VIVIANA CAUDURO MATESCO

SISTEMÁTICA DE THYREOCORIDAE AMYOT & SERVILLE (HEMIPTERA: HETEROPTERA: PENTATOMOIDEA): REVISÃO DE *ALKINDUS* DISTANT, MORFOLOGIA DO OVO DE DUAS ESPÉCIES DE *GALGUPHA* AMYOT & SERVILLE E ANÁLISE CLADÍSTICA DE *CORIMELAENA* WHITE, COM CONSIDERAÇÕES SOBRE A FILOGENIA DE THYREOCORIDAE, E MORFOLOGIA DO OVO DE 16 ESPÉCIES DE PENTATOMIDAE COMO EXEMPLO DO USO DE CARACTERES DE IMATUROS EM FILOGENIAS

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do Título de Doutor em Biologia Animal.

Área de concentração: Biologia Comparada
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“Sistemática de Thyreocoridae Amyot & Serville (Hemiptera: Heteroptera: Pentatomoidea): revisão de *Alkindus* Distant, morfologia do ovo de duas espécies de *Galgupha* Amyot & Serville e análise cladística de *Corimelaena* White, com considerações sobre a filogenia de Thyreocoridae, e morfologia do ovo de 16 espécies de Pentatomidae como exemplo de uso de caracteres de imaturos em filogenias”

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Tese apresentada como parte dos requisitos para obtenção de grau de Doutor em Biologia Animal, área de concentração Biologia Comparada.

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SUMÁRIO

ORGANIZAÇÃO DA TESE

A presente tese está organizada em seis partes principais. A primeira parte corresponde a um capítulo introdutório, o qual comporta uma revisão bibliográfica sobre o táxon estudado, bem como um resumo da metodologia utilizada e dos resultados obtidos. Esta primeira parte está redigida em português, a fim de atender às exigências regimentais (artigo 43) do Programa de Pós-Graduação em Biologia Animal, e não será publicada.

Os capítulos 1 a 4 correspondem a quatro artigos independentes, porém correlacionados. O capítulo 1 traz a revisão do gênero *Alkindus* Distant (Thyreocoridae: Corimelaeninae), e o capítulo 2 traz a descrição do estágio de ovo de duas espécies de *Galgupha* Amyot & Serville (Thyreocoridae: Corimelaeninae), bem como uma discussão sobre os ovos de Thyreocoridae. Ambos foram publicados na revista Zootaxa [Qualis B1, fator de impacto (FI) = 0,974], cujas normas encontram-se em anexo (Anexo I).

O capítulo 3 trata da análise cladística do gênero *Corimelaena* White (Thyreocoridae: Corimelaeninae), com considerações sobre a filogenia de Thyreocoridae. O artigo está redigido conforme as normas do Zoological Journal of the Linnean Society (Qualis A2, FI = 2,583) (Anexo II), ao qual será encaminhado para publicação após correções e sugestões da banca. O capítulo 4 traz a descrição da morfologia dos ovos de 16 espécies de Pentatomidae (Pentatomoidea) e sugere caracteres de ovos passíveis de inclusão em análises filogenéticas dentro de Pentatomoidea. Este artigo foi aceito para publicação na Zootaxa. A última parte corresponde a um capítulo conclusivo, em que são feitas considerações finais sobre as contribuições do presente trabalho ao conhecimento do grupo em estudo.

RESUMO

Thyreocoridae (Hemiptera: Heteroptera: Pentatomoidea) compreende 212 espécies em 12 gêneros, ocorrendo principalmente nas regiões Neártica e Neotropical. O grupo foi considerado próximo a Cydnidae e Parastrachiidae. Há uma hipótese cladística de monofilia para a família, porém as relações entre os seus gêneros não são conhecidas. Informações sobre estágios imaturos, plantas hospedeiras e distribuição geográfica estão dispersas na literatura. Na presente tese, 1) o gênero *Alkindus* é revisado; 2) os ovos de *Galgupha* (*Euryscytus*) *difficilis* e *Galgupha (Gyrocnemis) fossata* são descritos; 3) uma análise cladística de Thyreocoridae, com ênfase no gênero *Corimelaena*, é realizada com base em dados morfológicos, e 4) os ovos de 16 espécies de Pentatomidae são descritos e alguns caracteres de ovos são testados em duas análises cladísticas. Adultos de *Alkindus* spp. e ovos de *Galgupha* spp. e de espécies de Pentatomidae foram medidos, examinados em estereomicroscopia e microscopia eletrônica de varredura e fotografados e/ou ilustrados. Os ovos foram obtidos de fêmeas coletadas a campo e mantidas em laboratório até a oviposição. Adultos para a revisão de *Alkindus* e análise de *Corimelaena* foram provenientes de coleções. Registros de distribuição, plantas hospedeiras e caracteres de ovos foram compilados da literatura. Na análise de *Corimelaena*, foram incluídos 114 caracteres e 40 espécies, representando Thyreocoridae, Parastrachiidae, Cydnidae, Canopidae e Plataspididae. Uma lista de 40 caracteres de ovos foi compilada e alguns desses caracteres foram incluídos nas análises cladísticas de *Nezara* (seis caracteres) e grupo *Chinavia obstinata* (cinco caracteres). Todas as análises foram realizadas no TNT com pesos iguais para todos os caracteres. Ambas espécies de *Alkindus*, incluindo o macho de *A. crassicosta*, foram revisadas com base em caracteres morfológicos. Uma chave adaptada e uma lista de plantas potencialmente hospedeiras foram fornecidas, e os registros de distribuição foram expandidos. Os ovos de *G. difficilis* e *G. fossata* são depositados isoladamente, cada ovo é cilíndrico, branco, com cório translúcido e brilhante e processos micropilares curtos, pedunculados e clavados. São similares aos ovos de outros corimeleníneos, bem como de Parastrachiidae e Cydnidae. No entanto, hábitos de oviposição e cuidado maternal diferem entre esses grupos. A análise cladística de *Corimelaena* resultou em seis árvores mais parcimoniosas com 418 passos. A árvore de consenso estrito suporta a monofilia de *Corimelaena*, *Strombosoma*, Corimelaeninae e Thyreocoridae. A monofilia de Thyreocorinae, *Alkindus*, *Galgupha* e dos subgêneros de *Corimelaena* não foi suportada. Sugere-se a manutenção do status de família para Thyreocoridae e o abandono dos subgêneros de *Corimelaena*. Os ovos da maioria das espécies de Pentatomidae estudadas têm forma de barril, cório translúcido e espinhoso e processos aero-micropilares curtos e clavados. Padrões morfológicos foram identificados em Carpocorini, Procleticini, *Chinavia*, *Euschistus*, *Mormidea* e *Podisus*. Na análise cladística de *Nezara* e grupo *C. obstinata*, a inclusão dos caracteres de ovos foi informativa, porém não alterou a topologia original das árvores. Esta tese consiste em importante contribuição para o conhecimento de Thyreocoridae, agregando informações sobre diversos aspectos da biologia do grupo.

ABSTRACT

Thyreocoridae (Hemiptera: Heteroptera: Pentatomoidea) comprises 212 species in 12 genera, occurring mainly in the Neartic and Neotropical regions. The group has been considered related to the Cydnidae and Parastrachiidae. There is a cladistic hypothesis of monophyly for the family, but the relationships among its genera are unknown. Information on the immature stages, host plants and distribution are scattered in the literature. In this thesis, 1) the genus *Alkindus* is revised; 2) the eggs of *Galgupha* (*Euryscytus*) *difficilis* and *Galgupha (Gyrocnemis) fossata* are described; 3) a cladistic analysis of the Thyreocoridae, with emphasis on the genus *Corimelaena*, is performed based on morphological data, and 4) the eggs of 16 species of Pentatomidae are described and some egg characters are tested in two cladistic analyses. Adults of *Alkindus* spp. and eggs of *Galgupha* spp. and Pentatomidae species were measured, examined under stereomicroscopy and scanning electron microscopy and photographed and/or illustrated. Eggs were obtained from females collected in the field and kept in the laboratory until oviposition. Adults for the revision of *Alkindus* and the analysis of *Corimelaena* were obtained from collections. Distribution records, plant records and egg characters were compiled from the literature. In the analysis of *Corimelaena*, 114 characters and 40 species, representing the Thyreocoridae, Parastrachiidae, Cydnidae, Canopidae, and Plataspididae were included. A list of 40 egg characters has been compiled and some of these characters were included in the cladistic analyses of *Nezara* (six characters) and *Chinavia obstinata* group (five characters). All analyses were performed in TNT with equal weighting of characters. Both species of *Alkindus*, including the male of *A. crassicosta*, are revised based on morphological characters. An adapted key and a compiled list of potential host plants are provided and distribution records are expanded. The eggs of *G. difficilis* and *G. fossata* are laid singly, each egg cylindrical, white, with shiny and translucent chorion and micropylar processes short, stalked, and clubbed. They are similar to the eggs of other corimelaenines, as well as Parastrachiidae and Cydnidae. Oviposition habits and maternal care, however, differ among those groups. The cladistic analysis of *Corimelaena* resulted in six most parsimonious trees with 418 steps. The strict consensus tree supports the monophyly of *Corimelaena*, *Strombosoma*, Corimelaeninae, and Thyreocoridae. The monophyly of the Thyreocorinae as well as *Alkindus*, *Galgupha*, and the subgenera of *Corimelaena* were not supported by our results. We suggest the maintenance of family status to

Thyreocoridae and the abandonment of the subgenera of *Corimelaena*. The eggs of most species of Pentatomidae studied were barrel-shaped, with chorion translucent and spinose and aero-micropylar processes short and clubbed. Patterns of egg morphology could be identified in Carpocorini, Procleticini, *Chinavia*, *Euschistus*, *Mormidea*, and *Podisus*. In the cladistic analyses of *Nezara* and *C. obstinata* group, the inclusion of egg characters were somewhat informative but did not affect the original topology of the trees. This thesis is an important contribution to the knowledge of Thyreocoridae, adding information on various aspects of the biology of the group.

INTRODUÇÃO GERAL

1. Sistemática de Hemiptera e seus subgrupos

Hemiptera compreende o maior e mais diverso grupo de insetos não holometábolos, com aproximadamente 89.000 espécies descritas (Grazia *et al.* 2012). O grupo é considerado monofilético e pode ser reconhecido pela estrutura única de suas peças bucais (Carver *et al.* 1991; Schuh & Slater 1995). Heteroptera compreende sete infraordens e inclui mais de 40.000 espécies descritas (Weirauch & Schuh 2011). A subordem é considerada monofilética e suas sinapomorfias estão relacionadas às peças bucais e às glândulas odoríferas (Carver *et al.* 1991; Wheeler *et al.* 1993).

Análises filogenéticas em todos os níveis taxonômicos e o desenvolvimento da sistemática molecular influenciaram de modo crescente a compreensão das relações dentro de Heteroptera (Forero 2008; Weirauch & Schuh 2011). Hipóteses cladísticas explícitas existem para as relações entre as sete infraordens e para as relações dentro de cinco infraordens (Forero 2008; Weirauch & Schuh 2011). Schuh (1986) resumiu as hipóteses filogenéticas até então disponíveis para todas as infraordens de Heteroptera. Forero (2008) atualizou as informações sobre as principais hipóteses filogenéticas para Hemiptera e seus subgrupos. Mais recentemente, Weirauch & Schuh (2011) discutiram o progresso do conhecimento da sistemática e evolução do grupo.

Schuh (1979) propôs o primeiro esquema filogenético para as infraordens de Heteroptera, reanalisando os dados de adultos e ninfas apresentados por Cobben (1978). Wheeler *et al.* (1993) utilizaram sequências de rDNA 18S e caracteres morfológicos para resolver as relações entre as sete infraordens de Heteroptera. Os resultados corroboram em grande parte os de Schuh (1979), com evidências de monofilia de todas as infraordens, inclusive Pentatomomorpha.

Pentatomomorpha é a segunda maior infraordem de Heteroptera, contendo mais de 14.000 espécies descritas em cinco ou seis superfamílias e 40 famílias (Schuh & Slater 1995; Henry 1997; Weirauch & Schuh 2011). A análise de Pentatomomorpha baseada em morfologia feita por Henry (1997) incluiu 53 táxons, usando famílias, subfamílias e tribos como terminais, numa abordagem de plano básico. O autor incluiu Pentatomoidea como táxon terminal único, fornecendo evidência de sua monofilia, mas mostrando a dificuldade de posicionamento de Thaumastellidae. Os resultados evidenciam a monofilia das seis superfamílias. Li *et al.* (2005) analisaram as relações dos grupos dentro de Pentatomomorpha utilizando sequências de DNA nuclear ribossomal 18S e DNA mitocondrial. Embora tenham recuperado a monofilia de Pentatomomorpha, os demais agrupamentos não estiveram em acordo com as hipóteses morfológicas prévias, tendo Pentatomoidea aparecido como grupo parafilético.

Os limites taxonômicos de Pentatomoidea são bastante claros, sendo provavelmente o grupo mais bem conhecido de Heteroptera no nível específico (Schuh 1986). A monofilia de Pentatomoidea é amplamente aceita e embasada em análises cladísticas (Gapud 1991; Henry 1997; Grazia *et al.* 2008). A classificação em nível de família, subfamília e tribo, no entanto, é ainda muito controversa ou mesmo confusa (Schaefer 2003). Schuh (1986) aponta como principal causa da situação da classificação de Pentatomoidea, além da falta de catálogos recentes para a maioria dos táxons e da regionalização do trabalho dos sistematas, a falta de estudos rigorosos baseados na metodologia cladística. Nos últimos anos, entretanto, essa situação vem sendo modificada pela publicação de estudos cladísticos sobre as relações entre famílias e grupos superiores dentro de Pentatomoidea, principalmente dentro de Pentatomidae (Grazia 1997; Barcellos & Grazia 2003; Fortes & Grazia 2005; Campos & Grazia 2006; Bernardes *et al.* 2009; Ferrari *et al.* 2010; Genevcius *et al.* 2012; Simões *et al.* 2012; Garbelotto *et al.* 2013), Dinidoridae (Kocorek & Lis 2000; Lis *et al.* 2012a, 2012b) e Tessaratomidae (Kment & Vilímová 2010a; Lis *et al.* 2012b). Cydnidae e as famílias próximas (“grupo Cydnoidea”) ainda permanecem pouco estudadas do ponto de vista filogenético.

2. Sistemática de Thyreocoridae Amyot & Serville

2.1. Caracterização e histórico

Os membros da família Thyreocoridae, também conhecidos como *negro bugs*, são percevejos pequenos (entre 3 e 6 mm), ovais, fortemente convexos, brilhantemente negros, com aparência de besouros. O escutelo é grande e se estende até o ápice do abdome, cobrindo parte deste e das asas. Possuem antenas com cinco segmentos, tarsos com três segmentos e tricobótrios geralmente arranjados transversalmente. Podem também ser confundidos com pequenos percevejos da família Scutelleridae, mas são muito menores e apresentam fortes espinhos na tíbia (Miller 1971; Triplehorn & Johnson 2005; Marshall 2006).

A classificação do grupo é bastante confusa e não há consenso entre os autores sobre o posicionamento e o status do grupo, nem sequer sobre o nome da família. Tanto Thyreocoridae Amyot & Serville quanto Corimelaenidae Uhler têm sido amplamente utilizados, mediante diferentes justificativas por diversos autores.

A primeira proposição de reunião desses insetos em um grupo de gêneros foi feita por Amyot & Serville (1843), sob a denominação de Thyréocorides. Dentro deste grupo, os autores incluíram seis gêneros (*Chlaenocoris* Burmeister, *Coptosoma* Laporte, *Heterocrates* Amyot & Serville, *Plataspis* Westwood, *Strombosoma* Amyot & Serville e *Thyreocoris* Schrank). No entanto, apenas dois desses gêneros são incluídos atualmente em Thyreocoridae: *Strombosoma* e *Thyreocoris* (Dolling 1981). Os demais pertencem atualmente a Canopidae (*Chlaenocoris*) e a Plataspididae (*Coptosoma*, *Heterocrates* e *Plataspis*). Na mesma publicação, os autores reúnem, sob o nome de Odontoscélides, *Coreomelas* Amyot & Serville (sinônimo júnior de *Thyreocoris*), *Galgupha* Amyot & Serville (atualmente Thyreocoridae) e *Odontoscelis* Laporte (atualmente Scutelleridae). Na visão de Rolston & McDonald (1979), Thyréocorides deveria ser considerado sinônimo de Plataspididae, visto que a maioria das espécies incluídas pertence a esta família.

Uhler (1872) introduz o nome Corimelaenidae para incluir os gêneros *Galgupha* e *Corimelaena* White, sendo o nome mais amplamente aceito pelos pesquisadores norte-americanos. A partir de então, muitos autores rejeitaram o nome Thyreocoridae em favor de Corimelaenidae com base no uso (Rolston & McDonald 1979) ou considerando inválido o nome Thyréocorides; pois, embora nomes de grupos terminando em "-ides" tenham sido aceitos como Latim, a mesma terminação usada por Amyot & Serville (1843) seria francês (Leston 1953). Outros autores defendem Thyreocoridae como nome mais antigo, cujo uso deveria ser continuado para fins de estabilidade da nomenclatura (Stys & Davidová 1979; Froeschner 1988; Triplehorn & Johnson 2005; Marshall 2006).

Distant (1880) menciona nove espécies de Thyreocoridae (dentro de Pentatomidae: Cydninae) pertencentes ao gênero *Thyreocoris*, considerando-o sinônimo de *Corimelaena* e *Galgupha*. Lethierry & Severin (1893) consideraram Corimelaenidae como subfamília de Pentatomidae, incluindo os gêneros *Alkindus* Distant, *Canopus* Fabricius, *Chlaenocoris*, *Caenina* Walker, *Corimelaena*, *Cursula* Walker, *Cyrtaspis* Stål, *Eucoria* Mulsant & Rey, *Eumetopia* Westwood e *Strombosoma*.

Horvath (1919) trata o grupo como subfamília de Cydnidae (Thyreocorinae) e separa os gêneros *Canopus* (e seus sinônimos *Chlaenocoris* e *Cursula*) e *Cyrtaspis* na tribo Canoparia e os demais na tribo Thyreocoraria, junto com *Galgupha*, *Thyreocoris* e sete novos gêneros. McAtee & Malloch (1928a) excluem *Cyrtaspis* (= *Megaris* Stål) e *Canopus* de Thyreocorinae, criando táxons superiores para comportá-los (atualmente, Megarididae e Canopidae, respectivamente). Os mesmos autores posteriormente removem de Thyreocorinae os gêneros *Caenina* (considerado próximo a *Eysarcoris* Hahn), *Eumetopia* e *Strombosoma* (McAtee & Malloch 1933).

McAtee & Malloch (1933) fazem ampla revisão do grupo, considerando Thyreocorinae como subfamília de Pentatomidae, incluindo chaves para os gêneros, subgêneros, espécies e variedades cromáticas, além da descrição de 114 novas espécies. No entanto, o status de subfamília desses autores é considerado equivalente às atuais famílias de Pentatomoidea (Rolston & McDonald 1979; Ahmad & McPherson 1990). O trabalho inclui valiosas informações e um estudo extenso e criterioso das espécies do grupo; porém, não inclui ilustrações para todas as espécies, não discute caracteres de genitália de reconhecida importância e está desatualizado devido a posteriores modificações taxonômicas e descrições de espécies novas.

McAtee & Malloch (1933) reconhecem nove gêneros: *Alkindus*, *Allocoris* McAtee & Malloch, *Amyssonotum* Horvath, *Cydnoides* Malloch, *Galgupha*, *Godmania* Horvath, *Pericrepis* Horvath, *Pruhleria* McAtee & Malloch e *Thyreocoris*. Os gêneros *Carrabas* Distant e *Strombosoma* são considerados *incertae sedis*, pois, apesar de se assemelharem a Thyreocoridae, apresentam diferenças no comprimento do cório e no grau de desenvolvimento do evaporatório metapleural.

Sailer (1945) sinonimiza *Eucoria marginipennis* Mulsant & Rey a *Corimelaena pulicaria* (Germar) e sugere o uso do nome Eucoriinae baseado em Eucoriens Mulsant & Rey, pelo princípio da prioridade. A proposição, porém, baseia-se em um nome genérico que é sinônimo júnior de *Corimelaena*, tendo sido praticamente esquecido e nunca aplicado na literatura recente (Stys & Davidová 1979). Dolling (1981) considera Eucoriens *nomen oblitum*.

Froeschner (1960) exclui Corimelaenidae (equivalente a Thyreocorinae de McAtee & Malloch) de Cydnidae, dando a ambos os grupos status de famílias independentes. O autor concorda com McAtee & Malloch (1933), confirmando as características morfológicas apresentadas para distinguir Thyreocoridae de Cydnidae:

curta exposição do clavo e presença de uma área lisa de cutícula atrás dos olhos na superfície ventral da cabeça.

Stys & Davidová (1979) revisam o gênero *Thyreocoris* e conferem a Thyreocoridae o status de família.

Dolling (1981) reconhece Thyreocorinae e Corimelaeninae como duas subfamílias independentes dentro da família Cydnidae. Thyreocorinae incluiria três gêneros do Velho Mundo (*Carrabas*, *Strombosoma* e *Thyreocoris*) e Corimelaeninae incluiria nove gêneros americanos (incluindo *Eumetopia*). Os gêneros de Thyreocorinae são reunidos com base em características da cabeça, evaporatório, morfologia da asa e da genitália do macho e da fêmea, pelas quais diferem das espécies americanas. Corimelaeninae caracteriza-se pela morfologia da asa e da genitália do macho e da fêmea. Segundo o autor, os corimelenínеos americanos não têm nada em comum com os três gêneros de Thyreocorinae, exceto os caracteres básicos de cidnídeos e o escutelo extremamente ampliado, concluindo pela separação das formas do Velho Mundo e do Novo Mundo.

Em seu catálogo das espécies paleárticas, Lis (2006) adota o status de família para Thyreocoridae, seguindo Stys & Davidová (1979), e sua divisão em duas subfamílias, Thyreocorinae e Corimelaeninae, segundo proposto por Dolling (1981).

Após o catálogo de McAtee & Malloch (1933), apenas publicações esparsas trazem informações relevantes sobre insetos dessa família. Embora muitas das espécies de Thyreocoridae sejam comuns, poucas foram estudadas em maior detalhe. Novas espécies foram descritas (Sailer 1940, 1941b; Kormilev, 1956a, 1956b; McPherson & Sailer 1978; Ahmad & Moizuddin 1982) e outros estudos trazem considerações sobre a taxonomia de espécies do grupo (Sailer 1941a; McPherson 1978b).

Thyreocoridae tem status de família e compreende 212 espécies em 12 gêneros dividos em duas subfamílias: Thyreocorinae e Corimelaeninae (Lis 2006) (Tabelas 1 e 2). A maioria dos gêneros e espécies está amplamente distribuída nas regiões Neártica e Neotropical, enquanto poucos gêneros ocorrem nas regiões Paleártica, Oriental e Afrotropical (McAtee & Malloch 1933; Stys & Davidová 1979; Ahmad & Moizuddin 1982).

Thyreocorinae compreende sete espécies em três gêneros (Stys & Davidová 1979; Dolling 1981; Ahmad & Moizuddin 1982). Tem ocorrência somente no Hemisfério Oriental e geralmente é definida pelo lobo jugal na asa metatorácica inteiro, não perfurado (Dolling 1981). McAtee & Malloch (1933) consideraram *Carrabas* e *Strombosoma* como *incertae sedis*, mas Dolling (1981) posteriormente incluiu ambos os gêneros em Thyreocorinae.

Corimelaeninae compreende 205 espécies em nove gêneros (McAtee & Malloch 1933; Sailer 1940, 1941b; Kormilev 1956a, 1956b; McPherson & Sailer 1978; Dolling 1981). O grupo é restrito ao Hemisfério Ocidental e é definido pela asa metatorácica com uma perfuração oval no lobo jugal (Dolling 1981). Um gênero, *Galgupha*, contém cerca de três quartos da diversidade de Thyreocoridae e é dividido em 15 subgêneros. O único gênero cuja posição já foi contestada é *Eumetopia*, excluído de Thyreocoridae por McAtee & Malloch (1933), mas posteriormente incluído em Corimelaeninae por Dolling (1981).

2.2. Estudos morfológicos

Dentro de Thyreocoridae, poucas características morfológicas foram exploradas em estudos comparativos, impondo dificuldades para a seleção de caracteres. Para poucas espécies, há investigações sobre aspectos das estruturas das pernas (Lis 2010; Barão *et al.* 2013), sistema eferente odorífero externo (Kment & Vilímová 2010b) e genitália interna de machos (McAtee & Malloch 1933; Ahmad & McPherson 1990; Davidová-Vilímová & McPherson 1991), fêmeas (Pendergrast 1957; Scudder 1959; Pluot-Sigwalt & Lis 2008) ou ambos os sexos (McDonald 1966; Stys & Davidová 1979; Dolling 1981).

Quanto às pernas dos tireocorídeos, já foram estudadas pelo menos três estruturas: pentes coxais, pentes tibiais e aparato tibial. A presença de pentes coxais foi considerada uma sinapomorfia de Corimelaenidae (= Thyreocoridae) e de Cydnidae *sensu lato* (incluindo ou não Thyreocoridae) (Dolling 1981; Gapud 1991; Grazia *et al.* 2008). Esta estrutura já havia sido mencionada para Thyreocoridae por outros autores (e.g., McAtee & Malloch 1933; Schuh & Slater 1995; Grazia *et al.* 2008). Mais recentemente, Lis (2010) fotografou em microscopia eletrônica de varredura (MEV) os pentes coxais de *Thyreocoris scarabaeoides* (Linnaeus) e *Strombosoma impictum* Amyot & Serville, observando um padrão de cerdas tipo calha, encontrado também em alguns grupos de Cydnidae (Lis 2010).

Os pentes tibiais estão presentes em todas as infraordens terrestres de Heteroptera. Lis & Schaefer (2005) estudaram essas estruturas em vários representantes de Cydnidae e Parastrachiidae em MEV. Nenhuma espécie de Thyreocoridae foi incluída neste estudo, mas os autores mencionam que os pentes tibiais estão presentes nas pernas anteriores de espécies dessa família, bem como em várias outras famílias de Pentatomoidea. Recentemente, Barão *et al.* (2013) estudaram os pentes tibiais de 10 espécies de Thyreocoridae, além de espécies de Pentatomidae e Scutelleridae. Os autores concluíram que os tireocorídeos são caracterizados pela presença de um complexo de pentes tibiais, o qual é característico de Cydnidae. Os pentes tibiais, porém, diferem dos de Pentatomidae e de Scutelleridae apenas quanto ao número de cerdas.

O aparato da tíbia anterior está presente na maioria dos grupos de pentatomóideos (McAtee & Malloch 1928a; Dolling 1981), sendo considerada uma característica única dos Pentatomoidea "superiores" (Grazia *et al.* 2008). Sua presença em Thyreocoridae foi observada por Grazia *et al.* (2008) e Barão *et al.* (2013). O aparato tibial de Pentatomidae, Scutelleridae e Thyreocoridae difere apenas no número de cerdas (Barão *et al.* 2013).

As glândulas odoríferas dorso-abdominais dos adultos foram estudadas por Davidová-Vilímová & Podoubský (1999) em *T. scarabaeoides*. O sistema eferente odorífero externo em Thyreocoridae foi muito pouco estudado. Ahmad & Moizuddin (1982) ilustram esta estrutura em *Thyreocoris pakistanensis* Ahmad & Moizuddin e Stys & Davidová (1979) em outras três espécies de *Thyreocoris*. Kment & Vilímová (2010b) fornecem imagens em MEV de *T. scarabaeoides* e desenhos de *Galgupha impressa* (Horvath). Em ambos estudos, os autores ressaltam que as espécies de Thyreocoridae exibem similaridades morfológicas com espécies de Cydnidae.

Aspectos dos segmentos pré-genitais e genitais em ninfas e adultos foram estudados por McPherson *et al.* (2012) em *Corimelaena incognita* (McAtee & Malloch). A genitália de ambos os sexos foi descrita em relativamente poucas espécies de Thyreocoridae. A genitália externa de machos e/ou fêmeas de vários tireocorídeos foi ilustrada por McAtee & Malloch (1933).

Outras espécies já ilustradas incluem *Carrabas maurus* Distant, *Corimelaena lateralis* (Fabricius), *C. obscura* McPherson & Sailer, *C. pulicaria*, *Cydnoides ciliatus* McAtee & Malloch, *Eumetopia fissipes* Westwood, *Galgupha aterrima* Malloch, *G. atra* Amyot & Serville, *G. caudiculata* McAtee & Malloch, *G. denieri* Kormilev, *G. durionei* Kormilev, *G. fritzi* Kormilev, *G. magna* Sailer, *G. torresi* Kormilev, *Strombosoma unipunctatum* Amyot & Serville, *Thyreocoris fulvipennis* (Dallas), *T. ohridanus* Kormilev, *T. pakistanensis* e *T. scarabaeoides* (Sailer 1941b; Kormilev 1956a; Scudder 1959; McDonald 1966; McPherson & Sailer 1978; Stys & Davidová 1979; Dolling 1981; Ahmad & Moizuddin 1982; Davidová-Vilímová & McPherson 1991).

A genitália interna da fêmea foi estudada e ilustrada apenas em *C. pulicaria*, *Galgupha nitiduloides* (Wolff), *G. ovalis* Hussey, *T. fulvipennis*, *T. pakistanensis* e *T. scarabaeoides* (Pendergrast 1957; McDonald 1966; Stys & Davidová 1979; Ahmad & Moizuddin 1982; Pluot-Sigwalt & Lis 2008).

A genitália interna do macho foi ilustrada, porém não descrita, para várias espécies por McAtee & Malloch (1933). Há descrições e ilustrações da genitália interna do macho apenas para as quatro espécies de *Thyreocoris*, *C. maurus*, *C. ciliatus*, *C. laterais*, *C. obscura*, *G. atra* e *S. unipunctatum* (McPherson & Sailer 1978; Dolling 1981; Ahmad & Moizuddin 1982; Ahmad & McPherson 1990).

Pendergrast (1957) estudou a espermateca de duas espécies de Thyreocoridae, concluindo que *T. scarabaeoides* é semelhante a espécies de Cydnidae, porém *G. ovalis* é muito diferente. O autor sugere que Cydninae e Thyreocorinae deveriam ser consideradas apenas como subfamílias de Cydnidae.

Scudder (1959) faz referências à genitália da fêmea na família, concluindo que as diversas espécies de Coriomelaeinae (*sic*) apresentam genitália bastante especializada e indicam um grupo homogêneo. A genitália da fêmea em *Thyreocoris* é significativamente diferente, indicando que o gênero estaria posicionado erroneamente na família ou representaria um estoque ancestral na região Paleártica.

McDonald (1966) estuda a genitália do macho de *C. pulicaria*, concluindo que o pigóforo apresenta semelhanças com o de *T. scarabaeoides*. O phallus, porém, apresenta diferenças importantes, sendo mais semelhante aos das espécies de Corimelaeninae ilustradas por McAtee & Malloch (1933).

Stys & Davidová (1979) revisam o gênero *Thyreocoris*, reconhecendo três espécies válidas restritas à região Paleártica e fornecendo importantes informações sobre a genitália das espécies. Os autores concluem que vários aspectos da genitália do macho e da fêmea de *Thyreocoris* spp. seriam plesiomórficos dentro da família.

Ahmad & Moizuddin (1982), com base no estudo de características da glândula metatorácica e da genitália masculina e feminina, concordam com o posicionamento do grupo como subfamília de Cydnidae, considerando ainda Thyreocorinae como próximo de Scutellocorini (Cydnidae, Cydninae), descrita por Ahmad & Moizuddin (1980).

Ahmad & McPherson (1990) descrevem e ilustram a genitália masculina das espécies tipo dos gêneros *Corimelaena*, *Galgupha* e *Cydnoides* e comparam com dados sobre *Thyreocoris*. Com base no grau de similaridade geral da genitália, indicam que os grupos de distribuição no Velho e no Novo Mundo deveriam ser alocados em diferentes tribos da mesma subfamília, porém apontam que apenas o exame da genitália de ambos os sexos em um maior número de gêneros e espécies poderia sustentar o posicionamento dos grupos.

Pluot-Sigwalt & Lis (2008) estudaram a espermateca de várias espécies de Cydnidae e grupos próximos. Os autores ressaltam que a espermateca de *T. scarabaeoides* apresenta semelhanças com espécies de Sehirinae (Cydnidae) e Pentatomidae, sendo seus caracteres intermediários entre estes dois grupos.

2.3. Posição filogenética

As relações filogenéticas dentro de Thyreocoridae não são conhecidas; nenhum dos 12 gêneros foi investigado num contexto cladístico. A validade dos subgêneros dos gêneros mais diversos, *Corimelaena*, *Cydnoides* e *Galgupha*, ainda precisa ser testada. A posição de Thyreocoridae na evolução de Pentatomoidea, no entanto, já foi discutida por Gapud (1991), Grazia *et al.* (2008) e Lis *et al.* (2012), geralmente sugerindo uma relação próxima com Cydnidae.

A hipótese de Gapud (1991) das relações filogenéticas dentro de Pentatomoidea com base na morfologia reconhece que os grupos Cydnidae e Thyreocoridae estão fortemente associados pela presença de franjas coxais e espinhos tibiais. Cynidae, porém, se separa de Thyreocoridae pelas pontuações setígeras na cabeça e pronoto. Thyreocoridae possui caracteres relativamente fracos compartilhados com outras famílias, como o escutelo amplo cobrindo o abdome, freno curto e laterotergitos 9 contíguos.

Grazia *et al.* (2008) analisaram as relações dentro de Pentatomoidea, empregando 135 terminais e 57 caracteres morfológicos e dados de sequências das regiões dos genes rDNA 18S, rDNA 16S, rDNA 28S e COI. O estudo suporta a monofilia de Corimelaenidae (=Thyreocoridae), representada por *Thyreocoris* e *Allocoris* (=*Corimelaena*), com base em sete sinapomorfias homoplásticas. As sinapomorfias são: ângulos humerais e posteriores do pronoto não desenvolvidos; asas posteriores com *stridulitrum* A1; prosterno profundamente sulcado; prosterno fortemente carenado; coxas com uma franja de setas, cerdas ou escamas; tíbias anteriores com uma fileira de cerdas robustas na margem lateral, e gonocoxitos 9 unidos medianamente por membrana.

Enquanto nas análises morfológicas Corimelaenidae apareceu como grupo basal dentro Cydnidae, nas análises moleculares *Allocoris* apareceu em algumas árvores como grupo irmão de Parastrachiidae (*Parastrachia* Distant e *Dismegistus* Amyot & Serville). Grazia *et al.* (2008) sugerem que Parastrachiidae receba status de subfamília e seja tratada como parte de Thyreocoridae.

A análise de Lis *et al.* (2012) testa a monofilia de Dinidoridae e sua posição sistemática dentro de Pentatomoidea analisando sequências de rDNA 12S e 16S. Embora a análise de Thyreocoridae não tenha sido parte do objetivo dos autores e os resultados referentes à família não tenham sido discutidos no artigo, são incluídos três terminais: *Galgupha difficilis* (Breddin), *S. impictum* e *T. scarabaeoides*. Em nenhuma das análises (rDNA 12S, rDNA 16S e análise combinada rDNA 12S e 16S), Thyreocoridae foi recuperada como monofilética. Na análise combinada, *S. impictum* e *T. scarabaeoides* aparecem como grupos irmãos (sustentando Thyreocorinae) e *G. difficilis* aparece num ramo distante.

2.4. Distribuição e diversidade

Para Thyreocoridae, informações básicas (como ciclo de vida e distribuição geográfica) são incompletas, imprecisas ou faltam para muitas espécies (McPherson 1974). As áreas de ocorrência das espécies, bem como os países em que já foram registradas, são apresentadas na Tabela 2.

Em estudos de diversidade e em buscas dirigidas, os percevejos dessa família são coletados em abundância (McPherson 1974). Em análises recentes da diversidade de Pentatomoidea em áreas naturais do sul do Brasil, Thyreocoridae apresenta grande riqueza e abundância, geralmente aparecendo com a segunda família mais abundante, depois de Pentatomidae (Bunde 2005; Barcellos 2006; Bertolin 2007, Schmidt & Barcellos 2007; Mendonça *et al.* 2009).

O estado atual de conhecimento de suas espécies, no entato, impede a identificação de todos os exemplares coletados, dificultando assim tanto as análises de diversidade quanto o acúmulo de informações sobre esses insetos na natureza. Bunde (2005) atribui essa dificuldade à falta de material depositado em coleções, à ausência de inventários recentes e de estudos taxonômicos. Mendonça *et al.* (2009) atribuem a impossibilidade de identificação até o nível de espécie ao status do conhecimento taxonômico do grupo na região Neotropical.

Mesmo assim, após a revisão de McAtee & Malloch (1933), muitos tratamentos regionais foram dados ao grupo, principalmente na forma de catálogos de Hemiptera ou Pentatomoidea que fizeram referência à ocorrência de espécies de Thyreocoridae em determinadas regiões.

Para a região Etiópica, Linnavuori (1977, 1993) menciona as espécies que ocorrem no Sudão e outras regiões da África. Para a região Paleártica, há o catálogo de Lis (2006) e a menção de espécies para Polônia (Lis 1989) e regiões da República Tcheca (Stehlík 1983) e Turquia (Fent & Aktaç 2007).

