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SISTEMÁTICA E EVOLUÇÃO DE FIDICININI DISTANT, 1905 (CICADINAE) E DE HEMIDICTYINI DISTANT, 1905 (TETTIGOMYIINAE) (HEMIPTERA, AUCHENORRHYNCHA, CICADIDAE)

PORTO ALEGRE

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Área de concentração: Biologia Comparada

Orientador(a): Prof. Dr. Luiz Alexandre Campos

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Aprovada em ____ de ____________ de _____.

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Aos meus pais e ao meu amor Alexandre eu dedico.

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“*O conhecimento deve ser compartilhado, trocado e colocado à disposição de todos*”.

Alexander Von Humboldt

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RESUMO

Cicadidae é uma família composta por insetos conhecidos popularmente como cigarras, caracterizados pelo som emitido pelos machos para atrair as fêmeas para cópula. A família é dividida em quatro subfamílias: Cicadinae, Cicadettinae, Tettigomyiinae e Tibicininae. Cicadettinae e Tettigomyiinae apresentam um grupo peculiar de cigarras caracterizadas pela asa anterior com aspecto de "folha", devido à coloração verde e a área apical da asa reticulada. Essas cigarras estão distribuídas em cinco gêneros de quatro tribos, Chlorocystini, Hemidictyini e Prasiini (Cicadettinae) e Lacetasini (Tettigomyiinae). Análises cladísticas já incluiram os gêneros dessas tribos exceto os dois classificados em Hemidictyini. Nós testamos a monofilia de Hemidictyini, sua relação com as outras três tribos e analisamos quantas vezes ocorreu o surgimento de asas com aspecto de folha dentro das linhagens. Também discutimos sobre a história biogeográfica de Chlorocystini, Hemidictyini e Prasiini com base em possíveis disjunções. Dentre as subfamílias de Cicadidae, Cicadinae é a mais diversa composta por 30 tribos com distribuição global e Fidicinini é a segunda tribo mais diversa da subfamília, com 25 gêneros e 221 espécies. No entanto, a sistemática e taxonomia dentre os gêneros de Fidicinini carecem de estudos minuciosos com adequado conhecimento das espécies tipo. A monofilia da tribo nunca foi testada e as estruturas das genitálias dos machos nunca foram comparadas com as das outras tribos de Cicadinae. Nós propusemos homologias primárias para testar a monofilia da tribo e avaliar as relações entre os gêneros. A ausência de terminologias para estruturas da genitália do macho em Cicadidae torna difícil a proposição de homologias consequentemente enfraquecendo a sistemática do grupo. Algumas estruturas foram observadas na theca e na vesica das espécies de Fidicinini. Através de microscopia eletrônica de varredura, foi possível determina-las como ornamentações que apresentavam diferentes formas e distribuição na vesica de cada espécie, sendo possível nomeá-las a partir dessas características. Observando como as estruturas de machos e fêmeas interagem durante a cópula, nós inferimos funções de "hook" e "grab" para essas ornamentações. Nós investigamos a presença ou ausência desses traços nas espécies de outras 17 tribos de Cicadinae e, a partir disso, foi realizada uma reconstrução de estado ancestral para a subfamília. A dinâmica de cópula de uma espécie de Cicadomorpha é descrita pela primeira vez.

PALAVRAS CHAVE: cigarras, filogenia, biogeografia, taxonomia, edeago, cornuti, ampola seminal, cópula.

ABSTRACT

Cicadidae is a family composed by insects popularly known as cicadas, characterized by the sound emitted by males to attract females for copula. The family is divided in four subfamilies: Cicadinae, Cicadettinae, Tettigomyiinae e Tibicininae. Cicadettinae and Tettigomyiinae present a peculiar group of cicadas characterized by the leaf-winged due to the green coloration and the apical area of forewings reticulated. These cicadas are distributed in five genera of four tribes, Chlorocystini, Hemidictyini e Prasiini (Cicadettinae) e Lacetasini (Tettigomyiinae). Cladistic analyses have been included the genera of these tribes except the two classified in Hemidictyini. We tested the monophyly of Hemidictyini, its relationship to the other three tribes, and analyzed how many times the leaf-winged arise within the lineages. We also discussed about the biogeographic history of Chlorocystini, Hemidictyini and Prasiini based on possible disjunctions. Among the subfamilies of Cicadidae, Cicadinae is the most diverse composed of 30 tribes with global distribution, and Fidicinini is the second most diverse tribe in the subfamily, with 25 genera and 221 species. However, the systematics and taxonomy among Fidicinini genera lack detailed studies with adequate knowledge of the type species. The monophyly of tribe has never been tested and the structures of the male genitalia have never been compared with those of the other tribes of Cicadinae. We proposed primary homologies to test the monophyly of the tribe and to evaluate the relationship between the genera. The absence of terminology for structures of the male genitalia in Cicadidae makes difficult the proposing of homologies consequently weakening the systematics of group. Some structures were observed in theca and vesica of species of Fidicinini. Through scanning electron microscopy, was possible to determine them as ornamentations with variable shapes and distribution in the vesica of species, and assign names based in these characteristics. We observed how the structures of males and females interact during copulation, and infered "hook" and "grab" functions for these ornaments. We investigated the presence or absence of these traits in the species of other 17 tribes of Cicadinae, and an ancestral state reconstruction was performed for the subfamily. The copulation dynamics of a cicadomorphan species is described for the first time.

KEYWORDS: cicadas, phylogeny, biogeography, taxonomy, aedeagus, cornuti, seminal ampoule, copula.

INTRODUÇÃO

Sistemática de Cicadidae

Hemiptera Linnaeus, 1758 é a mais diversa ordem de insetos hemimetábolos, dividida em quatro subordens representadas por percevejos (Heteroptera Linnaeus, 1758), cigarras e cigarrinhas (Auchenorrhyncha Duméril, 1806), cochonilhas e pulgões (Sternorrhyncha Amyot & Serville, 1843) e coleorrincos (Coleorrhyncha). A diversidade da ordem é relacionada à coevolução e radiação das angiospermas, além das inovações adaptativas apresentadas dentro de Heteroptera, como cabeça prognata e a diversidade de habitats e hábitos alimentares (Grimaldi & Engel 2005; Li *et al*. 2017).

Dentre as subordens de Hemiptera, Auchenorrhyncha é a segunda com maior número de espécies descritas, caracterizada pelo rostro emergindo da região posterior da cabeça, e dividida em duas infraordens, Cicadomorpha e Fulgoromorpha (Cavichioli & Takiya 2012). A posição filogenética dessas duas infraordens formando o grupo monofilético Auchenorrhyncha tem sido questionada ao longo dos anos (Forero 2008), com resultados baseados em evidência tanto morfológica quanto molecular que corroboram (Yoshizawa & Saigusa 2001; Urban & Cyran 2007; Cyran & Urban 2012; Yoshizawa *et al*. 2017) e refutam (Campbell *et al*. 1995; Misof *et al*. 2014; Li *et al*. 2017) a monofilia do grupo.

Cicadoidea é uma das três superfamílias de Cicadomorpha, composta por duas famílias: Tettigarctidae Distant, 1905 e Cicadidae Latreille, 1802, a primeira caracterizada pelo pronoto extremamente grande, ocultando grande parte do mesonoto, tímbalos presentes em machos e fêmeas e tímpanos ausentes em ambos os sexos, ao contrário dos cicadídeos que apresentam pronoto menor, não ocultando o mesonoto, tímbalos presentes apenas em machos e tímpanos presentes em ambos os sexos (Moulds 2005). Tettigarctidae é composta por duas espécies com distribuição apenas na Austrália, e Cicadidae distribuição global sendo composta por cerca de 2000 espécies (Moulds 2003; Sanborn 2013).

A sistemática geral de Cicadidae pode ser considerada em um estágio muito inicial quando comparada a outras famílias de Auchenorryncha, como Cicadellidae, Cercopidae e Membracidae (Dietrich *et al*. 2001; Dietrich *et al*. 2017; Krishnankutty *et al*. 2016; Paladini *et al*. 2014; Evangelista *et al*. 2017). Ao longo dos anos, tentativas de classificação de Cicadidae foram feitos por muitos autores, inclusive gerando certa confusão. Em 1905, Distant propôs uma subdivisão em três subfamílias: Cicadinae Latreille, 1802, Gaeaninae Distant, 1905 e Tibicininae Distant, 1905. Essa classificação se tornou a base para proposições dos grupos atualmente aceitos e foi embasada no desenvolvimento da cobertura timbálica de machos das espécies, sendo feita da seguinte forma: Cicadinae e Gaeaninae com cobertura timbálica presente, sendo que em Cicadinae oculta inteiramente o orifício do tímbalo e Gaeaninae com coberturas timbálicas expondo parcialmente os orifícios (Fig. 1A, B), e Tibicininae não apresentando cobertura timbálica (Fig. 1C, D) (Distant 1905; 1906). Em 1916, Van Duzze apresentou uma subdivisão de Cicadidae com o novo nome Tibiceninae, como substituição ao nome Cicadinae Distant, mudando Gaeaninae Distant para o nome Cicadinae (Van Duzze 1915), e mantendo Tibicininae Distant. A semelhança entre a grafia de Tibiceninae e Tibicininae provocou muitos erros na história taxonômica da família.

A primeira análise cladística de Cicadidae com uma ampla revisão de terminologias para a morfologia externa e interna do grupo foi publicada por Moulds (2005). Os resultados corroboraram Cicadoidea composta por Tettigarctidae e Cicadidae, ambas monofiléticas, e esta última dividida em três subfamílias: Cicadinae, Cidadettinae Buckton, 1889 e Tettigadinae Distant, 1905 (equivalente a Tibicininae, sensu Distant). Moulds (2005) propõe o abandono do nome Tibicininae em favor do próximo nome disponível dentro da subfamília, Tettigadinae, para representar um novo conceito para o grupo recuperado na filogenia e eliminar o histórico de erros taxonômicos associados a esse nome. No entanto, nenhum caso de supressão do nome Tibicininae foi apresentado à Comissão Internacional de Nomenclatura Zoológica e, portanto Tibicininae continuou em uso em trabalhos subsequentes (Sanborn 2013; Marshall *et al*. 2018).

Apesar de a análise cladística de Moulds (2005) ser de grande importância para a sistemática de Cicadidae por ser a primeira classificação proposta a partir de um método filogenético, tribos africanas e neotropicais não foram amostradas nessa análise. Para testar as relações propostas por Moulds (2005) incorporando os táxons faltantes dessas regiões, Marshall *et al*. (2018) realizaram uma filogenia baseada em dados moleculares. Os autores recuperaram novas relações entre as tribos, corroborando a classificação proposta por Moulds (2005) para as subfamílias e propondo uma nova subfamília formada por gêneros africanos, Tettigomyiinae Distant, 1905. Cicadidae ficou subdividida em quatro subfamílias: Cicadinae, Cicadettinae, Tettigomyiinae e Tibicininae (Marshall *et al*. 2018). Essa divisão foi baseada em caracteres de morfologia externa e de genitália e não apenas na cobertura timbálica dos machos. Inclusive grupos taxonômicos agrupados historicamente por caracteres relacionados às estruturas de produção de som foram fracamente suportados na análise molecular (Marshall *et al*. 2018), demonstrando que as mudanças morfológicas dessas estruturas podem ser resultado de convergência evolutiva e não ancestralidade comum.

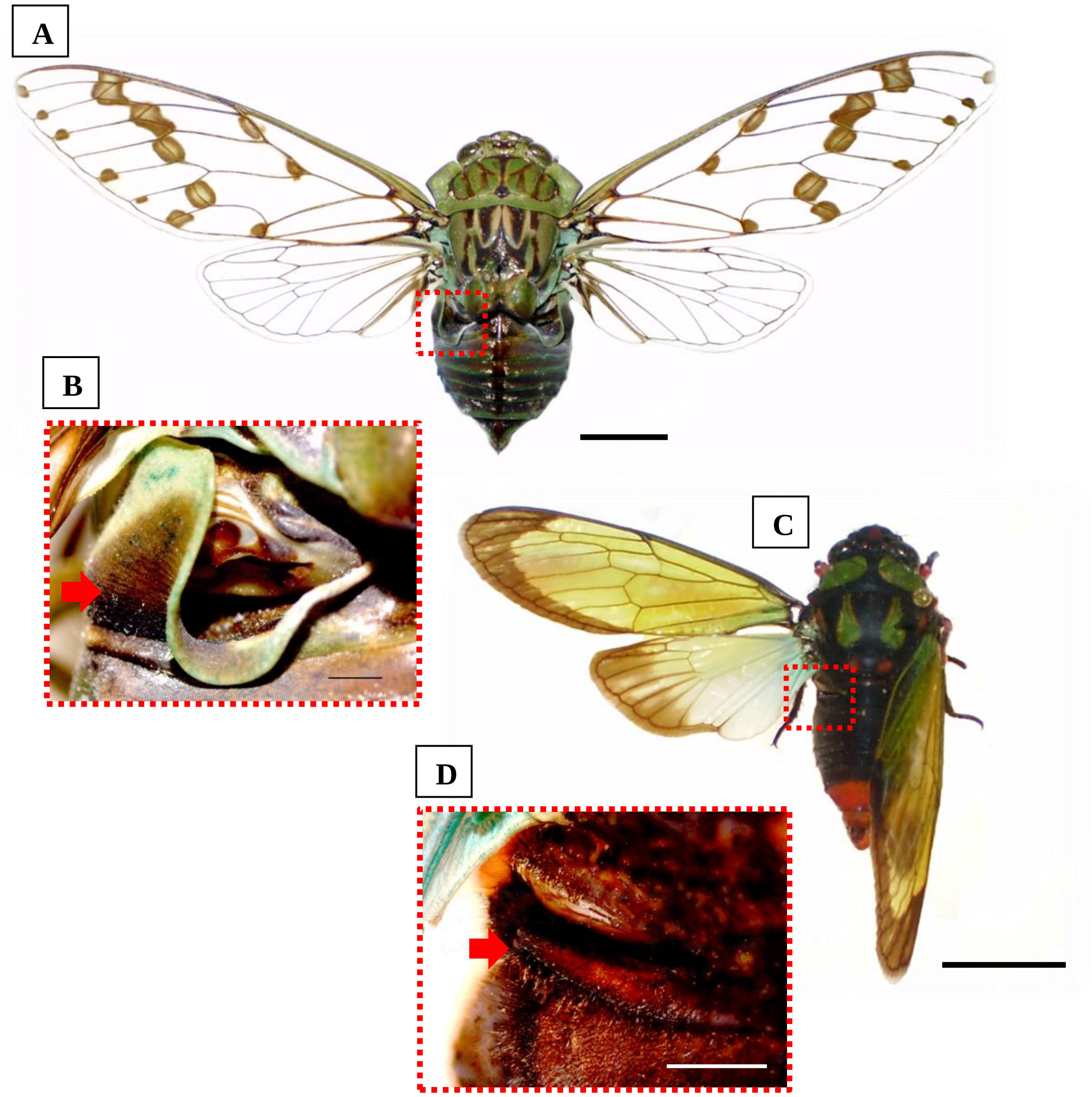

Figura 1. A. *Zammara tympanum* (Fabricius, 1803), macho em vista dorsal; **B.** Timbalo em vista latero-dorsal, a seta indica a cobertura timbálica; **C.** *Carineta diardi* (Guérin-Méneville, 1829), macho em vista dorsal; **D.** Tímbalo em vista latero-dorsal, a seta indica a ausência de cobertura timbálica. Escalas: A-B: 10 mm; B-C: 1 mm.

Fidicinini Distant, 1905 (Cicadinae) e Hemidictyini Distant, 1905 (Tettigomyiinae)

Cicadinae é a subfamília mais diversa composta por 30 tribos com distribuição global (Marshall *et al*. 2018). Dentre as tribos da subfamília, Fidicinini Distant, 1905 é a segunda mais diversa e representa cerca de metade da fauna do Brasil (Marshall *et al*. 2018; Ruschel & Carvalho 2019). A tribo foi descrita sobre o nome de "divisão" Fidicinaria dentro da antiga subfamília Gaeaninae sensu Distant (hoje Cicadinae), proposta para alocar gêneros neotropicais e com ocorrência no sul da região neártica, apresentando o orifício timpânico (sic) mais ou menos exposto (Distant 1905a; Distant 1914). Em Distant (1905), a tribo contemplava os gêneros *Ariasa* Distant, 1905; *Fidicina* Amyot & Serville, 1843; *Hemisciera* Amyot & Serville, 1843; *Majeorona* Distant, 1905; *Ollanta* Distant, 1905; *Pacarina* Distant, 1905; *Proarna* Stål, 1864; e *Tympanoterpes* Stål, 1861. Após Distant (1905), novos gêneros foram inseridos na tribo, tais como *Dorisia* Delétang, 1919 (modificada para *Dorisiana* por Metcalf, 1952), *Beameria* Davis, 1934, *Elassoneura* Torres, 1964, *Pompanonia* Boulard, 1982 e *Prasinosoma* Torres, 1963.

A primeira e única revisão da tribo foi realizada por Boulard & Martinelli (1996) com a proposição de três novos gêneros, *Bergalna*, *Fidicinoides* e *Guyalna*, apresentados em uma chave dicotômica que não contemplou todos os gêneros da tribo. Recentemente, *Cracenpsaltria* foi proposto por Sanborn (2018) como um novo gênero para a tribo. Infelizmente a sistemática e taxonomia dentre os gêneros da tribo carecem de estudos minuciosos com adequado conhecimento das espécies tipo. Além disso, tanto Fidicinini como outras tribos Neotropicais de Cicadidae necessitam de estudos taxonômicos e principalmente filogenéticos. Ao contrário destas, táxons com ocorrência na Austrália e Estados Unidos são amplamente abordados em estudos filogenéticos envolvendo análises morfológicas e moleculares (Lee & Hill 2010; Moulds 2005, 2012, 2014; Moulds & Hill 2015; Hill *et al*. 2015).

Hemidictyini é uma tribo que foi proposta por Distant (1905b) pra alocar nove gêneros, incluindo três com a característica de asas anteriores com aspecto de folha (*Cystosoma* Westwood, 1842, *Hemidictya* Burmeister, 1835, e *Hovana* Distant, 1905), devido às nervuras e à coloração esverdeada que elas apresentavam. Essa característica foi usada por Kato (1932) para propor que Hemidictyini fosse composta apenas por esses gêneros, e mais tarde por Moulds (1990) que acrescentou um gênero monotípico à tribo, *Cystopsaltria* Goding & Froggatt, 1904 com essa mesma característica. Destes quatro gêneros, o monotípico *Hemidictya* era o único com ocorrência no Brasil, sendo os demais na Austrália (*Cystosoma* e *Cystopsaltria*) e em Madagascar (*Hovana*). *Hemidictya frondosa* Burmeister, 1835 ficou conhecida no livro "Insetos do Brasil" de Costa Lima (1942) por ser apresentada como "uma bela cigarra de aspecto bizarro que lembra uma esperança ou um fulgorídeo".

Após a transferência de *Cystosoma* e *Cystopsaltria* para Chlorocystini Distant, 1905 em uma análise cladística que não amostrou *Hemidictya* e *Hovana* (Boer 1995), Hemidictyini ficou composta por esses dois gêneros cuja relação filogenética nunca foi testada com nenhum outro que apresentasse a característica de asa de folha. Além de *Cystosoma*, *Cystopsaltria*, *Hemidictya* e *Hovana*, o gênero *Lacetas* previamente classificado em Prasiini Matsumura, 1917 e com distribuição na África também apresenta esse aspecto peculiar. Após a proposição de uma tribo monotípica para *Lacetas* por Marshall *et al*. (2018) em Tettigomyiinae, diferente de Hemidictyini e Chlorocystini ainda classificadas em Cicadettinae, uma analíse cladística que analisasse conjuntamente essas quatro tribos Hemidictyini, Chlorocystini, Prasiini e Lacetasini tornou-se imprescindível para o entendimento das relações entre as espécies.

Cicadidae: ciclo de vida, comportamento sexual e hábito alimentar

Os insetos classificados em Cicadidae são chamados popularmente de cigarras conhecidos pelo som emitido pelos machos para atrair as fêmeas para cópula, um sinal acústico intraespecífico de longo alcance (Boulard 1977). Esse complexo mecanismo de comunicação sonora envolve várias estruturas como os tímbalos e os tímpanos. O som é realizado a partir de movimentos de contração e relaxamento de músculos ligados a uma membrana chamada tímbalo, localizada em ambos os lados do primeiro segmento abdominal dos machos. Sacos de ar revestidos por membranas localizados dentro do abdômen tem a função de ressonância para a frequência de vibração dos tímbalos que é alterada pela expansão do abdome através dos seus músculos laterais e pelo levantamento do mesmo fazendo com que aumente a abertura entre este e os opérculos. Os opérculos protegem os tímpanos e atuam na sincronização do som emitido. Os tímpanos são membranas delicadas situadas sob os opérculos entre o primeiro e o segundo esternitos e que funcionam como órgão auditivo nas cigarras, sendo mais desenvolvidos nas fêmeas (Pringle 1954; Moulds 2003). Os tímbalos podem se apresentar totalmente ou parcialmente cobertos por uma cobertura, chamada cobertura timbálica (Fig. 1A, B), cuja função ainda não foi explorada. Algumas cigarras apresentam a cobertura pouco desenvolvida, como uma borda parcialmente virada (Fig. 1C, D), ou a perda total da mesma (Marshall *et al*. 2018). Além disso, foi observada a perda total dos tímbalos em machos de alguns gêneros africanos (Boulard, 2012).

Estudos têm revelado comportamentos de pré e pós-cópula diferentes entre espécies de cigarras. O sinal acústico que caracteriza o comportamento pré-cópula pode ser realizado por vários machos de forma sincronizada a partir da formação de coros (*leks*) para atrair as fêmeas para esses locais. Os machos então procuram pelas fêmeas que sinalizam a reciprocidade com um bater de asas fazendo um dueto com o som do macho (Cooley & Marshall 2004). Esse comportamento é característico de algumas espécies de *Magicicada* Davis, 1905 que permanecem em cópula por um período longo quando comparado com outras espécies, cerca de três a quatro horas (Cooley, 1999). Após a cópula os machos inserem "plugs seminais" na abertura genital das fêmeas, formados de fluido seminal seco. Segundo Cooley (1999) a inserção dos "plugs" está mais relacionada a uma estratégia de garantia da paternidade do que a evitar que as fêmeas realizem outras cópulas com outros machos. Em outras espécies estudadas, como as dos gêneros *Okanagana* Distant, 1905, *Tibicen* Latreille, 1825 e *Diceroprocta* Stål, 1870, os machos realizam o sinal acústico isoladamente, com poucos machos por árvore, são as fêmeas que se aproximam dos machos, e não há inserção de "plug seminal" após a cópula (Cooley, 1999).

Enquanto poucos comportamentos pré e pós-cópula são conhecidos, nunca foi explorados quais e como as estruturas genitais de machos e fêmeas interagem durante a cópula. Apesar de terem sido observadas, essas estruturas genitais nunca foram nomeadas na literatura e suas funções permanecem desconhecidas.

O ciclo de vida das cigarras consiste de uma fase adulta muito mais breve em comparação com a fase ninfal. As fêmeas depositam os ovos em ramos vivos ou mortos (dependendo da espécie) que são cortados pelo seu ovipositor, muitas vezes em mais de uma fenda e em mais de um sítio de oviposição. Após cerca de 100 dias as ninfas descem ao solo onde escavam galerias subterrâneas e procuram as raízes para se alimentarem da seiva. Os cinco ínstares são realizados sob o solo, porém antes de realizarem a última ecdise as ninfas abandonam as galerias e sobem pelo primeiro suporte encontrado abandonando a sua última exúvia (Boulard 1965; Moulds 2003). A duração do ciclo de vida é conhecida somente para poucas espécies, sendo os casos mais extremos o das cigarras periódicas *Magicicada* spp. que apresentam períodos ninfais de 13 e 17 anos (Williams & Simon 1995). O período de vida adulta dura de duas a quatro semanas, porém a estimativa pode variar dependendo do hábitat de cada espécie, como gramíneas (três a quatro dias) e topos de árvores (oito semanas ou mais) (Moulds 2003).

Devido ao hábito alimentar fitófago apresentado pelas ninfas e pelos adultos, muitas espécies de cigarras são consideradas pragas no Brasil e em outros países do mundo. Há registros de danos causados por *Cicadatra persica* Kirkaldy, 1909 em plantações de maçã na Síria (Dardar *et al.* 2012), *Fidicina mannifera* (Fabricius, 1803) em erva-mate na Argentina (Pachas 1966), *Mogannia minuta* Matsumura, 1907 em cana-de-açúcar no Japão (Hayashi 1976) e *Amphipsalta zelandica* (Boisduval, 1835) em kiwi na Nova Zelândia (Logan *et al.* 2014). No Brasil muitas espécies são associadas ao cafeeiro nos estados de São Paulo, Minas Gerais, Goiás e Paraná (Fonseca & Araujo 1939; Martinelli & Zucchi 1997).

Estrutura da tese

No primeiro capítulo eu realizei uma análise cladística de Hemidictyini, Chlorocystini, Prasiini e Lacetasini para testar a monofilia de Hemidictyini, a relação entre as quatro tribos e se a característica de "asas de folha" teve uma ou múltiplas origens dentre dessas linhagens. Devido à interessante distribuição das quatro tribos e para detectar as possíveis disjunções que moldaram a distribuição das espécies eu desempenhei uma análise biogeográfica através do programa VIP que resultou em uma interessante interpretação de eventos de vicariância e dispersão.

No capítulo 2 eu realizei um profundo estudo morfológico dentre 18 tribos de Cicadinae com o objetivo de entender como algumas ornamentações presentes na genitália dos machos interagem durante a cópula, quais suas funções e a partir disso como evoluíram dentro da subfamília. Para a reconstrução de estado ancestral eu fiz duas análises, de parcimônia e de verossimilhança.

No capítulo três, eu realizei a primeira análise cladística de Fidicinini baseada em dados morfológicos e propus uma chave dicotômica e ilustrada para a identificação dos gêneros. A análise cladística foi feita através de busca heurística e pesagem

implícita. Homologias e definições para as estruturas de genitália masculina são determinadas. Novas combinações e sinonímias são propostas para algumas espécies da tribo.

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CAPÍTULO 1

Phylogeny and biogeography of the leaf-winged cicadas (Hemiptera, Auchenorrhyncha, Cicadidae)[1]

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Short running title: **Phylogeny of the leaf-winged cicadas**

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ABSTRACT

The leaf-winged cicadas include five genera classified in Chlorocystini, Hemidictyini and Prasiini (Cicadettinae). The tribe Hemidictyini has not previously been treated phylogenetically. We provide a hypothesis of relationships among Hemidictyini, Chlorocystini and Prasiini, and perform a biogeographical analysis to detect possible disjunctions that may have shaped the distribution of the species. Trees were calculated in TNT by heuristic searches using the implied weighting procedure, and the resulting strict consensus trees were compared using SPR distances. Biogeographical hypotheses are proposed for Hemidictyini, Chlorocystini and Prasiini on the most parsimonious tree**.** An expanded concept of Hemidictyini is proposed transferring *Lacetas*, *Iruana* and *Sapantanga* to the tribe. The remaining Prasiini and Chlorocystini are recovered as monophyletic. Hemidictyini is tentatively classified in Tettigomyiinae, with Lacetasini syn. nov. as a junior synonym. The VIP analysis resulted in 180 reconstructions with 10 disjunction nodes between the Ethiopian, Neotropical, Australian, and Oriental regions. A Gondwanan origin of the groups studied is contrary to the fossil evidence of Cicadidae, and more recent vicariant and dispersal events can explain the biogeographic evolution of the leaf-winged cicadas.

ADDITIONAL KEYWORDS: Chlorocystini – *Hemidictya* – Hemidictyini – *Hovana* – Lacetasini – *Lacetas* – Prasiini.

INTRODUCTION

Cicadidae is a widespread family occurring in all biogeographical regions with most of its 2000 species found in the tropics and subtropics (Moulds, 2003). This diverse fauna has been subject of several studies addressing its phylogeny and diversification (e.g. Moulds, 2005; Hill *et al*., 2015; Marshall *et al*., 2016; Marshall *et al*., 2018), but for the Neotropical cicadas modern taxonomic works and phylogenetic investigations are just starting to be made. The most recent classification (Marshall *et al*., 2018) subdivides Cicadidae in four subfamilies: Cicadinae Latreille, 1802, Cicadettinae Buckton, 1889, Tettigomyiinae Distant, 1905, and Tibicininae Distant, 1905 (= Tettigadinae). Cicadettinae is characterized by the uncus absent or very small and duck-bill shaped, clasper usually large and not spined, and the aedeagus restraint by claspers (Marshall *et al*., 2018). The leaf-winged cicadas include five genera classified in four tribes, being three of Cicadettinae, namely Chlorocystini Distant, 1905, Hemidictyini Distant, 1905, Prasiini Matsumura, 1917 (Sanborn, 2013), and Lacetasini Moulds & Marshall, 2018 (Tettigomyiinae; Marshall *et al*., 2018). These four tribes share morphological characteristics, such as the narrow head relative to pronotum, and a taxonomic history of genera being transferred among them.

Hemidictyini Distant, 1905 is one of the most remarkable tribes of Cicadettinae due to the distinctive appearance and distribution of species. The tribe currently contains two monotypic genera, *Hemidictya* Burmeister, 1835 (*Hemidictya frondosa* Burmeister, 1835) and *Hovana* Distant, 1905 (*Hovana distanti* (Brancsik, 1893)), described respectively from Brazil and Madagascar. Both species present green body, small size, and leaf-like forewings. Boulard (1985; 1997; 2007) documented and termed “phyllomorphy” this peculiar wing morphology, also observed in other cicadas, such as, in species of *Cystosoma* Westwood, 1842 and *Cystopsaltria* Goding & Froggatt, 1904 (Chlorocystini), and *Lacetas* Karsch, 1890 (Lacetasini).

Hemidictyini was proposed to include nine genera characterized by "the narrow head, which (including eyes) is about or scarcely more than half the width of mesonotum at base, and the abdomen of males more or less globose and usually longitudinally dorsally ridged" (Distant, 1905b: 275). In a comparative note about *Lacetas* Karsch, 1890, then classified in Tibiceninae, Distant (1905b) indicated the genus could belong to Hemidictyini, a classification adopted later (Distant, 1906). This classification of Hemidictyini with ten genera remained until the proposition of Prasiini by Matsumura (1917) to include *Prasia* Stål, 1863. Subsequently, Kato (1932) transferred to Prasiini all the other genera of Hemidictyini except *Cystosoma*, *Hemidictya* and *Hovana*. Hemidictyini remained with three genera until Moulds (1990) transferred the monotypic *Cystopsaltria* Goding & Froggatt, 1904 from Chlorocystini to Hemidictyini based on "the narrow head, inflated male abdomen, and reticulated tegmina" (p. 197) (Fig. 1).

Prasiini currently comprises nine genera distributed in the Oriental and Ethiopian regions, but only the "oriental Prasiini" (i.e. *Arfaka*, *Jacatra*, *Lembeja* and *Prasia*) have been proposed to form a monophyletic group (Boer, 1995a). Three genera (i.e. *Iruana* and *Lacetas*, both from Africa, and *Sapantanga* with unknown distribution) had their placement in Prasiini questioned (Jong, 1985; Moulds, 2005), and considered more closely related to Chlorocystini (Boer, 1995a). *Lacetas* was removed from Prasiini to former the tribe Lacetasini in Tettigomyiinae (Marshall *et al.*, 2018) (Fig. 1). For the three genera not included in the phylogenies by Boer (1995a) and Marshall *et al.* (2018), *Bafutalna*, *Mariekea* and *Murphyalna* (Boulard, 1993; Jong & Boer, 2004; Boulard, 2012), the first has been considered closely related to *Iruana* (Boulard, 1993), the second was proposed for the *harderi* group of *Lembeja* (Jong & Boer, 2004), and the third as closely related to *Bafutalna* by having vestigial timbals (Boulard, 1993; Boulard, 2012). Morphology of sound production characters as vestigial timbals, and the presence of timbal covers have been used in previous classifications of suprageneric groups in Cicadidae, but Marshall *et al*. (2018) argued that morphological changes of these structures may have resulted of evolutionary convergences rather from common ancestry.

Chlorocystini was proposed by Distant (1905a) to include 12 genera with characteristics very similar to Hemidictyini. The number of genera classified in Chlorocystini was increased to 20 by the time of publication of Metcalf's catalogue (1963) (Fig. 1). The monophyly of Chlorocystini was proposed and supported by an S-shaped aedeagus with winged lateral crests for 14 genera, including *Cystosoma* and *Cystopsaltria* transferred from Hemidictyini to Chlorocystini (Boer, 1995a). Currently 24 genera are placed in the tribe (Marshall *et al*., 2018) (Fig. 1), distributed mainly in the Oriental and Australian regions.

Moulds (2005; 2014) in a cladistic analysis of Cicadidae corroborated the monophyly of Chlorocystini, finding the tribe sister to Parnisini, and the clade Chlorocystini + Parnisini sister to Prasiini. A recent molecular phylogeny of Cicadidae recovered Prasiini sister to Chlorocystini, and Parnisini as not closely related to Chlorocystini or Prasiini (Marshall *et al*., 2018). However, none of the four phylogenetic analyses (Boer, 1995a; Moulds, 2005; 2014; Marshall *et al*., 2018) included the two currently remaining Hemidictyini (i.e. *Hemidictya* and *Hovana*) nor the Prasiini *Iruana* and *Sapantanga*, and therefore the relationships between Hemidictyini, Chlorocystini and Prasiini remain obscure.

Here we seek to determine how many time leaf-like wings have evolved independently (convergently) during cicada evolution. We also test the monophyly of Hemidictyini and its phylogenetic relationships with Chlorocystini, Lacetasini and Prasiini, and performed a biogeographical analysis to detect possible disjunctions that may have shaped the distribution of the species. The type species of *Hemidictya* and *Hovana* are redescribed and illustrated based on morphological characters including the yet undocumented genital morphology, the female of *H. frondosa* is described for the first time and a key is proposed to the tribe.

MATERIAL AND METHODS

TAXON SAMPLING

The material examined belong to the following collections: Natural History Museum – NHMUK (London, England), Australian Museum – AMS (Sydney, Australia), Illinois Natural History Survey – INHS (Champaign, USA), Universidade Federal do Paraná – DZUP (Curitiba, Brazil), and Universidade Federal de Minas Gerais – UFMG (Belo Horizonte, Brazil). Photographs of the type specimens of *Hemidictya frondosa*, *Lacetas annulicornis* and *L. longicollis* were provided by the Museum für Naturkunde – ZMHB (Berlin, Germany), and of *Hovana distanti* by the Hungarian Natural History Museum – HNHM (Budapest, Hungary).

The ingroup included *Hemidictya frondosa* and *Hovana distanti*, plus 16 species of Chlorocystini, two of Lacetasini and 12 species of Prasiini. For the outgroup we sampled, upon specimen availability, one species of Cicadettini, two species of Lamotialnini Boulard, 1976, two species of Parnisini and one species of Taphurini Distant, 1905. The outgroup was selected based on the taxonomic history and on the relationships between tribes proposed in the phylogenies of Cicadidae (Moulds, 2005; Marshall *et al.*, 2018). The species *Carineta diardi* (Guérin-Méneville, 1829)

(Carinetini) was selected for character polarization and rooting of trees, totaling 39 taxa in the analysis (Table 1).

