraproct simple (Fig. 43I), shell-like, with a lot of little tubercles and bristles, with strong bristles at apical margin. Subgenital plate with a pair of elongated stily (Fig. 26G), and backward oriented; disc with an apical V-shaped emargination. Phallus with thin microstructures on laterals of lobe **dl** (Figs 11E, 44E,F). Sclerites **TS+VS** completely attached to lobe **dl**; fold **vdl** dorsally everted, together with the sclerites **TS+VS**. Both sclerites (**TS+VS**) are widely separated from each other at midline. There is not lobe **fdl**. The vesicles are oval and small; the apodemes **ap** are elongated and barely sclerotized. The lobe **vl** is large, comprising two folds, two upper, and two lower pairs; the apex of each lobe have rounded tips.

**Female.** Tergite X divided at midline, with a protruding, strong apical projection dorsally. Epiproct and paraprocts triangular. Cerci simple, short, cylindrical and acuminate. Subgenital plate with basal region as wide as the apical one (Fig. 23H). Ovipositor boomerang-shaped, shorter than hind femura, upcurved; boomerang-shaped; dorsal valve about three times as wide as lower one, ventral valve with constant width over the entire length, apex of ovipositor rounded; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** Unlike other species of *Agraeciini*, which are mostly brownish and yellowish, species of this genus have greenish colors (Fig. 48).

**Distribution.** **Gen. nov. 4** is distributed only on the Colombian Andean region (Fig. 47), which is classified within the Pacific domain of the Brazilian subregion (*sensu* Morrone 2014). Several katydids that inhabits the Cauca province and Western Ecuador province, which are within the Pacific domain, have been also registered in the south and north of the Chocó-Darién province (*e.g.* *Phylloptera dimidiata* Brunner von Wattenwyl, *Scudderia paronae* Griffini, *Ceraia peraccae* Griffini, *Eubliastes pollonerae* (Griffini), etc.). This fact reinforces the idea that *Agraecia festae* can be the same species of **Gen. nov. 4 pulchella**, or a closely related species.

**Gen. nov. 4** comprises two species, **Gen. nov. 4 pulchella** (Hebard, 1927) **comb. nov.**, and *S. vittata* (Redtenbacher, 1891). As type species was selected **Gen. nov. 4 pulchella comb. nov.** instead of the first described *S. vittata comb. nov.*, because

the latter was based on an immature female, making difficult the delimitation of diagnostic characters.

**Gen. nov. 4 *vittata* (Redtenbacher, 1891) comb. nov.**

*Agraecia vittata* Redtenbacher, 1891: 454

**Holotype female** (NMW): Columbia (Coll. Brunner).

This species was described based on an immature female, from Colombia, devoid of more accurate locality collection data.

It is suspected that **Gen. nov. 4 *vittata* comb. nov.** and **Gen. nov. 4 *pulchella* comb. nov.** are the same species (Hugel 2009). Adults of **Gen. nov. 4 *vittata* comb. nov.** have not been collected after its description. Additionally immature of **Gen. nov. 4 *pulchella* comb. nov.** are very similar to the immature holotype of **Gen. nov. 4 *vittata* comb. nov.**, they have the same pattern of colocation (female immature of **Gen. nov. 4 *pulchella* comb. nov.** examined in MUSENUV (21858)). Additionally as noted by Hugel (2009), adult and immature specimens of **Gen. nov. 5 *cesairei* comb. nov.** have different coloration, a feature that could be extrapolated to the entire Agraeciini, and for this reasons, coloration in immature stages alone, are unreliable characters.

**Gen. nov. 4 *pulchella* (Hebard, 1927) comb. nov.**

(Figs 3F, 11E, 24G,H, 26G,H, 27B, 43H–L, 44E,F, 47, 48)

*Agraecia pulchella* Hebard, 1927: 346.

**Holotype female** (ANSP): Muzo, Boyacá, Colombia (From A. Maria.) [Hebard Collection, Type No. 1076.].

**Diagnostic description** (based in new collected material). General features as in the description of the genus. **Male.** Tegmina with left stridulatory file as shown in Fig. 24G. Tergite X strongly prolonge behind in two straight projectios which configures an U-shaped emargination, cutting about of the half length of the tergite. Cercus flat dorso-ventrally (Fig. 43J–L); three protruding projections at apical portion; the first projection at inner side, acute; a second projection at outer side, more robust and rounded; and a

third finger-like projection on lateral ventral side. Paraproct simple (Fig. 43I), triangular with a lot of dense tubercles. Subgenital plate as shown in Fig. 26G. Phallus as shown in Figs 11E, 44E.

**Female.** Subgenital plate and ovipositor as shown in Fig. 26H.

**Coloration.** Based on alive females (Fig. 48): general coloration mostly greenish. Tegmina, femora, and lateral portion of pronotum and head greenish. Tibiae a mixture between greenish and brownish. Pronotal disc and dorsal portion of head light brownish, additionally with two blackish bands on each side. Pronotum with a blackish stripe on the entire edge. Lateral ocelli whitish. Eyes, upper half dark brownish, lower half greenish. Thoracic pleuron and coxae with blackish marks (see Fig. 48B). Females still retain the color when they are preserved. Old males preserved specimens are paler than females, but there are not registers of alive males. Male abdomen and postabdomen blackish.

Immature females bear different coloration than the adults. Immature have only two wide black stripes at each lateral side of head and pronotum, and at the midline there is a greenish stripe, similar to the coloration of **Gen. nov. 4 vittata** (Redtenbacher, 1891) **comb. nov.**

**Distribution.** **Gen. nov. 4 pulchella comb. nov.** is distributed through the Colombian Andean region (Fig. 47), there are registers for the departments of Boyacá, Cundinamarca, Risaralda, Santander and Valle del Cauca (Chamorro-Rengifo *et al.* 2011).

**Calling song (Fig. 27B).** One male recorded in the field called continuously for one and a half minutes, probably longer. It produced a series of short calls of somewhat irregular repetition rate, with intervals of one to two seconds. An individual call is a zip sound consisting of three directly succeeding syllables. A syllable consists of a very low initial pulse, probably corresponding to the opening stroke of the tegmina, and a quick and noisy crescendo of rapidly decaying impulses, probably corresponding to tooth-scraper impacts during the closing stroke. The spectrum is fairly broad, with most energy between 10 and 15 kHz, apparently not reaching into ultrasound (although there might be isolated components not covered by the sampled frequency range with maximum 22 kHz).

**Specimens examined.** One adult male (MUSENUV) labeled \Colombia, Valle, Bosque Yotoco, altura 1500, Hosp: vegetación, Fecha: May 18-96. Col: F. Vargas [printed and handwritten on white paper] \ 21857 [printed on white paper] \ *A. pulchella* [printed on white paper]\. Five adult females labelled (MUSENUV) labeled \Colombia,

Valle, Vía mar nueva Km: 18. altura: 220 m. Hosp: Bromelia. Fecha: May 16-17. Col: G. Morris [printed and handwritten on white paper] \ 21856 [printed on white paper] \ *A. pulchella* [printed on white paper]\. \Colombia, Valle, Cali, Univalle. altura: 1000 msnm. Hosp: Vegetación. Fecha: Nov, 30, 87. Col: M.C. Mendoza [printed and handwritter on white paper] \ 21855 [printed on white paper] \ *A. pulchella* [printed on white paper]\. \Colombia, Valle, Bosque Yotoco, altura: 1500, Hosp: Vegetación, Fecha: Abril 12/92. Col: F. Montealegre [printed and handwritten on white paper] \ 21359 [printed on white paper] \ *A. pulchella* [printed on white paper]\. One adult female (MUSENUV) labeled \Colombia, valle, Chicoral. Altura: 1600 msnm, Hosp: vegetación, Fecha: 01-03-2004, col: Juliana Chamorro [printed and handwritten on white paper] \ 21381 [printed on white paper] \ *A. pulchella* [printed on white paper]\. One adult female (MUSENUV) labeled \Colombia, valle, Chicoral. Altura: 1600 msnm, Hosp: vegetación, Fecha: 16-10-2002, col: Juliana Chamorro [printed and handwritten on white paper] \ 21383 [printed on white paper] \ *A. pulchella* [printed on white paper]\. One immature female (MUSENUV) labeled \Colombia, Valle del Cauca, 20-10-1993, hospedero: arbusto, col: F. Montealegre [printed and handwritten on white paper] \ 21858 [printed on white paper] \ *A. pulchella*, det. F. Montealegre [printed on white paper]\.

**Habitat.** Quite possibly the distribution of the species is restricted to the presence of Bromeliads, since there are collection and observational records (pers. obs), of specimens inhabiting the interior of this plants. But apparently there is no specialization for forest type, as they have been captured in both Tropical dry and Premontane rain forest.

Although there are records of males in literature (Chamorro-Rengifo *et. al.* 2011), this is the first time the male is described.

### **Gen. nov. 6**

(Fig. 47)

Based on original description in Piza (1978) and Hugel (2009).

**Type species. Gen. nov. 6** *viridipennis* (Redtenbacher, 1891) **comb. nov.**

**Diagnosis** (Based on Hugel 2009 and Piza 1978). This genus differs from the remaining Agraeciini by the following combination of features: fastigium verticis thinner and shorter than scapus. Male postabdomen with posterior portion of tergite X strongly dorsally prolonged with two large lobes on ventral margin; paraprocts consisting of a disc and a lateral upward projection; cercus very long, longer than subgenital plate, apical portion thinner, and with lateral projections; subgenital plate with an U-shaped emargination; titillator with sclerites TS symmetrical short, wider than high, joined in the middle, well sclerotized, apex with denticles upwardly. Female postabdomen with tergite X straight; subgenital plate trapezoidal with two lateral projections forming an U-shaped emargination.

**Redescription.** (Male and female similar, except for sexual features). Head more or less conical, hypognathous. Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus about twice as long and wide as pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular, shorter and narrower than scapus, reaching the middle of scapus and with a blunt apex; projected straight between scapus and pedicellus; dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to the size of head, weakly protruding. Face longer than wide. Fastigium frontis triangular, not distinctly protruding. Frons flat and smooth devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium usually well defined, comparatively large, about two times the size of one eye; each lateral ocellus defined over each lateral portion of fastigium verticis, close to its base. Pronotum mostly smooth; disc broadly rounded into paranota and posterior portion shouldered; in profile with dorsal line and in transverse section straight, without higher or protruding zones. Metazona produced caudad, leaving exposed or only covering the basal portion of the stridulatory region. Pronotal disc with same width from pro- to metazona. Anterior margin concave; posterior margin backward concave; principal transverse sulcus deep, curved, continuous at midline; devoid of second transverse sulcus; metazona without traces of longitudinal keel. Humeral sinus weakly indicated. Paranota wider than deep; with a sulcus prolonged to the metazona on disc; ventral margin obliquely truncate; ventro-caudal angle almost right; caudal margin weakly oblique, almost straight. Anterior portion of mesopleurum with a vertical and thick carina. Thoracic auditory spiracle hidden under the auditory swelling. Prosternum armed with a pair of long spine. Meso- and metabasisternal lobes trapezoidal, projected downward; lateral margins concave; inner margins concave, both separated at the base. Possibly each posterior

angle of mesobasisternal lobes with one strong tubercle-like projection. Metasternal medial plate with one delicate tubercle at each lateral portion of the posterior margin. Wings in both sexes fully developed (macropterous species). Tegmina coriaceous with multiple secondary veins and cells; usually elongated and slender, surpassing apices of hind femora. Pro coxae with an elongated, strong and forwardly curved spine-like projection dorsally. Mid coxae with a small anterior and dorsal spine and a tubercle at apical portion, ventrally. Hind coxae unknown. Fore femora armed with spines (3–5) ventrally only on inner margins; midfemora with spines (4–6) on outer margins; and hindfemora on both margins (inner, 1–2; outer 7–8). Inner genicular lobes of Fore femora with an acute spine, outer lobe external slightly acute ventrally; inner and outer genicular lobes of mid femora armed with an acute tiny spine; inner and outer lobes of hindfemora armed with one acute and strong spine. Fore- and mid tibiae armed with spines on both margins but only ventrally; spines  $\frac{1}{4}$  to  $\frac{1}{2}$  diameter of tibia; hind tibiae armed on all four dorsal and ventral margins; apex of each hind tibia with one pair dorsally and one pair ventrally of movable spurs. Tympanal region weakly swollen; each tympanal slit on Fore tibiae very narrow, facing forward; with a pair of small, elongated pits below and close to each tympanal slit. Dorsal surface of abdominal terga smooth, unmodified.

**Male.** Tegmina with basal and apical portion of costal and anal margin concave, mid portion straight; posterior margin outwardly concave. Pre-costal region usually narrowing toward apex. Details of ramifications of veins unstudied. Cubital region of each tegmen large, with dense network of veinlets. Stridulatory file 1.80 mm long. Teeth lamelliform, homogeneously arranged on the file; usually few teeth dispersed at the right portion of the file. Vein **CuPb** of right tegmen much narrower than the left one. Left mirror cup-shaped; comparatively short, away from the costal margin of the tegmen, anterior margin oblique; very pigmented. Right mirror oval; completely membranous. Stridulatory region with dense little spiny-like microstructures ventrally. Tergite IX with lateral portions a bit longer than the remaining. Tergite X with lateral portion as wide as tergite IX, with a cone-shaped, dorsal portion strongly projected. Cerci very elongated. Paraprocts unknown. Subgenital plate with a pair of long stily, backward oriented; disc with an apical U-shaped emargination. Phallus with symmetric sclerites **TS**.

**Female.** Tergite X divided at midline, straight, devoid of projections. Cerci simple, short, cylindrical and acuminate. Subgenital plate with basal portion wider than apical portion; apical portion sometimes emarginated. Ovipositor concave, as long as or

shorter than hind femur, upcurved; dorsal valve about three times as wide as ventral one, somewhat expanded at midlength; ventral valves at basal portion with a spiny projections; apex of ovipositor pointed.

**Coloration.** Males and females seem to bear the same coloration pattern. A homogenous light brownish apparently devoid of distinctive marks.

**Distribution.** This genus is distributed in French Guiana to northeastern of Brasil (Fig.47). **Gen. nov. 6** *viridipennis* **comb. nov.** is recorded for the French Guyana and for an uncertain locality in the state of Maranhão in Brazil, it can be deduced that this species is distributed through the northeastern Brazilian coast, in the areas classified as Roraima and Paraná Provinces (*sensu* Morrone 2014). It is possible that this species can be collected on a large extension of the Amazonian biome.

**Gen. nov. 6** comprises only the species **Gen. nov. 6** *viridipennis* (Redtenbacher, 1891).

**Gen. nov. 6** *viridipennis* (Redtenbacher, 1891) **comb. nov.**  
(Fig. 47)

*Agraecia viridipennis* Redtenbacher, 1891: 453; Hugel (2009): 135.

*Agraecia malkini* Piza, 1978, syn.: 185.

**Holotype female** (NMW) \Coll. Br. v. W. ex. Coll. Fischer Brasilien [type- and handwritten on white paper] \ det. Redtenb. *Agraecia viridipennis* [type- and handwritten on white paper] \ 656 [handwritten on white paper] \ HOLOTYPE TYPUES [handwritten on red paper].

**Diagnostic description.** General features as in the description of the genus.  
**Male.** Tergite X cone-shaped, with dorsal portion projected, ventral margin comprise two weak large lobes with a little emargination at midline. Cerci longer than subgenital plate, slender and cylindrical, with apical portion thinner than basal one, apices overlapping over each other, downward curved, Subapical portion with a strong and lateral spine-like projection. Subgenital plate with an U-shaped emargination cutting about of less than one-quarter the length of the plate; stylies as long as one quarter the length of the plate.

**Female.** Subgenital plate with basal portion than apical; apical portion with a concave and superficial emargination at the entire dorsal margin.

**Specimen examined.** One male labeled (ESALQ): \Garápé Gurupi - Uma Aldeia Araçu, Ma. 50 km e. de Canindé 20 V. 1963 malkin col. [typewritten on brown paper] \Agraecia malkini Piza Tipo [handwritten on white paper].

**Comment.** **Gen. nov. 6** *viridipennis* (Redtenbacher, 1891) was originally described based on a female collected in Brazil; there is no accurate specific locality (Fig. 47). Hugel (2009) identified three females collected from the French Guiane as **Gen. nov. 6** *viridipennis* (Redtenbacher, 1891) **comb. nov.** (= *A. viridipennis*), and he got associated the females with a male of the species. The male from the French Guiane is similar to the male holotype of *Agraecia malkini* which was collected in the Brazilian state of Maranhão. Hugel (2009) established *A. malikini* as a synonym of *A. viridipennis*.

Maranhão is relatively close to French Guiane. Nevertheless, as the checked brazilian species of genera *Agraecia* and **Gen. nov. 1** seem to have a restricted or short distribution, the specimens of **Gen. nov. 6** *viridipennis* **comb. nov.** from the two localies must to be studied, and should make a comparison of the morphology of phalli.

As the only male available was the holotype of *Agraecia malkini*, an old and delicate specimen, it was not possible to dissect the phallus.

## **Gen. nov. 5**

(Fig. 47)

Based on original description and images in Hugel (2009; figs 1–15, 27)

**Type species.** **Gen. nov. 5** *cesairei* (Hugel, 2009) **comb. nov.:**130

**Diagnosis.** This genus differs from the remaning Agraeciini by the following combination of features: fastigium verticis thinner and shorter than scapus, and with a blunt apex. Cerci very elongated, slender; basal portion broader than apical portion; with tubercles and many bristles; apical portion smooth; apex with an acute teeth-like projection. Subgenital plate with a deep shallow V-shape emargination. Phallus with two sclerites **TS** with closes bases, and divergent apex. Female postabdomen with tergite X straight; subgenital plate trapezoidal, with two elongated projections which configures an U-shaped emargination.

**Redescription.** Male and female similar, except when specified). Head more or less conical, hypognathous. Vertex of head normal, not dorsally protruding. Antennae long, filiform, overreaching the body. Scapus little longer and two times wider than pedicellus; apex straight, devoid of protruding projections. Fastigium verticis triangular; narrower than scapus, and with a blunt apex; projected straight between scapus and pedicellus; dorsal portion at base smooth, devoid of secondary structures. Eyes small relative to size of head, weakly protruding. Face longer than wide. Fastigium frontis semitriangular, not distinctly protruding. Frons flat and smooth, devoid of dots or wrinkles. Tegumen of genae smooth, without traces of genal carinae. Mandibles and clypeus symmetrical. Ocellus medium comparatively small. Pronotum mostly smooth; with disc broadly rounded into paranota and posterior area shouldered; in profile with dorsal line and in transverse section straight, without higher or protruding zones. Metazona produced caudad, covering only the basal portion of the stridulatory region. Anterior margin concave; posterior margin almost straight, slightly concave. Humeral sinus weakly indicated. Paranota with ventral margin slightly concave. Prosternum armed with a pair of long spines. Wings in both sexes fully developed (macropterous species). Tegmina longer than postabdomen. Forecoxae with a spine on dorsal portion. Mid coxae with a small spine on basal portion dorsally and tubercle on posterior portion ventrally. Fore femora armed with spines ventrally on inner (5–7), and outer (3–5) margin; midfemora mostly armed on outer margin (6–10); and hindfemora on both margins (inner, 1–2; outer 7–9). Genicular lobes of fore- and midfemora with an acute projection at inner margins; hindfemora with a spiny-like projection on inner and outer margin.

**Male.** Tegmina with vein **CuPb** of left tegmen mostly straight, uniform, with margins slightly concave. Left stridulatory file with 68–71 teeth. Teeth lamelliform, homogeneously arranged over the file. Left mirror square; comparatively short; away from the anal margin; anterior margin oblique. Left mirror mostly squart; membranous. Right mirror square; membranous. Tergites IX and X as long as the remaining. Tergite X with apical portion with a concave and wide emargination. Epiproct slightly indented. Cerci very elongated, slender, basal portion as long as and broader than apical portion, with tubercles and many bristles; apical portion smooth; apex with an acute teeth-like projection. Paraprocts unknown. Subgenital plate elongate; with a V-shape emargination; with a pair of long stily.

**Female.** Tergite X, epiproct and paraprocts unknown. Cercus simple, short, cylindrical and acuminate. Subgenital plate with basal portion wider than the apical one,

usually emarginated. Ovipositor concave, shorter than hind femur, upcurved; dorsal valve about three times as wide as ventral one, somewhat expanded at middle; apex of ovipositor pointed; ventral valves smooth, devoid of processes on basal portion.

**Coloration.** General coloration dark brownish.

**Biology.** In captivity specimens were observed feeding on small insects, flowers and fruits (Hugel 2009).

**Distribution.** **Gen. nov. 5** was described from the Martinique island (Fig. 47), which is part of the Antillean subregion (*sensu* Morrone 2014). This monospecific genus can thus be endemic. The Martinique Island is classified together with other Caribbean island within the Lesser Antilles province; this province is inhabited by several endemic species of plants (*e.g.* Francisco-Ortega *et al.* 2007, Santiago-Valentin & Olmstead 2004) and vertebrates (*e.g.* Fouqueta *et al.* 2013, Breuil 2009). **Gen. nov. 5** has not been reported for any other locality on the South American continent. But it is also important to note that katydids' wildlife in the Caribbean islands and Venezuela, the nearest continental land, is practically unknown.

This genus is only known from the Martinique Island.

**Gen. nov. 5** comprises only the species **Gen. nov. 5** *cesairei* (Hugel, 2009) **comb. nov.**

**Gen. nov. 5** *cesairei* (Hugel, 2009) **comb. nov.**

(figs 2–9 in Hugel 2009)

*Agraecia cesairei* Hugel, 2009: 130.

**Holotype male** (MNHN) \Agraecia cesairei n.sp. Det Hugel 2009 [handwritten on white paper] \ 11 VIII 2008 MARTINIQUE Fol. St Denis, Plateau Boucher sentier du Carbet 650 m Alt 61°06'00''O, 14°43'09''N Rec. Hugel S. Vue de Nuit [handwritten on white paper] \ Enregistrement Mart n° 2008 081 [handwritten on white paper] \ MNHN-ENSIF 2074 [typewritten on white paper] \ Martinique2008 0081 [printed on white paper] \

\ HOLOTYPE [handwritten on red paper] \ 5 [handwritten on red paper].

**Allotype female** (MNHN) \Agraecia cesairei n.sp. Det Hugel S. 2009 [handwritten on white paper] \ 11 VIII 2008 MARTINIQUE Fd. ST Denis, Plateau

Boucher sentier du Cabert 650 m Alt 61°06'00''O, 14°43'09''N Rec Hugel S. Vue de Nuit [handwritten on white paper] \ Martinique 2008 0083 \ [printed on white paper] \ MNHN-ENSIF 2075 [typewritten on white paper] \ ALLOTYPÉ [handwritten on red paper] \ 7 [handwritten on red paper].

**Diagnostic description.** General features as in the description of the genus. **Male.** Tergite X with a lateral projection at each side, that configures a wide and concave emargination, about of half the length of the tergite. Paraprocts unknown. Cerci longer than subgenital plate, consisting of a wider basal portion and an apical finer one; ending in an acute tip; apical portions superimposed one over the other. Subgenital plate with the last quarter of the apical portion narrower than the remainder, where there is also, an U-shaped emargination. Titillator with sclerites **TS** symmetrical, higher than wide, arcuate outwardly, adjoining at middle, with tubercles in the upper part.

**Female.** Subgenital plate narrowing from basal to apical portion; each lateral side of apical portion projected in two acute projections which configures a square U-shaped emargination.

**Coloration.** General coloration dark brownish, with some areas blackish and others white. The following areas or structures are blackish: face, scapus, genicular lobes, apex of the tibiae, spines of femura. The following areas or structures are whitish: clypeus, labrum, palpi, median ocellus, lateral ocelli, apex of fastigium vertex. Abdomen of alive specimens yellowish.

**Distribution.** This species is only known from Martinique Island (Fig. 47).

**Gen. nov. 7 *reticulata*† (Piton & Théobald, 1939) comb. nov.**

(Fig. 49)

*Agraecia reticulata*† Piton & Théobald, 1939: 88

**Comments.** This species was erected based on a fossil of a tegmen dated from the Oligocene (Plate 1, fig. 3 in Piton & Théobald 1939) from the fossiliferous deposit of Puy-Saint-Jean in France. The authors considered the venation of the fossil similar to the venation in Agraeciini, and especially with *Agraecia* in its old sense. The authors considered *Agraecia* as a taxon comprised by 16 species, but it is not specified which species of the genus were observed for comparison.

Extant species of *Agraecia sensu novo* are all from Brazil. *Agraecia sensu novo* and the genera described here are based not only on the morphology of the tegmina, thus it is not possible to maintain this fossil species in *Agraecia* as here redefined. The venation of the tegmina differ from *Agraecia sensu novo* and the new genera because in the fossil, vein **M** diverges from **M+CuA** much after than extant genera (Fig. 49); basal portion diverging straight from **R**; vein **M** is widely separated from vein **R** from base, in extant genera this basal portion is curved; vein **ScP** diverging strongly from **R** since base, in extant species **ScP** runs close together to vein **R**. We consider that now it is better to transfer the fossil to a new genus.

### *Incertae sedis*

The following two species are here maintained in *Agraecia sensu novo*, but we believe they have to be located to other genera in the future.

### *Agraecia festae* Griffini, 1896

**Syntypes** (MRSNT), one adult male, one adult female, and one immature female: “Floreste del rio Lara (Darien)”.

Type material of *A. festae* is currently unavailable for revision. Collection of Museo Regionale di Storia Naturale, Torino (Italy) is closed and devoid of curator.

Original description (Griffini 1896) is very complete and contains important details, but it is insufficient for assigning it to an Agraeciini genus. Following description, specimens have yellowish marks, with two longitudinal lines on the dorsal portion of fastigium and pronotum. It possibly belongs to **Gen. nov. 4**

### *Agraecia fallax* Karny, 1911, nomen dubium

This species was described from a male collected in New Guinea. The holotype originally in Karny's collection at the NMW seems to be lost (Sigfrid Ingrisch pers. comm.), and the description does not provide enough information to assign it to any

genus. Following Karny (1911), *Agraecia fallax* is similar to *Secsiva differens* (Redtenbacher, 1891), originally described as *A. differens*.