Para a região Neártica, Uhler (1886) lista as espécies que ocorrem na América do Norte. Além do catálogo de Thyreocoridae do Canadá e Estados Unidos (EUA) (Froeschner 1988), há diversos levantamentos regionais para os EUA (McPherson, 1970, 1974, 1978a, 1979a, 1979b, 1980; McPherson & Mohlenbrock 1976).

Para a região Neotropical, há trabalhos sobre a fauna de Cuba (Barber & Bruner 1932), Porto Rico (Barber 1939), Jamaica (Van Duzee 1907), Nicarágua (Maes 1994), Granada (Uhler 1894), Trinidad (Callan 1948), Venezuela (Becker & Grazia-Vieira 1971), Guiana Francesa (Becker & Grazia-Vieira 1977), diferentes regiões do Brasil (McAtee & Malloch 1928b; Grazia *et al.* 1999; Barcellos 2006; Schmidt & Barcellos 2007; Mendonça *et al.* 2009; Grazia & Schwertner 2011), Equador (Froeschner 1981), Chile (Porter 1933) e Argentina (Berg 1879, 1884, 1891; Grazia *et al.*, no prelo).

2.5. Hábitos alimentares e importância econômica

Os tireocoríneos ocorrem abundantemente em gramíneas, plantas herbáceas e arbustos, onde encontram sua fonte primária de alimento, aparentemente concentrando sua atividade alimentar nas flores e sementes em desenvolvimento. Além de relatos dispersos de danos perceptíveis a plantas cultivadas e ornamentais, frequentemente é feita referência ao gosto desagradável conferido aos pequenos frutos cultivados em que esses insetos ocorrem (Froeschner 1988). Entretanto, nenhuma espécie de

Thyreocoridae é considerada entre os heterópteros de importância econômica (Schaefer & Panizzi 2000).

Schaefer (1988) compila dados de plantas hospedeiras para diversos grupos de Pentatomoidea, inclusive para a subfamília Corimelaeninae. Os dados não apontam preferências particulares por plantas hospedeiras no nível de subfamília ou gênero. A maioria das espécies alimenta-se nas partes reprodutivas ricas em nitrogênio (principalmente *Corimelaena* spp.); poucas ocorrem sobre o solo (principalmente *Cydnoides* spp.) (Schaefer 1988). Rider (2013) traz uma lista atualizada de diversos registros já publicados de plantas hospedeiras de Thyreocoridae. Pelo menos 32 espécies de Thyreocoridae têm algum registro de planta associada na literatura (Tabela 2).

Uma mesma espécie, *C. pulicaria*, foi registrada em diferentes plantas hospedeiras, de mais de 10 famílias de plantas (Schaefer 1988). No entanto, todas as espécies estudadas utilizaram durante seu ciclo de vida, em determinada área, apenas uma (Biehler & McPherson 1982) ou duas (Bundy & McPherson 1997) plantas como sítios preferenciais de alimentação, cópula e oviposição.

Todos os estudos sobre tireocorídeos em condições de campo ocorreram no Hemisfério Norte. As espécies podem ser uni-, bi- ou multivoltinas: um maior número de gerações por ano ocorre em baixas latitudes, enquanto que em latitudes mais altas apenas uma geração é possível (McPherson 1972; Lung & Goeden 1982; Bundy & McPherson 1997, 2009). Todas as espécies apresentam período de dormência no estágio adulto; durante esse período são encontradas sob folhiço, solo ou mesmo rochas. Os adultos deixam os sítios de dormência após o final do inverno ou início da primavera, se deslocam para as plantas hospedeiras e começam a se alimentar. Comportamento de pré-cópula foi descrito por Bundy & McPherson (1997): o macho se posiciona atrás da fêmea e inicia o contato por antenamento; após aceitação da fêmea, a cópula ocorre com os indivíduos posicionados em direções opostas, apenas as genitálias se tocando. A cópula pode durar horas.

2.6. Estágios imaturos

Os imaturos de Thyreocoridae foram pouco estudados, provavelmente devido ao seu pequeno tamanho, hábitos e falta de conhecimento sobre as plantas hospedeiras necessárias ao desenvolvimento ninfal (Yonke 1991). Características gerais dos ovos e ninfas de espécies de tireocorídeos foram brevemente descritas (Southwood 1956; Cobben 1968; Hinton 1981; Yonke 1991). Os estágios imaturos são conhecidos para apenas nove espécies, incluindo descrições de ovos e/ou ninfas e/ou biologia (Tabela 3).

Os ovos são alongados, com cório fino, aparentemente liso, podendo apresentar rugas quando observados em microscopia eletrônica de varredura (Bundy & McPherson 1997, 2009). A coloração inicial é branca, tornado-se avermelhada ou escurecida com o desenvolvimento do embrião, sendo possível observar as estruturas através do cório. Os processos aero-micropilares são pedunculados e curvados para o centro, localizados em torno do pólo apical; dependendo da espécie, ocorrem de 4 a 10 processos aero-micropilares, com diferenças no tamanho do pedúnculo. O opérculo está ausente, a linha de ruptura do ovo é irregular e ocorre transversalmente, iniciando no pólo apical e se estendendo lateralmente (Javahery 1994). Bundy & McPherson (2009) descrevem o *ruptor ovis* de *C. incognita* como sendo rombóide, com um pequeno processo mediano; Southwood (1956) e Cobben (1968) citam essa estrutura como reduzida em ambas subfamílias.

Os ovos são colocados individualmente e fixados lateralmente ao substrato, geralmente partes reprodutivas da hospedeira, menos frequentemente, ramos ou folhas. O tempo de desenvolvimento do ovo varia entre 8-11 dias, dependendo da espécie e também da temperatura e umidade. Parasitóides de ovos das famílias Tachinidae (Diptera) e Scelionidae (Hymenoptera) são os principais inimigos naturais registrados (Grazia *et al.* no prelo).

As ninfas têm a forma do corpo e da cabeça semelhante aos adultos. A coloração da maior parte do corpo é escura (negra ou castanha); a coloração do abdome varia de acordo com a espécie, podendo ser amarelado ou avermelhado, mas sempre com pontuações mais escuras. Outras características das ninfas de Thyreocoridae incluem: corpo fortemente convexo, com pontuações uniformemente distribuídas; espinhos tibiais presentes; placas dorsais medianas presentes em todos os segmentos abdominais, formando estruturas pareadas no primeiro e segundo segmentos; aberturas das glândulas odoríferas presentes entre os segmentos 3/4, 4/5 e 5/6, pareadas e alinhadas, e placas laterais subquadrangulares. Outras duas características são peculiares e parecem ser exclusivas para as ninfas de Thyreocoridae: no primeiro, segundo e terceiro instares, o metanoto nunca está completamente fusionado, e, no quinto instar, as margens posterior e anterior das placas abdominais dorsais do quarto e quinto segmentos, respectivamente, são contíguas (Grazia *et al.* no prelo).

Ninfas de primeiro instar são ativas; diferentemente das ninfas de outras famílias de Pentatomoidea, se alimentam e não têm comportamento gregário. Tempo de desenvolvimento das ninfas varia de 30-45 dias, provavelmente influenciado pelo alimento utilizado e também pelas condições de temperatura e umidade local (Grazia *et al.* no prelo).

2.7. Uso de caracteres de ovos em filogenias

A importância da estrutura do ovo para definir o status e as relações entre os grupos de Heteroptera já foi reconhecida. Em Pentatomoidea, padrões morfológios dos ovos já foram identificados em diferentes níveis taxonômicos (Leston 1955; Southwood 1956; Cobben 1968; Javahery 1994; Matesco *et al.* 2009). Embora a importância filogenética do estágio de ovo seja amplamente enfatizada na literatura, ela raramente foi testada em análises cladísticas (Hasan & Kitching 1993; Wheeler *et al.* 1993; Henry 1997; Grazia *et al.* 2008).

A presença de pseudopérculo e a ausência do canal micropilar interno são sinapomorfias de Pentatomidae (Pentatomoidea) (Hasan & Kitching 1993); a fenda de eclosão hexagonal é homoplásica para Artheneidae, Oxycarenidae e Piesmatidae (Lygaeoidea) (Henry 1997), e a presença de processos aero-micropilares suporta a monofilia de Pentatomomorpha (Grazia *et al.* 2008).

A mais importante lista de caracteres para os ovos de Pentatomoidea é a de Javahery (1994), que realizou uma análise filogenética baseada apenas no estágio de ovo. A matriz contém 22 caracteres para 23 gêneros de Pentatomoidea, incluindo somente espécies neárticas e paleárticas. Os caracteres de ovos já incluídos em análises cladísticas em Pentatomoidea encontram-se listados na Tabela 4.

O estágio de ovo ainda não foi descrito em quatro das 15 famílias de Pentatomoidea (Saileriolidae, Canopidae, Megarididae e Lestoniidae). Para a maiora das famílias, há trabalhos abrangentes sobre o estágio de ovo (Leston 1955; Southwood 1956; Cobben 1968; Hinton 1981; Javahery 1994), além de trabalhos dispersos na literatura com descrições de uma ou poucas espécies. Alguns trabalhos recentes trazem imagens em microscopia eletrônica de varredura, a maioria em Scutelleridae (Candan & Suludere 2003, 2006; Williams *et al.* 2005; Candan *et al.* 2007, 2011)

Dentro de algumas famílias (e.g., Dinidoridae, Tessaratomidae e Scutelleridae), a morfologia dos ovos parece ser relativamente bem conhecida, mas não há um levantamento do número de espécies já estudadas. Davidová-Vilímová (1987) revisaram os ovos de Plataspididae, e estudos mais recentes já foram feitos (Ren *et al.* 1990; Ren 1992; Candan *et al.* 2012). Para Thyreocoridae, nove das mais de 210 espécies do grupo já tiveram os ovos descritos (Tabela 3).

Por outro lado, os ovos de Pentatomidae foram descritos para mais espécies do que aqueles de qualquer outra família de Heteroptera (Southwood 1956; Hinton 1981; Wolf & Reid 2003), embora este tenha sido considerado o estágio do desenvolvimento menos estudado da família (Bundy & McPherson 2000). Matesco *et al.* (2009) listaram 125 espécies de Pentatomidae cujos ovos foram descritos em microscopia óptica ou em microscopia eletrônica de varredura.

OBJETIVOS

O objetivo geral desta tese é organizar, atualizar e ampliar o conhecimento sobre as espécies de Thyreocoridae, através da revisão do gênero *Alkindus*, da descrição dos ovos de duas espécies de *Galgupha* e da análise cladística do gênero *Corimelaena*. A fim de subsidiar o uso de caracteres de ovos em filogenias, estudaram-se também os ovos de 16 espécies de Pentatomidae.

Constituem objetivos específicos:

1) redescrever o gênero *Alkindus* e suas duas espécies, descrevendo pela primeira vez o macho de *Alkindus crassicosta*, fornecendo uma chave para as espécies, compilando registros de plantas associadas e ampliando registros de distribuição geográfica;

2) descrever os ovos de duas espécies neotropicais de *Galgupha* em microscopia óptica e microscopia eletrônica de varredura, compilando informações sobre a morfologia dos imaturos e os hábitos de oviposição em Thyreocoridae e grupos relacionados (Parastrachiidae e Cydnidae);

3) estabelecer uma hipótese das relações de parentesco entre as espécies de *Corimelaena*, testando a validade de seus subgêneros e a posição do gênero dentro da família, através da metodologia cladística, com base na morfologia de adultos e imaturos;

4) com base na mesma análise, testar a monofilia de Thyreocoridae, suas subfamílias e alguns de seus gêneros;

5) propor uma classificação para a família baseada nos grupos monofiléticos recuperados, e

6) caracterizar a estrutura coriônica externa dos ovos de 16 espécies neotropicais de Pentatomidae, discutindo padrões morfológicos em diferentes níveis taxonômicos, listando caracteres de ovos a serem utilizados em análises cladísticas e testando alguns desses caracteres em análises já existentes dentro de Pentatomidae.

MATERIAL E MÉTODOS

Estudo dos ovos e dos adultos

Para a revisão de *Alkindus* e para a análise de *Corimelaena*, analisaram-se espécimes adultos conservados a seco pertencentes a coleções entomológicas nacionais e estrangeiras, obtidos por empréstimo dos respectivos curadores.

Para o estudo dos ovos, analisaram-se exemplares preservados em álcool etílico 70% provenientes de fêmeas de duas espécies de Thyreocoridae e 16 espécies de Pentatomidae coletadas a campo na região sul do Brasil e mantidas em potes no laboratório até a oviposição. Devido ao pequeno número de exemplares coletados e à carência de informações sobre as plantas hospedeiras da maioria dessas espécies, não foi possível a criação das mesmas em laboratório. Exemplares testemunho de ovos e adultos estão depositados na Coleção Entomológica do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul (UFRG).

Os espécimes foram estudados em microscopia óptica e microscopia eletrônica de varredura (MEV). Para a obtenção de fotografias, utilizou-se equipamento digital fotográfico acoplado ao estereomicroscópio; o *software* Helicon Focus 4.77 foi utilizado para gerar imagens únicas a partir de imagens obtidas em vários planos de foco. As ilustrações foram confeccionadas com uso de câmara clara acoplada ao estereomicroscópio e, após, digitalizadas e vetorizadas no programa Adobe Illustrator®. Ovos e adultos foram medidos com auxílio de ocular de medição acoplada ao estereomicroscópio; as medidas são apresentadas em milímetros, como média ± desvio padrão, mínimo e máximo.

Para a análise em MEV, seguiu-se o protocolo descrito por Bianchi *et al.* (2011). As amostras foram submetidas a ponto crítico, quando necessário, e após montadas em stubs, metalizadas com ouro e analisadas no Centro de Microscopia Eletrônica da Universidade Federal do Rio Grande do Sul (CME/UFRGS).

A genitália interna de ambos os sexos não foi estudada devido à escassez de material e a dificuldades nos métodos de dissecção e preparação, bem como na interpretação das estruturas.

A terminologia seguiu Tsai *et al.* (2011) para a morfologia geral; Kment & Vilímová (2010b) para o sistema eferente odorífero externo; Lis & Schaefer (2005), Grazia *et al.* (2008) e Lis (2010) para as estruturas das pernas; Dupuis (1970) e Schaefer

(1977) para a genitália; Javahery (1994) e Bundy & McPherson (2009) para ovos de Thyreocoridae, e Matesco *et al.* (2009) para ovos de Pentatomidae.

Os registros de distribuição e a lista de plantas hospedeiras das espécies de *Alkindus*, bem como os caracteres de ovos de Pentatomoidea e seus respectivos estados foram compilados a partir da literatura.

Análises cladísticas

Na análise de *Corimelaena*, adotou-se a abordagem de táxon exemplar, em que os táxons terminais são espécies cujo complemento de caracteres é baseado na observação (Prendini 2001). Foram incluídas 40 espécies terminais, incluindo espécies representantes dos 12 gêneros de Thyreocoridae, bem como espécies de Canopidae, Cydnidae e Parastrachiidae. A espécie *Coptosoma scutellatum* (Geoffroy) (Plataspididae) foi utilizada com fins de polarização dos caracteres e enraizamento dos cladogramas.

A hipótese inicial de monofilia do grupo baseou-se nos resultados da análise cladística de Pentatomoidea de Grazia *et al.* (2008). A definição inicial de Thyreocoridae e dos limites dos gêneros constituintes da família foram feitas a partir da literatura (McAtee & Malloch 1933; Dolling 1981; Lis 2006). Quando possível, a escolha dos táxons terminais de Thyreocoridae buscou contemplar as espécies-tipo dos gêneros e subgêneros bem como outras espécies de modo a representar a diversidade morfológica contida em cada táxon. Para o terminal *Corimelaena (Epipora) signoretti* (McAtee & Malloch), os estados foram extraídos da literatura.

Para levantar hipóteses de parentesco entre os táxons, foi utilizada a metodologia cladística (Schuh 2000), empregando-se a análise por parcimônia (Kluge & Farris 1969). Foram analisados 114 caracteres (93 binários e 21 multiestado), relacionados à coloração do corpo (19 caracteres), morfologia da cabeça (18), tórax (38) e abdome da fêmea e do macho (32), imaturos (6) e comportamento materno (1). Foi utilizada a otimização de Fitch (1971), em que todos os caracteres multiestado foram codificados como não aditivos.

Entendendo que a evolução, como origem da hierarquia observada na natureza, deve de alguma forma refletir-se na classificação que os sistematas fazem dos seres vivos (Feliner 1999), propôs-se uma classificação para Thyreocoridae com base nos grupos monofiléticos recuperados pela análise. Para tanto, consideraram-se os clados presentes na árvore de consenso estrito.

Para testar o uso de caracteres de ovos em análises cladísticas, escolheram-se duas matrizes já publicadas em Pentatomidae para o gênero *Nezara* Amyot & Serville (Ferrari *et al.* 2010) e para o grupo *Chinavia obstinata* (Stål) (Genevcius *et al.* 2012). Os demais caracteres foram utilizados como nos artigos originais, adicionando-se seis caracteres de ovos à análise de *Nezara* (três discretos e três contínuos) e cinco à análise do grupo *C. obstinata* (dois discretos e três contínuos).

Tanto na análise de Thyreocoridae quanto nas de Pentatomidae, os estados dos caracteres de ovos foram extraídos da literatura (descrição dos imaturos das espécies terminais e espécies congenéricas). A descrição dos caracteres seguiu Sereno (2007). Para definir a polarização dos caracteres, foi utilizado o método do grupo externo (Nixon & Carpenter 1993). A construção e gerenciamento da matriz foram desenvolvidos no programa WinClada 1.00.08 (Nixon 2002), bem como a edição do cladograma resultante e a obtenção do número de passos e dos índices de consistência e retenção.

A busca pela solução mais parcimoniosa foi realizada no *software* TNT (Tree Analysis Using New Technology, Goloboff *et al.* 2008), utilizando somente pesos iguais. Os parâmetros de busca para a análise de Thyreocoridae incluíram reter 10000 árvores na memória; executar troca de ramos por *tree-bisection-reconnection* (TBR) em 10000 réplicas, e reter 500 árvores por replicação. Os valores de suporte de Bremer absoluto (Bremer 1994) foram calculados com TNT por TBR, retendo árvores subótimas com 10 passos extra. Para as análises em Pentatomidae, os parâmetros foram os mesmo dos artigos originais. Os caracteres contínuos foram normalizados entre 0 e 1, utilizando o script “stand 1”.

RESUMO DOS RESULTADOS

Capítulo 1

A morfologia externa de machos e fêmeas de *Alkindus atratus* Distant e *A. crassicosta* Horvath foi detalhadamente descrita, incluindo o sistema eferente odorífero externo. *A. atratus* possui registro de ocorrência em 12 países da região Neotropical, sendo Guatemala e Brasil novos registros. Pelo menos 14 espécies de plantas potencialmente hospedeiras em oito famílias já foram mencionadas para a espécie; *Ficus* sp. (Moraceae) constitui novo registro. *A. crassicosta* possui registro apenas para o Brasil (sendo Santa Catarina registro novo) e já foi registrada relacionada a uma espécie de Poaceae.

As espécies de *Alkindus* podem ser diferenciadas mediante uso de chave dicotômica adaptada, com base em caracteres do cório das asas e do abdome de machos e fêmeas. As características observadas no sistema eferente odorífero externo e nas pernas (pente coxal, pente tibial e aparato tibial) de ambas espécies de *Alkindus* são similares ao encontrado em outras espécies de Thyreocoridae. O estudo da morfologia da genitália da fêmea corrobora a inclusão de *Alkindus* em Corimelaeninae. Sugere-se que o gênero esteja mais relacionado a *Pericrepis*, como apontado previamente por outros autores.

Os registros de distribuição na região Neotropical das duas espécies de *Alkindus* são claramente disjuntos: *A. atratus* ocorre nos componentes Caribenho e Noroeste e *A. crassicosta* está restrito ao componente Sudeste. Apesar da escassez de dados de coletas e de espécimes identificados em museus, as duas espécies de *Alkindus* parecem estar restritas a áreas de florestas.

Capítulo 2

As espécies neotropicais *Galgupha* (*Euryscytus*) *difficilis* e *Galgupha* (*Gyrocnemis*) *fossata* McAtee & Malloch são similares quanto à estratégia de oviposição e à morfologia geral dos ovos. Os ovos são depositados isoladamente em partes da planta hospedeira. Caracterizam-se por serem cilíndricos, brancos, com cório brilhante, translúcido e com fracas carenas longitudinais. Os processos micropilares estão arranjados ao redor do polo anterior. Cada processo é branco ou translúcido, curto, pedunculado, capitado e com superfície irregular. Os ovos de *G. difficilis* e *G. fossata* diferem em tamanho (0,8 x 0,5 mm e 0,9 x 0,6 mm, respectivamente), superfície do cório (lisa e granulada, respectivamente) e número de processos micropilares (2–4 e 4–10, respectivamente).

Os ovos dessas duas espécies são similares aos de outros Corimelaeninae já estudados, cujo padrão parece incluir: ovos depositados isoladamente em partes da planta hospedeira, cilíndricos com as extremidades arredondadas e brancos antes do desenvolvimento embrionário; cório fino e brilhante com poucos (2–10) processos micropilares curtos e pedunculados ao redor do polo anterior; comprimento dos ovos e dos processos micropilares entre 0,65–1,08 mm e 0,03–0,05 mm, respectivamente. Portanto, a morfologia dos ovos em Thyreocoridae é conservada e se assemelha ao observado nos ovos de espécies de Parastrachiidae (exceto *Dismegistus*) e Sehirinae (Cydnidae). Estes últimos grupos, entretanto, diferem de Thyreocoridae no que tange aos hábitos de oviposição e ao cuidado maternal.

Capítulo 3

Os resultados da análise do gênero *Corimelaena* incluem uma breve explicação para cada caráter morfológico. A análise cladística resultou em seis cladogramas mais parcimoniosos com 418 passos, índice de consistência de 0,33 e índice de retenção de 0,61. O cladograma de consenso estrito possui apenas dois clados não resolvidos. A árvore de consenso suporta a monofilia dos gêneros *Corimelaena* (quatro sinapomorfias) e *Strombosoma* (duas sinapormofias), da subfamília Corimelaeninae (sete sinapormofias) e da família Thyreocoridae (seis sinapomorfias).

O gênero *Amyssonotum* é grupo irmão de *Corimelaena*, e *Godmania* é grupo irmão do clado *Amyssonotum* e *Corimelaena*. Os resultados não suportam a monofilia de Thyreocorinae, *Alkindus*, *Galgupha* (exceto o subgênero nominal) e dos subgêneros *Corimelaena* e *Parapora* McAtee & Malloch.

Corroborando os resultados de análises cladísticas prévias, Thyreocoridae é mais relacionado a Cydnidae (Sehirinae) e Parastrachiidae do que a Canopidae. Porém, como Parastrachiidae e Sehirinae parecem mais relacionados entre si do que a Thyreocoridae, sugere-se a manutenção do status de família para os táxons Thyreocoridae (incluindo os 12 gêneros já atribuídos ao grupo) e Parastrachiidae. Sugere-se ainda que se abandone a divisão de *Corimelaena* em subgêneros.

Capítulo 4

Foram estudados os ovos das seguintes espécies de Pentatomidae: *Banasa induta* Stål, *Capivaccius bufo* Distant, *Catulona pensa* Rolston, *Chinavia armigera* (Stål), *C. aseada* (Rolston), *C. brasicola* (Rolston), *C. runaspis* (Dallas), *Dichelops furcatus* (Fabricius), *Euschistus heros* (Fabricius), *E. riograndensis* Weiler & Grazia, *E. paranticus* Grazia, *Mormidea cornicollis* Stål, *Podisus distinctus* (Stål), *P. nigrispinus* (Dallas), *Serdia apicicornis* Stål e *Thoreyella maracaja* Bernardes, Schwertner & Grazia.

A maioria tem forma de barril, coloração branca, amarelada, esverdeada ou castanha, opérculo arredondado e convexo e cório translúcido e espinhoso. O ovo é esférico em *S. apicicornis* e tem as paredes laterais aplanadas em *T. maracaja*. O cório é liso em *C. pensa*, reticulado em *Chinavia* spp., *B. induta* e *C. bufo* e granulado em *S. apicicornis* e *T. maracaja*. O opérculo é achatado em *E. heros* e *T. maracaja*. Uma linha de eclosão está geralmente evidente, embora não tenha sido observada nos ovos de *Euschistus* spp., *M. cornicollis* e *T. maracaja*. Os processos aero-micropilares estão arranjados em círculo ao redor do polo anterior do ovo, são translúcidos a brancos, variando de curtos a longos, tubulares a fortemente clavados. Sua superfície é caracteristicamente esponjosa, exceto em *Podisus* spp., *C. pensa*, *D. furcatus*, *T. maracaja* e *C. bufo*.

Os padrões morfológicos já observados em nível de tribo foram corroborados em Carpocorini e Procleticini. Padrões em nível de gênero foram observados em *Chinavia* Orian, *Euschistus* Dallas, *Mormidea* Amyot & Serville e *Podisus* Herrich-Schäffer. *C. pensa* é a única espécie de Discocephalinae cujos ovos foram descritos em MEV. *C. bufo*, cujo gênero permanece não classificado em nenhuma tribo de Pentatomidae, apresenta características exclusivas, que dificultam o uso da morfologia dos imaturos para auxiliar na classificação.

A partir de dados da literatura, compilaram-se 286 espécies de Pentatomidae cujos ovos já foram descritos e descreveram-se 40 caracteres de ovos com potencial para uso em filogenias dentro de Pentatomoidea. Sete destes caracteres foram utilizados em duas análises cladísticas já publicadas em Pentatomidae. Na análise do gênero *Nezara*, nenhum dos caracteres foi informativo. Na análise do grupo *C. obstinata*, dois dos caracteres foram informativos: comprimento do ovo e número de processos aero-micropilares (ambos contínuos).

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Tabela 1. Lista de subfamílias, gêneros e subgêneros incluídos na família Thyreocoridae e respectivo número de espécies (McAtee & Malloch 1933; Sailer 1940, 1941b; Kormilev 1956a, 1956b; McPherson & Sailer 1978; Stys & Davidová 1979; Dolling 1981; Ahmad & Moizuddin 1982; Lis 2006).

Subfamília	Gênero	Subgênero	Nº de espécies
Thyreocorinae			7
	Carrabas Distant, 1908		1
	Strombosoma Amyot & Serville, 1843		2
	Thyreocoris Schrank, 1801		4
Corimelaeninae			205
	Alkindus Distant, 1889		2
	Amyssonotum Horvath, 1919		1
	Corimelaena White, 1839		31
		Corimelaena White, 1839	23
		Epipora McAtee & Malloch, 1933	1
		Parapora McAtee & Malloch, 1933	6
		Termapora McAtee & Malloch	1
	Cydnoides Malloch, 1919		9
		Cydnoides Malloch, 1919	3
		Sayocoris McAtee & Malloch, 1933	3
		Cosmarioides McAtee & Malloch, 1933	3
	Eumetopia Westwood, 1838		1
	Galgupha Amyot & Serville, 1843		155
		Acritophleps McAtee & Malloch, 1928	1
		Acrotmetus Horvath, 1919	6

		Astiroderma Horvath, 1919	2
		Bonaria McAtee & Malloch	1
		Charoda McAtee & Malloch, 1933	1
		Ctenopoda McAtee & Malloch, 1933	2
		Euryscytus Horvath, 1919	38
		Galgupha Amyot & Serville, 1843	8
		Gyrocnemis McAtee & Malloch, 1928	37
		Microcompsus Horvath, 1919	3
		Nothocoris McAtee & Malloch, 1928	27
		Orocoris McAtee & Malloch, 1933	1
		Psestophleps McAtee & Malloch, 1928	18
		Pteronomos McAtee & Malloch, 1933	9
		Trepocnemis McAtee & Malloch, 1933	1
	Godmania Horvath, 1919		1
	Pericrepis Horvath, 1919		4
	Pruhleria McAtee & Malloch, 1933		1

Tabela 2. Lista das espécies atualmente aceitas dentro de Thyreocoridae Amyot & Serville e suas respectivas plantas potencialmente hospedeiras e distribuição geográfica, considerando as áreas biogeográficas e os limites políticos dos países. Os dados foram retirados de McAtee & Malloch (1933), exceto quando mencionado.

Espécie	Família botânica	Planta associada	Distribuição
Carrabas maurus Distant	Casuarinaceae	*Casuarina* sp.	Oriental (Índia, Sri Lanka)
Strombosoma impictum (Stål)			Etiópica (Djibouti, República Democrática do Congo[32], África do Sul)
S. unipunctatum Amyot & Serville			Etiópica (Sudão[16], Senegal, Kenya[16], África do Sul[28])
Thyreocoris fulvipennis (Dallas)	Violaceae	*Viola tricolor* L.[55]	Paleártica (França[31], República Tcheca[31], Eslováquia[31], Áustria[31], Hungria[31], Romênia[31], Itália[31], Sérvia[31], Bulgária[31], Macedônia[31], Espanha[31], Portugal[31], Turquia[17], Algeria[31], Marrocos[31])
T. ohridanus Kormilev			Paleártica (Bulgária[31], Macedônia[31])
T. pakistanensis Ahmad & Moizuddin			Oriental (Paquistão[1])
T. scarabaeoides (Linnaeus)	Adoxaceae	*Sambucus* sp.[52]	Paleártica (Rússia[31], Noruega[31], Finlândia[31], Suécia[31], Estônia[31], Letônia[31], Grã-Bretanha[31], Irlanda[31], Dinamarca[31], Lituânia[31], Bielorrússia[31], Alemanha[31], Polônia[31], Holanda[31], Bélgica[31], Ucrânia[31], França[31], Luxemburgo[31], República Tcheca[31], Eslováquia[31], Áustria[31], Hungria[31], Moldávia[31], Romênia[31], Suiça[31], Liechtenstein[31], Itália[31], Eslovênia[31], Sérvia[31], Croácia[31], Bósnia Herzegovina[31], Bulgária[31], Macedônia[31], Espanha[31], Portugal[31], Grécia[31],Turquia[31], Azerbaijão[31], Irã[31], Algeria[31], Marrocos[31])
	Caryophyllaceae	*Gypsophila* sp.[30]	
	Fabaceae	*Ononis* sp.[30]	
	Hypericaceae	*Hypericum* sp.[30]	
	Lamiaceae	*Thymus* sp.[30]	
	Ranunculaceae	*Ranunculus* sp.[30]	
	Violaceae	*Viola tricolor* L.[55]	
Alkindus atratus Distant	Fabaceae	*Glycine* sp.[34]	México e Neotropical (Honduras[34], El salvador[34], Nicarágua, Aruba, Curaçao, Venezuela, Costa Rica, Colômbia, Panamá)
		Phaseolus sp.[34]	
	Malvaceae	*Gossypium* sp.[34]	
		Sida sp.[34]	
	Musaceae	*Musa* sp.[34]	
	Myrtaceae	*Eucalyptus* sp.[34]	

	Poaceae	*Cenchrus* sp.[34]	
		Echinochloa sp.[34]	
		Oryza sp.[34]	
		Sorghum sp.[34]	
		Zea mays L.[3]	
	Rubiaceae	*Coffea* sp.[34]	
	Sterculiaceae	*Theobroma* sp.[34]	
A. crassicosta Horvath	Poaceae	*Andropogon bicornis* L.[23]	Neotropical (Brasil)
Amyssonotum rastratum (Stål)			Neártica (EUA), México e Neotropical (Belize, Guatemala, Costa Rica, Trinidad, Colômbia, Panamá, Suriname, Brasil, Perú, Bolívia)
Corimelaena (Corimelaena) agrella McAtee			Neártica (EUA)
	Apiaceae	*Chaerophyllum procumbens* (L.) Crantz[40, 56]	
		Chaerophyllum tainturieri Hook[56]	
		Sanicula canadensis L.[56]	
	Juglandaceae	*Juglans nigra* L.[43]	
	Polemoniaceae	*Phlox pilosa* L.[39,40]	
C. (C.) alpina (McAtee & Malloch)			Neártica (EUA)
C. (C.) alticola (Horvath,)			México
C. (C.) barberi (McAtee & Malloch)			Neártica (EUA), México e Neotropical (Costa Rica)
C. (C.) championi (Distant)			Neotropical (Belize, Guatemala)
C. (C.) contrasta (McAtee & Malloch)			Neártica (EUA) e México
C.(C.) corallina (McAtee & Malloch)			México e Neotropical (Guatemala)
C. (C.) digitata (McAtee & Malloch			México
C. (C.) elegans (McAtee & Malloch)			México e Neotropical (Guatemala, Costa Rica, Panamá, Trinidad)

C. (C.) feminea (McAtee & Malloch)			Neártica (EUA)
C. (C.) harti Malloch			Neártica (EUA)
C. (C.) interrupta Malloch			Neártica (EUA), México e Neotropical (Guatemala, Honduras, Costa Rica)
C. (C.) lateralis (Fabricius)	Apiaceae	*Chaerophyllum procumbens* (L.) Crantz[40]	Neártica (EUA), México e Neotropical (Guatemala[20])
		Chaerophyllum tainturieri Hook[56]	
		Daucus carota L.[37, 38, 40, 56]	
		Torilis japonica (Houtt.) DC.[56]	
	Asteraceae	*Erigeron philadelphicus* L.[40]	
		Solidago altissima L.[38]	
	Geraniaceae	*Geranium carolinianum* L.[40, 56]	
		Geranium maculatum L.[35]	
	Juglandaceae	*Juglans nigra* L.[43]	
	Poaceae	*Bromus tectorum* L.[56]	
		Elymus hystrix L.[40]	
	Ranunculaceae	*Ranunculus macranthus* Scheele[22]	
	Rubiaceae	*Galium aparine* L.[2, 56]	
	Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	
C. (C.) limata (McAtee & Malloch)			
C. (C.) marginella Dallas	Annonaceae	*Asimina parviflora* (Michx.)	Neártica (EUA)

		Dunal.[9,57]	
C. (C.) micans (McAtee & Malloch)			Neotropical (Guatemala)
C. (C.) minuta Uhler			Neártica (EUA[20]) e Neotropical (Cuba, Haiti, República Dominicana, Porto Rico, Jamaica)
C. (C.) nigra Dallas	Ranunculaceae	*Ranunculus* sp.[29]	Neártica (EUA) e México
C. (C.) obscura McPherson & Sailer	Apiaceae	*Chaerophyllum tainturiera* Hook[11,56]	Neártica (EUA[41])
		Cryptotaenia canadensis L.[11,56]	
		Sanicula canadensis L.[11, 41, 56]	
		Torilis japonica (Houtt.) DC.[11, 56]	
	Apocynaceae	*Apocynum cannabinum* L.[11]	
	Poaceae	*Elymus virginicus* L.[56]	
	Scrophulariaceae	*Verbascum thapsus* L.[41, 56]	
C. (C.) palmeri (McAtee & Malloch)			México
C. (C.) polita Malloch			Neártica (EUA)
C. (C.) pulicaria (Germar)	Anacardiaceae	*Rhus glabra* L.[19]	Neártica (Canadá, EUA), México[15] e Neotropical (Guatemala, Martinica, Venezuela[3])
	Apiaceae	*Daucus carota* L.[38, 40, 56]	
		Chaerophyllum procumbens (L.) Crantz[40]	
		Torilis japonica (Houtt.) DC.[56]	
	Apocynaceae	*Apocynum cannabinum* L.[40, 56]	
	Asclepiadaceae	*Asclepias incarnata* L.[40]	
	Asteraceae	*Antennaria plantaginifolia* (L.) Richardson[40]	

		Baccharis neglecta Britton[44]	
		Cirsium arvense (L.) Scop.[36]	
		Erigeron philadelphicus L.[40]	
		Erigeron strigosus Muhlenberg[43, 56]	
		Eupatorium sp.[58]	
		Iva frutescens L.[26]	
	Geraniaceae	*Geranium maculatum* L.[35]	
	Juglandaceae	*Juglans nigra* L.[42, 43]	
	Liliaceae	*Uvularia* sp.[19]	
	Plantaginaceae	*Veronica peregrina* L.[18, 57]	
	Poaceae	*Sorghum halepense* L. (Pers.)[56]	
	Polygonaceae	*Polygonum* sp.[19]	
	Rhamnaceae	*Caenothus americanus* L.[18, 57]	
	Rubiaceae	*Galium verum* L.[2]	
	Scrophulariaceae	*Linaria vulgaris* Mill.[36, 53]	
		Verbascum thapsus L.[40]	
C. (C.) tibialis (Fabricius, 1803)			México e Neotropical (Jamaica, Costa Rica, Panamá, Colômbia, São Vicente e Granadinas, Granada, Venezuela, Trinidad, Guiana, Suriname, Guiana Francesa, Brasil, Equador, Bolívia)
C. (Epipora) signoretii (McAtee & Malloch)			Neotropical (Brasil)
C. (Parapora) californica Van Duzee			Neártica (EUA)
C. (P.) cognata (Van Duzee)	Loasaceae	*Eucnide* sp.[61]	Neártica (EUA), México e Neotropical (Cuba, Jamaica, Nicarágua, Colômbia,