MORPHOLOGY AND TAXONOMY

The morphological characters were observed, scored, measured, and illustrated using a stereoscopic microscope. The male genitalia were extracted with aid of forceps, heated in potassium hydroxide aqueous solution (10% KOH), and posteriorly washed in water. Genital pieces were conserved in micro vials filled with glycerin and attached to the specimen pin. Photographs were obtained with a Nikon AZ100M and stacked with the Nikon NIS–Elements Ar Microscope Imaging Software. Vectorized drawings were made on the photographs. The terminology of Moulds (2005) and Marshall *et al*. (2018) is adopted for morphological descriptions. The abbreviations used are as follows: aed, aedeagus; as, anal styles; bc, basal cell; bl, basal lobe of pygofer; cl, clasper; C, costal vein; CS, shelf-like of costal vein; clv, clavus; db, dorsal beak; dc, distal curvature; ds, distal shoulder; gx, gonocoxites; la, lateral angle of pronotal collar; lc, lateral crest; ll, lateral lobe of pronotum; mc, meracanthus; mc, medial cell; mc, median curvature; mes, mesonotum; met, metanotum; mg, median groove of pronotum; o, ovipositor; op, operculum; os, ovipositor sheath; pa, paranota; pc, proximal curvature; pl, paramedian lobe; pro, pronotum; pyg, pygofer; rc, radial cell; R+Sc, radius + subcostal veins; scl, scutellum; sp, spines; st, sternite; t, tergite; tc, tympanal cavity; th, theca; tim, timbal; u, ulnar cell; un, uncus; upl, upper lobe of pygofer; ve, vesica. Measurements (mean values) are given in millimeters for the following morphometric parameters: length of body, width of head including eyes, length of head, width of pronotum including pronotal collar, length of pronotum including pronotal collar, width of mesonotum, length of mesonotum, length of forewings, width of forewings, length of hindwings, and width of hindwings. For the type of *Hovana distanti* the measurements were made on photographs with the software IC Measure version 1.2.0.265. (2016). The species distributions were retrieved from the Cicadoidea catalogues of Metcalf (1963), Duffels & van der Laan (1985), and Sanborn (2013), and from the specimens' labels. New distribution records are indicated by an asterisk.

The criteria used for classifying the genera of Hemidictyini and Prasiini were the phylogenetic results represented by the recovered monophyletic groups and synapomorphies and, for the genera not sampled for the cladistic analysis (i.e. *Bafutalna* Boulard; *Murphyalna* Boulard; and *Mariekea* Jong & Boer), the morphological characters as available in the literature.

CLADISTIC ANALYSIS

The data matrix was made in the software Mesquite version 2.75 (Maddison & Maddison, 2001). The symbols "?" and "–" were used for missing and non-applicable data, respectively. The characters and character states were described following Sereno (2007), treated as discrete and unordered, and character polarization followed the outgroup method (Nixon & Carpenter, 1993). The cladistic analysis was performed using TNT v1.5 (Goloboff *et al*., 2008a) by heuristic searches using the implied weighting procedure proposed by Mirande (2009) as detailed by Garbelotto *et al.* (2013) with 11 K–values calculated for an average character fit ranging from 50 to 90% of a perfectly hierarchical character. A similarity matrix of Subtree Pruning Regrafting (SPR) distances of the consensus trees was constructed, and higher sums of SPR similarity were used as the criterion for choosing the trees (Garbelotto *et al*., 2013). The quantitative weighting of the characters has been defended as a reliable means of improving phylogenetic results (Farris, 1969; Goloboff, 1993, 2014; Goloboff *et al*., 2008b; Mirande, 2009), and the use of implied weighting against homoplasies in morphological data sets was demonstrated to improve measures of the quality and stability of trees (Goloboff *et al*., 2008b; Goloboff, 2014). The total fit was calculated for the consensus tree, and the fit and extra steps (homoplasy) were calculated for each character. The visualization of cladograms was performed in WinClada 1.00.08 (Nixon, 2002). For the most parsimonious cladogram relative Bremer support values (Goloboff & Farris, 2001) were calculated by tree bisection-reconnection, retaining suboptimal trees of 10 to 20 extra steps and a relative fit difference of 0.9. Jackknife absolute frequencies (Farris *et al*., 1996) with symmetric resampling were calculated with 33 of removal probability and 10000 replicates. We opted for using this particular Jackknife procedure for its more reliable behavior compared to other resampling methods in morphological data sets (Goloboff *et al*., 2003; Kopuchian & Ramírez, 2010).

BIOGEOGRAPHICAL ANALYSIS

The collection sites were retrieved only from specimen labels to ensure the reliability of species identifications, and geographically referenced using Global Gazetteer version 2.3 (2017) and Google Earth (2001) (Supplementary Material S1). The biogeographical hypotheses were proposed for Hemidictyini, Chlorocystini, and Prasiini on the most parsimonious topology resulting from the cladistic analysis. We could not include the Prasiini *Bafutalna* Boulard; *Murphyalna* Boulard; and *Mariekea* Jong & Boer; as well as five genera of Chlorocystini in our analyses as we could not obtain specimens, but the distributions of such genera is within the range of the genera analyzed (Supplementary Material S2). We also didn’t have samples of other 11 genera of Chlorocystini from Africa and South and Central Americas (genera with asterisk in S2); future studies including these genera may improve the knowledge about the biogeographical history of Chlorocystini. It is worthy to note that the tribal classification of 10 of these 11 genera known by the time was considered doubtful by Boer (1995a), and two of them (*Durangona* Distant, 1911 and *Nablistes* Karsh, 1891) were removed from Chlorocystini by Marshall *et al*. (2018) (Fig. 1).

The biogeographical analysis was conducted with the Vicariance Inference Program (VIP) (Arias, 2010) through an algorithm for spatial analysis of vicariance (Arias *et al*., 2011). We using a 0.5 x 0.5 grid with maximum fill of 1 (Von Neumann neighborhood), maximum overlapping of 10%, and a cost of distribution removal of 2. These parameters were chosen to minimize problems of lacking of distributional records, and to maximize vicariance (Arias, 2011). For the heuristic search we tested three different schemes: (1) 10000 iterations and 100 hold; (2) 5000 iterations and 100 hold; and (3) 5000 iterations and 10 hold. All analyses were made with full sector search, accept equals 50%, and a sector size of 8, as recommended by Arias (2011). We adopted the biogeographical regionalization of the world sensu Morrone (2015).

RESULTS

CHARACTERS

A total of 67 morphological characters, 48 out of these of general morphology of both sexes and 19 of male genitalia, were coded and included in a matrix (Table 1). Thirty nine characters are proposed for the first time in a phylogenetic framework and are indicated by an asterisk, the remaining 28 are reinterpreted from Boer (1995a) and Moulds (2005, 2012, 2014) as indicated in the following commented character list. Each character is followed by the values of the character fit and the extra steps in parentheses.

CHARACTER LIST

Head (characters 1–12)

1. *Eyes, lateral margin, relative to the lateral margin of head in dorsal view: (0) protruding (Figs. 2A-C, G, H); (1) not protruding (Figs. 2D-F). Note: When the lateral margin of eyes is protruding, the largest linear dimension of the eye is perpendicular to the longitudinal axis of the body. When the lateral margin is not protruding, the largest linear dimension of the eye is oblique to the longitudinal axis of the body. (0.00000; 0)

2. *Supra-antennal plate, width relative to the ocelli: (0) narrow (Figs. 2A, C, E-H); (1) wide (Figs. 2B, D). (0.54166; 6)

3. *Scape, length relative to pedicel: (0) subequal (Figs. 3A, B); (1) longer (twice the size) (Fig. 3D). (0.00000; 0)

4. Lateral ocelli, distance to each other compared to the distance between each lateral ocellus to the median one: (0) widely separated, distance between the lateral ocelli greater than between each lateral to the median (Figs. 2B-E, G); (1) closely spaced, distance between any two ocelli equal (Figs. 2A, F, H). Note: Equivalent to Boer's (1995a) characters 11 and 12. Similar to step 8 in Moulds’ (2005) key to the tribes of Australian Cicadinae. (0.16455; 1)

5. Vertex, width relative to the distance between lateral ocellus and eyes: (0) narrow, equal than diameter of ocellus (Figs. 2A, E, H); (1) wide, greater than diameter of ocellus (Figs. 2B-D, F, G). Note: Equivalent to step 132 in Moulds' (2012) key. (0.37143; 3)

6. *Vertex, lateral ocelli, in frontal view, height compared to median ocellus: (0) higher (Figs. 3A, D); (1) not higher (Figs. 3B, C). (0.16455; 2)

7. *Postclypeus, apex, length relative to vertex in dorsal view: (0) long (Fig. 2E); (1) equal (Figs. 2C, D, F-H); (2) short (Figs. 2A, B). (0.49618; 5)

8. Postclypeus, angle in lateral view: (0) obtuse (Fig. 3H); (1) right (Fig. 3G). Note: Equivalent to Boer's (1995a) character 5 and Moulds' (2005) character 3, but with different interpretation of states. (0.28261; 2)

9. Postclypeus, anterior margin in dorsal view, shape: (0) arched (Figs. 2A-C, F-H); (1) v-shaped (Figs. 2D, E). Note: Equivalent to Boer's (1995a) character 4, the anterior outline called “anterior edge”. (0. 28261; 2)

10. *Postclypeus, shape in ventral view: (0) oval (Fig. 3E) (1) rectangular (Fig. 3F). (0.00000; 0)

11. *Postclypeus, transverse grooves area, shape in frontal view: (0) convex (Figs. 3A, C); (1) flat (Fig. 3B); (2) projected in keel (Fig. 3D). (0.00000; 0)

12. Postclypeus, transverse groove, tumid processes: (0) absent (Figs. 3B, C); (1) present (Figs. 3A, D). Note: Equivalent to Boer's (1995a) character 7. (0. 28261; 2)

Thorax (characters 13–41)

13. *Pronotum, lateral lobe, width relative to paramedian lobe: (0) larger (Figs 2D-H); (1) subequal (Figs. 2A-C). Note: Here we adopted these terminologies for the lateral and paramedian lobes. (0.37143; 3)

14. Pronotum, pronotal lobes: (0) thick (Figs. 2A-C, F-H); (1) flat (Figs. 2D, E). Note: Equivalent to Boer's (1995a) character 13. (0.16455; 1)

15. Pronotum, median groove: (0) absent; (1) present (Figs. 2A-H). Note: Equivalent to Boer's (1995a) character 16. Here we adopted these terminologies for median groove. (0.00000; 0)

16. *Pronotum, median groove, shape: (0) wide and shallow (Figs. 2A, B, H); (1) narrow and deep (Figs. 2C-F); (2) narrow and shallow (Fig. 2G). (0.44067; 4)

17. *Pronotum, pronotal collar, paranota: (0) absent (Figs. 2A, B); (1) present (Figs. 2C-H). (0.37143; 3)

18. *Pronotum, lateral angle of pronotal collar, margin, shape: (0) round (Figures 2A-C, G, H); (1) truncate (Figs. 2D-F). (0.00000; 0)

19. Mesonotum, scutellum, shape: (0) cruciform (Fig. 4A); (1) sub rectangular (Fig. 4B); (2) sub triangular (Fig. 4C); (3) triangular (Fig. 4D). Note: Similar to Moulds' (2005) character 11. (0.00000; 0)

20. *Mesonotum, scutellum, lateral area, angle: (0) obtuse (Figs. 4A-C); (1) straight (Fig. 4D). (0.00000; 0)

21. *Mesonotum, scutellum, lateral area, width relative to the anterior projections: (0) wide (Figs. 4A, C); (1) narrow (Fig. 4B). Note: Inapplicable if the lateral area of scutellum is straight. (0.00000; 0)

22. *Metanotum, middle portion relative to scutellum: (0) not expanded (Fig. 5E); (1) expanded (Figs. 5D, F). (0.37143; 3)

23. Metapleura, operculum, size relative to tympanal cavity (males) in ventral view: (0) large, covering completely the tympanal cavity (Fig. 4E); (1) small, covering at least half of the tympanal cavity (Fig. 4F). Note: The operculum is considered small when the aperture of the tympanal cavity is left exposed in ventral view, and large when the aperture is completely covered, not allowing the visualization of timbal and tympanum. Moulds (2005, 2014) compared the development of operculum relative to the margin of the tympanal cavity (characters 38 and 13, respectivelly). (0. 37143; 3)

24. *Metapleura, operculum, posterior extension relative to sternite II (males): (0) reaching or almost reaching (Fig. 5B); (1) not reaching (Fig. 5A). (0. 37143; 3)

25. Metapleura, operculum, meracanthus, length relative to posterior margin of operculum (males): (0) shorter (Fig. 4E); (1) longer (Fig. 4F). Note: Equivalent to Boer's (1995a) character 43. (0.28261; 2)

26. *Metanotum, operculum, proportion: (0) longer than wide (Fig. 4F); (1) wider than long (Fig. 4E). (0.44067; 4)

27. Forewings, pigmentation: (0) pigmented, but translucent (Figs. 6A, J); (1) colorless (Figs. 6B, C, H, I); (2) semi opaque (Figs. 6D-G). Note: Equivalent to Boer's (1995a) character 24 and to Moulds' (2005) character 28. Boer (1995a) coded four states for the color of forewings, hyaline wings (1) opaque greenish or reddish (2) slightly reddish but still hyaline (3) and bronzed (4). The species of both *Cystopsaltria* and *Cystosoma* were coded by Boer (1995a) as opaque greenish or reddish. Moulds (2005) coded two character states, (0) hyaline; (1) maculated, tegmen-like, opaque, and considered both genera apomorphic. (0. 44067; 4)

28. Forewings, alternated paired spots along the margins of veins: (0) absent (Figs. 6B-J); (1) present (Fig. 6A). Note: Equivalent to Boer's (1995a) character 25. (0.00000; 0)

29. *Forewings, extension relative to ventral margin of abdomen in lateral view: (0) narrow, leaving the ventral margin of abdomen exposed (Figs. 20B, 21B); (1) wide, covering the whole abdomen (Figs. 13B, 16B). Note: Wide forewings hide the thoracic pleura and the abdomen in lateral view, and the wings touch each other ventrally. (0.00000; 0)

30. Forewings, distance of vein C to vein R+Sc: (0) contiguous (Fig.7A, B); (1) distant (Fig. 7C, D). Note: Equivalent to Boer's (1995a) character 29. (0.00000; 0)

31. *Forewings, vein C, expansion (shelf-like): (0) present (Figs. 7B, D, 8A, B); (1) absent. Note: Terminology "shelf-like" from Moulds (2012). (0.28261; 2)

32. *Forewings, vein C, width relative to R+Sc: (0) wide (Figs. 6A-F, H); (1) equal (Figs. 6G, I); (2) narrow (Fig. 6J). (0.16455; 1)

33. *Forewings, vein C, height relative to R+Sc: (0) higher; (1) equal. (0.28261; 2)

34. Forewing, vein RA, direction relative to vein Sc: (0) parallel (Figs. 6A, D-J); (1) divergent (Figs. 6B, C). Note: Veins RA and Sc were possibly considered by Boer (1995a) as the costal area of forewings (character 29), coded with the states "narrow to apex" (plesiomorphic) and "widening to apex" (apomorphic). Our interpretation and species coding are similar to that of Moulds (2005) for his character 23. (0.54166; 6)

35. Forewings, ulnar cell (u3), direction relative to medial cell (mc): (0) parallel (Figs. 6A, B); (1) angled (Figs. 6C-J). Note: Equivalent to Moulds' (2005, 2014) characters 18 and 4, respectivelly, but Moulds compared the position of the ulnar cell (u3) to the radial cell (rc). (0.49618; 5)

36. *Forewings, ulnar cell (u3) length relative to medial cell (mc): (0) subequal (Figs. 6A-D, F, I, J); (1) shorter (half the size) (Fig. 6E); (2) longer (twice the size) (Figs. 6G, H). (0.37143; 3)

37. Forewings, apical area: (0) not reticulated (Figs. 6A-C, H-J); (1) reticulated (Figs. 6D-G). Note: The cells forming the reticulated apical area are organized in a network shape. This character is equivalent to Boer's (1995a) character 27. (0.16455; 1)

38. Forewings, apical cells, number: (0) few, 8 to 10 (Figs. 6A, B, I, J); (1) many, twelve or more (Figs. 6C-H). Note: This character is similar to Boer's (1995a) character 30, to character 15 in Moulds (2005) and to character 1 in Moulds (2014). Boer (1995a) coded the species of *Cystosoma* and *Cystopsaltria* as having "more than twenty" cells, while Moulds (2005) coded them as with "multiple reticulation", and later (Moulds, 2014) considered the same genera as unknown or irrelevant for this character. We observed at least twelve cells in species of *Cystosoma*, *Cystopsaltria*, *Hemidictya*, and

Hovana, and we also found variation in the number of cells between the forewings in the same specimen. (0.28261; 2)

39. Forewings, subapical cells: (0) absent (Figs. 6A, B, H-J); (1) present (Figs. 6C-G). Note: Equivalent to Boer's (1995a) character 32 and to Moulds' (2005) character 16. Note: More than two subapical cells was the criterion for definition of presence (0. 28261; 2)

40. Forewings, marginal area: (0) present (Figs. 6B, C, J); (1) absent (Figs. 6A, D-I). Note: Equivalent to Boer's (1995a) character 28. (0.44067; 4)

41. *Forewings, ulnar cell (u2) position relative to ulnar cell (u3): (0) parallel (Figs. 6A, B, E, H); (1) angled (Figs. 6C, D, F, G, I, J). (0.49618; 5)

Male abdomen (characters 42–47)

42. Shape: (0) fusiform (Fig. 5G); (1) globose (Fig. 5H). Note: Fusiform abdomens clearly present a fold between the tergites and the sternites. Such a fold is absent in globose abdomens. This character is equivalent to Boer's (1995a) character 56, Moulds' (2014) character 15, and Moulds' (2005) character 40, the latter a homoplastic synapomorphy to Chlorocystini. (0.16455; 1)

43. *Tergite 1, posterior margin, shape: (0) convex (Figs. 5D, E); (1) straight (Fig. 5F). (0.37143; 2)

44. *Tergite 2, middle portion, length relative to timbal: (0) short, reaching the base of timbal (Figs. 5E, F); (1) long, reaching half of timbal (Fig. 5D). (0.16455; 1)

45. *Timbal, length relative to tergite 2: (0) equal (Fig. 5E); (1) longer (Figs. 5D, F). (0. 16455; 1)

46. *Sternite I, relative to metacoxa: (0) exposed (Figs. 5A, B); (1) covered (Fig. 5C). (0.49618; 5)

47. *Sternite II, anterior margin, median portion, shape: (0) arched (Fig. 5A); (1) nearly straight (Fig. 5B). (0.22857; 5)

Male genitalia (characters 48–67)

48. Uncus: (0) present (Figs. 9A, C, E, 10D); (1) absent (Figs. 10A-C, E, F). Note: Modified from Moulds’ (2005) character 63. (0.37143; 3)

49. Clasper: (0) absent (Figs. 9A, C, E); (1) present (Figs. 10A-F). Note: Modified from Moulds’ (2005) character 61. (0.44067; 4)

50. Claspers, apex: (0) distally parallel (Figs. 10A, C-F); (1) diverging towards their distal ends (Fig. 10B). Note: Equivalent to Moulds’ (2005) character 62 and to step 194 in Moulds' (2012) key. (0.37143; 3)

51. *Claspers, apex, direction: (0) anteriorly (Figs. 10A-F); (1) posteriorly (Figs. 14E, G, 22B, C). (0.00000; 0)

52. Pygofer, upper lobe: (0) present (Figs. 9E, 10A-E, 17C); (1) absent (Figs. 9A, C, 10F, 14E). Note: Equivalent to Moulds’ (2005) character 52. (0.28261; 2)

53. *Pygofer, secondary upper lobe: (0) absent; (1) present. (0.00000; 0)

54. *Pygofer, upper lobe, relative to anal styles: (0) short (Figs. 10A-C, E); (1) longer or the same length (Figs. 9E, 10D, 17C). (0.16455; 1)

55. Pygofer, basal lobe: (0) well-defined (Figs. 9A, C, 10F); (1) ill-defined (Figs. 10A-E). Note: Equivalent to Moulds’ (2005) character 58. (0.28261; 2)

56. Pygofer, dorsal beak: (0) absent (Figs. 9A, C); (1) present (Figs. 9E, 10A-F). Note: Equivalent to Moulds’ (2005) character 59. (0. 28261; 2)

57. *Aedeagus, spines: (0) absent (Figs. 10G-I); (1) present (Figs. 9B, D, F). (0.37143; 3)

58. *Aedeagus, apex, shape: (0) tubular (Figs. 10G, I); (1) bilobed (Figs. 9F, 10H). (0.44067; 4)

59. *Aedeagus, vesica: (0) exposed (Figs. 9B, D); (1) not exposed (Figs. 9F, 10G-I). (0.28261; 2)

60. *Aedeagus, proximal curvature: (0) present; (1) absent. (0.16455; 1)

61. *Aedeagus, proximal curvature, angle: (0) obtuse; (1) acute. (0.16455; 1)

62. *Aedeagus, median curvature: (0) absent (Figs. 9B, D, F); (1) present (Figs. 10G, I). Note: Boer (1995a) proposed an apomorphic state of the aedeagus as weakly S-shaped (character 132), recovered as a synapomorphy to Chlorocystini. We observed that not all species in the tribe fit this shape, so a new interpretation considering differences in their curvatures was necessary. Moulds (2005) interpreted this character similarly as Boer (1995a), also emerging as a synapomorphy to Chlorocystini (character 73). Moulds (2014) re-interpreted the states of this character and coded the species of Chlorocystini with the apomorphic state “S shaped or tending so” (character 19). (0. 16455; 2)

63. Aedeagus, distal curvature: (0) absent (Figs. 9B, D, F); (1) present (Figs. 10G, H). Note: Boer (1995a) coded as apomorphic for character 133 the apical part of aedeagus Z-curved. Possibly the author referred to the distal curvature. (0. 16455; 1)

64. *Aedeagus, lateral crest: (0) absent (Figs. 9B, D, F); (1) present (Figs. 10G, H). Note: Equivalent to Boer's (1995a) character 136. (0. 16455; 1)

65. *Aedeagus, lateral crest, shape: (1) short and projected (Fig. 10G); (2) long and low, not projected (Fig. 10H). Note: Equivalent to Boer's (1995a) character 138. (0.00000; 0)

66. *Aedeagus, conjunctival claw: (0) absent; (1) present. (0.00000; 0)

67. Theca, pseudoparameres: (0) absent; (1) present. Note: Aedeagal appendage process in Jong (1985). Equivalent to Moulds’ (2005) character 74. (0. 16455; 1)

CLADISTIC ANALYSIS

The higher sums of SPR similarity of consensus trees were obtained for the 7th *k*-value (*k*=5.077), resulting in two trees with 208 steps and total fit of 16.271585. The strict consensus tree is one step longer (Fig. 11).

The monophyly of Hemidictyini (clade A) was recovered including *Hemidictya frondosa*, *Hovana distanti*, three species of Prasiini, i.e. *Iruana rougeoti*, *I. sulcata*, and *Sapantanga nutans*, and two of Lacetasini, i.e. *Lacetas annulicornis*, *L. longicollis*, therefore, hence we propose classifying all these genera in Hemidictyini. Clade A is supported by one exclusive synapomorphy, though present only in *S. nutans* and *H. distanti*, the apex of claspers posteriorlly directed (51_1), and by three homoplastic synapomorphies: lateral ocelli not higher than median ocellus in frontal view (6_1), upper lobe of pygofer absent (52_1), and dorsal beak of pygofer absent (56_0). The two later homoplastic synapomorphies reverse in *Hovana distanti*; the first also evolves independently in *Venustria superba* (Chlorocystini).

The monophyly of clade B was recovered in all *k*-values, supported by two exclusive synapomorphies: lateral margin of eyes not protruding (1_1) and lateral angle of pronotal collar truncate (18_1); and by eight homoplastic synapomorphies. Clade B split in clade C (*Hemidictya* + *Hovana*) and D (*Lacetas* + *Iruana*). *Hovana distanti* and *Hemidictya frondosa* emerged as sister taxa (clade C) supported by four exclusive synapomorphies: scutellum triangular (19_3), lateral area of scutellum straight (20_1), forewings wide, covering the whole abdomen (29_1) and the veins C and R+Sc of forewings distant (30_1).

The monophyly of *Lacetas* + *Iruana* (clade D) was recovered in 72% of *k*-values and is supported by three homoplastic synapomorphies. The monophyly of *Lacetas* is recovered in all *k*-values and supported by two exclusive synapomorphies: scutellum sub rectangular (19_1) (only under delayed transformations character optimization) and lateral area of scutellum narrow (21_1).

The monophyly of *Iruana* is recovered in 72% of *k*-values, supported by two homoplastic synapomorphies: the posterior extension of operculum reaching or almost reaching the sternite II (24_0), and forewings pigmented, but translucent (27_0). The first is in parallelism with the *Prasia* clade and reverses in both the Hemidictyini + Prasiini clade and in clade N (24_1); the second reverses in the clade M (27_2).

Prasiini (clade E) is recovered monophyletic grouping the genera *Arfaka*, *Jacatra*, *Lembeja* and *Prasia*, and as sister group to Hemidictyini sensu novo. The Hemidictyini + Prasiini clade and the monophyly of Prasiini were recovered in all *k*-values. Hemidictyini + Prasiini is supported by four homoplastic synapomorphies: operculum small, covering at least half of the tympanal cavity (23_1), posterior extension of operculum not reaching the sternite II (24_1), meracanthus longer than posterior margin of operculum (25_1) and the upper lobe of pygofer reaching or longer than the anal styles (54_1). Among these, only character 24 is proposed for the first time. Character 54_1 is shared between Prasiini and *H. distanti*, the only species of Hemidictyini with upper lobe in pygofer. Prasiini sensu novo is supported by two exclusive synapomorphy: the scape longer, twice the pedicel size (3_1), and the postclypeus projected in keel (11_2); and by two homoplastic synapomorphies, lateral ocelli closely spaced (4_1) and a narrow vertex (5_0). The first is homoplastic with *Beaturia bicolorata* (clade J), and the second with *Lacetas* (Hemidictyini) and clade J in Chlorocystini.

Chlorocystini (clade H) is recovered monophyletic in 72% of *k*-values and sister to Prasiini sensu novo + Hemidictyini sensu novo in 81% of *k*-values. This relationship is supported by one exclusive and one homoplastic synapomorphy: postclypeus rectangular in ventral view (10_1); timbal longer than tergite 2 (45_1). The monophyly of

Chlorocystini is supported by four homoplastic synapomorphies: supra-antennal plate wide (2_1), apex of postclypeus short relative to vertex in dorsal view (7_2), vein RA divergent to vein Sc of forewings (34_1), and uncus absent (48_1).

BIOGEOGRAPHICAL ANALYSIS

All the VIP analyses resulted in 180 reconstructions, with 11 disjunction nodes and a cost of 16, the consensus reconstruction showed 10 disjunction nodes (A-J) (Fig. 12). One disjunction (node A) was recovered between Hemidictyini sensu novo (Ethiopian + Neotropical) and Prasiini sensu novo (Australian + Oriental). Disjunctions were recovered within the clade Hemidictyini in the Ethiopian region and between the Neotropical and the Ethiopian regions (nodes B and C).

Four disjunction nodes were recovered for the Prasiini in the Oriental and Australian regions: between Oriental Java in Indonesia (*Jacatra typica* in blue) and Sulawesi (Indonesia) + New Guinea (*Arfaka*, *Prasia* and *Lembeja* in red) (node D); between Sulawesi in Indonesia (*Prasia* in red) and New Guinea (*Arfaka fulva* in blue) (node E); between Northern Sulawesi in Indonesia (*L. elongata* and *L. minahassae* in red) + Papua in Indonesia (*L. robusta* in red) and Papua New Guinea (*L. papuensis* in blue) (node F); and between Northern Sulawesi (*Prasia princeps* in blue) and Occidental Sulawesi in Indonesia (*Prasia sarasinorum* in red) (node G).

Chlorocystini presents three disjunction nodes recovered in the Australian region. The first (node H) between New Guinea (*P. diodes*, *T. lanceola* and *T. globosa* in red) and Australia (*Chlorocysta suffusa* and *C. vitripennis* in blue); the second and the third within New Guinea (*Papuapsaltria diodes* in blue and *Thaumastopsaltria lanceola* and *T. globosa* in red) (node I); and *T. lanceola* in red and *T. globosa* in blue (node J).

DISCUSSION

CLADISTIC ANALYSIS

Hemidictyini sensu novo was recovered monophyletic in all *k*-values and split into *Sapantanga nutans* and clade B. Despite a great morphological differences from the other species of Hemidictyini, *S. nutans* has the male genitalia very similar to *H. frondosa*, mainly for the claspers' shape (Figs. 14E, G, 22B, C). Boer (1995a) presumed the type locality of *S. nutans* should be in South America, and considered it related to *Prosotettix* Jacobi, 1907 (Taphurini) and *Selymbria* Stål, 1861 (Selymbriini Moulds & Marshall, 2018, which was placed in the subfamily Tibicininae and not close to Taphurini). However, Walker (1850) reported unknown locality for *S. nutans,* and no country or collection site is recorded in the labels of the holotype (examined by TPR). Moreover, the species of Taphurini in our analysis was always recovered well outside the Hemidictyini clade, showing no close relationships with *S. nutans*.

The synapomorphies of *Hovana distanti* + *Hemidictya frondosa* (clade C) are also distinctive characteristics for both genera, except for the distance between veins C and R+Sc of forewings which is also found in *Tettigarcta* White, 1845 (Tettigarctidae) and in *Cyclochila* Amyot & Audinet-Serville, 1843 (Cicadinae). The male genitalia differs between *H. frondosa* and *H. distanti,* the first presenting claspers and lacking both the upper lobe and the dorsal beak of pygofer, and the second with uncus instead of claspers and presenting the upper lobe and the dorsal beak. We consider these characteristics distinctive enough to keep both species in separate genera.

Lacetas was recently placed by Marshall *et al*. (2018) after a molecular phylogeny in a new African subfamily Tettigomyiinae and so outside of Cicadettinae. We consistently recovered *Lacetas* in all analysis in the sister clade to *Hemidictya* + *Hovana*, and its classification proposed here reasserts former ideas by Distant (1905b) and Boer (1995a; 1997) about the possibility of including *Lacetas* in Hemidictyini. Boer (1995a) described “a strongly streamlined head and pronotum, with anterior margins of postclypeus and vertex lobes forming a nearly straight and almost continuous line with margin of the eyes and lateral edges of pronotum” as shared characteristics between *Lacetas*, *Hemidictya* and *Hovana*. These were coded here as characters 1_1 and 14_1, the first an exclusive synapomorphy of clade B, and the second resulting in ambiguous transformations but present only in *Hemidictya*, *Hovana* and *Lacetas*. *Iruana* was recovered as sister to the *Lacetas* clade (clade D), in line with early ideas on the proximity of these genera (Distant, 1905b).

Prasiini sensu novo groups *Arfaka*, *Jacatra*, *Lembeja* and *Prasia*, these genera form the “oriental Prasiini” sensu Boer (1995a). Prasiini was recovered monophyletic by Moulds (2005), but not by Boer (1995a) who proposed only the oriental Prasiini should form a monophyletic group sister to Chlorocystini. However, neither the Hemidictyini nor the Neotropical genera were included in Boer's analysis. Here Prasiini sensu novo is recovered sister to Hemidictyini sensu novo, whereas the clade Prasiini + Hemidictyini was recovered sister to Chlorocystini.

The monophyly of Chlorocystini was recovered in previous phylogenies supported by the forewings venation, the aedeagal basal plate short, and the “S-shaped” theca with winged lateral crests (Boer, 1995a; Moulds, 2005). We proposed four characters (60-63) referring to the curvatures of aedeagus (proximal, median and distal) rather than loosely characterizing the aedeagus as S-shaped. We also considered the presence and shape of the lateral crests in the aedeagus (64-65). The presence of both median and distal curvatures (that together correspond to the S-shaped aedeagus) is observed only in the sampled species of *Baeturia* and in *Gymnotympana rubricata* (clade J), rather than in all

Chlorocystini. Also, the lateral crests (64_1) are observed in the species of clade J and in *Chlorocysta*, but they are morphologically distinct between these groups (clade J: 65_1; *Chlorocysta*: 65_2).

In the recent phylogeny of Cicadidae by Marshall *et al*. (2018) ten African genera not included in the previous cladistic analysis by Moulds (2005) were sampled, resulting in three separate clades outside any of the three subfamilies of Cicadidae. Marshall *et al*. (2018) transferred those ten genera, along with all other African genera not sampled in their study, to a new subfamily Tettigomyiinae composed by four tribes, the new ones Lacetasini Moulds & Marshall (including only *Lacetas*) and Malagasini Moulds & Marshall, and the Tettigomyiini and Ydiellini that were previously part of Cicadettinae. Marshall *et al*. pointed out that their concept of Tettigomyiinae and its tribes may change after a thorough review of all African genera and their inclusion in phylogenetic studies. Among the genera not sampled by Marshall *et al*. (2018) are the Hemidictyini *Hovana* (African) and *Hemidictya* (South American), and the former Prasiini *Iruana* (African), all of them were recovered in our analysis within the clade including *Lacetas* (African) and *Sapantanga* (unknown distribution). *Lacetas* has been already considered as taxonomically related to *Hovana* and *Hemidictya* (Distant, 1905b; Boer, 1995a, 1997; Moulds, 2005), whereas *Iruana* was cited by the same authors as not related to Prasiini. In the classification proposed by Marshall *et al*. (2018) Hemidictyini sensu stricto (i.e. including only *Hovana* and *Hemidictya*), and Prasiini (including *Iruana* and *Sapantanga*) are still classified in Cicadettinae. Future studies including molecular samples of all these genera here classified in Hemidictyini sensu novo may unravel their phylogenetic placement relative to the clades of Tettigomyiinae.

We recovered a monophyletic Chlorocystini as did Marshall *et al*. (2018), however with diverse sister-group relationships. In the phylogeny by Marshall *et al*. Chlorocystini is sister to Prasiini, represented in their study only by one species of *Lembeja*, whereas we found Chlorocystini sister to Prasiini+ Hemidictyini, the later including *Lacetas*. We also recovered *Parnisa* (Parnisini) as not closely related to Chlorocystini or Prasiini, and the former Taphurini *Abroma* as not closely related to *Taphura*. Although Parnisini and Taphurini were part of the outgroup in the present study, our results are partially in accordance with Marshall *et al*., particularly regarding the classification of *Abroma* outside Taphurini. The relationships between Chlorocystini, Prasiini and Hemidictyini are well supported in our analysis.