## **Discussion**

With this revision, the neotropical Agraeciini comprise 22 genera and 66 species, but they are still insufficiently studied. The limits of the tribe, its suprageneric classification and internal phylogenetic relationships remain unresolved. For instance, the genus *Subria* Stål is as problematic as *Agraecia* was, needs to be revised and redefined. In addition, six of the previously genera are monospecific (*Acanthacara* Scudder, *Cestrophorus* Redtenbacher, *Erechthis* Bolívar, *Hyperomerus* Redtenbacher, *Paranelytra* Karny and *Parasubria* Karny), and others contain only few species. This is a consequence mainly of insufficient taxonomic and biodiversity studies on neotropical katydids. There are plenty of unidentified specimens in Brazilian museums and part of them certainly belong to new taxa. In the Andes of southern Ecuador were also found several undescribed and mostly brachypterous species, partly representing unknown genera (Braun 2008). Moreover, the katydid fauna of large portions of the South American subcontinent, including entire biomes, remains unsurveyed. The diversity of Agraeciini is certainly much higher, unestimable at this moment.

**Morphological comparisons.** Individuals of *Agraecia* and of the new genera described here share some similar characteristics, which may have been the reason why all previous species determined as *Agraecia* were included in a single genus. Overall similarity is insufficient for classifying species in a single genus and more emphasis should be given to comparative morphology of specific structures. The form of fastigium verticis and fastigium frontis, presence or absence of spines on sternum and development of tegmina have been traditionally used as diagnostic characters to differentiate genera of South American Agraeciini. Recent revisions of particular genera include more significant details, for example the morphology of postabdominal structures (*e.g.* Hugel 2009, Montealegre-Z. & Morris 2003, Naskrecki 2000b). Below we discuss structures traditionally mentioned in katydid taxonomy, the ones emphasized in modern works, and also features usually not mentioned or carefully compared (*e.g.* the stridulatory file of the right tegmen and phallus).

Specimens of Agraeciini are characteristically light or dark brownish colored (*e.g.* species of *Agraecia* and **Gen. nov. 1**) and it seems that greenish and lighter species as **Gen. nov. 4**

are rare (see also Ingrisich 1998). Face is rather uniform among the treated genera, being shiny and smooth, uniformly colored, devoid of marks, except for species of **Gen. nov. 2**, in which the face is slightly wrinkled with a large black marking on the frons. However, in the latter case it is not as wrinkled as in some Oriental Agraeciini, which can also bear conspicuous markings (*e.g.* species of *Pseudonicsara* Karny). The fastigium verticis is conical in dorsal view, laterally compressed, and with a blunt tip. This type of fastigium is very different from that of some other genera of American Agraeciini, for instance in *Eppia* Stål, *Dectinomima* Caudell and *Uchuca* Giglio-Tos, in which it is wider and completely obtuse. The length of the fastigium verticis varies among *Agraecia* and the new genera, but length can also vary among species of a particular genus (*e.g.* in **Gen. nov. 1**). Beside of this, in genera with a narrow fastigium verticis, the fastigium frontis is also narrow, while in species with an obtuse fastigium verticis (not treated here), the fastigium frontis is usually wider.

The pronotum is superficially similar among species of genera treated here; however it varies in angles, relative proportions and shape in general. For instance, in *Agraecia agraecioides* **comb. nov.**, the metazona is strongly projecting caudally, covering the stridulatory region of the tegmina. And although in almost all genera the sinus humeralis is well-developed, in **Gen. nov. 6** it is very weakly-differentiated. In all taxa treated here, the auditory spiracle bears a finger-like projection on the posterior edge, which is also present in other Agraeciini such as *Eppia* and some genera of Copiphorini (*e.g.* *Pyrgocorypha* Stål, *Caulopsis* Redtenbacher) (Naskrecki 2000b). The spiracle is also characteristically surrounded by bristles, which protects it against the intrusion of small particles, and possibly also against the ingress of water. It is known that some species of Agraeciini can dive in water accumulated inside bromeliads (see below).

Presence and length of prosternal spines are important characters for diagnosing the tribe and its genera. Most Agraeciini genera and species have two prosternal spines, as shown here, but there are also genera in which species are lacking these spines, like *Parasubria* and *Dectinomima* Caudell (Montealegre-Z. and Morris 2003). *Agraecia* and almost all the genera described here have short spines, and **Gen. nov. 4** has very long ones. And as is described here, species of *Agraecia* and the new genera have additional spines on the meso- and metasternal lobes. Katydidids of other major groups, as

Listroscelidinae, have a similar type of armature, that can be related to predatory behavior (Cohn 1957, Rentz 1995, Fialho *et al.* 2014).

Tegmina vary widely within Agraeciini. There are long-winged genera, others are micropterous (*e.g.* *Dectinomima* Caudell), and in some genera occur long- and short-winged species (*e.g.* *Uchuca*). Almost all species treated here have long tegmina, except for some females of *A. agraecioides* **comb. nov.** with shortened tegmina (see below). Species of a particular genus of Agraeciini share a similar venation pattern, but there is variation of relative length of veins, as well as size and shape of tegmina. In the Brazilian Agraeciini tegmina are similar between species, and only *Parasubria vittipes* **comb. nov.** and **Gen. nov. 4** *pulchella* **comb. nov.** show different shape and venation pattern. Stridulatory regions of left and right tegmen of all studied species are asymmetrical. All species have asymmetrical stridulatory files, in which the right one is always reduced. As usual in Tettigoniidae taxonomy, characteristics of the left file are considered diagnostic. It should be noted that the right cubital vein and file differ widely between genera treated here, but not so much between species of a particular genus. Here, we report for the first time that this right cubital vein and file can be used for differentiation of genera. The right file should be studied in detail in other major groups of Tettigoniidae, because provides complementary information useful for establishing phylogenetic relationships (Chamorro-Rengifo *et al.* 2014). An additional characteristic previously unstudied in Agraeciini American genera and rarely considered in taxonomic studies are features on the ventral surface of the tegmina. Tegmina of species of *Agraecia* and the new genera bear dense spine-like microstructures on the stridulatory region. These microstructures are present in other Agraeciini as well, like *Eschatoceras* (pers. obs), and are also reported for the Oriental *Pseudonicsara* Karny (Ingrisch 2009, fig. 85). Those spinules are also present in Copiphorini, like species of *Conocephalus* and *Neoconocephalus* (pers. obs), as well as in species of Armadillagraeciini like *Kapalgagraecia brayi* Rentz, Su, Ueshima & Robinson (Rentz *et al.* 2010). But there are also some Agraeciini without such microstructures, like **Gen. nov. 4** and *Eppia* (pers. obs.), and they are also absent in other Tettigonioidea (Listroscelidinae, Meconematinae, Phaneropterinae and Pseudophyllinae; pers. obs.). In Grylloidea were found sensory bristles (Masaki *et al.* 1987, fig. 6; Elliott and Koch 1983), which may take part in keeping the tegmina in the right position at rest and in motion. It is still unknown whether these microstructures have the same mechanical function as in Conocephalinae.

The number of ventral spines on the femora is variable among species of a particular genus, but the number and position of spines are very similar. Brazilian genera, including **Gen. nov. 6**, are devoid of spines on the outer margin of fore femora and the inner margin of mid femora. In contrast species of **Gen. nov. 5** have spines on the outer margin of the fore femora, while **Gen. nov. 4** has spines on the inner margin of the mid femora. Although the spines seem to be very variable components, they do serve to separate genera and perhaps groups of genera in American Agraeciini.

Postabdominal structures show a great variety of quite elaborated forms in Agraeciini. This is expected for structures that rapidly change by sexual selection (Eberhard 2010). Tergite X, cerci, paraprocts and phallus vary greatly and in a discontinuous manner between genera. The combinations of forms of these structures are the most robust characters for separating genera. The tergite X in Brazilian Agraeciini is only weakly elongated caudally (except for *Parasubria*), with a very weak median incision. In contrast in **Gen. nov. 4** and *Parasubria* the posterior portion is strongly elongated and divided into two lobes which are separated by a deep emargination, similar to American *Eppia* and some Oriental Agraeciini (e.g. *Rhynchocerus modiglianii* (Griffini) in Ingrisch 1998; *Nahlaksia bidadari* Ingrisch & Tan). Female tergite X is very uniform and unmodified in Brazilian genera, different from that in female **Gen. nov. 4**, with two pointed lobes, which is most similar to the female tergite X of *Eppia*.

In the tribe, male cerci are often simple, very large and devoid of processes (e.g. *Oxylakis singaporensis* Ingrisch & Tan). In all genera treated here, cerci are modified, possibly adapted for grasping (*Agraecia*, **Gen. nov. 6** and **Gen. nov. 4**), or only with apical processes that may also exert a certain pressure on the female postabdomen during copula. Paraprocts are simple structures in Agraeciini (**Gen. nov. 2** and **Gen. nov. 1**, and also other examples in Oriental Agraeciini), but in *Agraecia sensu novo* they are modified and possibly participate during copula as a grasping structure in conjunction with the cerci. These modified paraprocts are a derived condition. They have a cylindrical and sometimes finger-like process near the dorsal basal portion of the cerci. These processes were found in all examined genera, including **Gen. nov. 4**, where they are broader than in the Brazilian genera. Species of *Uchuca* and *Dectinomima* have similar finger-like process on the cerci. In the studied species, where paraprocts are fused with the base of the cerci, forming an almost continuous structure, these processes are located between paraprocts and cerci.

The shape of the male subgenital plate seems to be more uniform within each genus, compared to the more variable ones of the females, which seem to be under more selective pressure, and are an important character for species identification.

The phallus varies widely among genera and to a lesser extent among species. It is an important character for separating species belonging to one genus. In all revised Agraeciini sclerites **TS** consist always of two separated sclerotized bars, which are ventrally fused with sclerite **VS**, forming the complex **TS+VS**. The opposite state are separate sclerites as in *Conocephalus* sp. (Chamorro-Rengifo & Lopes-Andrade 2014). It seems that in all male Agraeciini have two sclerites, which vary in form, position and in the way they are fused. In Brazilian Agraeciini the lobe **vdl** is large, while it is absent in **Gen. nov. 4 pulchella comb. nov.** from Colombia. This large lobe **vdl**, together with the remaining components of the lobe **dl**, may be everted during copula, providing more expansion and consequently more contact surface with the female's genitalic chamber. Between the two sclerites **TS**, on the anterior portion of the phallus, there is a fold **fdl** which varies from very large (**Gen. nov. 1**; **Gen. nov. 2**) to fairly short (*Agraecia* and also in *E. truncatipennis*), or can be absent (**Gen. nov. 4 pulchella comb. nov.**). This fold is also present in *Conocephalus* sp. (Chamorro-Rengifo & Lopes-Andrade 2014). The functionality of this fold during copula is unknown, but it occurs only in phalli with two sclerites **TS** that are very close to each other. On the other hand, this fold is absent in phalli with widely separated sclerites **TS**, as in **Gen. nov. 4 pulchella comb. nov.** Additionally to the sclerites **TS**, the titillator may include processes **ti** located at each lateral portion of lobe **dl**, consisting of groups of conspicuous scale-like microstructures. These microstructures can be densely packed (*Agraecia* spp.) or be more scattered (**Gen. nov. 1** spp.; **Gen. nov. 2 nigrifrons**). This kind of processes **ti** are also present in other Agraeciini, like *Eppia truncatipennis*, where it is very large; but can also be completely absent in others, like *Uchuca ferreirai* and *Eschatoceras* sp. (Chamorro-Rengifo & Lopes-Andrade 2014). Oriental Agraeciini have similar processes **ti** (e.g. fig. 10 in Ingrisch & Tan 2012). The vesicles **ejv** are round or oval. In Brazilian Agraeciini they are smaller in relation to the size of the phallus, and also smaller compared with the **ejv** in other tribes (*Conocephalus* sp. in Chamorro-Rengifo & Lopes-Andrade 2014). The size of these vesicles **ejv** is similar among Brazilian Agraeciini, and similar to the size in some Australian Armadillagraeciini (*Kapalgagraecia nauma* Rentz *et al.*; fig. 12D in Rentz *et al.* 2010). In contrast **ejv** are very small in **Gen. nov. 4 pulchella comb. nov.**, in fact this species has the smallest

ones of all examined Agraeciini. There is little information on **ejv** in Oriental Agraeciini, but they seem to be also very small (*e.g.* fig. 406 in Ingrisch 2009).

Ovipositor forms are similar among species of *Agraecia* and the new genera, except for **Gen. nov. 4**, which has a more robust ovipositor with obtuse apex. Agraeciini in general show a great variety of ovipositors (Ingrisch 1998; 2009), including rather strange forms (*e.g.* *Oxylakis singaporensis* Ingrisch & Tan, *Ingrischia macrocephala* Naskrecki & Rentz).

The shape of the ovipositor can be associated with the oviposition substrate (Ingrisch 1998, 2001), which means that unrelated taxa with similar ovipositor shape may be the result of convergence. But similar ovipositors may also be a signal for close phylogenetic relationships (*e.g.* species of *Pseudomacroxiphus* Willemse and *Paramacroxiphus* Willemse; Ingrisch 2008). In this case **Gen. nov. 4** could belong to a phylogenetic lineage different from all other genera treated here. And it is important to note that **Gen. nov. 6** *viridipennis* **comb. nov.** bears two projections on the basal portion of the ovipositor, not found in any other Agraeciini.

**Biology and ecology.** All specimens collected during surveys were captured manually. Agraeciini are usually easy to capture, except for individuals of *Agraecia agraecioides* **comb. nov.**, which walk fast and can escape easily. They were very difficult to photograph in the field. Several specimens of *Agraecia* and **Gen. nov. 1** loaned from museums collections were caught with Malaise traps, indicating that individuals fly for locomotion inside the forest. Almost all individuals captured by this kind of trap are females, which can be related to flight associated with phonotactic behaviour (Forrest 1983), or simply with unequal sex-ratio in the population.

Some species are very rare, and individuals were only found after intense survey in specific microhabitats inside the forest. For instance, males of *Agraecia agraecioides* **comb. nov.** in the P. N. do Caparaó were found only in the more humid and best preserved areas, mostly walking on moss. The difficulty of collecting this species is confirmed by the fact that there is an old specimen loaned by CEIOC, which was collected in 1948 from the P.N. Itatiaia, while no individual could be found in this national park during the recent survey. During six days of field work in this same conservation unit only two individuals of *Agraecia* **sp. nov. 3** were collected. The population densities are possibly low or the katydids may be associated with an unknown microhabitat. This scarcity contrasts with the twenty individuals of **Gen. nov. 1** *maculata* **comb. nov.** found at this site. Additionally the proportion of individuals by

genera differs between localities. For instance, in the reserve PERD the number of collected individuals of **Gen. nov. 1** and *Agraecia* are relatively similar, while 23 individuals of *A. punctata* and only two of **Gen. nov. 1 sp.2 nov.** were collected in P. N. do Pau Brasil. This phenomenon cannot be explained yet.

Number of captured males and females varies between species and populations of a particular species. For example, all individuals of *Agraecia agraecioides* **comb. nov.** from P. N. do Caparaó are males, while fourteen females and no male were found in RPPN Sítio do Zaca. It is unknown if there were really more individuals of one gender, or if individuals of one gender were collected less frequently because they are more difficult to find.

Little is known about the biology of South American Agraeciini. Most data comes from observations made at the time of capture. There are few specific studies or observations on development, behavior and life cycle. Most available information is on the type of habitat or microhabitat in which specimens were captured. **Gen. nov. 4 pulchella** **comb. nov.** is frequently found inside bromeliads, which has been recorded several times on collection labels (pers. obs.). It is unknown whether there is a strict dependency of this species on these plants, and if the distribution or presence of **Gen. nov. 4 pulchella** depends on the availability of bromeliads. There are records in literature of Tettigonioidea using bromeliads. Immatures of certain Conocephalinae and Pseudophyllinae live inside bromeliads, where they find refuge and food (Costa Lima 1939, Burmeister 1985, Picado 1913, Lang and Römer 2007). Adult males of *Camposiella notabilis* Hebard (Pseudophyllinae) were found singing inside a spiny terrestrial bromeliad, where they are protected against predators (Braun 2002). A female of **Gen. nov. 1 sp.2 nov.** was collected from inside a bromeliad (data on old label). It was documented that species of Agraeciini may be predators (Leong 2011). In this case Agraeciini species can find little animals to eat inside bromeliads (Frank and Lounibos 2009). Bromeliaceae are distributed throughout the Neotropical region, and only one species has been reported from Africa (Givnish *et al.* 2007), which means that such biological relationships, if any, would appear mostly in Neotropical katydids. At any rate, more field observations are necessary to establish the importance of bromeliads for the life history of Agraeciini and other katydids.

Among the four individuals of *Agraecia agraecioides* **comb. nov.** from RPPN Sítio do Zaca, all females, one had normally developed tegmina, well extending beyond the abdomen (Fig. 18D). The others had greatly reduced tegmina, leaving a third of the abdomen unconcealed (Fig. 18E). RPPN Sítio do Zaca is the most disturbed

conservation unit that was surveyed, consisting of a little and isolated forest in process of recovery, surrounded by cultivated pasture, and these females were collected within secondary vegetation. How this type of environment could lead to a loss of the ability to fly is somewhat mysterious.

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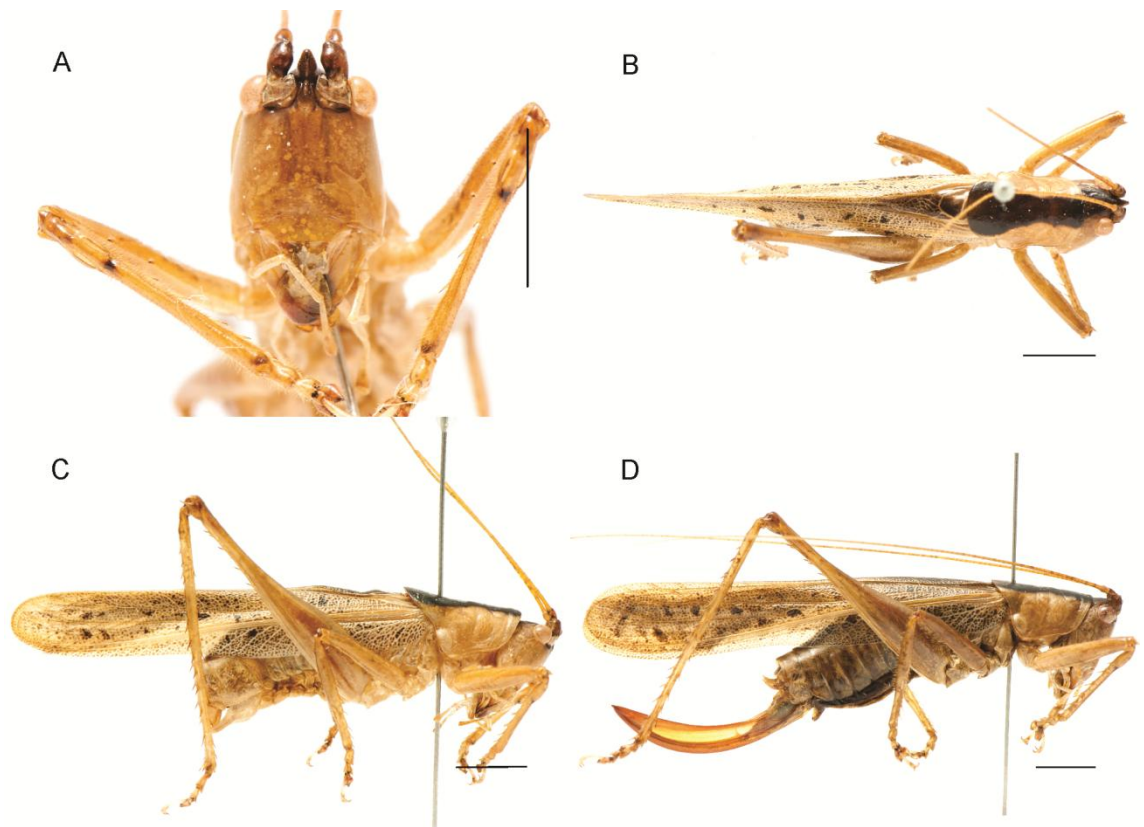
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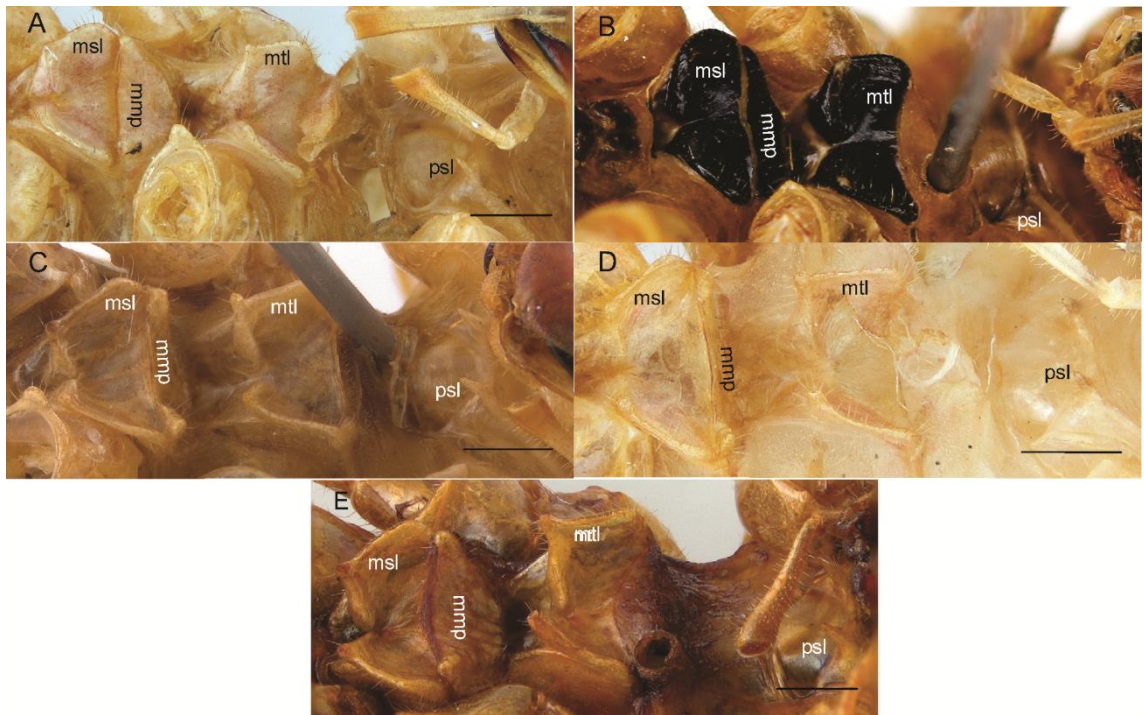
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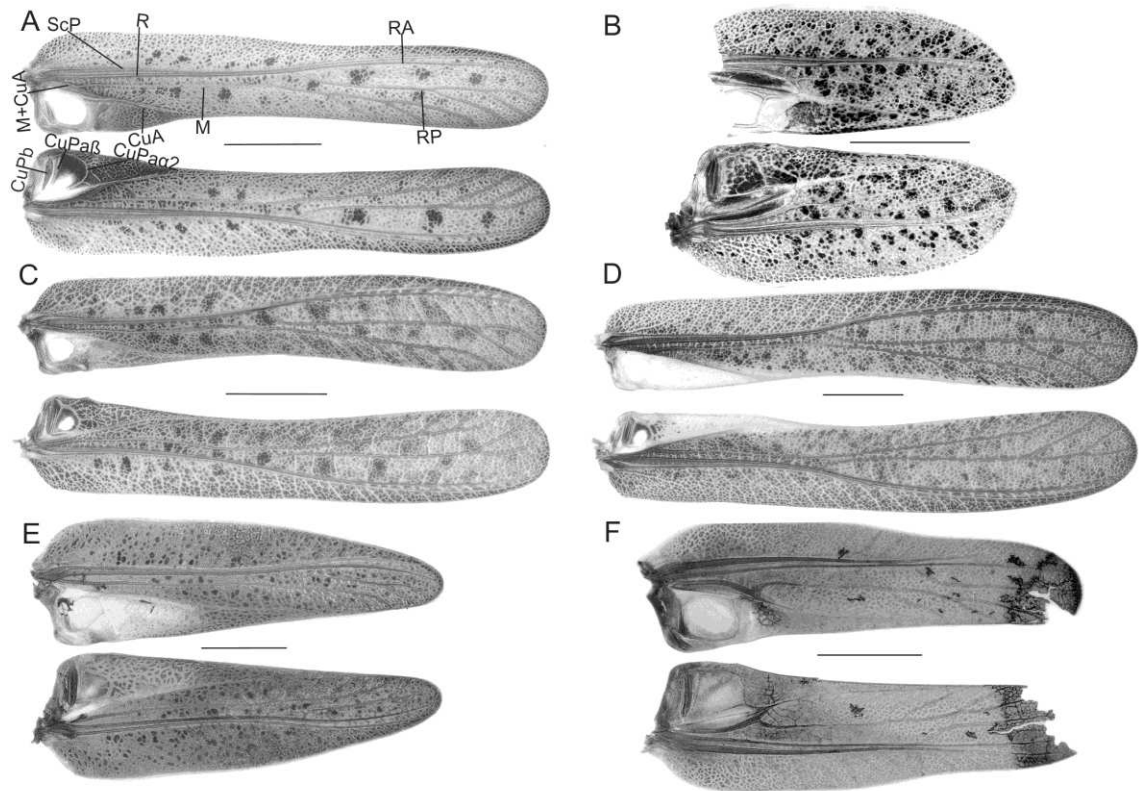
FIGURES



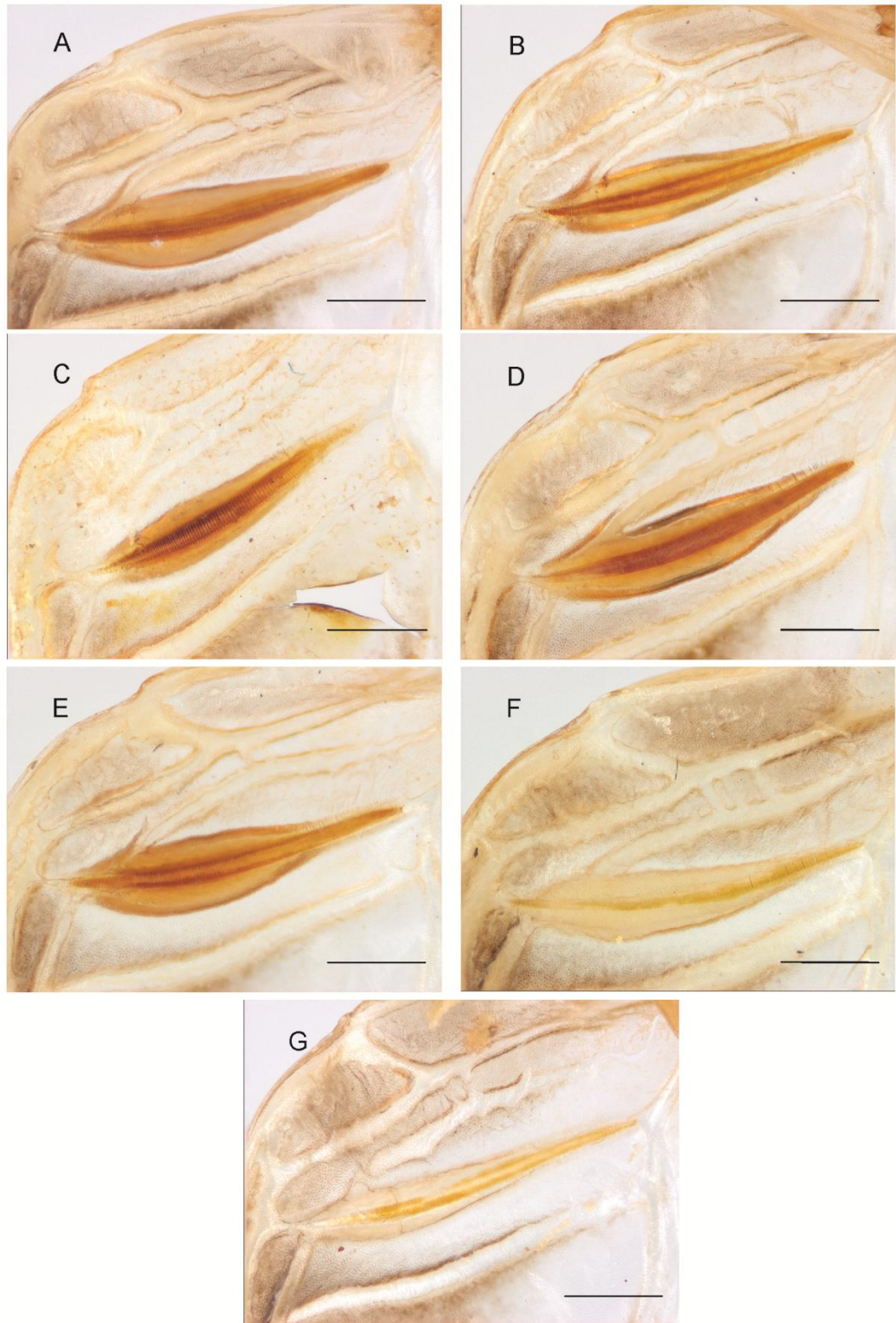
**Figure 1. Habitus of *Agraecia punctata* (Saint-Fargeau & Audinet-Serville).** A–C alloplesiotype male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) Plesiotype female, lateral view. Scale bars = 0.50 mm.