			Venezuela[3])
C. (P.) extensa Uhler	Asteraceae	*Baccharis salicifolia* (Ruiz & Pav.) Pers.[10]	Neártica (EUA) e México[20]
	Scrophulariaceae	*Linaria vulgaris* Mill.[53]	
	Solanaceae	*Nicotiana glauca* Graham[33]	
C. (P.) incognita (McAtee & Malloch)	Chenopodiaceae	*Atriplex* sp.[7]	Neártica (Canadá, EUA) e México
	Scrophulariaceae	*Leucophyllum frutescens* (Berland.) I.M.Johnst.[12]	
	Solanaceae	*Nicotiana glauca* Graham[22]	
		Nicotiana obtusifolia Martens & Galeotti[22]	
C. (P.) parana McAtee & Malloch			Neotropical (Brasil)
C. (P.) virilis (McAtee & Malloch)	Plantaginaceae	*Antirrhinum* sp.	Neártica (EUA)
	Solanaceae	*Nicotiana* sp.[27]	
C. (Termapora) minutissima Malloch			Neártica (EUA) e México
Cydnoides (*Cydnoides*) *ciliatus* (Uhler)	Euphorbiaceae	*Euphorbia* sp. [57]	Neártica (EUA) e México
	Fabaceae	*Cassia marilandica* L.[9, 57]	
C. (*C.*) *confusus* McAtee & Malloch,	Euphorbiaceae	*Euphorbia* sp.	Neártica (EUA) e México
C. (*C.*) *renormatus* (Uhler)			Neártica (EUA)
C. (*Sayocoris*) *albipennis* (Say)	Fabaceae	*Glycyrrhiza lepidota* (Nutt.) Pursh	Neártica (EUA)
C. (*S.*) *obtusus* (Uhler)	Euphorbiaceae	*Euphorbia polycarpa* Benth.[57]	Neártica (EUA) e México[20]
C. (*S.*) *peregrinus* McAtee & Malloch			Neártica (EUA) e México[57]

C. (*Cosmarioides*) *nitens* McAtee & Malloch			Neotropical (Brasil)
C. (*C.*) *reticulatus* McAtee & Malloch			Neotropical (Brasil)
C. (*C.*) *setiventris* McAtee & Malloch			Neotropical (Bolívia, Paraguai)
Eumetopia fissipes Westwood			Neotropical (Brasil)
Galgupha (*Acritophleps*) *luteomarginata* McAtee & Malloch			Neotropical (Brasil, Bolívia)
G. (*Acrotmetus*) *brasilianus* (Jensen-Haarup)			Neotropical (Brasil, Bolívia, Paraguai)
G. (*A.*) *crassa* McAtee & Malloch			Neotropical (Brasil)
G. (*A.*) *grossa* McAtee & Malloch			Neotropical (Guiana Francesa, Brasil, Paraguai[24])
G. (*A.*) *minuenda* McAtee & Malloch			Neotropical (Brasil)
G. (*A.*) *schulzii* (Fabricius)	Rubiaceae	*Spermacoce verticillata* L.[13]	México e Neotropical (Panamá, Trinidad[13], Guiana Francesa, Brasil, Argentina)
	Solanaceae	*Solanum tuberosum* L.[46]	
G. (*A.*) *tucumanus* (Horvath)			Neotropical (Brasil, Argentina)
G. (*Astiroderma*) *albipennis* (Eschsholtz)			Neotropical (Guatemala, Guiana Francesa, Brasil, Argentina, Uruguai)
G. (*A.*) *breddini* McAtee & Malloch			Neotropical (Brasil, Argentina[24])
G. (*Bonaria*) *longirostris* (Berg)			Neotropical (Argentina)
G. (*Charoda*) *simplex* McAtee & Malloch			Neotropical (Brasil, Chile, Argentina[24])
G. (*Ctenopoda*) *castor* McAtee & Malloch			Neotropical (Brasil)
G. (*C.*) *maculosa* (Berg)			Neotropical (Brasil, Paraguai, Argentina[4])
G. (*Euryscytus*) *aliena* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *apicata* McAtee & Malloch			Neotropical (Suriname, Guiana Francesa)

G. (*E.*) *assimilis* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *australis* McAtee & Malloch			Neotropical (Brasil, Bolívia, Paraguai, Argentina)
G. (*E.*) *basalis* (Germar)	Moraceae	*Ficus* sp.[14]	Neotropical (Jamaica[60], Brasil)
G. (*E.*) *caudata* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *caudiculata* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *contra* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *contracta* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *corvina* (Horvath)			Neotropical (Brasil, Argentina)
G. (*E.*) *cruenta* (Horvath)			México
G. (*E.*) *curvata* McAtee & Malloch			Neotropical (Brasil, Bolívia[24])
G. (*E.*) *curvatula* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *difficilis* (Breddin)			Neotropical (Brasil, Argentina)
G. (*E.*) *foveolata* (Jensen-Haarup)			Neotropical (Brasil)
G. (*E.*) *insula* McAtee & Malloch			Neotropical (Paraguai, Argentina)
G. (*E.*) *jaczewskii* McAtee & Malloch			Neotropical (Brasil, Argentina[24])
G. (*E.*) *labrata* McAtee & Malloch			
G. (*E.*) *laevis* (Stål)			Neotropical (Brasil)
G. (E.) lucretia McAtee & Malloch			México e Neotropical (Guatemala)
G. (*E.*) *mammula* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *nitida* McAtee & Malloch			Neotropical (Panamá)
G. (*E.*) *obesa* McAtee & Malloch, 1933			Neotropical (Paraguai)
G. (*E.*) *opacifrons* McAtee & Malloch			Neotropical (Brasil)

G. (*E.*) *opercula* McAtee & Malloch, 1933			México
G. (*E.*) *parae* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *parallela* McAtee & Malloch			Neotropical (Brasil, Bolívia)
G. (*E.*) *punctata* McAtee & Malloch			México
G. (*E.*) *rasilis* (Horvath)			Neotropical (Colômbia, Guiana, Suriname, Guiana Francesa, Brasil, Bolívia)
G. (*E.*) *regularis* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *romana* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *rostrata* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *sahlbergi* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *signatipennis* (Germar)			Neotropical (Brasil, Paraguai, Argentina)
G. (*E.*) *smidtii* (Fabricius)			Neotropical (Brasil)
G. (*E.*) *valvata* McAtee & Malloch			Neotropical (Guiana Francesa)
G. (*E.*) *varipennis* McAtee & Malloch			Neotropical (Brasil)
G. (*E.*) *vulnerata* (Horvath)			Neotropical (Brasil, Paraguai)
G. (*Galgupha*) *aterrima* Malloch	Aceraceae	*Acer negundo* L.[56]	Neártica (Canadá, EUA)
	Asteraceae	*Erigeron annuus* (L.) Pers.[56]	
	Cyperaceae	*Carex retroflexa* Muhl. ex Willd.[40]	
	Euphorbiaceae	*Euphorbia maculata* L.[62]	
	Juglandaceae	*Juglans nigra* L.[42]	
	Scrophulariaceae	*Veronica arvensis* L.[40]	
G. (*G.*) *atra* Amyot & Serville	Asteraceae	*Helianthus decapetalus* L.[40]	Neártica (EUA) e México
	Euphorbiaceae	*Euphorbia*	

		maculata L.[62]	
	Juglandaceae	*Juglans nigra* L.[43]	
	Plantaginaceae	*Plantago aristata* Michaux[54, 57]	
	Rosaceae	*Rubus allegheniensis* Porter[40]	
	Scrophulariaceae	*Castilleja sessiflora* Pursh[54]	
		Verbascum thapsus L.[40]	
G. (*G.*) *carinata* McAtee & Malloch	Asteraceae	*Amphiachyris dracunculoides* (DC.) Nutt.	Neártica (EUA)
		Sitilias grandiflora (Nutt.) Greene	
	Brassicaceae	*Ledipidium* sp.	
	Juglandaceae	*Juglans nigra* L.[42]	
	Oxalidaceae	*Oxalis* sp.[21]	
G. (*G.*) *denudata* (Uhler, 1863)			Neártica (EUA) e México
G. (*G.*) *hesperia* McAtee & Malloch			Neártica (EUA)
G. (*G.*) *loboprostethia* Sailer	Fabaceae	*Medicago* sp.[49]	Neártica (EUA[48])
	Juglandaceae	*Juglans nigra* L.[42]	
G. (*G.*) *monostira* Horvath			México
G. (*G.*) *ovalis* Hussey	Asteraceae	*Vernonia interior* Small[51]	Neártica (EUA), México e Neotropical (Guatemala)
	Juglandaceae	*Juglans nigra* L.[42]	
	Plantaginaceae	*Plantago aristata* Michaux[8]	
G. (*Gyrocnemis*) *acuta* McAtee & Malloch			Neotropical (Brasil)
G. (*G.*) *basigrapha* (Horvath)			Neotropical (Perú, Bolívia[24])
G. (*G.*) *bicornis* McAtee & Malloch			Neotropical (Brasil)
G. (*G.*) *concava* McAtee & Malloch			Neotropical (Brasil, Bolívia, Paraguai, Argentina)

G. (*G.*) *cruralis* (Stål)	Aquifoliaceae	*Ilex paraguariensis* A. St. Hil.[47]	Neotropical (Brasil, Bolívia, Argentina)
	Poaceae	*Sorghum bicolor* L. Moench[46]	
		Oryza sativa L.[46]	
		Zea mays L.[6]	
	Rutaceae	*Citrus* sp.[46]	
	Solanaceae	*Solanum tuberosum* L.[5, 6]	
G. (*G.*) *cydnoidea* McAtee & Malloch			Neotropical (Colômbia, Venezuela)
G. (*G.*) *differentialis* McAtee & Malloch			Neotropical (Brasil, Perú, Bolívia, Paraguai)
G. (*G.*) *diminuta* (Van Duzee)			Neártica (EUA)
G. (*G.*) *dimorpha* McAtee & Malloch			Neotropical (Bolívia, Paraguai)
G. (*G.*) *diversa* McAtee & Malloch			Neotropical (Paraguai, Argentina)
G. (*G.*) *durionei* Kormilev			Neotropical (Bolívia[24])
G. (*G.*) *fossata* McAtee & Malloch			Neotropical (Brasil, Paraguai, Argentina)
G. (*G.*) *geayi* McAtee & Malloch			Neotropical (Venezuela)
G. (*G.*) *guttiger* (Stål)	Arecaceae	*Elaeis* sp.[34]	Neártica (EUA), México e Neotropical (Cuba, Haiti, República Dominicana, Jamaica, Belize[15], Guatemala, Honduras, Nicarágua, Costa Rica, Panamá, Colômbia, Venezuela, Trinidad, Bolívia)
	Brassicaceae	*Brassica* sp.[34]	
	Cucurbitaceae	*Cucurbita* sp.[34]	
	Fabaceae	*Cajanus* sp.[34]	
		Phaseolus sp.[34]	
	Lauraceae	*Persea* sp.[34]	
	Malvaceae	*Gossypium* sp.[34]	
		Sida sp.[34]	
	Nyctaginaceae	*Boerhaavia* sp.[34]	
		Bougainvillea sp.[34]	
	Pedaliaceae	*Sesamum* sp.[34]	

	Poaceae	*Oryza* sp.[34]	
		Sorghum sp.[34]	
		Zea sp.[34]	
	Rubiaceae	*Coffea* sp.[34]	
	Solanaceae	*Lycopersicon* sp.[34]	
		Nicotiana sp.[34]	
		Solanum sp.[34]	
G. (*G.*) *impressa* (Horvath)			Neotropical (Venezuela, Brasil, Perú, Bolívia, Argentina)
G. (*G.*) *inaequalis* McAtee & Malloch			Neotropical (Colômbia, Venezuela, Bolívia)
G. (*G.*) *intermedia* McAtee & Malloch			Neotropical (Brasil, Argentina[24])
G. (*G.*) *lineata* McAtee & Malloch			Neotropical (Brasil, Argentina)
G. (*G.*) *maculipennis* (Germar)			Neotropical (Brasil[4], Paraguai, Argentina)
G. (*G.*) *morbiloci* McAtee & Malloch			México
G. (*G.*) *nitens* (Breddin)			Neotropical (Brasil, Colômbia, Perú, Bolívia)
G. (*G.*) *nitidipennis* McAtee & Malloch			Neotropical (Venezuela)
G. (*G.*) *notha* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *novatra* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *novella* McAtee & Malloch			Neotropical (Brasil)
G. (*G.*) *occulta* McAtee & Malloch			Neotropical (Brasil)
G. (*G.*) *omissa* McAtee & Malloch			Neotropical (Brasil)
G. (*G.*) *parva* McAtee & Malloch			Neotropical (Brasil, Paraguai)
G. (*G.*) *punctifer* McAtee & Malloch			Neártica (EUA), México e Neotropical (Belize, Guatemala, Costa Rica, Panamá, Colômbia, Bolívia)
G. (*G.*) *quadrisignata* (Stål)	Verbenaceae	*Lantana* sp.[45]	México e Neotropical (Belize,

			Guatemala, Honduras, El Salvador, Costa Rica)
G. (*G.*) *reinhardti* (Jensen-Haarup)			Neotropical (Venezuela, Brasil)
G. (*G.*) *singularis* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *soror* McAtee & Malloch			México
G. (*G.*) *texana* McAtee & Malloch			Neártica (EUA)
G. (*G.*) *torresi* Kormilev			Neotropical (Argentina[24])
G. (*G.*) *triconcava* McAtee & Malloch			Neotropical (Brasil, Bolívia, Paraguai, Argentina)
G. (*G.*) *unica* McAtee & Malloch			Neotropical (Colômbia)
G. (*Microcompsus*) *daldorfii* (Fabricius)			Neotropical (Brasil)
G. (*M.*) *haywardi* Kormilev			Neotropical (Argentina[25])
G. (*M.*) *vinculata* (Germar)	Rubiaceae	*Spermacoce verticillata* L.[13]	Neotropical (Colômbia, Venezuela, Trinidad, Suriname, Guiana Francesa, Brasil, Bolívia, Paraguai, Argentina)
G. (*Nothocoris*) *akarna* McAtee & Malloch			Neotropical (Argentina)
G. (*N.*) *alutacea* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *bakeri* McAtee & Malloch			Neártica (EUA)
G. (*N.*) *boliviana* McAtee & Malloch			Neotropical (Brasil, Bolívia)
G. (*N.*) *brevis* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *brunnipennis* (Germar)			Neotropical (Brasil, Paraguai)
G. (*N.*) *caracasana* McAtee & Malloch			Neotropical (Venezuela)
G. (*N.*) *chilocoroides* (Walker)			México e Neotropical (Guiana Francesa, Brasil)
G. (*N.*) *chrostowskii* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *coccineloides* Horvath			Neotropical (Guiana Francesa, Brasil, Bolívia, Paraguai, Argentina)

G. (*N.*) *eas* McAtee & Malloch			Neártica (EUA)
G. (*N.*) *fossula* McAtee & Malloch			México
G. (*N.*) *grenadensis* McAtee & Malloch			Neotropical (Colômbia)
G. (*N.*) *inornata* McAtee & Malloch			Neotropical (Argentina)
G. (*N.*) *juno* McAtee & Malloch			Neotropical (Argentina)
G. (N.) magna Sailer			México[50]
G. (*N.*) *marginalis* McAtee & Malloch			Neotropical (Colômbia)
G. (*N.*) *marginicollis* Horvath			Neotropical (Colômbia, Venezuela, Granada)
G. (*N.*) *microphthalma* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *nitiduloides* (Wolff)	Asteraceae	*Helenium* sp.	Neártica (EUA), México e Neotropical (Guatemala, Nicarágua[34], Costa Rica, Brasil)
	Fabaceae	*Glycine* sp.[34]	
	Malvaceae	*Gossypium* sp.	
	Plantaginaceae	*Plantago patagonica* Jacq.[57, 59]	
	Poaceae	*Saccharum* sp.	
	Verbenaceae	*Lantana* sp.[45]	
G. (*N.*) *oculata* McAtee & Malloch			Neotropical (Paraguai)
G. (*N.*) *parvula* Horvath			Neotropical (Perú)
G. (*N.*) *repetita* McAtee & Malloch			
G. (*N.*) *semilimbata* Horvath			Neotropical (Brasil, Paraguai)
G. (*N.*) *stramineipennis* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *surda* McAtee & Malloch			Neotropical (Brasil)
G. (*N.*) *terminalis* (Walker)			Neotropical (Brasil, Bolívia, Paraguai, Uruguai)
G. (*Orocoris*) *arizonensis* (Van Duzee)			Neártica (EUA)

G. (*Psestophleps*) *altera* McAtee & Malloch	Neotropical (Brasil)
G. (*P.*) *bergiana* McAtee & Malloch	Neotropical (Brasil, Perú, Paraguai, Argentina)
G. (*P.*) *bisignata* McAtee & Malloch	Neotropical (Brasil, Argentina)
G. (*P.*) *carbonata* McAtee & Malloch	Neotropical (Argentina)
G. (*P.*) *casta* McAtee & Malloch	Neotropical (Argentina)
G. (*P.*) *costomaculata* McAtee & Malloch	Neotropical (Brasil, Paraguai)
G. (*P.*) *denieri* Kormilev	Neotropical (Argentina[24])
G. (*P.*) *fimbriata* McAtee & Malloch	Neotropical (Venezuela, Suriname)
G. (*P.*) *imitans* McAtee & Malloch	Neotropical (Venezuela[3], Brasil)
G. (*P.*) *inops* McAtee & Malloch	Neotropical (Brasil)
G. (*P.*) *mayana* McAtee & Malloch	Neotropical (Honduras)
G. (*P.*) *media* McAtee & Malloch	Neotropical (Guiana, Suriname)
G. (*P.*) *mexicana* McAtee & Malloch	México
G. (*P.*) *neobisignata* McAtee & Malloch	Neotropical (Guiana Francesa, Brasil, Paraguai, Argentina, Uruguai)
G. (*P.*) *obovata* McAtee & Malloch	Neotropical (Argentina)
G. (*P.*) *pallipennis* McAtee & Malloch	Neotropical (Brasil)
G. (*P.*) *porcata* Horvath	Neotropical (Brasil, Paraguai, Argentina)
G. (*P.*) *tabellula* McAtee & Malloch	Neotropical (Suriname)
G. (*Pteronomos*) *amitta* McAtee & Malloch	Neotropical (Argentina)
G. (*P.*) *china* McAtee & Malloch	Neotropical (Brasil, Perú, Bolívia, Argentina)
G. (*P.*) *fritzi* Kormilev	Neotropical (Chile[24])

G. (*P.*) *meridiana* McAtee & Malloch			Neotropical (Paraguai, Argentina)
G. (*P.*) *oblonga* McAtee & Malloch			Neotropical (Brasil, Paraguai, Argentina)
G. (*P.*) *punctifrons* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *ruficornis* (Dallas)			Neotropical (Colômbia)
G. (*P.*) *vianai* Kormilev			Neotropical (Argentina[25])
G. (*P.*) *vittifrons* McAtee & Malloch			Neotropical (Bolívia, Argentina)
G. (*Trepocnemis*) *anomala* McAtee & Malloch			Neotropical (Argentina)
Godmania aterrima Horvath			México e Neotropical (Guatemala)
Pericrepis afer McAtee & Malloch			Neotropical (Argentina)
P. bergi Kormilev			Neotropical (Argentina[25])
P. bosqui Kormilev			Neotropical (Argentina[25])
P. callosula Horvath			Neotropical (Brasil, Paraguai[24], Argentina)
Pruhleria incerta (Uhler)	Musaceae	*Musa* sp.	Neotropical (Cuba, Nicarágua[15])

Referências: 1, Ahmad & Moizuddin 1982; 2, Batra 1984; 3, Becker &Grazia-Vieira 1971; 4, Berg 1891; 5, Bertels 1962; 6, Bertels & Baucke 1966; 7, Bibby 1961; 8, Biehler & McPherson 1982; 9, Blatchley 1926; 10, Boldt & Robbins 1990; 11, Bundy & McPherson 1997; 12, Bundy & McPherson 2009; 13, Callan 1948; 14, Costa Lima 1936; 15, Distant 1880; 16, Dolling 1981; 17, Fent & Aktaç 2007; 18, Forbes 1905; 19, Froeschner 1941; 20, Froeschner 1988; 21 Hoffman 1971; 22, Jones 1993; 23, Klein *et al.* 2013; 24, Kormilev 1956a; 25, Kormilev 1956b; 26, Lago & Testa 2000; 27, Lattin 1955; 28, Linnavuori 1993; 29, Linsley & MacSwain 1959; 30, Lis 1989; 31, Lis 2006; 32, Lis *et al.* 2011; 33, Lung & Goeden 1982; 34, Maes 1994; 35, Martin 1965; 36, Maw 1976; 37, McPherson 1971; 38, McPherson 1972; 39, McPherson 1974; 40, McPherson & Mohlenbrock, 1976; 41, McPherson & Sailer 1978; 42, McPherson & Weber 1990; 43, Nixon *et al.* 1975; 44, Palmer 1987; 45, Palmer & Pullen 1995; 46, Quintanilla *et al.* 1976; 47, Quintanilla *et al.* 1981; 48, Sailer 1940; 49, Sailer 1941a; 50, Sailer 1941b; 51, Schwitzgebel & Wilbur 1942; 52, Singer 1952; 53, Smith 1959; 54, Stoner 1920; 55, Stys & Davidová 1979; 56, Tecic & McPherson 2005; 57, Torre-Bueno 1939; 58, Uhler 1894; 59, van Duzee 1904; 60, van Duzee 1907; 61, van Duzee 1923; 62, Wheeler 1981.

Tabela 3. Lista das espécies de Thyreocoridae cujos imaturos (ovos e/ou ninfas) já foram descritos e/ou cuja biologia é conhecida.

Táxon	**Ovos**		**Ninfas**	**Biologia**
	MEV*	**MO***		
Thyreocorinae				
Thyreocoris scarabaeoides (Linnaeus)		Cobben 1968		
Corimelaeninae				
Corimelaena sp.		Southwood 1956		
Corimelaena (*Corimelaena*) *lateralis* (Fabricius)		McPherson 1972	McPherson 1972	McPherson 1971, 1972
Corimelaena (C.) obscura McPherson & Sailer	Bundy & McPherson 1997		Bundy & McPherson 1997	Bundy & McPherson 1997
Corimelaena (*Parapora*) *extensa* Uhler		Lung & Goeden 1982	Lung & Goeden 1982	Lung & Goeden 1982
Corimelaena (P.) incognita (McAtee & Malloch)	Bundy & McPherson 2009		Bundy & McPherson 2009	Bundy & McPherson 2009
Corimelaena (*P.*) *virilis* (McAtee & Malloch)		Lattin 1955		
Galgupha (Galgupha) atra Amyot & Serville		Javahery 1994		
Galgupha (*G.*) *ovalis* Hussey		Biehler & McPherson 1982	Biehler & McPherson 1982	Biehler & McPherson 1982

* MEV = microscopia eletrônica de varredura; MO = microscopia óptica.

Tabela 4. Caracteres de ovos previamente utilizados em análises cladísticas em Pentatomoidea.

Caráter e respectivos estados	**Referência**
Textura coriônica: lisa; rugosa	Hasan & Kitching (1993)
Ruptor ovis: pequeno e fracamente esclerotizado; grande e bem esclerotizado	Hasan & Kitching (1993)
Canal micropilar interno: presente; ausente	Hasan & Kitching (1993)
Fenda no cório à eclosão: longitudinal; ao redor do opérculo	Hasan & Kitching (1993)
Ovos nunca com micrópilas e aerópilas arranjadas em anel externamente ao opérculo; ovos com micrópilas e aerópilas arranjadas em anel externamente ao opérculo	Wheeler *et al.* (1993)
Forma da micrópila: como tubérculo; com pedúnculo	Javahery (1994)
Projeção micropilar: muito pequena; muito longa	Javahery (1994)
Número de micrópilas: menos do que 35; 35 ou mais	Javahery (1994)
Número de micrópilas: menos do que 11; entre 11 e 34	Javahery (1994)
Forma do *ruptor ovis*: em forma de "Y"; em forma de "T"	Javahery (1994)
Esclerotização do *ruptor ovis*: pequeno e fracamente esclerotizado; grande e fortemente esclerotizado	Javahery (1994)
Localização do *ruptor ovis*: no centro do polo anterior; sob a linha circular micropilar	Javahery (1994)
Espessura do cório: fina, entre 2 e 5 µm; mais espessa, mais de 6 µm	Javahery (1994)
Cório: brilhante; opaco	Javahery (1994)
Cório: escavado; piloso	Javahery (1994)
Cório: sem qualquer reticulação e espinhos; espinhoso	Javahery (1994)
Coloração do cório: nunca colorido; castanho, negro ou com 2-3 bandas coloridas e manchas dispersas	Javahery (1994)
Orientação embrionária: para uma direção; reverso ou de frente para o centro da postura	Javahery (1994)
Forma: similar a Lygaeidae; forma de barril	Javahery (1994)
Forma: esférica; cilíndrica	Javahery (1994)
Fenda de eclosão: linha longitudinal reta; seguindo o anel micropilar	Javahery (1994)
Casca: sem uma barra de vedação; com uma barra de vedação	Javahery (1994)
Oviposição: ovos depositados em uma massa; ovos depositados em várias massas	Javahery (1994)
Oviposição: ovos depositados individualmente; ovos depositados em massas de diferentes números	Javahery (1994)
Oviposição: ovos depositados em fendas no solo; ovos depositados em plantas	Javahery (1994)

Comprimento do ovo: cerca de 1 mm ou menos; mais de 1 mm	Javahery (1994)
Proteção do ovo: ovos guardados pela fêmea; ovos nunca guardados	Javahery (1994)
Fratura de eclosão: fenda simples; hexagonal	Henry (1997)
Processos aero-micropilares: ausentes; presentes	Grazia *et al.* (2008)

CAPÍTULO 1

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Revision of the genus *Alkindus* Distant (Hemiptera: Heteroptera: Thyreocoridae: Corimelaeninae)

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Abstract

The neotropical genus *Alkindus* Distant is revised based on morphological characters (general morphology, including the external scent efferent system and leg structures, and external genital morphology). The male of *Alkindus crassicosta* Horvath is here described for the first time. Illustrations, an adapted key to species, and a compiled list of plants associated with both species are provided. Distribution records are expanded to include Guatemala and Brazil (Roraima) for *Alkindus atratus* Distant and Brazil (Santa Catarina) for *A. crassicosta*.

Key words: taxonomy, morphology, genitalia, Neotropical region, scanning electron microscopy

Introduction

The genus *Alkindus* was described by Distant (1889) for a single species, *Alkindus atratus*, based on a male and a female from Panama. He considered *Alkindus* allied to *Thyreocoris* Schrank at that time considered a senior synonym of the Neotropical genera *Corimelaena* White and *Galgupha* Amyot & Serville. According to Distant (1889), *Alkindus* and *Thyreocoris* share characters of general structure, but differ in the shape and size of the head. Horvath (1919) described a second species, *Alkindus crassicosta*, based on a female from Brazil (São Paulo).

Distant (1889) included *Alkindus* in the family Pentatomidae, subfamily Cydninae. Lethierry & Severin (1893) placed it within the subfamily Corimelaeninae (Pentatomidae) removing it from the subfamily Cydninae. Horvath (1919) treated the group as the subfamily Thyreocorinae of the Cydnidae and recognized two tribes: Canoparia and Thyreocoraria, including *Alkindus* among the latter. McAtee and Malloch (1928) excluded the Canoparia from Thyreocorinae, and the same authors (McAtee & Malloch 1933), in their broad revision of the group, recognize *Alkindus* within the Thyreocorinae, a subfamily of the Pentatomidae. Dolling (1981) recognized Thyreocorinae and Corimelaeninae as subfamilies of Cydnidae; *Alkindus* was included in Corimelaeninae. Lis (2006) considered both Thyreocorinae and Corimelaeninae as subfamilies of Thyreocoridae.

McAtee and Malloch (1933) redescribed the genus and both species, and included a key to separate the species of *Alkindus*. In the same paper, distribution records of *A. atratus* were expanded to Mexico, Nicaragua, Aruba, Curaçao, Venezuela, Costa Rica, and Colombia. Becker and Grazia-Vieira (1971) identified 125 specimens (60 males and 65 females) of *A. atratus* from Venezuela. Maes (1994) included this species in the catalog of the Pentatomoidea from Nicaragua, recording it also from Honduras and El Salvador. Grazia *et al.* (1999) and Grazia and Schwertner (2011) included *A. crassicosta* in the checklist of the Pentatomoidea from the state of São Paulo, Brazil, based on literature data. Klein *et al.* (2013) recently recorded *A. crassicosta* from the state of Rio Grande do Sul, Brazil. Biological data are not available, except for records of plants associated with *Alkindus* spp. (Table 1).

The status (family vs. subfamily) and the name of the group (Thyreocoridae vs. Corimelaenidae) have been intensely disputed (e.g. Leston 1953; Rolston & McDonald 1979; Stys & Davidová 1979; Dolling 1981; Ahmad & Moizuddin 1982; Froeschner 1988), but its composition has remained almost unchanged (McAtee & Malloch

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1933; Dolling 1981; Lis 2006). The Thyreocoridae [*Thyreocoris* + *Allocoris* McAtee & Malloch (junior synonym of *Corimelaena*)] has been considered a monophyletic group by Grazia *et al.* (2008) in their analysis of the Pentatomoidea. The placement of *Alkindus* in the family, although never formally tested, has never been disputed.

In this paper, the genus *Alkindus* and both species are redescribed, and the male of *A. crassicosta* is described for the first time. A key to the species, complementing the one included in McAtee and Malloch (1933), is offered. Records of plants from which the insects were collected are compiled and distribution records are expanded.

TABLE 1. Records of plants associated with *Alkindus atratus* Distant and *A. crassicosta* Horvath.

Insect species	Plant family	Plant species	Reference
A. atratus	Fabaceae	*Glycine* sp.	Maes 1994
		Phaseolus sp.	Maes 1994
	Malvaceae	*Gossypium* sp.	Maes 1994
		Sida sp.	Maes 1994
	Moraceae	*Ficus* sp.	New record
	Musaceae	*Musa* sp.	Maes 1994
	Myrtaceae	*Eucalyptus* sp.	Maes 1994
	Poaceae	*Cenchrus* sp.	Maes 1994
		Echinochloa sp.	Maes 1994
		Oryza sp.	Maes 1994
		Sorghum sp.	Maes 1994
		Zea mays	Becker & Grazia-Vieira 1971
	Rubiaceae	*Coffea* sp.	Maes 1994
	Sterculiaceae	*Theobroma* sp.	Maes 1994
A. crassicosta	Poaceae	*Andropogon bicornis*	Klein *et al.* 2013

Material and methods

The specimens examined belong to the following collections, acronyms and curators in parenthesis: Hungarian Natural History Museum, Budapest, Hungary (HNHM—Dr. Dávid Rédei); Natural History Museum, London, United Kingdom (BMNH—Dr. Mick Webb); Florida State Collection of Arthropods, Joseph E. Eger personal collection, Florida, USA (JEEC—Dr. Joseph E. Eger); Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (MCNZ—Dra. Aline Barcellos); Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (UFRG—Dra. Jocelia Grazia).

Photographs of the female type of *A. crassicosta* have been taken using digital camera. General and external genital morphology were illustrated using stereomicroscope and drawing tube. Female genitalia were cleared in 10% KOH and stained with Congo Red; internal genitalia have been observed but not illustrated, and brief comments are made in the description of the genus. Male internal genitalia are not addressed in this paper due to difficulties in dissection and preparation methods as well as interpretation of the structures.

The terminology followed Tsai *et al.* (2011) for general morphology; Kment and Vilímová (2010) for the external scent efferent system; Lis and Schaefer (2005), Grazia *et al.* (2008), and Lis (2010) for leg structures; Dupuis (1970) and Schaefer (1977) for the genitalia. Morphometric parameters measured: total length, abdominal width, head length, head width, eye width, interocular distance, anteocular length, length of antennal segments I to V, pronotal length, pronotal width, scutellar length, scutellar width, corium length, and rostrum length. Measurements [mean (range) ± standard deviation] are given in millimeters.

For scanning electron microscopy (SEM) analysis, whole specimens were kept submersed in contact lens solution (Renu®) for 24h, agitated in a sonicator with water and detergent during three minutes, and air-dried at 50ºC for 24h. Later, they were mounted on stubs, coated with gold, and analyzed with a JEOL scanning electron microscope, JSM 6060, at the Centro de Microscopia Eletrônica da Universidade Federal do Rio Grande do Sul (CME/UFRGS).

The distribution records for purposes of map plotting were obtained from literature data and from labels of specimen collections. Geographic coordinates were searched for at Glosk (2007), Global Gazeteer Version 2.2 (2010), and Species Link (2013) and then plotted on the map using DIVA-GIS Version 7.5 (2011). When the location was not specified, it was considered the capital of the country/state/department/province and, when there was more than one city with the same name, it was considered the most populous one.

Results

Alkindus Distant, 1889

Type species: *Alkindus atratus* Distant, by monotypy.

Alkindus Distant, 1889: 309; Lethierry & Severin 1893: 14 (catalogue); Horvath 1919: 231; McAtee & Malloch 1933: 347–348 (redescription).

Description. Ovoid (Fig. 1), dorsally convex (Fig. 3), about 1.5 times longer than wide.

Coloration. Black, shining; eyes yellowish brown to reddish brown; antennae yellowish ocher, sometimes infuscated; rostrum dark brown to ocher; legs dark brown to black, except for the tarsi, yellowish ocher, sometimes infuscated; venter black, except for abdominal sternites IV to VII sometimes with reddish brown lateral stripes.

Head (Figs. 2, 5, 7). Subtrapezoidal, more than two times wider than long, declivent; densely and deeply punctate, especially on anterior and lateral areas; clypeus nearly impunctate, except subapically. Mandibular plates slightly longer than clypeus, convergent at apex, not covering completely the apex of clypeus; external margins broadly convex, slightly deflected and emarginated. Maxillary plate concave between eye and rostrum; rostrum reaching mid coxae.

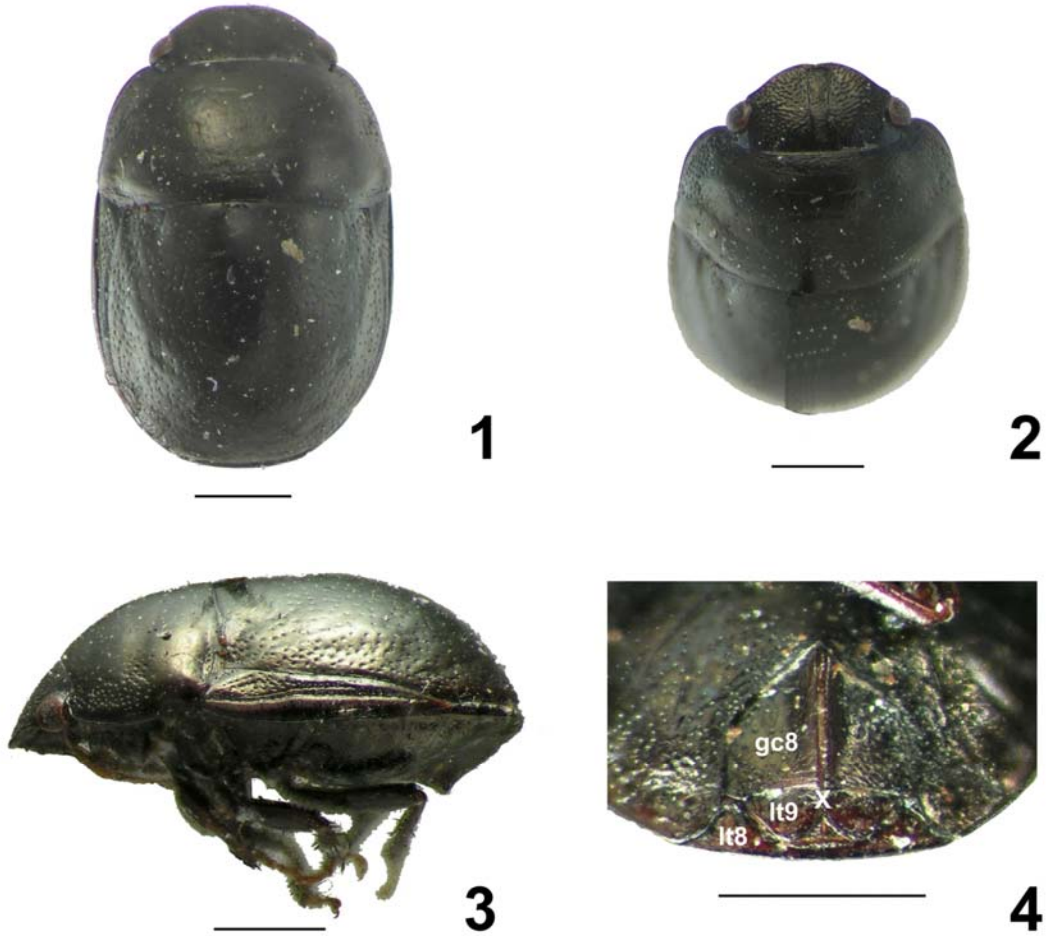
Pronotum (Figs. 1–3). Subrectangular. Disc with small and shallow punctures, sometimes inconspicuous; lateral area strongly punctate, punctures denser and deeper than on disc. Lateral margins emarginate. Humeral angles broadly rounded; posterolateral angles tumid and rounded.

Scutellum (Figs. 1, 3). Base slightly depressed laterally; apex rounded, clearly surpassing posterior margin of tergite VII in both sexes, almost reaching apex of abdomen, covering lateral part of abdomen and the membrane of hemelytra. Disc impunctate, surrounded by dense and regularly distributed punctures, smaller and denser near lateral and posterior margins.