We sampled species from a large number of genera in three tribes historically treated as related (Distant, 1905a; 1905b; Kato, 1932; Moulds, 1990; Boer, 1995a), i.e. Chlorocystini, Prasiini and Hemidictyini, the latter included for the first time in a phylogenetic study. The Hemidictyini *Hovana* and *Hemidictya* share the forewing veins C and R+Sc widely separated, a characteristic listed by Marshall *et al*. (2018) as diagnostic for the new tribe Lacetasini. After examining several specimens and photographs of the holotypes of two species of *Lacetas*, including the type species *L. annulicornis* Karsch, 1890, we can confirm the forewing veins C and R+Sc in *Lacetas* are contiguous, not widely separated as considered by Marshall *et al*. (2018) (as in Fig. 7A, B).

Since *Lacetas* was recovered within the Hemidictyini sensu novo clade in our analysis, we also evaluated the eleven characteristics listed by Marshall *et al*. for Tettigomyiinae to determine if the Hemidictyini fit in this subfamily. Five out of the eleven characteristics are also present in Cicadetiinae, and the remaining six listed as diagnostic of Tettigomyiinae are found in different combinations in the genera of Hemidictyini sensu novo. The metanotum is covered in the midline in *Lacetas* (Figs. 20A, 21A), *Hemidictya* (Fig. 14A), *Hovana* (Fig. 17A), *Iruana rougeoti* (Fig. 18A) and

Iruana sulcata (Fig. 19A) (but not in *Sapantanga nutans*, Fig. 22A); the pygofer with the distal shoulder well developed and lacking the upper lobe is observed in all genera except *Hovana* (Figs. 16C, 17C); the uncus long, directed distally and not retractable within the pygofer as well the absence of claspers are characteristics of *Hovana* (Figs. 16C, 17C), *Lacetas* (Figs. 9A, C, 20C, 21C, D), and *Iruana* (Figs. 18B, C, 19B, C); and the aedeagal restraint before or below the uncus is present only in the Hemidictyini having a developed uncus (i.e., *Hovana*, *Iruana* and *Lacetas*). Regarding the diagnostic characteristics of Cicadettinae, the metanotum is exposed in the midline in *Sapantanga nutans* (Fig. 22A); the pygofer with distal shoulder undeveloped and with upper lobe is present in *Hovana* (Fig. 17C); and the uncus is absent in *Hemidictya* and *Sapantanga*, however contrary to the putative autapomorphy of Cicadettinae sensu Marshall *et al*. (2018) the aedeagus is not restrained by the claspers in these two genera (Figs. 14E, 22B, C).

The Hemidictyni sensu novo clade is supported by synapomorphies considered diagnostic of either Cicadettinae (character 51_1) or Tettigomyiinae (character 52_1), thus the tribe's classification remains uncertain, demanding for the acquisition of more evidence such as molecular data not only for Hemidictyni sensu novo (i.e., *Hemidictya*, *Hovana*, *Iruana* and *Sapantanga*) but also of Prasiini (e.g., *Arfaka*, *Jacatra* and *Prasia*). Because our results are partially conflicting with those in Marshall *et al*. (2018) regarding the phylogenetic placement of *Lacetas* and the classification of the remaining genera of Hemidictyini sensu novo, we propose provisionally transferring Hemidictyini to Tettygominae and considering Lacetasini a junior synonym of Hemidictyini.

CLASPERS AND UNCUS

The presence or absence of claspers and uncus have been considered key characteristics grouping taxa in Cicadidae. Notwithstanding this importance some suprageneric taxa are variable regarding the presence of uncus and claspers between the containing genera (i.e., in Cicadettinae the uncus is absent or small; in Cicadinae the claspers are absent except in some Dundubiini (Marshall *et al*., 2018). We found the presence of uncus and claspers variable in Hemidictyini sensu novo. According to Moulds (2005), the uncus is a process originating adjacent to the median portion of the anal tube (10th segment) and may diverge into two arms, the uncal lobes. On the other hand the claspers are a pair of processes originating from below the uncus, on the basal part of the 10th segment. The absence of a "medial uncal lobe" (here 48_1) was considered by Boer (1995a) to separate "*Baeturia* and related genera complex" in the Chlorocystini from other tribes of Cicadettinae (Tibicinidae sic Boer 1995a), and it would also be absent or strongly reduced in the "oriental Prasiini". Moulds (2005) also considered the uncus absent in Prasiini and in Taphurini, though described its presence earlier in *Abroma guerinii* (a former Taphurini) (Moulds, 2003).

We coded two characters for the presence of uncus and claspers. We found claspers but no uncus in Chlorocystini; both uncus and claspers together in Prasiini sensu novo; and either uncus or claspers in Hemidictyini sensu novo. The short lateral processes observed in the uncus were considered here as lateral branches of uncus. According to Boer (1995a) and Marshall *et al*. (2018), the median lobe of uncus (medial uncus lobe sic Moulds 2005) is absent in *Abroma*, however we considered the uncus present following Moulds (2003). Boer (1995a) also considered Chlorocystini the only group in Cicadettinae (Tibicinidae sic Boer, 1995a) lacking the uncus, though we observed them also in Parnisini (*Parnisa*) and Hemidictyini (*S. nutans* and *H. frondosa*). We observed a strongly reduced uncus in the Prasiini *Lembeja* and *Prasia* as reported by Jong (1985, 1986, 1987) and Boer (1995a) contrary to Moulds (2005, 2012) and Marshall *et al*. (2018) who considered the uncus absent in these genera. Due this disagreement about the definition of claspers and uncal lobes, a morphological study addressing the origins of these processes would be valuable.

MORPHOLOGY OF THE FOREWINGS

The apical area of forewings reticulated, together with the narrow head and inflated male abdomen was used by Moulds (1990) to transfer *Cystopsaltria immaculata* to Hemidictyini. We gave attention to the morphology of the forewings (characters 27 to 41) so variation in veins and cells, color, and the peculiar reticulated apical area were properly evaluated in a phylogenetic perspective. The character 30 refers to the distance between veins C and R+Sc, being distant only in *Hemidictya* and *Hovana* (Fig. 7C, D). Character 34 refers to the direction of RA relative to SC, divergent in the same species considered by Boer (1995a) as with “costal area widening to apex”, i.e. *Gymnotympana rufa*, *G. varicolor*, *Chlorocysta vitripennis*, *C. suffusa* and *Glaucopsaltria viridis*. The character 31 refers to the expansion of vein C, considered by Moulds (2012) as a very wide sclerotized area (shelf-like) anterior to costal vein (Fig. 8A). Through the dissection of a costal vein we observed this sclerotized area is indeed an expansion of the costal vein rather a separate sclerotization (Fig. 8B). The vein C is not expanded only in *H. distanti*, *S. nutans* and clade P (31_1).

Boer (1995a) coded in his analysis the color and vein reticulation of the forewings (Boer’s characters 24 and 27, respectively), finding the forewings “apically pointed” (character 26) and with “venation reticulated” synapomorphic to the *Cystopsaltria* – *Cystosoma* clade. Boer (1997) deemed the opaque and reticulate forewings shared characteristics between *Cystopsaltria*, *Cystosoma*, *Hemidictya* and *Hovana* but that it would be "difficult regarded a synapomorphy due to variation of reticulation in the four genera" (Boer, 1997). Boer (1997) did not include the species of Hemidictyini in his analysis and argued that "the male genitalia of *Hemidictya frondosa* do not suggest relationship to Chlorocystini". Indeed forewings with apical area reticulated (37_1) are homoplastic between clades M and C. The same occurs between clades M and B for the semi opaque forewings (27_2) when accelerated transformations character optimization is applied. Our results support the hypothesis that leaf-like wings are an adaptive characteristic of these groups of cicadas.

BIOGEOGRAPHY OF HEMIDICTYINI, CHLOROCYSTINI AND PRASIINI

Disjunct distributions can be explained either by vicariant events or by dispersal across a pre-existing barrier. Vicariance hypotheses can be tested by concordance between the phylogenetic and distribution patterns of different taxa, but dispersal through barriers are explanations difficult to test with current methods, since it can be temporary and cause different effects on different species (Morrone & Crici, 1995; Ronquist, 1997; Samartín & Ronquist, 2004). The knowledge about the distribution of lands in geological times, the variation of the spacing between them, and the characteristics of taxa are important for the inference of biogeographic hypotheses. Cicadas are known to present poor colonization ability and to be less dispersive compared to other insects due their large size, low flight activity and a long subterranean nymphal stage contrasting to a short adult life (Duffels, 1983, 1986).

The current distribution of Hemidictyini, Chlorocystini and Prasiini would point to a possible Gondwanan origin. Biogeographical studies on insects with similar distribution suggest a Gondwanan vicariance (Popham, 2000; Liu *et al.*, 2015), or transoceanic dispersal events (Fuller *et al*., 2005; Forthman & Weirauch, 2016) considering the time of origin of the taxa. Recent studies of the tribe Cicadettini in the southern hemisphere using molecular clock dating methods supported the diversification and continual radiation of subclades of Cicadettini in the late Cenozoic during the Oligocene, Miocene, Pliocene and Pleistocene (following the opening of the Drake Passage and the glaciation of Antartica, in concert with the aridification of the Southern Hemisphere (Marshall *et al*., 2008; Owen *et al*., 2015; Marshall *et al*., 2016). Colonization of New Zealand by long-distance dispersal rather than an originally hypothesized Gondwanan origin was strongly supported with possible invasion routes into New Zealand from Australia and New Caledonia in the mid Miocene (Arensburger *et al*., 2004; Buckley & Simon, 2007; Marshall *et al*., 2008; Hill *et al*., 2009; Marshall *et al*., 2012; Owen *et al*., 2015a). The molecular phylogeny of Marshall *et al*. (2016) also strongly supported the later spread world-wide of members of the tribe Cicadettini in two waves by long distance dispersal through the Palearctic, Ethiopian and Nearctic regions starting in the early to mid Miocene. On the other hand, studies employing methods of cladistic biogeography on the Oriental Chlorocystini, Prasiini and Cosmopsaltriina (Indo-Pacific sic Duffels, 1986; West-Pacific sic Boer, 1995b) suggest a vicariance evolution caused by the fragmentation of West- and South-West Pacific island arcs and a possible Gondwanan origin (Duffels, 1983, 1986; Boer, 1995b; Boer & Duffels, 1996). The high rate of endemism of cicadas in the Oriental region is mainly attributed to the geotectonic history of the area and the poor dispersal abilities of cicadas (Boer & Duffels, 1996). However, a Gondwanan origin (Mesozoic) of these subgroups of cicadas is contrary to the fossil evidence that point to a more recent origin of Cicadidae. Thirthy two fossils are dated from the Cenozoic era (65Myr), most of them classified in extant tribes in the family, and only one (*Burmacicada protera* Poinar & Kritsky, 2011) from the Late

Cretaceous in the Mesozoic (99 Myr) (Cooper, 1941; Kaulfuss & Moulds, 2015; Moulds, 2018), whose familial classification has been put into question since it is represented by a first instar nymph that could actually belong to Tettigarctidae (Moulds, 2018). Thus, the origin of Cicadidae in the Mesozoic is doubtful. Unfortunately the identification of these fossils is based mainly in isolated wings leading to a doubtful placement in the classification and to difficulties in dating the origin of the family (Grimaldi & Engel, 2005).

The Gondwanan continent had the first rifting with the opening of a narrow ocean between Africa and Antarctica, Madagascar, India and Australia (~160 Myr). Africa and South America begin separation from the eastward moving India-Australia-Antarctica (~140 Myr) both in the Mesozoic (Boer, 1995b; Yoder & Nowack, 2006). The disjunction nodes A (between Hemidictyini and Prasiini), B and C (both within Hemidictyini) could be associated to the vicariant events separating the Ethiopian and Oriental regions, continental Ethiopian and Madagascar, and the Ethiopian and Neotropical regions. However to assume a Gondwanan vicariance to Hemidictyini and Prasiini would be inferring a possible origin of Cicadidae from 60 million years before its oldest known fossil, so we sought alternative explanations.

Several hypotheses describing putative dispersal routes between the biogeographical regions originated from Gondwana have been proposed. According to Yoder & Nowack (2006) there was an interval of perhaps 20 million years when the exchange of fauna between western and eastern Gondwana was kept. During the drift until the current position of the continents the existence of terrestrial connections among these landmasses is suggested, as the Gunnerus Ridge (Late Cretaceous, ~85 Myr), that may have been a potential dispersal route between Madagascar and South America via Antarctica (Rage 2003). The existence of discontinuous dispersal routes from the Late

Cretaceous to the earliest Cenozoic between Africa and South America through land connection or series of islands acting as stepping stones, and a trans-Atlantic passage have been proposed to explain the occurrence of fossil pollen, and crocodilian, and living groups as primates, rodents and reptiles in both continents (Morley, 2003; Sereno *et al*., 2004; Poux *et al*., 2006; Vidal *et al*., 2008). Likewise, hypotheses about possible dispersal events from the Ethiopian to the Oriental region before the subcontinent of India joined Asia at 45 Myr are defended, occurring between Madagascar and Asia through India and Seychelles and Mascarenes Plateaus in the Late Cretaceous, and through the contact of northeastern India with western Indonesia and subsequently Sumatra in the Late Paleocene (Rage, 2003; Ali & Aitchison, 2008; Warren *et al*., 2010). Another dispersal hypothesis considers the steppingstones of Seychelles, the Comores, and the Chagos archipelagos between Africa and Indonesia, and the channel opened by the collision between the Afro-Arabian plate and Asia in the Miocene (Li *et al*., 2009; Warren *et al*., 2003).

Despite a possible Gondwanan origin of Cicadidae defended by Duffels (1983, 1986), Boer (1995b), and Boer & Duffels (1996), the many dispersal hypotheses described may explain the disjunction nodes A, B and C. Following such hypotheses a possible scenario is the divergence between Hemidictyini, Chlorocystini, and Prasiini in Africa (node A) with posterior dispersals to the Oriental and Australian regions, though preceding the oldest known Cenozoic fossil of Cicadidae about 25 to 30 My in the Late Cretaceous. The disjunctions recovered in Hemidictiyni (nodes B and C) separating South America and Madagascar from continental Africa are consistent with proposed dispersal routes for mammals and lizards between South America and Madagascar through Antarctica during the Late Cretaceous (Rage, 2003).

The disjunction nodes D to G (Prasiini) and H to J (Chlorocystini) are related with islands in southeastern Asia, i.e. Sulawesi, Java and New Guinea. These islands consist of fragments of multiple geologic origins and are considered areas of endemism (Duffels, 1986; Boer & Duffels, 1996; Hall, 2002; Turner *et al*., 2001). The geological evolution of southeastern Asia is complex, involving collisions between several ocean plates (Pacific, Indian, Philippine) and land plates (Eurasian, Indian, Australian) in the Cenozoic (~50 Myr), although this process may have started in the early Paleozoic (~400 Myr). This region is a mosaic of microplates and numerous fragments from the margins of Australia, Sundaland, and Asia (Hall, 2002; Turner *et al*., 2001). The biogeographical history of the west-pacific cicadas (i.e. Cosmopsaltriaria, Chlorocystini and Prasiini) was accounted to vicariant and dispersal events after a possible Gondwanan origin (Duffels, 1983, 1986; Boer, 1995b; Boer & Duffels, 1996). However, whether the vicariant explanation requires extending the origin of cicadas well before the oldest known fossil, dispersalist explanations occurring in the Cenozoic are consistently found for several taxa distributed in southeast Asia (Emerson *et al*., 2000; Karns *et al*., 2000; Blackburn *et al*., 2010; Thomas *et al*., 2012; Schutze *et al*., 2012).

Almost all cicadas found in Sulawesi, an island in the center of the Indo-Australian Archipelago, are endemic and some even restricted to only part of the island. The origin of endemic taxa in Sulawesi is controversial, supported either by dispersal events across the Wallace line or vicariance between Asia and Australia (Stelbrink *et al*., 2012). Vicariance has been used to explain disjunctions in Sulawesi to monkeys and toads, considering Sulawesi was formed from a past archipelago (Evans *et al*., 2003). However, according to Stelbrink *et al*. (2012) the island was predominantly colonized by dispersal, and speciation inside Sulawesi would have not occurred before the

Miocene. Following the dispersal hypothesis the invasion of Sulawesi by the ancestral Prasiini from the Oriental region may be dated between the Late Cretaceous and Miocene.

The disjunction recovered between Java and Sulawesi + New Guinea (node D) can be explained following the reconstruction proposed by Hall (2002), with west Sulawesi more related to Java, and southeast Sulawesi more related to New Guinea. The split between *Jacatra typica* and the remainder taxa in clade D may be linked to a vicariant event between Java and west Sulawesi in the early Eocene about 55 Myr. The subsequent drift of west Sulawesi closing to the other current parts of the island and to New Guinea may have allowed to dispersals followed by speciation corresponding to disjunctions E, F and G, between 30 Myr and 5 Myr. We found disjunction E between *Arfaka fulva* (New Guinea) and *Prasia* (Sulawesi), disjunction G within *Prasia* separating west and northeast Sulawesi, and disjunction F within *Lembeja* in New Guinea and Sulawesi. New Guinea is more related to north and northeast Sulawesi, while south New Guinea and the Bird’s Head region are associated to the Australian continental margin (Hall, 2002). Additionaly, north Sulawesi coincides with the multiple tectonic origins of both islands and is better explained by dispersal events from Sulawesi. Similar conclusions favouring dispersal were postulated by Boer (1995b) for Cosmopsaltriaria, Prasiini and Chlorocystini.

The first disjunction within Chlorocystini (node H), between the species of *Chlorocysta* distributed on the east coast of Australia and *Papuapsaltria* + *Thaumastopsaltria* in New Guinea, match the vicariant event separating the northern margin of Australia from south New Guinea from Late Triassic to Late Jurassic (200 – 150 Myr) (Audley-Charles *et al.*, 1988). Posterior dispersal in New Guinea (disjunctions I and J) are consistent with the fragmented origin of the island as already discussed.

Despite the low dispersal abilities attributed to cicadas, this was possibly the most common process driving the biogeographic evolution of the leaf-winged cicadas, since vicariant events are much older than the documented origin of Cicadidae. Our conclusions are compatible with an origin of Cicadidae between the Paleocene (Cenozoic) to the Late Cretaceous (Mesozoic).

TAXONOMY

FAMILY CICADIDAE LATREILLE, 1802
SUBFAMILY TETTIGOMYIINAE DISTANT, 1905
TRIBE HEMIDICTYINI DISTANT, 1905

Hemidictyini Distant, 1905: 275.

Synonyms: Lacetasini Moulds & Marshall, 2018: 49. **syn. nov.**

Type genus: Hemidictya Burmeister (type species *Hemidictya frondosa* Burmeister).

Included genera: Bafutalna Boulard, 1993; *Hemidictya* Burmeister, 1835; *Hovana* Distant, 1905; *Iruana* Distant, 1905; *Lacetas* Karsch, 1890; *Murphyalna* Boulard, 2012; and *Sapantanga* Distant, 1905.

Included species: Bafutalna mirei Boulard, 1993; *Hemidictya frondosa* Burmeister, 1835 (Figs. 13A, B); *Hovana distanti* (Brancsik, 1893) (Figs. 16A, B); *Iruana brignolii* Boulard, 1982; *I. meruana* Boulard, 1990; *I. rougeoti* Boulard, 1975 (Fig. 18A); *I. sulcata* Distant, 1905 (Fig. 19A); *Lacetas annulicornis* Karsch, 1890 (Fig. 20A-D); *L. breviceps* Schumacher, 1912; *L. jacobii* Schumacher, 1912; *L. longicollis* Schumacher, 1912 (Fig. 21A-E); *Murphyalna mughessensis* Boulard, 2012; *Sapantanga nutans* Distant, 1905 (Fig. 22A-C).

Diagnosis: Head with supra-antennal plate meeting eye; eyes not protruding laterally (except in *Sapantanga*); supra-antennal plates narrow, almost the same width of ocelli (except in *Hemidictya*); lateral ocelli widely spaced, not higher than median ocellus in frontal view; ocular tubercle absents; vertex wider than eyes diameter; apex of postclypeus longer than or equal to the vertex in dorsal view, right in lateral view (except in *Sapantanga*) and round in frontal view; tumid processes absents in transverse grooves. Pronotum with median groove present; pronotal lobes flat (except in *Iruana* and *Sapantanga*); paranota present (except in *Sapantanga*); lateral angle of pronotal collar truncate (except in *Sapantanga*). Mesonotum with scutellum cruciform (*Iruana* and *Sapantanga*), triangular (*Hemidictya* and *Hovana*) or sub rectangular (*Lacetas*); operculum small, covering at least half of the tympanal cavity; meracanthus longer than posterior margin of operculum. Forewings opaque (*Lacetas*, *Hemidictya* and *Hovana*), pigmented, but translucent (*Iruana*) or colorless (*Sapantanga*); expansion of vein C (shelf-like) present (except in *Hovana* and *Sapantanga*); vein RA aligned closely with subcosta (Sc) for its length (except in *Sapantanga*); apical area of forewings not reticulated (except in *Hemidictya* and *Hovana*); apical cells in number of eight to ten (except in *Hemidictya* and *Hovana*); subapical cells absent (except in *Hemidictya* and *Hovana*); marginal area absent (except in *Iruana* and *Sapantanga*); ulnar cell (u3) angled to medial cell (mc); ulnar cell (u3) subequal to medial cell (mc) (except in *Hovana* that is longer (twice the size)). Male abdomen fusiform (tergites with sides straight). Sternite I not exposed (except in *Sapantanga*). Uncus present (except in *Sapantanga* and *Hemidictya*). Claspers, when presents, with apex posteriorlly directed (only for *Sapantanga* and *Hemidictya*). Pygofer upper lobe and dorsal beak absents (except in *Hovana*); pygofer secondary upper lobe absent; basal lobe of pygofer well-defined. Aedeagus lateral crest absent. Pseudoparameres absent.

*Distinguishing characters***:** Lateral ocelli widely spaced; ocular tubercle absent; anal lobe of hindwings very wide, the apex forming an obtuse angle; abdomen fusiform; pygofer with basal lobe well-defined; uncus, when present, ventrally developed, tube-shaped; clasper, when present, posteriorly developed, U-shaped; uncus and claspers never present together; aedeagus tubular, without median and distal curvatures, lateral crest or pseudoparameres.

Remarks: The only existing diagnosis for Hemidictyini was proposed by Distant (1905b), based in an old classification including genera now classified in Chlorocystini and Prasiini. Therefore, the characteristics listed by Distant (1905b), such as narrow head and the more or less globose and usually longitudinally dorsally ridged abdomen, are not useful to distinguish the Hemidictyini.

GENUS *HEMIDICTYA* BURMEISTER, 1835

Hemidictya Burmeister, 1835: 178.

Type species: *Hemidictya frondosa* Burmeister, 1835. By monotypy.

Diagnosis: Lateral margin of eyes not salient relative to the lateral margins of head; lateral angle of pronotal collar truncate; pronotal lobes flat; scutellum triangular; forewings covering the whole abdomen and pleurae in lateral view, anterior margins touching each other ventrally to the abdomen; forewings with veins C and R+Sc apart from each other; apical area of forewings reticulated; marginal area of forewings absent; expansion of vein C (shelf-like) in forewings present; apex of claspers posteriorly directed; uncus absent.

HEMIDICTYA FRONDOSA BURMEISTER, 1835
(FIGS13-15)

Hemidictya frondosa Burmeister, 1835: 178

Lectotype male here designated: Rio de Janeiro, Brazil, male (ZMHB). Type Cat. no. 5671. (Fig. 13A).

Paralectotype male here designated: same data as lectotype. Type Cat. no. 5671. (Fig. 13B).

Diagnosis: Apical area reticulated separate from proximal area by a median line; ulnar cell (u3) subdivided; clavus (clv) pigmented; basal cell sub rectangular; apex of claspers posteriorly directed; aedeagus curved with two apical parallel spines.

Coloration: Green in live specimens, yellow in dried specimens.

Description: Male. Head (Fig. 14A) narrow, smaller than mesonotum. Lateral margin of eyes reaching the lateral margin of pronotum, not salient relative to the lateral margins of head. Posterior margin of eyes not reaching the anterior margin of pronotum. Supra-antennal plates not prominent. Region of ocelli flat, without tubercles, the lateral ocelli not higher than the median. Lateral ocelli widely spaced, the distance between them about the same distance between each lateral ocellus and eye. Postclypeus long, anterior outline V-shaped, rectangular in ventral view and slightly salient in lateral view. Flagellum with three segments, all almost the same length, distal article black at apex in one specimen. Anteclypeus and carina bearing tuft of setae. Labium short, reaching mesocoxae.

Pronotum (Fig. 14A) with a narrow and deep median grove; lateral lobes larger than paramedian lobes. Paranota developed. Pronotal collar wide, lateral angles truncate reaching the articulation of forewings. Mesonotum (Fig. 14A) with a long triangular scutellum reaching tergite 2 and bearing a central crest. Parapsidal suture poorly marked, lateral and submedian sigilla pale black. Operculum (Fig. 14B) thin and short, not covering the tympanal cavity and not reaching sternite II. Meracanthus (Fig. 14B) exceeding the size of operculum, apex directed posteriorly. Gutter across the margin of operculum. Profemora with three small spines, the primary leaning forward against the ventral margin of femur. Tarsi with three articles. Forewings (Fig. 14D) semi opaque and wide, covering the whole abdomen and pleurae in lateral view, apex acute. Veins C and R+Sc apart from each other. Basal cell subretangular, longer than wide. Ulnar cell (u3) subdivided and angled to medial cell (mc). Apical area reticulated, separated from the proximal area by a median line. Clavus (clv) pigmented. Posterior margin absent.

Abdomen fusiform, apex triangular. Sternite I not completely covered by metacoxae, touching sternite II whose median portion of anterior margin is nearly straight. Sternite VII subrectangular, obtuse at apex (Fig. 14C).

Pygofer (Fig. 14E) with distal shoulders developed and rounded. Claspers posteriorly developed in U-shape (Fig. 14G), process close not enfolding the aedeagus, apex obtuse. Upper lobe undeveloped. Aedeagus (Figs. 14E, F) C-shaped, angle of proximal curvature obtuse, bearing two apical spines.

Female (Figs. 15A-D). Somatic characteristics as described for male except the operculum that almost covers the tympanal cavity, meracanthus reaching sternite II (Fig. 15A), the later not projected anteriorly at midline; posterior margin of sternite VII concave (Fig. 15B). Tergite 9 with the mesial margin concave becoming convex in the middle (Fig. 15B). The tip of ovipositor sheath with same length of dorsal beak of tergite 9 (Fig. 15C, D).

Measurements (mm): male, n = 3, mean (range). Length of body: 12.79 (12.48-13.10); width of head including eyes: 3.66 (3.55-3.90); length of head: 1.60 (1.42-1.70); width of pronotum including pronotal collar: 5.20 (4.97-5.67); length of pronotum including pronotal collar: 1.69 (1.63-1.76); width of mesonotum: 4.29 (3.97-4.66); length of mesonotum: 4.34 (4.18-4.53); width of forewing: 9.41 (9.20-9.67); length of forewing: 18.72 (17.94-20.28). Female, n = 2, mean (range). Length of body: 16.53 (16.38-16.69); width of head including eyes: 4.67 (4.30-5.04); length of head: 2.02 (1.90-2.14); width of pronotum including pronotal collar: 6.85 (6.50-7.20); length of pronotum including pronotal collar: 2.15 (2.00-2.30); width of mesonotum: 5.50 (5.20-5.80); length of mesonotum: 5.75 (5.50-6.00); width of forewing: 12.24 (11.70-12.79); length of forewing: 25.42 (23.40-27.45).

Material examined: **Mato Grosso**: Chap. Guimarães – MT \ 03-05.XII.1983 \ Exc. Dep. Zool. UFPR \ (Polonoroeste) \ Malaise \\ Dpto. Zoll.\UF-Paraná, 1 male (DZUP); CHAPADA – MT \ Brasil XI.63 \ M. Alvarenga, 2 males (DZUP); **Minas Gerais**: BRA, MG, Marliéria \ Timóteo, Parque Estadual \ do Rio Doce, 14.XI.1980-\ 16.XI.1980, M.A. Vulcano *et al*. leg., 1 female (UFMG); **Espírito Santo**: Linhares \ ES- Brasil \ XII-196 5\ A. Maller \\ Dpto Zoo l\ UF-PARANÁ, 1 female (DZUP).

Distribution: Brazil (Mato Grosso*, Minas Gerais*, Espírito Santo*, Rio de Janeiro).

Remarks: H. frondosa is included in clade C as sister group to *Hovana distanti*. The species present one homoplastic synapomorphy: uncus absent (48_1).

GENUS *HOVANA* DISTANT, 1905

Hovana Distant, 1905: 279

Type species: *Hemidictya distanti* Brancsik, 1893. By monotypy.

Diagnosis: Lateral margin of eyes not salient relative to the lateral margins of head; lateral angle of pronotal collar truncate; pronotal lobes flat; scutellum triangular; forewings covering the whole abdomen and pleurae in lateral view, anterior margins touching each other ventrally to the abdomen; forewings with veins C and R+Sc apart from each other; apical area of forewings reticulated; marginal area of forewings absent; expansion of vein C (shelf-like) in forewings absent; uncus present; upper lobe and dorsal beak of pygofer present.

Included species: Hovana distanti (Brancsik, 1893).

HOVANA DISTANTI (BRANCSIK, 1893)
(FIGS16, 17)

Hemidictya distanti Brancsik, 1893: 253; *Hovana distanti*; Distant, 1905: 280.

Holotype: Nosy Be, Madagascar, male (HNHM). The specimen labelled as “type” is considered here as holotype by monotypy (ICZN, art. 73.2.1) (Figs. 16A, B).

Diagnosis: Costal area in forewings pigmented; basal cell sub polygonal; apical area reticulated, not separated by a median line from proximal area; ulnar cell (u3) longer (twice the size) than medial cell (mc) of forewings.

Coloration: Green in live specimens, yellow in dried specimens.

Description: Male. Head (Fig. 17A) narrow, smaller than mesonotum. Lateral margin of eyes reaching the paramedian margins of pronotum, not salient relative to the lateral margins of head. Posterior margin of eyes not reaching the anterior margin of pronotum. Supra-antennal plates not prominent. Region of ocelli flat, without tubercles, lateral ocelli not higher than median. Lateral ocelli widely spaced, the distance between them about the same distance between each lateral ocellus and eye. Postclypeus long, anterior outline V-shaped, rectangular in ventral view and slightly salient in lateral view. Labium short, reaching mesocoxae.

Pronotum (Fig. 17A) bearing a narrow and deep median grove, lateral lobes larger than the paramedian. Paranota developed. Pronotal collar wide, lateral angles truncate reaching the articulation of forewings. Mesonotum (Fig. 17A) with long triangular scutellum reaching the tergite 2 and with a central crest. Parapsidal suture and sigilla not marked. Forewings (Fig. 17B) semi opaque and wide, covering the whole abdomen in lateral view, apex acute. Veins C and R+Sc apart from each other. Costal area pigmented. Basal cell subrectangular. Ulnar cell (u3) twice the size of medial cell (mc). Radial cell (rc) and ulnar cell (u3) of equal length. Apical area reticulated.

Abdomen fusiform. Uncus present, upper lobe of pygofer longer than anal styles, dorsal beak of pygofer present (Fig. 17C).

Measurements (mm): Type. Length of body: 20.23; width of head including eyes: 5.14; length of head: 3.11; width of pronotum including pronotal collar: 9.51; length of pronotum including pronotal collar: 3.53; width of mesonotum: 8.08; length of mesonotum: 7.35; length of forewing: 26.78; width of forewing: 14.62; length of hindwing: 15.27; width of hindwing: 7.85.

Distribution: Madagascar.

Remarks: Hovana distanti is included in clade C as sister group to *Hemidictya frondosa*. The species present five homoplastic synapomorphies: expansion (shelf-like) of vein C in forewings absent (31_1), vein C equal in width to R+Sc (32_1), ulnar cell (u3) longer (twice the size) than the medial cell (mc) in forewings (36_2), upper lobe of pygofer present (52_0) and dorsal beak of pygofer present (56_1).

KEY TO THE GENERA OF HEMIDICTYINI SENSU NOVO

1. Forewings semi opaque (Figs. 6D-G)… 2

– Forewings pigmented but translucent (Fig. 6A) or colorless (Fig. 6B)… 3

2. Forewings wide, covering the whole abdomen in lateral view (Figs. 13B, 16B)… 4

– Forewings narrow, leaving the ventral margin of abdomen exposed in lateral view (Figs. 20B, 21B)… *Lacetas*

3. Paranota present (Fig. 2F)… *Iruana*

– Paranota absent (Fig. 22A)… *Sapantanga*

4. Apical area reticulated separated from proximal area by a median line (Figs. 13A, B; 14D)… *Hemidictya*

– Apical area reticulated not separated from proximal area by a median line (Figs. 16A, B; 17B)… *Hovana*

FAMILY CICADIDAE LATREILLE, 1802
SUBFAMILY CICADETTINAE BUCKTON, 1890
TRIBE PRASIINI MATSUMURA, 1917

Prasinaria Matsumura, 1917: 209.

Prasiini Kato, 1932: 188.

Type genus: Prasia Stål (type species *P. faticina* Stål).

Included genera: Arfaka Distant, 1905; *Jacatra* Distant, 1905; *Lembeja* Distant, 1892; *Mariekea* Jong & Boer, 2004; *Prasia* Stål, 1863.

Included species: Arfaka fulva (Walker, 1870); *A. hariola* (Stål, 1863); *Jacatra typica* Distant, 1905; *Lembeja brendelli* Jong, 1986; *L. consanguinea* Jong, 1987; *L. dekkeri* Jong, 1986; *L. distanti* Jong, 1986; *L. elongata* Jong, 1986; *L. fatiloqua* (Stål, 1870); *L. foliata* (Walker, 1858); *L. fruhstorferi* Distant, 1897; *L. hollowayi* Jong, 1986; *L. incisa* Jong, 1986; *L. lieftincki* Jong, 1987; *L. maculosa* (Distant, 1883); *L. majuscula* Jong, 1986; *L. minahassae* Jong, 1986; *L. mirandae* Jong, 1986; *L. oligorhanta* Jong, 1986; *L. papuensis* Distant, 1897; *L. paradoxa* (Karsch, 1890); *L. parvula* Jong, 1987; *L. pectinulata* Jong, 1986; *L. robusta* Distant, 1909; *L. roehli* Schmidt, 1925; *L. sangihensis* Jong, 1986; *L. sanguinolenta* Distant, 1909; *L. sumbawensis* Jong, 1987; *L. tincta* (Distant, 1909); *L. vitticollis* (Ashton, 1912); *L. wallacei* Jong, 1987; *Mariekea acuta* Jong, 2004; *M. euharderi* Jong, 2004; *M. floresiensis* Jong, 2004; *M. groenendaeli* Boer, 2004; *M. harderi* (Schmidt, 1925); *M. major* Jong, 2004; *Prasia breddini* Jong, 1985; *P. faticina* Stål, 1863; *P. nigropercula* Jong, 1985; *P. princeps* Distant, 1888; *P. sarasinorum* Jong, 1985; *P. senilirata* Jong, 1985; *P. tuberculata* Jong, 1985.