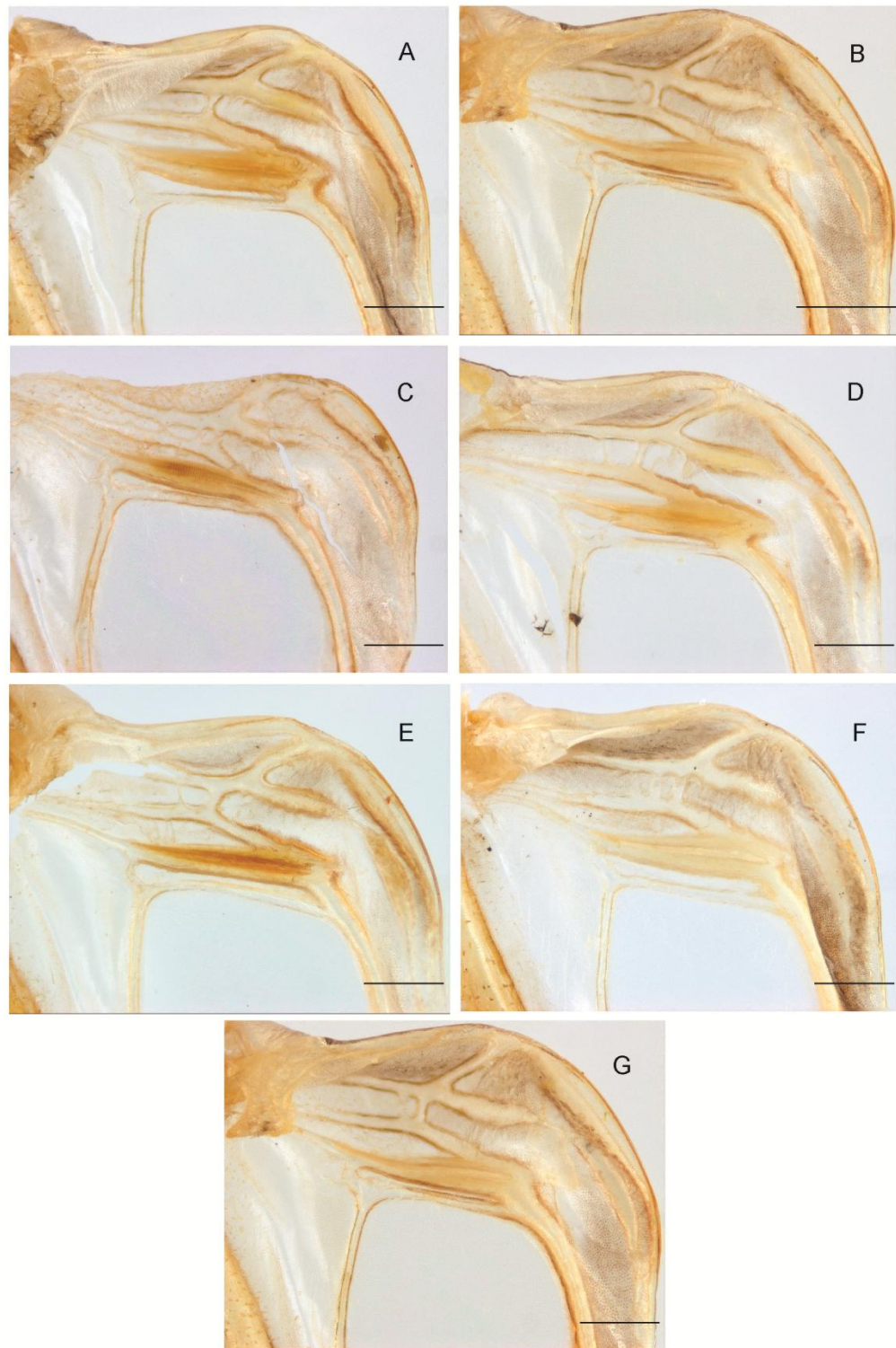
**Figure 2. Thoracic male sternites.** (A) *Agraecia punctata* (Saint-Fargeau & Audinet-Serville). (B) *Parasubria vittipes* (Redtenbacher) **comb. nov.** (C) **Gen. nov. 1** *maculata* (Redtenbacher) **comb. nov.** (D) **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.** (E) **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** Abbreviations: metasternal medial plate **mmp**; mesobasisternal lobe **msl**; metabasisternal lobe **mtl**; probasisternal lobe **psl**. Scale bars = 1.00 mm.



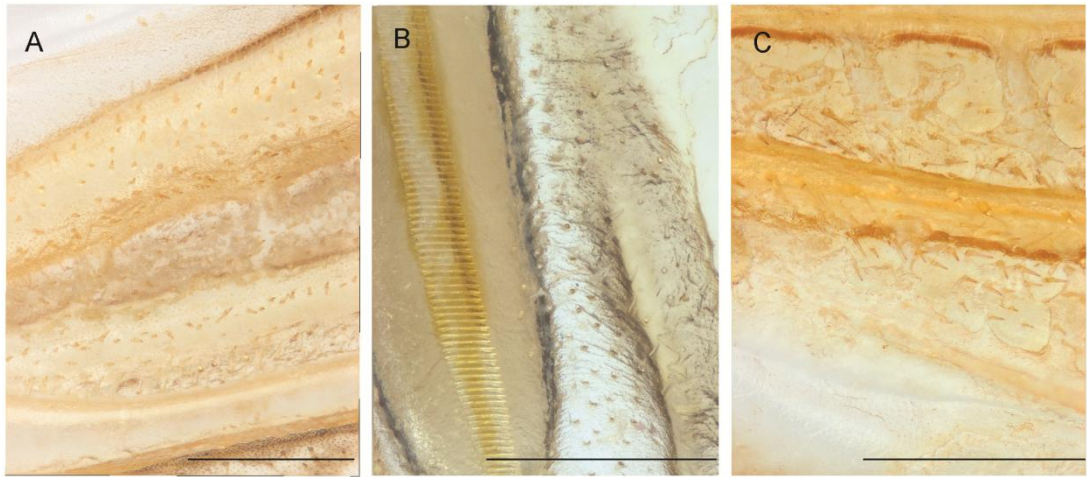
**Figure 3. Male Tegmina of each genera.** Dorsal view of right (above) and left (below) tegmen. (A) *Agraecia punctata* (Saint-Fargeau & Audinet-Serville). (B) *Parasubria vittipes* (Redtenbacher) **comb. nov.** (C) **Gen. nov. 1** *maculata* (Redtenbacher) **comb. nov.** (D) **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.** (E) **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** (F) **Gen. nov. 4** *pulchella* (Hebard) **comb. nov.** (F) Scale bars = 5.00 mm.



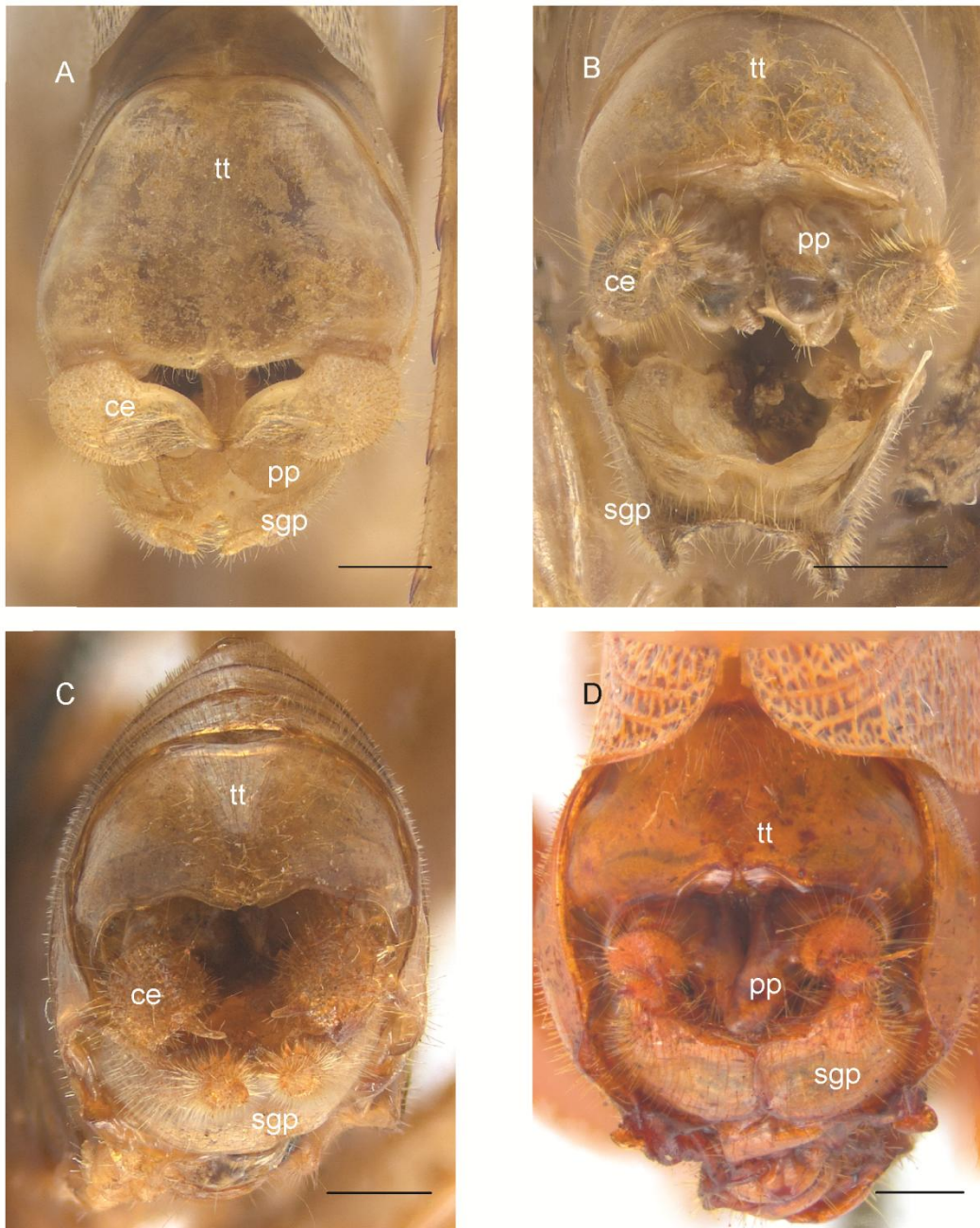
**Figure 4. Left Stridulatory file of male *Agracia* species.** (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) *A. dorsalis* Karny. (C) *A. agracioides* (Rehn) **comb. nov.** (D) *Agracia* **sp. nov. 1** (E) *Agracia* **sp. nov. 2** (F) *Agracia* **sp. nov. 3** (G) *Agracia* **sp. nov. 4**. Scale bars = 0.50 mm.



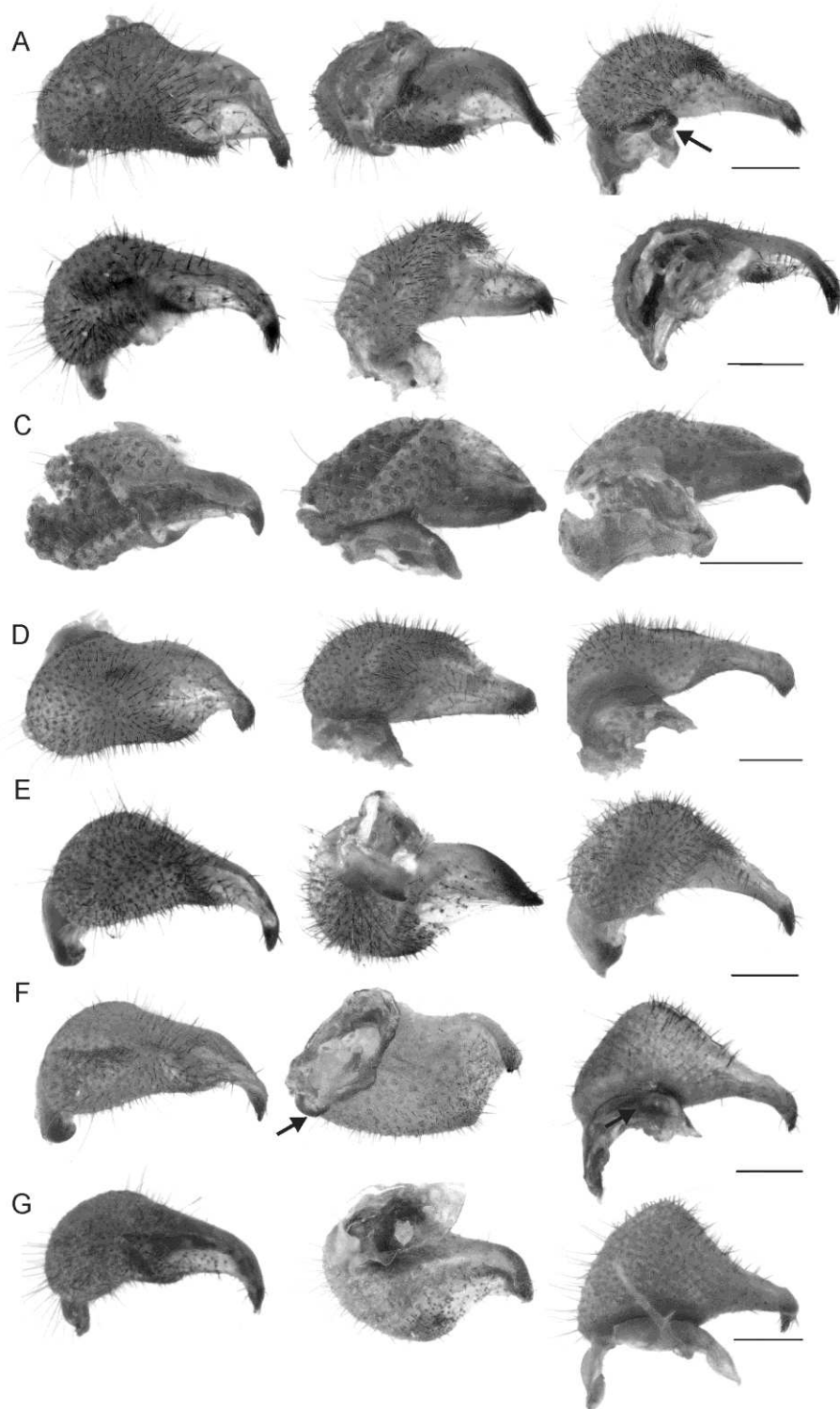
**Figure 5. Right file of male *Agraecia* species.** (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) *A. dorsalis* Karny. (C) *A. agraecioides* (Rehn) **comb. nov.** (D) *Agraecia* **sp. nov. 1** (E) *Agraecia* **sp. nov. 2** (F) *Agraecia* **sp. nov. 3** (G) *Agraecia* **sp. nov. 4**. Scale bars = 0.50 mm.



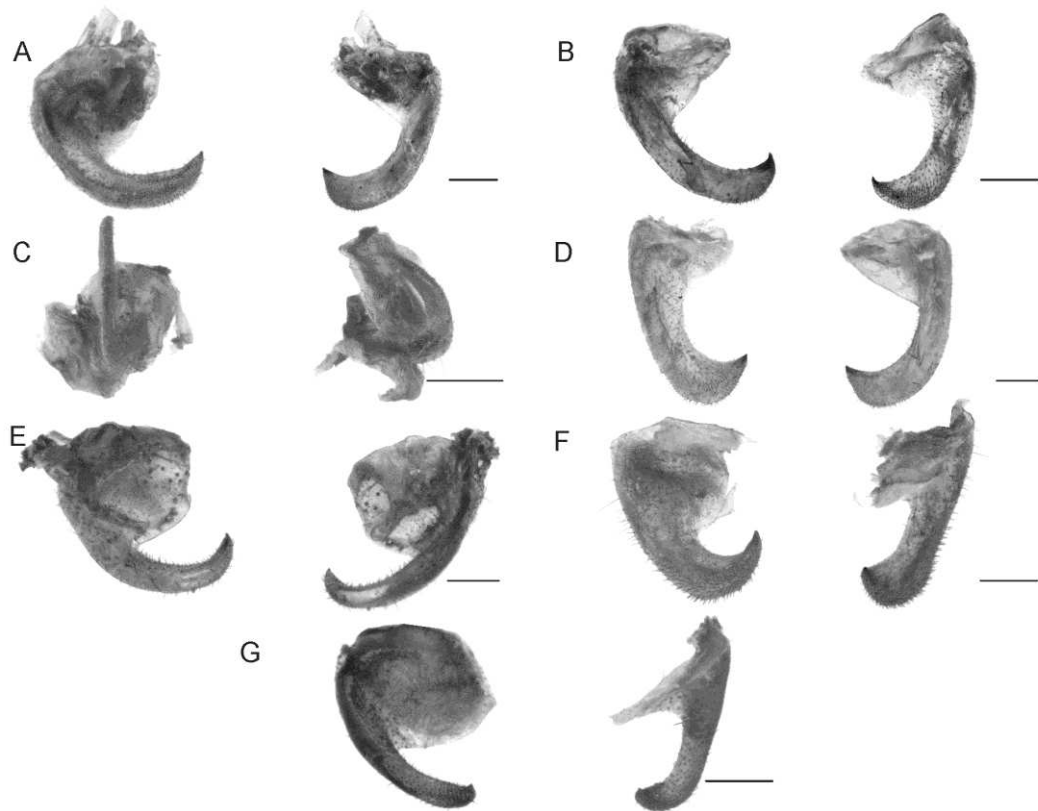
**Figure 6. Spiny-like microstructures on ventral portion of tegmina.** (A) *Agraecia punctata* (Saint-Fargeau & Audinet-Serville). (B) **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.** (D) **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** Scale bars = 0.50 mm.



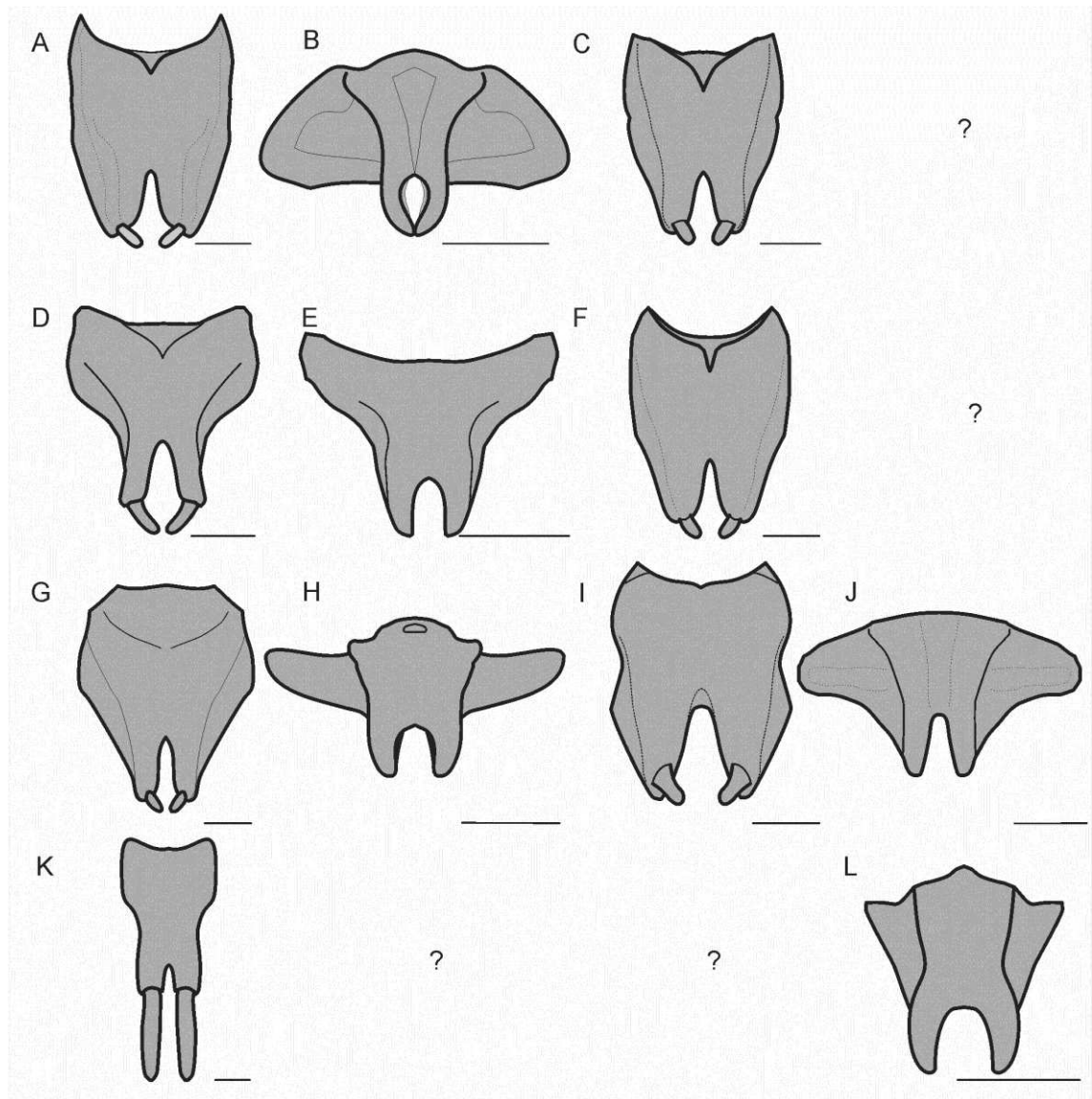
**Figure 7. Male postabdomen of genera.** Dorsal-posterior view. (A) *Agraecia punctata* (Saint-Fargeau & Audinet-Serville). (B) **Gen. nov. 1 sp.1 nov.** (C) **Gen. nov. 2 nigrifrons** (Redtenbacher) **comb. nov.** (D) **Gen. nov. 3 abbreviata** (Redtenbacher) **comb. nov.** Abbreviations: cercus **ce**; paraproct **pp**; subgenital plate **sgp**; tergite X **tt**. Scale bars = 1.00 mm.