Hemelytra (Figs. 3, 6, 8). Corium narrow, acute at apex. Punctures at clavus, endocorium, and along veins; punctures at costa smaller and shallower. Costa emarginated, declivent, smooth and shiny. Exocorial vein bifurcated from middle third, strongly impressed from the base, forming a shallow groove along its external branch. Cubital vein deeply impressed from the base. Corium usually reaching base of abdominal segment VI.

Thoracic venter (Figs. 17–28). Anterior half of propleura strongly punctate, posterior half less punctate and concave; prosternal median sulcus moderately deep, margins deflected and more widely separated anteriorly. Anterior half of mesopleura polished and strongly punctate, mesopleural evaporatorium not reaching anterior margin of the segment, macrosculpture showing gyrification (Figs. 17, 18, 21, 23) mycoid microsculpture with mushroom-like bodies; pseudoperitreme present (Figs. 17, 21, 23); mesosternal median carina shallow, with a small posterior projection. Metapleural evaporatorium not reaching lateral margin of the segment, macrosculpture showing gyrification (Figs. 17, 18, 21, 22) and mycoid microsculpture with mushroom-like bodies (Figs. 19, 20); vestibular scar present (Figs. 17, 21), peritremal groove covering 3/4 of the segment width; peritremal surface nearly smooth (Figs. 18, 22); posterior half of metapleura polished, sparsely punctate; metasternum with small projection between coxae, posteriorly directed and medially sulcated (Fig. 24). Coxal combs present on all legs (Fig. 24); foretibial combs present, consisting of a row of 17 setae, two outer setae only slightly longer than the remaining ones, basal longitudinally ridged spines placed slightly posteriorly to the line of tibial comb, tibial fossula hardly distinguishable, surrounded by pilosity (Figs. 25, 27); foretibial apparatus present, consisting of four setae (Figs. 26, 28). All tibiae flattened dorsally; hind tibiae scarcely sulcate.

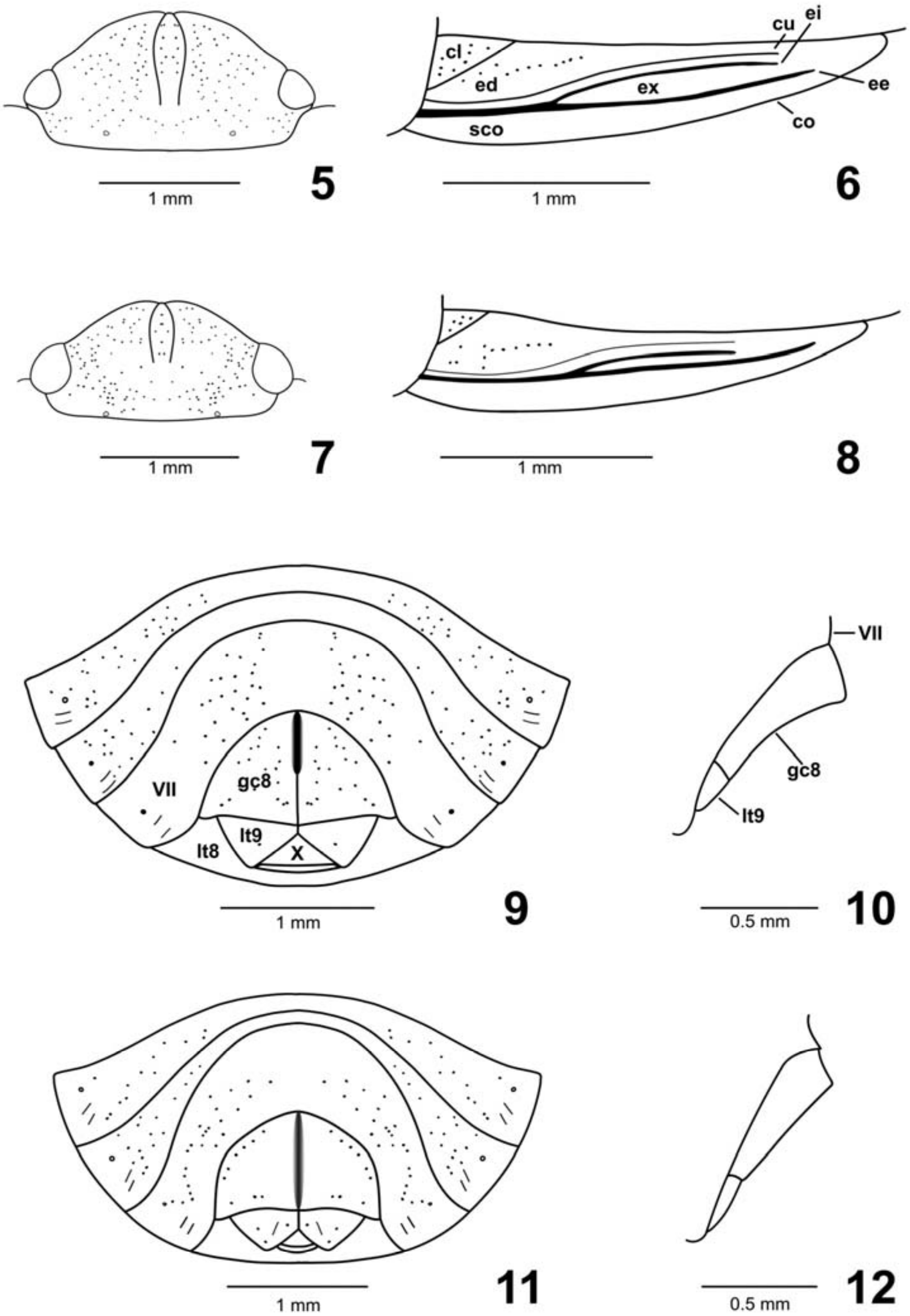
Abdominal venter (Figs. 9, 11, 13, 15). Sternites IV and especially V and VI medially constricted; punctures sparse on all segments, denser laterally, median area impunctate; paired trichobothia at sternites III–VII, longitudinally arranged, although slightly oblique, with the anterior trichobothrium innermost; spiracles nearer to the trichobothria than to the lateral margins of sternites; sometimeswith single long paramedian bristle on each side of sternite VII in the male.



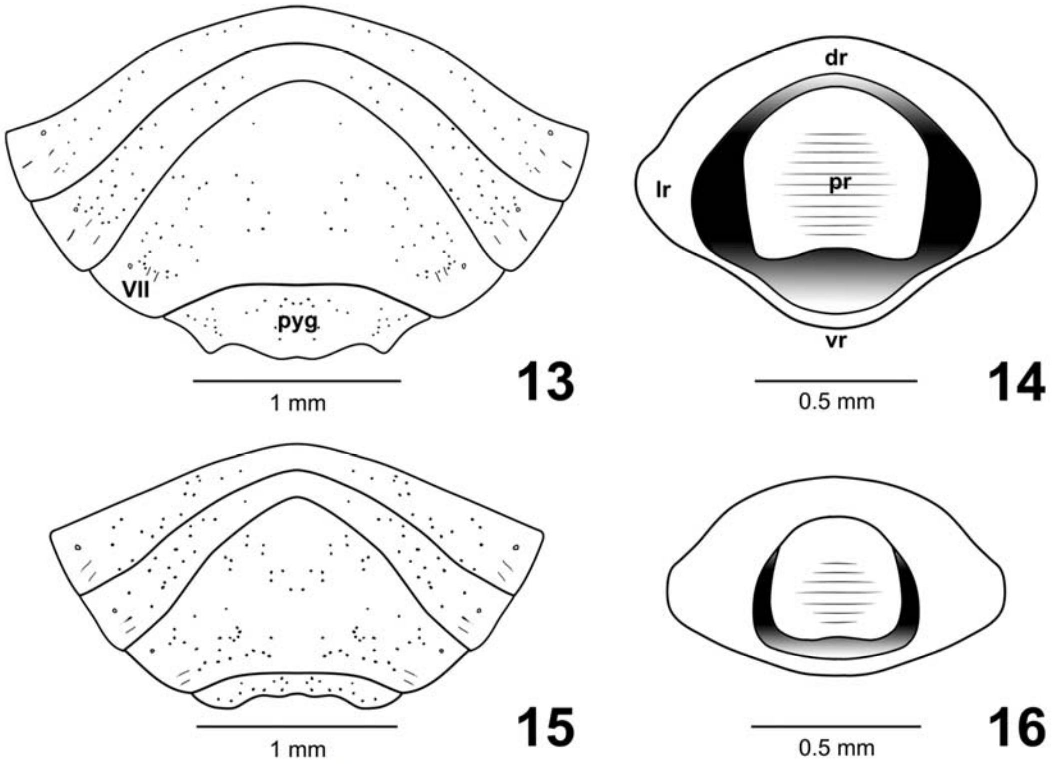
FIGURES 1–4. *A. crassicosta* Horvath, female holotype. Fig. 1. Dorsal view. Fig. 2. Head, dorsal view. Fig. 3. Lateral view. Fig. 4. Genital plates, ventral view. Scale bar = 1 mm. Abbreviations: X—segment X, gc8—gonocoxites 8, lt8—laterotergites 8, lt9—laterotergites 9.

Male genitalia (Figs. 13–16, 30, 31). Ventral exposure of pygophore punctate. Ventral rim variable in shape. Dorsal rim flattened. Lateral rims enlarged, with dense punctures and pilosity. Proctiger wide and transversely striated, ventral half depressed. Parameres not visible externally, concealed by the proctiger.

Female genitalia (Figs. 4, 9–12, 29). Gonocoxites 8 free from each other, triangular, sparse and finely punctate; posterior margins concave; mesial margins ventrally projected. Laterotergites 8 fused mesially, each bearing spiracle, with deep and sparse punctures. Gonocoxites 9 not visible externally; not fused mesially. Laterotergites 9 not fused, but meeting mesially, partially covering segment X, triangular, well developed, about 0.4 times the length of gonocoxites 8 at mesial margins, with deep and sparse punctures. Both tergum X and sternum X visible ventrally, the former with a median suture line. Presence of paired elongate sacs attached to base of gonocoxites 9. Ring sclerites absent. *Orificium receptaculi* surrounded by a narrow sclerotized groove. *Ductus receptaculi* connecting both to a sac-like dilation (not observed in *A. atratus*) and to the *pars intermedialis* (with only the proximal flange developed) plus the semicircular *capsula seminalis*, this without projections.



FIGURES 5–12. General and female genital morphology. Figs. 5, 6. *A. atratus.* Fig. 5. Head, dorsal view. Fig. 6. Corium of the left forewing, lateral view. Figs. 7, 8. *A. crassicosta*. Fig. 7. Head, dorsal view. Fig. 8. Corium of the left forewing, lateral view. Figs. 9, 10. *A. atratus,* genital plates. Fig. 9. Ventral view. Fig. 10. Lateral view. Figs. 11, 12. *A. crassicosta*, genital plates. Fig. 11. Ventral view. Fig. 12. Lateral view. Abbreviations: VII—7th sternite, X—segment X, cl—clavus, co—costa, cu—cubital vein, ed—endocorium, ee—external branch of the exocorial vein, ei—internal branch of the exocorial vein, ex—exocorium, gc8—gonocoxites 8, lt8—laterotergites 8, lt9—laterotergites 9, sco—subcostal area.

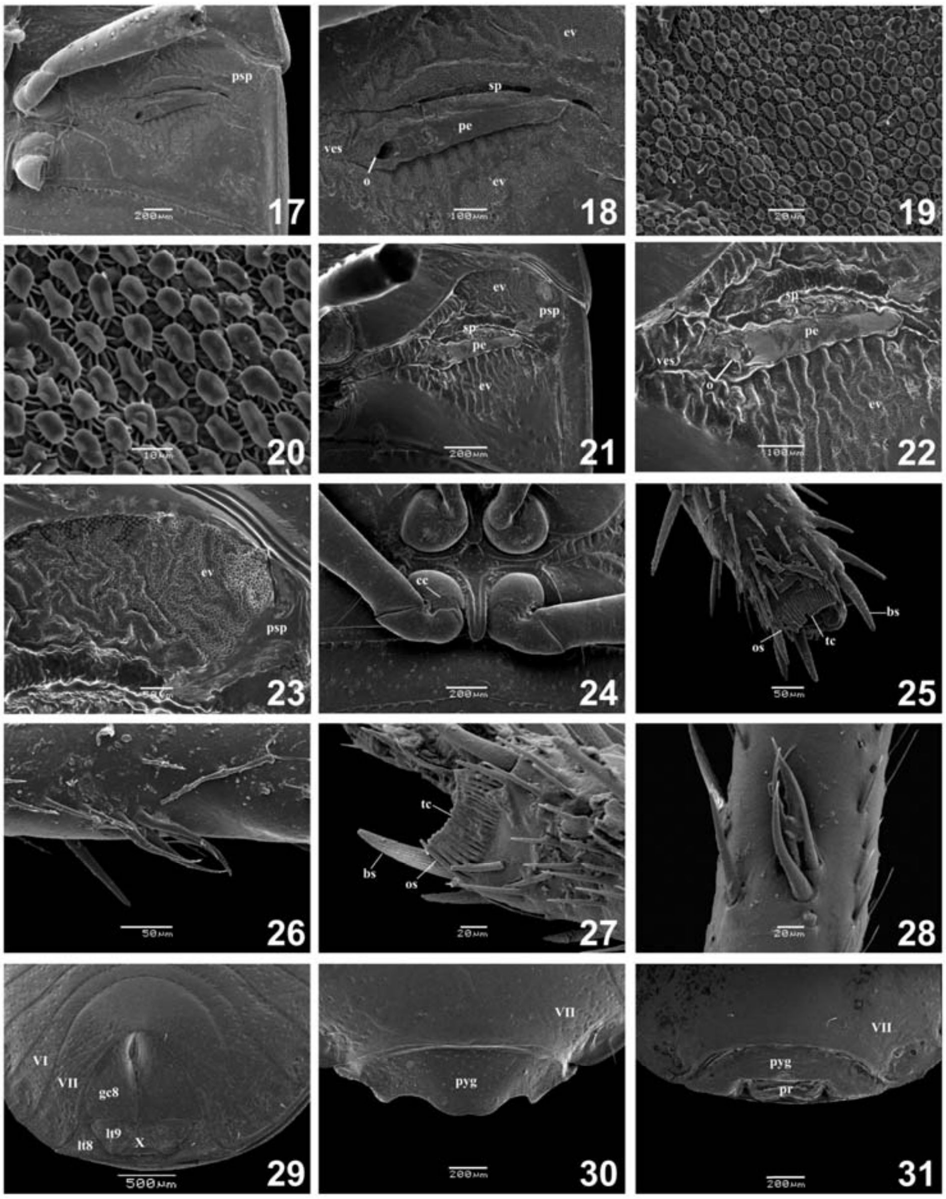


FIGURES 13–16. Pygophore. Figs. 13, 14. *A. atratus*. Fig. 13. Ventral view. Fig. 14. Posterodorsal view. Figs. 15, 16. *A. crassicosta*. Fig. 15. Ventral view. Fig. 16. Posterodorsal view. Abbreviations: VII—7th sternite, dr—dorsal rim, lr—lateral rim, pr—proctiger, pyg—pygophore, vr—ventral rim.

Distribution. Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Aruba, Curaçao, Venezuela, Costa Rica, Colombia, Panama, and Brazil (Fig. 32).

Comments. Diagnosis. In the absence of a hypothesis of relationships among thyreocorid species, preventing the construction of a better key to the genera, specimens of *Alkindus* can be identified using McAtee and Malloch's (1933) key. However, species of *Alkindus* are similar to, and can be confused with, those of *Pericrepis* Horvath, as already noted by Horvath (1919). Both genera share similarities in general color (especially with *Pericrepis afer* McAtee & Malloch and *P. bergi* Kormilev), head shape, position of the ocelli, elevation of the area between the costa and the exocorial vein, and female genitalia. McAtee and Malloch (1933) emphasize the sternites with bristles laterad of the trichobothria as a main character of *Alkindus*, while they are mostly lacking in *Pericrepis*. However, the presence of lateral bristles in the abdomen is not a constant character within the genus *Alkindus*, since they are mostly lacking in *A. crassicosta*. In addition to having the hind tibia dorsally sulcate, the species of *Alkindus* seem unique in the external morphology of male and female genitalia, allowing easy differentiation from species of *Pericrepis*.

External scent efferent system. The external scent efferent system of the Thyreocoridae has been poorly described. Kment and Vilímová (2010) provided SEM images of *Thyreocoris scarabaeoides* (Linnaeus) and line drawing of *Galgupha (Gyrocnemis) impressa* (Horvath). The vestibular scar, as observed in *Alkindus* spp., is present in *T. scarabaeoides*, as well as in several other families of Pentatomoidea, (Thaumastellidae, Cydnidae, and Plataspididae) (Kment & Vilímová 2010). The pseudoperitreme, especially developed in *A. crassicosta*, has been observed in representatives of the Thyreocoridae, some Cydnidae and Plataspididae (Kment & Vilímová 2010). A verrucose peritremal surface was described in *T. scarabaeoides,* differing from the smooth peritremal surface in *Alkindus* spp.



FIGURES 17–31. External scent efferent system, leg structures, and genital morphology with the scanning electron microscope. Figs. 17–20. *A. atratus*, external scent efferent system. Fig. 17. Meso- and metapleuron. Fig. 18. Detail of ostiole, peritremal groove, and evaporatorium. Fig. 19. Mycoid microsculpture of the evaporatorium. Fig. 20. Mycoid microsculpture of the evaporatorium in greater detail, evidencing the mushroom bodies. Figs. 21–23. *A. crassicosta*, external scent efferent system. Fig. 21. Meso- and metapleuron. Fig. 22. Detail of ostiole, peritremal groove, and evaporatorium. Fig. 23. Detail of mesopleural evaporatorium and pseudoperitreme. Fig. 24. *A. atratus*, metasternum with median projection and coxal combs. Figs. 25, 26. *A. atratus*. Fig. 25. Foretibial comb. Fig. 26. Foretibial apparatus. Figs. 27, 28. *A. crassicosta*. Fig. 27. Foretibial comb. Fig. 28. Foretibial apparatus. Figs. 29, 30. *A. atratus*. Fig. 29. Female genital plates, ventral view. Fig. 30. Pygophore, ventral view. Fig. 31. *A. crassicosta*, pygophore, ventral view. Abbreviations: VI—6th sternite, VII—7th sternite, X—segment X, bs—basal spines, cc—coxal comb, ev—evaporatorium, gc8—gonocoxites 8, lt8—laterotergites 8, lt9—laterotergites 9, o—ostiole, os—outer setae, pe—peritreme, pr—proctiger, psp—pseudoperitreme, pyg—pygophore, sp—metathoracic spiracle, tc—tibial comb, ves—vestibular scar.

FIGURE 32. Distribution records of *Alkindus atratus* Distant (black triangles) and *A. crassicosta* Horvath (black circles), according to the provinces of Latin America and the Caribbean islands proposed by Morrone (2006). Numbers refer to the following provinces (mentioned only those in which the species occur): 8—Transmexican Volcanic Belt, 9—Balsas Basin, 11—Mexican Pacific Coast, 14—Chiapas, 15—Eastern Central America, 16—Western Panamanian Isthmus, 25—Maracaibo, 26—Venezuelan Coast, 29—Venezuelan Llanos, 39—Roraima, 51—Pampa, 53—Brazilian Atlantic Forest, 56—North Andean Paramo.

Leg structures. The presence of coxal combs has been regarded as a synapomorphy for the Corimelaenidae (= Thyreocoridae) and for the Cydnidae *sensu lato* (including or not the Thyreocoridae) (Dolling 1981; Grazia *et al.* 2008). The presence of this structure in the Thyreocoridae has been pointed out previously by some authors (e.g., McAtee & Malloch 1933; Schuh & Slater 1995; Grazia *et al.* 2008). More recently, Lis (2010) illustrated in SEM the coxal combs of *T. scarabaeoides* and *Strombosoma impictum* Amyot & Serville (both Thyreocorinae). In *Alkindus* spp., the coxal combs seem compatible with the pattern of gutter-like setae observed for other thyreocorids and some groups of Cydnidae (Lis 2010).

Tibial combs are present in all infraorders of terrestrial Heteroptera; however, their presence and degree of development in the three pairs of tibiae varies greatly, as revised by Lis and Schaefer (2005). The same authors studied the tibial combs in several representatives of the Cydnidae and the Parastrachiidae, also in SEM. No Thyreocoridae species were included in their study, but they stated that the tibial combs of the fore legs are present in this family, as well as in several other pentatomoid families (Acanthosomatidae, Dinidoridae, Pentatomidae, Plataspididae, Scutelleridae, Tessaratomidae, and Urostylididae). Barão *et al.* (2013) studied the tibial comb of ten species of Thyreocoridae, in addition to Pentatomidae and Scutelleridae. They concluded that the thyreocorids differ from the pentatomids and scutellerids by the presence of the tibial comb complex (which is characteristic of the Cydnidae), but tibial combs of thyreocorids differed only in the number of setae. According to the same authors, the number of setae in the Thyreocorinae (14–16) is usually smaller than in the Corimelaeninae (14–21), which is compatible with our observations in *Alkindus* spp. (19).

The foretibial apparatus is present in most groups within the superfamily (McAtee & Malloch 1928; Dolling 1981), being a unique feature of "higher" Pentatomoidea (Grazia *et al.* 2008). Its presence in Thyreocoridae was observed by Grazia *et al.* (2008) and, recently, by Barão *et al.* (2013). In the latter study, the foretibial apparatus of the Pentatomidae, the Scutelleridae and the Thyreocoridae differed only in the number of setae; for the Thyreocoridae, the number of setae (4–5) overlaps with the Pentatomidae (3–23). The additional data provided by the study of *Alkindus* spp. suggest that this number is quite conserved within the family.

Female genitalia. The female genitalia were described in only a few species of Thyreocoridae. External genitalia of several thyreocorids were illustrated by McAtee and Malloch (1933), *Galgupha magna* Sailer by Sailer (1941), *Galgupha durionei* Kormilev, *Galgupha fritzi* Kormilev, and *Galgupha torresi* Kormilev by Kormilev (1956a), *Galgupha atra* Amyot & Serville by Scudder (1959), *Corimelaena pulicaria* (Germar) by McDonald (1966), *Corimelaena lateralis* (Fabricius) and *Corimalena obscura* McPherson & Sailer by McPherson & Sailer (1978), *Thyreocoris* spp. by Stys & Davidová (1979), *Carrabas maurus* Distant, *Strombosoma unipunctatum* Amyot & Serville, and *T. scarabaeoides* by Dolling (1981), *Thyreocoris pakistanensis* Ahmad & Moizuddin by Ahmad & Moizuddin (1982). Female internal genitalia have been studied and illustrated only in *C. pulicaria*, *Galgupha nitiduloides* (Wolff), *Galgupha ovalis* Hussey, and *T. scarabaeoides* (Pendergrast 1957; McDonald 1966; Stys & Davidová 1979; Pluot-Sigwalt & Lis 2008).

In almost all of those species, as well as in *Alkindus* spp., the laterotergites 8 are fused medially and the paired gonocoxites 8 and laterotergites 9 are free from each other (Scudder 1959; McDonald 1966). According to Dolling (1981), in *T. scarabaeoides*, the laterotergites 8 have a median suture line and, in *S. unipunctatum*, they are not fused. In *Allocoris* sp. (= *Corimelaena*) (Corimelaeninae), the laterotergites 9 are contiguous, partially covering the segment X, as in *Alkindus* spp. (Grazia *et al.* 2008). In *T. scarabaeoides*, they are separate, with segment X between them (Grazia *et al.* 2008), as found in the other Thyreocorinae (Dolling 1981).

The gonocoxites 9 appear to be even more variable in their degree of fusion. As observed in *Alkindus* spp., the gonocoxites 9 are independent from each other in the Thyreocorinae (*C. maurus*, *S. unipunctatum*, and *T. scarabaeoides*) (Dolling 1981), although Grazia *et al.* (2008) considered them to be joined medially by membrane in *T. scarabaeoides*. In *Allocoris* sp., they are fused, but with a distinct median fusion line (Grazia *et al.* 2008). In Thyreocorinae, the gonocoxites 9 are visible externally, lying between the laterotergites 9 (Dolling 1981). According to the description of McDonald (1966) for *C. pulicaria* and *G. nitiduloides*, the gonocoxites 9 are not visible externally, a condition found in all other Corimelaeninae illustrated and observed so far (including *Alkindus* spp.).

The *receptaculum seminis* (= spermathecae) appears to differ radically within the family (McDonald 1966), but this structure could not be adequately observed in *Alkindus* spp. The narrow sclerotized groove surrounding the *orificium receptaculi* was described in *G. nitiduloides* (McDonald 1966) and is similar to the observed for the Scutelleridae by Grazia *et al.* (2008). Among the thyreocorid species whose ectodermal female genital ducts have been studied, a dilation was present in *G. nitiduloides*, *G. ovalis*, and, in a very different shape, in *T. scarabaeoides* (Pendergrast 1957; McDonald 1966; Stys & Davidová 1979; Pluot-Sigwalt & Lis 2008). According to McDonald (1966), *C. pulicaria* would lack a dilation, but at least in one species of *Corimelaena*, this structure is clearly present (J. Grazia, personal communication). In *A. atratus*, the dilation could not be recognized, but it appears to be present as an amorphous structure in *A. crassicosta*. The presence of two accessory sacs has been described already in *C. pulicaria*, *G. atra*, and *G. nitiduloides*, but their function is unknown (Scudder 1959; McDonald 1966). The absence of ring sclerites has been observed for other representatives of the family (Scudder 1959; McDonald 1966; Dolling 1981; Pluot-Sigwalt & Lis 2008). Those few observations support the closest relation of *Alkindus* with other Corimelaeninae and reinforce the need for a comprehensive comparative study on the female internal genitalia in Thyreocoridae.

Biogeographical notes. Distribution of *Alkindus* spp. is restricted to the Neotropical region *sensu lato* (Morrone 2013). This, however, is not a geological or geographically unique or homogeneous entity (Amorim 2012). Distribution records from both species are clearly disjunct. *A. atratus* is present in the Caribbean and Northwest components of the Neotropical region (Amorim & Pires 1996), widely distributed from Mexico to northern Brazil. On the other hand, *A. crassicosta* is restricted to southern and southeastern Brazil, occupying part of the Southeast Neotropical component, restricted to the Atlantic Forest, with a single record to the northwest of Pampa (Amorim & Pires 1996). This disjunct distribution is consistent with the second dichotomy of the Neotropical region *sensu stricto* into a north-western and a south-eastern component, as found by Morrone (2013).

Considering the classification of the Neotropical region proposed by Morrone (2013) and the biogeographical regionalization into provinces compiled by Morrone (2006), *A. atratus* occurs in the Mexican transition zone, the Amazonian subregion, and the South American transition zone. In the Mexican transition zone, the species occupies two provinces: the Transmexican Volcanic Belt and the Balsas Basin. In the Amazonian subregion, it occurs in all provinces of the Mesoamerican dominion (except the Mexican Gulf), in three provinces of the North-western South American dominion (Maracaibo, Venezuelan Coast, and Venezuelan Llanos), and in one province of the Northern Amazonian dominion (Roraima). The species has been collected in only one province of the South American transition zone (North Andean Paramo). *A. crassicosta*, in turn, occurs in the Chacoan subregion, more precisely in the Pampa and the Brazilian Atlantic Forest Provinces.

Lack of data from field sampling and identified museum specimens, as well as lack of hypotheses of relationships among thyreocorid genera prevent further biogeographical discussions. However, it is worth mentioning that both species of *Alkindus* are restricted to forest areas, since records in open formations are missing. The large gap observed in their distribution could be explained either by lack of sampling and identification or by extinction of the taxon in intervening areas. Alternatively, there may be undescribed species in areas of Cerrado and Caatinga, which should be further explored.

The availability of phylogenetic information within Thyreocoridae would be especially interesting to test the presumptive relatedness between *Alkindus* and *Pericrepis*. The latter genus is comprised of four species, distributed in Argentina (all species), Brazil (two species), and Paraguay (one species) (McAtee & Malloch 1933; Kormilev 1956b; collection data).

Key to the species of *Alkindus*

(modified from McAtee & Malloch, 1933)

1 Smaller (3.0–4.8 mm); subcostal smooth area of corium broader throughout, distinctly widened in the middle of its length, the branches of exocorial vein more crowded together and subparallel (Fig. 8); posterior margin of abdominal sternite VII slightly projected ventrally in the female, accompanying the gonocoxites 8; gonocoxites 8 ventrally projected along entire mesial margins (Figs. 4, 11, 12); ventral rim of pygophore broadly concave at median 3/5, scarcely covering the proctiger (Figs. 15, 31); distributed in southeastern and southern Brazil . . . . *A. crassicosta* Horvath

1' Larger (4.5–5.6 mm); subcostal smooth area of corium narrower, slightly broader at base, the branches of exocorial vein divergent in middle part of their course (Fig. 6); posterior margin of abdominal sternite VII not ventrally projected in the female; gonocoxites 8 ventrally projected at anterior half (Figs. 9, 10, 29); ventral rim of pygophore convex at median third, slightly bilobate, completely covering the proctiger, with 1 + 1 acute posterior projections at lateral thirds (Figs. 13, 30); distributed in Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Aruba, Curaçao, Venezuela, Costa Rica, Colombia, Panama, and northern Brazil. . . . . *A. atratus* Distant

Alkindus atratus Distant, 1889

(Figs. 5, 6, 9, 10, 13, 14, 17–20, 24–26, 29, 30)

Type locality: Tolé, Panama.

Alkindus atratus Distant, 1889: 309; Lethierry & Severin 1893: 14 (catalogue); McAtee & Malloch 1933: 348–349 (redescription); Becker & Grazia-Vieira 1971: 9 (distribution records); Maes 1994: 21 (catalogue).

Diagnosis. Head (Fig. 5). Ocelli almost equidistant from middle of vertex and from eyes; head posterior to ocelli about 2.2 times the diameter of ocelli.

Pronotum. Broad lateral punctate area. Callus slightly rastrate.

Hemelytra (Fig. 6). Width of subcostal area uniform at first half, narrower posteriorly. Branches of exocorial vein divergent in middle part of their course.

Abdominal venter (Figs. 9, 13). Sternite VII on average 0.6 and 1.2 times the length of segments III–VI in female and male, respectively; anterior margin of sternite VII broadly rounded in female and narrowly rounded to sub angulate in male, posterior margin rounded in both sexes. Lateral bristles present on all visible abdominal segments (including laterotergites 8 and 9 in female), these longer and thicker than the trichobothria, located laterally and in line with anterior trichobothria.

Male genitalia (Figs. 13, 14, 30). Ventral exposure of pygophore long, about 0.4 times the length of urosternite VII, more densely punctate anteriorly and laterally. Ventral rim convex at median third, slightly bilobate; with 1 + 1 acute posterior projections at lateral thirds.

Measurements (n=9). Total length 4.7 (4.5–5.0) ± 0.2; head length 0.9 (0.9–1.1) ± 0.1, width 2.0 (1.9–2.1) ± 0.1; eye width 0.2 (0.2–0.3) ± 0.0; interocular distance 1.5 (1.4–1.6) ± 0.1; anteocular length 0.4 (0.4–0.5) ± 0.0; length of antennal segments: I—0.4 (0.4–0.5) ± 0.0; II—0.2 (0.1–0.2) ± 0.0; III—0.3 ± 0.0; IV—0.4 (0.3–0.4) ± 0.0; V—0.5 (0.4–0.5) ± 0.0; pronotal length 1.4 (1.3–1.5) ± 0.1, width 3.1 (3.0–3.4) ± 0.1; scutellar length 2.9 (2.6–3.2) ± 0.2, width 2.7 (2.5–2.8) ± 0.1; abdominal width 3.0 (2.9–3.3) ± 0.1; corium length 2.1 (2.0–2.3) ± 0.1; rostrum length 1.7 (1.7–1.8) ± 0.0.

Female genitalia (Figs. 9, 10, 29). Posterior margins of gonocoxites 8 slightly concave; anterior half of mesial margins ventrally projected; mesial margins about 1.3 times the length of abdominal sternite VII at midline and 1.3 times the length of posterior margins of gonocoxites 8.

Measurements (n=7). Total length 5.1 (4.7–5.6) ± 0.3; head length 1.0 (1.0–1.1) ± 0.1, width 2.2 (2.1–2.3) ± 0.1; eye width 0.3 ± 0.0; interocular distance 1.6 (1.6–1.8) ± 0.1; anteocular length 0.4 (0.4–0.5) ± 0.0; length of antennal segments: I - 0.5 (0.4–0.5) ± 0.1; II - 0.2 ± 0.0; III - 0.3 (0.3–0.4) ± 0.0; IV - 0.4 ± 0.0; V - 0.5 (0.5–0.6) ± 0.0; pronotal length 1.5 (1.4–1.8) ± 0.1, width 3.5 (3.3–3.7) ± 0.2; scutellar length 3.1 (2.9–3.3) ± 0.2, width 3.0 (2.8–3.3) ± 0.2; abdominal width 3.4 (3.2–3.6) ± 0.2; corium length 2.3 (2.1–2.4) ± 0.1; rostrum length 1.9 (1.8–2.1) ± 0.1.

Distribution. Mexico (States of Jalisco, Colima, and Guerrero), Guatemala (Department of Escuintla), Honduras, El Salvador, Nicaragua (Departments of Matagalpa, Chinandega, Boaco, León, Managua, Zelaya, Masaya, Granada, Carazo, and Rivas), Aruba, Curaçao, Venezuela (States of Sucre, Aragua, Anzoategui, Guarico, Zulia, Monagas, Portuguesa, Trujillo, and Bolívar), Costa Rica (Provinces of Guanacaste, Cartago, and San Jose), Colombia (Departments of Magdalena, Boyaca, and Cundinamarca), Panama (Provinces of Panama, Cocle, and Chiriqui), and Brazil (State of Roraima). Provinces 8, 9, 11, 14, 15, 16, 25, 26, 29, 39, and 56, according to Morrone (2006) (Fig. 32).

Type material (examined). Holotype ♂ and paratype ♀. Tolé, Panama, Champion; Tierra Colorado, Guerrero, 2.000 ft., October, H. H. Smith (BMNH).

Material examined. GUATEMALA, **Escuintla**: 5 km S Siguinala, 1 ♀, down fig tree, 7-26-2008, C. W. & L. B. O'Brien, F. Skillman, J. Monzon cols. (JEEC); COSTA RICA, **Guanacaste**: Sta. Rosa N. Pk., Nat. Trail, 1 ♀, IX-3-1998, C. W. & L. B. O'Brien cols. (JEEC); VENEZUELA, **Aragua**: El Limon, 450 m, 1 ♀, 2-VII-54; J. Gonzalez col. (UFRG); El Limon, 450 m, 1 ♀, 19-VII-56, en gallingo, Fco. Fdez. Y. col. (UFRG); Carmen de Cura, 850 m, 1 ♂, 11-VII-1966, F. Fernandez, Y. C. J. Rosales cols. (UFRG); **Anzoategui**: 3 km W Clarines, 250', 1 ♂, Aug. 2 1988, C. & L. O'Brien & G. Wibmer cols. (JEEC); **Guarico**: 1 km S Dos Caminos, 570', 1 ♀, 7-27-1988, C. & L. O'Brien & G. Wibmer cols. (JEEC); Hato Las Lajas, 3 ♂, 15-VIII-1964, A. Dascoli col. (UFRG); **Monagas**: Josepin, 1 ♂, 14-IX-1965, F. Fernandez, Y. C. J. Rosales cols. (UFRG); BRAZIL, **Roraima**: Ilha de Maracá, 3 ♂, 2 ♀, 21–25/09/1987, M. H. Galileo leg. (MCNZ).

Alkindus crassicosta Horvath, 1919

(Figs. 1–4, 7, 8, 11, 12, 15, 16, 21–23, 27, 28, 31)

Type locality: São Paulo, Brazil.

Alkindus crassicosta Horvath, 1919: 232; McAtee & Malloch 1933: 349–350 (redescription); Grazia *et al.* 1999: 108 (list); Grazia & Schwertner 2011: 12 (list); Klein *et al.* 2013: 242 (distribution record).

Diagnosis. Head (Figs. 2, 7). Ocelli nearer eyes than to middle of vertex; head posterior to ocelli about 1.6 times the diameter of ocelli.

Pronotum. Lateral punctate area proportionally smaller than in *A. atratus*. Callus inconspicuously rastrate.

Hemelytra (Figs. 3, 8). Subcostal smooth area of corium broader than in *A. atratus*; largest width at median third. Exocorial vein with internal and external branches subparallel, closer to each other than in *A. atratus*.

Abdominal venter (Figs. 11, 15). Sternite VII on average 0.8 and 1.0 times the length of segments III–VI in female and male, respectively; anterior margin of sternite VII broadly rounded in female and narrowly rounded to slightly angulate in male, posterior margin broadly rounded in male and angulate and ventrally projected at middle in female. Lateral bristles absent. Based solely on the absence of such bristles, the specimens of *A. crassicosta* would key to the genus *Pericrepis*, because McAtee & Malloch (1933) mistakenly consider the presence of lateral bristles as characteristic of the genus *Alkindus*.

Male genitalia (Figs. 15, 16, 31). Ventral exposure of pygophore shorter than in *A. atratus*, about 0.2 times the length of urosternite VII, punctate, with median transverse striations. Ventral rim broadly concave, almost subrectilinear at median 3/5, not covering the proctiger.