Diagnosis: Head with supra-antennal plate meeting eye (Moulds, 2005); eyes protruding laterally, wider than vertex; scape longer, twice the size of pedicel; supra-antennal plates narrow, almost the same width of ocelli; ocellus closely spaced (Boer, 1995a); ocular tubercle present; vertex narrow (Boer, 1995a), width equal than diameter of ocellus; length of postclypeus equal to the vertex in dorsal view; postclypeus very prominent and obtuse in lateral view, keel-shape in frontal view; tumid processes present in transverse grooves (except *Lembeja*). Pronotum with median groove present; pronotal lobes thick; paranota absent (except *Prasia*); pronotal collar with lateral margin confluent with adjoining lateral lobes (as pronotal sclerites in Moulds, 2005); lateral angle of pronotal collar round. Mesonotum with scutellum cruciform with lateral area obtuse; operculum small, covering at least half of the tympanal cavity. Metanotum expanded. Forewing veins C and R+Sc close together (Moulds, 2005); expansion (shelf-like) of vein C present; vein RA aligned closely with subcosta (Sc) for its length (Moulds, 2005); apical area of forewings not reticulated; apical cells in number of eight; subapical cells absent; marginal area absent. Hindwing with anal lobe either broad or narrow and vein 3A either separated or adjacent to wing margin (Moulds, 2005). Male abdominal tergites with sides straight or convex in cross-section (Moulds, 2005); tergites 2 and 3 similar in size to tergites 4-7 (Moulds, 2005); tergite 2 short, reaching the base of timbal; timbals extend below wing bases (Moulds, 2005). Uncus present. Clasper present (except in *Arfaka*) and distally directed. Pygofer with upper lobe present, thickened rather than flat (Moulds, 2005), longer or the same length of anal styles; pygofer secondary upper lobe absent; pygofer basal lobe ill-defined (except in *Arfaka*); dorsal beak present. Aedeagus lateral crest absent. Theca straight or curved in a gentle arc (Moulds, 2005) with apex bilobed; pseudoparameres present in some species.

Distinguishing characters: Scape long, twice the size of pedicel; vertex narrow; ocelli closely spaced; postclypeus keel-shaped in frontal view; clasper and uncus present together, the uncus poorly developed and the claspers, located below, distally developed. The long scape and the keel-shaped postclypeus are proposed for the first time as diagnostic to Prasiini.

Remarks: Some of the characters proposed by Boer (1995a), as a large obconical and triangularly protruding postclypeus; a very narrow hyaline border along the hind margin of the wing; and well-developed and posteriorly projecting protuberances on the lateral lobes of the male pygofer (used here as characters 7, 8, 40 and 52) cannot be used as diagnostic to Prasiini because they are also present in species of Hemidictyini and Chlorocystini.

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FIGURES AND TABLE

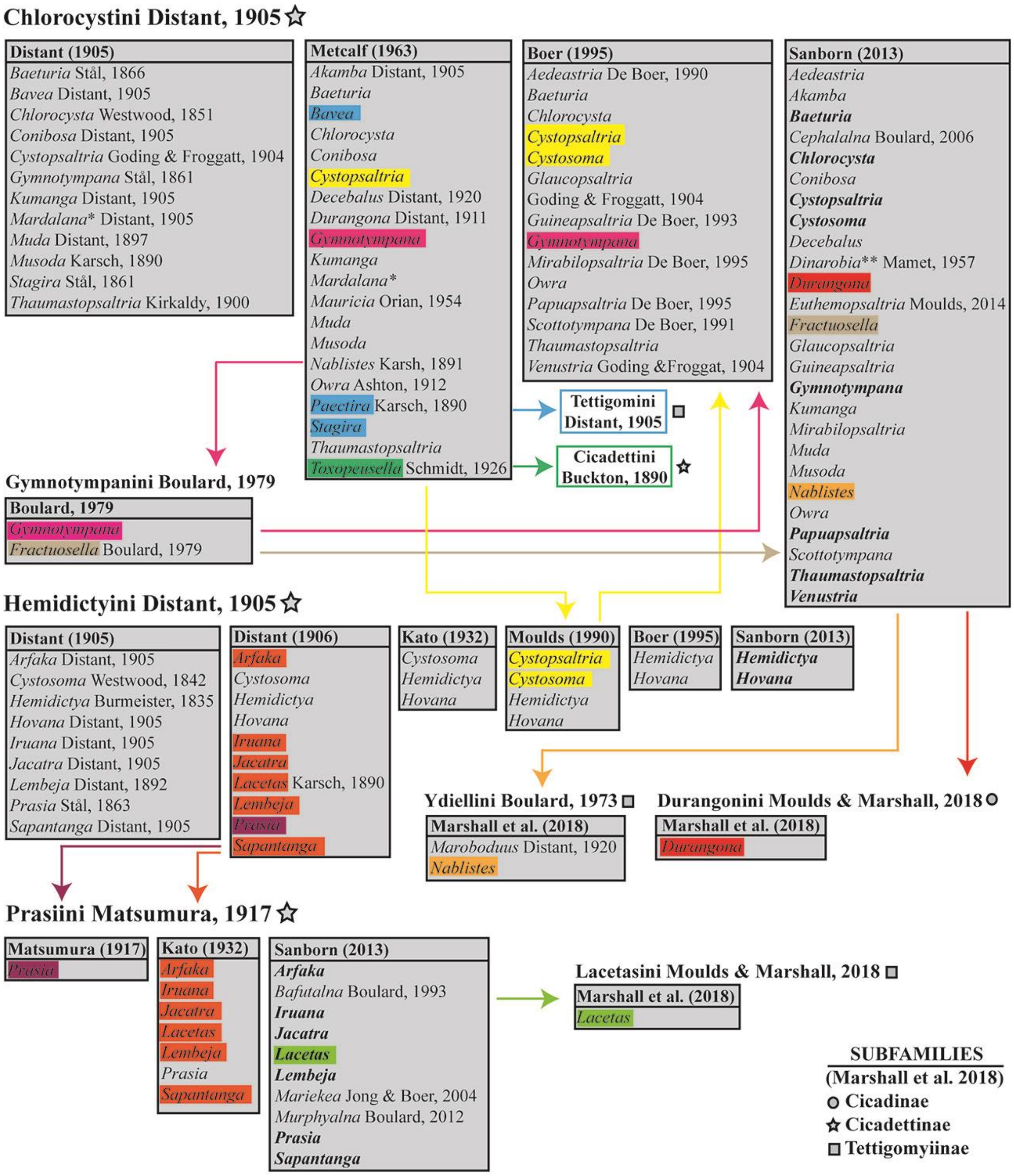

Figure 1. Diagram of taxonomic history of Chlorocystini, Prasiini and Hemidictyini.

Table 1. Character matrix of the 39 taxa and 67 characters used in the cladistic analysis of the leaf-winged cicadas. The symbols '?' and '–' were used for missing and non-applicable data, respectively.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Carineta diardi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0
Diemeniana hirsuta	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0
Parnisa lineaviridia	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	1	0	?	?	0	0	0
Parnisa viridis	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	0	0	0	1	?	?	1	?	?	0	?	?
Abroma ferraria	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	-	-	0	1	0	0	1	0	0	0	1	?	0
Abroma guerinii	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	-	-	0	1	0	0	1	0	0	0	1	?	0
Taphura misella	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	0	0	0
Baeturia bicolorata	0	0	0	1	0	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Baeturia edauberti	0	0	0	0	0	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Baeturia laminifer	0	0	0	0	0	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Cystosoma saundersii	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	0	2	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Cystosoma schmeltzi	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	0	2	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Cystopsaltria immaculata	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1	0	2	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1
Chlorocysta vitripennis	0	1	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0
Chlorocysta suffusa	0	1	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	1	0	1	0
Glaucopsaltria viridis	0	1	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Gymnotympana rubricata	0	1	0	0	0	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1
Gymnotympana varicolor	0	1	0	0	1	1	2	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Gymnotympana rufa	0	1	0	0	1	1	2	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	1	0
Papuapsaltria dioedes	0	1	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	0
Thaumastopsaltria globosa	0	0	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	1	2	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0
Thaumastopsaltria lanceola	0	0	0	0	1	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	1	2	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0
Venustria superba	0	1	0	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	-	0	1	0	0	1	0	1	0
Arfaka fulva	0	0	1	1	0	0	1	0	1	1	2	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	-	-	0	0	1	0	1	1	1	1	0	?	0
Iruana rougeoti	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	-	-	1	0	-	0	0	1	0	0	0	?	0
Iruana sulcata	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	-	-	1	0	-	0	0	?	?	?	0	0	0
Jacatra typica	0	0	1	1	0	0	1	0	0	1	2	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lacetas annulicornis	1	0	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0	-	-	1	0	-	0	0	1	0	0	0	0	0
Lacetas longicollis	1	0	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0	-	-	1	0	-	0	0	1	0	0	0	0	0
Lembeja elongata	0	0	1	1	0	0	1	0	0	1	2	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0
Lembeja minahassae	0	0	1	1	0	0	1	0	0	1	2	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	?	0
Lembeja papuensis	0	0	1	1	0	0	1	0	0	1	2	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0
Lembeja robusta	0	0	1	1	0	0	1	0	0	1	2	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0
Prasia faticina	0	0	1	1	0	0	1	0	0	1	2	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0
Prasia princeps	0	0	1	1	0	0	1	0	0	1	2	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0
Prasia sarasinorum	0	0	1	1	0	0	1	0	0	1	2	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0
Sapantanga nutans	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	1	0	-	0	0	0	0	1	0	0	0
Hemidictya frondosa	1	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	3	1	-	0	1	1	1	1	2	0	1	1	0	0	0	0	1	0	1	1	1	1	-	0	0	0	1	1	1	1	1	0	1	1	0	-	0	0	1	0	1	0	0	0
Hovana distanti	1	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	3	1	-	0	1	1	1	1	2	0	1	1	1	1	0	0	1	2	1	1	1	1	1	0	0	0	1	1	1	0	0	-	-	0	0	1	?	1	?	?	?	?	?	?

Table 1. Continued.

	63	**64**	**65**	**66**	**67**
Carineta diardi	0	0	-	0	0
Diemeniana hirsuta	0	0	-	0	0
Parnisa lineaviridia	0	0	-	0	0
Parnisa viridis	?	0	-	0	0
Abroma ferraria	0	0	-	1	0
Abroma guerinii	0	0	-	1	0
Taphura misella	0	0	-	0	0
Baeturia bicolorata	1	1	1	0	0
Baeturia edauberti	1	1	1	0	0
Baeturia laminifer	1	1	1	0	0
Cystosoma saundersii	0	0	-	0	0
Cystosoma schmeltzi	0	0	-	0	0
Cystopsaltria immaculata	0	0	-	0	0
Chlorocysta vitripennis	1	1	2	0	0
Chlorocysta suffusa	1	1	2	0	0
Glaucopsaltria viridis	0	0	-	0	0
Gymnotympana rubricata	1	1	1	0	0
Gymnotympana varicolor	0	0	-	0	0
Gymnotympana rufa	0	0	-	0	0
Papuapsaltria dioedes	0	0	-	0	0
Thaumastopsaltria globosa	0	0	-	0	0
Thaumastopsaltria lanceola	0	0	-	0	0
Venustria superba	0	0	-	0	0
Arfaka fulva	0	0	-	0	0
Iruana rougeoti	0	0	-	0	0
Iruana sulcata	0	0	-	0	0
Jacatra typica	?	?	?	?	?
Lacetas annulicornis	0	0	-	0	0
Lacetas longicollis	0	0	-	0	0
Lembeja elongata	0	0	-	0	1
Lembeja minahassae	0	0	-	0	1
Lembeja papuensis	0	0	-	0	0
Lembeja robusta	0	0	-	0	1
Prasia faticina	0	0	-	0	0
Prasia princeps	0	0	-	0	1
Prasia sarasinorum	0	0	-	0	1
Sapantanga nutans	0	0	-	0	0
Hemidictya frondosa	0	0	-	0	0
Hovana distanti	?	?	?	?	?

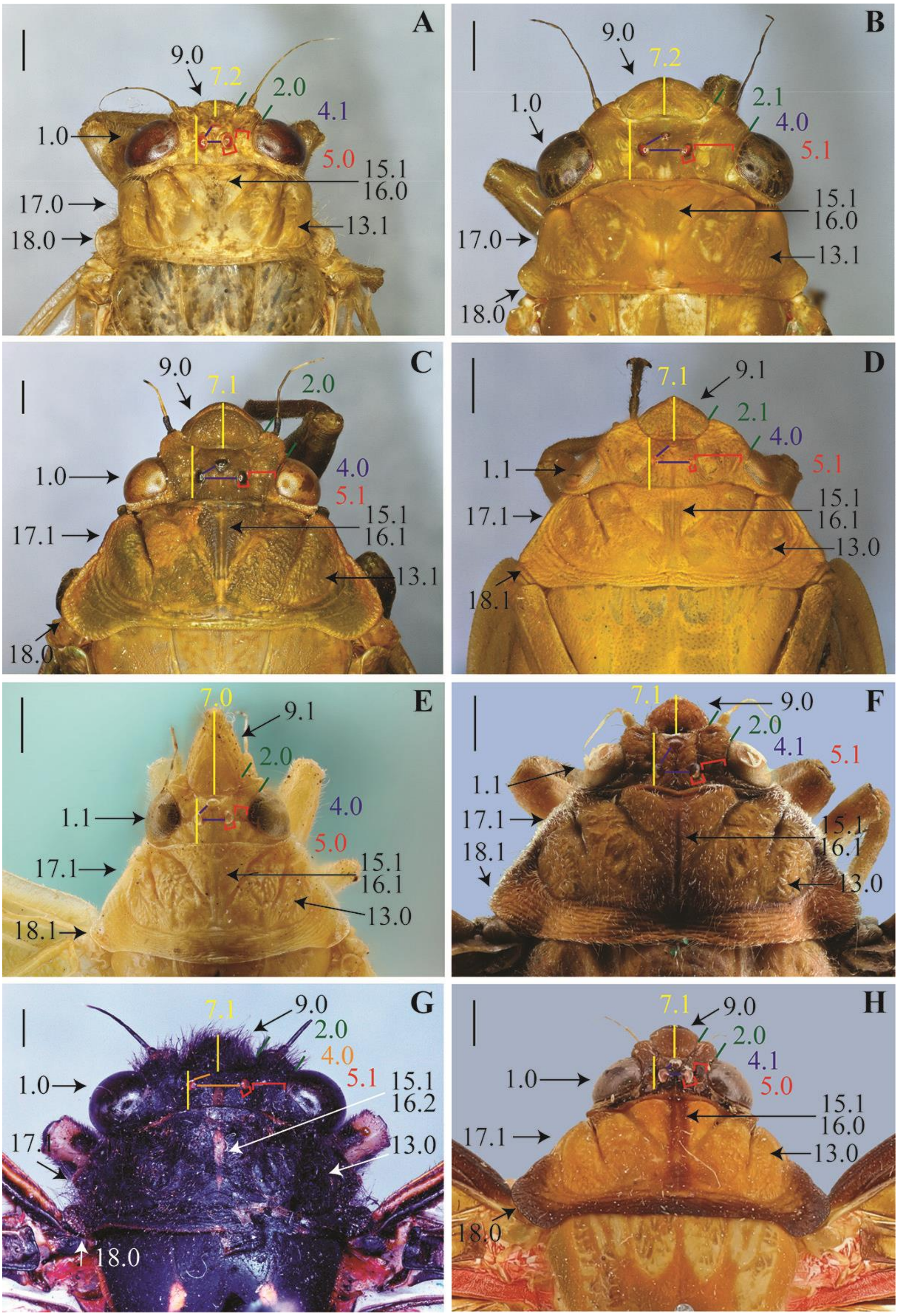

Figure 2. Characters of head and pronotum in dorsal view. A. *Baeturia bicolorata*; B. *Chlorocysta vitripennis*; C. *Cystosoma saundersii*; D. *Hemidictya frondosa*; E. *Lacetas annulicornis*; F. *Iruana sulcata*; G. *Diemeniana hirsuta*; H. *Prasia culta*. Scales: 1 mm.

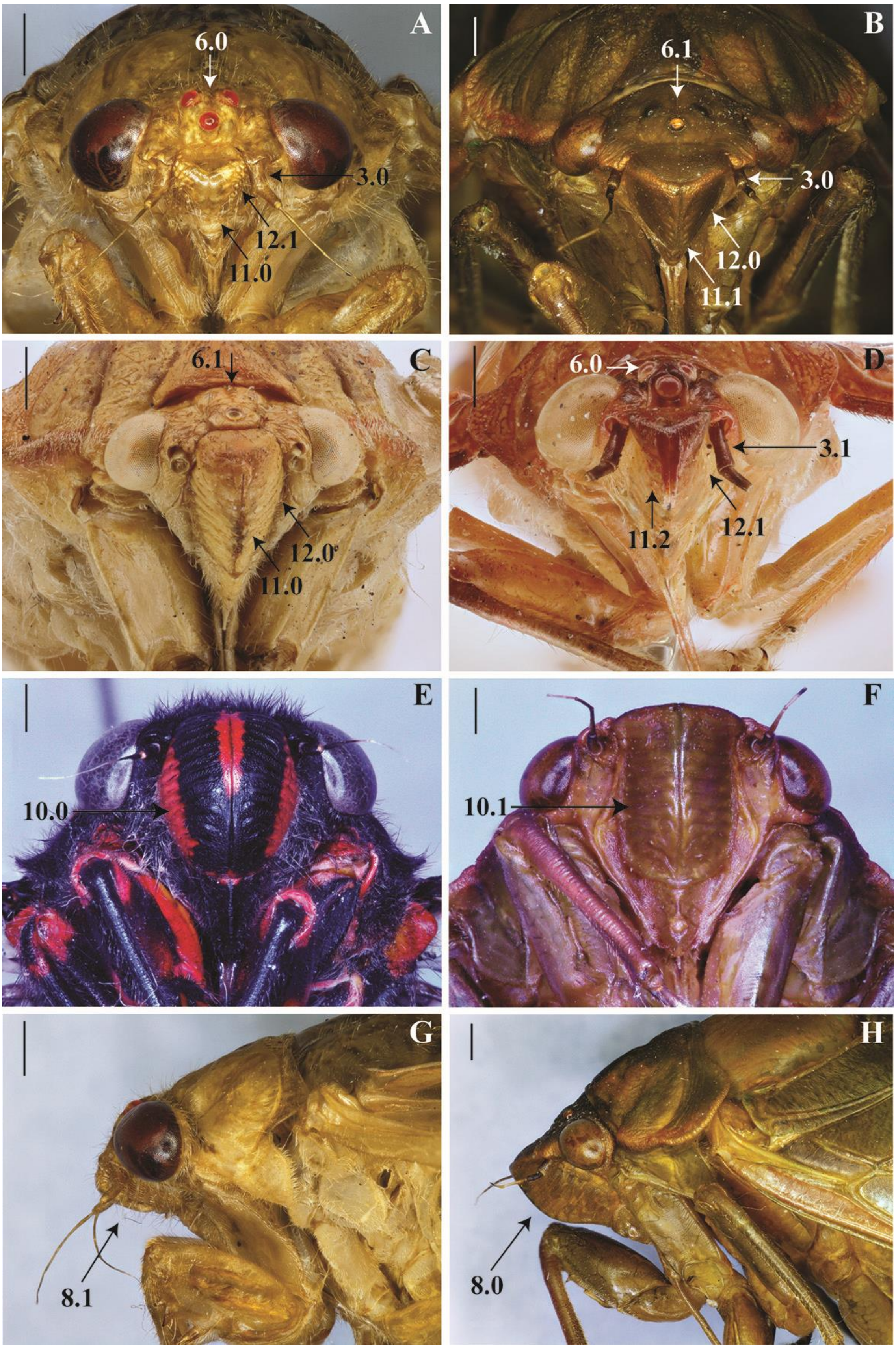

Figure 3. Characters of head. A. *Baeturia bicolorata* in frontal view; B. *Cystosoma saundersii* in frontal view; C. *Iruana sulcata* in frontal view; D. *Prasia culta* in frontal view; E. *Carineta diardi* in ventral view; F. *Cystosoma saundersii* in ventral view; G. *Baeturia bicolorata* in lateral view; H. *Cystosoma saundersii* in lateral view. Scales: 1 mm.

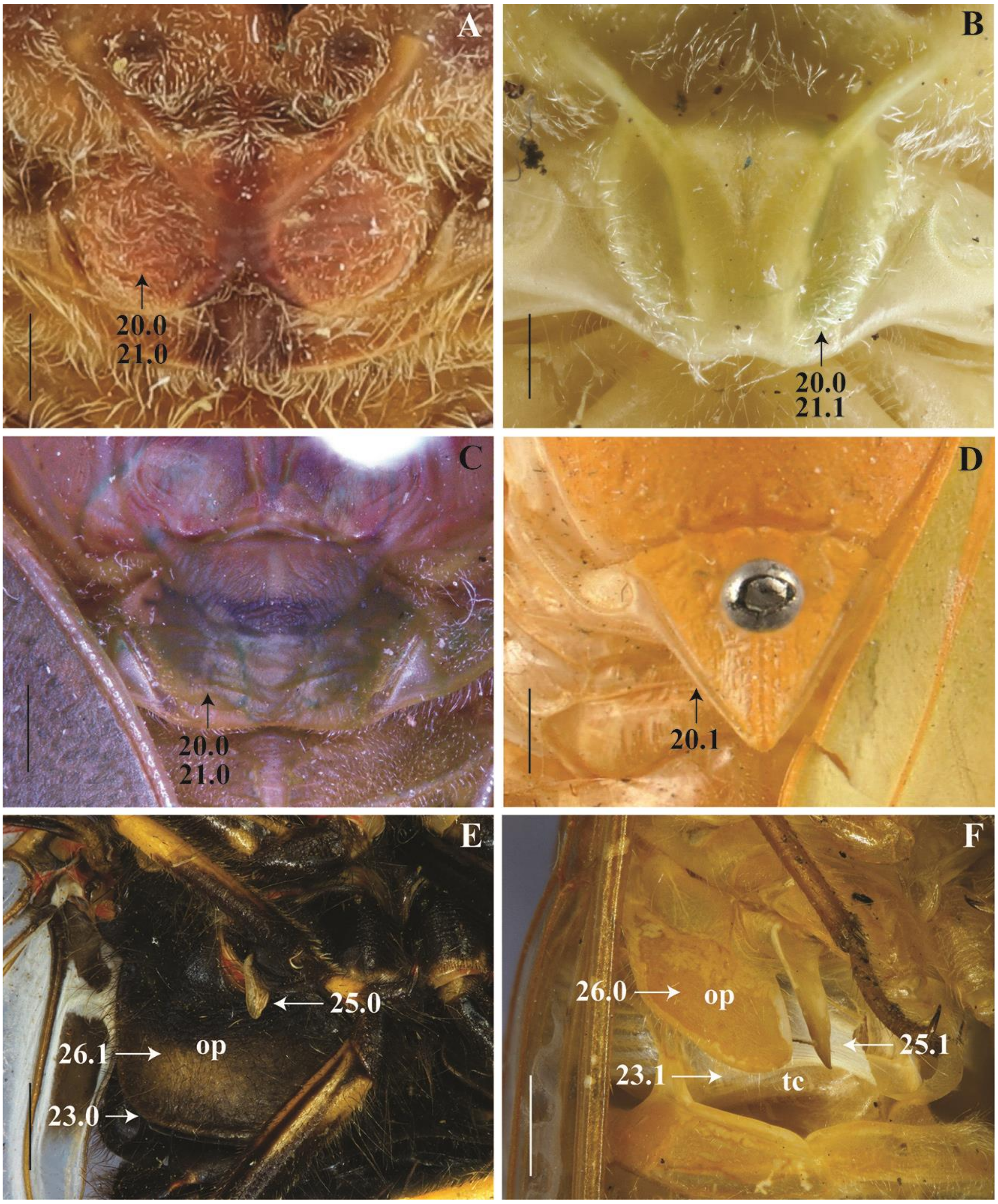

Figure 4. Characters of scutellum and male operculum. A. Scutellum of *Lembeja papuensis* in dorsal view; B. Scutellum of *Lacetas annulicornis* in dorsal view; C. Scutellum of *Cystosoma saundersii* in dorsal view; D. Scutellum of *Hemidictya frondosa* in dorsal view; E. Operculum of *Diemeniana hirsuta* in ventro-lateral view; F. Operculum of *Papuapsaltria dioedes* in ventro-lateral view. Scales: 1 mm.

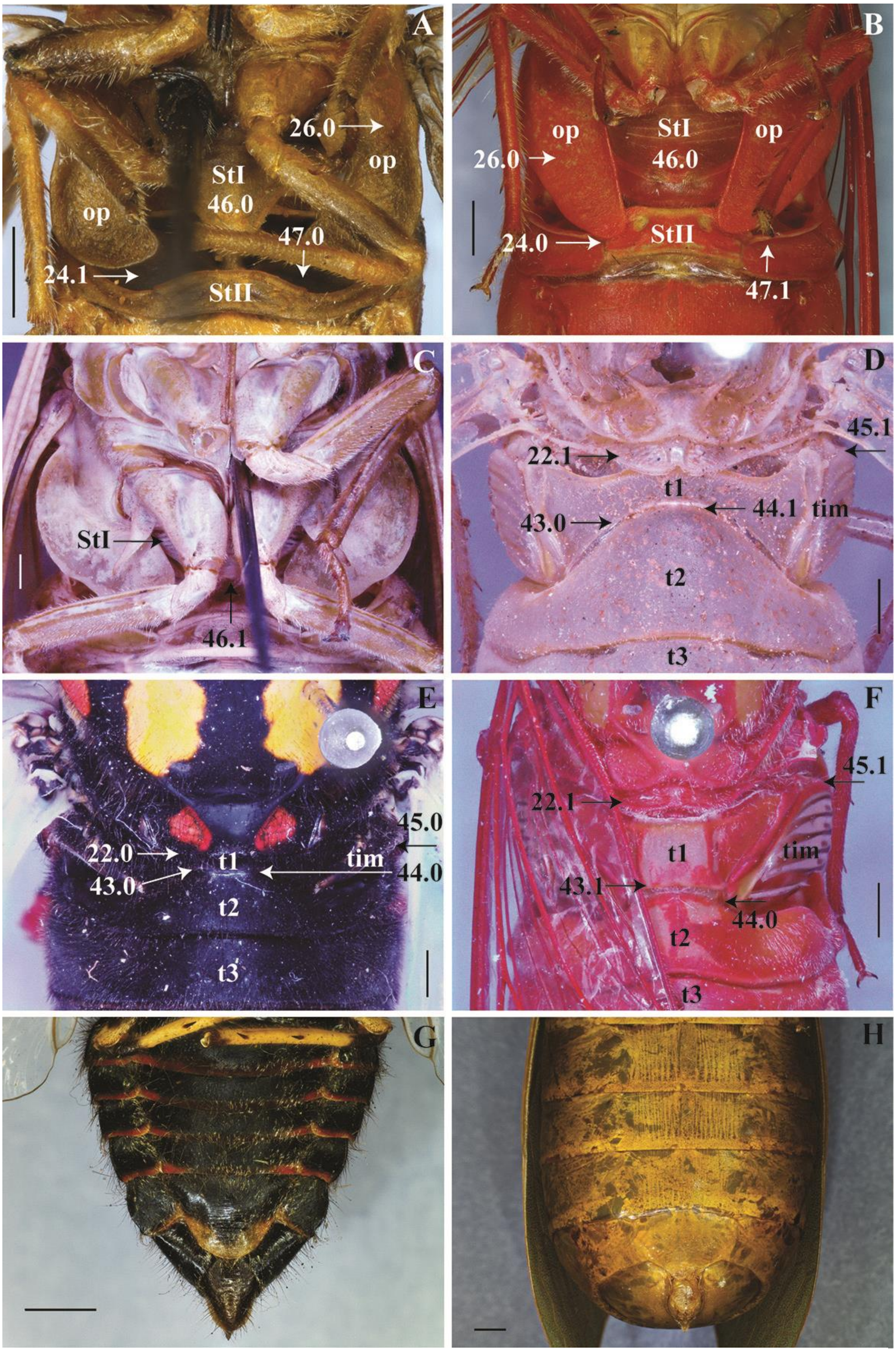

Figure 5. Characters of male: thorax in ventral view (A-C); anterior portion of abdomen in dorsal view (D-F) and posterior portion in ventral view (G, H). A. *Parnisa lineaviridia*; B. *Gymnotympana varicolor*; C. *Cystopsaltria immaculata*; D. *Thaumastopsaltria globosa*; E. *Carineta diardi*; F. *Gymnotympana varicolor*; G. *Diemeniana hirsuta*; H. *Cystosoma saundersii*. Scales for A-F = 1 mm, G and H = 2 mm.

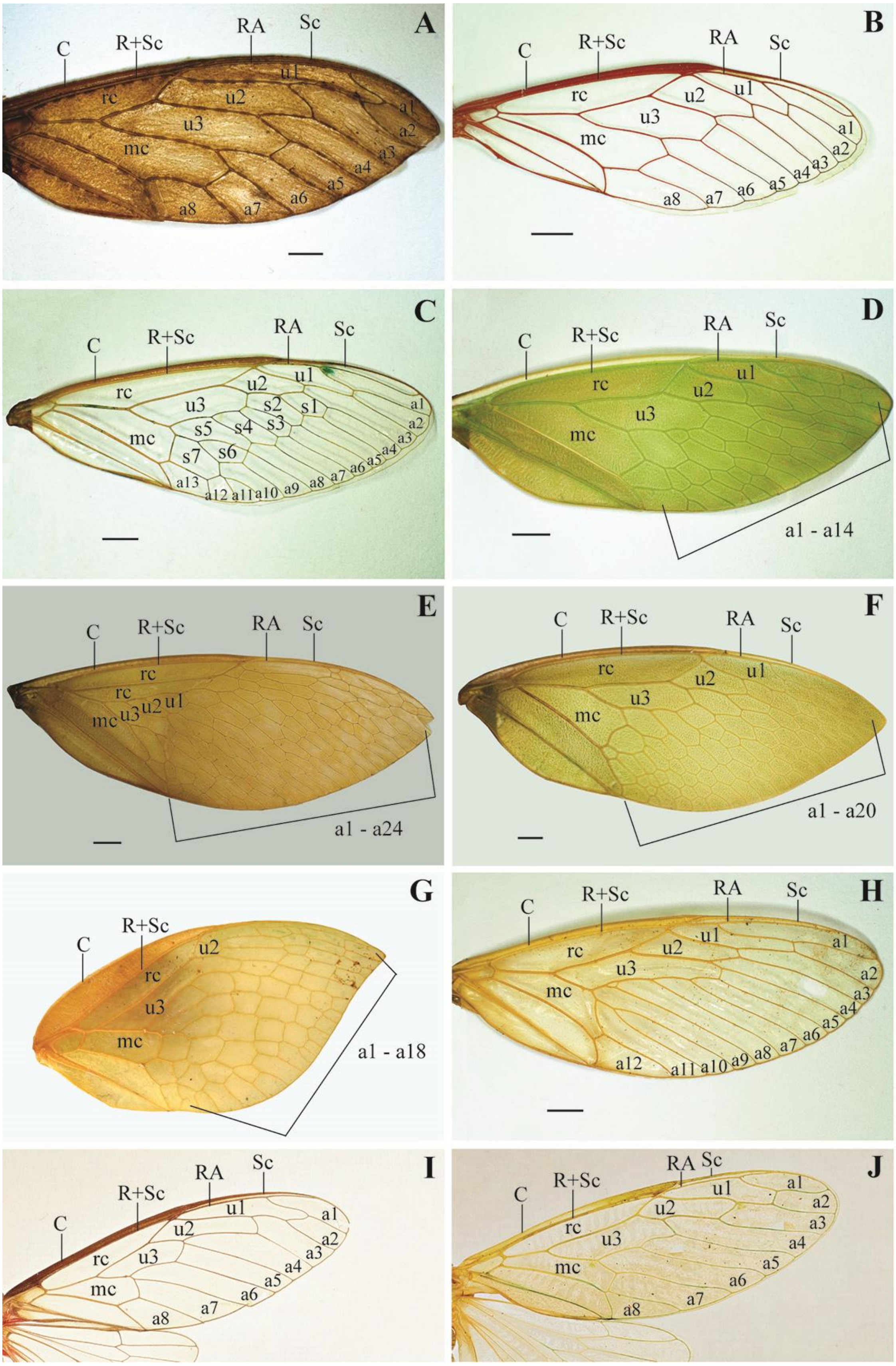

Figure 6. Characters of forewings in dorsal view. A. *Lembeja papuensis*; B. *Gymnotympana varicolor*; C. *Chlorocysta vitripennis*; D. *Cystosoma schmeltzi*; E. *Cystopsaltria immaculata*; F. *Cystosoma saundersii*; G. *Hovana distanti*; H. *Thaumastopsaltria lanceola*; I. *Prasia culta*; J. *Iruana rougeoti*. Scales: 2 mm.

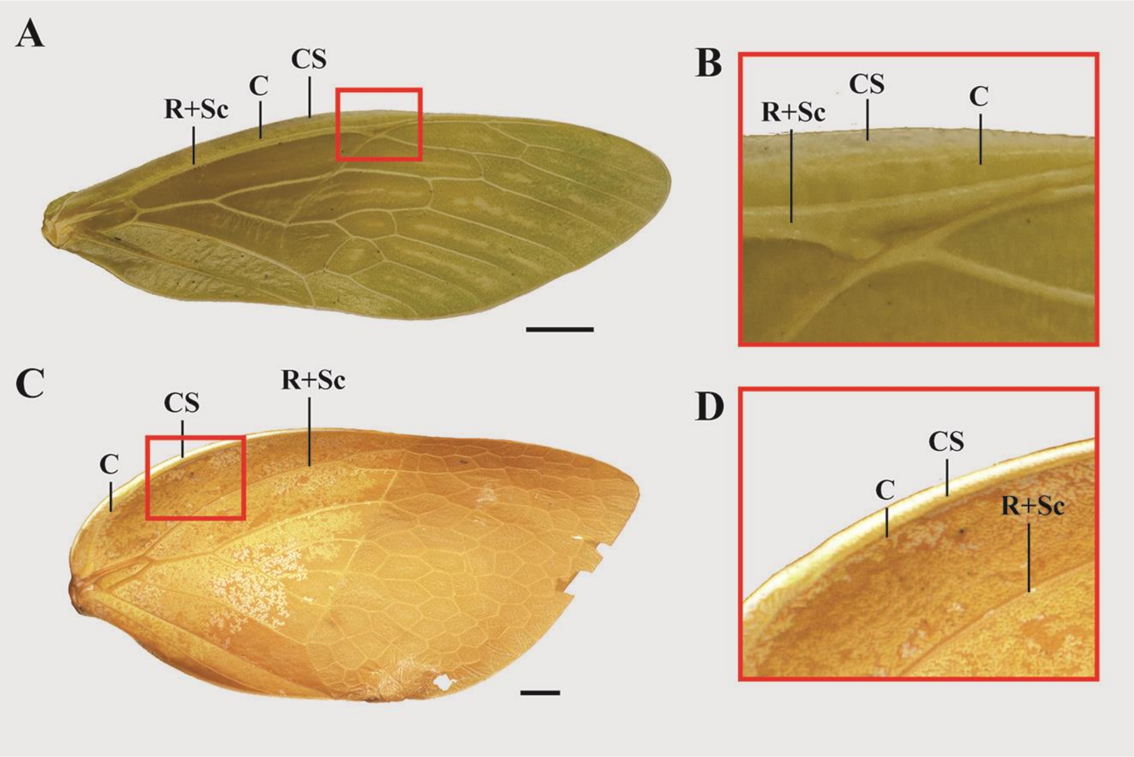

Figure 7. Right forewing in dorsal view. *Lacetas annulicornis* (A, B) and *Hemidictya frondosa* (C, D). B and D, detail of veins costal (C), radius + subcostal (R+Sc) and the expansion (shelf-like) of vein C (CS). Scales: 2 mm.