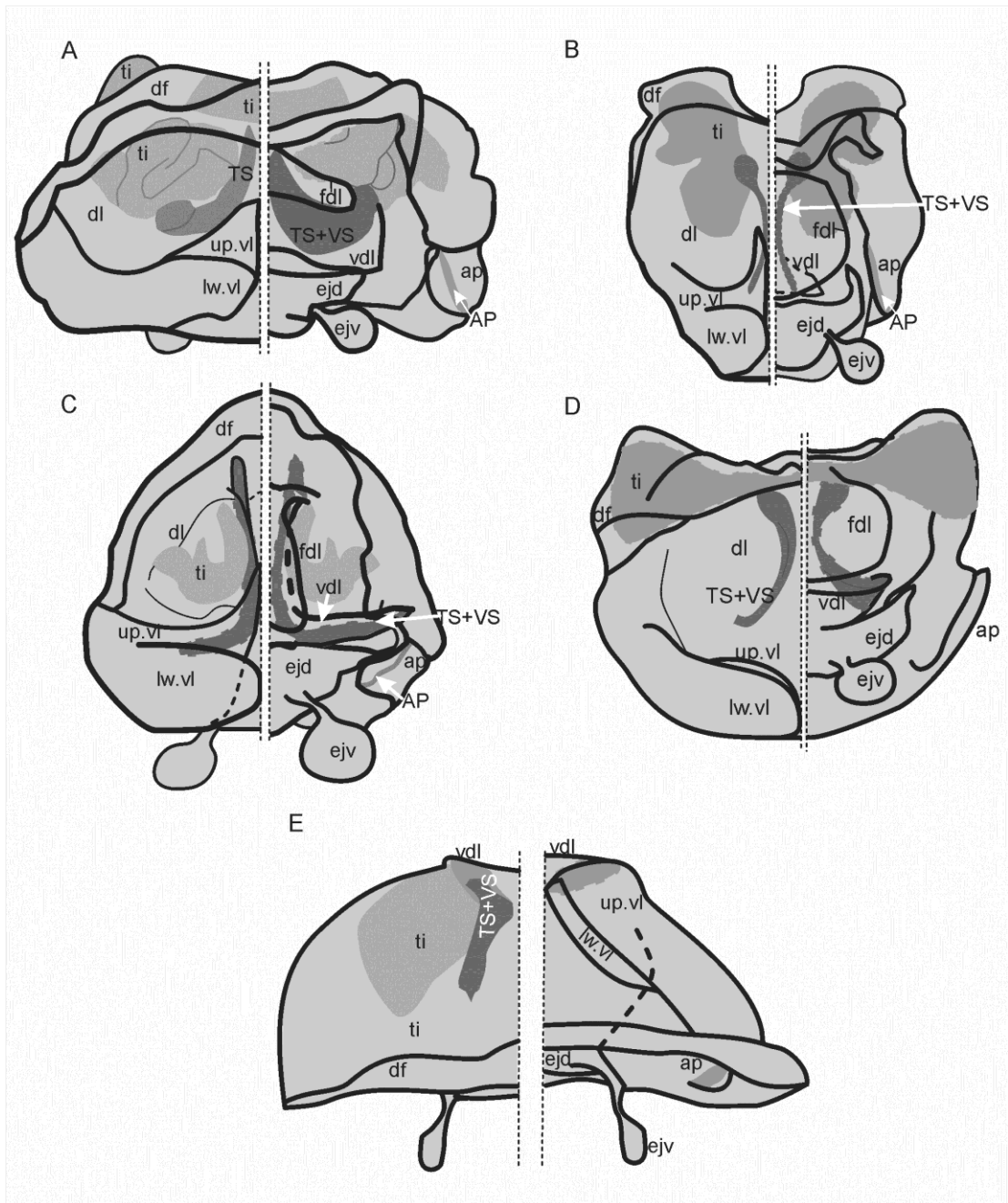
**Figure 8. Cerci of male *Agraecia* species.** Posterior, interior and dorsal views. (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) *A. dorsalis* Karny. (C) *A. agraecioides* (Rehn) **comb. nov.** (D) *Agraecia* **sp. nov. 1** (E) *Agraecia* sp. nov. 2 (F) *Agraecia* **sp. nov. 3** (G) *Agraecia* **sp. nov. 4**. Arrow showing digitiform process. Scale bars = X.



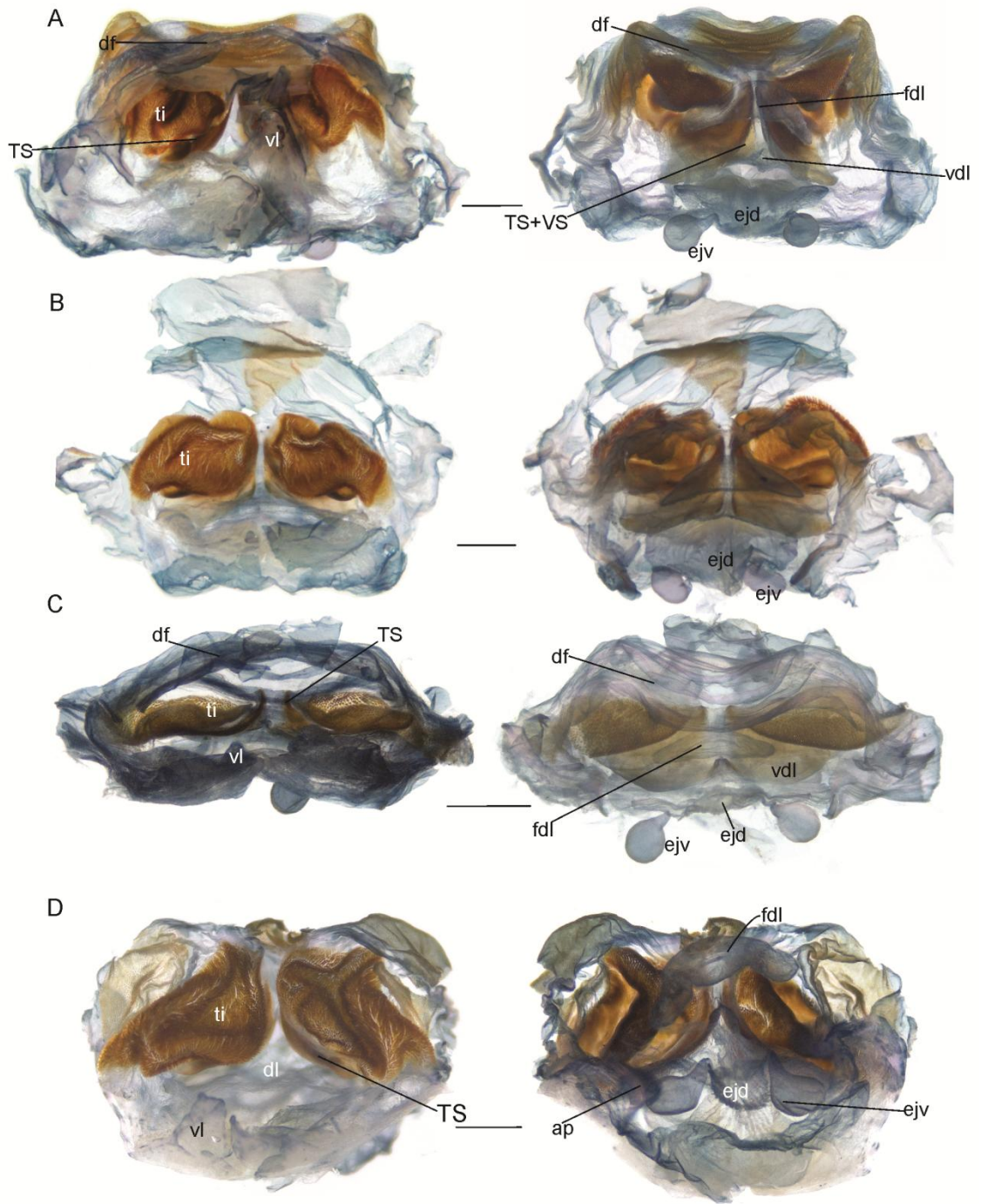
**Figure 9. Paraprocts of male *Agraecia* species.** Posterior and interior views. (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) *A. dorsalis* Karny. (C) *A. agraecioides* (Rehn) **comb. nov.** (D) *Agraecia* **sp. nov. 1** (E) *Agraecia* **sp. nov. 2** (F) *Agraecia* **sp. nov. 3** (G) *Agraecia* **sp. nov. 4**. Scale bars = 0.5 mm.



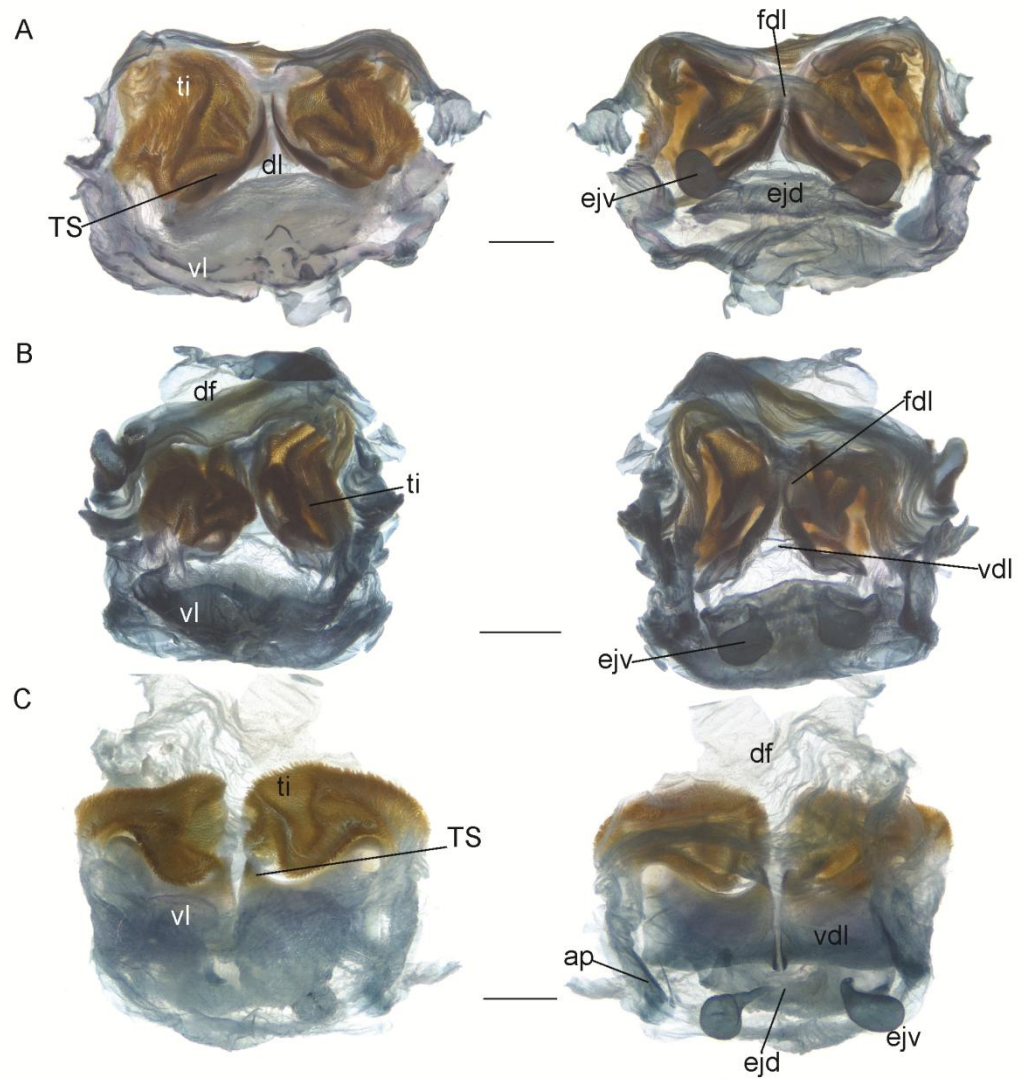
**Figure 10. Subgenital plates of male and female *Agraecia* species.** Ventral view. A–B *A. punctata* (Saint-Fargeau & Audinet-Serville), (A) male, (B) female. (C) *A. dorsalis* Karny, male. D–E *A. agraecioides* (Rehn) **comb. nov.**, (D) male, (E) female. (F) *Agraecia* **sp. nov. 1**, male. G–H *Agraecia* **sp. nov. 2**, (G) male, (H) female. I–J *Agraecia* **sp. nov. 3**, (I) male, (J) female. (K) *Agraecia* **sp. nov. 4**, male. L. subgenital plate of female from Sooretama. Symbol ? indicates that the male or female is unknown. Scale bars = 1.00 mm.



**Figure 11. Comparative schemes of phallus morphology.** (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) **Gen. nov. 1** *maculata* (Redtenbacher) **comb. nov.** (C) **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.** (D) **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** (E) **Gen. nov. 4** Abbreviations: anterophallic apodemes **ap**; sclerites of apodemes **AP**; dorsal fold **df**; dorsal lobe(s) **dl**; ejaculatory duct **ejd**; ejaculatory vesicles **ejv**; fore fold of dorsal lobe **fdl**; lower folds of ventral lobe **lw.vl**; titillatory process(es) **ti**; titillator's sclerite(s) **TS**; **up.vl** upper folds of ventral lobe; ventral fold(s) of dorsal lobe **vdl**; sclerite(s) of ventral fold of dorsal lobe **VS**.



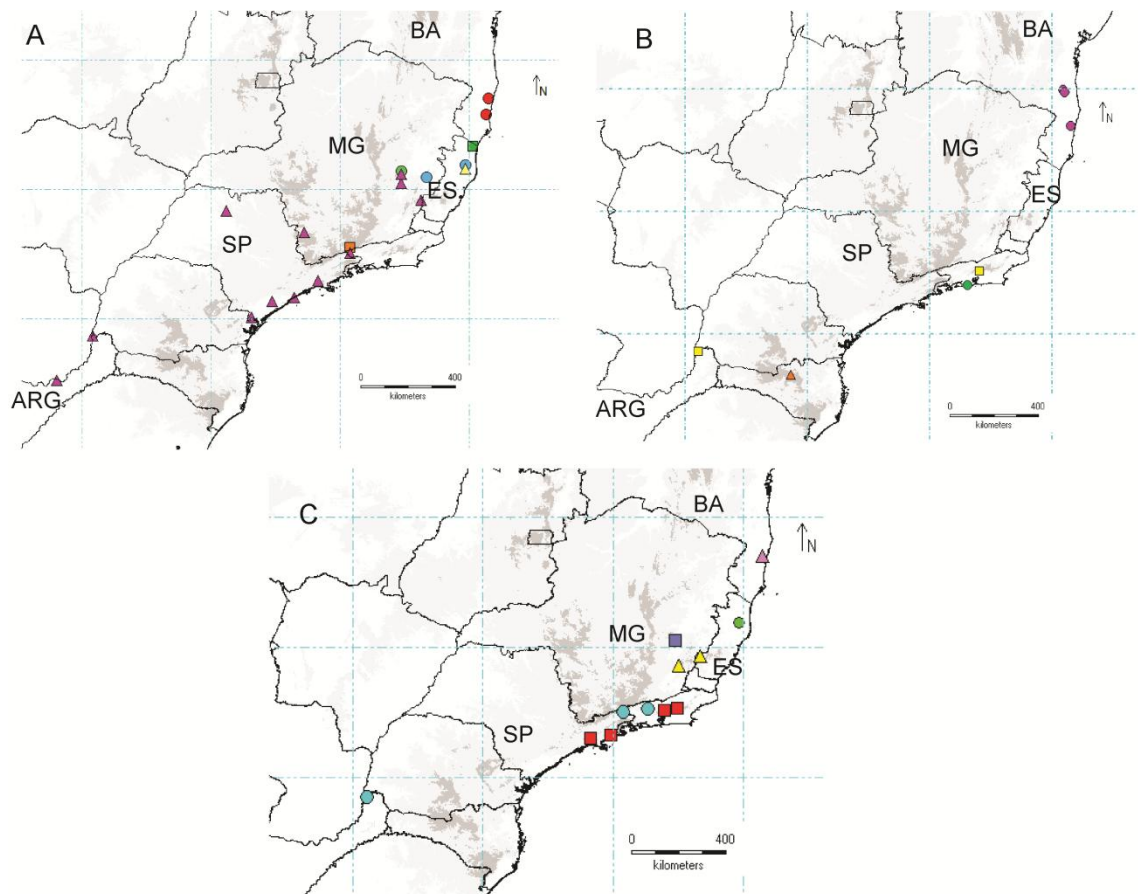
**Figure 12. Phallus of *Agraecia* species, dorsal and ventral views. (A) *A. punctata* (Saint-Fargeau & Audinet-Serville). (B) *A. dorsalis* Karny. (C) *A. agraecioides* (Rehn) **comb. nov.** (D) *Agraecia* **sp. nov. 1** Abbreviations: anterophallic apodemes **ap**; dorsal fold **df**; dorsal lobe(s) **dl**; ejaculatory duct **ejd**; ejaculatory vesicles **ejv**; fore fold of dorsal lobe **fdl**; lower folds of ventral lobe **lw.vl**; titillatory process(es) **ti**; titillator's sclerite(s) **TS**; ventral fold(s) of dorsal lobe **vdl**; ventral lobe **vl**; sclerite(s) of ventral fold of dorsal lobe **VS**. Scale bars = 0.50 mm.**



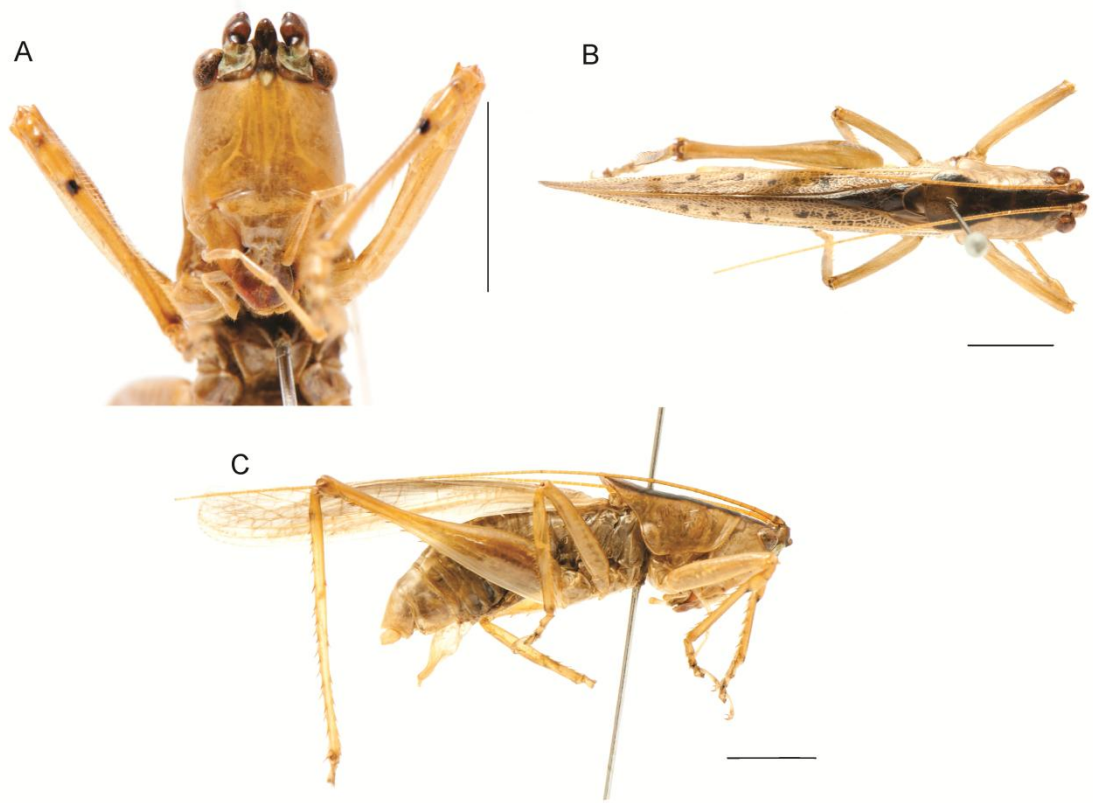
**Figure 13. Phallus of *Agraecia* species, dorsal and ventral views. (A) *Agraecia* sp. nov. 2 (B) *Agraecia* sp. nov. 3 (C) *Agraecia* sp. nov. 4.** Abbreviations: anterophallic apodemes **ap**; dorsal fold **df**; dorsal lobe(s) **dl**; ejaculatory duct **ejd**; ejaculatory vesicles **ejv**; fore fold of dorsal lobe **fdl**; lower folds of ventral lobe **lw.vl**; titillatory process(es) **ti**; titillator's sclerite(s) **TS**; ventral fold(s) of dorsal lobe **vdl**; ventral lobe **vl**; sclerite(s) of ventral fold of dorsal lobe **VS**. Scale bars = 0.50 mm.



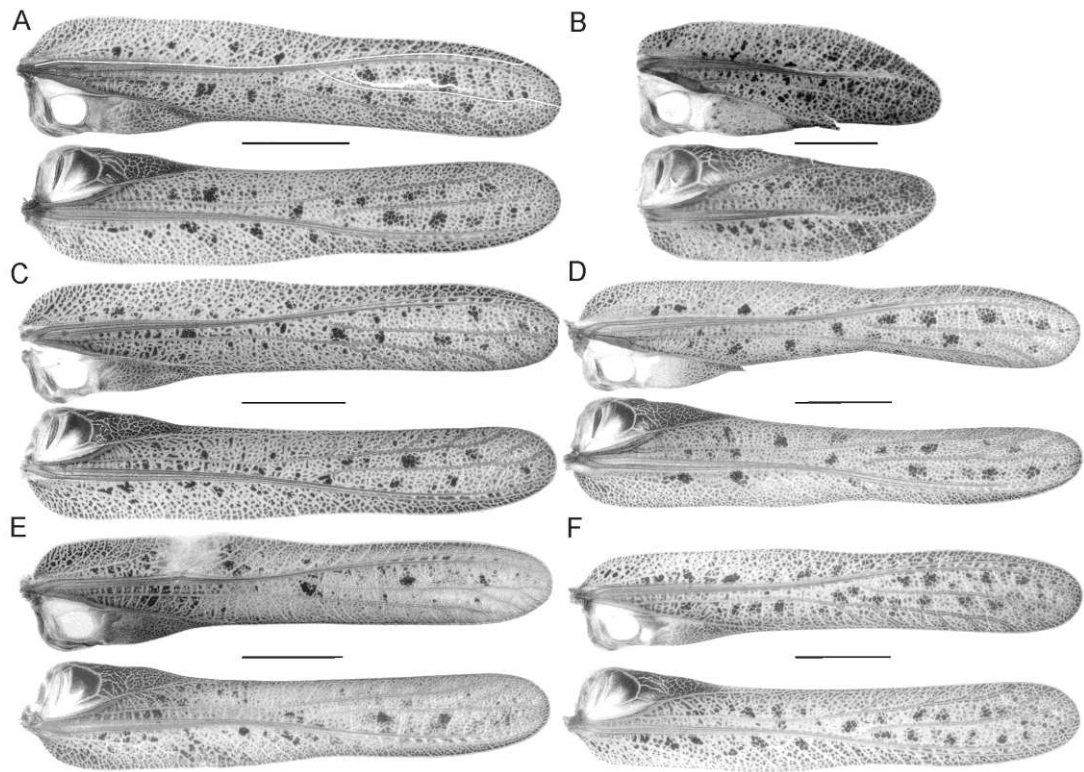
**Figure 14. Live individuals of *Agraecia* Audinet-Serville species.** (A) Female of *A. punctata* (Saint-Fargeau & Audinet-Serville) dorso-lateral view. B–D *A. agraeioides* (Rehn) **comb. nov.** (B) Male dorsal view; (C) long-wing female, dorso-lateral view; (D) short-wing female, dorso-lateral view. (E) Female of *Agraecia* **sp. nov. 2**, dorsal view. (F) Female of *Agraecia* **sp. nov. 3**, dorso-lateral view.



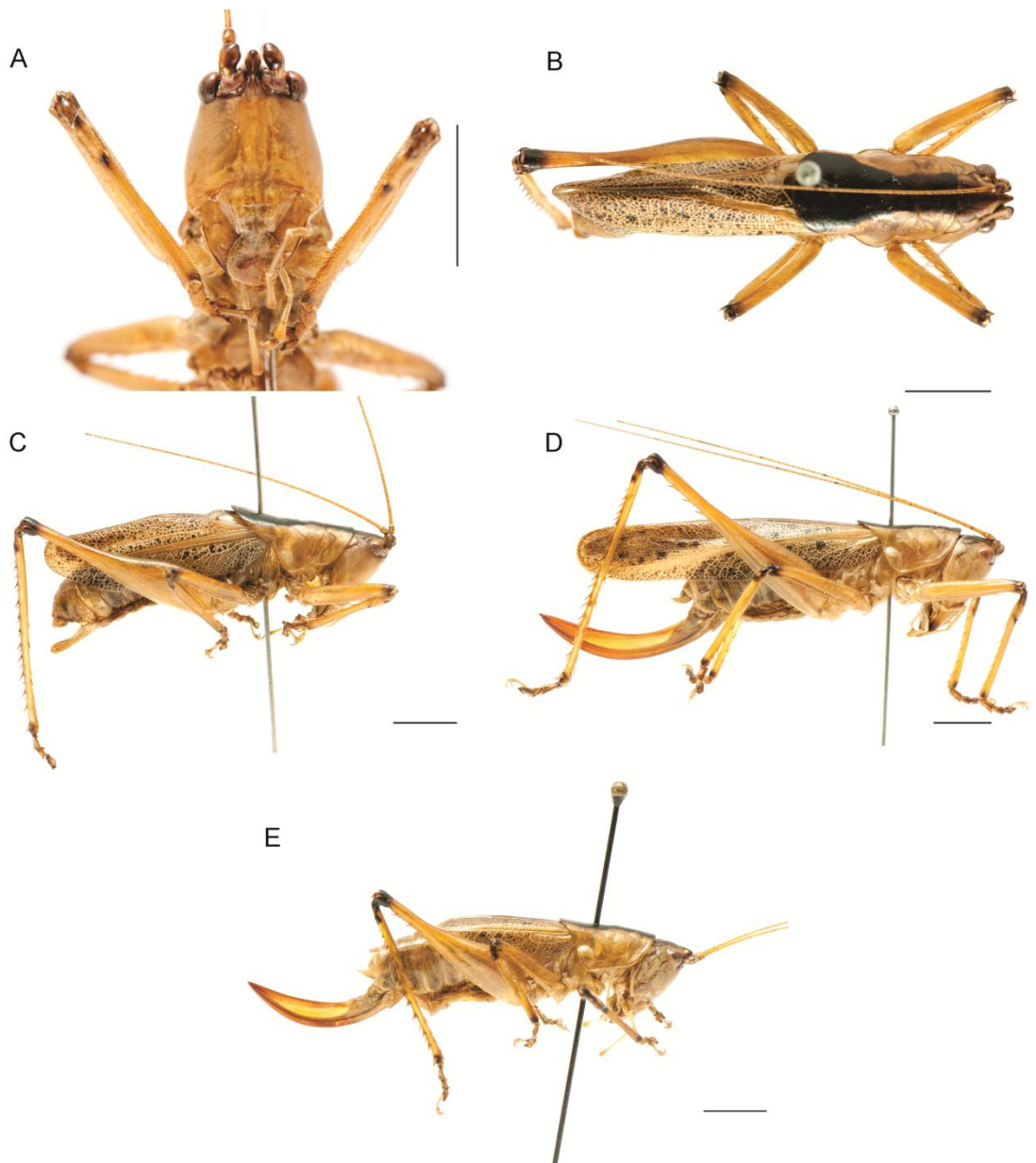
**Figure 15. Geographic distribution.** (A) Species of *Agracia*: *Agracia punctata* (Saint-Fargeau & Audinet-Serville) (red circle); *Agracia* **sp. nov. 2** (green square); *Agracia dorsalis* Karny (blue circle); *Agracia agracioides* (Rehn) **comb. nov.** (pink triangle); *Agracia* **sp. nov. 3** (brown square); *Agracia* **sp. nov. 4** (yellow triangle) (B) **Gen. nov. 2** *nigrifrons* (Redtenbacher, 1891) **comb. nov.** (pink circle); **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** (green circle); *Parasubria vittipes* (Redtenbacher) **comb. nov.** (yellow square); *Parasubria ziczac* Karny (orange triangle). (C) Species of **Gen. nov. 1**: **Gen. nov. 1 sp.2 nov.** (pink triangle); **Gen. nov. 1 sp.1 nov.** (green circle); **Gen. nov. 1 sp.3 nov.** (blue square); **Gen. nov. 1** *subulata* (Redtenbacher, 1891) (yellow triangle); **Gen. nov. 1 sp.2 nov.** (red square).