Measurements (n=5). Total length 4.1 (3.0–4.6) ± 0.6; head length 0.8 (0.8–0.9) ± 0.1, width 1.9 (1.8–1.9) ± 0.0; eye width 0.3 ± 0.0; interocular distance 1.3 (1.3–1.4) ± 0.0; anteocular length 0.3 (0.3–0.4) ± 0.0; length of antennal segments: I—0.4 ± 0.0; II —0.1 (0.1–0.2) ± 0.0; III—0.2 (0.2–0.3) ± 0.0; IV—0.3 (0.3–0.4) ± 0.0; V—0.4 (0.4–0.5) ± 0.0; pronotal length 1.4 (1.3–1.4) ± 0.0, width 2.9 (2.8–3.0) ± 0.1; scutellar length 2.7 (2.5–3.0) ± 0.2, width 2.3 (2.3–2.4) ± 0.0; abdominal width 2.7 (2.6–2.9) ± 0.1; corium length 1.9 (1.7–2.2) ± 0.2; rostrum length 1.5 (1.5–1.7) ± 0.1.

Female genitalia (Figs. 11, 12). Gonocoxites 8 more elongate than in *A. atratus*; mesial margins strongly projected ventrally, especially at anterior and median third, projection evanescent posteriorly; mesial margins about 1.1 times the length of abdominal sternite VII at midline and 1.4 times the length of posterior margins of gonocoxites 8.

Measurements (n=2). Total length 4.8 (4.7–4.8) ± 0.1; head length 0.9 (0.9–1.0) ± 0.1, width 2.0 ± 0.0; eye width 0.3 ± 0.0; interocular distance 1.5 ± 0.0; anteocular length 0.4 ± 0.0; length of antennal segments: I—0.5 ± 0.0; II—0.2 ± 0.0; III—0.3 ± 0.0; IV— 0.4; V—0.5; pronotal length 1.5 (1.4–1.5) ± 0.1, width 3.1 ± 0.0; scutellar length 3.0 (2.9–3.0) ± 0.1, width 2.6 ± 0.0; abdominal width 2.9 (2.9–3.0) ± 0.1; corium length 2.2 (2.2–2.3) ± 0.0; rostrum length 1.7 (1.6–1.8) ± 0.1.

Distribution. Brazil (States of São Paulo, Santa Catarina, and Rio Grande do Sul). Provinces 51 and 53, according to Morrone (2006) (Fig. 32).

Type material (photographs examined). Holotype ♀. Labels: 1) Brasilia, S. Paulo; 2) *crassicosta* det. Horvath (HNHM).

Material examined. BRAZIL, **Santa Catarina**: Maracajá, 1 ♂, 21-X-2005, Bertolin, T. col. (UFRG); **Rio Grande do Sul**: Triunfo, 1 ♂, 20/X/1977, H. A. Gastal leg. (MCNZ); Eldorado do Sul, 3 ♂, 12.05.2010, Joana Klein col. (UFRG); Barra do Quaraí, Fazenda Espinilho, 2 ♀, 1ª varredura, campo, 10/I/2004, Bunde; Schwertner cols. (UFRG).

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CAPÍTULO 2

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Article

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Egg ultrastructure of two species of *Galgupha* Amyot & Serville, with a discussion of the eggs and oviposition patterns of thyreocorid and allied groups (Hemiptera: Heteroptera: Pentatomoidea: Thyreocoridae)

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Abstract

Immature stages are known in only 11 species of the Thyreocoridae. In this paper, the eggs of *Galgupha* (*Euryscytus*) *difficilis* (Breddin) and *Galgupha (Gyrocnemis) fossata* McAtee & Malloch are described and illustrated. Egg morphology and oviposition habit in the Thyreocoridae and Cydnidae are reviewed. Adults of both species were collected in São Francisco de Paula municipality, state of Rio Grande do Sul, Brazil, and maintained in the laboratory for oviposition. The eggs were examined by stereomicroscopy and scanning electron microscopy and photographed. In *G. (E.) difficilis*, the eggs were laid singly or in pairs; each egg is cylindrical (0.8 x 0.5 mm) and white and the chorion is shiny, translucent, and smooth; the micropylar processes (2–4) are short and stalked. In *G.* (*G.*) *fossata*, the eggs were laid singly; each egg is cylindrical (0.9 x 0.6 mm) and white and the chorion is shiny, translucent, and granulated; the micropylar processes (4–10) are short, stalked, and transversely constricted. The eggs of both species are similar to those of other thyreocorids, especially of other corimelaenines. The Thyreocoridae in the broadest sense (including the Parastrachiinae) is not a uniform group concerning egg morphology, oviposition behavior, and maternal care. Within the Pentatomoidea, based on egg morphology, the Cydnidae is the group nearest to the Thyreocoridae. The evolution of the eggs in the Pentatomoidea should be investigated within a phylogenetic framework, including egg characters, in future cladistic analyses.

Key words: Corimelaeninae, *Galgupha* (*Euryscytus*) *difficilis*, *Galgupha* (*Gyrocnemis*) *fossata*, Cydnidae, Pentatomoidea, scanning electron microscopy

Introduction

The Thyreocoridae Amyot & Serville (= Corimelaenidae Uhler) is a common but poorly studied group in the Pentatomoidea. It includes the Thyreocorinae, with seven species in three genera, and Corimelaeninae, with 206 species in nine genera (McAtee & Malloch 1933; Sailer 1940, 1941; Kormilev 1956a, 1956b; McPherson & Sailer 1978; Štys & Davidová 1979; Dolling 1981; Ahmad & Moizuddin 1982). Grazia *et al.* (2008), in a cladistic analysis of the Pentatomoidea, suggested that the Parastrachiinae Schaefer, Dolling, and Tachikawa should be treated as part of a more broadly conceived Thyreocoridae, adding two genera and eight species (Kirkaldy 1909; Jeannel 1913; Hesse 1925; Sweet & Schaefer 2002). Following Grazia *et al.* (2008), Thyreocoridae is treated here as comprising three subfamilies.

Galgupha Amyot & Serville (Corimelaeninae) is widely distributed in the Americas, with 15 subgenera and 156 species (McAtee & Malloch 1933; Sailer 1940, 1941; Kormilev 1956a, 1956b). The subgenera *Euryscytus* Horvath and *Gyrocnemis* McAtee & Malloch, including 38 species each, are the most diverse (McAtee & Malloch 1933; Kormilev 1956a).

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Basic information (e.g., life cycle, geographical distribution) for many species is either incomplete, inaccurate, or lacking (McPherson 1974), especially in the Neotropics. Thyreocorid immatures have been broadly overlooked, probably due to their minute size, somewhat secretive habits, and lack of knowledge about host plants, which is required for nymphal development (Yonke 1991). General features of the eggs and nymphs of thyreocorid species have been briefly described (Southwood 1956; Cobben 1968; Hinton 1981; Yonke 1991). Immature stages are known only for 11 species, including descriptions of eggs and/or nymphs, and/or life history (Table 1).

Galgupha (*Euryscytus*) *difficilis* (Breddin) and *Galgupha* (*Gyrocnemis*) *fossata* McAtee & Malloch are known through the original descriptions of the adults and reviews of the family by Breddin (1914) and McAtee and Malloch (1928, 1933). Distribution records include Brazil and Argentina for the former species, and Brazil, Argentina, and Paraguay for the latter (McAtee & Malloch 1933).

This paper provides the first description of the eggs of exclusively Neotropical thyreocorid species viewed by stereomicroscopy (SM) and scanning electron microscopy (SEM). Egg morphology and oviposition habit in species of the Thyreocoridae and Cydnidae (historically considered close to the former family) are reviewed and discussed according to the hypotheses of relationships in the Pentatomoidea presented by Grazia *et al*. (2008).

Material and methods

Adults of *G. (E.) difficilis* and *G. (G.) fossata* were collected on *Buddleia brasiliensis* (Scrophulariaceae) in "Floresta Nacional de São Francisco de Paula," São Francisco de Paula municipality, state of Rio Grande do Sul, Brazil (29°42’91”S, 50°39’34”W; 29°42’81”S, 50°39’03”W, respectively). In the laboratory, the insects were kept in plastic containers (Gerbox®, 11x11x3 cm) with branches of *B. brasiliensis* for oviposition. Eggs were preserved in 70% ethanol. Species were identified using McAtee and Malloch's (1933) keys and comparison with material deposited at the "Museo Argentino de Ciencias Naturales Bernardino Rivadavia" (MACN; Buenos Aires, Argentina) and at the "Museo de La Plata" (MLPA; La Plata, Argentina).

Eggs and ovipositional habits were examined with a stereomicroscope coupled with a digital camera and photographed; the eggs also were examined with a scanning electron microscope and photographed. Egg length and width were measured in millimeters (mean ± standard deviation, minimum, and maximum) and micropylar processes were counted. Terminology followed Javahery (1994) and Bundy and McPherson (2009). For SEM analysis, three eggs of each species were fixed and prepared according to Bianchi *et al*. (2011). Samples were submitted to a critical point drying process, mounted in stubs, metalized with gold, and analyzed in a JEOL JSM 6060 scanning electron microscope at the "Centro de Microscopia Eletrônica da Universidade Federal do Rio Grande do Sul" (CME/UFRGS).

Voucher specimens are deposited at the "Coleção Entomológica do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul" (UFRG).

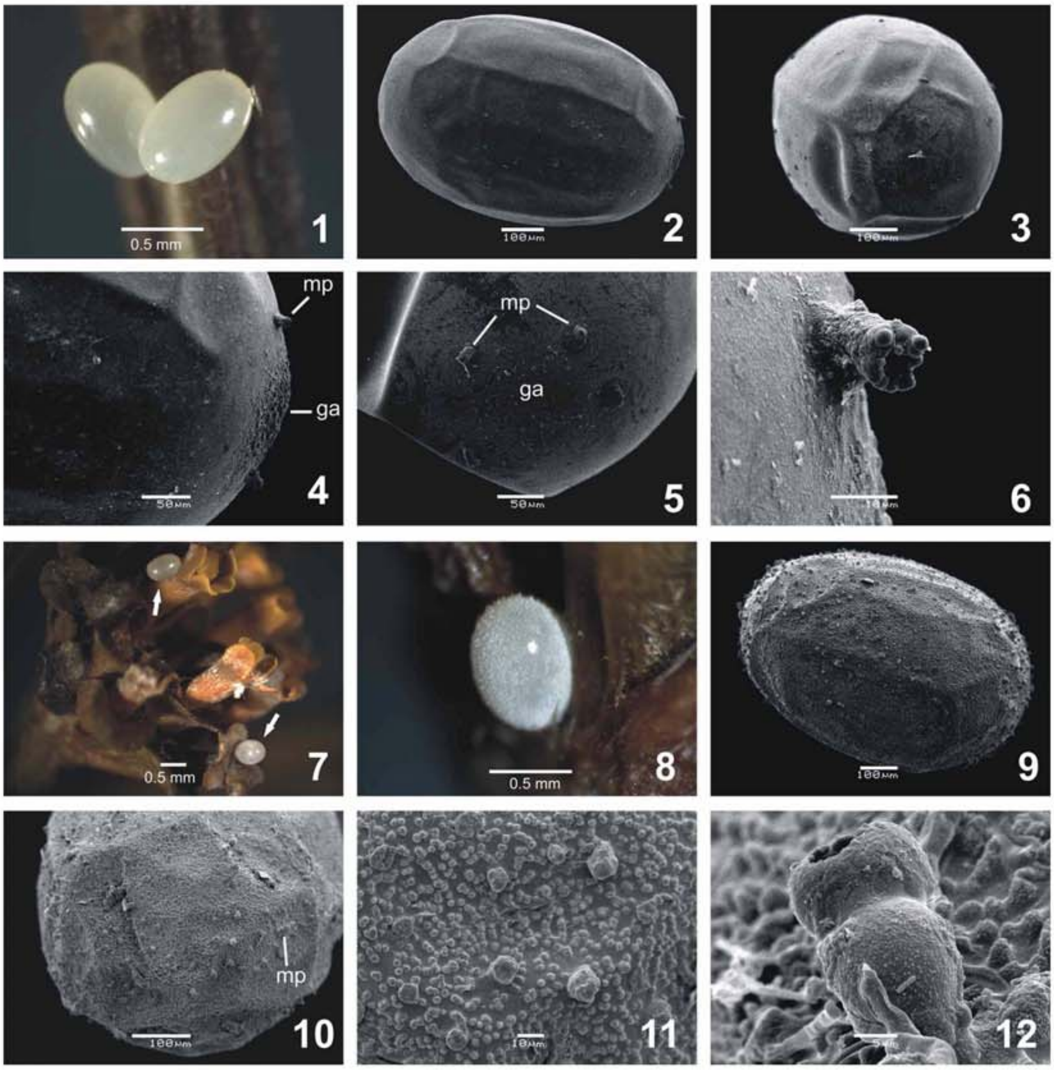
Results and Discussion

Galgupha* (*Euryscytus*) *difficilis (Figs. 1–6). Eggs were deposited on the bottom of the plastic container or at the bases of the plant branches; they were laid singly or in pairs and, if paired, attached to each other at a right angle (Fig. 1).

Description. Egg cylindrical with rounded ends, slightly narrower at anterior pole, white; chorion shiny and translucent (Fig. 1). Chorion surface, either with SM or SEM, generally smooth but often with faint longitudinal carinae (Figs. 1–3). Under SEM, center of anterior pole granulated (Fig. 4), sometimes mostly smooth (Fig. 5). Length: 0.8 ± 0.01; width: 0.5 ± 0.02 (0.5–0.6) (n = 7). Micropylar processes (MP) circularly arranged around anterior pole (Figs. 4, 5); mean number of MP 3 ± 0.6 (2–4). Each MP translucent, short, stalked, slightly capitate; apical opening circular; under higher magnification, surface not spongy (Fig. 6).

Galgupha* (*Gyrocnemis*) *fossata (Figs. 7–12). Eggs were deposited on the host plant inflorescences and laid singly (Fig. 7).

Description. Egg cylindrical with rounded ends, slightly wider at anterior pole, white; chorion shiny and translucent (Fig. 8). Chorion surface, under SM, with small protuberances (Fig. 8); under SEM, dense granulation evident, interspaced with larger tubercles, usually with faint longitudinal carinae (Figs. 9–11). Length: 0.9 ± 0.04 (0.8–1.0); width: 0.6 ± 0.07 (0.5–0.7) (n = 20). MP circularly arranged around anterior pole but slightly displaced posteriorly (Fig. 10); mean number of MP 7 ± 1.5 (4–10). Each MP white, short, almost indistinguishable from the chorionic sculpture under SM, stalked, oblong, capitate, with transverse constriction near middle; apical opening circular; under higher magnification, surface irregular but not spongy (Fig. 12).



FIGURES 1–12. Eggs of *Galgupha* (*Euryscytus*) *difficilis* and *Galgupha* (*Gyrocnemis*) *fossata*. 1— Eggs of *G.* (*E.*) *difficilis* laid in pair, at right angle to each other, attached to branch of ***Buddleia brasiliensis***, viewed with stereomicroscope (SM). 2–6— Eggs of *G.* (*E.*) *difficilis* viewed with scanning electron microscope (SEM): 2— lateral view, 3— anterior view, 4— magnification of anterior pole in lateral view, 5— magnification of anterior pole in anterior view, 6— micropylar process, with circular apical opening. 7–8— Eggs of *G.* (*G.*) *fossata* in SM: 7— Eggs laid singly (arrows), attached to inflorescence of ***B. brasiliensis***, 8— Egg attached to branch of the plant, with conspicuous chorion sculpture. 9–12— Eggs of *G.* (*G.*) *fossata* viewed with SEM: 9— lateral view, 10— anterior view, 11— magnification of anterior pole; chorion sculpture with granules and tubercles, 12— micropylar process, with transverse constriction and circular apical opening. Abbreviations: ga—granulated area, mp—micropylar process.

General morphology

The importance of the structure of eggs to define status and relationships among heteropteran groups long has been recognized. Morphological similarities are expected among eggs of species belonging to the same taxon, and patterns actually have been identified at different levels in the Pentatomoidea (Leston 1955; Southwood 1956; Cobben 1968; Javahery 1994; Matesco *et al.* 2009). Although the phylogenetic importance of the egg stage is widely emphasized, it has been rarely tested in cladistic analyses (Hasan & Kitching 1993; Wheeler *et al.* 1993; Henry 1997; Grazia *et al.* 2008).

In thyreocorid eggs, no pattern has been recognized yet at the generic level. Egg characters in the family are scarce – the egg structure is simple – and basic information is available for only a few species. Detailed descriptions and SEM studies in more genera (e.g., *Thyreocoris* Schrank, *Parastrachia* Distant, *Dismegistus* Amyot & Serville, and other corimelaenine genera) are highly desirable and essential for further discussion.

Eggs of *Galgupha* studied here are similar to other corimelaenine eggs. Based on the egg morphology of eight corimelaenine species (Table 1), a consistent pattern can be outlined: eggs are laid singly on parts of the host plants; each egg is cylindrical with rounded ends and white before embryonic development; the chorion is thin and shiny with a few (2–10) short, stalked MP around anterior pole; lengths of eggs and MP are 0.65–1.08 and 0.03–0.05 mm, respectively.

TABLE 1. List of thyreocorid species with described immatures (eggs and/or nymphs) and/or immature biology*.

Taxon	Egg		Nymph	Biology
	SEM	SM		
Parastrachiinae				
Dismegistus sanguineus (De Geer)		Dolling 1981		
Parastrachia japonensis (Scott)		Tachikawa & Schaefer 1985	Tachikawa & Schaefer 1985	Tachikawa & Schaefer 1985
Thyreocorinae				
Thyreocoris scarabaeoides (Linnaeus)		Cobben 1968		
Corimelaeninae				
Corimelaena sp.		Southwood 1956		
Corimelaena (*Corimelaena*) *lateralis* (Fabricius)		McPherson 1972	McPherson 1972	McPherson 1971, 1972
Corimelaena (C.) obscura McPherson & Sailer	Bundy & McPherson 1997		Bundy & McPherson 1997	Bundy & McPherson 1997
Corimelaena (*Parapora*) *extensa* Uhler		Lung & Goeden 1982	Lung & Goeden 1982	Lung & Goeden 1982
Corimelaena (P.) incognita (McAtee & Malloch)	Bundy & McPherson 2009		Bundy & McPherson 2009	Bundy & McPherson 2009
Corimelaena (*P.*) *virilis* (McAtee & Malloch)		Lattin 1955		
Galgupha (*Euryscytus*) *difficilis* (Breddin)	this study			
Galgupha (Galgupha) atra Amyot & Serville		Javahery 1994		
Galgupha (*G.*) *ovalis* Hussey		Biehler & McPherson 1982	Biehler & McPherson 1982	Biehler & McPherson 1982
Galgupha (*Gyrocnemis*) *fossata* McAtee & Malloch	this study			

* SEM = scanning electron microscopy; SM = stereomicroscopy.

As observed in *G. (E.) difficilis*, the chorion is usually smooth as described for other two *Galgupha* and five *Corimelaena* species (Lattin 1955; McPherson 1972; Biehler & McPherson 1982; Lung & Goeden 1982; Javahery 1994; Bundy & McPherson 1997, 2009). The chorion sculpture in *G. (G.) fossata* is possibly similar to that of *Thyreocoris scarabaeoides* (Linnaeus) (Thyreocorinae), which shows a rough appearance and is beset with pegs, according to the description of Cobben (1968). In other aspects, it probably fits the pattern described above for the Corimelaeninae.

Because embryonated or hatched eggs of *G.* (*E.*) *difficilis* and *G.* (*G.*) *fossata* were not observed, the presence of the pseudoperculum and egg-burster could not be determined. The pseudoperculum is not apparent in thyreocorid eggs (McPherson 1972; Javahery 1994), although Lattin (1955) considered it the area defined by the MP. The absence of the pseudoperculum is congruent with the thinness of the chorion and its irregular split at eclosion, described by previous authors (Southwood 1956; McPherson 1971; Biehler & McPherson 1982; Lung & Goeden 1982; Javahery 1994; Bundy & McPherson 1997). The egg-burster was rarely described in the group, but Javahery (1994) stated that hatching could not take place in these bugs in the absence of this structure. When observed, it was dark brown, small and weakly sclerotized, "Y"-shaped, placed in the center of anterior pole, with an acute median spine (Lattin 1955; Lung & Goeden 1982; Javahery 1994; Bundy & McPherson 1997, 2009).

The micropylar processes are short, stalked, capitate, and apparently lack the spongy appearance in thyreocorid species. At greater magnification, however, the four species studied under SEM (Table 1) are slightly different from each other in the shape and orientation of the MP and placement of the opening (Bundy & McPherson 1997, 2009; this study).

Oviposition behavior and maternal care

The Thyreocoridae in the broadest sense (including the Parastrachiinae: *Parastrachia* and *Dismegistus*) is not a uniform group concerning egg morphology, oviposition behavior, and maternal care. The eggs of *Parastrachia japonensis* (Scott) are superficially similar to those of other thyreocorids: oval, broadly rounded at each end, pale, without pseudoperculum, and with six micropyles evenly distributed subapically, although not borne on micropylar processes (Tachikawa & Schaefer 1985; Schaefer *et al.* 1988; Sweet & Schaefer 2002). Nonetheless, although most of the thyreocorids disperse their eggs on plants, singly over space and time and abandon them, females of *P. japonensis* lay eggs in a round mass (60-100 eggs) in chambers in the ground, and guard them (Tachikawa & Schaefer 1985). This species is considered subsocial, and nymphs are provisioned with food as well as with trophic eggs, which are functionally and morphologically differentiated (Tsukamoto & Tojo 1992; Nomakuchi *et al.* 2001; Hironaka *et al.* 2005).

Similar subsocial behavior, egg guarding, progressive provisioning, and eventually trophic egg production have been recorded in species of the Sehirinae (Cydnidae): *Adomerus triguttulus* (Motschulsky), *Adomerus variegatus* (Signoret), *Canthophorus niveimarginatus* Scott, and *Sehirus cinctus* (Palisot de Beauvois) (Kight 1997; Kudo & Nakahira 2004, 2005; Filippi *et al.* 2009; Mukai *et al.* 2010). These aspects seem to be associated with ephemeral food resources and high predation risks (Filippi *et al.* 2001). *Parastrachia*, in fact, has been considered related to the Sehirinae because of similarities in maternal behavior, oviposition habits, and certain features of external morphology (Schaefer *et al.* 1988). However, even among the subsocial species, *P. japonensis* is considered unique, as a strict specialist feeder with a life history marked at each stage with unusual characteristics (Filippi *et al.* 2001).

The evolution of maternal care and subsociality in the Heteroptera is contentious. Tallamy and Schaefer (1997) considered that parental care is plesiomorphic in the Pentatomoidea. According to this hypothesis, it was only when host-plant seasonality or other unidentified phenomena prevented the distribution of eggs over space and time that relict maternal care persisted. Most pentatomoids would have abandoned maternal care for more effective, less costly means of protecting eggs.

In this context, there is a clear relationship between oviposition habit and the retention of maternal care, which could be exemplified by *P. japonensis* and species of the Sehirinae that lay eggs in unstructured masses within soil crevices. In spite of maternal care, protection afforded by this habit of oviposition is considered slightly lower [protection index (pi) = 4] than that afforded by eggs glued singly to plants (Thyreocorinae and Corimelaeninae; pi = 5) and much lower than eggs buried singly in soil (Cydninae; pi = 20) (see Tallamy & Schaefer 1997 for explanation of the protection index). Clustering eggs in one spot, an essential component of parental care, is more attractive to predators and parasitoids than isolated eggs and is usually accompanied by selection for increased clutch size to justify the large time commitment allocated to a single clutch. Still, the terrestrial substrate is considered less efficient than natural crevices as an oviposition site because of desiccation and predation threats (Tallamy & Schaefer 1997).

Notwithstanding, Schaefer *et al.* (1988) considered maternal behavior an apomorphy in both *Parastrachia* and the Sehirinae, but suggested that the features shared by them have been independently acquired. Also, Filippi *et al.* (2001) considered subsociality an apomorphic character in *Parastrachia japonensis*.

On the other hand, reports on eggs of *Dismegistus* spp. (Parastrachiinae) are scarce. Dolling (1981) described a large batch (122 eggs) of *Dismegistus sanguineus* (De Geer) attached to a leaf whose eggs bore a pseudoperculum and an egg-burster as well as two concentric rings of numerous MP. This is quite unlike anything that has been reported for the Thyreocoridae or Cydnidae; a double row of MP has been reported only briefly in *Chrysocoris* sp. (Scutelleridae) and *Leptocoris augur* (Fabricius) (Rhopalidae) (Southwood 1956; Hinton 1981).

Previous evidence based on adult morphology has stressed similarities among species of *Dismegistus* and *Parastrachia* and/or the Cydnidae (Lis 2002, 2010a, 2010b; Lis & Schaefer 2005; Pluot-Sigwalt & Lis 2008). Cladistic analyses based on morphological and molecular data (analyzed separately and in the form of a total evidence analysis) consistently support the monophyly of *Parastrachia* + *Dismegistus* (Grazia *et al.* 2008). Thus, confirmation of the striking egg characters in *Dismegistus sanguineus* and other congeneric species are needed for further conclusions.

Considerations on the relationships within the Pentatomoidea

Several authors have considered thyreocorid eggs similar to those of other related families, especially the Cydnidae (Lattin 1955; Southwood 1956; Cobben 1968; Hinton 1981). The Corimelaeninae and Thyreocorinae historically have been included among the Cydnidae (Dolling 1981), along with the Amnestinae, Cydninae, Garsauriinae, Cephalocteinae (= Scaptocorinae), Sehirinae, and Thaumastellinae. The egg of *Thaumastella aradoides* Horvath (now Thaumastellidae) is atypical for the Pentatomomorpha: the chorion is thin and has a faint hexagonal pattern, the anterior pole bears a small projection in the shape of a rosette; there are just three micropyles, but they lack the usual spongy layer and do not project above the surface (Cobben 1968; Hinton 1981). In those few species of the Cydninae and Cephalocteinae (both Cydnidae), whose eggs are known, they are laid singly in the ground. Eggs are 1.35–1.80 mm in length, oval, and white; the chorion is smooth and shiny, and the MP are absent or inconspicuous (Ayyar 1930; Southwood 1956; Cobben 1968; García & Bellotti 1980; Hinton 1981; Lis *et al.* 2000; J. Grazia, personal information).

Eggs of the Sehirinae (Cydnidae) are similar to those of the Thyreocoridae with regard to shape, size, and color; all aspects of chorion structure; size, and number of MP, and degree of development; and shape of the egg-burster. However, some special features can be highlighted: MP are sessile, eggs are laid in round masses in the soil, and the female usually cares for the eggs (Stokes 1950; Paul 1953; Leston 1955; Southwood 1956; Cobben 1968; McDonald 1968; Hinton 1981; Sites & McPherson 1982; Javahery 1994; Kudo & Nakahira 2004; Mukai *et al.* 2010), as in *P. japonensis*.

Lattin (1955) considered the Cydnidae (including the Corimelaeninae) a well-defined family within the Pentatomoidea, at least regarding the egg-burster. Southwood (1956) generalized egg characters for the Corimelaeninae, Sehirinae, and Cydninae, considering them a unique and somewhat ancient group with a thin simple chorion, poles gently rounded, small micropylar processes, and a weakly sclerotized egg-burster. Southwood (1956) felt the eggs were sharply distinguished from those of the Pentatomidae and showed similarities to those of the Pyrrhocoridae and some Lygaeidae. Cobben (1968) recognized a reasonably stable pattern of chorion structure for the eggs of 15 species of the Corimelaeninae, Sehirinae, and Cydninae.

In a cladistic analysis with morphological and molecular characters of the Pentatomoidea, however, the Cydnidae *sensu* Dolling could not be recovered as monophyletic except in the analysis of morphological data alone (Grazia *et al.* 2008). Instead, the Thyreocoridae was considered monophyletic, including the Parastrachiinae (*Parastrachia* and *Dismegistus*) and probably Sehirinae.

The new data presented here, together with earlier reports on the egg stage, show that egg morphology is conserved in the Thyreocoridae *sensu stricto* (Thyreocorinae and Corimelaeninae). The inclusion of *Parastrachia* in the family does not invalidate the pattern recognized for the eggs of the Thyreocorinae and Corimelaeninae, and also may support the proximity with the Sehirinae [suggested by the cladistic analysis of Grazia *et al.* (2008)] because of similarities in oviposition habit and maternal care. Egg morphology in *Dismegistus sanguineus* and other species of the genus is poorly known and remains intriguing. Within the Pentatomoidea, the Cydnidae is the group more similar to the Thyreocoridae regarding egg morphology, but further studies of the former family are required.

Most characters regarding egg stage shared by thyreocorid species, as well as other pentatomoid families, could be plesiomorphic or alternatively highly associated with oviposition in semi-exposed sites (Southwood 1956) (although aspects of oviposition behavior and maternal care vary in the group). Relationship hypotheses developed by Grazia *et al.* (2008) and the evolution of eggs in the Pentatomoidea can be clarified only by further studies, including additional data and within a phylogenetic framework. In this context, we believe that egg morphology, oviposition behavior, and maternal care will help unravel evolutionary relationships between taxa. Therefore, these egg characters should be included in future cladistic analyses. Nevertheless, further information about the egg stage in individual species of the Thyreocoridae and allied groups is still needed.

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CAPÍTULO 3

Cladistic analysis of *Corimelaena* White based on morphology, with considerations on the phylogeny of the Thyreocoridae (Hemiptera: Heteroptera: Pentatomoidea)

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Abstract

The relationships among the species of *Corimelaena* White, the position of the genus within Thyreocoridae, and the monophyly of Thyreocoridae were tested using morphological data of adult and immature stages in a cladistic analysis. A phylogenetic classification was proposed based on the monophyletic groups recovered. We include 40 species as terminal taxa: 36 species of Thyrecoridae and four species representing the families Parastrachiidae, Cydnidae, Canopidae, and Plataspididae. A total of 114 characters were analyzed with equal weighting of characters. The strict consensus tree supports the monophyly of the genera *Corimelaena* and *Strombosoma* Amyot & Serville, the subfamily Corimelaeninae, and the family Thyreocoridae. The monophyly of the Thyreocorinae, the genera *Alkindus* Distant and *Galgupha* Amyot & Serville (except for the nominal subgenus), and the subgenera of *Corimelaena* (*Corimelaena* and *Parapora* McAtee & Malloch) was not supported by our results. This is the first hypothesis of relationships within the Thyreocoridae as well as the first cladistic evidence of monophyly of *Corimelaena*. We suggest the maintenance of family status to Thyreocoridae and the abandonment of the subgenera of *Corimelaena*.

Keywords: Corimelaeninae – Cydnidae – egg characters – *Galgupha* – Parastrachiidae – Pentatomoidea – Thyreocorinae.

Introduction

The monophyly of the Pentatomoidea is well supported by cladistic analyses (Gapud, 1991; Henry, 1997; Grazia, Schuh & Wheeler, 2008), although the relationships among family groups and even the monophyly of some of them are still unresolved (Grazia *et al*., 2008). The placement of the Thyreocoridae within Pentatomoidea was discussed by Gapud (1991), Grazia *et al.* (2008), and Lis *et al.* (2012), usually suggesting a close relationship with the Cydnidae.

Grazia *et al.* (2008) supported the monophyly of the Thyreocoridae, represented by *Thyreocoris* Schrank and *Allocoris* McAtee & Malloch, based in seven homoplasious synapomorphies. The analysis also hypothesized a close relationship between Thyreocoridae and Parastrachiidae (*Parastrachia* Distant and *Dismegistus* Amyot & Serville). The authors suggested that Parastrachiidae should be given subfamily rank and treated as part of a broadly conceived Thyreocoridae. This classification was followed by Matesco *et al.* (2012), but not by other authors (Lis, 2010a, 2010b; Lis, Ziaja & Lis, 2011; Barão, Ferrari & Grazia, 2013), who still confer family status to the group.

Thyreocoridae was first established by Amyot & Serville (1843) as *Thyréocorides*. Uhler (1872) suggested the name Corimelaenidae to include the genera *Galgupha* Amyot & Serville and *Corimelaena* White. Since then, many authors rejected the name Thyreocoridae in favor of Corimelaenidae based on use (Rolston & McDonald, 1979) or considering the name Thyreocorides invalid because it would be French (Leston, 1953). Other authors emphasized that Thyreocoridae is the oldest name, advocating its adoption for purposes of nomenclature stability (Stys & Davidová, 1979; Froeschner, 1988; Triplehorn & Johnson, 2005; Marshall, 2006).

Lethierry & Severin (1893) gave this group subfamily rank within Pentatomidae and was followed by McAtee & Malloch (1933) in their revision of the group. Horvath (1919) treats the group as subfamily of the Cydnidae, but Froeschner (1960) separated Thyreocoridae from the Cydnidae, giving it status of family. Stys & Davidová (1979) revised the genus *Thyreocoris* and gave Thyreocoridae family status. Dolling (1981) formally recognized Thyreocorinae and Corimelaeninae as two independent subfamilies within Cydnidae. Lis (2006), in the catalog of Palaearctic species, confers family status to Thyreocoridae, following Stys & Davidová (1979), dividing it into two subfamilies, according to Dolling (1981).

Thyreocoridae is currently given family status and comprises 212 species in 12 genera divided in two subfamilies: Thyreocorinae and Corimelaeninae (Lis, 2006) (Table 1). Most genera and species are widely distributed in the Neartic and Neotropical regions, while a few genera occur in the Palaearctic, Oriental or Afrotropical regions (McAtee & Malloch, 1933; Stys & Davidová, 1979; Ahmad & Moizuddin, 1982). Also known as *negro bugs* in North America, the group comprises black insects of usually ovoid and gibbous form with the scutellum covering most, or all, of the abdomen (McAtee & Malloch, 1933).

Thyreocorinae comprises seven species in three genera (Table 1) (Stys & Davidová, 1979; Dolling, 1981; Ahmad & Moizuddin, 1982). It occurs only in the Eastern Hemisphere and is usually defined by the metathoracic wing with the jugal lobe entire, not perforated (Dolling, 1981). McAtee & Malloch (1933) considered *Carrabas* and *Strombosoma* as *incertae sedis*, but Dolling (1981) later included both in the Thyreocorinae.

Corimelaeninae comprises 205 species in nine genera (Table 1) (McAtee & Malloch, 1933; Sailer, 1940, 1941; Kormilev 1956a, 1956b; McPherson & Sailer, 1978; Dolling, 1981). It is restricted to the Western Hemisphere and is defined by the metathoracic wing with an oval perforation in the jugal lobe (Dolling, 1981). The genus *Galgupha* contains about three-fourths of the described diversity of Thyreocoridae (~150 spp.) and is divided in 15 subgenera. The only genus whose position has been disputed is *Eumetopia*, excluded from Thyreocoridae by McAtee & Malloch (1933), but later included in the group by Dolling (1981).

The monograph of McAtee & Malloch (1933) included keys to genera, subgenera, species and chromatic varieties, besides the description of 114 new species.

After this revision, systematic work in the group has been restricted to descriptions of a few species (Sailer, 1940, 1941; Kormilev, 1956a, 1956b; McPherson & Sailer, 1978; Ahmad & Moizudin, 1982) and regional studies (Porter, 1933; McPherson, 1970, 1979a, 1979b; Becker & Grazia-Vieira, 1971, 1977; Nixon, McPherson & Cuda, 1975; Linnavuori, 1977, 1993; Froeschner, 1981, 1988; Lis, 1989, 2006; Maes, 1994; Fent & Aktaç, 2007; Grazia, Matesco & Schwertner, in press). The phylogenetic relationships within the group are unknown; none of the 12 genera has been investigated in a cladistic framework. The monophyly of the subgenera of the most diverse genera, *Corimelaena*, *Cydnoides*, and *Galgupha*, remains to be tested.

Within Thyreocoridae, few morphological characters have been explored in comparative basis, difficulting the selection of characters to phylogenetic studies. There are limited investigations on aspects of leg structures (Lis, 2010a; Barão *et al.*, 2013; Matesco & Grazia, 2013), external scent efferent system (Kment & Vilímová, 2010b; Matesco & Grazia, 2013), and internal genitalia (McAtee & Malloch, 1933; Pendergrast, 1957; Scudder, 1959; McDonald, 1966; Stys & Davidová, 1979; Dolling, 1981; Ahmad & McPherson, 1990; Davidová-Vilímová & McPherson, 1991; Pluot-Sigwalt & Lis, 2008). The eggs of thyreocorids, on the other hand, are known for 11 species (reviewed by Matesco *et al.*, 2012).

Corimelaena is the second most diverse genus of Thyreocoridae and was established in 1839 by White, designating *Tetyra lateralis* Fabricius as type. Van Duzee (1917) and others cited species of *Corimelaena* under the name *Thyreocoris*. However, Malloch (1919) stated that the palaearctic species *T. scarabaeoides* (Linnaeus) is not congeneric with the American species and reestablished *Corimelaena*. McAtee & Malloch (1933) considered the type of *Corimelaena* unidentifiable and proposed a new name for the group, *Allocoris*. Sailer (1945) synonymized *Allocoris* and *Eucoria* Mulsant & Rey to *Corimelaena*.

The species of *Corimelaena* occurs on both Neartic and Neotropical regions, with most of the group diversity found in the former (McAtee & Malloch, 1933). The genus currently comprises 31 species (McAtee & Malloch, 1933; McPherson & Sailer, 1978), most of them in the nominal subgenus (23 species), and in three other subgenera, proposed by McAtee & Malloch (1933): *Epipora* (1 species), *Parapora* (6 species), and *Termapora* (1 species). The subgenera are based on differential position of the spiracles on sternites IV-VII in relation to the lateral margin.