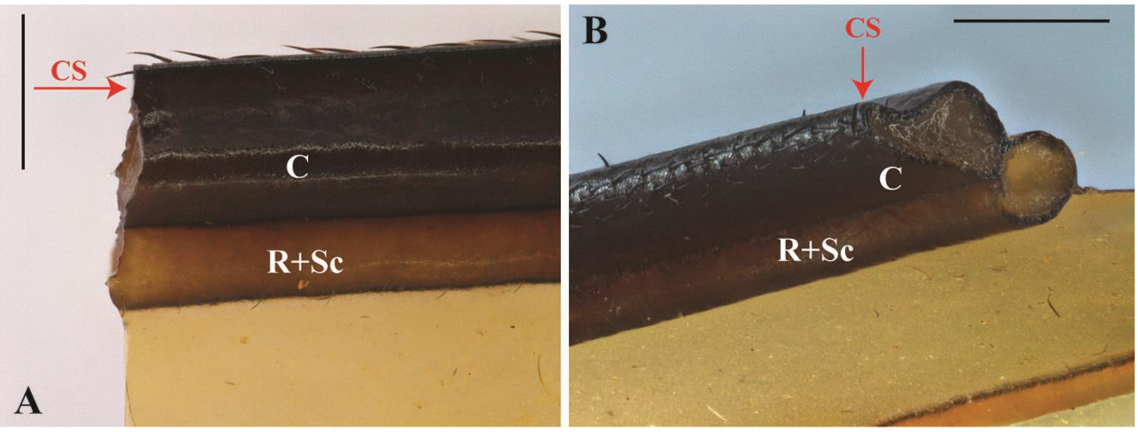

Figure 8. Forewing of *Carineta diardi*, transversal cut of the veins costal (C) and radius + subcostal (R+Sc) in dorsal (A) and fronto-ventral (B) views. The arrow indicates the expansion (shelf-like) of vein costal (CS). Scales: 5 mm.

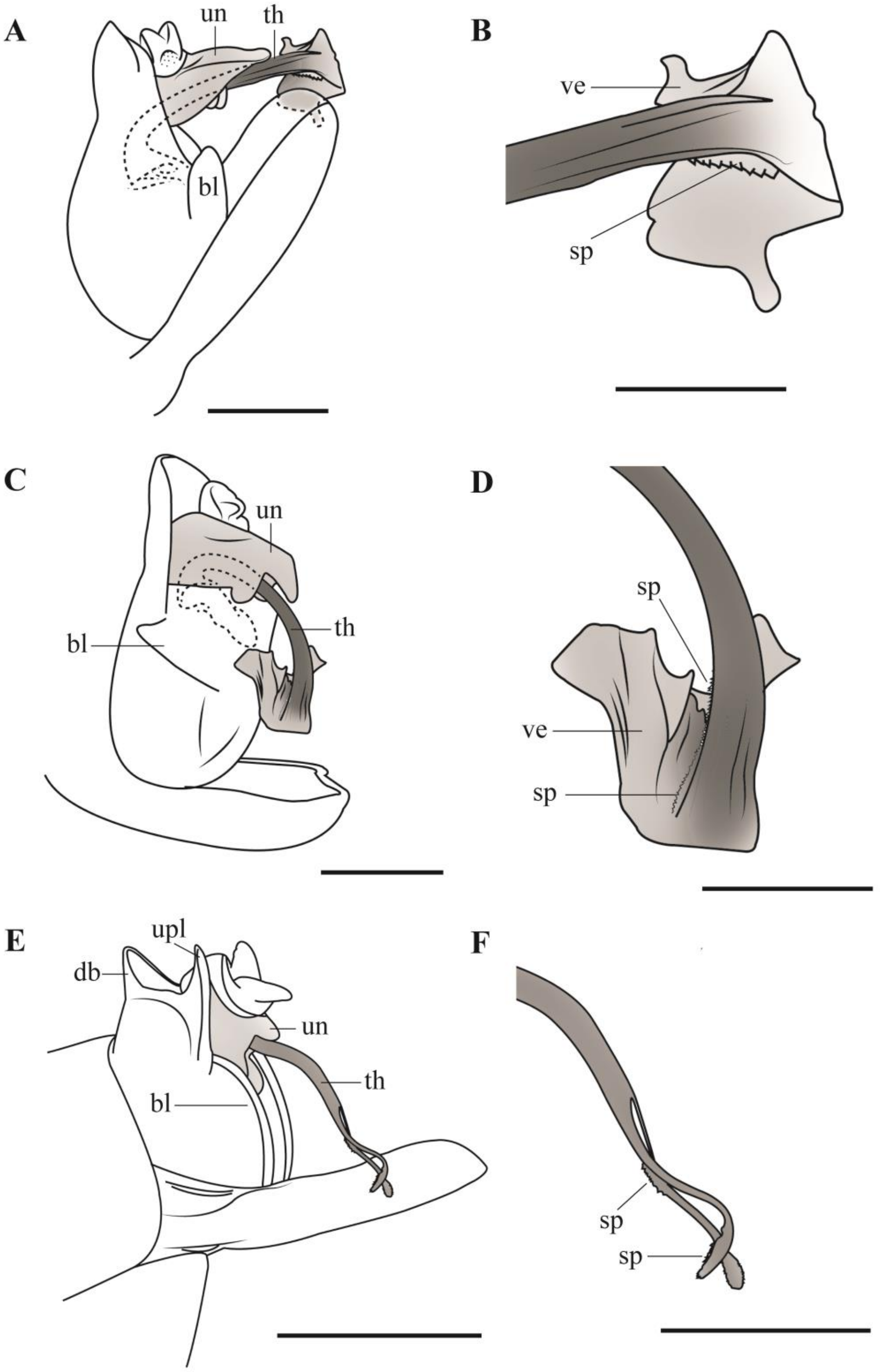

Figure 9. Characters of pygofer and aedeagus. A. Pygofer of *Lacetas annulicornis* in lateral view; B. Aedeagus of *L. annulicornis* in dorsal view; C. Pygofer of *Lacetas longicollis* in lateral view; D. Aedeagus of *L. longicollis* in dorsal view; E. Pygofer of *Arfaka fulva* in lateral view; F. Aedeagus of *A. fulva* in lateral view. Scales: 1 mm.

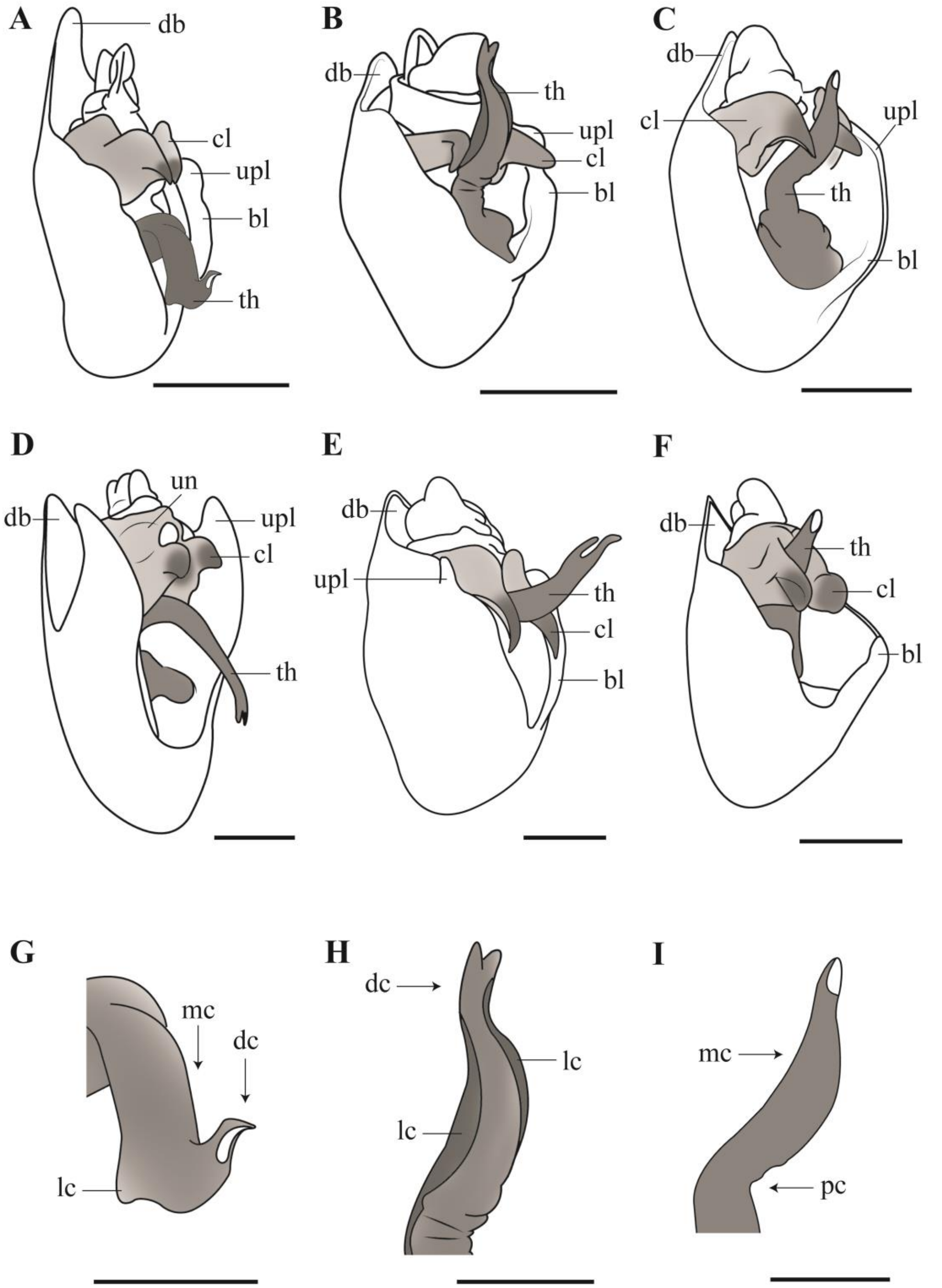

Figure 10. Characters of pygofer in ventro-lateral view (A-F) and aedeagus (G-I). A. *Baeturia bicolorata*; B. *Chlorocysta suffusa*; C. *Cystosoma schmeltzi*; D. *Lembeja papuensis*; E. *Cystopsaltria immaculata*; F. *Venustria superba*; G. *B. bicolorata* fronto-lateral view; H. *C. suffusa* in ventro-lateral view; I. *C. schmeltzi* in ventro-lateral view. Scales: 1 mm.

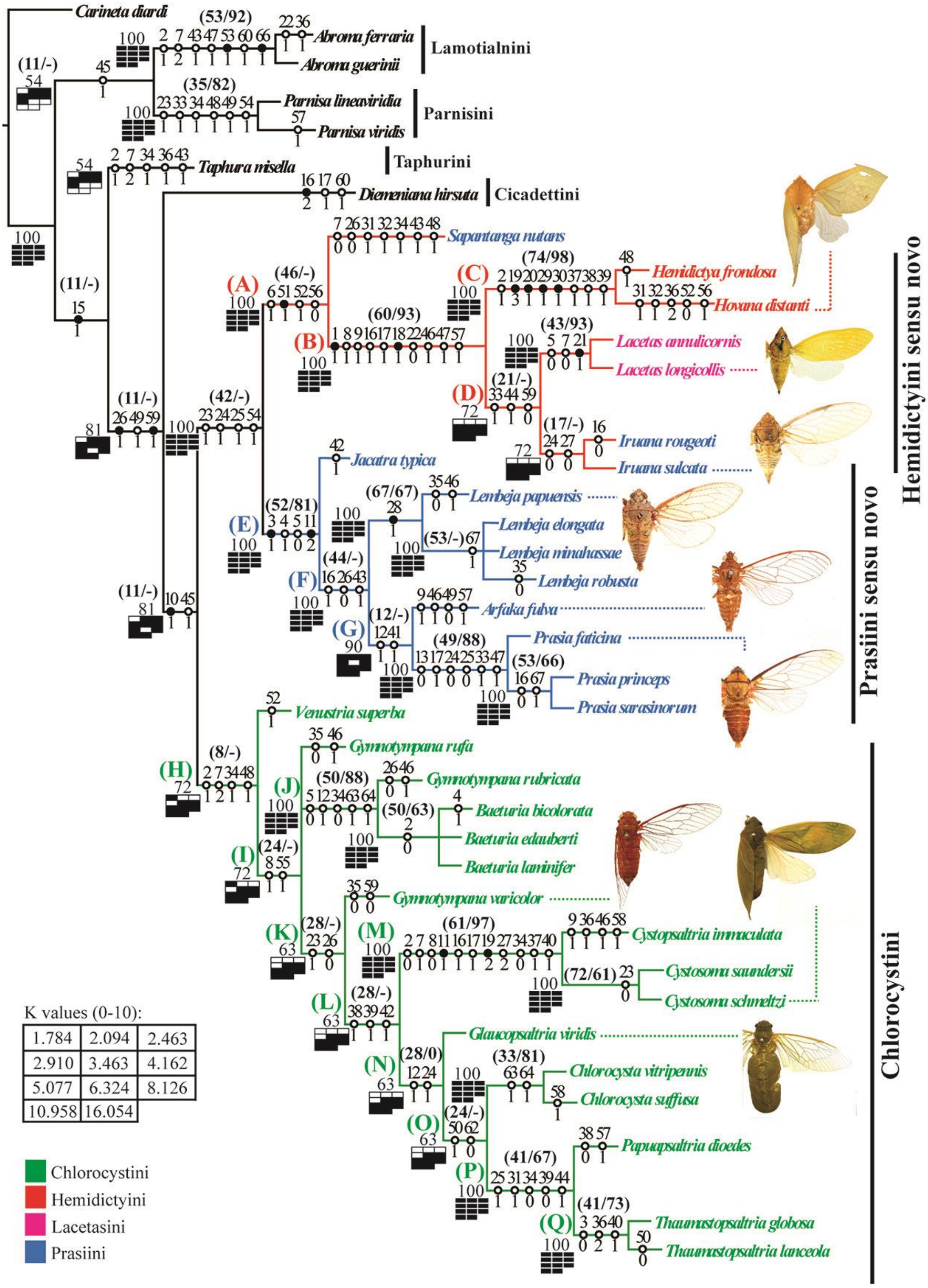

Figure 11. Strict consensus cladogram resulting from analyses under implied weighting. Ambiguos transformations not shown. (● = nonhomoplasious transformations; ○ = homoplasious transformations; capital letters in parentheses indicate the clades referred in discussion; numbers in parentheses above the branches indicate relative Bremer support and Jackknife with symmetric resampling, respectively. Taxa and branch colours refer to the tribal classification in Marshall et al. (2018). Filled rectangles represent the concavity constants (k-values) for which the clades are recovered (the values are presented in the legend).

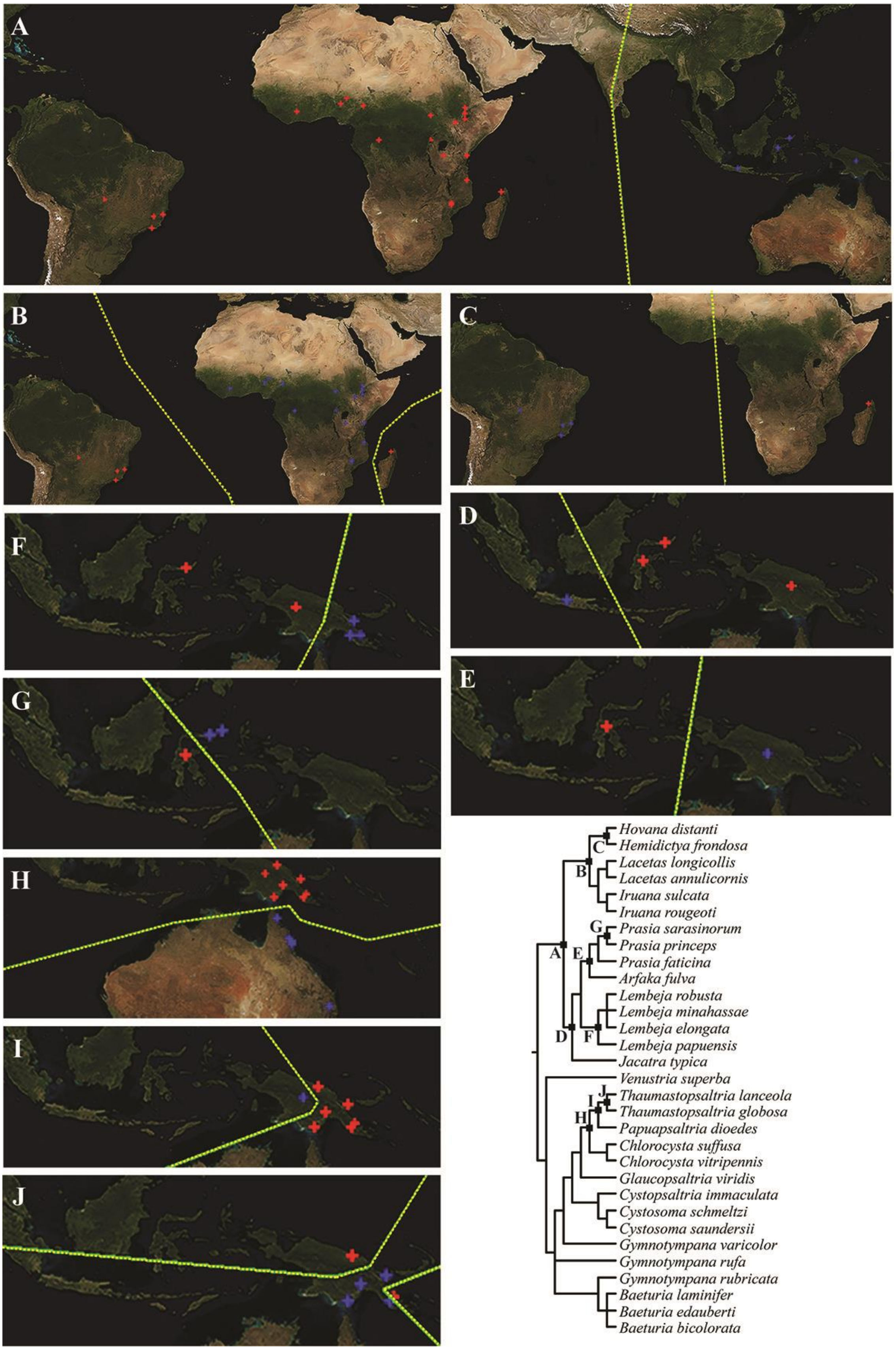

Figure 12. Clades of the ingroup used in the VIP analysis. Black squares represent the disjunction nodes (A-J). Blue and red crosses correspond to distributions of terminals in the respective A-J maps. Dotted yellow lines represent the Voronoi lines.

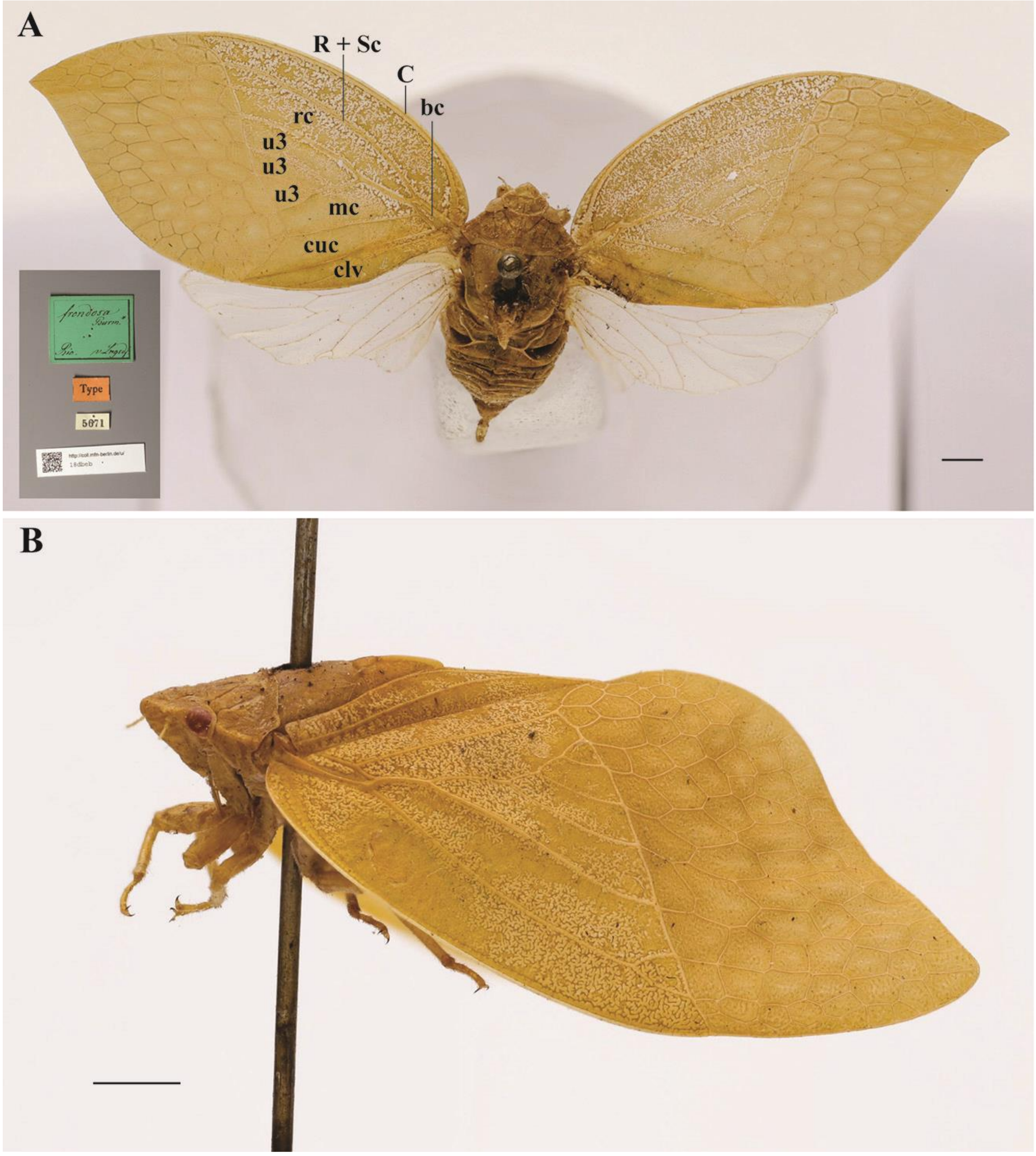

Figure 13. Lectotype (A) and paralectotype (B) male of *Hemidictya frondosa* (ZMHB) in dorsal and lateral view, respectively. Scales: 1 mm.

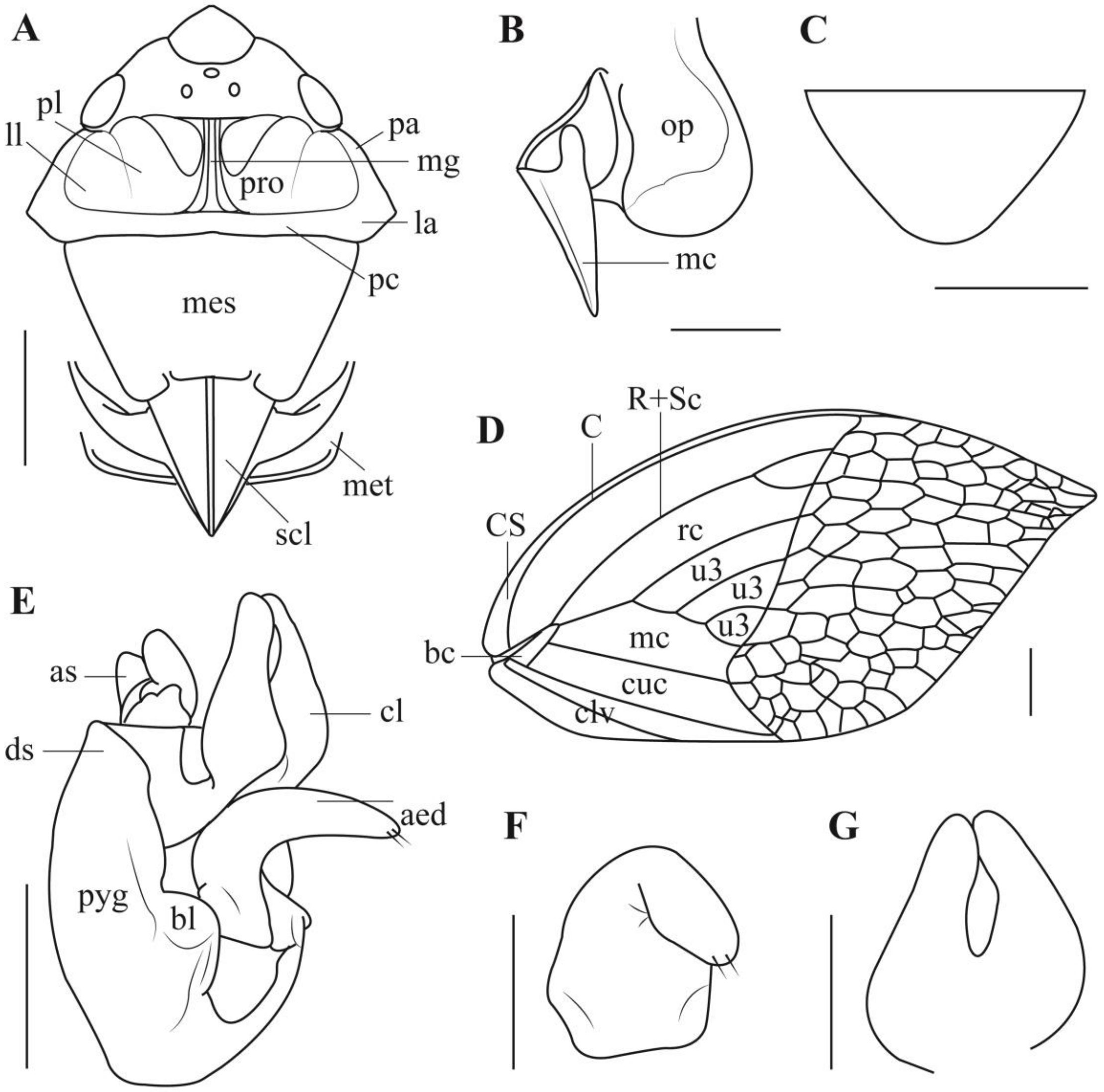

Figure 14. *Hemidictya frondosa* (male). A. Head, pronotum and mesonotum in dorsal view; B. Operculum and meracanthus in ventral view; C. Sternite VII in ventral view; D. Forewing in dorsal view; E. Pygofer in lateral view; F. Aedeagus in frontal view; G. Claspers in ventral view. Scales: A, D = 2mm, B, C, E = 1mm, F, G = 0.5mm.

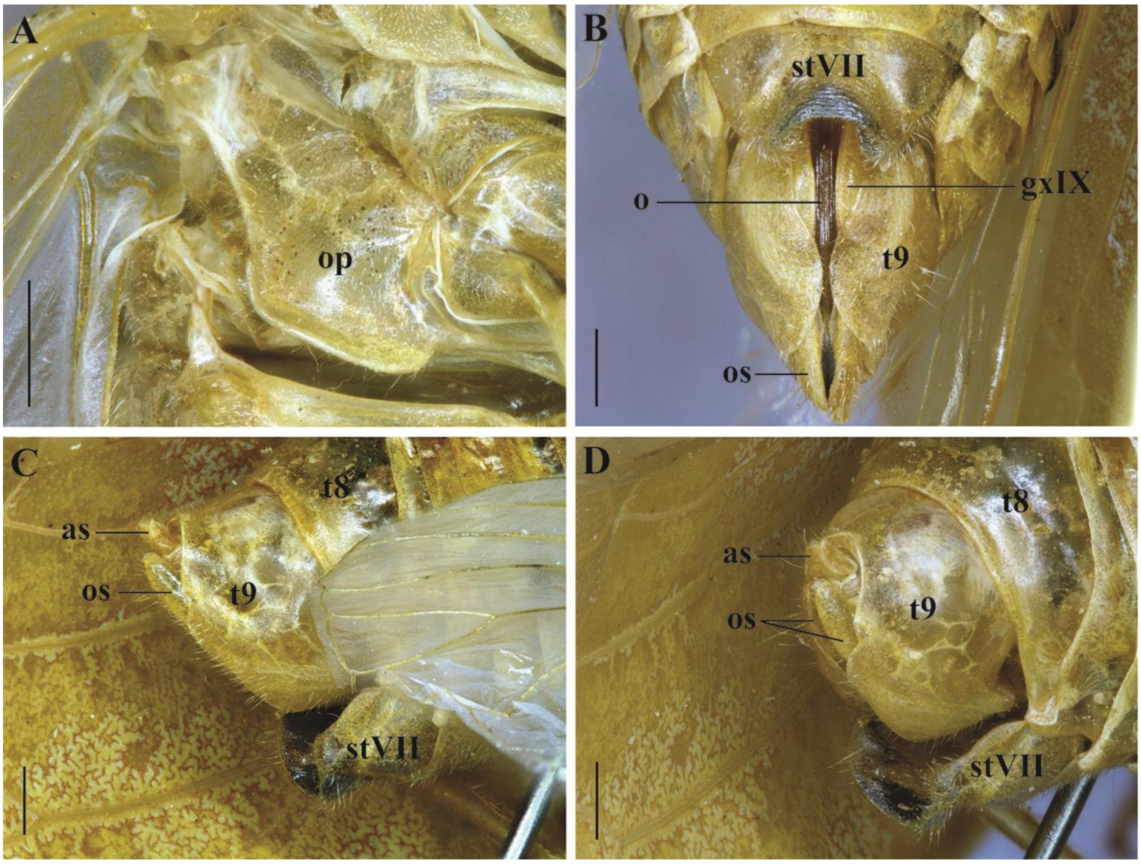

Figure 15. *Hemidictya frondosa* (female) (DZUP). A, operculum in ventral view; B, terminalia in ventral view, lateral view (C) and postero-lateral view (D). Scales: 1 mm.

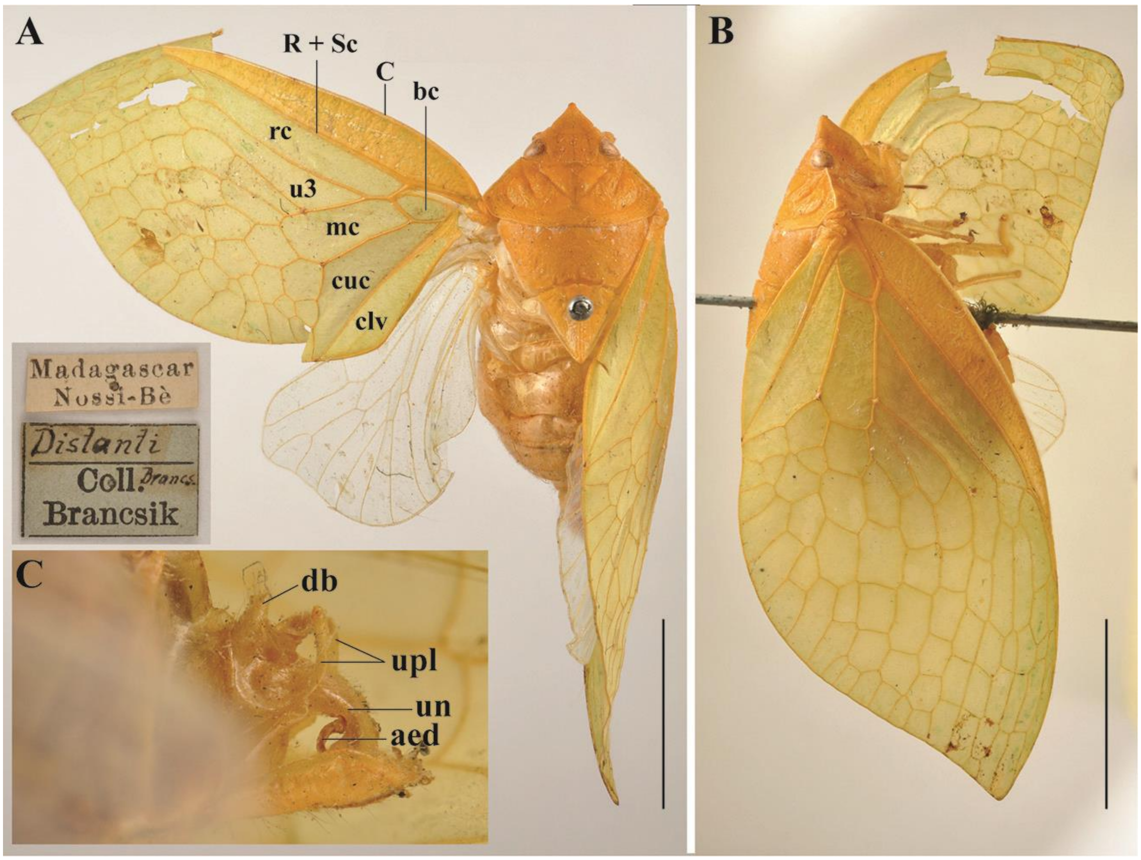

Figure 16. Holotype male of *Hovana distanti* in dorsal (A) and lateral views (B), and pygofer in lateral view (C) (HNHM). Scales: 1 cm.