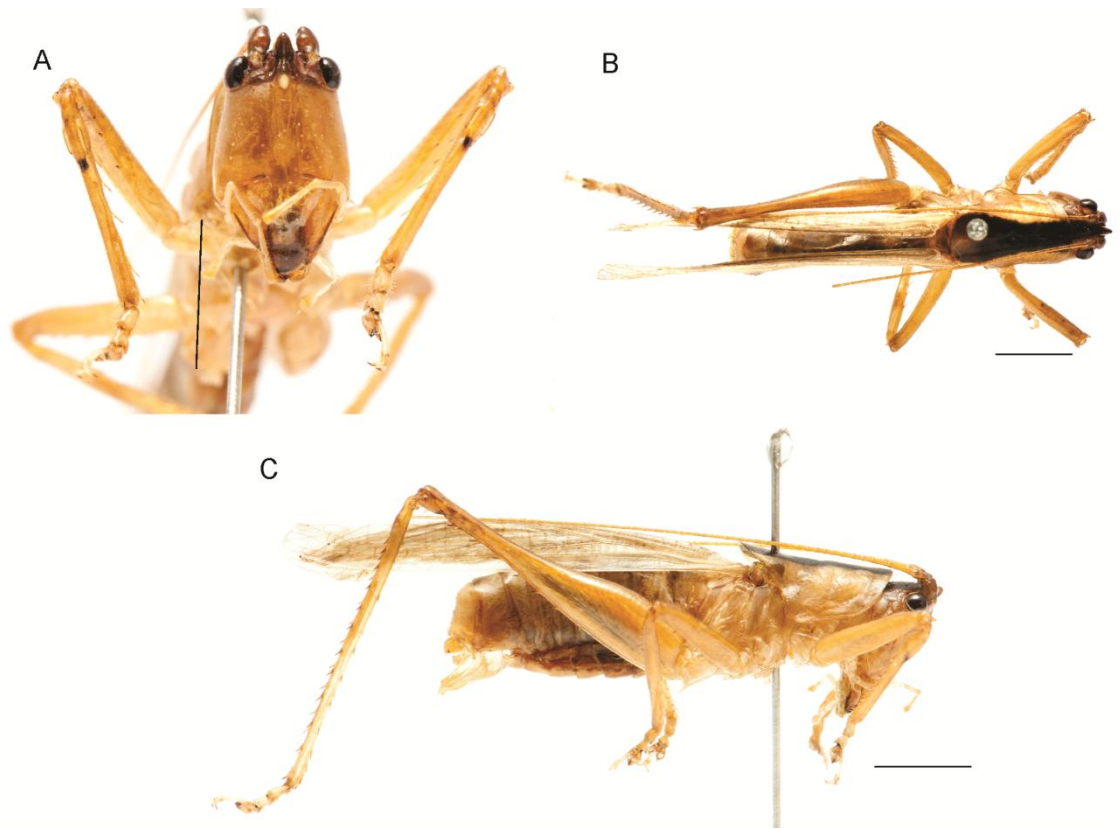
**Figure 16. Habitus of *Agraecia dorsalis* Karny. male (A) frontal view, (B) dorsal view, (C) lateral view. Scale bars = 0.50 mm.**



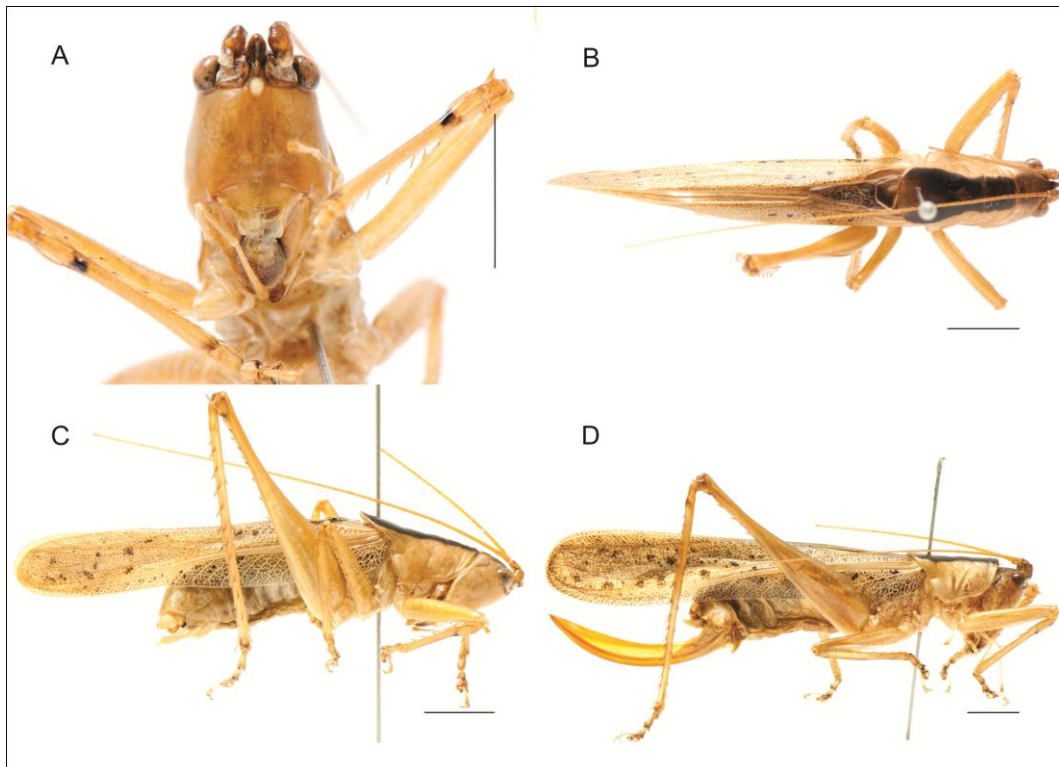
**Figure 17. Tegmina of male *Agraecia* species.** Dorsal view of right (above) and left (below) tegmen. (A) *A. dorsalis* Karny. (B) *A. agraecioides* (Rehn) **comb. nov.** (C) *Agraecia* **sp. nov. 1** (D) *Agraecia* **sp. nov. 2** (E) *Agraecia* **sp. nov. 3** (F) *Agraecia* **sp. nov. 4**. Scale bars = 5.00 mm.



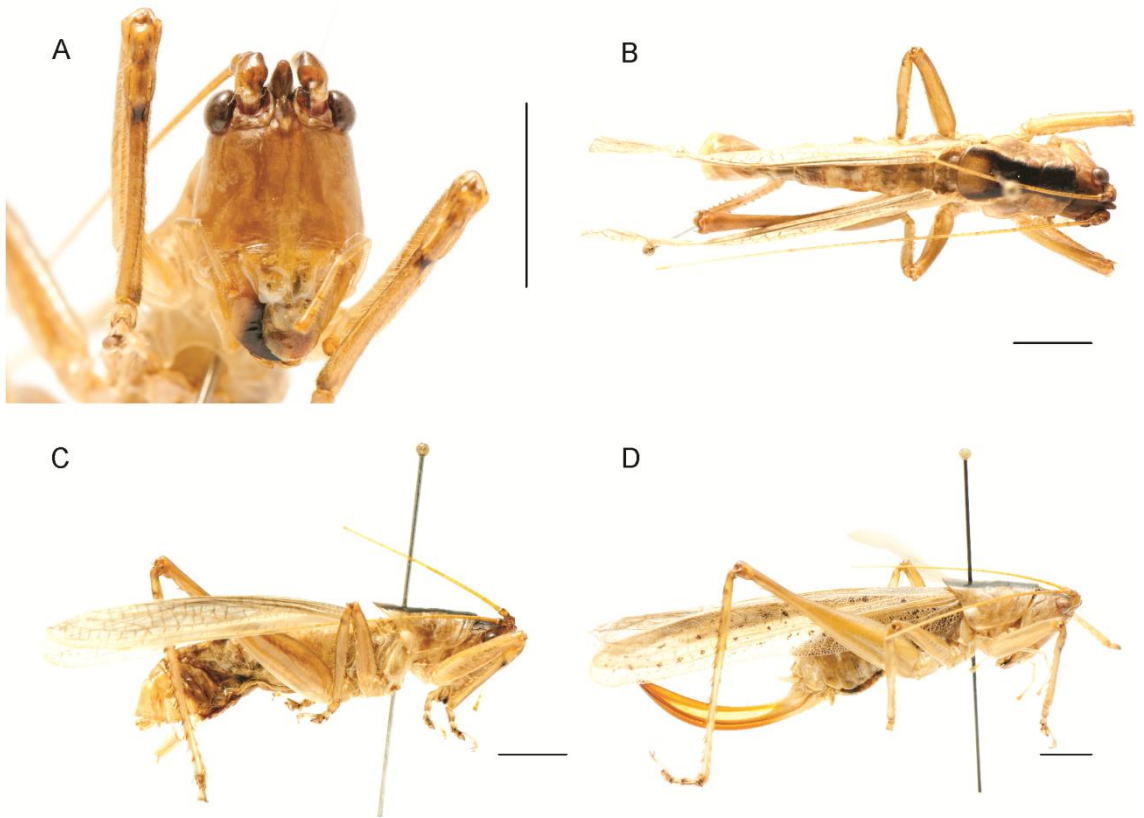
**Figure 18. Habitus of *Agraecia agraeioides* (Rehn) comb. nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) long-wing female, lateral view. (E) short wing female. Scale bars = 0.50 mm.



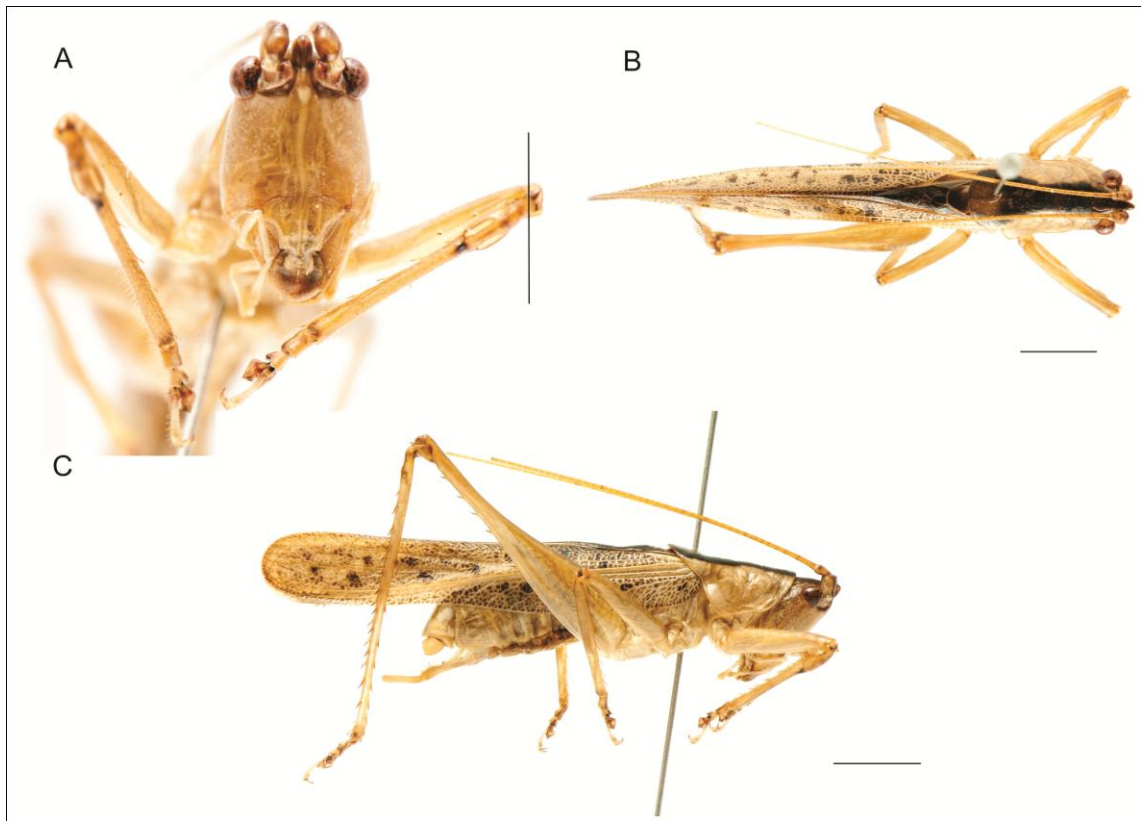
**Figure 19.** Habitus of *Agraecia* sp. nov. 1, male (A) frontal view, (B) dorsal view, (C) lateral view. Scale bars = 0.50 mm.



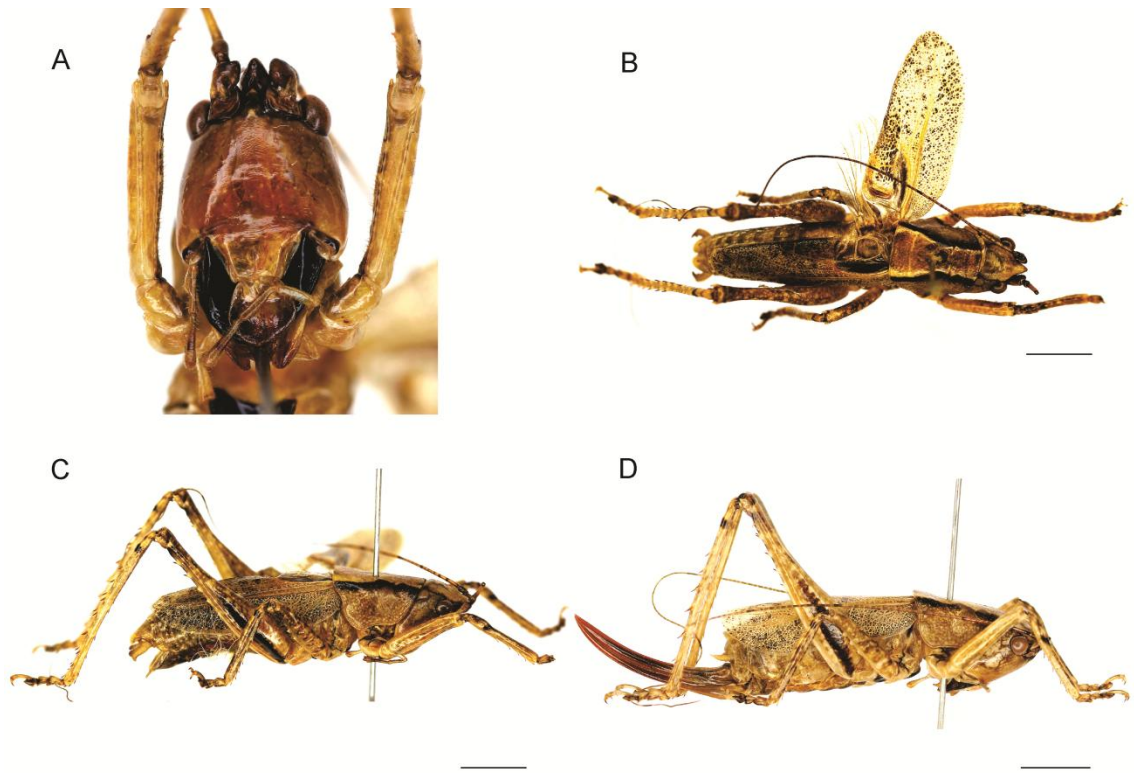
**Figure 20. Habitus of *Agraecia* sp. nov. 2.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



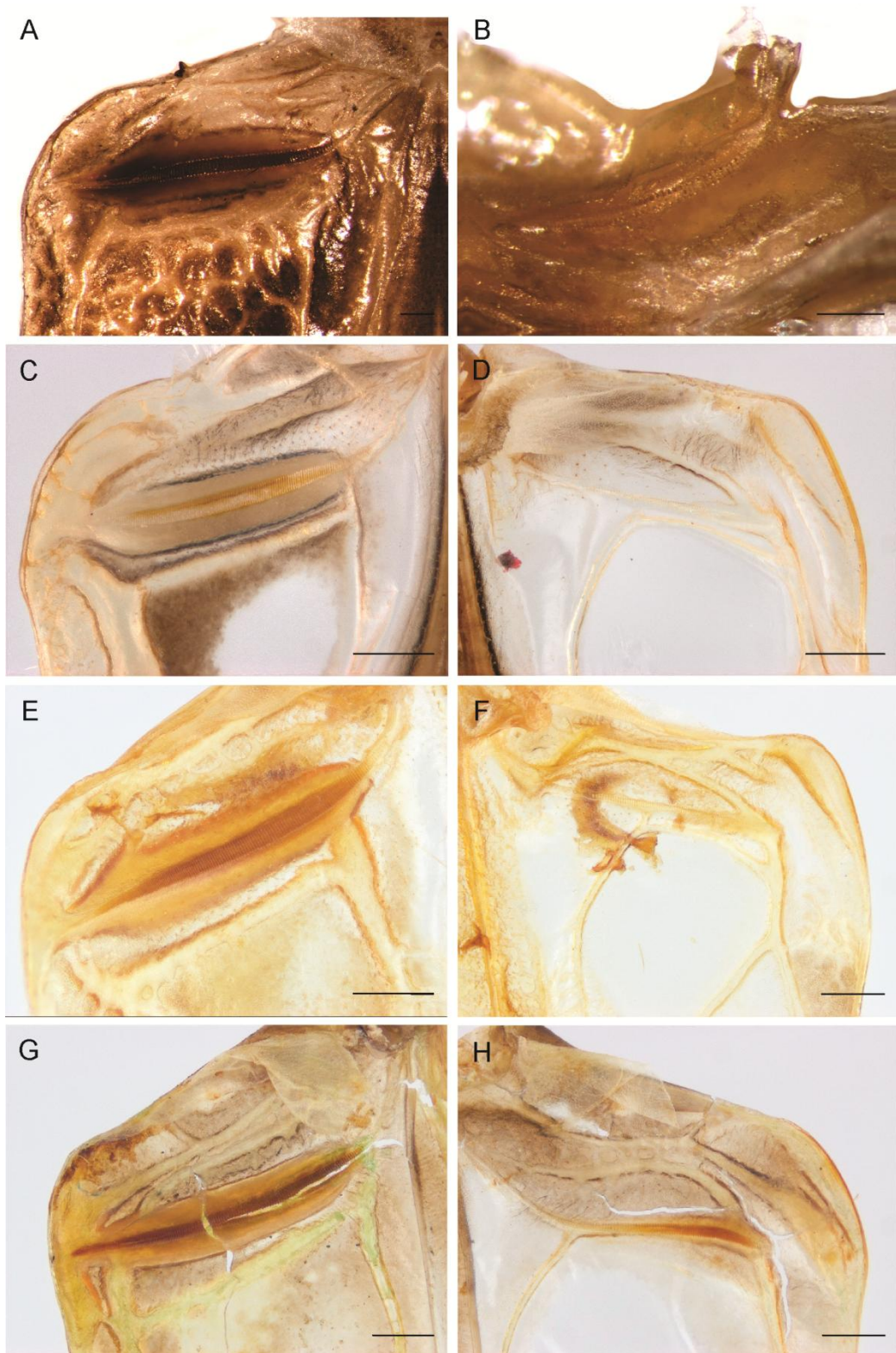
**Figure 21. Habitus of *Agraecia* sp. nov. 3.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



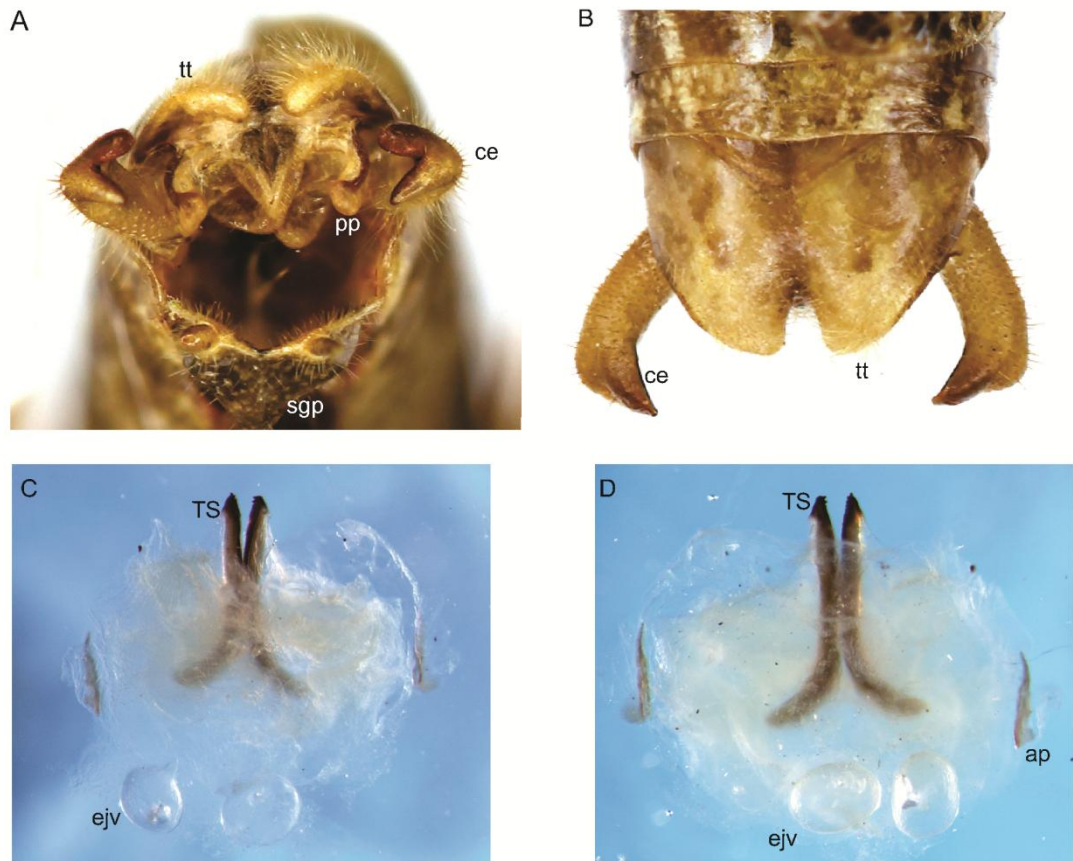
**Figure 22. Habitus of *Agraecia* sp. nov. 4. male (A) frontal view, (B) dorsal view, (C) lateral view. Scale bars = 0.50 mm.**



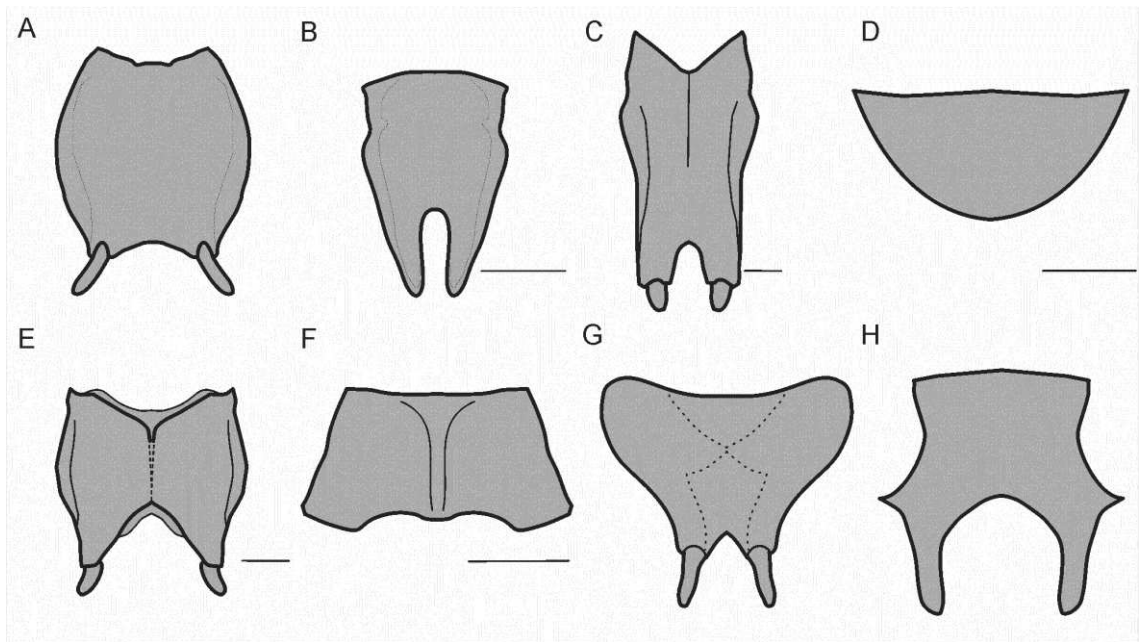
**Figure 23. Habitus of *Parasubria vittipes* (Redtenbacher) comb. nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



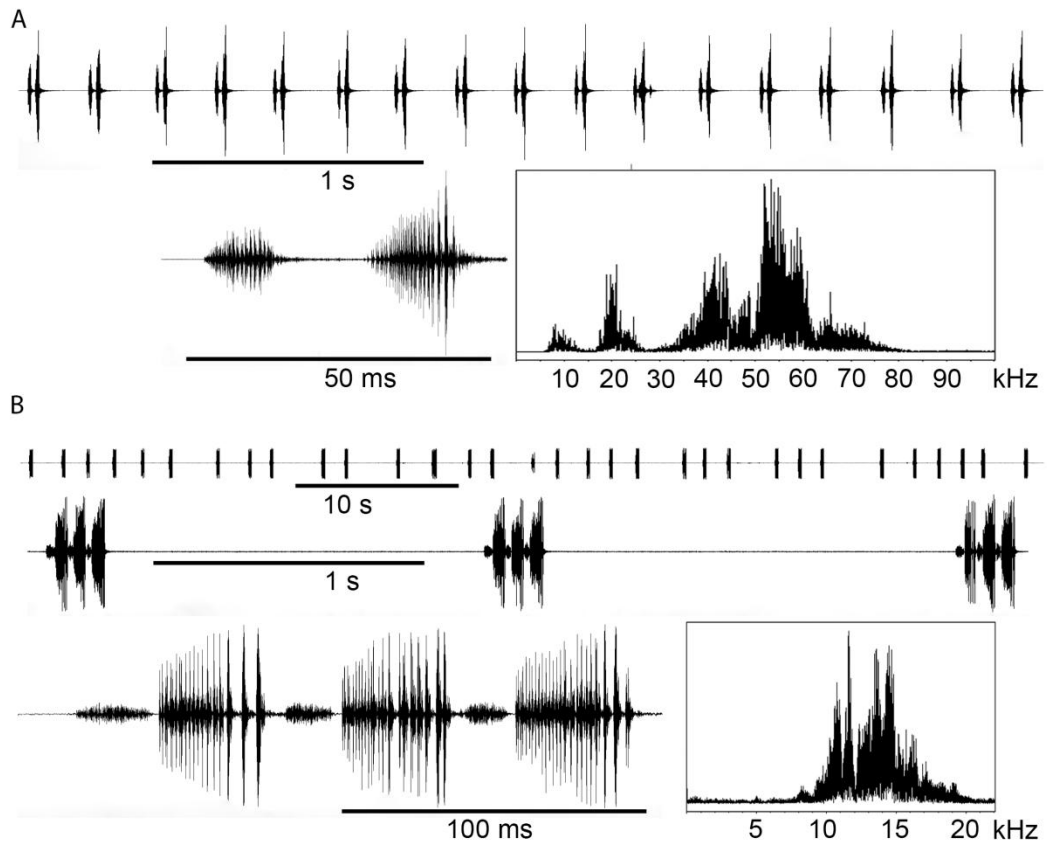
**Figure 24.** Left Stridulatory file (left column) and right (vein CuPb) file (right column). A–B *Parasubria vittipes* (Redtenbacher) **comb. nov.** C–D **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.** E–F **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.** G–H **Gen. nov. 4** *pulchella* (Hebard) **comb. nov.** Scale bars = 0.50 mm.