In this study, relationships among the species of *Corimelaena* and the position of the genus within Thyreocoridae were evaluated using morphological data of adult and immature stages in a cladistic analysis. We aim to discuss the limits and relationships of the genus and its subgenera. In addition, the monophyly of the family, its subfamilies, as well most of thyreocorid genera was also tested. A phylogenetic classification was formulated based on the monophyletic groups recovered within Thyreocoridae.

Material and Methods

Taxon sampling

We include 40 species as terminal taxa in the current analysis: 36 species of the 12 genera of Thyreocoridae (including representatives of both subfamilies, Thyreocorinae and Corimelaeninae) in addition to four species representing the families/subfamilies Parastrachiidae (*Parastrachia japonensis* (Scott)), Cydnidae: Sehirinae (*Sehirus cinctus* Palisot de Beauvois), Canopidae (*Canopus caesus* (Germar)) and Plataspididae (*Coptosoma scutellatum* (Geoffroy)). *Coptosoma scutellatum* (Plataspididae) was chosen for character polarization and rooting of the cladograms, following Grazia *et al.* (2008).

Within Thyreocoridae, all genera are represented (Tabel 1); the availability of material determined when the genera was represented by more than one species in order to test monophyly. Whenever possible, terminal species within Thyreocoridae correspond to the type species of the genus or subgenus; some terminal species were chosen due to the availability of information on egg stage.

For a few species, only one sex could be examined: *Pruhleria incerta* (Uhler) (male), *Strombosoma unipunctatum* Amyot & Serville, and *Corimelaena (Parapora) californica* Van Duzee (female). Some *Corimelaena* species are known only by one of the sexes; when we were able to identify the other sex, this was included in the matrix: *Corimelaena (Parapora) parana* McAtee & Malloch and *Corimelaena (Parapora) virilis* (McAtee & Malloch) (female). Specimens of *Corimelaena (Epipora) signoretii* (McAtee & Malloch) were not examined; coding of the characters was based on the literature (McAtee & Malloch, 1933). For characters related to immature morphology and maternal behavior, coding was based exclusively on the literature, including data from other congeneric species for *S. cinctus* and *C. scutellatum* (Stokes, 1950; Paul, 1953; Lattin, 1955; Southwood, 1956; Cobben, 1968; McDonald, 1968; McPherson, 1971, 1972; Biehler & McPherson, 1982; Lung & Goeden, 1982; Sites & McPherson, 1982; Tachikawa & Schaefer, 1985; Davidová-Vilímová, 1987; Ren, 1992; Javahery, 1994; Filippi-Tsukamoto *et al.*, 1995a; Filippi-Tsukamoto, Nomakuchi & Tojo, 1995; Kight, 1995; Bundy & McPherson, 1997, 2009; Hironaka *et al.*, 2005; Matesco *et al.*, 2012).

Character sampling

A total of 114 characters were defined, including characters related to body coloration (19 characters) and morphology of the head (18), thorax (38), female and male abdomen, with external genitalia (32). Characters of immatures (6) and maternal behavior (1) were also used. Internal female and male genitalia were not addressed owing to scarcity of material, difficulties in dissection and preparation methods and interpretation of the structures.

Elaboration of character statements follows Sereno (2007). Ninety-three characters were coded as binary and 21 as multistate. All characters were treated as discrete, and multistate characters were treated as non-additive (Fitch, 1971). Characters and character states were scored in a data matrix using WinClada (Nixon, 2002). The symbols “?” and “-” were used for unobserved and noncomparable data, respectively.

Photographs and illustrations were taken using digital camera and camera lucida respectively, adapted to a stereomicroscope. Photographs were taken in different focal planes, and then stacked with Helicon Focus Lite 5.4.7 software. Drawings were edited with the software Adobe Illustrator®. Scanning electron microscopy photographs were obtained according to Matesco *et al.* (2012) and Matesco & Grazia (2013).

Cladistic analysis

Relationships were hypothesized using parsimony criteria. Character polarization followed the outgroup method (Nixon & Carpenter, 1993). A traditional search analysis with equal weighting was carried out in TNT (Goloboff, Farris & Nixon, 2008), using the following parameters: hold 10000 trees in memory; perform tree-bisection-reconnection (TBR) branch-swapping on 10000 replicates; hold 500 trees per replication. Absolute Bremer support values (Bremer, 1994) were calculated with TNT by TBR, retaining suboptimal trees with 10 extra steps. Visualization of cladograms and computation of descriptive indices (number of steps, retention index, and consistency index) were performed in WinClada. For the character discussion, we use the notation “$X^{[y]}$”, in which X represents the character and Y represents the state. The resulting strict consensus tree was used to document and discuss character transformation with unambiguous changes only and the classification proposed. Every additional step required is treated as homoplastic.

Results

Cladistic analysis

Full character list and data matrix are in Tables 2 and 3, respectively. Characters 32, 39, 43–45, 47, 50, 51, 70, 72, 83, and 94 were based on Grazia *et al.* (2008), characters 65–68 on Kment & Vilímová (2010a), and characters 108–112 and 114 on Matesco *et al.* (in press). The remainig characters are proposed and discussed for the first time in this work. Comments on the characters were made when considered necessary.

Characters

Color

1. Body, predominant color: (0) black; (1) castaneous; (2) red; (3) ocher.

2. Body, predominant color, pattern: (0) variegated; (1) uniform.

Characters 1 and 2. Froeschner (1960) states that the most common color in the cydnids is brownish black to black without conspicuous or important markings. In the Cydnidae *sensu* Dolling (1981), the prevailing color is black or brown without a conspicuous color pattern. The Thyreocoridae are known as the *negro bugs* (McAtee & Malloch, 1933), and all species are predominantly black (Figs. 1B-C), except for *Eumetopia fissipes* Westwood, which is predominantly ocher or mottled brown (Figs. 1A, 1D-E) (Dolling, 1981). However, only a few species are completely dark (uniform pattern) (Fig. 1B). Some species in the Sehirinae and Corimelaeninae have white, yellow or red spots, in strong contrast with the dark ground color (variegated pattern) (Figs. 1A, 1D-E, 2A-H) (Dolling, 1981). Those maculae have been used in taxonomic keys within Thyreocoridae, mainly for recognition at species level (e.g., within *Corimelaena* and *Galgupha*) (McAtee & Malloch, 1933) and are recognized as separated characters.

The predominant black color occurs in other groups out of Thyreocoridae (Plataspididae and Cydnidae), but the uniform coloration is a homoplasious synaphomorphy of the clade *Thyreocoris* and Corimelaeninae (node 6), with two important reversals: in the clade *Galgupha* in part and *Pruhleria* (node 15) and in the genus *Corimelaena* (node 20).

3. Thorax black variegated, pronotum, yellow lateral spot: (0) absent; (1) present.

4. Thorax black variegated, propleuron, yellow lateral spot: (0) absent; (1) present.

Characters 3 and 4. In most of the species with predominantly black color, the prothorax has the same pattern. However, in few species there is a submarginal pale strip near the anterolateral margin, on the pronotum or on the propleuron (Fig. 1G).

5. Thorax black variegated, scutellum, color: (0) completely dark; (1) posterior margin yellow; (2) posterior half yellow.

Character 5. In the predominantly black colored species, the scutellum may be completely dark or bear yellow markings; these markings occupy only the posterior margin or the posterior half of this structure.

6. Thorax black variegated, forewing, corium, color: (0) yellow; (1) black.

Character 6. In Thyreocoridae, as well as in other families within Pentatomoidea, the forewing (=hemelytron) consists of corium and membrane (Lis, 2002). The corium is the anterior coriaceous portion of hemelytron (Lis, 2002). Several predominantly black species display a yellow corium (Figs. 2A-E); in others the corium is black (Figs. 2F-H). Despite its predominant color, other spots can be present on the corium, which are considered independent characters.

7. Thorax, forewing, corium yellow, mescorium, black spot: (0) absent; (1) present.

8. Thorax, forewing, corium yellow, mesocorium, black spot, extent: (0) completely covering mesocorium; (1) confined to the apical half; (2) confined to the internal margin; (3) confined to the mesocorial vein.

Characters 7 and 8. According to Froeschner (1960), the corium is divided into clavus, next to the scutellum; mesocorium, between the clavus and the radial vein [corresponding to the endocorium (Nichols, 1989)]; and exocorium, between the radial vein and the costa. McAtee & Malloch (1933) do not provide a definition of their use of the terms meso- and exocorium, but in the illustration of the corium of *Galgupha (Gyrocnemis)* sp., they apparently divide these two areas according to the position of the cubital vein instead of the radial vein. Although poorly stated, we adopt the definition of McAtee & Malloch (1933) because it adapts better to the descriptions of color markings, since the cubital vein limits most of the spots on the corium.

In those species in which the corium is yellow, there can be a black spot on the mesocorium (Figs. 2A-E), which covers it completely (Figs. 2A-B) or is restricted to the apical half (Fig. 2C), to the internal margin (Fig. 2D) or covers only the mesocorial vein (Fig. 2E). The mesocorium entirely black is a homoplasious synapomorphy of the clade *C. agrella*, *C. harti* and *C. marginella* (node 27).

9. Thorax, forewing, corium yellow, exocorium, black spot: (0) absent; (1) present.

10. Thorax, forewing, corium yellow, exocorium, black spot, extent: (0) confined to the median third; (1) confined to the inner margin.

Characters 9 and 10. In those species with a yellow corium, the exocorium can have a black spot (Figs. 2B-C), which is confined to the median third (Fig. 2C) or covers only its inner margin (Fig. 2B). Some authors mention the yellowish exocorium as characteristic of the Thyreocoridae (e.g., Grazia *et al.*, in press). In our analysis, the exocorium completely yellow is a homoplasious synapomorphy of an internal clade within *Corimelaena* (node 22). The presence of a black spot confined to the inner margin of the exocorium is a nonhomoplasious synapomorphy to all species of *Corimelaena* except *C. interrupta*.

11. Thorax, forewing, corium black, costa, yellow margin: (0) present (Fig. 2F); (1) absent (Figs. 2G-H).

12. Thorax, forewing, corium black, base, yellow spot: (0) absent; (1) present.

13. Thorax, forewing, corium black, apex, yellow spot: (0) present; (1) absent.

Characters 12 and 13. In species with a black corium, a broad yellow spot (sometimes orange or reddish) can be present at the base of the corium, occupying part of the meso- and exocorium (Fig. 2G). Alternatively, a yellow spot can be present at the apex of the corium (Figs. 2F, 2H). Both spots rarely occur together but they are present in apparently unrelated species among different subgenera of *Galgupha* (McAtee & Malloch, 1933). In the analysis, the presence of the basal spot and the absence of the apical spot (corium apex black) are nonhomoplasious synapomorphies of the clade *Galgupha* in part and *Pruhleria* (node 15).

14. Abdomen black variegated, sternite VI, yellow lateral spot: (0) present; (1) absent.

15. Abdomen black variegated, sternite VII, yellow lateral spot: (0) present; (1) absent.

16. Abdomen black variegated, sternite VII, yellow lateral spot, shape: (0) strip; (1) semicircular.

17. Abdomen black variegated, sternite VII, yellow lateral spot, extent: (0) occupying the entire margin of the sternite; (1) not occupying the entire margin of the sternite.

18. Female, abdomen black variegated, laterotergites 8, yellow spot: (0) present; (1) absent.

Characters 14 to 18. Among the predominantly black species, yellow lateral spots in either one or more abdominal sternites can be present in the sternites VI (Figs. 3C-D, 3H), VII (Figs. 3A-D, 3H), and in the laterotergites 8 among females (Figs. 3A, 3C, 3H). It can occupy the entire margin of the sternite (Figs. 3A-D) or be confined to its middle third (Fig. 3H). The former condition is usually, but not exclusively, related to a spot in the shape of a strip (Figs. 3A-D) and the latter to a semicircular shaped spot (Fig. 3H).

The absence of those lateral yellow spots on sternites VI, VII and laterotergites 8 is a homoplasious synapomorphy of the clade *Carrabas* and *Strombosoma* (node 4). The absence of the spot on sternite VI is also a homoplasious synapomorphy of *Corimelaena* except *C. interrupta* (node 21). When present, a semicircular spot occupying part of the margin of the sternite is synapomorphic to the clade *Pruhleria*, *Psestophleps* and *Gyrocnemis* (node 16) and the spot occupying part of the margin of the sternite also supports the clade *Epipora* and *Parapora* (node 31).

19. Male, abdomen black variegated, pygophore, ventral surface, color: (0) black; (1) yellow.

Character 19. In black species, the ventral surface of the pygophore can display the same coloration (Fig. 3B) or be partially or completely yellow (Fig. 3D). This feature has been used in taxonomic keys, mainly for species recognition (McAtee & Malloch, 1933). The ventral surface of the pygophore yellow is a homoplasious synapomorphy of the clade containing *C. minuta* (node 25), with a reversal to a black pygophore in the clade *C. harti* and *C. marginella* (node 28).

Characters 3 to 19 were treated as inapplicable for the uniformly colored species.

Head

20. Clypeus and mandibular plates, sexual dimorphism: (0) absent; (1) present.

Character 20. In most Thyreocoridae species, as well as in most Pentatomoidea, male and female do not differ in terms of head morphology. In *Carrabas* and *Eumetopia* (Figs. 1D-E), however, male head presents a very striking shape of the clypeus and mandibular plates, while female head is more or less similar to the other thyreocorid species.

21. Area before the eyes, shape: (0) trapezoidal; (1) triangular.

Character 21. Most Thyreocoridae, including the species of *Galgupha*, have a broad head, usually truncate at apex, resembling trapezoidal in shape (Figs. 1E, 4A). On the other hand, in *Corimelaena* as well as in some other genera, the head is narrower, usually with an acute apex, giving it a triangular shape (Figs. 1F, 4C). The triangular outline of the head is an homoplasious synapomorphy for the clade *Godmania*, *Amyssonotum* and *Corimelaena* (node 18).

22. Anterior margin, degree of deflection: (0) not deflected; (1) deflected.

In some thyreocorids, the head is not deflected (Fig. 1G), whereas in others the anterior margin of the head in conspicuously deflected. A deflected head is synapomorphic to the clade Thyreocoridae, *Sehirus* and *Parastrachia* (node 1), with several reversals, including node 14.

23. Anterior margin, carina: (0) present; (1) absent.

Character 23. The anterior margin of the head can be emarginated, bearing a carina, or not. The absence of this carina is a homoplasious synapomorphy of *Corimelaena* (node 20), with a reversal to the presence of the carina in the clades *C. nigra* and *C. pulicaria* (node 24) and *Termapora*, *Epipora* and *Parapora* (node 30).

24. Clypeus, protuberance: (0) absent; (1) present.

Character 24. The apex of the clypeus in most Thyreocoridae is rounded or blunt (Fig. 1G). In some species of *Corimelaena*, the anterior tip of the clypeus is extended into a prominent process (Fig. 1F). A similar condition was described in some Reduviidae, a distantly related group, by Weirauch (2008). The presence of this protuberance is a homoplasious synapomorphy of an internal clade within *Corimelaena* (node 25).

25. Clypeus, apex, length compared to the mandibular plates: (0) sub equal; (1) longer; (2) shorter.

Character 25. In most thyreocorid genera, the clypeus attains the apex of the head (Fig. 4A), usually surpassing the mandibular plates (Figs. 1E-F, 4C). In a few species, including the Thyreocorinae, the clypeus is shorter and enclosed by the mandibular plates. In our analysis, the clypeus apex sub equal to the mandibular plates is a homoplasious synapomorphy of Corimelaeninae (node 7) and the apex of the clypeus longer than the mandibular plates is synapomorphic to the clade *Godmania*, *Amyssonotum* and *Corimelaena* (node 18).

26. Mandibular plates, apex, level compared to the level of clypeus: (0) at the same level; (1) at a higher level.

Character 26. In most Pentatomoidea, the apex of the mandibular plates is at the same level of the apex of the clypeus, when the head is observed in lateral view (Fig. 1G). Among the species sampled, only in the genera *Parastrachia* and *Carrabas*, the apex of the mandibular plates is at a higher level than the clypeus.

27. Mandibular plates, lateral margins, shape: (0) convex; (1) straight; (2) sinuate.

Character 27. The external or lateral margins of the mandibular plates can be either curved (=convex) (Figs. 1E, 4A), straight or sinuate (Figs. 1F, 4C). The condition found in every case has been described by McAtee & Malloch (1933), as important to the differentiation among thyreocorid species. The straight lateral margins of the mandibular plates are a homoplasious synapomorphy that supports a big clade within Thyreocoridae (node 11). The sinuate margins of the mandibular plates are synapomorphic to *Corimelaena* except *C. interrupta* and *C. lateralis* (node 22).

28. General punctuation: (0) present; (1) absent.

29. Punctation, density: (0) low, distance between two adjacent punctures greater than the diameter of one puncture; (1) high, distance between two adjacent punctures similar to the diameter of one puncture.

30. Area between the eye and the ocellus, punctuation: (0) absent; (1) present.

31. Occiput, punctuation: (0) absent; (1) present.

Characters 28 to 31. Within Thyreocoridae, all species display punctations on the head (Figs. 1D-F, 4A, 4C). In most species, the head is densely punctate (Figs. 1F, 4A) as opposed to some species in which the punctation is rather sparse (Figs. 1D-E, 4C). Even when the head is densely punctate, the presence of punctations in the area between the eye and the ocellus and at the occipital strip is variable. Those features are used as diagnostic at species level by McAtee & Malloch (1933).

The high density of the head punctation is a homoplasious synapomorphy of Thyreocoridae (node 3), with several reversals to a low density punctuation (29^0). The most important reversals support the monophyly of the subgenus *Galgupha* (node 13) and the clade *Galgupha* in part and *Pruhleria* (node 15). The presence of punctation in the area between the eye and the ocellus is synapomorphic to three groups: Thyreocoridae (node 3), the clade 23 within *Corimelaena (Corimelaena)*, and the clade 33 within *Corimelaena (Parapora)*. The absence of punctation in this area is synapomorphic to the clade 14 within Corimelaeninae.

32. Antenniferous tubercles, dorsal view, relation to the mandibular plates: (0) completely covered; (1) partially visible.

Character 32. This character was extracted from Grazia *et al.* (2008). According to the authors, the antenniferous tubercles placed ventrally on the head and partially obscured by the mandibular plates is found in most of the families of the Pentatomoidea. In Thyreocoridae and some other families (e.g., Canopidae, Plataspididae), the antenniferous tubercles are completely covered by the mandibular plates in dorsal view. In the present analysis, the antenniferous tubercles partially visible in dorsal view are synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

33. Bucculae, length compared to the length of the head: (0) short, not surpassing half of the head; (1) long, nearly reaching posterior margin.

Character 33. The bucculae in the Pentatomoidea vary from long, extending nearly to the posterior margin of the head (Fig. 1H), to short, not surpassing half of the head length. The long bucculae occurs in most Thyreocoridae and in *Canopus*, and the shortened bucculae is a more restricted condition. A very similar character has been used by Henry (1997) and Grazia *et al.* (2008).

34. Labium, segment I, length compared to the bucculae: (0) longer; (1) shorter.

35. Labium, segment I, length compared to the anterior margin of the prosternum: (0) not reaching; (1) reaching.

Characters 34 and 35. In most Thyreocoridae species, the first labium segment surpasses the bucculae and reaches the anterior margin of the prosternum, while the segment enclosed within the bucculae and not reaching the prosternum is a more restricted condition. In a few species, the segment I is longer than the bucculae but do not reach the prosternum (Fig. 1H).

36. Labium, segment II, length compared to the procoxae: (0) reaching; (1) surpassing; (2) not reaching.

Character 36. The second labial segment in most thyreocorids reaches the procoxae. In a few species it either does not reach the procoxae or surpasses them.

37. Rostrum, apex: (0) reaching metacoxae; (1) reaching urosternite III; (2) reaching mesocoxae.

Character 37. In the Thyreocoridae, the rostrum is usually middle sized, not shorter than the procoxae nor reaching the apex of the abdomen; its length, however, varies. The rostrum shorter, reaching mesocoxae, is a homoplasious synapomorphy of Corimelaeninae (node 7), with several reversals to the condition in which the rostrum apex reaches metacoxae, supporting *Gyrocnemis* and *Psestophleps* (node 17), *C. nigra* and *C. pulicaria* (node 24), and *C. extensa* and *C. virilis* (node 34). The apex of the rostrum reaching urosternite III is a homoplasious synapomorphy of *Godmania*, *Amyssonotum* and *Corimelaena* (node 18).

Thorax

38. Pronotum, lateral margins, shape: (0) convex; (1) straight.

Character 38. In most thyreocorids, the lateral margins of the protonum are convex (Figs. 1A-E). The shape of the lateral margins of pronotum is used as diagnostic feature in the key to species within *Corimelaena (Parapora)*. In the analysis, the lateral margins straight are synapomorphic to *Sehirus* and *Parastrachia* (node 2).

39. Pronotum, posterior angles, development: (0) developed; (1) not developed.

Character 39. In the Thyreocoridae, the pronotum is nearly rectangular, because neither the humeral nor the posterior angles are developed (Figs. 1A-E). According to *Grazia et al.* (2008), from whom this character has been adapted, this condition is found in most non-pentatomoid pentatomomorphans. The posterior angles not developed are a nonhomoplasious synapomorphy of the clade Thyreocoridae, *Sehirus* and *Parastrachia* (node 1).

40. Pronotum, rastration: (0) absent; (1) present.

41. Pronotum, rastration, extent: (0) restricted to the lateral area; (1) two posterior thirds.

Characters 40 and 41. Several thyreocorid species display deep markings at the pronotum, appearing to be originated by the irregular coalescence of punctures. These markings are more or less parallel and have been called rastrate by McAtee & Malloch (1933). In most species in which the pronotum is rastrate, these markings are restricted to the area near the cicatrices of the pronotum. Only in *Cydnoides* and *Amyssonotum*, they occupy the two posterior thirds of the pronotum. McAtee & Malloch (1933) used the pronotum decidedly rastrate posteriorly as diagnostic feature of *Amyssonotum* in their key to genera, but the authors do not consider the rastration a character of generic significance because it is more or less developed in other genera. The absence of rastration supports the nodes 8 (*Eumetopia*, *Alkindus* and *Pericrepis*) and 30 (*Termapora*, *Epipora* and *Parapora*).

42. Propleuron, punctuation: (0) absent; (1) present.

Character 42. In some thyreocorid species, the propleurum is coarsely punctate throughout (e.g., *Thyreocoris*), while in others a considerable portion of its extent is impunctate (e.g., most Corimelaeninae) (McAtee & Malloch, 1933). The absence of punctation in the propleuron is a homoplasious synapomorphy of *A. crassicosta* and *P. callosula* (node 10).

43. Prosternum, sulcus: (0) present; (1) absent.

Character 43. A similar character has been used by Grazia *et al.* (2008), considering the presence of the prosternal sulcus as restricted to a few families within Pentatomoidea. In all Thyreocoridae species, the prostenum is sulcate as to accommodate the rostrum (Fig. 1H). In the present analysis, the absence of this sulcus is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

44. Prosternum, carinae: (0) absent; (1) present.

45. Prosternum, carinae, degree of development: (0) strongly carinate, completely surrounding the rostrum; (1) moderately carinate, not surrounding completely the rostrum.

46. Prosternum, carinae, direction: (0) parallel-sided; (1) flaring anteriorly.

Character 44 to 46. At each side of the prosternal sulcus, there is an elevated carina (Fig. 1H). Among our terminal species, only in *Coptosoma scutellatum* the sulcus is present while the carinae are absent. The presence and the degree of development of the prosternal carina were treated in a single character by Grazia *et al.* (2008). The authors considered the strongly carinate prosternum as found in restricted families within Pentatomoidea. Among the Thyreocoridae, the carinae can be either strongly developed (Fig. 1H), surpassing the rostrum in height in lateral view, or moderately developed, not surpassing the rostrum in height. Independently of its degree of development, the carinae can be either parallel-sided (straight) (Fig. 1H) or flaring anteriorly ("V"-shaped). McAtee & Malloch (1933) use the prosternal sulcus parallel-sided as taxonomic character for *Thyreocoris* in their key to genera.

In the analysis, the carinae moderately developed supports the monophyly of Corimelaeninae (node 7), with a reversal supporting an apical clade within *Corimelaena* (*Parapora*) (node 33). The carinae flaring anteriorly is synapomorphic to Corimelaeninae (node 7), with reversals in the subgenera *Galgupha* (node 13) and *Parapora* (node 33).

47. Scutellum, length in relation to the urosternites: (0) surpassing VII; (1) reaching VII; (2) reaching V.

Character 47. Along with the predominantly black color and the ovoid shape, the scutellum covering most, or all, of the abdomen (Figs. 1A-C) is one of the characters of Thyreocoridae highlighted by McAtee & Malloch (1933). A similar character has been used by Grazia *et al.* (2008), who considered the condition found in Canopidae and Plataspididae different from that found in Thyreocoridae. In the present analysis, the scutellum short, reaching only urosternite V, is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

48. Scutellum, shape: (0) broadly rounded; (1) triangular.

Character 48. According to Dolling (1981), in a number of Pentatomoidea including some Cydnidae, development of the scutellum surpasses the usual pentatomoid type and it is modified into a large shield of rounded outline largely concealing the abdomen and at least part of the hemelytra at rest. The triangular scutellum is present in a number of cydnid species, including the Sehirinae, whereas the scutellum semi to sub-circular, broadly rounded in outline, is present in Thyreocorinae and Corimelaninae (Figs. 1A-C). In the present analysis, the triangular scutellum is a synapomorphy of the clade *Sehirus* and *Parastrachia* (node 2).

49. Scutellum, margin: (0) emarginated; (1) not emarginated.

Character 49. In our analysis, the scutellum is emarginated only in *Canopus* and *Coptosoma*. The scutellum not emarginated is therefore a nonhomoplasious synapomorphy of Thyreocoridae, *Sehirus* and *Parastrachia* (node 1).

50. Scutellum, frena: (0) absent; (1) present.

51. Scutellum, frena, length in relation to the length of scutellum: (0) long, surpassing middle of scutellum; (1) short, not surpassing middle of scutellum.

Characters 50 and 51. The presence and degree of development of the frena were used as a single character by Grazia *et al.* (2008). The authors stated their absence in some families, as the Canopidae and Plataspididae. In the present analysis, the presence of the frena is synapomorphic to the clade Thyreocoridae, *Sehirus* and *Parastrachia* (node 1).

52. Forewing, corium, length in relation to the urosternites: (0) reaching IV; reaching V; (2) reaching VI.

Character 52. Extent of the exposed corium in relation to the abdominal sternites is used as diagnostic feature in the key differentiating *Thyreocoris*, *Carrabas* and *Strombosoma* (McAtee & Malloch, 1933). In *Carrabas* and *Strombosoma*, the corium attains only the IV segment, while it is longer in *Thyreocoris*.

53. Forewing, clavus, length: (0) short, not surpassing middle of scutellum; (1) elongate, surpassing middle of scutellum.

Character 53. Based on the statement of McAtee & Malloch (1933), the Thyreocoridae may be separated from the Cydnidae by the exposure of the clavus. In the Thyreocoridae, it is very short, briefly triangular and does not extend much beyond the base of the scutellum (Figs. 2A-E, 2G-H, 4B, 4D); in the Cydnidae, it is elongate and reaches to, or almost to, the apex of the scutellum (Fig. 2F), with a corresponding prolongation of the groove in the side of the scutellum in which it rests. In the present analysis, the elongate clavus is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

54. Forewing, corium, apex, shape: (0) acute; (1) rounded; (2) truncate.

Character 54. McAtee & Malloch (1933) included the shape of the corium at apex as diagnostic feature in their keys to the subgenera of *Galgupha* and to the species of *Corimelaena (Corimelaena)*. In the Thyreocoridae, the corium apex can be either acute (pointed) (Figs. 2A, 2C, 4B), rounded (Figs. 2B, 2D-E, 2H, 4D) or truncate (Figs. 2F-G). The apex of the corium rounded is a homoplasious synapomorphy to the clade *Godmania*, *Amyssonotum*, and *Corimelaena* (node 18) and the apex of the corium truncate is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

55. Forewing, corium, mesocorial vein: (0) absent; (1) present.

Character 55. McAtee & Malloch (1933) used to a great extent the venation of the hemelytra in their generic, subgeneric, and specific differentiations. The authors consider that the genera *Galgupha*, *Amyssonotum*, and *Alkindus* have the most complete venation, while *Pruhleria* and *Corimelaena* have the greatest reduction. However, *Corimelaena* spp. have the mesocorial vein much more developed than is the case in any other genus of Thyreocoridae. In *Pruhleria*, on the other hand, the mesocorial vein is entirely lacking (McAtee & Malloch, 1933).

The mesocorium with a vein paralleling scutellum and connivent, or nearly so, posteriorly with cubitus (Figs. 2A-B, 2D-E, 2G-H, 4D) is a feature present in the genera *Godmania* and *Corimelaena*. Most other genera lack this vein (Figs. 2C, 4B), except for some subgenera of *Galgupha*. The presence of the mesocorial vein is a homoplasious synapomorphy of the clade *Godmania*, *Amyssonotum* and *Corimelaena* (node 18).

56. Forewing, corium, exocorial vein (radial + mesial veins): (0) absent; (1) present.

57. Forewing, corium, exocorial vein, base: (0) deeply impressed; (1) evanescent.

58. Forewing, corium, exocorial vein, inner branch (mesial vein): (0) apparent; (1) obsolete.

59. Forewing, corium, exocorial vein, outer branch (radial vein): (0) apparent; (1) obsolete.

Characters 56 to 59. According to Wootton & Betts (1986), the radial vein and median vein fused for some distance from the wing base, but diverging before the corium margin, is a common character in extant Heteroptera. Within Cydnidae, Lis (2002) observed that, in species of *Sehirus*, the radial vein (R) is entirely coalescent with the median vein (M) in their basal half, the apical part of the median vein is clearly visible, and the cubital vein is widely separated from R+M. The same author states that non-coalescence of M with R is more likely plesiomorphic to coalescence, and he could observe several steps of the fusion of M with R. An intermediate derived state would be M coalescent with R in the basal third, which is present in several cydnids, including *Sehirus* (Fig. 2F), and *Dismegistus* (currently Parastrachiidae).

McAtee & Malloch (1933) mention the presence of an exocorial vein, usually divided in an inner and an outer branch. In comparison with the interpretation of the venation in Cydnidae by Lis (2002), we consider the outer branch of the exocorial vein to be the radial vein and the inner branch to be the median vein. Among the thyreocorids, the exocorial vein is usually present (Figs. 2C, 2G, 4B), but is obsolete or almost so in the genera *Godmania* and *Corimelaena* (Figs. 2A-B, 2D-E, 2H, 4D) (McAtee & Malloch, 1933). In some species in which the exocorial vein is present, its base is as deeply impressed as the cubital vein (Figs. 2C, 2F, 2G), as in the subgenera *Galgupha*, *Gyrocnemis*, and *Euryscytus* of *Galgupha*. In others, it is characteristically evanescent, as in the subgenera *Astiroderma* and *Psestophleps* of *Galgupha*. Either the outer or the inner branch can be obsolete or well developed.

The presence of an exocorial vein is a homoplasious synapomorphy of the clade Thyreocoridae, *Sehirus* and *Parastrachia* (node 1). The inner branch of the exocorial vein obsolete is a homoplasious synapomorphy for the clade *Carrabas* and *Strombosoma* (node 4).

60. Forewing, area between the costa and the exocorial vein, degree of elevation: (0) not elevated; (1) elevated.

Character 60. In most thyreocorid species, the area between the costa and the exocorial vein is at the same plane as the rest of the corium. In *Alkindus* and *Pericrepis*, as well as in some subgenera of *Galgupha*, this part of the corium is clearly elevated. In the analysis, the elevation of the area between the costa and the exocorial vein is a nonhomoplasious synapomorphy of the clade *Alkindus* and *Pericrepis* (node 9).

61. Forewing, corium, costa, shape: (0) rounded; (1) carinate.

Character 61. In a lateral view of the corium, the costa is either rounded or bears a carina. In their key to the genera of Thyreocoridae, McAtee & Malloch (1933) distinguish *Godmania* from *Corimelaena* by the costa carinate in the former opposed to a rounded costa, lacking a carina, in the latter. The rounded shape of the costa is a homoplasious synapomorphy of *Corimelaena* (node 20).

62. Metapleuron, lateral area to evaporatorium, punctuation: (0) present; (1) absent.

Character 62. In those species in which the evaporatorium does not reach the lateral margin of the metapleuron, there is a glossy lateral portion. The presence of punctation in this area (Fig. 5A) is variable; some genera are defined by the lateral area impunctate (McAtee & Malloch, 1933). The absence of punctation laterad to the metapleural evaporatorium is a homoplasious synapomorphy of the clade *Cydnoides* and subgenus *Galgupha* (node 12).

63. External scent efferent system, mesopleuron, pseudoperitreme: (0) absent; (1) present.

Character 63. The pseudoperitreme, a mesopleural structure functioning as a prolongation of the metapleural peritreme, is present in representatives of the Thyreocoridae, Cydnidae, and Plataspididae (Kment & Vilímová, 2010b). It has been previously described in *Thyreocoris scarabaeoides*, *Galgupha (Gyrocnemis) impressa* and *Alkindus* spp. (Fig. 5A) (Kment & Vilímová, 2010b; Matesco & Grazia, 2013). In our analysis, the presence of a pseudoperitreme is a nonhomoplasious synapomorphy of the Thyreocoridae (node 3).

64. External scent efferent system, metapleuron, evaporatorium, extent in relation to the lateral margin of the segment: (0) clearly reaching; (1) scarcely attaining.

Character 64. In their key to genera, McAtee & Malloch (1933) distinguish *Thyreocoris* from the other genera of Thyreocoridae by the metapleural evaporatorium extending clear to the lateral margin of the metapleurum. In the remaining genera (Corimelaeninae), the evaporatorium scarcely attains the lateral margin of the metapleurum (Fig. 5A), being separated from it by a glossy portion.

65. External scent efferent system, metapleuron, ostiole, position: (0) laterad, placed in the middle of metapleuron; (1) basal, between meso- and metacetabulum.

Character 65. This character has been adapted from the analysis of Tessaratomidae (Kment & Vilímová, 2010a). The basal position of the ostiole occurs in some groups of Pentatomoidea; the lateral position occurs in Thyreocoridae, among other families (Fig. 5A). In our analysis, the basal position of the ostiole in the metapleuron is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

66. External scent efferent system, metapleuron, peritreme, shape: (0) spout; (1) auricle; (2) disc; (3) groove.

Character 66. According to Kment & Vilímová (2010b), there are six basic shapes of peritreme in the Pentatomoidea. However, they assume that at least some of these types evolved several times independently. This character has been previously used by Kment & Vilímová (2010a). In all thyreocorids, the peritreme is groove-shaped (Fig. 5A), a condition also present in representatives of the Pentatomidae and Scutelleridae (Kment & Vilímová, 2010b).

67. External scent efferent system, evaporatorium, extent: (0) very large, covering pro-, meso-, and metapleuron; (1) well developed, covering both meso- and metapleuron; (2) reduced, covering metapleuron only.

Character 67. The evaporatorium is always present on metapleuron, surrounding the ostiole and peritremal surface, and extending onto mesopleuron, rarely even onto propleuron. This character has been used by Kment & Vilímová (2010a). The evaporatorium well-developed both on the meso- and metapleuron (Fig. 5A) occurs in many groups within the Pentatomoidea, the state being reduced several times independently. A very large evaporatorium extending on the prothorax would be exclusive of the Plataspididae.

68. External scent efferent system, metapleuron, evaporatorium, gyrification, development: (0) present in form of low wrinkles and furrows; (1) not developed, evaporatorium smooth.

Character 68. The surface of evaporatorium can have a pattern of shallow to deep furrows and low to high wrinkles, resembling the brain surface. This macrosculpture, termed gyrification, has been described in several species of the Pentatomoidea. This character has been previously used by Kment & Vilímová (2010a). In our analysis, the absence of gyrification in the metapleural evaporatorium is a nonhomoplasious synapomorphy of the clade *Sehirus* and *Parastrachia* (node 2).

69. Metasternum, median projection: (0) absent; (1) present.

Character 69. The presence of a median projection at the posterior margin of the metasternum, projecting posteriorly between the metacoxae (Fig. 5B), is extremely variable within Thyreocoridae. In the analysis, its presence is a homoplasious synapomorphy for the clades *Thyreocoris* and Corimelaeninae (node 6), *C. nigra* and *C. pulicaria* (node 24), and *Corimelaena (Parapora)* except *C. parana* (node 33). The absence of the median projection of the metasternum supports the clade *Amyssonotum* and *Corimelaena* (node 19).

70. Legs, coxae, coxal combs: (0) absent; (1) present.

Character 70. The presence of a comb-like row of flattened setae at the apices of the mid and hind coxae distinguishes Cydnidae and Thyreocoridae from the other pentatomoids (McAtee & Malloch, 1933; Froeschner, 1960; Dolling, 1981). Dolling (1981) considered that this structure is universal in the Cydnidae (including Thyreocoridae, and Thaumastellidae) and is unknown elsewhere in the Heteroptera. The same character has been used in previous cladistic analyses of Pentatomoidea (Gapud, 1991; Grazia *et al.*, 2008). Lis (2010a) provided a formal definition of the coxal combs, indicated its presence in all coxae, and confirmed its occurrence in all families of the "cydnoid" complex (i.e., Cydnidae *sensu lato*, Parastrachiidae, Thaumastellidae, and Thyreocoridae).