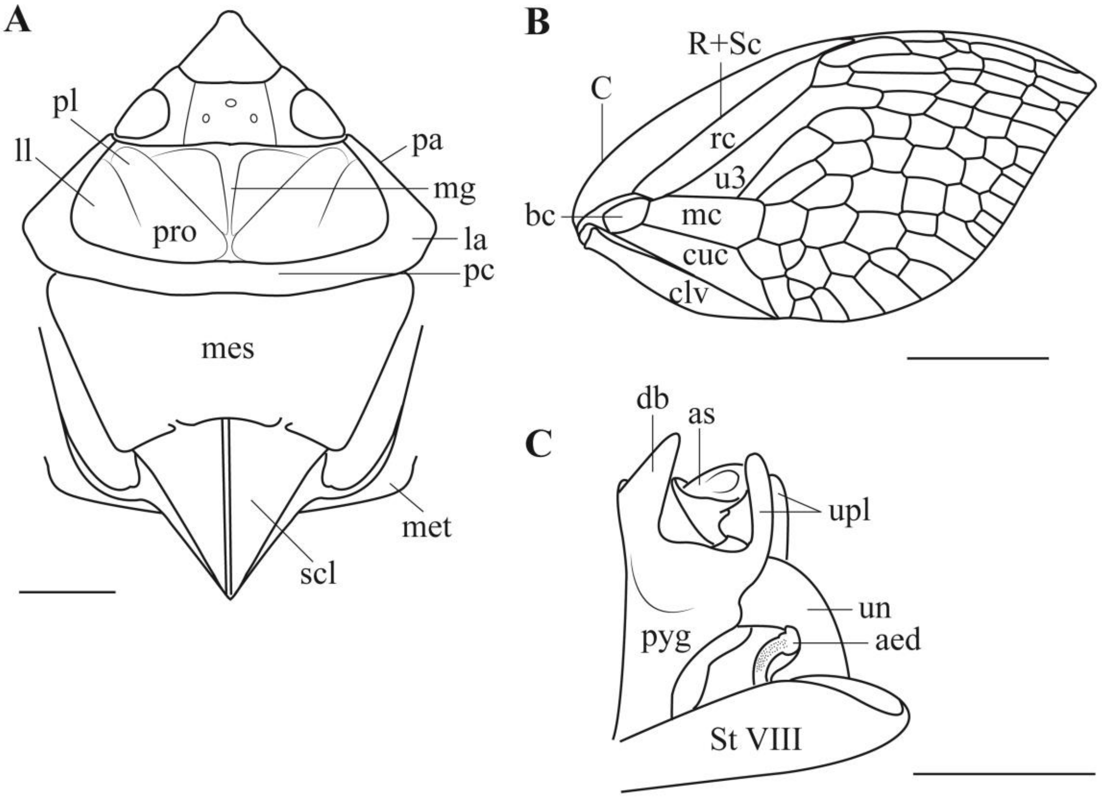

Figure 17. *Hovana distanti* (male). A. Head, pronotum and mesonotum in dorsal view; B. Forewing in dorsal view; C. Pygofer in lateral view. Scales: A, B = 2 mm, C = 1 mm.

Figure 18. A. *Iruana rougeoti* (male) in dorsal view (NHMUK); pygofer in lateral (B) and postero-lateral views (C). Scales: A = 10 mm, B, C = 1 mm.

Figure 19. A. Syntype male of *Iruana sulcata* in dorsal view; pygofer in lateral (B) and ventral views (C). Scales: A = 10 mm, B, C = 1 mm.

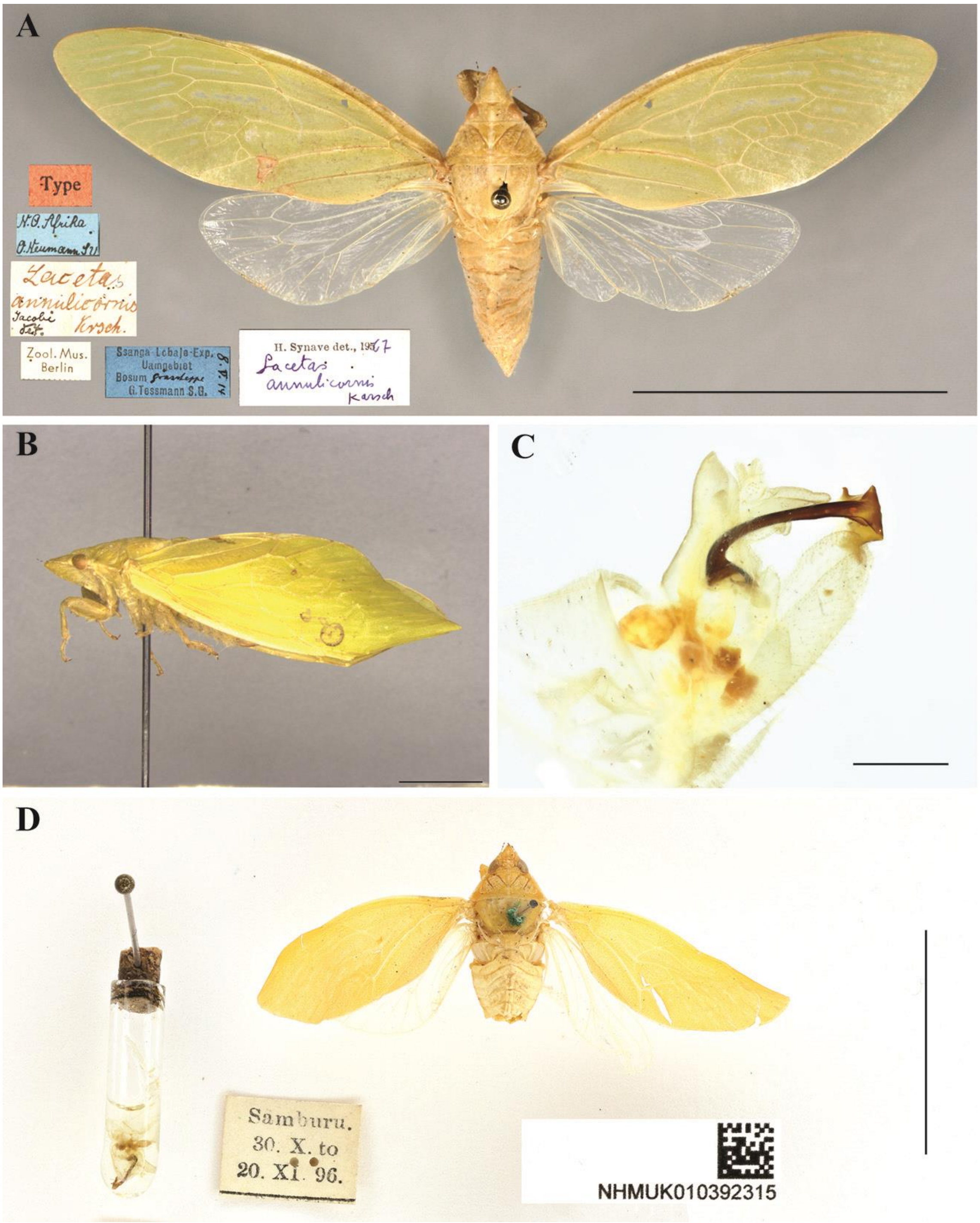

Figure 20. A. Holotype female of *Lacetas annulicornis* in dorsal (ZMHB); B. Specimen female of *Lacetas annulicornis* in lateral view (ZMHB); C. Pygofer in lateral view (NHMUK); D. Specimen male in dorsal view (NHMUK). Scales: A, B = 5 mm; C = 1 mm; D = 20 mm.

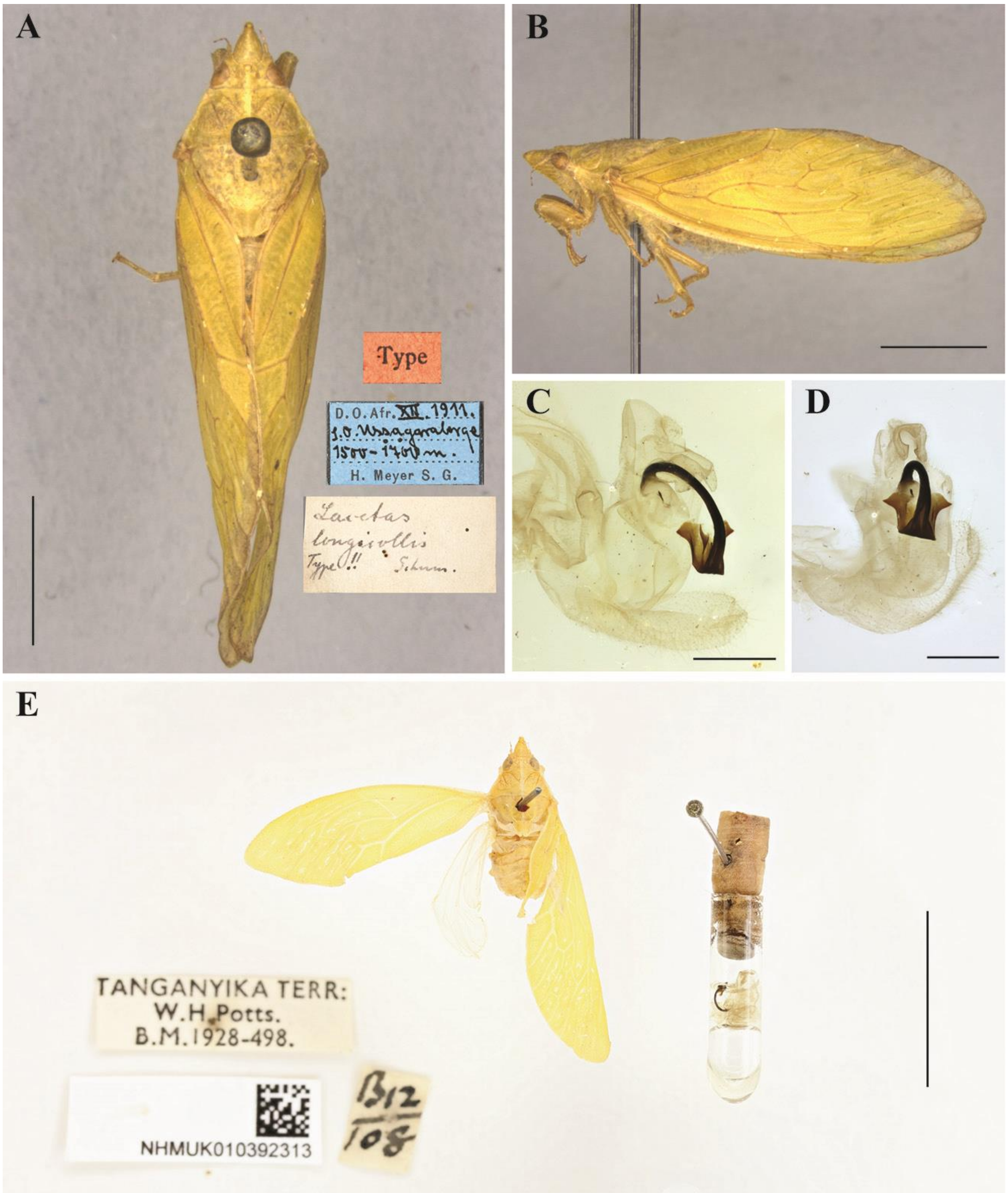

Figure 21. Syntype male of *Lacetas longicollis* in dorsal (A) and lateral view (B) (ZMHB); Pygofer in lateral (C) and ventral views (D) (NHMUK); Specimen male in dorsal view (E) (NHMUK). Scales: A, B = 5 mm; C and D = 1 mm; E = 20 mm.

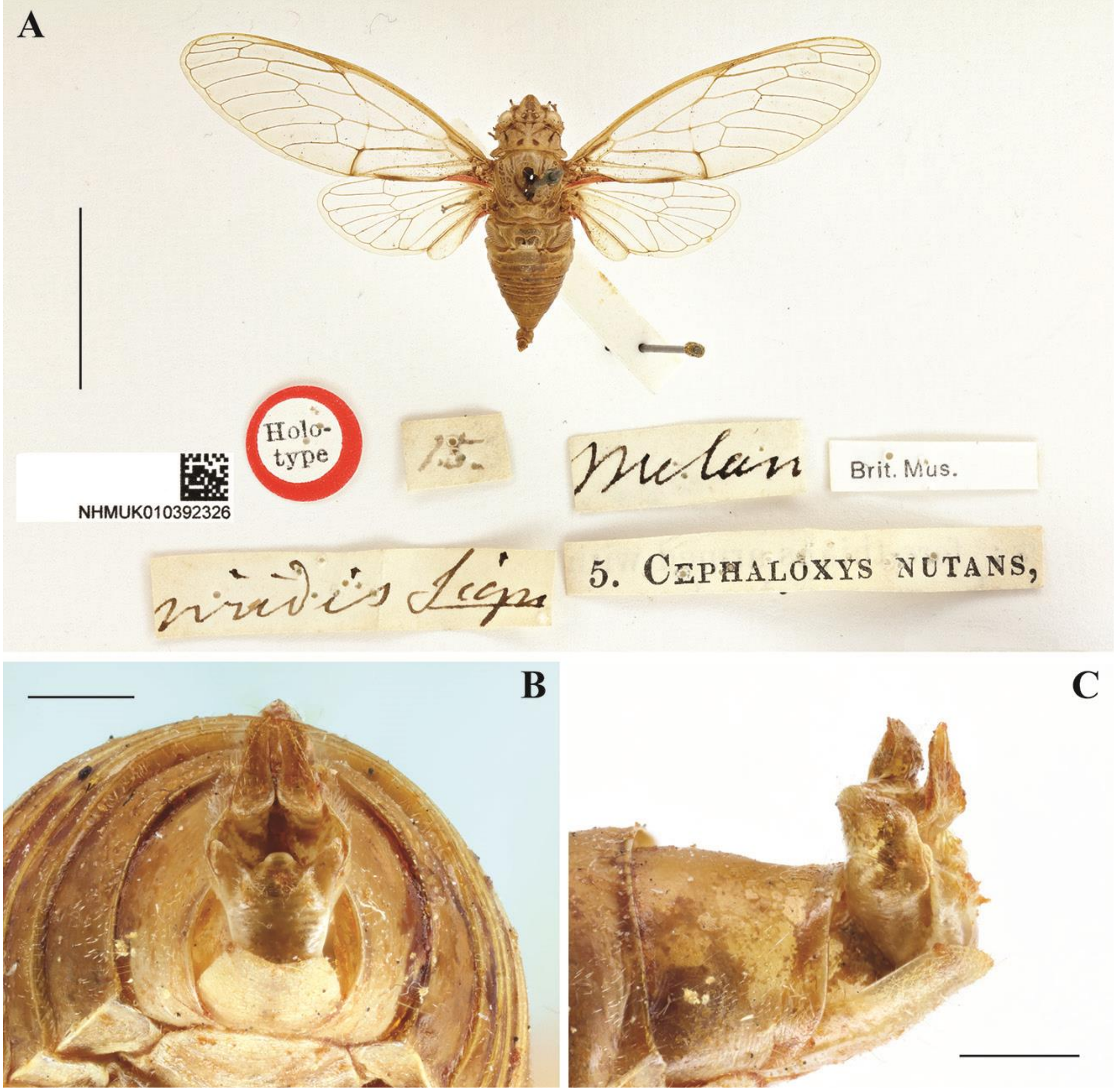

Figure 22. A. Holotype male of *Sapantanga nutans* in dorsal view (NHMUK); pygofer in ventral (B) and lateral view (C) (NHMUK). Scales: A = 10 mm, B, C = 1 mm.

SUPPORTING INFORMATION

S1 Geographical coordinates and deposit data of sampled species of Chlorocystini, Hemidictyini and Prasiini.

Tribe	Species	Author	Type	Deposition data	Long	Lat	Sex	Institution
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835	lectotype	frondosa\Burm.\Rio\\Type\\5671	-43,280000	-22,880000	♂	ZMHB
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835		Chap. Guimarães - MT\03-05.XII.1983\Exc. Dep. Zool. UFPR\(Polonoroeste)\Malaíse\\Dpto. Zoll.\UF-Paraná	-55,750000	-15,460000	♂	DZUP
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835		CHAPADA - MT\Brasil XI.63\M. Alvarenga	-55,750000	-15,460000	♂	DZUP
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835		CHAPADA - MT\Brasil XI.63\M. Alvarenga	-55,750000	-15,460000	♂	DZUP
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835		Linhares\ES- Brasil\XII-1965\A. Maller\\Dpto Zool\UF-PARANÁ	-40,060000	-19,390000	♀	DZUP
Hemidicityini	*Hemidictya frondosa*	Burmeister, 1835		BRA, MG, Marliéria/\Timóteo, Parque Estadual\do Rio Doce, 14.XI.1980-\16.XI.1980, M.A. Vulcano\et al. leg.	-42,750000	-19,720000	♀	UFMG
Hemidicityini	*Hemidictya distanti*	Brancsik, 1893	holotype	Madagascar\Nossi-Bè	48,263206	-13,320482	♂	HNHM
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890	holotype	(Ungaran) N.O. Africa\O. Neumann J.U.\\Lacetas\annulicornis\Karsch\Jacobi det.\\Type\\Zool. Mus.\Berlin			♀	ZMHB
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Ssanga Lobaje Exp.\Uamgablot\Bosum Grasdeppe\G.Tessmann S.G.\8.V.14\\H. Synave det., 1967\Lacetas\annulicornis\Karsch			♀	ZMHB
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Abyssinia\Lake Rudolph Exp.\Ph. C. Zaphiro.\1906-78	36,112432	4,529547	♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		ABYSSINIA\Provinces Ecuatoriales\Gofa Basketo Dime\MISSION\DU BOURG DE BOZAS 1903\\Distant Coll.\1911-383.			♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Bouaké\\Lacetas\annulicornis\Michel Boulard det. 1972	-5,039002	7,689368	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Bobo 24/6/75\Quattara\\UPPER VOLTA\P. Jolivet\\Pres by\Comm Inst Ent\B.M. 1978-1\\C.I.E. COLL.\A. 9610\\Lacetas\annulicornis\det. M.S.K. Ghauri, 1977 Kar.			♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		B.M. E. Africa Exp.\Tendaguru\13-XII-1925\F.W.H. Migeod.\B.M. 1926-42\\Lacetas\annulicornis J	39,116667	-10,050000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		B.M. E. Africa Exp.\Tendaguru\13-XII-1925\F.W. H. Migeod.\B.M. 1926-42	39,116667	-10,050000	♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Congo\\Distant Coll.\1911-383	16,132282	-0,263059	♀	BMNH
Hemidicityini	*Lacetas*	Karsch,		EAST AFRICA:\Tendaguru\21.I.1925\W.E.Cutler\B.M. 1930-	39,116667	-10,050000	♀	BMNH

	annulicornis	1890		489\\Tendaguru\21-I-25				
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		N. Nigeria\Zungeru.\Apl. 1911\J.W. Scott-Macfie.\1911-417	6,150000	9,810000	♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		N. Nigeria:\Yola.\Dr. L.N. Lee.\\Brit. Mus.\1924-420	12,495389	9,202341	♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		N. NIGERIA:\Zaria\Samaru\23.IV.1966\\Brit. Mus. 1967-684\\66/2?/94\\J.C. Deeming\m.v. trap.\\Lacetas sp.\det. P.S. Broomfield 1966	7,704949	11,109313	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		NIGERIA: \Samaru\18-25.v.1970\P.H. Ward.\B.M. 1970-604\\Mercury vapour\light trap.	7,630000	11,170000	2♂2♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		NIGERIA: \Samaru\1-2.vi.1970\P.H.Ward\B.M. 1970-604	7,630000	11,170000	♂♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		NIGERIA: \Samaru\1-2.vi.1970\P.H.Ward\B.M. 1970-604\\Mercury vapour\light trap.	7,630000	11,170000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		NIGERIA: \Samaru\3-10.vi.1970\P.H.Ward\B.M. 1970-604\\Mercury vapour\light trap.	7,630000	11,170000	2♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		NIGERIA: \Samaru\26-31.v.1970\P.H.Ward\B.M. 1970-604	7,630000	11,170000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Nyasaland.\Cholo\2700 ft.\R.C. Wood.\\Pres. By\Imp. Bur. Ent.\Brit. Mus.\1923-559\\Lacetas\annulicornis\Karsh\Det. B. Uvarov.	35,150000	-16,070000	♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Nyasaland\Cholo.\R. C. Wood.\\Pres. By\Imp. Inst. Ent.\B.M. 1936-27\\2289\Cholo.\\Lacetas\annulicornis\Karsh\Det. B. Uvarov.	35,150000	-16,070000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Nyasaland\Chiromo\R.C. Wood.\Pres. By\Imp. Bur. Ent.\Brit. Mus.\1923-559	35,160000	-16,550000	♂♀	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Samburu\30.X. to\20.XI.96	39,280000	-3,780000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		Sudan: Gell River Post.\70m from Bahr-el-Gebel.\5 54 N. 30 45 E.\Bimb. F. Moysey. 1923\\Brit. Mus. 1924-112	29,680000	6,810000	♂	BMNH
Hemidicityini	*Lacetas annulicornis*	Karsch, 1890		TANGANYICA\Old Shinyanga\20.XII.54\E. Burtt.\\COM. INST. ENT.\COLL. NO. 14251\\Pres by\Com Inst Ent\BM 1956-611\\Lacetas sp.\N.C.E. Miller det. 1955	33,400000	-3,550000	♂	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912	syntype	D-Ostafrika\Tendaguru, Lindi\XII.09.I.10\Janensch S.G.\\Zool. Mus. Berlin	39,116667	-10,050000	♂	ZMHB
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912	syntype	D.O. Afr. XII.1911\L.O.Ussaganaberge\15 nov.-1700 m\H. Meyer S.G.	39,116667	-10,050000		ZMHB

Hemidicityini	*Lacetas longicollis*	Schumacher, 1912	syntype	D.O. Afr. XII.1911\L.O.Ussagana-\berge 15 nov.-1700 m\H. Meyer S.G.	39,116667	-10,050000		ZMHB
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912	syntype	D. Ostafrika\Tendaguru, Lindi\XII.09-I.10\Janensch S.G.	39,116667	-10,050000		ZMHB
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		East Africa.\1923.\Capt. Moysey.\\Brit. Mus.\1931-538.			♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		EAST AFRICA:\Tendaguru\22.I.1925\W.E.Cutler\B.M. 1930-489\\Tendaguru\22-I-25	39,116667	-10,050000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Ilesha\So. Nigeria\(Capt. Humfrey).\\Brit. Mus.\1924-292.	4,740000	7,630000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		NYASALAND:\Ramens\18.XII.1946\\Grass: Ramens\18.12.46\\R.H. Lowe.\B.M. 1948-309\\Grass.			♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Karamoja 4 50\van Someren\M.t Labwor\Karamoja 4 50\\V.G.L. van Someren\Collection.\Brit. Mus. 1959-468\\COM. INST. ENT.\COLL. NO. 11740\\Lacetas sp.\N.C.E. Miller det. 1950	33,180000	4,110000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika Territory\Kilosa 15.xii.25\N.C.E. Miller\al light\\Pres. By\ Imp. Bur. Ent.\Brit. Mus.\1927-503	36,991825	-6,835078	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika Terr.\30.XI.1917\A. Loveridge.\\Pres. By\ Imp. Bur. Ent.\Brit. Mus.\1926-394	35,005485	-6,624416	♂	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika Terr:\W. H. Potts.\B.M.1928-498\\1312\108	35,005485	-6,624416	♂	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika Terr:\W.H.Potts.\B.M. 1928-498	35,005485	-6,624416	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika Territory\Kilosa 15.XII.25\N.C.E. Miller\al. light\\Pres. By\ Imp. Bur. Ent.\Brit. Mus.\1927-503	36,991825	-6,835078	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika:\Old. Shinyanga\2.I.55\E. Burtt.\\COM. INST. ENT.\COLL. NO. 14251\\Lacetas sp.\N.C.E. Miller det. 1955	33,400000	-3,550000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		Tanganyika:\Old. Shinyanga\in house\E. Burtt.\17.12.47Pres. by\Com Inst Ent \BM 1956-611	33,400000	-3,550000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		TANGANYIKA:\Old Shinyanga\E. Burtt.\20.XII.54\\Pres. By\Com Inst Ent \BM 1956-611	33,400000	-3,550000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		UGANDA \Lake George\iii.1933\HB Johnston\Short Grass\plains\\Lacetas\lon.\-gicollis Schum	30,120200	-0,01949	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		UGANDA \Lake George\iii.1933\HB Johnston\Short Grass\plains	30,120200	-0,01949	♀	BMNH

Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		UGANDA\Ankole\Gayaza\17.iii.1936\H.B. Johnston\\Acacia Bush\cut for\Tsetse control	32,615032	0,451199	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		UGANDA:\Nebbi\West Nile\grass on farm.\4.vi.1956\\Coll. P.E.S. & E.M. Whalley\B.M. 1961-343\\157	31,090000	2,480000	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		van Someren\Mt Labwor\Karamoja 4 50\\V.G.L. van Someren\Collection\Brit. Mus. 1959-468.	33,180000	4,110000	2♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		van Someren\Bwamba Valley\W. Uganda\May 1954\\V.G.L. van Someren\Collection\Brit. Mus. 1959-468	30,043358	0,833167	♀	BMNH
Hemidicityini	*Lacetas longicollis*	Schumacher, 1912		van Someren\MandiOpei\N: Uganda 5 51			♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905	syntype	Lagari\Mch. 1 to May 21\1900\(Mile 469)\\Brit E. Africa\C.S. Betton\1902-146\\Iruana\sulcata\type Dist.\\Type\\Syntype\\NHMUK010392330			♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905	syntype	Lagari\Mch. 1 to May 21\1900\(Mile 469)\\Brit E. Africa\C.S. Betton\1902-146\\Syntype\\NHMUK010392331			♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905	syntype	Lagari\Mch. 1 to May 21\1900\(Mile 469)\\Brit E. Africa\C.S. Betton\1902-146\\Syntype\\NHMUK010392332			♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Abyssinia: Djem-Djem Forest.\over 8000 ft.\10.x.1926\J. Omer Cooper\\Brit. Mus.\1927-127\\Box48	38,558998	8,974885	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Abyssinia: Djem-Djem Forest.\over 8000 ft.\7-9.x.1926\Dr. H. Scott.\\Brit. Mus.\1927-127\\Box41	38,558998	8,974885	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		ABYSSINIA:\Wolamo Prov.\Soddu\c. 6.800ft.\1-15.XI.1948\\ETHIOPIA:\1948-1949\Hugh Scott\B.M. 1949-184	37,750000	6,900000	♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Allan. Turner\KAIMOSI\Mch.Apl. 1932\\Iruana\sulcata Dist\Michel Boulard det. 1971	34,846296	0,124331	♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Allan. Turner\KAIMOSI\Mch.Apl. 1932	34,846296	0,124331	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Allan. Turner\KAIMOSI\Mch. Apl, 1932	34,846296	0,124331	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		Brit. E. Africa\C.S. Betton\1902-146\\Lagari\Mch. 1 to May 21\1900\(Mile 469)			♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		H.J.A. Turner\ Kakamega\AUG 1933	34,750000	0,280000	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		H.J.A. Turner\West Aberdares\Above 9000 ft.\Mch. Apl. 1934\\Iruana\sulcata Dist\Michel Boulard det. 1972 (sem o abdomen)	36,666211	-0,414626	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		KENYA: Muguga\26-III-1952\I.W.B.Nye\\N973\\At light	36,660000	-1,190000	♀	BMNH

Hemidicityini	*Iruana sulcata*	Distant, 1905		Nairobi 3-26	36,820000	-1,280000	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		UGANDA: Ruwenzori Range\Nyinabitaba\8,650 ft. 7-13.vii.1952\D.S. Fletcher\\Iruana\sulcata Dist.\Michel Boulard det. 1972\\24\\Ruwenzori Exped.\B.M. 1952-566	29,871688	0,385822	♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		UGANDA: Ruwenzori Range\XII.1934-I.1935\B.M.E. Afr. Exp.\B.M. 1935-203\\Namwamba Valley\6.500 ft\F.W. Edwards	29,871688	0,385822	♀	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		van Someren\Kitale\July Aug 1932	35,010000	1,020000	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		van Someren\ Kitale\Jan, 1933	35,010000	1,020000	♂	BMNH
Hemidicityini	*Iruana sulcata*	Distant, 1905		van Someren\Nyeri (S.)\Kenya 10 48\\COM INST ENT.\COLL. NO. 11740\\Gen. nov.??? BM\N.C.E. Miller det. 1950\\V.G.L. van Someren\Collection\Brit. Mus. 1959-468	36,950000	-0,420000	♂	BMNH
Hemidicityini	*Iruana rougeti*	Boulard, 1975	holotype	Kebre-Mengist (1 800-2 000 m, au Nord de la province Sidamo), les 17-19-XI-1973	38,983333	5,883333	♂	MNHN
Hemidicityini	*Iruana rougeti*	Boulard, 1975	paratype	Koffole (2 200 m, dans le Sud de I'Arusi) le 31-X-1973	38,749997	7,000006	♀	MNHN
Hemidicityini	*Iruana rougeti*	Boulard, 1975		Abyssinia:\Djem-Djem Forest\8000-9000 ft.\22-26.ix.1926\Dr. H. Scott\\Brit. Mus.\1927-127\\Box\26	38,558998	8,974885	♂	BMNH
Hemidicityini	*Sapantanga nutans*	Walker, 1850	holotype	Locality Unknown			♂	BMNH
Chlorocystini	*Baeturia bicolorata*	Distant, 1892		Papua New Guinea, Western Province, Kiunga (6° 05' S, 141° 15' E) 18/07/1970 - 18/07/1970, McCaw, O. K.(Collector)	141,250000	-6,083333	♀	AMS
Chlorocystini	*Baeturia bicolorata*	Distant, 1892		Papua New Guinea, Gulf Province, Kikori, Doibu village (7° 25' S, 144° 14' E) 1956 - 1956, Dawson, P(Collector), Field Collected - Terrestrial	144,233333	-7,416667	♂	AMS
Chlorocystini	*Baeturia edauberti*	Boulard, 1979		Solomon Islands, Temotu Province, Santa Cruz Islands, Peu, Vanikoro (11° 41' S, 166° 50' E) /08/1926 - /08/1926, Troughton, E.(Collector), Livingstone, A. A.(Collector), Field Collected - Terrestrial	166,833333	-11,683333	♀	AMS
Chlorocystini	*Baeturia edauberti*	Boulard, 1979		Vanuatu, Sanma Province, Espiritu Santo, Hog Harbour 10/01/1923 - 10/01/1923, Barnard, T. T.(Collector), Field Collected - Terrestrial	167,100000	-15,130000	♂	AMS
Chlorocystini	*Baeturia edauberti*	Boulard, 1979		Vanuatu, Shefa Province, Efate, Efate Island (17° 40' S, 168° 23' E) 05/02/1907 - 05/02/1907, Field Collected - Terrestrial	168,383333	-17,666667		AMS
Chlorocystini	*Baeturia edauberti*	Boulard, 1979		Solomon Islands, Temotu Province, Santa Cruz Islands, Reef Island (10° 15' S, 166° 10' 00" E) 23/07/1926 - 23/07/1926, Troughton, E.(Collector), Livingstone, A. A.(Collector), Field Collected - Terrestrial	166,166667	-10,250000		AMS

Chlorocystini	*Baeturia laminifer*	Blöte, 1960		Papua New Guinea, Western Province, Kiunga (6° 05' S, 141° 15' E) 18/07/1970 - 18/07/1970, McCaw, O. K.(Collector)	41,250000	-6,083333	♂	AMS
Chlorocystini	*Baeturia laminifer*	Blöte, 1960		Papua New Guinea, Northern Province (Oro), Mount Lamington District (8° 57' S, 148° 09' E) 1928 - 1928, McNamara, Charles Terence(Collector), Field Collected - Terrestrial	148,150000	-8,950000	♀	AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Glen Innes (29° 44' 06" S, 151° 44' 19" E) 29/11/1963 - 29/11/1963, Moulds, Dr. Max S. - Australian Museum - Science(Collector)	151,738611	-29,735000	♂	AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Glen Innes (29° 44' 06" S, 151° 44' 19" E) 29/11/1963 - 29/11/1963, Moulds, Dr. Max S. - Australian Museum - Science(Collector)	151,738611	-29,735000	♂	AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Horseshoe Creek, near Kyogle (28° 33' S, 153° 03' E) 04/12/1987 - 04/12/1987, Scambler, D. J.(Collector), at light - see Notes	153,037175	-28,538162	♀	AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		[BRITTON 2006/032] Australia, Queensland, Eungella National Park, Broken River visitor area (21° 10' 07" S, 148° 30' 19" E) 21/04/2006 - 21/04/2006, Britton, Dr David R. - Australian Museum - Science(Collector), Weiner, Jean R. - Australian Museum - Natur	148,505278	-21,168611	♀	AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Laidley (27° 38' S, 152° 24' E) 19/02/1978 - 19/02/1978, Woodhead, W J(Collector)	152,400000	-27,633333		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Tenterfield (29° 03' S, 152° 01' E) 11/12/1946 - 11/12/1946, Pullen, R J(Collector), Accession	152,016667	-29,050000		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Kempsey (31° 05' S, 152° 50' E) 27/01/1981 - 27/01/1981, Day, Mr Barry J. - Australian Museum - Science(Collector), Gray, Dr Michael R. - The Australian Museum - Arachnology Department(Collector)	152,833333	-31,083333		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Eungella (21° 07' 02" S, 148° 29' 02" E) /04/1998 - /04/1998, Cassis, Dr Gerasimos A. - Australian Museum(Collector)	148,483889	-21,117222		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Lismore (28° 48' 25" S, 153° 17' 09" E) 10/12/1907 - 10/12/1907	153,285833	-28,806944		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Hastings River (31° 25' S, 152° 22' E), Chisholm, A H(Collector)	152,366667	-31,416667		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Terrigal (33° 26' 56" S, 151° 26' 35" E) /01/1950 - /01/1950, Peach, B(Collector)	151,443056	-33,448889		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Ash Island (32° 51' S, 151° 43' E)	151,716667	-32,850000		AMS

Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Gosford (33° 25' 25" S, 151° 20' 29" E) /11/1993 - /11/1993, Bray, M(Collector)	151,341389	-33,423611		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Tweed River (28° 20' 28" S, 153° 22' 09" E) 12/11/1909 - 12/11/1909	153,369167	-28,341111		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Glen Innes (29° 44' 06" S, 151° 44' 19" E) 11/12/1950 - 11/12/1950, Lowry, E.(Collector)	151,738611	-29,735000		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Sydney, Ryde (33° 48' 55" S, 151° 06' 04" E) 09/12/1951 - 09/12/1951, Muller, V C(Collector)	151,101111	-33,815278		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Eungella Range, Crediton State Forest (21° 14' 02" S, 148° 35' 10" E) 01/05/1995 - 05/05/1995, Theischinger, Gunther - Department of Environment and Conservation(Collector), Mueller, L.(Collector), Field Collected - Terrestrial	148,586111	-21,233889		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, 7 Burke St, Telopea (33° 47' 58" S, 151° 02' 28" E) 01/01/1979 - 01/01/1979, Smith, J.(Collector), Smith, K.(Collector), Field Collected - Terrestrial	151,041111	-33,799444		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, North-East New South Wales (31° 0' S, 150° 0' E), Field Collected - Terrestrial	150,000000	-31,000000		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Wyoming (33° 24' 19" S, 151° 21' 05" E) 20/10/1995 - 20/10/1995, Nedved, L(Collector), Field Collected - Terrestrial	151,351389	-33,405278		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Crediton National Park (21° 12' S, 148° 34' E) 29/04/1975 - 29/04/1975, P. Colman(Collector), Field Collected - Terrestrial	148,5666667	-21,200000		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Windsor Tableland, N of Mount Carbine (16° 14' S, 145° 01' E) 16/04/1994 - 16/04/1994, Moulds, Dr. Max S. - Australian Museum - Science(Collector), Field Collected - Terrestrial	145,016667	-16,233333		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Cedar Rd., Huonbrook, nr Mullumbimby (28° 32' S, 153° 21' E) 01/02/1991 - 15/02/1991, Ralph, T.(Collector), at light - see Notes, Field Collected - Terrestrial	153,350000	-28,533333		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, New South Wales, Upper Horseshoe Creek (28° 31' 54" S, 153° 04' 04" E) /12/1987 - /12/1987, Scambler, D. J.(Collector), at light - see Notes	153,067778	-28,531667		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Lower Beechmont (28° 04' 38" S, 153° 14' 54" E) 01/01/1982 - 04/01/1982, Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector)	153,248333	-28,077222		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Bunya Mountains National Park (26° 51' 30" S, 151° 36' 22" E) 06/01/1970 - 06/01/1970, Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector)	151,606111	-26,858333		AMS

Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Broken River Range, Eungella National Park (21° 03' S, 148° 17' E) 08/12/1961 - 08/12/1961, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	148,283333	-21,050000		AMS
Chlorocystini	*Cystosoma saundersii*	(Westwood, 1842)		Australia, Queensland, Mulgrave River, 7km W of Gordonvale (17° 07' S, 145° 43' E) 18/01/1991 - 18/01/1991, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Day, Mr Barry J. - Australian Museum - Science(Collector), Field Collected -	145,716667	-17,116667		AMS
Chlorocystini	*Cystosoma schmeltzi*	Distant, 1882		Australia, New South Wales, Narrabri (30° 19' 54" S, 149° 46' 04" E) 15/01/1982 - 15/01/1982, Everingham, Greg(Collector)	149,767778	-30,331667	♂	AMS
Chlorocystini	*Cystosoma schmeltzi*	Distant, 1882		Australia, Queensland, Carnavon Range (25° 30' S, 149° 50' E) 12/12/1938 - 12/12/1938, Geary, N.(Collector)	149,833333	-25,500000	♂	AMS
Chlorocystini	*Cystosoma schmeltzi*	Distant, 1882		Carnarvon Rge.\Q. 12 Dec. 1938\N. Geary	148,666677	-25,333411	♀	AMS
Chlorocystini	*Cystosoma schmeltzi*	Distant, 1882		Australia, Queensland, Mundubbera (25° 35' 17" S, 151° 17' 56" E) 06/12/1996 - 06/12/1996, Smith, Mr Derek John - Australian Museum - Science(Collector), Freebairn, C(Collector), Field Collected - Terrestrial	151,298889	-25,588056	♀	AMS
Chlorocystini	*Cystopsaltria immaculata*	Goding & Froggat, 1904		Australia, Queensland, Broken River Range, Eungella National Park (21° 03' S, 148° 17' E) 08/12/1961 - 08/12/1961, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	148,283333	-21,050000	♀	AMS
Chlorocystini	*Cystopsaltria immaculata*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 28/01/1972 - 28/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♀	AMS
Chlorocystini	*Cystopsaltria immaculata*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 28/01/1972 - 28/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♂	AMS
Chlorocystini	*Cystopsaltria immaculata*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 28/01/1972 - 28/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♂	AMS
Chlorocystini	*Cystopsaltria immaculata*	Goding & Froggat, 1904		Australia, Queensland, Kuranda (16° 49' 12" S, 145° 38' 13" E) /11/1910 - /11/1910, Dodd, Frederick Parkhurst(Collector)	145,636944	-16,820000		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Comboyne (31° 35' 55" S, 152° 28' 04" E) /12/1924 - /12/1924, Chisholm, Dr E. C.(Collector)	152,467778	-31,598611	♀	AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Lower Beechmont (28° 04' 38" S, 153° 14' 54" E) 01/01/1982 - 04/01/1982, Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector)	153,248333	-28,077222	♀	AMS

Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Huonbrook (28° 32' S, 153° 21' E) 27/02/1965 - 28/02/1965, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	153,350000	-28,533333	♂	AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Lansdowne (31° 46' 55" S, 152° 32' 06" E) 29/12/1980 - 29/12/1980, Williams, G.(Collector)	152,535000	-31,781944	♂	AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Terania Ck, nr. Lismore (28° 37' S, 153° 18' E) 05/02/1983 - 05/02/1983, D.K. McAlpine & K.C. Khoo(Collector), at light	153,300000	-28,616667		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Wilson River Bridge nr Bluff Point Picnic area (31° 13' S, 152° 39' E) 06/01/1999 - 06/01/1999, B.J. & R. Day(Collector), at light	152,650000	-31,216667		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Mullimbimby (=Mullumbimby) (28° 32' 56" S, 153° 30' 04" E) 14/02/1992 - 27/02/1992, Ralph, T.(Collector), at light - see Notes, Field Collected - Terrestrial	153,501111	-28,548889		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Huonbrook (28° 32' S, 153° 21' E) 04/12/1961 - 04/12/1961, Lossin, R.(Collector)	153,350000	-28,533333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Ballina (28° 51' 51" S, 153° 33' 56" E) 25/09/1922 - 25/09/1922, Waterhouse, Gustavus Athol - Australian Museum(Collector)	153,565556	-28,864167		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Horseshoe Creek, near Kyogle (28° 33' S, 153° 03' E) 06/11/1987 - 06/11/1987, Scambler, D. J.(Collector)	153,050000	-28,550000		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Ballina (28° 51' 51" S, 153° 33' 56" E) 07/10/1922 - 07/10/1922, Burns, Alexander Noble(Collector)	153,565556	-28,864167		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Bellingen (30° 27' S, 152° 54' E) 04/01/2000 - 04/01/2000, Day, Mr Barry J. - Australian Museum - Science(Collector)	152,900000	-30,450000		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Tweed River (28° 20' 28" S, 153° 22' 09" E) 07/11/1909 - 07/11/1909	153,369167	-28,341111		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Caringbah (34° 02' S, 151° 08' E) 15/10/1998 - 15/10/1998, McCormick, Jeff(Collector)	151,133333	-34,033333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, East Dorrigo (30° 20' 25" S, 152° 42' 45" E) 03/12/1929 - 03/12/1929, Heron, W.(Collector), Field Collected - Terrestrial	152,712500	-30,340278		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Fernleigh (28° 45' 55" S, 153° 29' 51" E) 12/02/1995 - 12/02/1995, James, C R(Collector), Field Collected - Terrestrial	153,497500	-28,765278		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Wilson River, Bluff Point Picnic Area (31° 0' S, 153° 0' E) 03/01/2001 - 07/01/2001, Day, Mr Barry J. - Australian	153,000000	-31,000000		AMS

				Museum - Science(Collector), Day, K. A.(Collector), Day, E M(Collector), Field Collected - Terrestria				
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Lamington National Park, Monkey Duck Creek Road (28° 14' S, 153° 0' E) 08/12/1993 - 08/12/1993, Cassis, Dr Gerasimos A. - Australian Museum(Collector), At light, Field Collected - Terrestrial	153,000000	-28,233333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Montville, Palmwoods, North Coast Line (26° 41' 23" S, 152° 53' 34" E) /12/1928 - /12/1928, McCartney, H C(Collector), Field Collected - Terrestrial	152,892778	-26,689722		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Laidley (27° 38' S, 152° 24' E) 19/02/1978 - 19/02/1978, Woodhead, W J(Collector)	152,400000	-27,633333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Tamborine (27° 51' 23" S, 153° 07' 11" E) 28/12/1912 - 28/12/1912	153,119722	-27,856389		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Wilson River, Bluff Point Picnic Area (31° 0' S, 153° 0' E) 03/01/2001 - 07/01/2001, Day, Mr Barry J. - Australian Museum - Science(Collector), Day, K. A.(Collector), Day, E M(Collector), Field Collected - Terrestrial	153,000000	-31,000000		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Ulong (30° 13' 55" S, 152° 53' 06" E)	152,885000	-30,231944		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Tweed River (28° 20' 28" S, 153° 22' 09" E) /11/1907 - /11/1907	153,369167	-28,341111		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Nightcap National Park, nr. Terania Creek (28° 35' S, 153° 10' E) 28/12/1993 - 30/12/1993, Williams, Dr Geoff A. - Australian Museum - Science(Collector)	153,166667	-28,583333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, New South Wales, Minyon Falls Rd. (28° 36' 48" S, 153° 23' 29" E) 26/02/1965 - 26/02/1965, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Field Collected - Terrestrial	153,391389	-28,613333		AMS
Chlorocystini	*Chlorocysta vitripennis*	(Westwood, 1851)		Australia, Queensland, Binna Burra, Lamington National Park (21° 10' S, 139° 49' E) 02/02/1961 - 02/02/1961, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	139,816667	-21,166667		AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Kuranda (16° 49' 12" S, 145° 38' 13" E) 20/02/1972 - 20/02/1972, Davies, G.(Collector)	145,636944	-16,820000	♀	AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Hutchinson Creek, near Daintree River (16° 13' 02" S, 145° 25' 23" E) 08/01/1967 - 08/01/1967, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(	145,423056	-16,217222	♀	AMS

Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Kuranda (16° 49' 12" S, 145° 38' 13" E) 20/02/1972 - 20/02/1972, Davies, G.(Collector)	145,636944	-16,820000	♂	AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Kuranda (16° 49' 12" S, 145° 38' 13" E) 20/02/1972 - 20/02/1972, Davies, G.(Collector)	145,636944	-16,820000	♂	AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Laidley (27° 38' S, 152° 24' E) 19/02/1978 - 19/02/1978, Woodhead, W J(Collector)	152,400000	-27,633333		AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Gordonvale (17° 05' 38" S, 145° 47' 12" E) /12/1917 - /12/1917, Jarvis, Edmund - Queensland Government - Department of Agriculture and Stock(Collector)	145,786667	-17,093889		AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Cairns (16° 55' 20" S, 145° 46' 33" E) 11/01/1951 - 11/01/1951, Brooks, Dr. J. G.(Collector)	145,775833	-16,922222		AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Claudie River, near Lamond Hill (12° 44' 44" S, 143° 16' 40" E) 21/12/1971 - 21/12/1971, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collec	143,277778	-12,745556		AMS
Chlorocystini	*Chlorocysta suffusa*	(Distant, 1907)		Australia, Queensland, Kuranda (16° 49' 12" S, 145° 38' 13" E)	145,636944	-16,820000		AMS
Chlorocystini	*Glaucopsaltria viridis*	Goding & Froggat, 1904		Australia, Queensland, Mount Tamborine (27° 58' 21" S, 153° 11' 52" E) /10/1924 - /10/1924, Musgrave, Mr Anthony - Australian Museum(Collector), Geissmann, C.(Collector)	153,197778	-27,972500	♀	AMS
Chlorocystini	*Glaucopsaltria viridis*	Goding & Froggat, 1904		Australia, Queensland, Buderim (26° 41' 06" S, 153° 03' 14" E) 06/03/1988 - 06/03/1988, Fisher, J(Collector), Field Collected - Terrestrial	153,053889	-26,685000	♂	AMS
Chlorocystini	*Glaucopsaltria viridis*	Goding & Froggat, 1904		Australia, New South Wales, Ballina (28° 51' 51" S, 153° 33' 56" E) 07/10/1922 - 07/10/1922, Burns, Alexander Noble(Collector)	153,565556	-28,864167		AMS
Chlorocystini	*Glaucopsaltria viridis*	Goding & Froggat, 1904		Australia, Queensland, Brisbane (27° 28' 16" S, 153° 01' 27" E)	153,024167	-27,471111		AMS
Chlorocystini	*Gymnotympana rubricata*	(Distant, 1897)		Papua New Guinea, Northern Province, Ijivitari, Popondetta, Awala (8° 46' S, 148° 14' E) 04/11/1963 - 04/11/1963, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Field Collected - Terrestrial	148,233333	-8,766667	♀	AMS
Chlorocystini	*Gymnotympana rubricata*	(Distant, 1897)		Papua New Guinea, Northern Province (Oro), Mount Lamington District (8° 57' S, 148° 09' E) /01/1929 - /02/1929, McNamara, Charles Terence(Collector), Field Collected - Terrestrial	148,150000	-8,950000	♂	AMS

Chlorocystini	*Gymnotympana rufa*	(Ashton, 1914)		Australia, Queensland, Claudie River, near Lamond Hill (12° 44' 44" S, 143° 16' 40" E) 07/01/1972 - 07/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collec	143,277778	-12,745556	♂	AMS
Chlorocystini	*Gymnotympana rufa*	(Ashton, 1914)		Australia, Queensland, Claudie River, near Lamond Hill (12° 44' 44" S, 143° 16' 40" E) 07/01/1972 - 07/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collec	143,277778	-12,745556	♂	AMS
Chlorocystini	*Gymnotympana rufa*	(Ashton, 1914)		Mulgrave R. 4Mi.\W of Gordonvale\NQld 28 Jan 1972\D.K. McAlpine	145,750000	-17,141389	♂	AMS
Chlorocystini	*Gymnotympana rufa*	(Ashton, 1914)		Australia, Queensland, Lloyd Bay, 3 miles North of Claudie River mouth (12° 47' 33" S, 143° 21' 40" E) 14/01/1972 - 14/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomolog	143,361111	-12,792500		AMS
Chlorocystini	*Gymnotympana rufa*	(Ashton, 1914)		Australia, Queensland, Iron Range, Claudie River, 5 miles West of Lamond Hill (12° 44' 34" S, 143° 14' 15" E) 02/01/1972 - 02/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - En	143,237500	-12,742778		AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Cardstone (17° 50' 28" S, 145° 42' 58" E) 15/01/1967 - 15/01/1967, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector), at light - see N	145,716111	-17,841111	♂	AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Edmonton (17° 01' 10" S, 145° 44' 37" E) 01/01/1951 - 01/01/1951, Brooks, Dr. J. G.(Collector), Field Collected - Terrestrial	145,743611	-17,019444	♂	AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Cardstone (17° 50' 28" S, 145° 42' 58" E) 15/01/1967 - 15/01/1967, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector), at light - see N	145,716111	-17,841111	♀	AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Coopers Ck, Cape Tribulation (16° 05' S, 145° 29' E) 13/04/1994 - 13/04/1994, Moulds, Dr Max S. - The Australian Museum - Entomology Section(Collector)	145,483333	-16,083333	♀	AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Gap Creek (15° 50' 36" S, 145° 19' 52" E) 14/04/1994 - 14/04/1994, Moulds, Dr. Max S. - Australian Museum - Science(Collector)	145,331111	-15,843333		AMS
Chlorocystini	*Gymnotympana*	(Distant,		Australia, Queensland, Gordonvale (17° 05' 38" S, 145° 47' 12" E),	145,786667	-17,093889		AMS

	varicolor	1907)		Illingworth, J. F.(Collector), light trap				
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Cairns (16° 55' 20" S, 145° 46' 33" E), J.F. Illingsworth(Collector)	145,775833	-16,922222		AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, Annan River (15° 31' 19" S, 145° 13' 23" E) /07/1995 - /07/1995, Field Collected - Terrestrial	145,223056	-15,521944		AMS
Chlorocystini	*Gymnotympana varicolor*	(Distant, 1907)		Australia, Queensland, 5 miles East of Cardstone (17° 53' 03" S, 145° 46' 13" E) 13/01/1967 - 13/01/1967, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector),	145,770278	-17,884167		AMS
Chlorocystini	*Papuapsaltria dioedes*	Boer, 1995		Papua New Guinea, Western Province, Star Mountains (5° 15' S, 141° 05' E) 14/05/1970 - 14/05/1970, McCaw, O. K.(Collector), Field Collected - Terrestrial	141,083333	-5,250000	♂	AMS
Chlorocystini	*Papuapsaltria dioedes*	Boer, 1995		Papua New Guinea, Western Province, Star Mountains (5° 15' S, 141° 05' E) 14/05/1970 - 14/05/1970, McCaw, O. K.(Collector), Field Collected - Terrestrial	141,083333	-5,250000	♀	AMS
Chlorocystini	*Thaumastopsaltria globosa*	(Distant, 1897)		Papua New Guinea, Western Province, Mabaduan (9° 16' 35" S, 142° 44' 15" E) 06/04/1921 - 06/04/1921, Pockley, E. O.(Collector), Field Collected - Terrestrial	142,737500	-9,276389	♂	AMS
Chlorocystini	*Thaumastopsaltria globosa*	(Distant, 1897)		Papua New Guinea, Gulf Province, Kikori (7° 25' S, 144° 14' E) 1956 - 1956, Dawson, P(Collector), Accession	144,233333	-7,416667	♀	AMS
Chlorocystini	*Thaumastopsaltria globosa*	(Distant, 1897)		Papua New Guinea (6° 25' S, 147° 12' E) 02/11/1921 - 02/11/1921, Pockley, E. O.(Collector), Field Collected - Terrestrial	147,200000	-6,416667		AMS
Chlorocystini	*Thaumastopsaltria globosa*	(Distant, 1897)		Papua New Guinea, Iorabaiwa to Urikituru (9° 17' S, 147° 31' E) 21/06/1921 - 21/06/1921, Pockley, E. O.(Collector), Field Collected - Terrestrial	147,516667	-9,283333		AMS
Chlorocystini	*Thaumastopsaltria lanceola*	Boer, 1992		Papua New Guinea, East Sepik Province, Kuminibus (3° 38' S, 143° 02' E) 17/12/1963 - 17/12/1963, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	143,033333	-3,633333	♀	AMS
Chlorocystini	*Thaumastopsaltria lanceola*	Boer, 1992		Papua New Guinea, Northern Province (Oro), Mount Lamington District (8° 57' S, 148° 09' E), McNamara, Charles Terence(Collector), Field Collected - Terrestrial	148,150000	-8,950000	♂	AMS
Chlorocystini	*Venustria superba*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 28/01/1972 - 28/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♂	AMS
Chlorocystini	*Venustria superba*	Goding &		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17°	145,750000	-17,141389	♂	AMS

		Froggat, 1904		08' 29" S, 145° 45' 00" E) 25/01/1972 - 25/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)				
Chlorocystini	*Venustria superba*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 25/01/1972 - 25/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♀	AMS
Chlorocystini	*Venustria superba*	Goding & Froggat, 1904		Australia, Queensland, Mulgrave River, 4 miles West of Gordonvale (17° 08' 29" S, 145° 45' 00" E) 25/01/1972 - 25/01/1972, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector)	145,750000	-17,141389	♀	AMS
Chlorocystini	*Venustria superba*	Goding & Froggat, 1904		Australia, Queensland, Laidley (27° 38' S, 152° 24' E) 19/02/1978 - 19/02/1978, Woodhead, W J(Collector)	152,400000	-27,633333		AMS
Chlorocystini	*Venustria superba*	Goding & Froggat, 1904		Australia, Queensland, 2 miles east of Cardstone (17° 50' 09" S, 145° 44' 12" E) 13/01/1967 - 13/01/1967, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector),	145,736667	-17,835833		AMS
Prasiini	*Arfaka fulva*	(Walker, 1870)	syntype	(New Guinea) N\Gui\Wallace\\fulva\\Type\\Syntype\\67\66\\N\\Brit. Mus.\\NHMUK010392325	141,345741	-5,016746	♂	BMNH
Prasiini	*Jacatra typica*	Distant, 1905	syntype	(Java)Syntype\\60 15\E.I.C.\\Brit. Mus.\\14	110,000000	-7,483333	♂	BMNH
Prasiini	*Jacatra typica*	Distant, 1905	syntype	(Java)Jacatra\typica\type Dist.\\Syntype\\60 15\E.I.C.\\Brit. Mus.\\14\\NHMUK010392328	110,000000	-7,483333	♂	BMNH
Prasiini	*Lembeja elongata*	Jong, 1986	paratype	Dumoga-Bone N.P., Clarke's Camp (="1440"), 1140 m, lightsheet, iii.1985, J.H. Martin	123,704376	0,578277	♂	BMNH
Prasiini	*Lembeja minahassae*	Jong, 1986	paratype	Indonesia:\Sulawest Utara\Dumoga-Bone N.P.\May 1985\\Rothamsted light\trap, site 1,\200 m. H. Barlow\\rR. Ent. Soc. Lond.\Project Wallace\B.M. 1985-10	123,704376	0,578277	♂	BMNH
Prasiini	*Lembeja papuensis*	Distant, 1897	lectotype	(British) New Guinea\ Dilo\ Loria VI.VII.90\\Lembeja\papuensis\type Dist.\\Brit. Mus\\Distant Coll.\1911-383\\Lembeja\papuensis Distant\det. M.R. de Jong, 1981\\Lectotype\Lembeja\papuensis Dist.\M.R. de Jong, 1981\\NHMUK010392334			♂	BMNH
Prasiini	*Lembeja papuensis*	Distant, 1897		Papua New Guinea, Northern Province, Ijivitari, Popondetta, Popondetta, Papua (8° 45' S, 148° 01' E) 11/12/1972 - 12/12/1972, Holloway, Mr Geoff A. - The Australian Museum - Entomology Section(Collector), Field Collected - Terrestrial	148,016667	-8,750000	♀	AMS
Prasiini	*Lembeja papuensis*	Distant, 1897		Papua New Guinea, Northern Province (Oro), Mount Lamington District (8° 57' S, 148° 09' E) 1927 - 1927, McNamara, Charles Terence(Collector),	148,150000	-8,950000	♂	AMS

				Field Collected - Terrestrial				
Prasiini	*Lembeja papuensis*	Distant, 1897		Papua New Guinea, Morobe Province, Lae (6° 45' S, 147° 00' E) 20/07/1951 - 20/07/1951, Brandt, W.(Collector)	147,000000	-6,750000		AMS
Prasiini	*Lembeja papuensis*	Distant, 1897		Papua New Guinea, Central Province, Aroa River, Aroana Estate (8° 59' S, 146° 50' E) 29/11/1963 - 29/11/1963, McAlpine, Dr. David Kendray - Australian Museum - Science(Collector), Field Collected - Terrestrial	146,833333	-8,983333		AMS
Prasiini	*Lembeja robusta*	Distant, 1909		B.N.Guinea\Keykey\(Pratt)\\Lembeja\robusta\Type Dist.\\Type\\Syntype\\NHMUK010392333	139,453387	-4,941852	♂	BMNH
Prasiini	*Prasia culta*	Distant, 1898	lectotype	(Malay Archipelago) S. Celebes\ Patunuang\Jan. 1896\H. Fruhstorfer\\culta\Dist.\\Distant Coll.\1911-383\\Brit. Mus.\\Type\\Syntype\\Lectotype\Prasia culta\Distant\M.R. de Jong, 1982\\NHMUK010392339	120,511178	-1,866799	♂	BMNH
Prasiini	*Prasia faticina**	Stål, 1863	holotype	Celebes\Wallace\\Type\\67\66\\Brit. Mus.\\faticina Stal\\HotoypePrasia faticina\Stal\M.R. de Jong, 1982			♀	BMNH
Prasiini	*Prasia princeps*	Distant, 1888	holotype	(North-eastern Celebes)Minahasa\Celebes\\princeps\Dist.\\Type\\Syntype\\Lectotype\Prasia princeps\Distant\M.R. de Jong, 1982\\Brit. Mus.\\NHMUK010392337	125,023919	1,440184	♀	BMNH
Prasiini	*Prasia princeps*	Distant, 1888		Indonesia:\Sulawest Utara\Dumoga-Bone N.P.\May 1985\\Rothamsted light\trap, site 1,\200 m. H. Barlow\\rR. Ent. Soc. Lond.\Project Wallace\B.M. 1985-10	123,704376	0,578277	♂	BMNH
Prasiini	*Prasia saranisorum*	Jong, 1985	holotype	Celebes\Mapane & Umgebg\ii.95 (Dres. Sarasin)\\Prasia distanti\Brit.\\Prasia culta?\\Distant Coll.\1911-383\\Holotype\Prasia\sarasinorum n.sp.\det. M.R. de Jong 1985\\Brit. Mus.\\NHMUK010392341	120,505246	-1,864654	♂	BMNH

S2 Geographic distribution of species of Chlorocystini, Hemidictyini and Prasiini sensu Sanborn (2013) from catalogues of Cicadoidea (Metcalf 1963; Duffels & van der Laan 1985; Sanborn 2013), labels of species and related articles to taxa.

Tribes	**Genera**	**Species**	**Distribution**
Chlorocystini (25)	Aedeastria (12)	*A. bullata* Boer, 1993	New Guinea, Papua New Guinea
		A. cheesmanae Boer, 1993	New Guinea, Indonesia (Western Papua (Waigeu Island, Misoöl))
		A. cobrops Boer, 1990	New Guinea, Indonesia (Western Papua (as Irian New Guinea), Vogelkop Peninsula)
		A. digitata (Blöte, 1960)	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
		A. dilobata Boer, 1993	Papua New Guinea (Papuan Peninsula)
		A. hastulata Boer, 1993	Indonesia (Maluku Islands (Bacan, Halmahera, Morotai, Ternate))
		A. kaiensis Boer, 1993	New Guinea, Indonesia (Maluku Islands (Kai Islands))
		A. latifrons (Blöte, 1960)	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Indonesia (Maluku Islands (Aru Islands)), Malaysia
		A. moluccensis Boer, 1993	Indonesia (Maluku Islands (Obi Island))
		A. obiensis Boer, 1993	Indonesia (Maluku Islands (Obi Island))
		A. sepia Boer, 1990	New Guinea, Indonesia (Western Papua (Vogelkop Peninsula)), Maluku Islands (Roon Island)
		A. waigeuensis Boer, 1993	New Guinea, Indonesia (Western Papua (Waigeu Island)
	Akamba* (1)	*A. aethiopica* Distant, 1905	West Africa, Sierra Leone, Kenya (as British East Africa), French West Africa (currently Islamic Republic of Mauritania, Senegal, Mali, French GuineaIvory Coast, Burkina Faso, Benin and Niger)
	***Baeturia* (69)**		
		B. arabuensis Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
		B. bemmeleni Boer, 1994	New Guinea, Indonesia (West Papua (as Iriayan Jaya))
		B. bicolorata Distant, 1892	New Guinea, Papua New Guinea, Indonesia (Maluku Islands (Aru Islands, Buru)
		B. bilebanarai Boer, 1989	Solomon Islands
		B. bipunctata Blöte, 1960	New Guinea, Indonesia (Western Papua (as Irian New Guinea))
		B. biroi Boer, 1994	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
		B. bismarkensis Boer, 1989	Papua New Guinea (Bismarck Archipelago)
		B. bloetei Boer, 1989	New Guinea, Indonesia (Maluku, Papua (Biak Island, Yapen Island (as Japen Island))), Papua New Guinea (Bismarck Archipelago (Admiralty Islands)), Solomon Islands, Vanuatu, Samoa, Tonga, Fiji (Rotuma Island)
		B. boulardi Boer, 1989	Vanuatu
		B. brandti Boer, 1989	Solomon Islands
		B. brongersmai Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
		B. colossea Boer, 1994	New Guinea, Papua New Guinea
		B. conviva (Stål, 1861)	New Guinea, Indonesia (Maluku Islands (Amboina, Bacan, Buru Island, Aru Islands, Ternate, Halmahera, Seram, Sula, Obi Island, Banda, Roon Island, Kai Islands)), Fiji (Ori Island), Timor, Papua (Larat)), Papua New Guinea (Duke of York Islands), Australia (Dorre Island)
		B. cristovalensis Boer, 1989	Solomon Islands
		B. daviesi Boer, 1994	Papua New Guinea (Papuan Peninsula)
		B. edauberti Boulard, 1979	Vanuatu (or New Hebrides)
		B. exhausta (Guérin-Méneville, 1831)	New Guinea, Indonesia (Maluku Islands (Amboina, Aru Islands, Buru Island,

	Halmahera, Seram, Sula, Sumba, Ternate, Banda, Kai Islands, Obi Island),Timor, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Samoa (Savaii, Upolu, Tutuila, Manua), Solomon Islands
B. fortuini Boer, 1994	New Guinea, Papua New Guinea
B. furcillata Boer, 1992	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
B. galeata Boer, 2000	Papua New Guinea
B. gibberosa Boer, 1994	Papua New Guinea (Papuan Peninsula, Normanby Island)
B. gressitti Boer, 1989	Solomon Islands
B. guttulinervis Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Indonesia (Maluku Islands, Banda (Roon Island))
B. guttulipennis Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
B. hamiltoni Boer, 1994	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
B. hardyi Boer, 1986	New Guinea, Indonesia (Banda (Roon Island))
B. hartonoi Boer, 1994	New Guinea, Papua New Guinea
B. inconstans Boer, 1994	New Guinea
B. intermedia Boer, 1982	New Guinea
B. karkarensis Boer, 1992	New Guinea, Papua New Guinea (Karkar Island)
B. laminifer Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula, Bismarck Archipelago (Admiralty Islands))
B. laperousei Boulard, 2005	Solomon Islands (Vanikoro)
B. laureli Boer, 1986	Indonesia (Maluku Islands (Halmahera, Morotai))
B. lorentzi Boer, 1992	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
B. loriae Distant, 1897	New Guinea, Papua New Guinea (Papuan Peninsula)
B. maai Boer, 1994	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
B. macgillavryi Boer, 1989	Indonesia (Maluku Islands (Buru Island, Halmahera, Moratai, Seram), Talaud Islands), Timor, Banda Islands
B. maddisoni Duffels, 1988	Tonga, Samoa
B. mamillata Blöte, 1960	Western New Guinea (as Irian New Guinea), Papua New Guinea
B. manusensis Boer, 1989	Papua New Guinea (Manus Island, Bismarck Archipelago (Admiralty Islands))
B. marginata Boer, 1989	Solomon Islands
B. marmorata Blöte, 1960	Western New Guinea (as Irian New Guinea)
B. mendanai Boer, 1989	Solomon Islands
B. mussauensis Boer, 1989	Papua New Guinea (Mussau Island, Bismarck Archipelago (Admiralty Islands))
B. nasuta Blöte, 1960	Western New Guinea (as Irian New Guinea), Papua New Guinea
B. papuensis Boer, 1989	New Guinea, Papua New Guinea
B. parva Blöte, 1960	Western New Guinea (as Irian New Guinea), Papua New Guinea (Bismarck Archipelago (Admiralty Islands, New Britain, New Ireland)), Indonesia (Biak Island, Western Papua (Misoöl), Obi Island)
B. pigrami Boer, 1994	New Guinea, Papua New Guinea
B. polhemi Boer, 2000	Papua New Guinea
B. quadrifida (Walker, 1868)	Western New Guinea (as Irian New Guinea), Indonesia (Maluku Islands (Aru

		Islands), Western Papua (Vogelkop Peninsula))
	B. reijnhoudti Boer, 1989	Solomon Islands
	B. retracta Boer, 1994	Papua New Guinea (Bismarck Archipelago (Admiralty Islands), Manus Island)
	B. roonensis Boer, 1994	New Guinea, Indonesia (Banda (Roon Island))
	B. rossi Boer, 1994	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Indonesia (Papua (Yapen Island))
	B. rotumae Duffels, 1988	Fiji (Rotuma Island)
	B. rufula Blöte, 1960	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
	B. schulzi Schmidt, 1926	Indonesia (Maluku Islands (Buru Island, Seram, Sula))
	B. sedlacekorum Boer, 1989	Solomon Islands
	B. silveri Boer, 1994	New Guinea, Papua New Guinea
	B. splendida Boer, 1994	New Guinea, Papua New Guinea
	B. tenuispina Blöte 1960	New Guinea, Papua New Guinea (D'Entrecasteaux Islands (Goodenough Island, Normanby Island))
	B. turgida Boer, 1992	New Guinea, Papua New Guinea
	B. uveiensis Boulard, 1996	Wallis Island
	B. valida Blöte, 1960	New Guinea, Papua New Guinea
	B. vanderhammeni Blöte, 1960	New Guinea
	B. versicolor Boer, 1994	Papua New Guinea (Papuan Peninsula)
	B. viridis Blöte, 1960	New Guinea
	B. wauensis Boer, 1994	New Guinea, Papua New Guinea
	B. wegeneri Boer, 1994	New Guinea, Papua New Guinea
*Cephalalna** (1)	*C. francimontanum* Boulard, 2006	Madagascar
***Chlorocysta* (3)**	*C. fumea* (Ashton, 1914)	Australia (Queensland)
	C. suffusa (Distant, 1907)	Australia (Queensland)
	C. vitripennis (Westwood, 1851)	Australia (New South Wales, Queensland)
*Conibosa** (1)	*C. occidentis* (Walker, 1858)	Mexico (Veracruz), Honduras, Costa Rica, Panama
***Cystosoma* (2)**	***C. saundersii*** (Westwood, 1842)	Australia (New South Wales, Queensland, Lord Howse Island)
	C. schmeltzi Distant, 1882	Australia (New South Wales, Queensland)
***Cystopsaltria* (1)**	***C. immaculata*** Goding & Froggat, 1904	Australia (Queensland)
*Decebalus** (1)	*D. ugandanus* Distant, 1920	Uganda
*Dinarobia** (1)	*D. claudeae* (Orian, 1954)	Mauritius
*Durangona** (1)	*D. tigrina* Distant, 1911	Ecuador, Colombia
*Fractuosella** (4)	*F. breoni* Boulard, 1989	Réunion Island
	F. darwini (Distant, 1905)	Mauritius
	F. vinsoni Boulard, 1979	Mauritius
	F. virginiae Boulard, 1979	Mauritius
***Glaucopsaltria* (1)**	***G. viridis*** Goding & Froggat, 1904	Australia (New South Wales, Queensland)
Guineapsaltria (8)	*G. chinai* (Blöte, 1960)	New Guinea, Papua New Guinea (Papuan Peninsula)
	G. flava (Goding & Froggatt, 1904)	New Guinea, Papua New Guinea, Indonesia (Aru Islands), Australia (Queensland)
	G. flaveola Boer, 1993	Papua New Guinea (Papuan Peninsula, Sideia Island)
	G. pallida (Blöte, 1960)	New Guinea
	G. pallidula Boer, 1993	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
	G. pennyi Boer, 1993	New Guinea, Papua New Guinea
	G. stylata (Blöte, 1960)	New Guinea, Papua New Guinea
	G. viridula (Blöte, 1960)	New Guinea, Papua New Guinea (Umboi Island, New Britain, Solomon Islands,