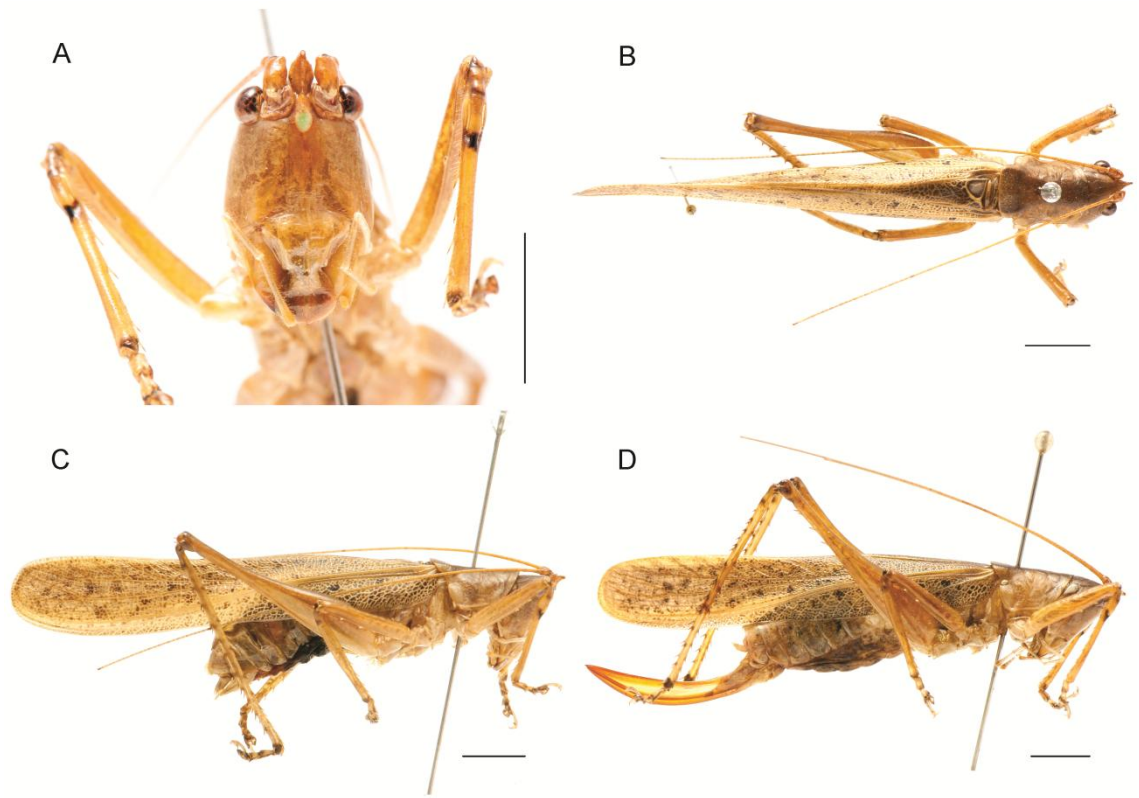
**Figure 25. Male postabdomen and phallus of *Parasubria vittipes* (Redtenbacher) comb. nov.** A–B postabdomen, (A) posterior view. (B) tergite X and cerci, dorsal view. C–D phallus, (C) phallus, dorsal view. (D) phallus, ventral view.



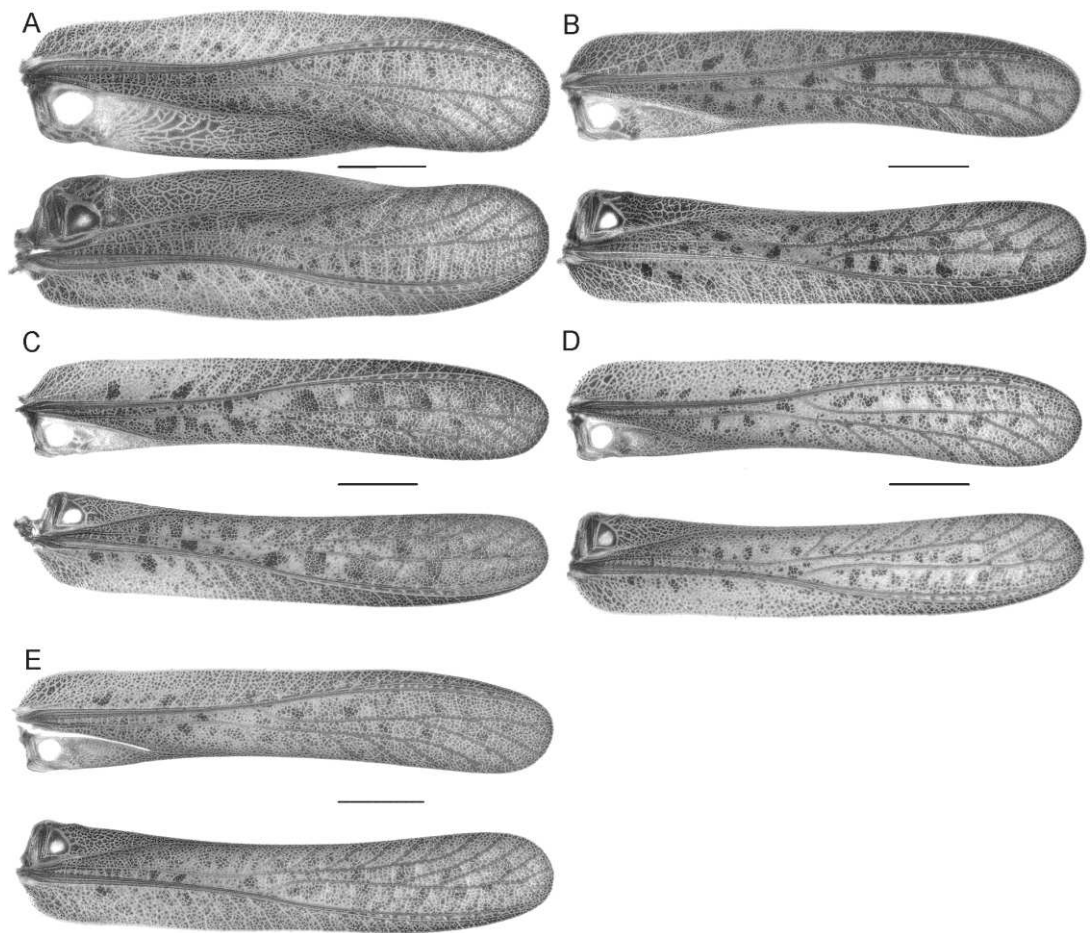
**Figure 26.** Subgenital plates of male and female *Agraeiini* genera. A–B *Parasubria vittipes* (Redtenbacher) **comb. nov.** (A) male, (B) female. C–D **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb.n.**, (C) male, (D) female. E–F **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.**, (E) male, (F) female. G–H **Gen. nov. 4** *pulchella* (Hebard) **comb. nov.** (drawing devoid of scale), (G) male, (H) female. Scale bar = 1.00 mm.



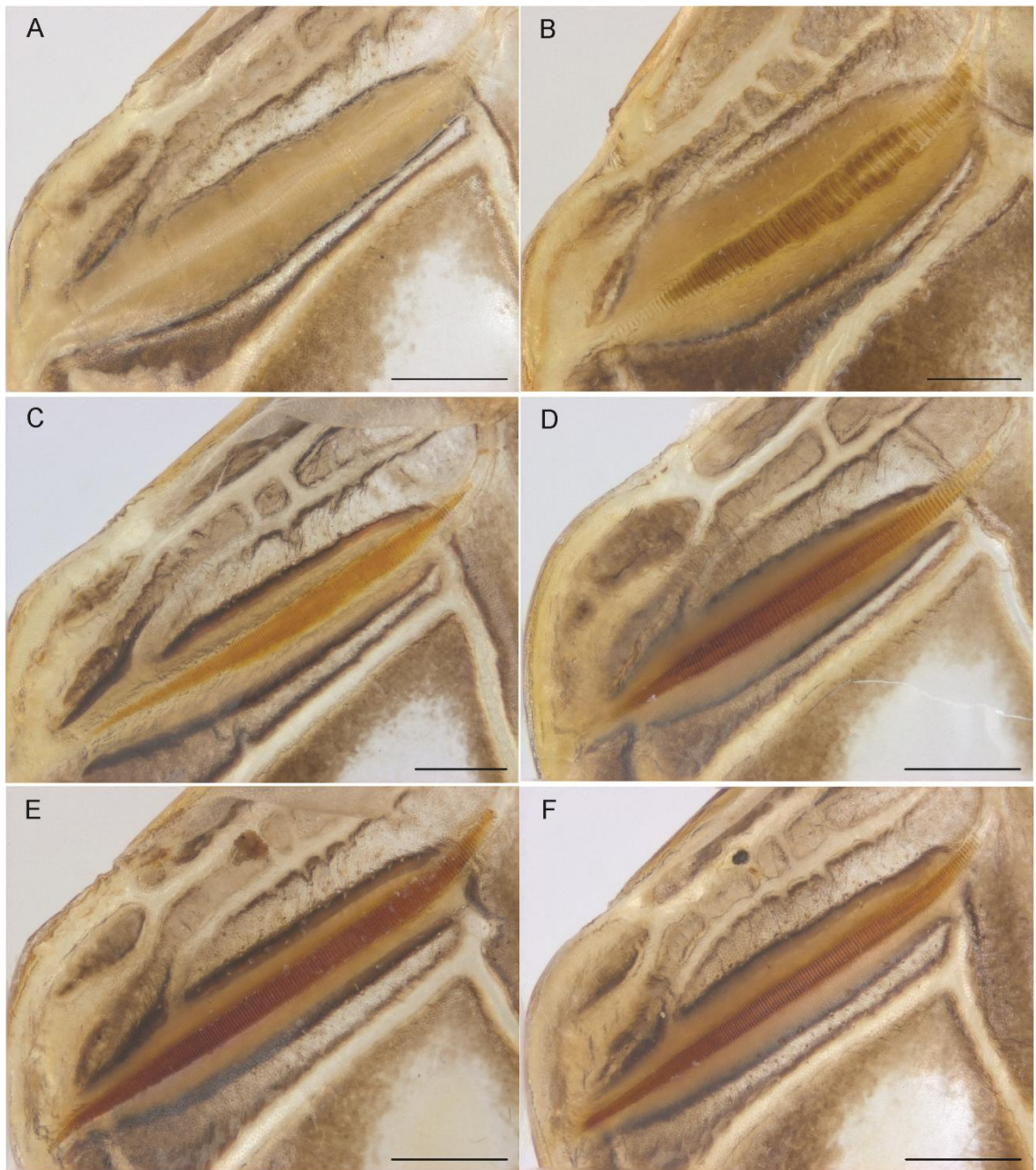
**Figure 27. Calling songs.** (A) *Parasubria vittipes* (Redtenbacher) **comb. nov.**, 4-s-fragment of continuous calling, one call in fine scale, and linear spectrogram; recorded at 27°C ambient temperature in cage (Parque Nacional Iguazú, Misiones, Argentina, February 2011, original recording M00025). (B) **Gen. nov. 4 pulchella** (Hebard) **comb. nov.**, one minute continuous calling, three subsequent calls and one call in finer scales, and linear spectrogram up to 22 kHz; recorded in the field, probably at much lower temperature (Santuario de fauna y flora Otún Quimbaya, Risaralda, Colombia), which contributes to lower repetition rate.



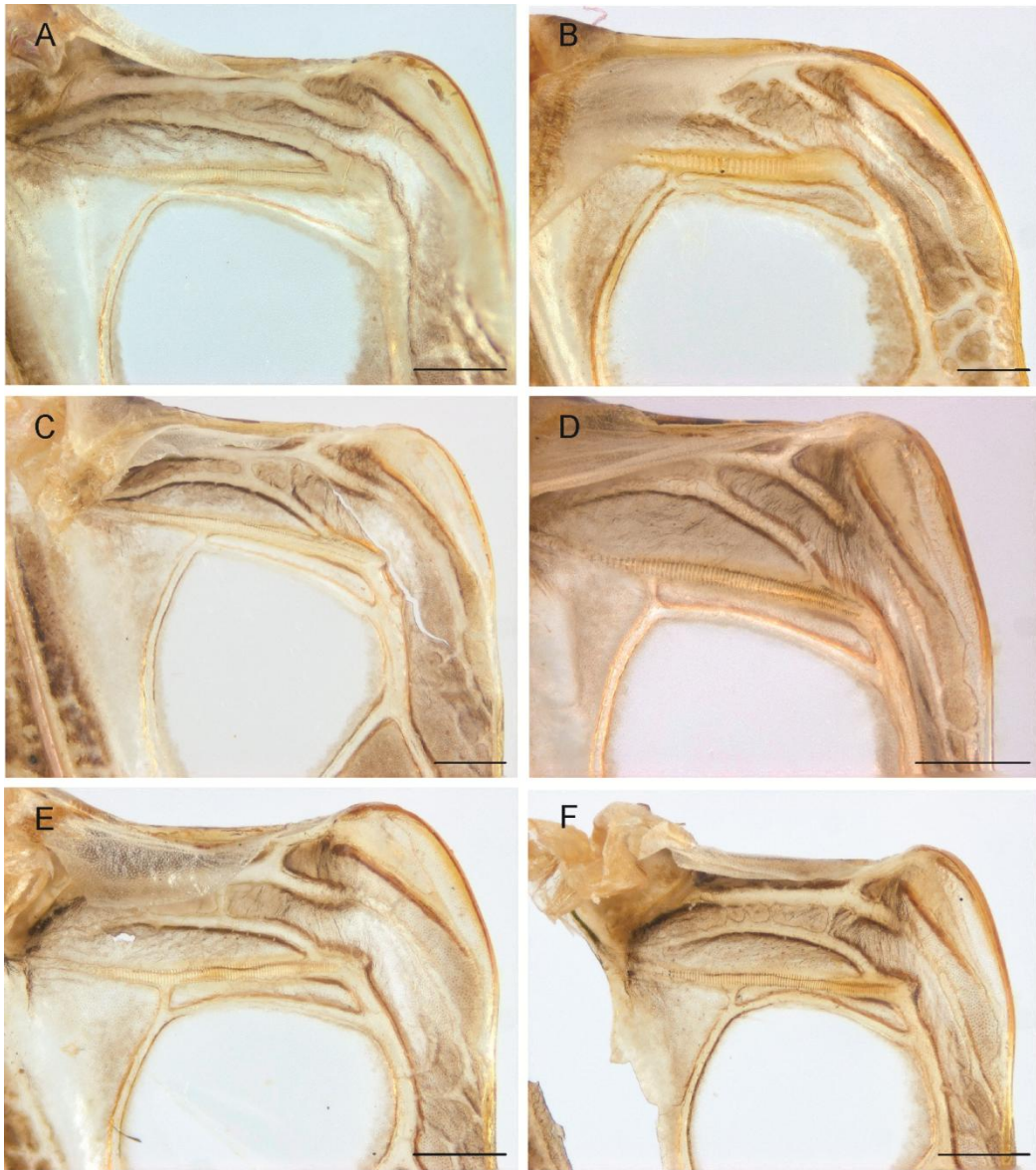
**Figure 28. Habitus of Gen. nov. 1 *maculata* (Redtenbacher) comb. nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



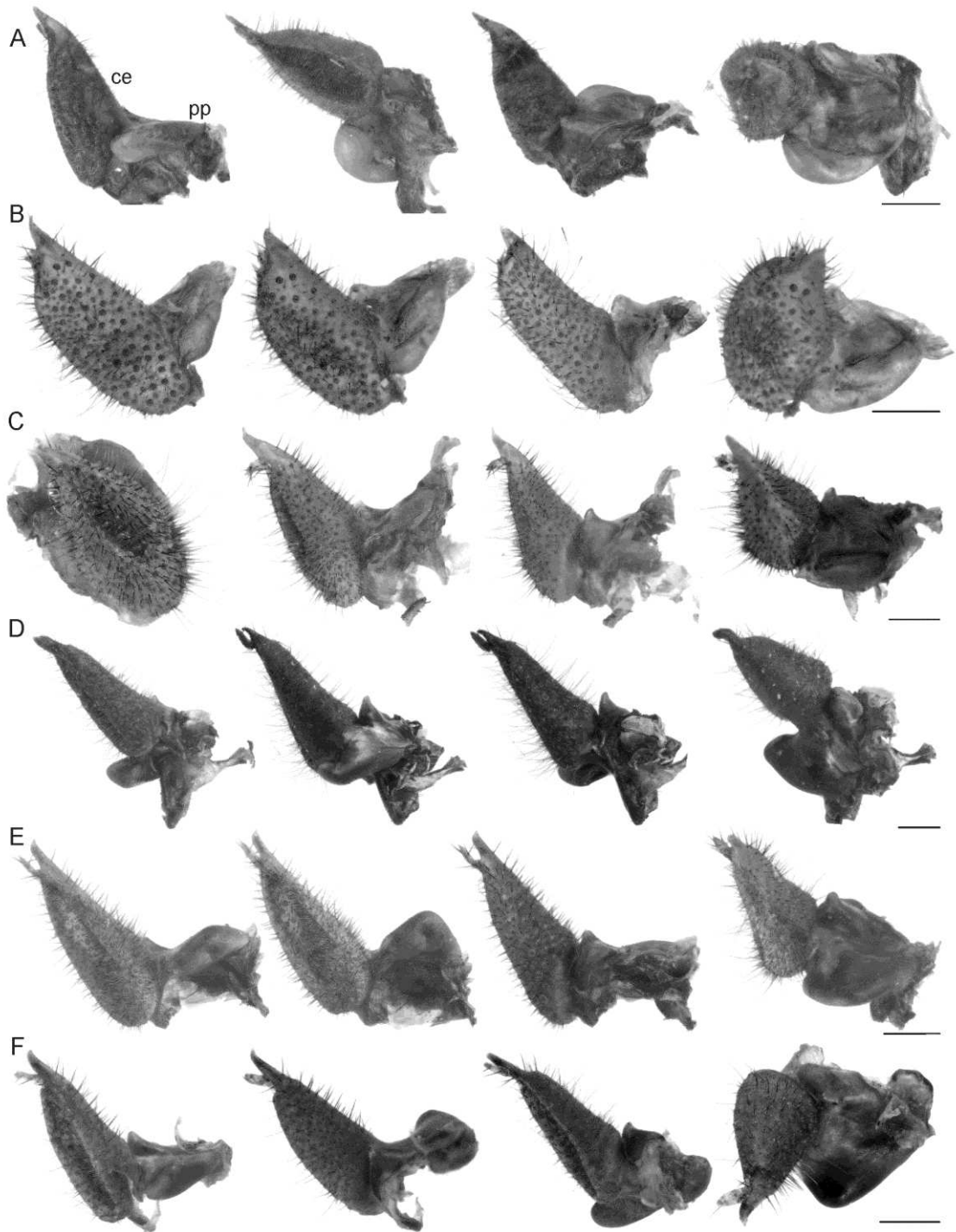
**Figure 29. Tegmina of male Gen. nov. 1 species. (A) Gen. nov. 1 *subulata* (Redtenbacher) comb. nov. (B) Gen. nov. 1 sp.2 nov. (C) Gen. nov. 1 sp.1 nov. (C) Gen. nov. 1 sp.3 nov. (D) Gen. nov. 1 sp.2 nov. Scale bars = 5.00 mm.**



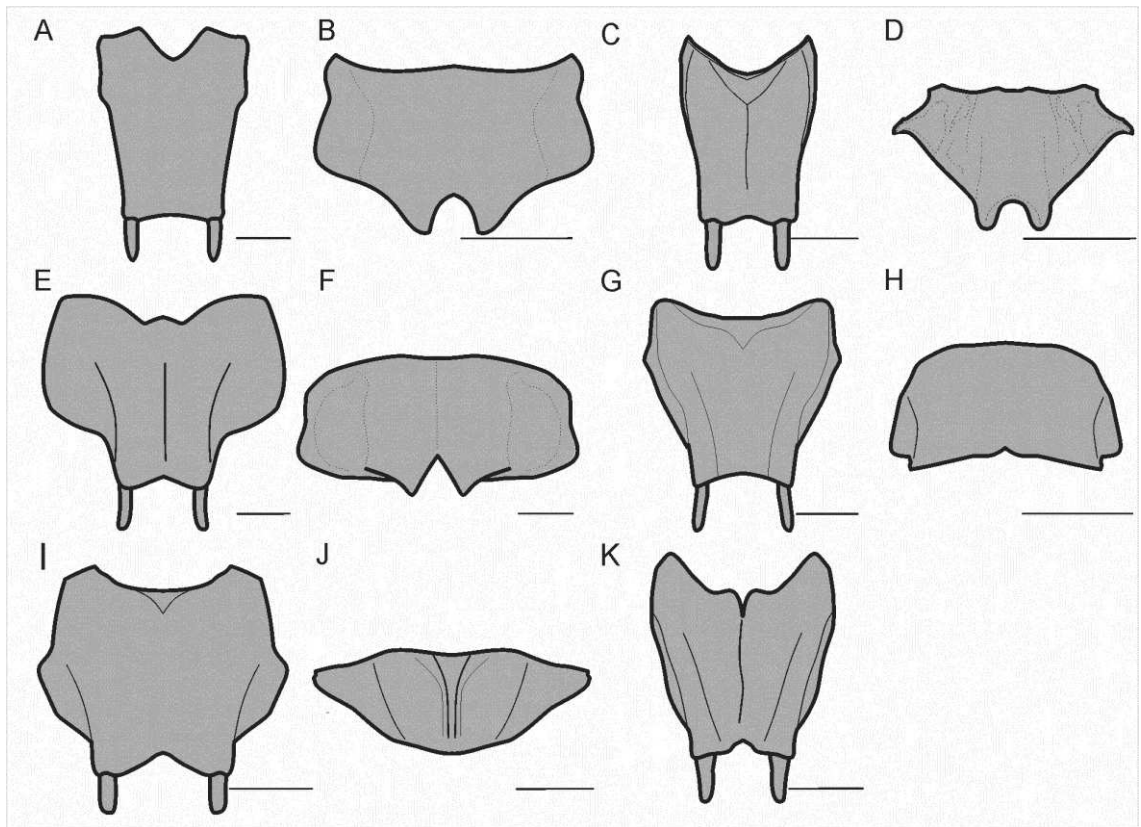
**Figure 30. Left Stridulatory file of male Gen. nov. 1 species. (A) Gen. nov. 1 *maculata* (Redtenbacher) **comb. nov.** (B) Gen. nov. 1 *subulata* (Redtenbacher) **comb. nov.** (C) Gen. nov. 1 **sp.2 nov.** (D) Gen. nov. 1 **sp.1 nov.** (E) Gen. nov. 1 **sp.3 nov.** (F) Gen. nov. 1 **sp.2 nov.** Scale bar = 0.50 mm.**