In our analysis, the presence of the coxal combs (Fig. 5B) is a nonhomoplasious synapomorphy of the clade Thyreocoridae, *Sehirus* and *Parastrachia* (node 1).

71. Legs, fore femora, lateral margin, row of spines: (0) absent; (1) present.

Character 71. Several leg characters have been used to segregate groups and individual species of Thyreocoridae in the keys of McAtee & Malloch (1933). The presence of the ventral armature of the fore femora in *Galgupha* is of value in distinguishing certain subgenera (McAtee & Malloch, 1933). In the analysis, the presence of a row of spines in the fore femora, although homoplastic, is synapomorphic to the subgenus *Galgupha* (node 13).

72. Legs, fore tibiae, lateral margin, row of spines: (0) absent; (1) present.

Character 72. McAtee & Malloch (1933) state that both Thyreocoridae and Cydnidae have distinct tibial bristles. According to Froeschner (1960), the leg armature may be simply an adaptative feature for the fossorial habits of these insects and not at all an indicator of phylogenetic relationships. However, Dolling (1981) noted that the tibiae of the Cydnidae (including Thyreocoridae) are furnished with stout spines which are presumed to assist in the burrowing activities of the bugs, but are well developed even in non fossorial species. Grazia *et al.* (2008), which applied this character to the phylogeny of Pentatomoidea, found a row of stout setae on the lateral margins of the fore tibiae only in the Cydnidae, Thaumastellidae, and Thyreocoridae. In the present analysis, the presence of a row of spines at the lateral margin of the fore tibiae is a homoplasious synapomorphy of the clades *Thyreocoris* and Corimelaeninae (node 6) and *C. extensa* and *C. virilis* (node 34).

73. Legs, hind tibiae, dorsally, shape: (0) cylindrical; (1) flattened; (2) sulcate.

Character 73. The conformation of the hind tibiae, whether sulcate or nonsulcate dorsally, is of value (McAtee & Malloch, 1933). In *Thyreocoris*, all tibiae are sulcate dorsally; in *Alkindus* and *Amyssonotum* the hind tibiae are flattened or sulcate dorsally. In the other genera, tibiae are in most cases cylindrical (McAtee & Malloch, 1933). In the analysis, the hind tibiae dorsally sulcate support the monophyly of the genus *Strombosoma* (node 5).

74. Legs, hind tibiae, posterior surface, carina: (0) absent; (1) present.

Character 74. In many species of the genus *Amyssonotum*, *Cydnoides* and *Galgupha*, there is a carina or raised line on the posterior, or inner, surface of the hind tibiae (McAtee & Malloch, 1933). The presence of a carina at the posterior surface of the hind tibiae, although homoplasious, supports the monophyly of *Cydnoides* and *Galgupha* (*Galgupha*) (node 12).

75. Legs, hind tibiae, posterodorsal bristles: (0) absent; (1) present.

Character 75. The posterodorsal armature of the hind leg is of value, especially within the subgenus *Parapora* of *Corimelaena* (McAtee & Malloch, 1933). The presence of posterodorsal bristles in the hind tibiae is a homoplasious synapomorphy of the clades *Thyreocoris* and Corimelaeninae (node 6) and *C. extensa* and *C. virilis* (node 34), with a reversal supporting an internal clade within *Corimelaena* (node 29).

Abdomen

76. Sternites III-VII, lateral bristles: (0) absent; (1) present.

Character 76. Strong, dark, lateral bristles are frequently present in thyreocorid species. One or two bristles on each side laterad of the trichobothria are present in *Alkindus* (Fig. 5C), *Amyssonotum*, *Cydnoides*, *Galgupha*, and *Godmania*. Sternites are mostly without lateral bristles in *Corimelaena*, *Pericrepis*, and *Pruhleria*. The presence of lateral bristles in the abdominal sternites III to VII is a homoplasious synapomorphy of the Corimelaeninae (node 7) and its absence supports the monophyly of *Corimelaena* (node 20) and the clade *Pericrepis* and *Alkindus crassicosta* (node 10).

77. Sternite II, spiracles, placement: (0) in the heavily sclerotized portion; (1) in the membranous anterior strip of the sternite.

Character 77. The anterior part of the second abdominal segment, including its spiracles, is membranous and usually concealed from view in the Cydnidae and Thyreocoridae (Froeschner, 1960; Dolling, 1981). Along with the presence of fringes of bristles in the apices of the coxae, the placement of the spiracles of the abdominal segment II in a membranous anterior strip of the sternite distinguishes Cydnidae and Thyreocoridae from the other pentatomoids (McAtee & Malloch, 1933).

78. Sternites III-VII, spiracles, callus: (0) present; (1) absent.

Character 78. In a few thyreocorid species, there is a callus surrounding the spiracles. In our analysis, the presence of a callus surrounding the spiracles in the abdominal sternites III to VII is not unique, but supports the monophyly of the genus *Strombosoma* (node 5).

79. Sternites V-VII, spiracles, placement: (0) closer to the trichobothria; (1) closer to the lateral margin.

Character 79. The spiracles are nearer to the lateral margins of sternites than to the trichobothria at least on segments V to VII in the genera *Godmania* and *Corimelaena* (Figs. 4F, 4H). In other thyreocorid genera, the spiracles are nearer to the trichobothria (Figs. 4E, 4G, 5C). McAtee & Malloch (1933) used this feature as diagnostic at genus level within the Thyreocoridae.

80. Sternite IV, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral; (2) dorsal.

81. Sternite V, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral.

82. Sternites VI-VII, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral.

Characters 80 to 82. A similar character has been used by Henry (1997) in his analysis of the Pentatomomorpha. According to the author, most Pentatomoidea have ventral abdominal spiracles. The differential position of the spiracles on sternites IV to VII is the basis for the division of *Corimelaena* spp. into four subgenera by McAtee & Malloch (1933).

In the present analysis, the spiracles of the IV and V sternites in a lateral position (Figs. 3H, 4F) are nonhomoplasious synapomorphies of the clade *Epipora* and *Parapora* (node 31). The spiracles of the VI and VII sternites in a lateral position (Figs. 3H, 4F, 4H) are a nonhomoplasious synapomorphy of the clade *Termapora*, *Epipora* and *Parapora* (node 30).

83. Sternites III-VI, trichobothria, placement: (0) longitudinal; (1) transverse.

Character 83. The trichobothria usually occur in pairs, sublaterally on abdominal sternites III to VII. Their disposition may be parallel to the body axis (=longitudinal) (Figs. 4E-H, 5C) or transverse (Dolling, 1981). According to McAtee & Malloch (1933), members of the Cydnidae and Thyreocoridae, with the exception of the Sehirinae, have the trichobothria longitudinally arranged, often nearly in line with the spiracles. In other families of the Pentatomoidea, the trichobothria are arranged transversely, or nearly so, behind the spiracles. Froeschner (1960), on the other hand, states that there are at least five trichobothrial patterns within Cydnidae. This character has been previously used by Grazia *et al.* (2008).

Female abdomen

84. Sternite VII, anterior margin, shape: (0) rounded; (1) subangulate.

Character 84. The anterior margin of the VII sternite subangulate in the female (Figs. 3A, 3C, 4F) supports two clades: *Carrabas* and *Strombosoma* (node 4) and an internal clade within Corimelaeninae (node 14). The reversal to the rounded shaped margin supports the clade *Gyrocnemis* and *Psestophleps* (node 17).

85. Sternite VII, posterior margin, caudal median projection: (0) absent; (1) present.

Character 85. In some species of *Corimelaena*, there is a median projection, caudally directed, at the posterior margin of the sternite VII. The presence of the caudal median projection of the posterior margin of the VII sternite is a homoplasious synapomorphy of the clade *C. extensa* and *C. virilis* (node 34).

86. Gonocoxites 8, punctuation: (0) present; (1) absent.

Character 86. In the Thyreocoridae, the gonocoxites 8 are usually punctuated (Figs. 3A, 3C, 3H, 4E-F). The absence of punctation on the gonocoxites 8 supports the relationship between *Sehirus* and *Parastrachia* (node 2).

87. Gonocoxites 8, posterior margins, shape: (0) straight; (1) convex; (2) concave.

Character 87. The posterior margins of the gonocoxites 8 straight (Fig. 3A) is homoplasiously synapomorphic to *Corimelaena* except *C. interrupta* (node 21). The convex shape of the posterior margins (Fig. 3C) supports an internal clade within *Corimelaena* (node 25) and the concave shape (Figs. 3H, 4E-F) is synapomorphic to the clade *C. (E.) signoretii* and *C. (P.) parana* (node 32).

88. Gonocoxites 8, posterior margins, position: (0) transverse; (1) oblique.

89. Gonocoxites 8, posterior margins oblique, direction: (0) posterior; (1) anterior.

Characters 88 and 89. The posterior margins of the gonocoxites 8 can be either transverse (Figs. 3A, 4E-F) or oblique (Fig. 3C). When oblique, they can be directed anteriorly (Fig. 3C) or posteriorly. The oblique position of the posterior margins of the gonocoxites 8 supports three clades: *Pericrepis* and *A. crassicosta* (node 10), *Gyrocnemis* and *Psestophleps* (node 17), and *Parapora* except *C. (P.) parana* (node 33).

90. Gonocoxites 8, sutural margins, ventral elevation: (0) absent; (1) present.

91. Gonocoxites 8, sutural margins, ventral elevation, degree of development: (0) slight; (1) strong.

92. Sternite VII, posterior margin, ventral elevation: (0) absent; (1) present.

Characters 90 to 92. In several species within Thyreocoridae, the sutural margins of the gonocoxites 8 are elevated ventrally (Fig. 4E), either slightly or strongly developed. McAtee & Malloch (1933) used this feature in their key to thyreocorid genera, separating *Alkindus* from *Amyssonotum* and *Pericrepis* from *Pruhleria*, based on the presence of this acute elevation in *Alkindus* and *Pericrepis*. In a few species, the posterior margin of the sternite VII is also elevated, accompanying the gonocoxites 8. The absence of the ventral elevation of the sutural margins of the gonocoxites 8 supports an internal clade within Corimelaeninae (node 11). The presence of a ventral elevation at the posterior margin of the VII sternite is synapomorphic to clade *Pericrepis* and *A. crassicosta* (node 10).

93. Laterotergites 8, posterior margins, shape: (0) straight; (1) sinuate.

Character 93. Shape of the posterior margins of the laterotergites 8 varies from straight (Fig. 3C, 4E-F) to sinuate (Fig. 3A). The posterior margins of the laterotergites 8 sinuate are a nonhomoplasious synapomorphy of the clade *Parapora* except *C. (P.) parana* (node 33).

94. Laterotergites 9, sutural margins, position in relation to each other: (0) contiguous; (1) not contiguous.

Character 94. In *Thyreocoris*, the laterotergites 9 are separated by the segment X and the gonocoxites 9 at base (Stys & Davidová, 1979). Within Corimelaeninae, the laterotergites 9 are contiguous or almost so in front (Fig. 3A, 3C, 4E-F) (McAtee & Malloch, 1933). This character has been previously described by Grazia *et al.* (2008), stating that both conditions are widespread among Pentatomoidea. In the present analysis, the sutural margins of the laterotergites 9 contiguous to each other are a homoplasious synapomorphy of the Corimelaeninae (node 7).

95. Laterotergites 9, shape: (0) triangular; (1) lanceolate.

Character 95. In most thyreocorids, the laterotergites 9 are well developed and triangular (Fig. 4E). In a few genera, they are rather small and lanceolate (Fig. 3A, 3C, 3H, 4F). The laterotergites 9 lanceolate are a homoplasious synapomorphy of the clade *Amyssonotum* and *Corimelaena* (node 19).

Male abdomen

96. Sternite VII, anterior margin, shape: (0) subangulate; (1) rounded; (2) angulate.

Character 96. Shape of the anterior margin of the VII sternite is used in differentiation among thyreocorid species by McAtee & Malloch (1933). The anterior margin of the VII sternite angulate in males (Figs. 3B, 4H) is a homoplasious synapomorphy of Thyreocoridae (node 3). The anterior margin rounded (Fig. 4G) is synapomorphic to the clade *Alkindus* and *Pericrepis* (node 9). The subangulate anterior margin (Fig. 3D) supports two groups: *Cydnoides* and *Galgupha (Galgupha)* (node 12) and *Pruhleria*, *Psestophleps* and *Gyrocnemis* (node 16).

97. Pygophore, ventral surface, transverse groove: (0) absent; (1) present.

Character 97. The ventral surface of the pygophore channeled is present in several thyreocorid species and has been used in taxonomic keys, mainly for recognition at species level (McAtee & Malloch, 1933). The absence of the transverse groove in the pygophore's ventral surface supports the clades *Carrabas* and *Strombosoma* (node 4) and *Pruhleria*, *Psestophleps* and *Gyrocnemis* (node 16).

98. Pygophore, ventral surface, punctuation: (0) present; (1) absent.

Character 98. Presence of punctation on the ventral surface of the pygophore (Figs. 3B, 3D, 4G-H) varies in the Thyreocoridae. The absence of punctation in the ventral surface of the pygophore is a homoplasious synapomorphy of the clade *C. harti* and *C. marginella* (node 28).

99. Pygophore, ventral rim, relation to the proctiger in ventral view: (0) not covering; (1) covering.

Character 99. In Thyreocoridae, the ventral surface of the pygophore is usually long enough as to cover the proctiger in ventral view (Figs. 3B, 3D, 4G-H). The ventral rim of the pygophore not covering the proctiger in ventral view is synapomorphic to the clades *Carrabas* and *Strombosoma* (node 4) and *C. agrella*, *C. harti* and *C. marginella* (node 27).

100. Pygophore, ventral rim, median third, outline: (0) convex; (1) straight; (2) concave.

Character 100. The shape of the ventral rim is considered the most important character to identify species among Thyreocoridae (McAtee & Malloch, 1933). The median third of the ventral rim of the pygophore convex (Fig. 3B, 3D, 4G-H) is a homoplasious synapomorphy of two clades: the subgenus *Galgupha* (node 13) and *Amyssonotum* and *Corimelaena* (node 19). The median third of the ventral rim of the pygophore concave is a homoplasious synapomorphy of the clade *C. harti* and *C. marginella* (node 28).

101. Pygophore, ventral rim, tumescence: (0) present; (1) absent.

Character 101. The presence of tumescence at the ventral rim of the pygophore (Fig. 3D) is a homoplasious synapomorphy of an internal clade within *Corimelaena* (node 26).

102. Pygophore, ventral rim, deflection: (0) not deflected; (1) deflected.

Character 102. The ventral rim of the pygophore not deflected is a homoplasious synapomorphy of an internal clade within *Corimelaena* (node 25).

103. Pygophore, dorsal rim, shape: (0) sloping inwardly; (1) flat; (2) excavated.

Character 103. The conformation of the dorsal rim of the pygophore is regarded by McAtee & Malloch (1933) as of considerable importance for the recognition of species and has been used by the authors in their keys to the Thyreocoridae. This feature is especially important in differentiating species of the subgenus *Parapora*.

104. Pygophore, dorsal rim, internal face, carina: (0) present; (1) absent.

105. Pygophore, dorsal rim, internal face, carina, shape: (0) convex; (1) straight.

Characters 104 and 105. The presence and shape of the carina at the internal face of the dorsal rim of the pygophore is used as diagnostic feature within *Corimelaena (Parapora)* (McAtee & Malloch, 1933). The absence of such carina is a homoplasious synapomorphy of the Thyreocoridae (node 3). The presence of the carina (Figs. 3E-G) is a homoplasious synapomorphy of the clade *Termapora*, *Epipora* and *Parapora* (node 30).

106. Pygophore, dorsal rim, internal face, carina, lateral elevations: (0) absent; (1) present.

Character 106. Associated with the carina at the dorsal rim of the pygophore, there can be a pair of lateral elevations (Fig. 3F), which are also used in differentiating species of *Parapora* (McAtee & Malloch, 1933).

107. Pygophore, parameres, degree of exposure: (0) completely exposed; (1) partially exposed; (2) not exposed, covered by the proctiger.

Character 107. In the dorsal surface of the pygophore of the Thyreocoridae, there is always a conspicuous depression in which lie the tips of the parameres, usually covered by the proctiger, but sometimes projecting to some degree (Fig. 3G) (McAtee & Malloch, 1933). The parameres partially exposed is a homoplasious synapomorphy of the Thyreocoridae (node 3). The parameres not exposed (Fig. 3E-F) is a homoplasious synapomorphy of the Corimelaeninae (node 7).

Immatures

108. Egg, chorion sculpture, pattern: (0) reticulate; (1) smooth; (2) granulate.

Character 108. Chorion sculpture varies within Heteroptera and bears taxonomic value both at generic and specific levels (Cobben, 1968; Candan, Suludere & Açikgöz, 2005; Matesco *et al*., 2009). Most non-Pentatomidae groups have smooth chorion, as *Sehirus*, *Parastrachia* and most species of Thyreocoridae (Fig. 5D). The chorion surface in some Thyreocoridae species is described as granulate (Fig. 5E). In Plataspididae, the reticulate chorion is the most common pattern. This character has been previously explored by Hasan & Kitching (1993), Javahery (1994), and Matesco *et al*. (in press).

109. Egg, aero-micropylar process, insertion: (0) pedunculate; (1) not pedunculate.

Character 109. Pentatomoid eggs are marked at the cephalic end by a ring of aero-micropylar processes. Their form varies in relation to genus and family (Javahery, 1994). In most pentatomoids, they are pedunculate (Fig. 5F). Sessile processes are present in *Sehirus* as well as other groups (e.g., within Scutelleridae). This character has been suggested by Matesco *et al*. (in press) based on the character described by Javahery (1994).

110. Oviposition, pattern: (0) in masses; (1) singly.

Character 110. Oviposition strategy varies in the Pentatomoidea, although the number of ovarioles is relatively conserved among species of different families (Javahery, 1994). In most pentatomoids, eggs are deposited in one or more masses during a females' life time. In a few scattered species and in all the thyreocorids studied so far, eggs are oviposited singly (Fig. 3I). This character has been suggested by Matesco *et al.* (in press) based on Javahery (1994).

111. Oviposition, position of the egg in relation to the substrate: (0) upright; (1) unstructured; (2) lengthwise.

Character 111. In Pentatomoidea, most species deposit their eggs in an upright position in relation to the substrate. Most cydnids and *P. japonensis*, lay eggs in a round mass, with eggs in different positions. The thyreocorids deposit their eggs lengthwise in relation to the substrate (Fig. 3I). This character has been suggested by Matesco *et al.* (in press).

112. Oviposition, site: (0) on plants; (1) in the soil.

Character 112. Several pentatomoids oviposit on plants, as the Plataspididae and Thyreocoridae (Fig. 3I). Species of Sehirinae and *P. japonensis* lay their eggs in the soil. This character has been suggested by Matesco *et al.* (in press.) based on Javahery (1994). In the present analysis, the oviposition in the soil is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

113. First instar, gregarious behavior: (0) present; (1) absent.

Character 113. In several pentatomoids, especially in the well studied Pentatomidae, first instar nymphs are gregarious. Javahery (1994) states that first instar nymphs of most species studied by him do not feed, and aggregate on or around the egg shells after emergence. *P. japonensis* is a highly gregarious species in most life stages (Hironaka *et al.*, 2005). On the other hand, in most thyreocorid species, the first instar does not display gregarious behavior.

Maternal behavior

114. Maternal care: (0) absent; (1) present.

Character 114. Most insects disperse eggs individually over space and time and abandon them, as in the Thyreocoridae. Postovipositional investment in offspring, or subsocial behavior, has evolved repeatedly in insects in response to a variety of environmental pressures (Filippi-Tsukamoto *et al.*, 1995a). Subsocial behavior has been reported for a number of families in the Hemiptera (Tallamy & Schaefer, 1997): maternal care is present in some species of Sehirinae (Sites & McPherson, 1982; Javahery, 1994; Kight, 1995; Kudo & Nakahira, 2004, 2005) and in *P. japonensis* (Tsukamoto & Tojo, 1992; Filippi-Tsukamoto *et al.*, 1995a). This character has been suggested by Matesco *et al.* (in press) based on Javahery (1994). In our analysis, the presence of maternal care is synapomorphic to the clade *Sehirus* and *Parastrachia* (node 2).

Trees

The analysis resulted in six most parsimonious trees with 418 steps, consistency index (Ci) of 0.33, and retention index (Ri) of 0.61. The strict consensus of these trees is shown in Figs. 6-8. Bremer support values were low.

The consensus tree supports the monophyly of the family Thyreocoridae (node 3), the genus *Strombosoma* (node 5), the subfamily Corimelaeninae (node 7) and the genus *Corimelaena* (node 20). *Parastrachia* and *Sehirus* (node 2) present sister-group relationship. *Godmania* is the sister group of the clade *Amyssonotum* and *Corimelaena* (node 18) and *Amyssonotum* was hypothesized as the sister group of *Corimelaena* (node 19). The monophyletic condition of the Thyreocorinae, of the genera *Alkindus* and *Galgupha*, and of the subgenera *Corimelaena* and *Parapora* was not supported by our results.

Monophyly of *Corimelaena*

Corimelaena is monophyletic on the basis of 4 homoplasious synapomorphies: color pattern of the body variegated (2^0), absence of carina at the anterior margin of the head (23^1), costa rounded (61^0), and absence of lateral bristles on sternites III to VII (76^0) (Fig. 8). All subgenera of *Corimelaena* are paraphyletic: *Corimelaena* is paraphyletic due to the inclusion of species of *Termapora*, *Parapora*, and *Epipora*, and *Parapora* is paraphyletic due to the inclusion of the only species of *Epipora* (node 31) (Fig. 8).

Godmania, *Amyssonotum*, and *Corimelaena*

The genus *Corimelaena* has sister group relationships with *Godmania* and *Amyssonotum* (node 18) based on 5 homoplasious synapomorphies (Fig. 8). The sister group relationship between *Amyssonotum* and *Corimelaena* is supported by 3 homoplasious synapomorphies (Fig. 8).

Polyphyly of Thyreocorinae and monophyly of *Strombosoma*

Thyreocoris is more related to the Corimelaeninae (node 6) than to the clade *Carrabas* and *Strombosoma* (node 4), rendering Thyreocorinae paraphyletic. The monotypic genus *Carrabas* has a sister group relationship with *Strombosoma* based on seven homoplasious synapomorphies (Fig. 7). The genus *Strombosoma* was recovered as monophyletic based on two homoplasious synapomorphies (Fig. 7).

Eumetopia, *Alkindus*, and *Pericrepis*

The genus *Alkindus* is paraphyletic because it includes the species of *Pericrepis* (node 9). There is a sister group relationship among *Eumetopia*, *Alkindus* and *Pericrepis* (node 8), based on one homoplasious synapomorphy (Fig. 7). The monophyly of *Alkindus* and *Pericrepis* (node 9) is supported by a nonhomoplasious synapomorphy and a homoplasious synapomorphy (Fig. 7).

Galgupha and *Cydnoides*

The genus *Galgupha* was recovered as polyphyletic, although represented only by 5 of its 15 subgenera. The subgenus *Galgupha* was hypothesized as monophyletic (node 13) on the basis of 4 homoplasious synapomorphies (Fig. 7). It appears to be more related to the genus *Cydnoides* (node 12) than to the other subgenera of *Galgupha* and this relationship is supported by three homoplasious synapomorphies (Fig. 7). The remaing subgenera, *Astiroderma*, *Euryscytus*, *Gyrocnemis*, and *Psestophleps*, are related to each other and to the monotypic genus *Pruhleria*. This group is supported by 2 nonhomoplasious synapomorphies and 2 homoplasious synapomorphies (Fig. 7).

Discussion

Monophyly of *Corimelaena* and subgenera

Corimelaena is monophyletic based on 4 synapomorphies. The costa rounded and the absence of lateral bristles on abdominal sternites have been already mentioned by McAtee & Malloch (1933) as major features of the genus. As discussed above, *Corimelaena* spp., like most thyreocorids, have a color pattern variegated (2^0), in constrast with the sister groups, *Amyssonotum* and *Godmania*, which are uniformly black. The carina at the anterior margin of the head is absent (23^1), but this feature occurs in other species of Thyreocoridae. In a lateral view of the corium, the costa is rounded in all species of *Corimelaena* (61^0), which is the character used by McAtee & Malloch (1933) to separate *Corimelaena* from *Godmania* in their key to the thyreocorid genera. The lateral bristles on sternites III to VII, which are very common in thyreocorids, are absent (76^0), as in the genera *Pericrepis* and *Pruhleria*.

Our results do not support the monophyly of the subgenera of *Corimelaena*, so we suggest that their use should be abandoned. McAtee & Malloch (1933) divided *Corimelaena* into four subgenera, only based on the position of the spiracles on the sternites IV to VII relative to the lateral margin. This character, as interpreted in the present analysis (with each group of spiracles as different characters and with each possible position as different states), provides three nonhomoplasious sinapomorphies for internal clades in *Corimelaena*. The spiracles of the IV and V sternites in a lateral position (80^1, 81^1) support the group *Epipora* and *Parapora*. A dorsal position of the spiracles of the IV sternite (80^2) is autapomorphic to *Epipora*. The spiracles of the VI-VII sternites in a lateral position (82^1) support the grouping of *Termapora*, *Epipora* and *Parapora*.

Godmania, *Amyssonotum*, and *Corimelaena*

Corimelaena is more related to *Amyssonotum*, and the grouping has a sister group relationship with *Godmania*. A close proximity between the genera *Godmania* and *Corimelaena* was already suggested by McAtee & Malloch (1933).

Monophyly of Thyreocoridae

The cladogram obtained is not congruent with the classic systematic organization of the Thyreocoridae. The family and some of its genera (*Corimelaena* and *Strombosoma*) are monophyletic, but Thyreocorinae, *Alkindus*, and the subgenera of *Corimelaena* are paraphyletic. The genus *Galgupha*, comprising the greater diversity within Thyreocoridae, is polyphyletic.

Although the lack of comprehensiveness of our outgroup sampling for the analysis of Thyreocoridae, the family was recovered as monophyletic, comprising the twelve genera already assigned to the group. Thus, the results of Grazia *et al.* (2008) are here corroborated.

Polyphyly of Thyreocorinae

Our analysis did not recover the monophyly of Thyreocorinae, because *Thyreocoris* is more related to the Corimelaeninae than to the clade *Carrabas* and *Strombosoma*. McAtee & Malloch (1933) excluded *Carrabas* and *Strombosoma* from Thyreocoridae. Later, Dolling (1981) grouped both genera to *Thyreocoris* into a single subfamily, Thyreocorinae. The author considered that the American Corimelaninae had nothing in common with the three Old World Thyreocorinae, except the basic cydnid characters and the greatly enlarged scutellum. Dolling (1981) grouped Thyreocorinae based on the absence of a perforation in the jugal lobe of the metathoracic wing, recognizing, however, that this is the condition found in all other Heteroptera. We were not able to evaluate this character because the metathoracic wing could not be expanded properly in most specimens. Other features pointed by Dolling (1981) are related to the internal male and female genitalia, the shape of the evaporatorium and the enclosed clypeus.

The only previous cladistic analysis including more than one representative of this subfamily is that of Lis *et al.* (2012), who studied the monophyly and systematic position of the Dinidoridae using mitochondrial 12S and 16S rDNA sequences. Although they did not aim to test nor did they discuss the monophyly of Thyreocoridae, the resultant tree of the combined analysis supports the Thyreocorinae (*Strombosoma impictum* and *Thyreocoris scarabaeoides*) as sister group to all other Pentatomoidea except Pentatomidae, but not grouping with *Galgupha difficilis*.

Similarities between species of *Carrabas* and *Strombosoma* have already been stated by McAtee & Malloch (1933) and Dolling (1981). The genus *Strombosoma* is monophyletic. *Thyreocoris*, on the other hand, is basal to and separated from the Corimelaeninae. It has already been pointed in the literature that this genus differs from the American species (=Corimelaeninae) in the form of the internal male and female genitalia (Dolling, 1981).

Based on our results, Thyreocorinae is not monophyletic, although there is low support. Complimentary studies, including further exploration of morphological characters in a comparative basis as well as molecular characters, should help define if the division of Thyreocoridae into subfamilies should be abandoned.

Monophyly of Corimelaeninae

The monophyly of Corimelaeninae, including all nine genera already assigned to the group, was recovered based on several features. McAtee & Malloch (1933) noted that in all Thyreocoridae, except *Thyreocoris*, there is an oval perforation of the jugal lobe of the metathoracic wing. Dolling (1981) uses this feature as diagnostic of the Corimelaeninae, placing in this subfamily all of the American species covered by the revision of McAtee & Malloch (1933). In addition, Dolling (1981) considered that the group differed from Thyreocorinae in body shape, pronotum shape and features of male and female internal genitalia. Most of these characters were not evaluated in our analysis. In our analysis, Corimelaeninae is supported by the clypeus sub equal to the mandibular plates (25^0), rostrum reaching mesocoxae (37^2), prosternum moderately carinate (45^1), carinae flaring anteriorly (46^1), presence of lateral bristles on sternites III-VII (76^1), laterotergites 9 contiguous (94^0), and parameres not exposed (107^2).

Eumetopia, *Alkindus*, and *Pericrepis*

The results of our analysis do not support a close affinity between *Eumetopia* and *Galgupha (Gyrocnemis)*, as suggested by Dolling (1981), because *E. fissipes* and *G. (Gy.) fossata* come out in different clades. *Eumetopia* has been placed in Thyreocoridae by Lethierry & Severin (1893). McAtee & Malloch (1933) considered the genus as not thyreocorine due to the venation, but the authors included *Galgupha (Gyrocnemis) tabida* (Stål) in the family. *G tabida* was catalogued by Stål (1876) as a species of *Eumetopia* and suggested it might be conspecific with *E. fissipes*. Dolling (1981) synonimized *G. tabida* to *E. fissipes* and included it within Corimelaeninae. In our analysis, we studied males and females of *E. fissipes*, and our results hypothesize the inclusion of *Eumetopia* within Corimelaeninae, as suggested by Dolling (1981). *Eumetopia* and *Carrabas* are the only groups in this family which display sexual dimorphism of the head shape, consisting in an autapomorphy for each genera.

The genus *Alkindus*, recently revised by Matesco & Grazia (2013), resulted not monophyletic, because the two species come up in a clade with *Pericrepis callosula*. Horvath (1919) suggested that those two genera might be close. However, McAtee & Malloch (1933) suggested that *Alkindus* is related to *Amyssonotum* and *Pericrepis* to *Pruhleria*.

Galgupha and *Cydnoides*

Galgupha is not supported as a monophyletic group in the present analysis. On the other hand, the monophyly of the nominal subgenus is corroborated (node 13). As discussed above, in the Thyreocoridae head punctation occurs in high density (29^1), except for some reversals to a low density punctation (29^0) in some groups (e.g., *Galgupha (Galgupha)*; *Galgupha* in part and *Pruhleria*). In the Corimelaeninae, the prosternal carinae are flaring anteriorly (46^1), but there are reversals to the prosternal carinae parallel-sided (46^0) in the subgenera *Galgupha* and *Parapora*. Within the genus *Galgupha*, comparative strength of the ventral armature of the fore femora is variable, but, among the species analyzed, only *Galgupha (Galgupha)* (besides *Alkindus* spp.) present a row of spines in the fore femora (71^1). The median third of the ventral rim of the pygophore is convex (100^0) only in the subgenus *Galgupha* and in *Amyssonotum* and *Corimelaena*.

The subgenus *Galgupha* is more related to the genus *Cydnoides,* which were coupled in the same step by McAtee & Malloch (1933) in their key. As only a small fraction of the diversity within the genus *Galgupha* was considered in the present analysis, the results need further testing and representatives of the remaining subgenera should be considered.

Thyreocoridae and relationships with related families

Grazia *et al.* (2008) consider the composition of the Cydnidae the most controversial among the family-group taxa within Pentatomoidea. Their total evidence analysis suggested a relationship among *Canopus* and members of the Cydnidae. All the analysis, except for the morphological data alone, failed to recognize the Cydnidae *sensu* Dolling (1981), but did not indicate how the constituent taxa should be related. Their analysis supported the concept of Thyreocoridae distinct from the Cydnidae and also indicated a close relationship among Parastrachiidae (*Parastrachia* and *Dismegistus*) and the Thyreocoridae. *Sehirus* appeared associated either with Thyreocoridae or Parastrachiidae or both. Grazia *et al.* (2008) suggested to maintain the family status of the Thyreocoridae and to give subfamily status to the Parastrachiidae, including it in the former family, and also recommend to await further analyses to decide whether the Sehirinae should also be included as part of this grouping.

Although Thyreocoridae has been historically related to the Cydnidae, the poor cydnid sample in our analysis precludes further discussion on the relationships among these groups. The inclusion of representatives of the other cydnid subfamilies can help clarify the position of Parastrachiidae, Sehirinae and Thyreocoridae among the “cydnoid complex”.

Conclusions

This paper is the first hypothesis of relationships within the Thyreocoridae as well as the first cladistic evidence of monophyly of the genus *Corimelaena*. Based on our results, we suggest the maintenance of family status of Thyreocoridae as suggested by Stys & Davidová (1979), including 12 genera (Table 4). Also, there is evidence of the monophyly of *Corimelaena*, but the subgenera should be abandoned. The relationship between the Thyreocoridae and the Cydnidae awaits further studies. Only a broader taxon sampling of Thyreocoridae and Cydnidae *sensu lato* and additional and more complete data sets will help clarify the status of equivocal taxa, in particular the relationships within the “cydnoid complex”.

Further phylogenetic studies within some thyreocorid genera are required to test the monophyly (e.g., *Pericrepis*, *Cydnoides*, and *Galgupha*). A stronger test of the present hypothesis will require analysis of a much larger taxon sample for the Cydnidae and Thyreocoridae, especially among *Galgupha*. This diverse lineage, with 15 subgenera, remains the greatest challenge to understand the evolution of the group and to set up a phylogenetic classification.

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TABLE 1. Check-list of Thyreocoridae and material examined for the cladistic analysis, with the respective number of males and females examined and their belonging collection.