		Bismarck Archipelago (Admiralty Islands), Manus Island)
***Gymnotympana* (20)**	*G. dahli* (Kuhlgatz, 1905)	New Guinea, Indonesia (Biak Island), Papua New Guinea (Bismarck Archipelag, D'Entrecasteaux Islands (Goodenough Island), Manus Island, New Britain, Papuan Peninsula)
	G. hirsuta Boer, 1995	Papua New Guinea
	G. langeraki Boer, 1995	Papua New Guinea (D'Entrecasteaux Islands (Goodenough Island), Normanby Island, Papuan Peninsula)
	G. membrana Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula)
	G. minoramembrana Boer, 1995	New Guinea
	G.montana Boer, 1995	Papua New Guinea (Papuan Peninsula)
	G. nigravirgula Boer, 1995	Papua New Guinea (Papuan Peninsula)
	G. obiensis Boer, 1995	Indonesia (North Maluku, Obi Island)
	G. olivacea Distant, 1905	New Guinea, Papua New Guinea (Papuan Peninsula)
	G. parvula Boer, 1995	Papua New Guinea (Papuan Peninsula)
	G. phyloglycera Boer, 1995	Papua New Guinea
	G. rubricata (Distant, 1887)	New Guinea, Papua New Guinea (D'Entrecasteaux Islands, Louisiade Archipelago, Papuan Peninsula)
	G. rufa (Distant, 1897)	Australia (Queensland)
	G. stenocephalis Boer, 1995	Papua New Guinea (Papuan Peninsula)
	G. strepitans (Stål, 1861)	New Guinea, Papua New Guinea (D'Entrecasteaux Islands, Louisiade Archipelago), Indonesia (Aru Islands), Australia
	G. stridens (Stål, 1861)	Indonesia (Maluku Islands (Bacan, Morotai, Obi Island, Ternate))
	G. subnotata (Walker, 1868)	Indonesia (Maluku Islands (Bacan, Halmahera, Morotai))
	G. varicolor (Distant, 1907)	Australia (Queensland)
	G. verlaani Boer, 1995	New Guinea, Papua New Guinea
	G. viridis Boer, 1995	Papua New Guinea (Papuan Peninsula)
*Kumanga** (1)	*K. sandaracata* (Distant, 1888)	Myanmar (as Burma)
Mirabilopsaltria (6)	*M. globosa* Boer, 1996	New Guinea, Papua New Guinea (Papuan Peninsula, Bismarck Archipelago)
	M. humilis (Blöte, 1960)	New Guinea, Indonesia (Biak Island)
	M. inconspicua Boer, 1996	New Guinea
	M. inflata Boer, 1996	New Guinea, Papua New Guinea (Bismarck Archipelago, New Britain, New Ireland)
	M. toxopeusi (Blöte, 1960)	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
	M. viridicata (Distant, 1897)	New Guinea, Papua New Guinea (Papuan Peninsula)
*Muda** (4)	*M. kuroiwae* (Matsumura, 1913)	Japan (Okinawa), Ryukyu Islands
	M. obtusa (Walker, 1858)	Indonesia (Java, Sumatra (Mentawei Islands)), Malaysia (Sabah, Peninsular Malaysia, Borneo (Sarawak), Banguey Island, Langkawi Island, Penang, Malacca, Perak, Johore), Singapore
	M. tua Duffels, 2004	Malaysia (Peninsular Malaysia)
	M. virguncula (Walker, 1857)	New Guinea, Indonesia (Java, Sumatra (Mentawei Islands), Sipora, Siberut), Malaysia (Borneo, Malacca), Singapore
*Musoda** (4)	*M. flavida* Karsch, 1890	Central African Republic, Cameroon, French West Africa (currently Islamic Republic of Mauritania, Senegal, Mali, French GuineaIvory Coast, Burkina Faso,

		Benin and Niger), Gabon, Democratic Republic of the Congo (as Zaire).
	M. gigantea Distant, 1914	Central African Republic, Cameroon
	M. occidentalis Boulard, 1974	Central African Republic, Nigeria, Togo, Bioko (as Fernando Pool), Ivory Coast
	M. orientalis Boulard, 1974	Kenya, Uganda
*Nablistes** (2)	*N. heterochroma* Boulard, 1986	Ivory Coast
	N. terebrata Karsch, 1891	Ivory Coast, Cameroon, Bioko (as Fernando Pool), Democratic Republic of the Congo
Owra (1)	*O. insignis* Ashton, 1912	Australia (Queensland)
***Papuapsaltria* (20)**	*P. angulata* Boer, 1995	Papua New Guinea (Papuan Peninsula)
	P. baasi Boer, 1995	New Guinea
	P. bidigitula Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Indonesia (Papua (Yapen Island))
	P. bosaviensis Boer, 2000	Papua New Guinea
	P. brassi Boer, 1995	New Guinea, Papua New Guinea
	***P. dioedes* Boer, 1995**	New Guinea, Papua New Guinea
	P. dolabrata Boer, 1995	Indonésia (Banda (Roon Island)), West Papua (Waigeu Island))
	P. goniodes Boer, 1995	New Guinea, Papua New Guinea
	P. lachlani Boer, 1995	New Guinea
	P. nana (Jacobi, 1903)	New Guinea, Papua New Guinea (D'Entrecasteaux Islands, Normanby Island)
	P. novariae Boer, 1995	New Guinea
	P. phyllophora (Blöte, 1960)	New Guinea, Papua New Guinea, Indonésia (West Papua (Waigeu Island))
	P. plicata Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula)
	P. pusilla Boer, 2000	Papua New Guinea
	P. spinigera Boer, 2000	New Guinea, Papua New Guinea
	P. stoliodes Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula)
	P. toxopei Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
	P. ungula Boer, 1995	New Guinea, Papua New Guinea (Papuan Peninsula)
	P. ustulata (Blöte, 1960)	New Guinea
	P. woodlarkensis Boer, 1995	Papua New Guinea (Woodlark Island, Papuan Peninsula)
Scottotympana (3)	*S. biardae* Boer, 1991	New Guinea, Papua New Guinea
	S. huibregtsae Boer, 1991	New Guinea, Papua New Guinea
	S. sahebdivanni Boer, 1991	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya))
***Thaumastopsaltria* (8)**	*T. adipata* (Stål, 1863)	New Guinea, Indonesia (West Papua (Misoöl Island)), Australia
	T. globosa (Distant, 1897)	New Guinea, Papua New Guinea, Australia (Queensland, Northern Territory, Grootte Island)
	T. lanceola Boer, 1992	New Guinea, Papua New Guinea (D'Entrecasteaux Islands, Fergusson Island, Normanby Island)
	T. pneumatica Boer, 1992	Papua New Guinea (Papuan Peninsula (as Irian Jaya))
	T. sarissa Boer, 1992	New Guinea
	T. sicula Boer, 1992	New Guinea, Papua New Guinea (Papuan Peninsula (as Irian Jaya)), Indonesia (West Papua (Waigeu Island))
	T. smithersi Moulds, 2012	Australia
	T. spelunca Boer, 1992	New Guinea, Papua New Guinea (Papuan Peninsula, Bismark Archipelago, Umboi Island, New Britain, Buka, Solomon Islands, Bougainville)

	***Venustria* (1)**	***V. superba*** Goding & Froggat, 1904	Australia (Queensland)
Hemidictyini (2)	***Hemidictya* (1)**	***H. frondosa*** Burmeister, 1835	Brazil (Mato Grosso*, Minas Gerais*, Espírito Santo*, Rio de Janeiro)
	***Hovana* (1)**	***H. distanti*** (Brancsik, 1893)	Madagascar
Prasiini (10)	***Arfaka* (2)**	***A. fulva*** (Walker, 1870)	New Guinea
		A. hariola (Stål, 1863)	New Guinea, Indonesia (Misoöl Island)
	***Bafutalna* (1)**	*B. mirei* Boulard, 1993	Southwest Cameroon
	***Iruana* (4)**	*I. brignolli* Boulard, 1982	Ethiopia
		I. meruana Boulard, 1990	Kenya
		I. rougeoti Boulard, 1975	Ethiopia (Kebre-Mengist, Kofele, Djem-Djem Forest*)
		I. sulcata Distant, 1905	Ethiopia (Djem-Djem Forest*), Congo/Uganda (Ruwenzori Range*), Kenya* (Nyeri, Kitale, Nairobi, Kaimosi, Kakamega, West Aberdares, Muguga)
	***Jacatra* (1)**	***J. typica*** Distant, 1905	Indonesia (Java, Sumatra)
	***Lacetas* (4)**	***L. annulicornis*** Karsch, 1890	Nigeria, Congo (cited as Zaire), Sudan, Central African Republic, Angola, Ethiopia*, Ivory Coast* (Bouake), Tanzania*, Kenya*(Samburu), Tanganyika*
		L. breviceps Schumacher, 1912	Northeastern Africa
		L. jacobii Schumacher, 1912	Togo (as Togoland)
		L. longicollis Schumacher, 1912	Nigeria*, Uganda* (Karamoja, Nebbi, Gayaza), Northern Africa, Tanganyika, Mozambique
	***Lembeja* (28)**	*L. brendelli* Jong, 1986	Sulawesi
		L. consanguinea Jong, 1987	Sulawesi
		L. dekkeri Jong, 1986	Sulawesi
		L. distanti Jong, 1986	Sulawesi
		***L. elongata* Jong, 1986**	Sulawesi
		L. fatiloqua (Stål, 1870)	New Guinea, Indonesia (Soemba, Sumba, Sumbawa), Malaysia (Borneo), Lesser Sunda Islands, Philippine Island (Mindanao), Australia (Queensland)
		L. foliata (Walker, 1858)	New Guinea, Indonesia (Flores, Sumba), Sulawesi (Sangihe Island)
		L. fruhstorferi Distant, 1897	Sulawesi
		L. hollowayi Jong, 1986	Sulawesi
		L. incisa Jong, 1986	Sulawesi
		L. lieftincki Jong, 1987	Sulawesi, Malaysia (Borneo), Philippine Island
		L. maculosa (Distant, 1883)	Sulawesi
		L. majuscula Jong, 1986	Sulawesi
		L. minahassae Jong, 1986	Sulawesi
		L. mirandae Jong, 1986	Sulawesi
		L. oligorhanta Jong, 1986	Sulawesi
		L. papuensis Distant, 1897	New Guinea
		L. paradoxa (Karsch, 1890)	New Guinea, Papua New Guinea, Australia (Queensland (Moa Island), Torres Strait Islands (Thursday Island)
		L. parvula Jong, 1987	Sulawesi
		L. pectinulata Jong, 1986	Sulawesi
		L. robusta Distant, 1909	New Guinea, Papua New Guinea (Papuan Peninsula), Indonesia (Obi Island), Australia (Queensland) (?)
		L. roehli Schmidt, 1925	Indonesia (Sumba), Lesse Sunda Islands
		L. sangihensis Jong, 1986	Sulawesi
		L. sanguinolenta Distant, 1909	Sulawesi
		L. sumbawensis Jong, 1987	Indonesia (Sumbawa), Lesse Sunda Islands
		L. tincta (Distant, 1909)	Sulawesi
		L. viticollis (Ashton, 1912)	Malaysia (Borneo), Philippine Island, Australia (Queensland)

	L. wallacei Jong, 1987	Sulawesi
Mariekea (6)	*M. harderi* Jong & Boer, 2004	Indonesia (Nusa Tenggara (Sumba))
	M. major Jong, 2004	Indonesia (Nusa Tenggara (Sumba))
	M. euharderi Jong, 2004	Indonesia (Nusa Tenggara (Sumba))
	M. acuta Jong, 2004	Indonesia (Nusa Tenggara (Flores))
	M. floresiensis Jong, 2004	Indonesia (Nusa Tenggara (Flores))
	M. groenendaeli Jong & Boer, 2004	Indonesia (Nusa Tenggara (Flores))
Murphyalna (1)	*M. mughessensis* Boulard, 2012	Nord Malawi (Thitipa District, Mughesse Forest, Misuku Hills)
***Prasia* (7)**	*P. breddini* Jong, 1985	Sulawesi
	P. faticina Stål, 1863	Sulawesi
	P. nigropercula Jong, 1985	Sulawesi (Muna Island)
	P. princeps Distant, 1888	Sulawesi
	P. sarasinorum Jong, 1985	Sulawesi
	P. senilirata Jong, 1985	Sulawesi
	P. tuberculata Jong, 1985	Sulawesi
***Sapantanga* (1)**	***S. nutans*** (Walker, 1850)	Locality Unknown

CAPÍTULO 2

In-depth morphological examination and evolution of male copulatory holding structures in Cicadinae (Hemiptera, Cicadidae)[2]

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Running head: **Functional evolution of male genitalia in Cicadinae**

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Abstract

The male intromittent organ is one of the most morphologically diverse structures within metazoa. The evolution of genitalia is highly influenced by male-female coevolution, and the anatomy of these structures has been related to specific functions during copulation. The male-female coupling interaction of Cicadomorpha has remained unknown, making primer studies on copulatory interaction and coevolution challenging. Here we explored the male-female structural interaction during copulation, assigned functions to the structures and ornamentations in Cicadinae, and also reconstructed the evolution of such ornamentations based on their function. We dissected a pair of cicadas in copula and described the interaction of genitalic structures. The morphology of the theca and vesica from 18 tribes of Cicadinae were analyzed. The ornamentations were classified according to their roles during copulation. Ancestral trait reconstructions under parsimony and maximum likelihood were mapped onto a Bayesian inference tree. We inferred a copulation pattern for male-female interaction for Auchenorrhyncha.

Keywords: cicadas, genitalia, morphology, copula, sexual selection, vesica.

Introduction

The evolution of mechanisms related to reproductive success is closely associated with genitalic variation, which in turn plays a crucial role in gamete transfer. Sexual selection is guided by different evolutionary processes in contrast to those acting in natural selection (Hunt, Breuker, Sadowski, & Moore, 2009), thus genitalic structures, in general, are under stronger selective pressure when compared to non-genitalic structures (Klaczko, Ingram, & Losos, 2015; Genevcius, Caetano, & Schwertner, 2017). Sexual selection has been accepted as the main driver of genitalic evolution and helps explain the high morphological diversification of these structures (phenotypes) (Eberhard, 1985; Simmons, 2014; Langerhans, Anderson, & Heinen-Kay, 2016). In cases of internal fertilization, which arose independently in many metazoan lineages (Margulis & Chapman, 2009), the male intromittent organs serve two basic functions: insertion into a mate and sperm transfer (Kelly, 2016). These functions are fulfilled in some organisms by a simple cylindrical tube, yet in others, by extravagant and morphologically diverse structures (Kelly & Moore, 2016).

The development of ornamentations on the intromittent organ is widespread in vertebrates and arthropods (Kelly, 2016). The anatomy of these structures varies largely, including ridges, craws, scales, flaps, stiff spines, and many others. Although many parts of these ornamentations have not been investigated in-depth (Brennan, 2016), they are likely associated with specific functions, for instance, stimulating the female by rubbing (Katandukila & Bennett, 2016), ejecting the sperm from a previous male rival (Simmons, 2014), acting as female coercion, or to damage by piercing (Lane, 2018). Another often conspicuous morphological modification is the inflatable tissue, especially common in arthropods [but also present in vertebrate lineages (Brennan, Clark, & Prum, 2010)] (Filippov, Kovalev, Matsumura, & Gorb, 2015; Kelly, 2016). In arthropods, the tissue is usually unfolded from inside the aedeagus by hydraulic pressure. It increases the working size of the intromittent organ and eventually acts as an anchor after expanding inside the female genitalia during copulation (Matsumura, Michels, Appel, & Gorb, 2017; Zlatkov, 2018). The incredible anatomical diversification of the male genitalia (Eberhard, 1985) is an important focus in evolutionary biology (Langerhans, Anderson, & Heinen-Kay, 2016).

Cicadas are phytophagous insects classified within Cicadidae Latreille, 1802, known by their short adult lifetime in contrast to a long subterranean nymphal stage, and also by intraspecific acoustic communication performed by the males (Boulard, 1965; Williams & Simon, 1995; Boulard, 2006). Among the four subfamilies, Cicadinae Latreille, 1802 is the most diverse comprising 30 tribes with a global distribution (Marshall *et al*., 2018). However ornamentations found on male genitalia were never explored missing studies about morphology and function.

The general morphology of male genitalia in Cicadidae is well-known, although the diversity of phenotypes of these structures is still underexplored. The male genitalia comprises the pygofer, uncus and/or claspers, and aedeagus. The aedeagus is composed of a theca attached to a basal plate, and contains the ejaculatory duct and vesica (Moulds, 2005). The vesica is a membranous inflatable structure that can bear different kinds of ornamentations (see results). On the other hand, the female genitalia of cicadas has received less attention compared to that of the male, mirroring a pattern observed for other metazoan lineages (Ah-King, Barron, & Herberstein, 2014). The external genitalia of the female is composed by the 9th abdominal segment and the ovipositor.

The female reproductive system includes the seminal ampoule, the dorsovaginal pouch, ovary, common and lateral oviducts, and different kinds of glands (Moulds, 2005). Given that the function and evolution of animal genitalia are highly influenced by their coevolution (Ah-King, Barron, & Herberstein, 2014), the relative lack of information associated with female genitalia hinders scientific research pertaining to copulation and requires attention.

The mating behavior of cicadas is known only for a few species, but are diverse nevertheless. There is a consensus that females tend to mate just once, as this may reduce the time spent finding mates, and that females are highly selective when acquiring males (Cooley & Marshall, 2004). There are also several mechanisms that could be interpreted as male adaptations to avoid or reduce intrasexual competition (Anderson & Simmons, 2006) such as mate guarding and/or the use of external ornamentations to grasp the female and increase the time in copula. For Auchenorrhyncha, the copulatory structures and male-female genitalic dynamics are known only for Fulgoromorpha (e.g. Bourgoin & Huang, 1991; Wang, Liang, & Webb, 2009), however, for Cicadomorpha, only mating behaviors have been documented to date (Hunt, 1993; Sueur, 2002; Sueur & Aubin, 2003).

Here, we assess for the first time the male-female coupling interaction of a cicadomorphan species and infer the function and evolution of the male genitalia observed in Cicadinae. We address the following questions: (1) What are the male and female structures interacting in copula and how do they interact? (2) What are the functions of different ornamentations on male genitalia? (3) How did these morphologically diverse ornamentation evolve across Cicadinae? We built our tests on two nonmutually exclusive hypotheses that pertain to their function and evolution: (I) The male genitalia intrudes deeply into the female genitalia, and the vesica inflates upon reaching the inner wall of the seminal ampoule and aid the male in anchoring to the female during copulation; (II) The multiple phenotypes present within Cicadinae are the result of a functional improvement to maintain copulation and have evolved independently along different lineages.

Material and Methods

Taxon sampling

A total of 24 species of 18 tribes of Cicadinae were studied. We sampled six species of Fidicinini, two of Zammarini, and one species for each of the other 16 tribes. *Diemeniana hirsuta* (Goding & Froggatt, 1904) (Cicadettinae) was selected to root the trees. We selected available species based on the Cicadinae clade recovered by Marshall *et al*. (2018), attempting to use the same species or genera. When we did not have access to the species used by Marshall *et al*. (2018), we used a different congeneric species and present only the genus name in the phylogeny. The material examined belongs to the following collections: Australian Museum – AMS (Sydney, Australia), Illinois Natural History Survey – INHS (Champaign, USA), Swedish Museum of Natural History – NHRS (Stockholm, Sweden), Musée de Zoologie Lausanne – MZLS (Lausanne, Switzerland), Zoological Museum of University of Copenhagen – ZMUC (Copenhagen, Denmark), Universidade Federal do Paraná – DZUP (Curitiba, Brazil), Universidade Federal de Minas Gerais – UFMG (Belo Horizonte, Brazil), and Instituto Nacional de Pesquisas da Amazônia – INPA (Manaus, Amazonas, Brazil).

Male-Female coupling interaction

Intending to understand the interaction between male and female genital structures, a dry pinned female specimen of *Guyalna bonaerensis* (Berg, 1879) (Cicadinae, Fidicinini) with a pygofer attached to female genitalia in complete mating position was dissected. The specimen was placed in potassium hydroxide aqueous solution (KOH 10%) for 24 hours. The abdomen was cut with histological scissors and placed in water. The dissection was made in stages, removing tergites and sternites until the reproductive system was exposed. Based on observations of coupling interaction we dissected another female specimen of *G. bonaerensis* for scanning electron microscopy (SEM). The seminal ampoule was cut to expose the inner walls and dehydrated in ethanol 80% and 96% for 10 minutes each. The dissected genitalia were then glued to metal supports with carbon tape for gold coating. The micrographs were made in a scanning electron microscope JEOL JSM 6060.

Theca preparation

Dry pinned specimens were placed in a pot with the apex of abdomen laid in hot water (~100ºC) for 15 minutes. The pygofer was removed with forceps, heated in a potassium hydroxide aqueous solution (KOH 10%) at 200ºC for 30 minutes, and posteriorly washed in water. The pygofers were held in water about 3 hours to inflate the vesica. With the vesica kept folded inside the theca, we exposed it by cutting the lateral wall of theca. Photographs of the pygofer and aedeagus were taken with an AxioCam ERc 5s digital camera attached to a stemi 2000 C P.06 stereoscopic microscope with Zen Lite 2011 software, and with a Nikon AZ100M followed by stacking with the Nikon NIS–Elements Ar Microscope Imaging Software before the preparation of theca for SEM. The thecae were cut with histological scissors and placed in Dietrich's (Kahle's) Fixative (Thompson & Hunt, 1966) for 24 hours for fixation of the vesica. Dietrich's (Kahle's) solution was prepared following Callis & Sterchi (2002). After fixation, the thecae were dehydrated in 80% and 96% ethanol for 10 minutes each, and glued to metal supports with carbon tape for gold coating. The micrographs were made for left-right sides of theca in JEOL JSM 6060.

Phylogenetic tree and ancestral trait reconstruction

For the 25 terminal taxa we used a subset of the concatenated matrix from Marshall *et al*. (2018) containing the alignment of the mitochondrial markers: cytochrome oxidase I (COI), cytochrome oxidase II (COII); and the nuclear markers: elongation factor 1 alpha (EF-1α), acetyltransferase (ARD1), and 18S ribosomal RNA (18S). Intending to obtain similar congruence to Marshall's results, we applied the same partitions and substitution models adopted by Marshall *et al*. (2018). Bayesian inference (BI) of the concatenated data was performed in the multithreading version of the software MrBayes 3.2.0 (Ronquist & Huelsenbeck, 2003), setting two million generations (nruns=2 nchains=4) with trees sampled every 1000 generations. Tracer v.1.6.0 (Rambaut, Suchard, Xie, & Drummond, 2016) was used to inspect for convergence of the chains to a stationary distribution. The first 10% of the generations were discarded as "burn-in", the ESS values were checked to be higher than 200 for each parameter, and then the chains were combined. The posterior probability and branch length were then estimated. Phylogenetic trees were visualized and edited using FigTree v1.4.0 (Rambaut, Suchard, Xie, & Drummond, 2016).

To investigate the evolutionary history of male genitalic ornamentations we, estimated their ancestral trait reconstruction using parsimony and maximum likelihood (Mk1 model with equal probability for any particular character change) using Mesquite 3.51 (Maddison & Maddison 2018). The morphology of male genitalia was analyzed by examining the dissected voucher specimens, and the traits were inferred based on the presence of specific ornamentation (see the results). Ancestral trait reconstructions were made on the topology of the resulting tree from Bayesian inference. The characters comprise ornamentations and microsculpturing present on the theca and vesica. For pairwise correlations between the discrete variables, we used Pagel’s (1994) test for correlation of binary characters with 999 simulations and 100 replications to evaluate the p-value. This analysis is used to identify biological traits that do not evolve independently and reveal any underlying correlation.

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CAPÍTULO 3

Phylogeny of Fidicinini Distant, 1905 (Hemiptera, Auchenorrhyncha, Cicadidae) based on morphological data with a key for the genera[3]

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[3] Manuscrito a ser submetido para *Arthropod Systematics & Phylogeny*.

Abstract

Fidicinini is the second more diverse tribe of Cicadinae widespread in the Nearctic and Palearctic regions. Diagnostic characteristics for the genera are doubtful and the absence of terminologies of male genitalia structures weakens the systematics of the tribe. Herein we tested for the first time the monophyly of tribe and relationships among genera based in phylogenetic methods coupled with the evaluation of overlooked morphological features. We performed a cladistic analysis by heuristic searches using the implied weighting procedure for 66 species and 88 characters. We identified and delimitate the structures of uncus in Fidicinini comparing with outgroup. An updated diagnosis for Fidicinini is presented and an illustrated key for the genera was elaborated.

Keywords: cicadas, cladistics, systematic, morphology.

1. Introduction

Fidicinini was erected by Distant to include species whose tympanal orifices are more or less exposed (DISTANT 1905: 310). Despite the proposition of new genera over time (DAVIS 1934; METCALF 1952; TORRES 1963; TORRES 1964; BOULARD 1982) the tribe only received a revision by BOULARD & MARTINELLI (1996) that divided Fidicinini into Fidicinina and Guyalnina based in the number of tarsal segments, and proposed new genera and species. Unfortunately, the new genera were presented in an incomplete key for the tribe, without a diagnosis or description, leading to doubtful species classification in future studies.

Several genera of Fidicinini were established based on a combination of characteristics of general morphology some of them are of questionable interpretation. The timbal cover of males was a structure strongly considered to classified species in subfamily level (DISTANT 1889; DISTANT 1906) and for the proposition of new combinations and diagnosis of genera (SANBORN 2016a; 2016b). However, this structure has distinct morphology among closely related species proved not be reliable characteristics in the delimitation of genera (RUSCHEL et al., in prep. A), and for suprageneric groups in Cicadidae (MARSHALL et al. 2018). On the other hand, characters of male genitalia have never been used in the proposition of genera. The absence of terminologies of male genitalia structures for Fidicinini genera make difficult the proposition of homologies and consequently weakening the systematics of the tribe.

Although taxonomic studies have been published for some genera of Fidicinini, most genera have outdated diagnoses, and taxonomic revisions with proper documentation of type species and genital morphology are absent. Among the genera of tribe, *Fidicina* Amyot & Audinet-Serville, 1843 and *Fidicinoides* Boulard & Martinelli, 1996 (Fidicinina) are the only ones with recent descriptions of species including male genitalia (BOULARD & MARTINELLI 1996; SANTOS & MARTINELLI 2009; SANTOS et al. 2010), and *Pacarina* Distant, *Guyalna* Boulard &Martinelli and *Ariasa* Distant (Guyalnina) have been the subjects of taxonomic revisions (SANBORN et al. 2012; SANBORN 2016a; 2016c). Nevertheless, there is a lack of comprehensive taxonomic keys or generic revisions including all species or type information. The first cladistics analysis of a genus of Fidicinini including a broader framework within the tribe was made recently (RUSCHEL et al., in prep. A). The monophyly of *Dorisiana* Metcalf, 1952 (Guyalnina) was tested, two new genera were proposed and a new concept for *Dorisiana* and two closely related genera (*Guyalna* and *Tympanoterpes* Stål, 1861) were presented.

The most recent phylogeny of Cicadidae based on molecular data was the first to include Fidicinini and hypothesizing relationships of tribe within Cicadinae (MARSHALL et al. 2018). A new diagnosis was proposed and six genera were transferred to the tribe: the monotypic *Nosola* Stål, 1866 from Taphurini Distant, 1905 (Cicadettinae), *Diceroprocta* Stål, 1870 and *Orialella* Metcalf, 1952 from Cryptotympanini (Cicadinae), and the three genera previously classified in Hyantiini Distant, 1905, with the tribe synonymized with Fidicinini. However analyses including all the genera of Fidicinini that test their phylogenetic relationships have never been conducted. Fidicinini is the second more diverse tribe of Cicadinae comprising 221 species classified in 25 genera widespread in Nearctic and Palearctic regions (METCALF 1963; SANBORN 2013; MARSHALL et al. 2018).

Here we tested the monophyly of Fidicinini and evaluated the relationships of genera. Homologies of structures of male genitalia are analysed and compared for the first time with species of other tribes. We presented new synonyms, new combinations and corroborate the classification proposed by MARSHALL et al. (2018) for Fidicinini and the new concepts for some genera suggested by RUSCHEL et al. (in prep. A). A complete and illustrated key for the genera of tribe is presented.

2. Material and Methods

2.1. Taxon sampling

The ingroup comprises all genera of Fidicinini except the monotypic *Mura*. We sampled one to four species per genus based on their diversity, totalizing 51 species. For outgroup we selected available species based on the relationship between Fidicinini and the other tribes of Cicadinae (see MARSHALL et al. 2018). We sampled six species of Zammarini (sister to Fidicinini), and one species for each of the others eight tribes, comprising a total of 66 species. *Carineta diardi* (Guérin-Méneville, 1829) (Cicadettinae) was selected for character polarization and rooting of trees.

The specimens examined in this study belong to the following collections: **AMNH** – American Museum of Natural History, New York, USA; **CMNH** – Cleveland Museum of Natural History, Cleveland, USA; **DZRJ** – Coleção Entomológica Prof. José Alfredo Pinheiro Dutra da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **DZUP** – Coleção Entomológica Padre Jesus Santiago Moure da Universidade Federal do Paraná, Curitiba, Brazil; **INHS** – Illinois Natural History Survey, Illinois, USA; **INPA** – Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil; **MAPA** – Museu Anchieta de Ciências Naturais, Porto Alegre, Rio Grande do Sul, Brazil; **MCNZ** – Museu de Ciências Naturais da Fundação Zoobotânica de Porto Alegre, Rio Grande do Sul, Brazil; **MCPM** – Milwaukee Public Museum, Wisconsin, USA; **MCTP** – Museu de Ciências e Tecnologia da PUCRS, Porto Alegre, Rio Grande do Sul, Brazil; **MNRJ** – Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MPUJ** – Museo Javeriano de Historia Natural, Bogota, Colombia; **MRGC** – Museu de Entomologia Prof. Ramiro Gomes Costa da Fundação Estadual de Pesquisa Agropecuária, Porto Alegre, Rio Grande do Sul, Brazil; **MZUSP** – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **NHMUK** – Natural History Museum, London, England; **NHRS** – Swedish Museum of Natural History, Stockholm, Sweden; **SIIS** – Staten Island Institute of Arts and Sciences, New York, USA; **UCDC** – Bohart Museum of Entomology at the University of California at

Davis, California, USA; **UMSP** – University of Minnesota Insect Collection, Minnesota, USA; **UFMG** – Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; **UFRG** – Coleção Entomológica da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **ZMUC** – Zoological Museum University of Copenhagen, Denmark.

Identification of some specimens was done based in keys and descriptions (e.g., GOGALA et al. 2015; GODING 1925; BOULARD 1982; BOULARD 1986; BOULARD & MARTINELLI 1996; SANTOS & MARTINELLI 2009; BOULARD & MARTINELLI 2011; DAVIS 1917, 1921, 1934; SANBORN 2007, 2011, 2016b; SANBORN et al. 2011; SANBORN et al. 2012; SANBORN & HEATH 2014; TORRES 1964); species described by Distant, Walker and Berg were identified through the study of type specimens deposited in **NHMUK** and **MACN** (Museo Argentina de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina); some pictures of type specimens were received from museus: **NHRS** for species of Stål; **MLPA** (Museo de La Plata, La Plata, Argentina) for species of Torres; **ZMHB** (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany) for species of Berg; and **ZMD** (Zoological Museum of Ivan Franko National University of Lviv, Lviv, Ukraine) for species of Germar. The knowledge about the type specimens was essential for the correct identification of species sampled in this analysis.

2.2. Morphology and taxonomy

Male specimens were studied in a stereoscopic microscope. For extraction of genitalia the specimens were placed in a pot with the apex of abdomen laid in hot water (~100ºC) for 15 minutes. The pygofer were extracted with forceps and heated in a potassium hydroxide aqueous solution (10% KOH) for about 30 minutes, and posteriorly washed in water. The genitalia were conserved in micro vials filled with glycerine and attached to the specimen pin. Photographs of morphological structures were obtained with an AxioCam ERc 5s digital camera attached to a stemi 2000 C P.06 stereoscopic microscope with Zen Lite 2011 software, and with a Nikon AZ100M followed by stacking with the Nikon NIS–Elements Ar Microscope Imaging Software. Terminologies adopted here follow MOULDS (2005; 2012) for general and genital morphology and MARSHALL et al. (2018) for genital morphology.

2.3. Cladistic analysis

The characters and states were described following the classification of neomorphic and transformational proposed by SERENO (2007). The data matrix was constructed using the software Mesquite version 2.75 (MADDISON & MADDISON 2001), and the symbols "?" and "–" were used for missing and nonapplicable data, respectively. All characteres were treated as discrete and non-additive, and polarized following NIXON & CARPENTER (1993). We used parsimony (cladistic method) for infer the phylogenetic relationships. The cladistic analysis was performed using TNT v1.5 (GOLOBOFF et al. 2008) by heuristic searches using the implied weighting script proposed by MIRANDE (2009), with 11 K–values calculated for an average character fit ranging from 50 to 90% of a perfectly hierarchical character. A similarity matrix of Subtree Pruning Regrafting (SPR) distances of the consensus trees was constructed, and higher sums of SPR similarity were used as the criterion for choosing the trees. We also used the script proposed by COSTA et al. (in prep.) to confirm the choice of tree by lower sum of SPR moves. The total fit was calculated for the consensus tree, and the fit and extra steps (homoplasy) were calculated for each character.

For the consensus tree, the Relative Bremer support values (GOLOBOFF & FARRIS 2001) were calculated by TBR, retaining suboptimal trees with ten extra steps and a relative fit difference of 0.9. The Jackknife absolute frequency (FARRIS et al. 1996) with symmetric resampling was calculated using 10.000 replicates (GOLOBOFF et al. 2003; KOPUCHIAN & RAMÍREZ 2010). The visualization of cladograms was performed in WinClada 1.00.08 (NIXON 2002).

We considered the phylogenetic results and morphological characters for the classification of genera of Fidicinini.

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CONSIDERAÇÕES FINAIS

Cicadidae é um grupo taxonômico com pouca atuação de pesquisadores em comparação com outras famílias de Auchenorrhycha ou até mesmo de Heteroptera. No Brasil o grupo é negligenciado resultando em um conhecimento incipiente sobre a real diversidade dos cicadideos. Os principais problemas em Cicadidae são: as errôneas determinações de espécies nos poucos trabalhos taxonômicos existentes, falta de análise de material tipo nas publicações, ausência de registros adequados da morfologia de genitália e carência de estudos empregando métodos cladísticos principalmente em tribos Neotropicais. Nós buscamos realizar estudos de sistemática e evolução de duas tribos com ocorrência Neotropical e de ampla (Neartica e Paleartica) e interessante (Brasil e Madagascar) distribuição a fim de ampliar o conhecimento sobre o grupo. Nós inferimos hipóteses filogenéticas para Fidicinini e Hemidictyini. Com Hemidictyini analisamos uma instigante caraceterísitca dessas cigarras e questionamos o período proposto para o surgimento de Cicadidae com base em nossos resultados e registros fósseis. Com Fidicinini conseguimos delimitar as estruturas de uncus e compará-las com as do grupo externo para propor homologias. Além disso, nomeamos ornamentações presentes na genitália dos machos e avaliamos como elas evoluíram dentro de Cicadinae. A maneira como essas estruturas interagem com a genitália das fêmeas e consequentemente como é a cópula em Cicadidae é muito similar às cópulas já descritas de espécies de Fulgoromorpha. Consequentemente é um grande avanço no conhecimento da função dessas ornamentações que são discutidos a partir de uma perspectiva ampla e podem ser interessantes para uma audiência maior pesquisando sobre Auchenorrhyncha, coevolução, cópula, pressão sexual, homologia, morfologia genital, morfologia funcional, comportamento, seleção sexual pós-moldada e conflito sexual.

Os resultados apresentados nessa tese são de estudos primordiais. A partir deles outras questões podem ser geradas tanto dentro dessas tribos quanto de Cicadidae, e espera-se que repercuta em novas pesquisas, principalmente a cerca de sistemática, taxonomia, evolução, história biogeográfica e morfologia comparada.