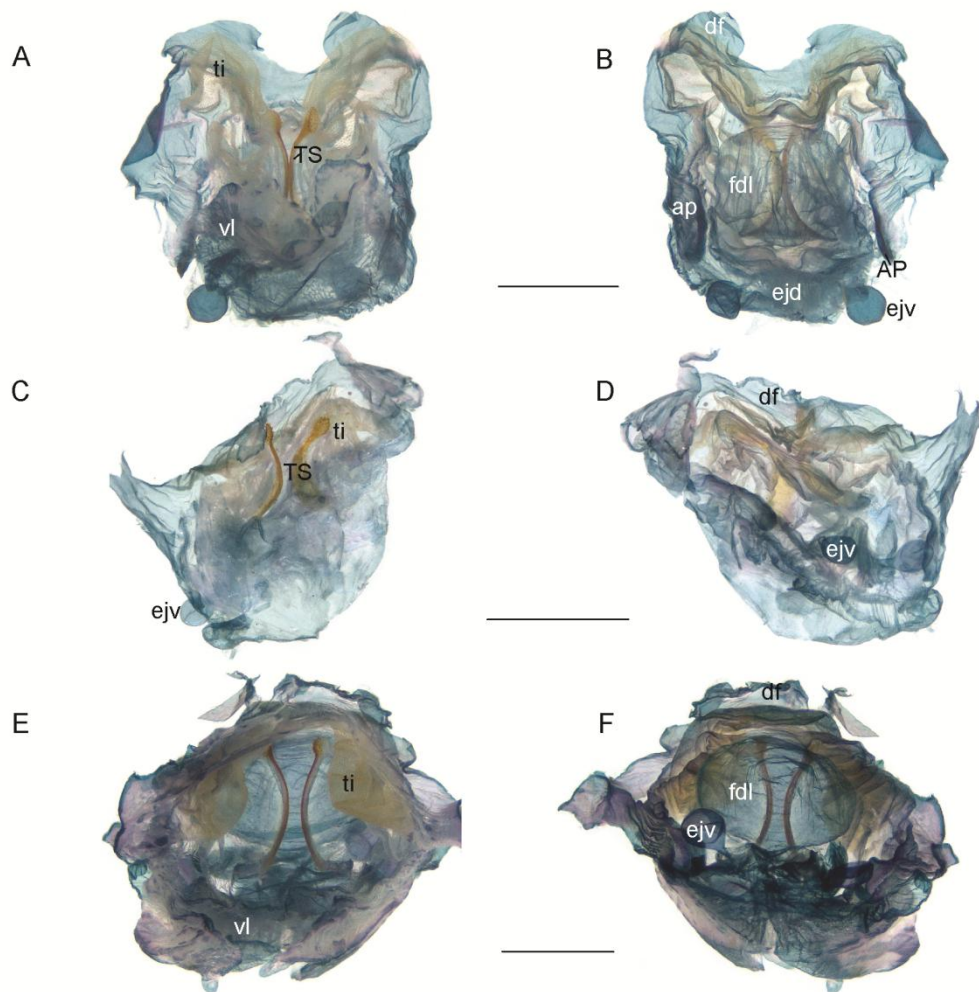
**Figure 31. Right file of male Gen. nov. 1 species. (A) Gen. nov. 1 *maculata* (Redtenbacher) **comb. nov.** (B) Gen. nov. 1 *subulata* **comb. nov.** (C) Gen. nov. 1 **sp.2** **nov.** (D) Gen. nov. 1 **sp.1** **nov.** (E) Gen. nov. 1 **sp.3** **nov.** (F) Gen. nov. 1 **sp.2** **nov.** Scale bar = 0.50 mm.**



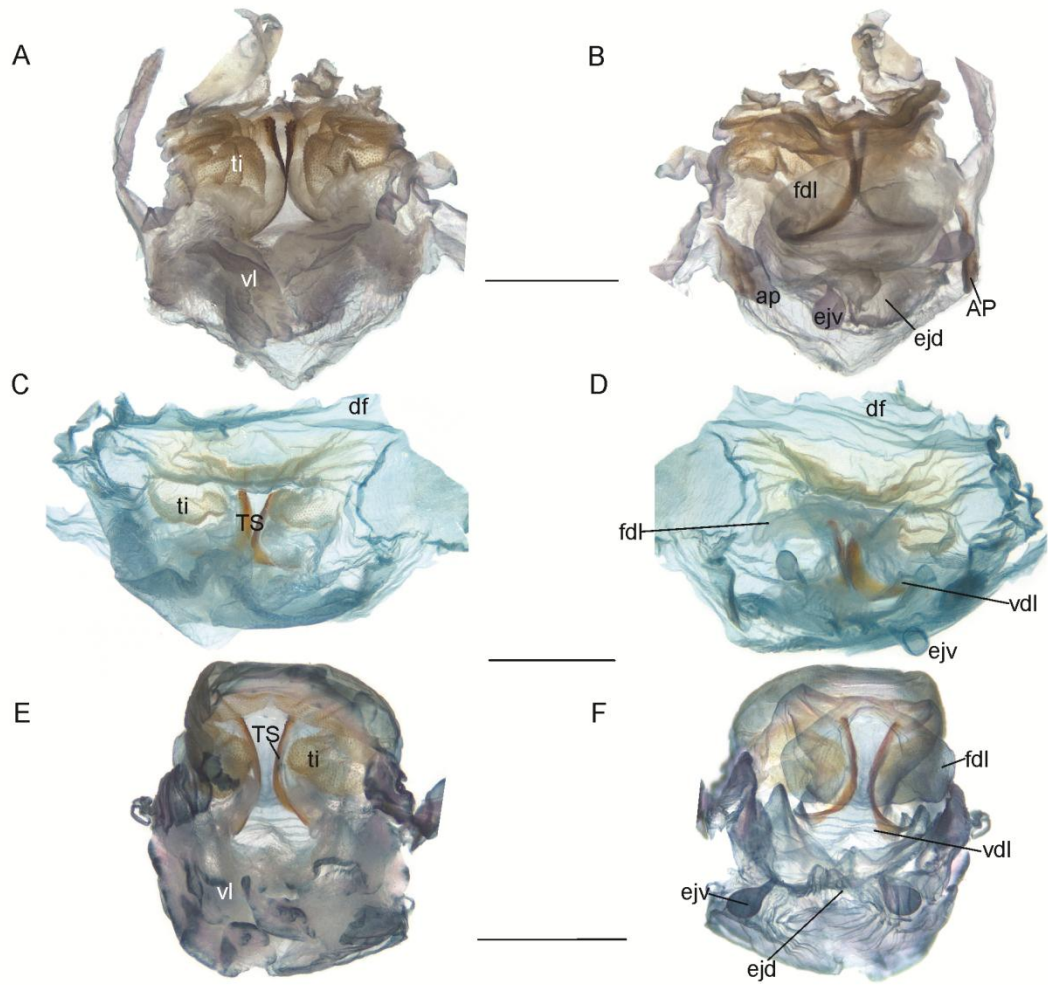
**Figure 32.** Cerci and paraprocts of male *Gen. nov. 1* species. (A) *Gen. nov. 1 maculata* comb. nov. (B) *Gen. nov. 1 subulata* comb. nov. (C) *Gen. nov. 1 sp.2* nov. (D) *Gen. nov. 1 sp.1* nov. (E) *Gen. nov. 1 sp.3* nov. (F) *Gen. nov. 1 sp.2* nov. Scale bar = 0.50 mm.



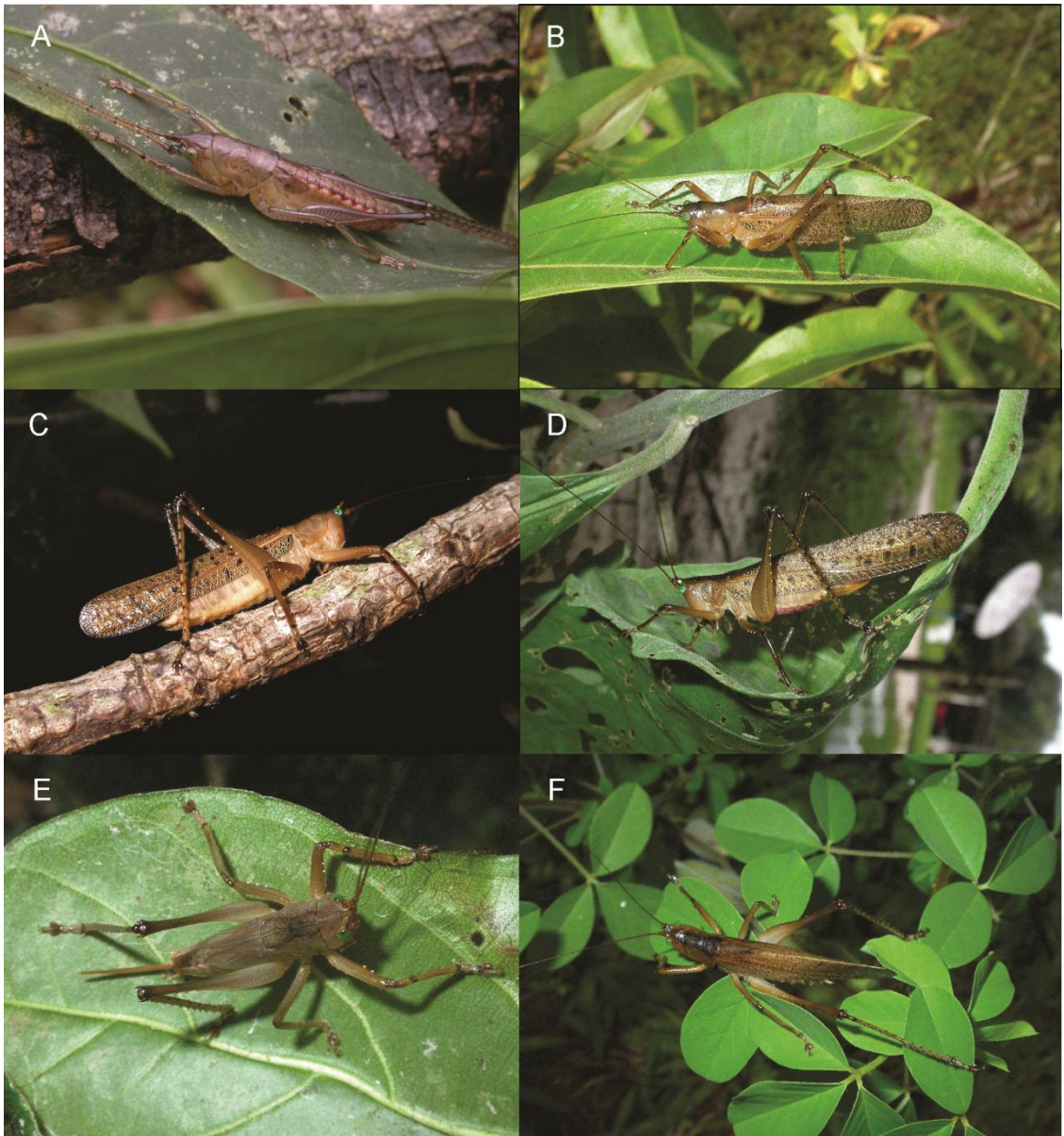
**Figure 33. Subgenital plates of male and female Gen. nov. 1 species. A–B Gen. nov. 1 maculata comb. nov., (A) male, (B) female. C–D Gen. nov. 1 subulata comb. nov., (C) male, (D) female. E–F Gen. nov. 1 sp.2 nov., (E) male, (F) female. G–H Gen. nov. 1 sp.1 nov., (G) male, (H) female. I–J Gen. nov. 1 sp.3 nov., (I) male, (J) female. (K) Gen. nov. 1 sp.2 nov., male. Scale bar = 1.00 mm.**



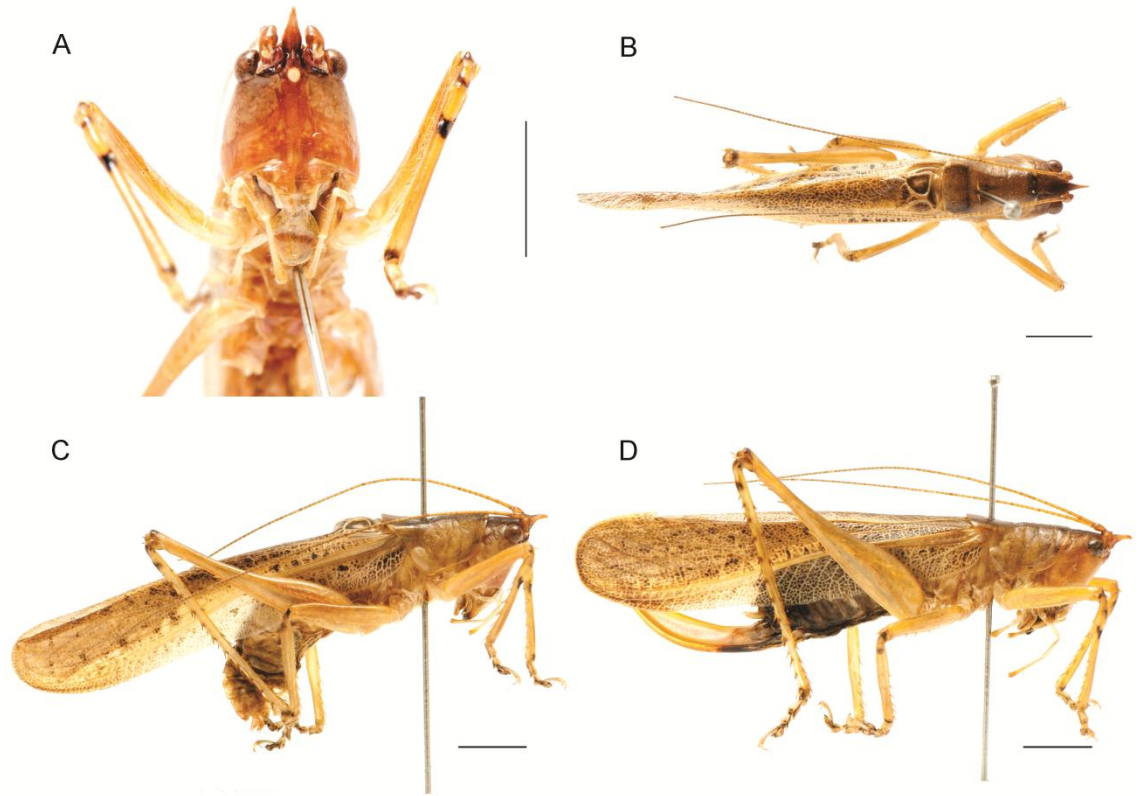
**Figure 34. Phallus of Gen. nov. 1 species.** A–B *Gen. nov. 1 maculata comb. nov.*, (A) dorsal, (B) ventral. C–D *Gen. nov. 1 subulata comb. nov.* (C) dorsal; (D) ventral. E–F *Gen. nov. 1 sp.2 nov.*, (E) dorsal, (F) ventral. Abbreviations: anterophallic apodemes **ap**; sclerites of apodemes **AP**; ejaculatory duct **ejd**; ejaculatory vesicles **ejv**; fore fold of dorsal lobe **fdl**; titillatory process(es) **ti**; titillator's sclerite(s) **TS**. Scale bar = 1.00 mm.



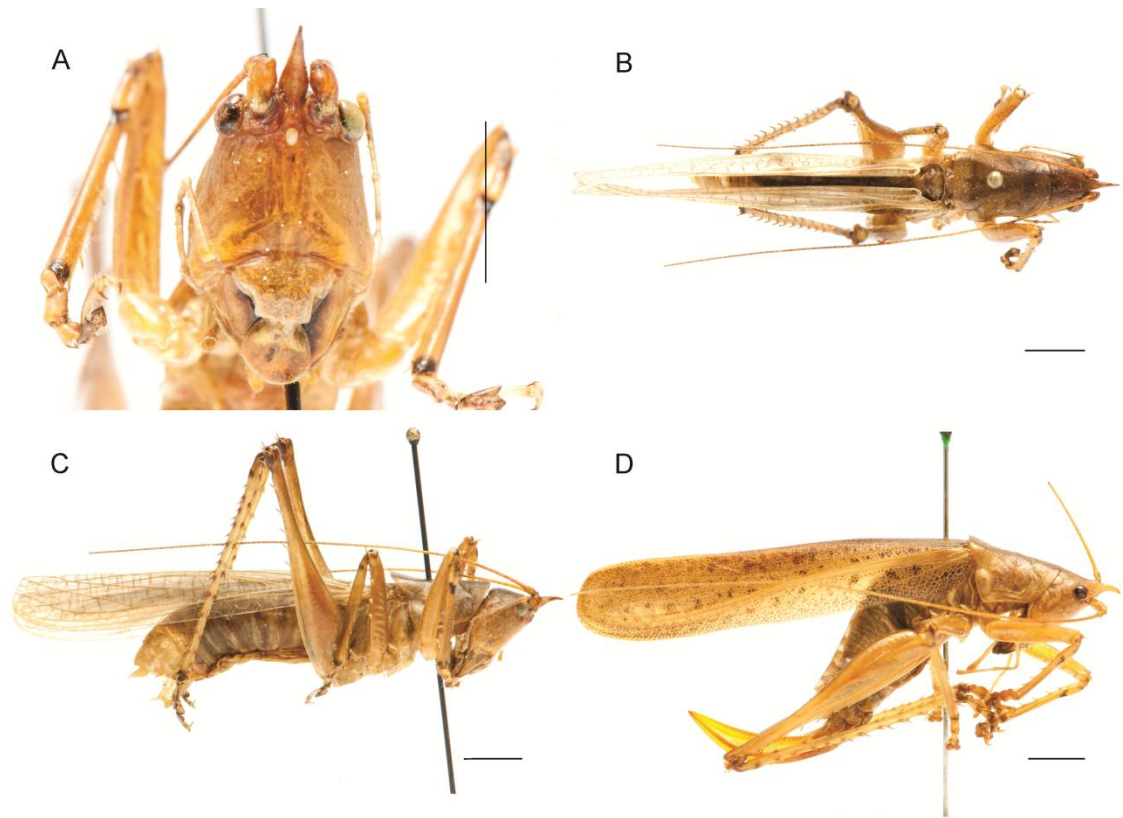
**Figure 35. Phallus of Gen. nov. 1 species.** A–B **Gen. nov. 1 sp.1 nov.**, (A) dorsal, (B) ventral. C–D **Gen. nov. 1 sp.3 nov.**, (C) dorsal, (D) ventral. E–F **Gen. nov. 1 sp.2 nov.**, (E) dorsal, (F) ventral. Abbreviations: anterophallic apodemes **ap**; sclerites of apodemes **AP**; ejaculatory duct **ejd**; ejaculatory vesicles **ejv**; fore fold of dorsal lobe **fdl**; titillatory process(es) **ti**; titillator's sclerite(s) **TS**. Scale bar = 1.00 mm.



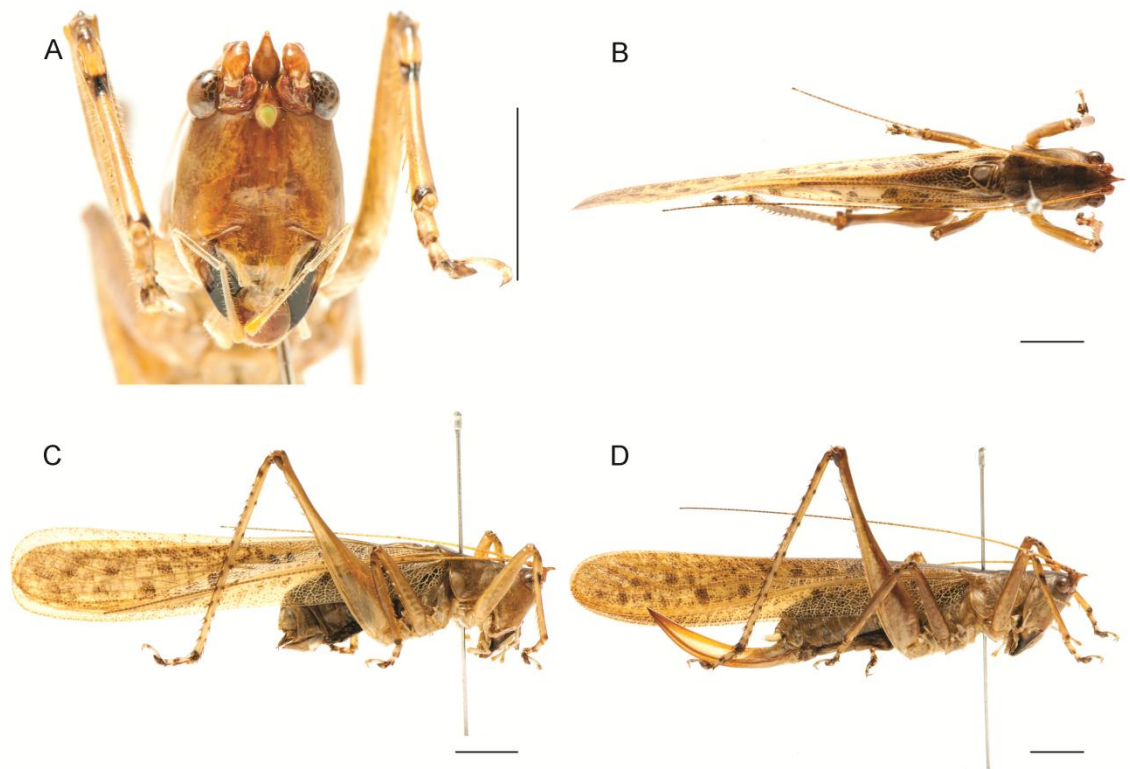
**Figure 36. Live individuals of Gen. nov. 1 species.** (A) Male of **Gen. nov. 1 maculata** (Redtenbacher) **comb. nov.**, dorso-lateral view. (B) Male of **Gen. nov. 1 subulata** (Redtenbacher) **comb. nov.**, dorso-lateral view. (C) Male of **Gen. nov. 1 sp.2 nov.**, lateral view. D–E **Gen. nov. 1 sp.1 nov.** (D) Adult female, lateral view; (E) Immature female, dorsal view. (F) Female of **Gen. nov. 1 sp.3 nov.**, dorsal view.



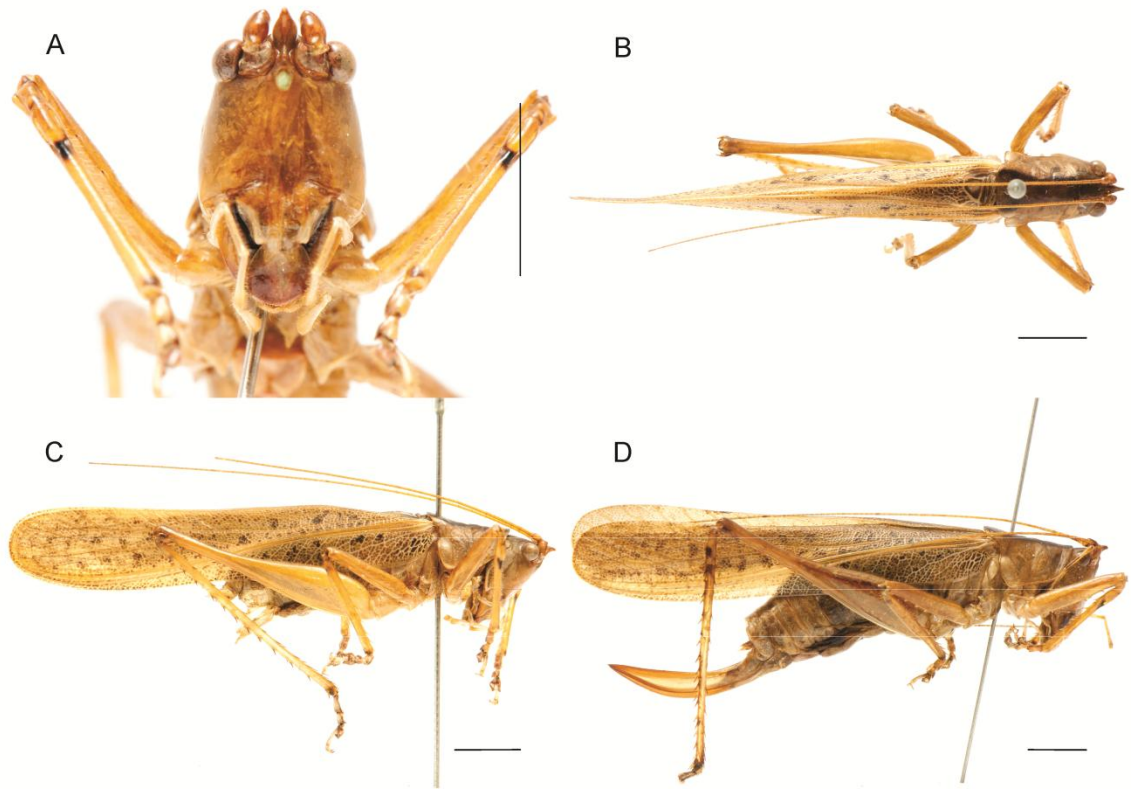
**Figure 37. Habitus of Gen. nov. 1 *subulata* (Redtenbacher, 1891) comb. nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



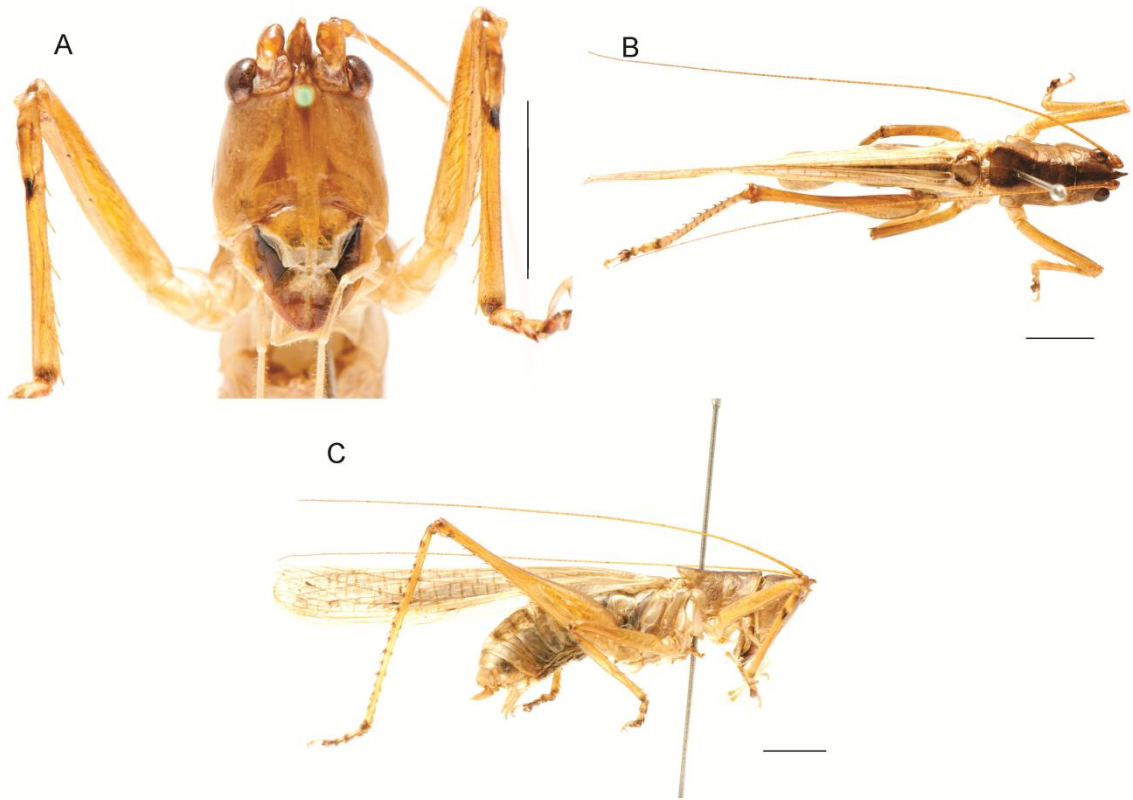
**Figure 38. Habitus of Gen. nov. 1 sp. 2 nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



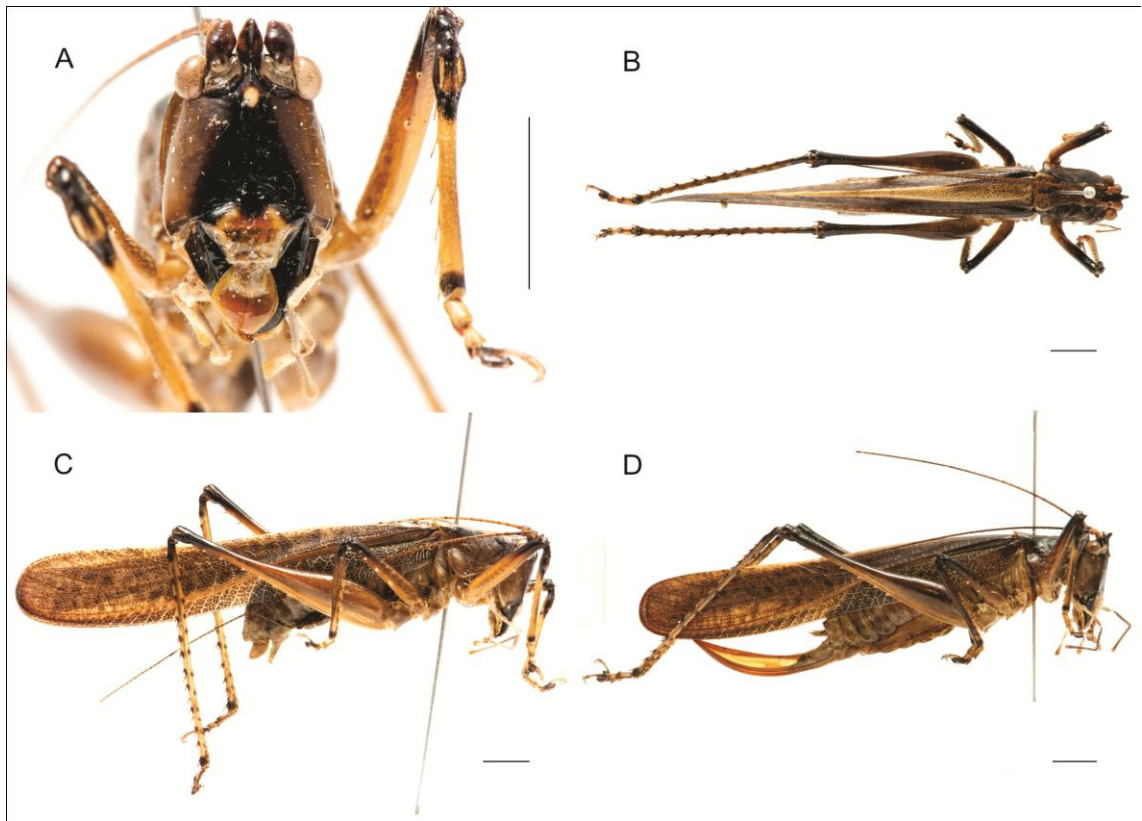
**Figure 39. Habitus of Gen. nov. 1 sp.1 nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



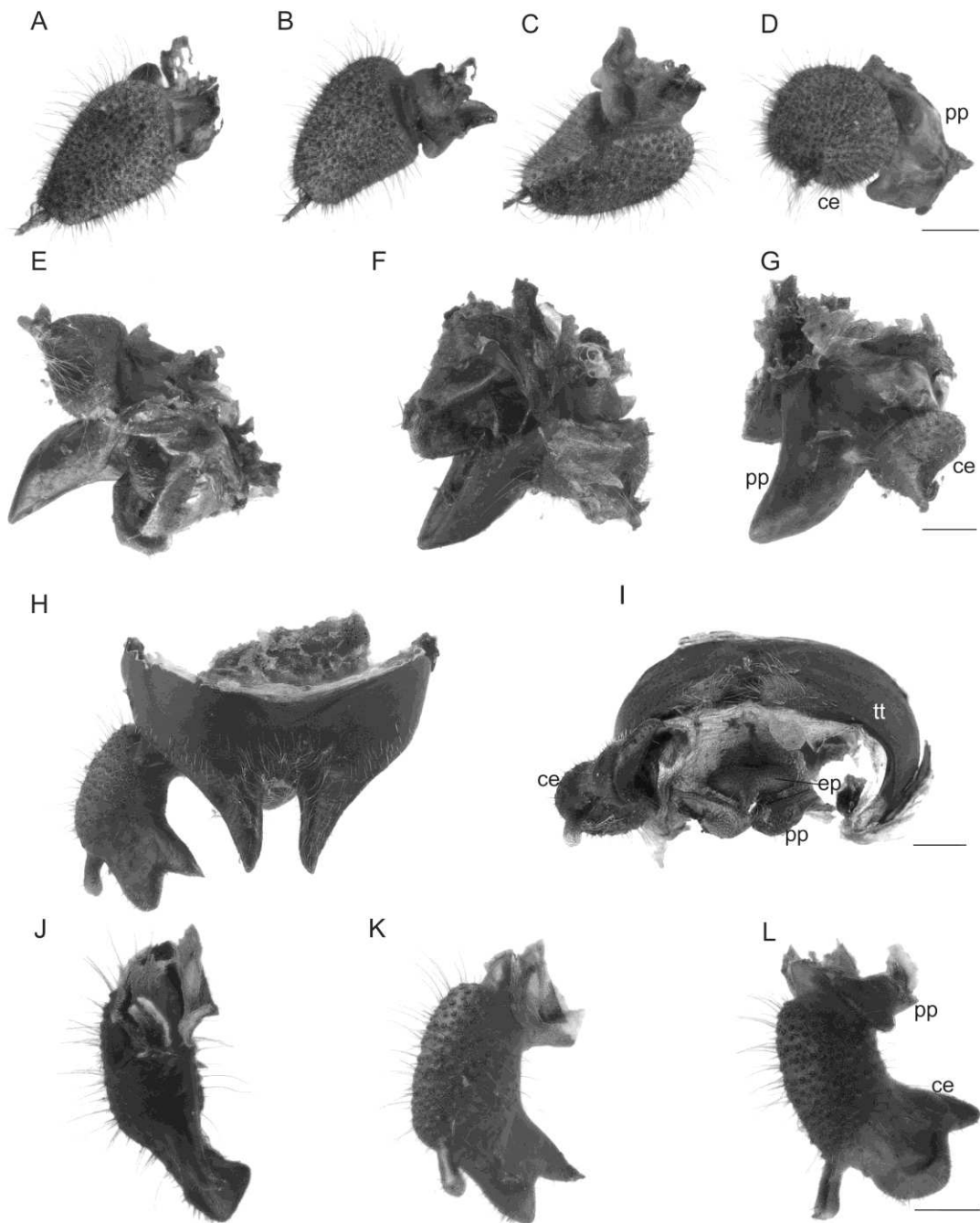
**Figure 40. Habitus of Gen. nov. 1 sp.3 nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



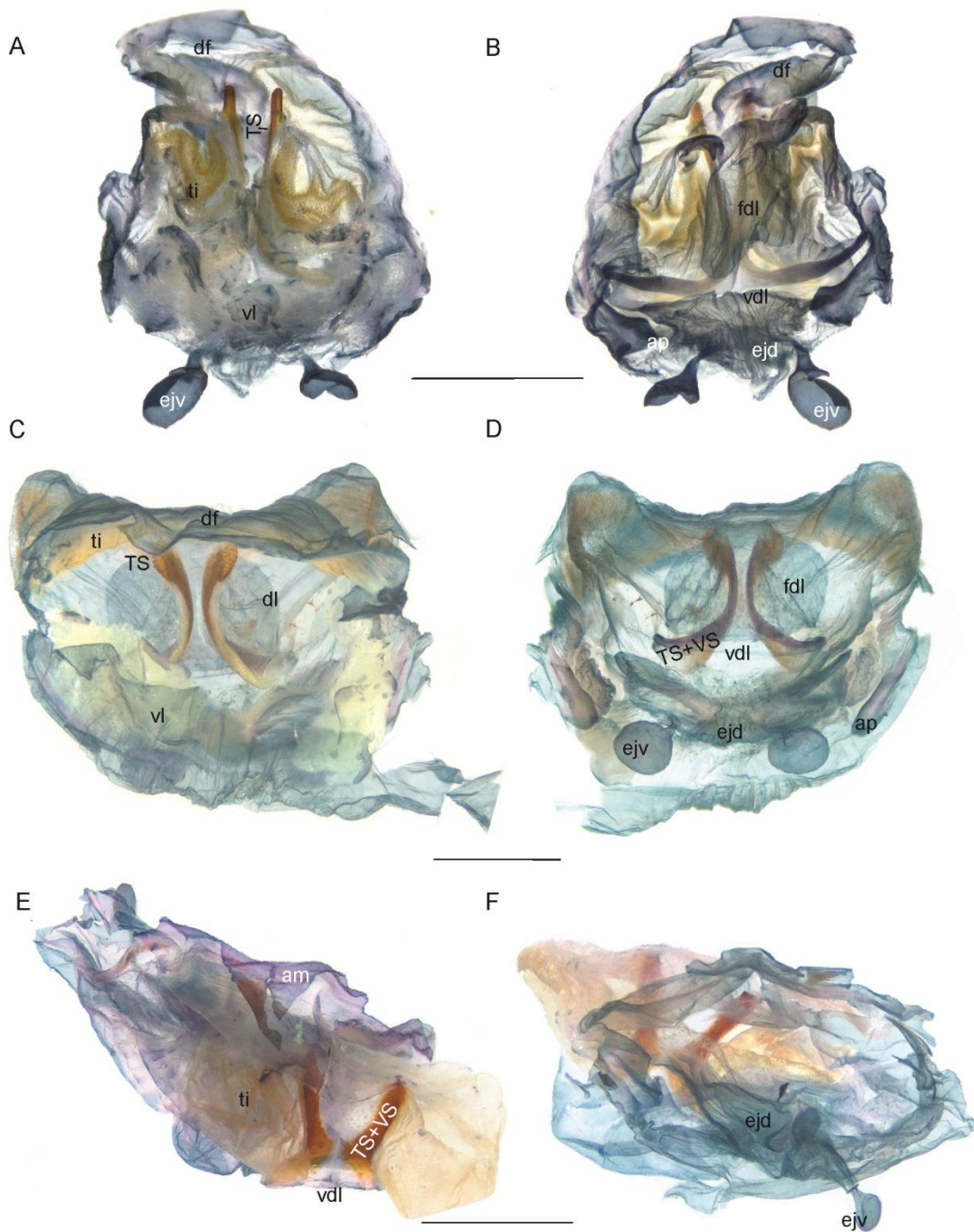
**Figure 41. Habitus of Gen. nov. 1 sp.4 nov. male (A) frontal view, (B) dorsal view, (C) lateral view. Scale bars = 0.50 mm.**



**Figure 42. Habitus of *Gen. nov. 2 nigrifrons* (Redtenbacher) comb. nov.** A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.



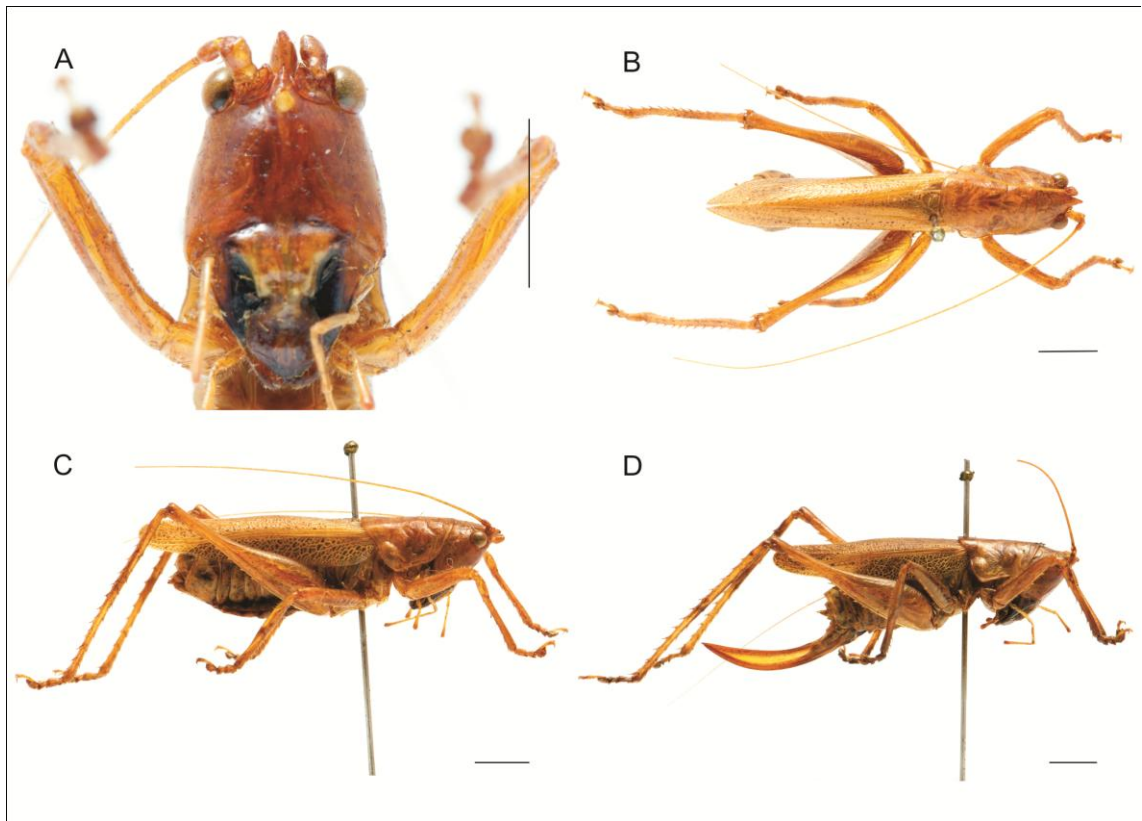
**Figure 43. Components of the postabdomen.** A–D **Gen. nov. 2** *nigrifrons* (Redtenbacher) **comb. nov.**, (A) lateral view, (B) latero-dorsalview, (C) lateral-ventral view (D) posterior view. E–G **Gen. nov. 3** *abbreviata* (Redtenbacher) **comb. nov.**, (E) latero-ventral view, (F) ventral view, (G) posterior view. H–L **Gen. nov. 4** *pulchella* (Hebard) **comb. nov.**, (H–I) tergite X and cerci, (H) dorsal view, and (I) dorso-posterior view; (J–L) cerci, (J) ventral view, lateral-ventral view, (K) dorsal view. Scale bars = 0.50 mm.



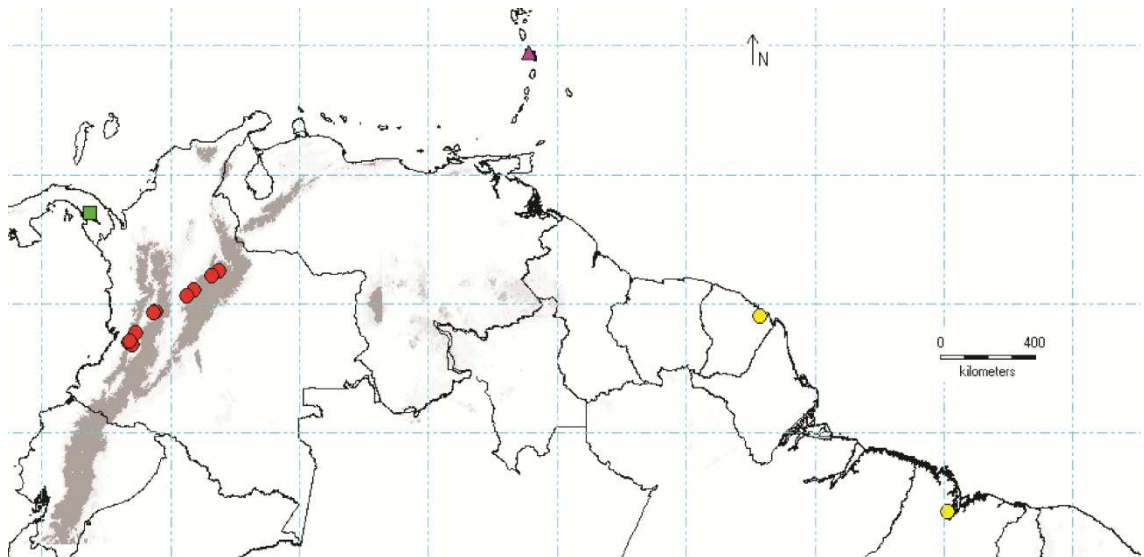
**Figure 44. Phallus of Agraeiini genera. A–B Gen. nov. 2 *nigrifrons* (Redtenbacher) **comb.n.** (A) dorsal, (B) ventral. C–D Gen. nov. 3 *abbreviata* (Redtenbacher) **comb. nov.**, (C) dorsal, (D) ventral. E–F Gen. nov. 4 *pulchella* (Hebard) **comb. nov.**, (E) dorsal; (F) ventral. Scale bar = 1.00 mm.**



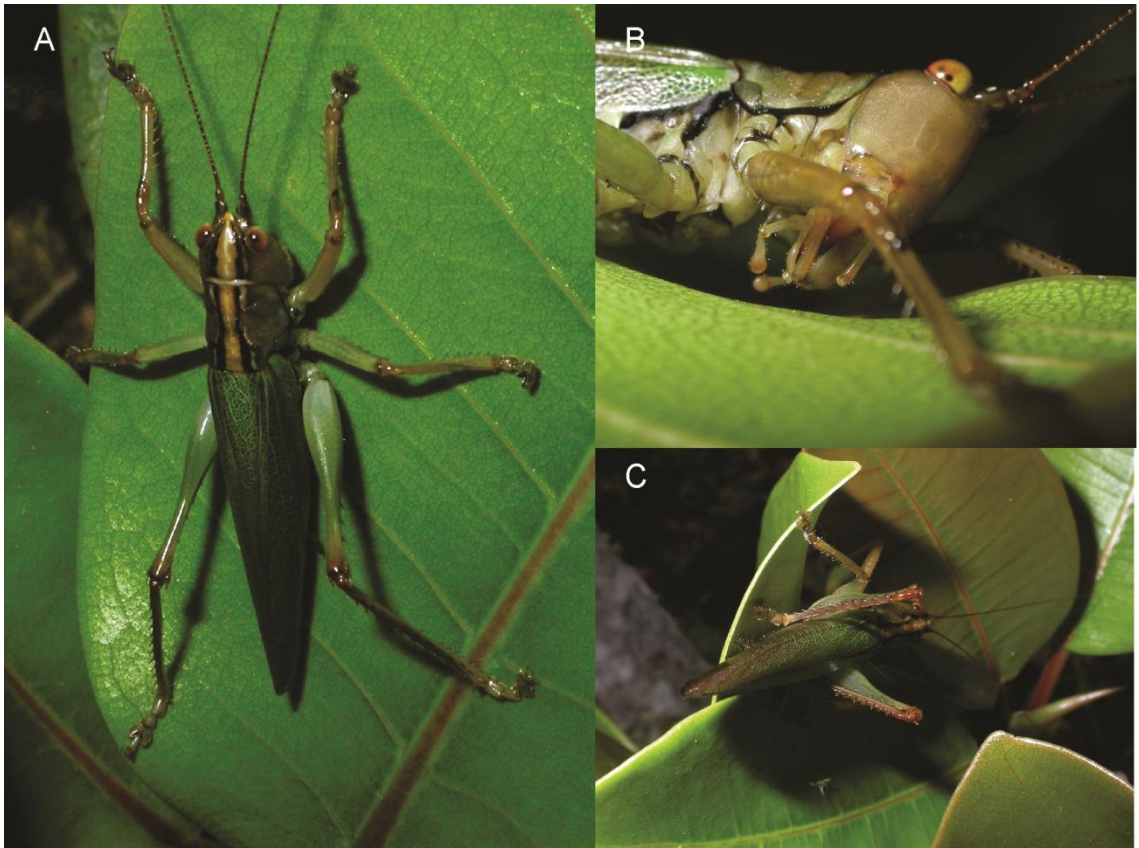
**Figure 45.** Live individuals of *Gen. nov. 2 nigrifrons* (Redtenbacher) *comb. nov.*, (A) adult female, lateral view, (B) female, immature latero-dorsal view, (C) male latero-dorsal view, (D) male, face, frontal view.



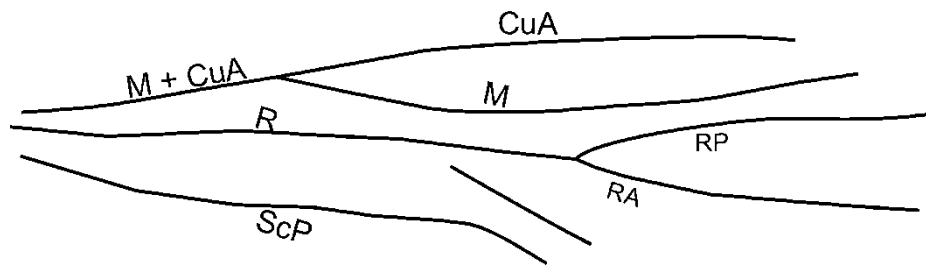
**Figure 46. Habitus of Gen. nov. 3 *abbreviata* (Redtenbacher, 1891) comb. nov. A–C male, (A) frontal view, (B) dorsal view, (C) lateral view. (D) female, lateral view. Scale bars = 0.50 mm.**



**Figure 47. Geographic distribution. Gen. nov. 5 cesairei** (Hugel) **comb. nov.** (purple triangle); *Agraecia festae* Griffini (green square); **Gen. nov. 4 pulchella** (Hebard) **comb. nov.** (red circle); *Gen. nov. 6 viridipennis* (Redtenbacher) **comb. nov.** (yellow circle).



**Figure 48.** Live individuals of *Gen. nov. 4 pulchella* (Hebard) *comb. nov.* male, (A) body dorsal view, (B) face, pronotum and thoracic sclerites, lateral view, (C) posterior view.



**Figure 49.** Schematic drawing of venation pattern of **Gen. nov. 7 *reticulata*†** (Piton & Théobald, 1939) **comb. nov.** Based on Plate 1, Fig. 3 in Piton & Théobald 1939.

## 6. CONCLUSÕES GERAIS

O falo em Tettigonioidea, visto como um todo, e junto com seus componentes por separado, é informativamente útil para efetuar a classificação de espécies, gêneros e agrupações supragenéricas. Além disso, a morfologia do falo pode ser usada como uma ferramenta robusta para inferir relações filogenéticas entre os táxons.

O falo é uma estrutura que deve ser considerada como uma parte do organismo que interage e funciona junto com outras estruturas, como cercos, paraproctos e placa subgenital. Mas o falo também pode fazer parte de processos mais amplos no organismo, como a produção do espermátóforo ou expressão de certos comportamentos. Devido a essas interações, e para poder entender a evolução do falo e seus componentes, deve-se entender também a sua funcionalidade durante a cópula.

As tégminas são estruturas informativamente úteis usadas para estabelecer relações entre categorias supragenéricas. A maior parte da história dos Pterygota está baseada no registro fóssil de tégminas. Assim, para ligar a diversidade de Tettigonioidea existente e entender o passado do grupo, o estudo da morfologia das tégminas é essencial.

Tanto a fileira estridulatória esquerda e a fileira direita em Tettigonioidea podem ser usadas como caracteres para a separação de táxons. E para elucidar a história evolutiva dos Tettigonioidea, há de se compreender melhor os fatores que influenciam a variação entre as tégminas esquerda e direita, como presença e ausência da fileira estridulatória, número de dentes das fileiras, morfologia do espelho, raspador e outras veias e componentes das tégminas.

As diagnoses e diferenciação entre *Agraecia* Audinet-Serville e os novos gêneros propostos neste estudo estão suportadas em caracteres tradicionalmente considerados na taxonomia de Agraeciini, como aparência geral do corpo, o formato do fastigio do vertex e fastígio da frente. Mas também na morfologia comparada detalhada das tégminas, incluindo a fileira estridulatória direita, o esterno, e as estruturas do pós-abdômen, incluindo o falo.

Devido às mudanças taxonômicas propostas aqui, a distribuição geográfica das únicas duas espécies mantidas em *Agraecia* restringe o gênero ao chamado Domínio Paraná da Região Neotropical, que compreende a porção suldeste do Brasil, e a porção norte da Argentina e Uruguai. Aparentemente, o gênero *Agraecia* Audinet-Serville, os gêneros novos e as espécies aqui tratadas possuem uma distribuição reduzida. Porém, é

preciso realizar mais coletas, principalmente em biomas pouco amostrados como o Cerrado e a Caatinga.

O problema taxonômico resolvido no presente estudo sobre o gênero *Agraecia* é uma amostra representativa da situação atual do conhecimento da diversidade e classificação de esperanças no Brasil. Por tal motivo, na atualidade não existem dados suficientes para fazer uma estimativa sobre a diversidade de Agraeciini brasileiros, muito menos dos neotropicais. A quantidade de espécies e gêneros deve ser muito maior do que é conhecida atualmente.