Higher taxa and species	**Number of specimens**	**Collection***
Plataspididae		
Coptosoma Laporte, 1832		
C. scutellatum (Geoffroy, 1785)	1♂, 1♀	AMNH
Canopidae		
Canopus Fabricius, 1803		
C. caesus (Germar, 1839)	2♂, 5♀	AMNH
Cydnidae		
Sehirus Amyot & Serville, 1843		
S. cinctus (Palisot de Beauvois, 1805)	1♂, 2♀	AMNH
Parastrachiidae		
Parastrachia Distant, 1883		
P. japonensis (Scott, 1880)	1♂, 2♀	AMNH, USNM
Thyreocoridae: Thyreocorinae		
Carrabas Distant, 1908		
C. maurus Distant, 1908	1♂, 1♀	BMNH
Strombosoma Amyot & Serville, 1843		
S. impictum (Stål, 1853)	1♂, 1♀	MNHN, NHRS
S. unipunctatum Amyot & Serville, 1843	1♀	MNHN
Thyreocoris Schrank, 1801		
Thyreocoris fulvipennis (Dallas, 1851)		
T. ohridanus Kormilev, 1936		
T. pakistanensis Ahmad & Moizuddin, 1982		
T. scarabaeoides (Linnaeus, 1758)	5♂, 9♀	AMNH, MACN, ZMHB
Thyreocoridae: Corimelaeninae		
Alkindus Distant, 1889		
A. atratus Distant, 1889	9♂, 7♀	JEEC, MCNZ, UFRG
A. crassicosta Horvath, 1919	5♂, 2♀	MCNZ, UFRG
Amyssonotum Horvath, 1919		
A. rastratum (Stål, 1862)	2♂, 6♀	FCAP, JEEC, UFRG
Cydnoides Malloch, 1919		
C. (Cydnoides) ciliatus (Uhler, 1863)	5♂, 6♀	JEEC, MACN, ZMHB

C. (*C.*) *confusus* McAtee & Malloch, 1933		
C. (*C.*) *renormatus* (Uhler, 1895)		
C. (*Sayocoris*) *albipennis* (Say, 1831)		
C. (*S.*) *obtusus* (Uhler, 1894)		
C. (*S.*) *peregrinus* McAtee & Malloch, 1933		
C. (*Cosmarioides*) *nitens* McAtee & Malloch, 1933		
C. (*C.*) *reticulatus* McAtee & Malloch, 1933		
C. (*C.*) *setiventris* McAtee & Malloch, 1933		
Eumetopia Westwood, 1838		
E. fissipes Westwood, 1838	4 ♂, 4 ♀	DZUP; MCNZ
Galgupha Amyot & Serville, 1843		
G. (*Acritophleps*) *luteomarginata* McAtee & Malloch, 1928		
G. (*Acrotmetus*) *brasilianus* (Jensen-Haarup, 1926)		
G. (*A.*) *crassa* McAtee & Malloch, 1933		
G. (*A.*) *grossa* McAtee & Malloch, 1928		
G. (*A.*) *minuenda* McAtee & Malloch, 1928		
G. (*A.*) *schulzii* (Fabricius, 1781)		
G. (*A.*) *tucumanus* (Horvath, 1919)		
G. (Astiroderma) albipennis (Eschscholtz, 1822)	7 ♂, 5 ♀	MACN, MLPA, MNHN, ZMHB
G. (*A.*) *breddini* McAtee & Malloch, 1933		
G. (*Bonaria*) *longirostris* (Berg, 1879)		
G. (*Charoda*) *simplex* McAtee & Malloch, 1933		
G. (*Ctenopoda*) *castor* McAtee & Malloch, 1933		
G. (*C.*) *maculosa* (Berg, 1891)		
G. (*Euryscytus*) *aliena* McAtee & Malloch, 1933		
G. (*E.*) *apicata* McAtee & Malloch, 1933		
G. (*E.*) *assimilis* McAtee & Malloch, 1933		
G. (*E.*) *australis* McAtee & Malloch, 1933		
G. (*E.*) *basalis* (Germar, 1839)		
G. (*E.*) *caudata* McAtee & Malloch, 1933		
G. (*E.*) *caudiculata* McAtee & Malloch,		

1933		
G. (*E*.) *contra* McAtee & Malloch, 1933		
G. (*E*.) *contracta* McAtee & Malloch, 1933		
G. (*E*.) *corvina* (Horvath, 1919)		
G. (*E*.) *cruenta* (Horvath, 1919)		
G. (*E*.) *curvata* McAtee & Malloch, 1933		
G. (*E*.) *curvatula* McAtee & Malloch, 1933		
G. (E.) difficilis (Breddin, 1914)	10 ♂, 10 ♀	MCNZ, UFRG
G. (*E*.) *foveolata* (Jensen-Haarup, 1926)		
G. (*E*.) *insula* McAtee & Malloch, 1933		
G. (*E*.) *jaczewskii* McAtee & Malloch, 1928		
G. (*E*.) *labrata* McAtee & Malloch, 1933		
G. (*E*.) *laevis* (Stål, 1862)		
G. (E.) lucretia McAtee & Malloch, 1933		
G. (*E*.) *mammula* McAtee & Malloch, 1933		
G. (*E*.) *nitida* McAtee & Malloch, 1933		
G. (*E*.) *obesa* McAtee & Malloch, 1933		
G. (*E*.) *opacifrons* McAtee & Malloch, 1933		
G. (*E*.) *opercula* McAtee & Malloch, 1933		
G. (*E*.) *parae* McAtee & Malloch, 1933		
G. (*E*.) *parallela* McAtee & Malloch, 1933		
G. (*E*.) *punctata* McAtee & Malloch, 1933		
G. (*E*.) *rasilis* (Horvath, 1919)		
G. (*E*.) *regularis* McAtee & Malloch, 1933		
G. (*E*.) *romana* McAtee & Malloch, 1933		
G. (*E*.) *rostrata* McAtee & Malloch, 1933		
G. (*E*.) *sahlbergi* McAtee & Malloch, 1933		
G. (*E*.) *signatipennis* (Germar, 1839)		
G. (*E*.) *smidtii* (Fabricius, 1803)		
G. (*E*.) *valvata* McAtee & Malloch, 1933		
G. (*E*.) *varipennis* McAtee & Malloch, 1933		
G. (*E*.) *vulnerata* (Horvath, 1919)		
G. (*Galgupha*) *aterrima* Malloch, 1919		
G. (G.) atra Amyot & Serville, 1843	3 ♂, 3 ♀	JEEC, MACN
G. (*G*.) *carinata* McAtee & Malloch, 1933		
G. (*G*.) *denudata* (Uhler, 1863)		
G. (*G*.) *hesperia* McAtee & Malloch, 1933		
G. (*G*.) *loboprostethia* Sailer,1940		

G. (*G*.) *monostira* Horvath, 1919		
G. (G.) ovalis Hussey, 1925	2 ♂, 1 ♀	JEEC, MACN
G. (*Gyrocnemis*) *acuta* McAtee & Malloch, 1933		
G. (*G*.) *basigrapha* (Horvath, 1919)		
G. (*G*.) *bicornis* McAtee & Malloch, 1933		
G. (*G*.) *concava* McAtee & Malloch, 1928		
G. (*G*.) *cruralis* (Stål, 1862)		
G. (*G*.) *cydnoidea* McAtee & Malloch, 1933		
G. (*G*.) *differentialis* McAtee & Malloch, 1928		
G. (*G*.) *diminuta* (Van Duzee, 1923)		
G. (*G*.) *dimorpha* McAtee & Malloch, 1933		
G. (*G*.) *diversa* McAtee & Malloch, 1933		
G. (*G*.) *durionei* Kormilev, 1956		
G. (G.) fossata McAtee & Malloch, 1928	10 ♂, 10 ♀	JEEC, MCNZ, UFRG
G. (*G*.) *geayi* McAtee & Malloch, 1933		
G. (*G*.) *guttiger* (Stål, 1862)		
G. (*G*.) *impressa* (Horvath, 1919)		
G. (*G*.) *inaequalis* McAtee & Malloch, 1933		
G. (*G*.) *intermedia* McAtee & Malloch, 1933		
G. (*G*.) *lineata* McAtee & Malloch, 1933		
G. (*G*.) *maculipennis* (Germar, 1839)		
G. (*G*.) *morbiloci* McAtee & Malloch, 1933		
G. (*G*.) *nitens* (Breddin, 1914)		
G. (*G*.) *nitidipennis* McAtee & Malloch, 1933		
G. (*G*.) *notha* McAtee & Malloch, 1933		
G. (*G*.) *novatra* McAtee & Malloch, 1933		
G. (*G*.) *novella* McAtee & Malloch, 1928		
G. (*G*.) *occulta* McAtee & Malloch, 1933		
G. (*G*.) *omissa* McAtee & Malloch, 1933		
G. (*G*.) *parva* McAtee & Malloch, 1933		
G. (*G*.) *punctifer* McAtee & Malloch, 1933		
G. (*G*.) *quadrisignata* (Stål, 1862)		
G. (*G*.) *reinhardti* (Jensen-Haarup, 1926)		
G. (*G*.) *singularis* McAtee & Malloch, 1933		

G. (*G.*) *soror* McAtee & Malloch, 1933
G. (*G.*) *texana* McAtee & Malloch, 1933
G. (*G.*) *torresi* Kormilev, 1956
G. (*G.*) *triconcava* McAtee & Malloch, 1933
G. (*G.*) *unica* McAtee & Malloch, 1933
G. (*Microcompsus*) *daldorfii* (Fabricius, 1803)
G. (*M.*) *haywardi* Kormilev, 1956
G. (*M.*) *vinculata* (Germar, 1839)
G. (*Nothocoris*) *akarna* McAtee & Malloch, 1933
G. (*N.*) *alutacea* McAtee & Malloch, 1933
G. (*N.*) *bakeri* McAtee & Malloch, 1933
G. (*N.*) *boliviana* McAtee & Malloch, 1933
G. (*N.*) *brevis* McAtee & Malloch, 1933
G. (*N.*) *brunnipennis* (Germar, 1839)
G. (*N.*) *caracasana* McAtee & Malloch, 1933
G. (*N.*) *chilocoroides* (Walker, 1867)
G. (*N.*) *chrostowskii* McAtee & Malloch, 1928
G. (*N.*) *coccineloides* Horvath, 1919
G. (*N.*) *eas* McAtee & Malloch, 1933
G. (*N.*) *fossula* McAtee & Malloch, 1933
G. (*N.*) *grenadensis* McAtee & Malloch, 1933
G. (*N.*) *inornata* McAtee & Malloch, 1933
G. (*N.*) *juno* McAtee & Malloch, 1933
G. (N.) magna Sailer, 1941
G. (*N.*) *marginalis* McAtee & Malloch, 1933
G. (*N.*) *marginicollis* Horvath, 1919
G. (*N.*) *microphthalma* McAtee & Malloch, 1933
G. (*N.*) *nitiduloides* (Wolff, 1802)
G. (*N.*) *oculata* McAtee & Malloch, 1933
G. (*N.*) *parvula* Horvath, 1919
G. (*N.*) *repetita* McAtee & Malloch, 1933

G. (*N.*) *semilimbata* Horvath, 1919		
G. (*N.*) *stramineipennis* McAtee & Malloch, 1933		
G. (*N.*) *surda* McAtee & Malloch, 1933		
G. (*N.*) *terminalis* (Walker, 1867)		
G. (*Orocoris*) *arizonensis* (Van Duzee, 1923)		
G. (*Psestophleps*) *altera* McAtee & Malloch, 1933		
G. (*P.*) *bergiana* McAtee & Malloch, 1933		
G. (*P.*) *bisignata* McAtee & Malloch, 1933		
G. (*P.*) *carbonata* McAtee & Malloch, 1933		
G. (*P.*) *casta* McAtee & Malloch, 1933		
G. (*P.*) *costomaculata* McAtee & Malloch, 1933		
G. (*P.*) *denieri* Kormilev, 1956		
G. (*P.*) *fimbriata* McAtee & Malloch, 1933		
G. (*P.*) *imitans* McAtee & Malloch, 1933		
G. (*P.*) *inops* McAtee & Malloch, 1933		
G. (*P.*) *mayana* McAtee & Malloch, 1933		
G. (*P.*) *media* McAtee & Malloch, 1933		
G. (*P.*) *mexicana* McAtee & Malloch, 1933		
G. (P.) neobisignata McAtee & Malloch, 1928	10 ♂, 10 ♀	MACN, MNHN, UFRG
G. (*P.*) *obovata* McAtee & Malloch, 1933		
G. (*P.*) *pallipennis* McAtee & Malloch, 1933		
G. (*P.*) *porcata* Horvath, 1919		
G. (*P.*) *tabellula* McAtee & Malloch, 1933		
G. (*Pteronomos*) *amitta* McAtee & Malloch, 1933		
G. (*P.*) *china* McAtee & Malloch, 1933		
G. (*P.*) *fritzi* Kormilev, 1956		
G. (*P.*) *meridiana* McAtee & Malloch, 1933		
G. (*P.*) *oblonga* McAtee & Malloch, 1933		
G. (*P.*) *punctifrons* McAtee & Malloch, 1933		
G. (*P.*) *ruficornis* (Dallas, 1851)		
G. (*P.*) *vianai* Kormilev, 1956		

G. (*P.*) *vittifrons* McAtee & Malloch, 1933		
G. (*Trepocnemis*) *anomala* McAtee & Malloch, 1933		
Godmania Horvath, 1919		
G. aterrima Horvath, 1919	1 ♂, 1 ♀	JEEC
Pericrepis Horvath, 1919		
P. afer McAtee & Malloch, 1933		
P. bergi Kormilev, 1956		
P. bosqui Kormilev, 1956		
P. callosula Horvath, 1919	5 ♂, 3 ♀	JEEC, MLPA, UFRG
Pruhleria McAtee & Malloch, 1933		
P. incerta (Uhler, 1863)	2 ♂	AMNH
Corimelaena White, 1839		
C. (Corimelaena) agrella McAtee, 1919	1 ♂, 1 ♀	NDSU
C. (C.) alpina (McAtee & Malloch, 1933)		
C. (C.) alticola (Horvath, 1919)		
C. (C.) barberi (McAtee & Malloch, 1933)		
C. (C.) championi (Distant, 1880)		
C. (C.) contrasta (McAtee & Malloch, 1933)		
C (C.) corallina (McAtee & Malloch, 1933)		
C. (C.) digitata (McAtee & Malloch, 1933)		
C. (C.) elegans (McAtee & Malloch, 1933)		
C. (C.) feminea (McAtee & Malloch, 1933)		
C. (C.) harti Malloch, 1919	1 ♂, 1 ♀	NDSU
C. (C.) interrupta Malloch, 1919	1 ♂, 1 ♀	NDSU
C. (C.) lateralis (Fabricius, 1803)	4 ♂, 3 ♀	JEEC, MACN, MNHN
C. (C.) limata (McAtee & Malloch, 1933)		
C. (C.) marginella Dallas, 1851	3 ♂, 3 ♀	JEEC, MACN
C. (C.) micans (McAtee & Malloch, 1933)		
C. (C.) minuta Uhler, 1863	2 ♂, 2 ♀	JEEC
C. (C.) nigra Dallas, 1851	1 ♂, 1 ♀	MACN
C. (C.) obscura McPherson & Sailer, 1978	1 ♂, 1 ♀	NDSU
C. (C.) palmeri (McAtee & Malloch, 1933)		
C. (C.) polita Malloch, 1919		
C. (C.) pulicaria (Germar, 1839)	3 ♂, 2 ♀	JEEC, MACN
C. (C.) tibialis (Fabricius, 1803)	6 ♂, 13 ♀	JEEC, MCNZ, MNHN, UFRG, ZMHB
C. (Epipora) signoretti (McAtee &	(literature data)	

Malloch, 1933)		
C. (Parapora) californica Van Duzee, 1929	2 ♀	USNM
C. (P.) cognata (Van Duzee, 1907)	4 ♂, 4 ♀	JEEC, NDSU
C. (P.) extensa Uhler, 1863	4 ♂, 3 ♀	JEEC, MACN, NDSU
C. (P.) incognita (McAtee & Malloch, 1933)	2 ♂, 2 ♀	MACN, NDSU
C. (P.) parana McAtee & Malloch, 1928	1 ♂, 1 ♀	MCNZ, UFRG
C. (P.) virilis (McAtee & Malloch, 1933)	2 ♂, 1 ♀	AMNH, MACN,
C. (Termapora) minutissima Malloch, 1919	1 ♂, 1 ♀	USNM

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* Museum acronyms, according to Evenhuis (2013), with curators in parenthesis: AMNH–American Museum of Natural History, New York, USA (Randall T. Schuh); BMNH–The Natural History Museum, London, United Kingdom (Mick Webb); DZUP–Museu de Entomologia Pe. Jesus Santiago Moure, Curitiba, Brazil (Luciane Marinoni); FCAP–Universidade Federal do Pará, Belém, Brazil (José A. M. Fernandes); JEEC–Joseph E. Eger personal collection, Florida, USA (Joseph E. Eger); MACN–Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (Arturo Roig-Alsina); MCNZ–Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (Aline Barcellos); MLPA–Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina (María del C. Coscarón); MNHN – Muséum National d'Histoire Naturelle, Paris, France (Eric Guilbert); NDSU–North Dakota State University, Fargo, USA (David A. Rider); NHRS–Naturhistoriska Riksmuseet, Stockholm, Sweden (Gunvi Lindberg); UFRG–Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (Jocelia Grazia); USNM–National Museum of Natural History, Washington, USA (Thomas Henry); ZMHB–Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Juergen Deckert).

TABLE 2. List of characters used in the cladistic analysis.

Color

1. Body, predominant color: (0) black; (1) castaneous; (2) red; (3) ocher.
2. Body, predominant color, pattern: (0) variegated; (1) uniform.
3. Thorax black variegated, pronotum, yellow lateral spot: (0) absent; (1) present.
4. Thorax black variegated, propleuron, yellow lateral spot: (0) absent; (1) present.
5. Thorax black variegated, scutellum, color: (0) completely dark; (1) posterior margin yellow; (2) posterior half yellow.
6. Thorax black variegated, forewing, corium, color: (0) yellow; (1) black.
7. Thorax, forewing, corium yellow, mesocorium, black spot: (0) absent; (1) present.
8. Thorax, forewing, corium yellow, mesocorium, black spot, extent: (0) completely covering mesocorium; (1) confined to the apical half; (2) confined to the internal margin; (3) confined to the mesocorial vein.
9. Thorax, forewing, corium yellow, exocorium, black spot: (0) absent; (1) present.
10. Thorax, forewing, corium yellow, exocorium, black spot, extent: (0) confined to the median third; (1) confined to the inner margin.
11. Thorax, forewing, corium black, costa, yellow margin: (0) present; (1) absent.
12. Thorax, forewing, corium black, base, yellow spot: (0) absent; (1) present.
13. Thorax, forewing, corium black, apex, yellow spot: (0) present; (1) absent.
14. Abdomen black variegated, sternite VI, yellow lateral spot: (0) present; (1) absent.
15. Abdomen black variegated, sternite VII, yellow lateral spot: (0) present; (1) absent.
16. Abdomen black variegated, sternite VII, yellow lateral spot, shape: (0) strip; (1) semicircular.
17. Abdomen black variegated, sternite VII, yellow lateral spot, extent: (0) occupying the entire margin of the sternite; (1) not occupying the entire the margin of the sternite.
18. Female, abdomen black variegated, laterotergites 8, yellow spot: (0) present; (1) absent.
19. Male, abdomen black variegated, pygophore, ventral surface, color: (0) black; (1) yellow.

Head

20. Clypeus and mandibular plates, sexual dimorphism: (0) absent; (1) present.
21. Area before the eyes, shape: (0) trapezoidal; (1) triangular.
22. Anterior margin, degree of deflection: (0) not deflected; (1) deflected.
23. Anterior margin, carina: (0) present; (1) absent.
24. Clypeus, apex, protuberance: (0) absent; (1) present.
25. Clypeus, apex, length compared to the mandibular plates: (0) sub equal; (1) longer; (2) shorter.
26. Mandibular plates, apex, level compared to the level of the clypeus: (0) at the same level; (1) at a higher level.

27. Mandibular plates, lateral margins, shape: (0) convex; (1) straight; (2) sinuate.

28. General punctation: (0) present; (1) absent.

29. Punctation, density: (0) low, distance between two adjacent punctures greater than the diameter of one puncture; (1) high, distance between two adjacent punctures similar to the diameter of one puncture.

30. Area between the eye and the ocellus, punctation: (0) absent; (1) present.

31. Occiput, punctation: (0) absent; (1) present.

32. Antenniferous tubercles, dorsal view, relation to the mandibular plates: (0) completely covered; (1) partially visible.

33. Bucculae, length compared to the length of the head: (0) short, not surpassing half of the head; (1) long, nearly reaching posterior margin.

34. Labium, segment I, length compared to the bucculae: (0) longer; (1) shorter.

35. Labium, segment I, length compared to the anterior margin of prosternum: (0) not reaching; (1) reaching.

36. Labium, segment II, length compared to the procoxae: (0) reaching; (1) surpassing; (2) not reaching.

37. Rostrum, apex: (0) reaching metacoxae; (1) reaching urosternite III; (2) reaching mesocoxae.

Thorax

38. Pronotum, lateral margins, shape: (0) convex; (1) straight.

39. Pronotum, posterior angles, development: (0) developed; (1) not developed.

40. Pronotum, rastration: (0) absent; (1) present.

41. Pronotum, rastration, extent: (0) restricted to the lateral area; (1) two posterior thirds.

42. Propleuron, puctation: (0) absent; (1) present.

43. Prosternum, sulcus: (0) present; (1) absent.

44. Prosternum, carinae: (0) absent; (1) present.

45. Prosternum, carinae, degree of development: (0) strongly carinate, completely surrounding the rostrum; (1) moderately carinate, not surrounding completely the rostrum.

46. Prosternum, carinae, direction: (0) parallel-sided; (1) flaring anteriorly.

47. Scutellum, length in relation to the urosternites: (0) surpassing VII; (1) reaching VII; (2) reaching V.

48. Scutellum, shape: (0) broadly rounded; (1) triangular.

49. Scutellum, margin: (0) emarginated; (1) not emarginated.

50. Scutellum, frena: (0) absent; (1) present.

51. Scutellum, frena, length in relation to the length of scutellum: (0) long, surpassing middle of scutellum; (1) short, not surpassing middle of scutellum.

52. Forewing, corium, length in relation to the urosternites: (0) reaching IV; (1) reaching V; (2) reaching VI.

53. Forewing, clavus, length: (0) short, not surpassing middle of scutellum; (1) elongate, surpassing middle of scutellum.

54. Forewing, corium, apex, shape: (0) acute; (1) rounded; (2) truncate.

55. Forewing, corium, mesocorial vein: (0) absent; (1) present.

56. Forewing, corium, exocorial vein (radial + mesial veins): (0) absent; (1) present.

57. Forewing, corium, exocorial vein, base: (0) deeply impressed; (1) evanescent.

58. Forewing, corium, exocorial vein, inner branch (mesial vein): (0) apparent; (1) obsolete.

59. Forewing, corium, exocorial vein, outer branch (radial vein): (0) apparent; (1) obsolete.

60. Forewing, area between the costa and the exocorial vein, degree of elevation: (0) not elevated; (1) elevated.
61. Forewing, corium, costa, shape: (0) rounded; (1) carinate.

62. Metapleuron, lateral area to evaporatorium, punctation: (0) present; (1) absent.

63. External scent efferent system, mesopleuron, pseudoperitreme: (0) absent; (1) present.

64. External scent efferent system, metapleuron, evaporatorium, extent in relation to the lateral margin of the segment: (0) clearly reaching; (1) scarcely attaining.
65. External scent efferent system, metapleuron, ostiole, position: (0) laterad, placed in the middle of metapleuron; (1) basal, between meso- and metacetabulum.
66. External scent efferent system, metapleuron, peritreme, shape: (0) spout; (1) auricle; (2) disc; (3) groove.
67. External scent efferent system, evaporatorium, extent: (0) very large, covering pro-, meso-, and metapleuron; (1) well developed, covering both meso- and metapleuron; (2) reduced, covering metapleuron only.
68. External scent efferent system, metapleuron, evaporatorium, gyrification, development: (0) present in form of low wrinkles and furrows; (1) not developed, evaporatorium smooth.
69. Metasternum, median projection: (0) absent; (1) present.

70. Legs, coxae, coxal combs: (0) absent; (1) present.

71. Legs, fore femora, lateral margin, row of spines: (0) absent; (1) present.

72. Legs, fore tibiae, lateral margin, row of spines: (0) absent; (1) present.

73. Legs, hind tibiae, dorsally, shape: (0) cylindrical; (1) flattened; (2) sulcate.

74. Legs, hind tibiae, posterior surface, carina: (0) absent; (1) present.

75. Legs, hind tibiae, posterodorsal bristles: (0) absent; (1) present.

Abdomen

76. Sternites III-VII, lateral bristles: (0) absent; (1) present.

77. Sternite II, spiracles, placement: (0) in the heavily sclerotized portion; (1) in the membranous anterior strip of the sternite.
78. Sternites III-VII, spiracles, callus: (0) present; (1) absent.

79. Sternites V-VII, spiracles, placement: (0) closer to the trichobothria; (1) closer to the lateral margin.
80. Sternite IV, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral; (2) dorsal.

81. Sternite V, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral.

82. Sternites VI-VII, spiracles, position in relation to the lateral margin: (0) ventral; (1) lateral.

83. Sternites III-VI, trichobothria, placement: (0) longitudinal; (1) transverse.

Female abdomen

84. Sternite VII, anterior margin, shape: (0) rounded; (1) subangulate.

85. Sternite VII, posterior margin, caudal median projection: (0) absent; (1) present.

86. Gonocoxites 8, punctation: (0) present; (1) absent.

87. Gonocoxites 8, posterior margins, shape: (0) straight; (1) convex; (2) concave.

88. Gonocoxites 8, posterior margins, position: (0) transverse; (1) oblique.

89. Gonocoxites 8, posterior margins oblique, direction: (0) posterior; (1) anterior.

90. Gonocoxites 8, sutural margins, ventral elevation: (0) absent; (1) present.

91. Gonocoxites 8, sutural margins, ventral elevation, degree of development: (0) slight; (1) strong.

92. Sternite VII, posterior margin, ventral elevation: (0) absent; (1) present.

93. Laterotergites 8, posterior margins, shape: (0) straight; (1) sinuate.

94. Laterotergites 9, sutural margins, position in relation to each other: (0) contiguous; (1) not contiguous.

95. Laterotergites 9, shape: (0) triangular; (1) lanceolate.

Male abdomen

96. Sternite VII, anterior margin, shape: (0) subangulate; (1) rounded; (2) angulate.

97. Pygophore, ventral surface, transverse groove: (0) absent; (1) present.

98. Pygophore, ventral surface, punctation: (0) present; (1) absent.

99. Pygophore, ventral rim, relation to the proctiger in ventral view: (0) not covering; (1) covering.

100. Pygophore, ventral rim, median third, outline: (0) convex; (1) straight; (2) concave.

101. Pygophore, ventral rim, tumescence: (0) present; (1) absent.

102. Pygophore, ventral rim, deflection: (0) not deflected; (1) deflected.

103. Pygophore, dorsal rim, shape: (0) sloping inwardly; (1) flat; (2) excavated.

104. Pygophore, dorsal rim, internal face, carina: (0) present; (1) absent.

105. Pygophore, dorsal rim, internal face, carina, shape: (0) convex; (1) straight.

106. Pygophore, dorsal rim, internal face, carina, lateral elevations: (0) absent; (1) present.

107. Pygophore, parameres, degree of exposure: (0) completely exposed; (1) partially exposed; (2) not exposed, covered by the proctiger.

Immature*s*

108. Egg, chorion sculpture, pattern: (0) reticulate; (1) smooth; (2) granulate.

109. Egg, aero-micropylar process, insertion: (0) pedunculate; (1) not pedunculate.

110. Oviposition, pattern: (0) in masses; (1) singly.

111. Oviposition, position of the egg in relation to the substrate: (0) upright; (1) unstructured; (2) lengthwise.

112. Oviposition, site: (0) on plants; (1) in the soil.

113. First instar, gregarious behavior: (0) present; (1) absent.

Maternal behavior

114. Maternal care: (0) absent; (1) present.

TABLE 3. Data matrix of character states of 114 characters and 40 taxa. Missing information is represented by “?” and inapplicable data by “–”.

	1 1 1 2 3 4 5 6 7 8 9 0 1 123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234
Coptosoma scutellatum	0000000–0——000000000000000000000000000–000—0000–00000——0–00000000000000?00000000000–0—00000000000000000000?0
Canopus caesus	11————————000001001——010111000–101000000–20000——1001011000000000010000000000–0—0101101111100010???????
Sehirus cinctus	001001——000000001001102000000100022111011 0—2111011201000000011211010100 10?1000010011100—0101101011100001101101
Parastrachia japonensis	20————————011002111——100101110–010—2111021201000011011221010000001100001 11110–10001011110000001 01?01101
Carrabas maurus	000001——10011—10101002100111000100011010100101??0000101001011031001000000110000110020–10001020000 1011—1???????
Strombosoma impictum	01————————001002000111010100011010100001??000010100101103100100200 0?00000110020–10001020002100???1???????
Strombosoma unipunctatum	000001——10011—1?001002000111010100011010100001??00001010010110310?1002000?00000110020–10001020002100???1???????
Thyreocoris scarabaeoides	01————————001002020111010020011010100101111010100101–10031011012010?10000000020–11001021012110 1—12??????
Alkindus atratus	01————————0010000001100100020 10–101110011110001000110110310111110111100000000 20–110000100101010002??????
Alkindus crassicosta	01————————0010000000100101020 10–00101001??10001000110110310111110 10?100000000211111000110021011—2???????
Amyssonotum rastratum	01————————010001010100010101011110101001??1011100001111031001012111?00000000020–0—101010101111—2???????
Cydnoides (C.) ciliatus	01————————0010000101100110220111001110011110101000011110310110101111100000000000–0—00001012112000 2???????
Eumetopia fissipes	30————————101101000010011002010–1011110111102110000101103101101001 1?10000000000–110000210121020000???????
Galgupha (A.) albipennis	000010100——000000000000010000010102011000111001111000110001011031011010011110000011020–0—00021010110011 2???????
Galgupha (E.) difficilis	000001——1110000000010000100000101020 10–0011100111102110000101103101101011111000001 0020–0—000210121101—210120?0
Galgupha (Ga.) atra	01————————001000010010010102011000110001111000100001111031011110111110000000002100—000010101121—21?1?0?0
Galgupha (Ga.) ovalis	01————————000000010010010102011000100001??10001000011110310111101111100000000 20–0—000110101121—21?12010
Galgupha (Gy.) fossata	0011101110——001100000000010000010100010–001111011110211000011110310110100111100000000 2100—000000121001—220120?0
Galgupha (P.) neobisignata	000001——11111—1000000001000001010001 0–00101001111000110001011031011010111110000000002100—000000111111—2???????
Godmania aterrima	01————————010001010100010111011010100001??10110——101103101101001 1?11000010010–0—000210121101—2???????
Pericrepis callosula	0000201110——00000000000000011001102201100011100 1??1000101011011031011010010?10000000011111100011012111 1—2???????
Pruhleria incerta	0000001110——0011?000010002010001110 2010–00111001??101011010101 10310?1000010?1000001?020–0—???000001011—2???????
Corimelaena (C.) agrella	0000001011——000001010111020100010100011010111001??10010——0011031001000010?1100001001110—001210000001—2???????
Corimelaena (C.) harti	000000100——100000101110201100101000110101110 01??10010——0011031001000010?1100001001110—001211020101—2???????
Corimelaena (C.) interrupta	0000101210——000000101010101000101000110101110 01??10110——0011031001000010?11000010020–0—00121010111000 2???????
Corimelaena (C.) lateralis	0000001011——100000010101010100010101011010111001111 0110——001103100101001 0?11000010000–0—101210101101—21012010
Corimelaena (C.) marginella	000000100——100000101110201100101110110101010 01??10010——0011031001000000?1100001001110—001211020001—2???????
Corimelaena (C.) minuta	000000120——100001010111020110010111011010101001??10010——0011031001000000?11000010010–0—001210101001—2???????
Corimelaena (C.) nigra	01————————010001020110010100011010101001??10110——0011031011010010?11000010000–100000210101100002???????
Corimelaena (C.) obscura	000001——100100000010101000100010101011010111001111 0110——0111031011000000?1100000000100—000010101101—21012010
Corimelaena (C.) pulicaria	000000120——10000000100010201100101000110101110011110110——0011031011000011?11000010000–0—001210111101—2???????
Corimelaena (C.) tibialis	000000120——00000101011102011001010101101011100111101 10——0011031001000010111000010011 10—001010100001—2???????
Corimelaena (E.) signoretti	0000?0120——10??0????0???201?0????????????????0????0?10——00?????????00?0??1211011020–0—?????0???????????????
Corimelaena (P.) californica	000000120——10110??1000102011001010001 0–10100001??10110——00110310?1000000?1111101000100—101??0???????????????
Corimelaena (P.) cognata	000010120——00010001000101011001010101101010000 1??10110——0011031011000000?1111101100100—101210121111—2???????
Corimelaena (P.) extensa	000010120——1001000100010201100101000 10–1010000111101 10——0011031011010010?1111101100100—101210121100002 1?1?000
Corimelaena (P.) incognita	000010120——100100010001020110010101010–1010100111101 10——0011031011000000?1111101000100—101210121120102101?010
Corimelaena (P.) parana	001120130——0011010101010102000001010111 0–10111001??10110——0011031001000010?11111010020–0—001210101100002???????
Corimelaena (P.) virilis	000010120——100100010001020110010100010–10110001??10110——00110310?1010010111111011 00100—101210121100112?0120?0
Corimelaena (T.) minutissima	000000120——000000010001020100010101010–10111001??10110——0011031001000000?11001010000–0—00121102110010 2?????? ?

TABLE 4. Classification of Thyreocoridae based on the results of the cladistic analysis.

Taxa	**Number of subgenera**	**Number of species**
Thyreocorinae		7
Carrabas Distant, 1908		1
Strombosoma Amyot & Serville, 1843		2
Thyreocoris Schrank, 1801		4
Corimelaeninae		205
Alkindus Distant, 1889		2
Amyssonotum Horvath, 1919		1
Cydnoides Malloch, 1919	3	9
Eumetopia Westwood, 1838		1
Galgupha Amyot & Serville, 1843	15	155
Godmania Horvath, 1919		1
Pericrepis Horvath, 1919		4
Pruhleria McAtee & Malloch, 1933		1
Corimelaena White, 1839		31
C. agrella McAtee, 1919		
C. alpina (McAtee & Malloch, 1933)		
C. alticola (Horvath, 1919)		
C. barberi (McAtee & Malloch, 1933)		
C. californica Van Duzee, 1929		
C. championi (Distant, 1880)		
C. cognata (Van Duzee, 1907)		
C. contrasta (McAtee & Malloch, 1933)		
C. corallina (McAtee & Malloch, 1933)		
C. digitata (McAtee & Malloch, 1933)		
C. elegans (McAtee & Malloch, 1933)		
C. extensa Uhler, 1863		
C. feminea (McAtee & Malloch, 1933)		
C. harti Malloch, 1919		
C. incognita (McAtee & Malloch, 1933)		
C. interrupta Malloch, 1919		
C. lateralis (Fabricius, 1803)		
C. limata (McAtee & Malloch, 1933)		
C. marginella Dallas, 1851		
C. micans (McAtee & Malloch, 1933)		
C. minuta Uhler, 1863		
C. minutissima Malloch, 1919		

C. nigra Dallas, 1851

C. obscura McPherson & Sailer, 1978

C. palmeri (McAtee & Malloch, 1933)

C. parana McAtee & Malloch, 1928

C. polita Malloch, 1919

C. pulicaria (Germar, 1839)

C. signoretti (McAtee & Malloch, 1933)

C. tibialis (Fabricius, 1803)

C. virilis (McAtee & Malloch, 1933)

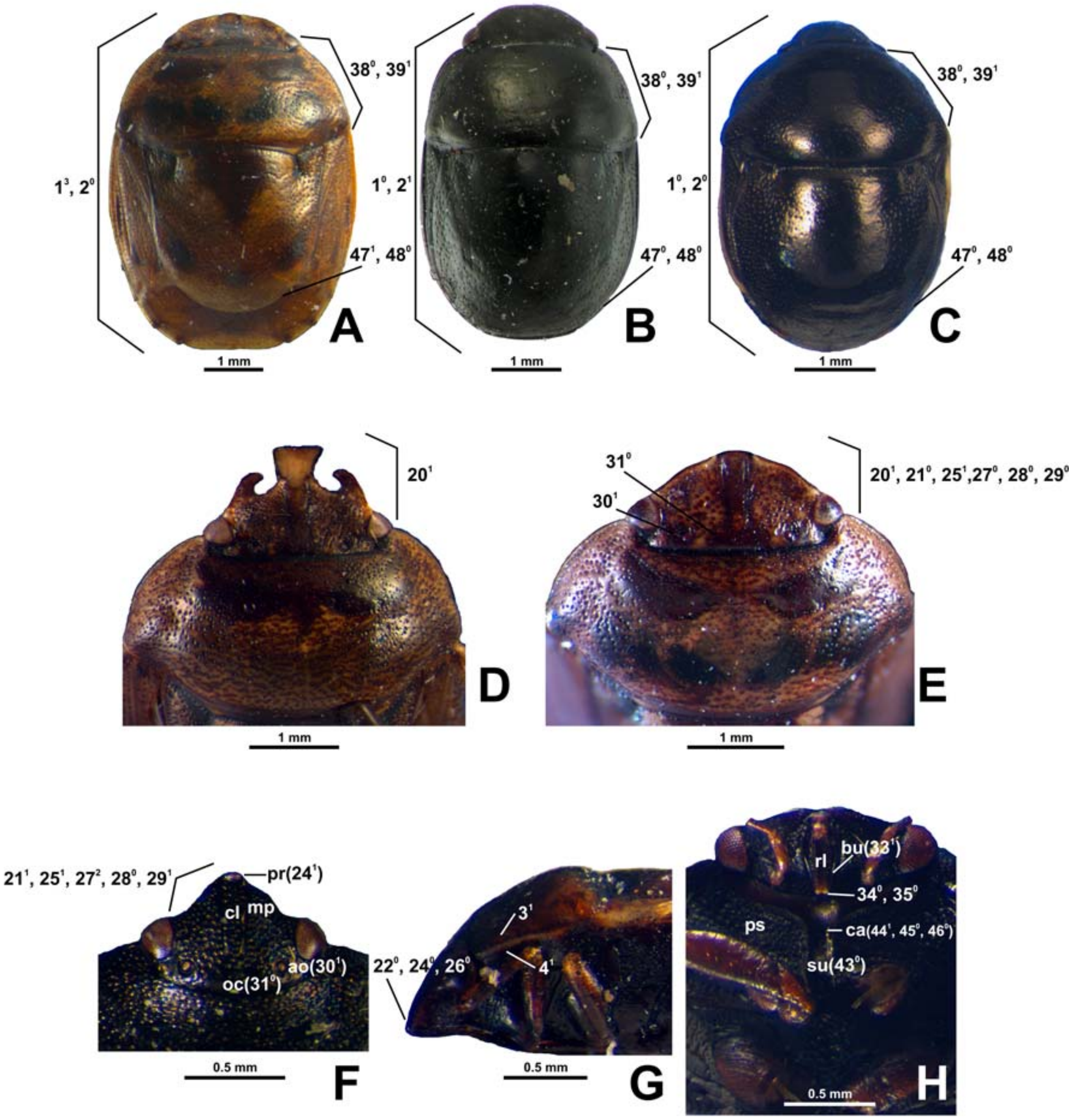

Figure 1. A-C, adult, dorsal view: A, *Eumetopia fissipes* Westwood; B, *Alkindus crassicosta* Horvath; C, *Corimelaena (Corimelaena) lateralis* (Fabricius). D-E, *E. fissipes*, head and pronotum, dorsal view: D, male; E, female. F, *C. (C.) marginella* Dallas, head, dorsal view. G, *Corimelaena (Parapora) parana* McAtee & Malloch, head and thorax, lateral view. H, *Thyreocoris scarabaeoides* (Linnaeus), head and thorax, ventral view. Abbreviations: ao–area between the eye and the ocellus, at–antenniferous tubercle, bu–bucula, ca–carina, cl–clypeus, mp–mandibular plate, oc–occiput, pr–protuberance, ps–prosternum, rI–rostrum I, su–sulcus.

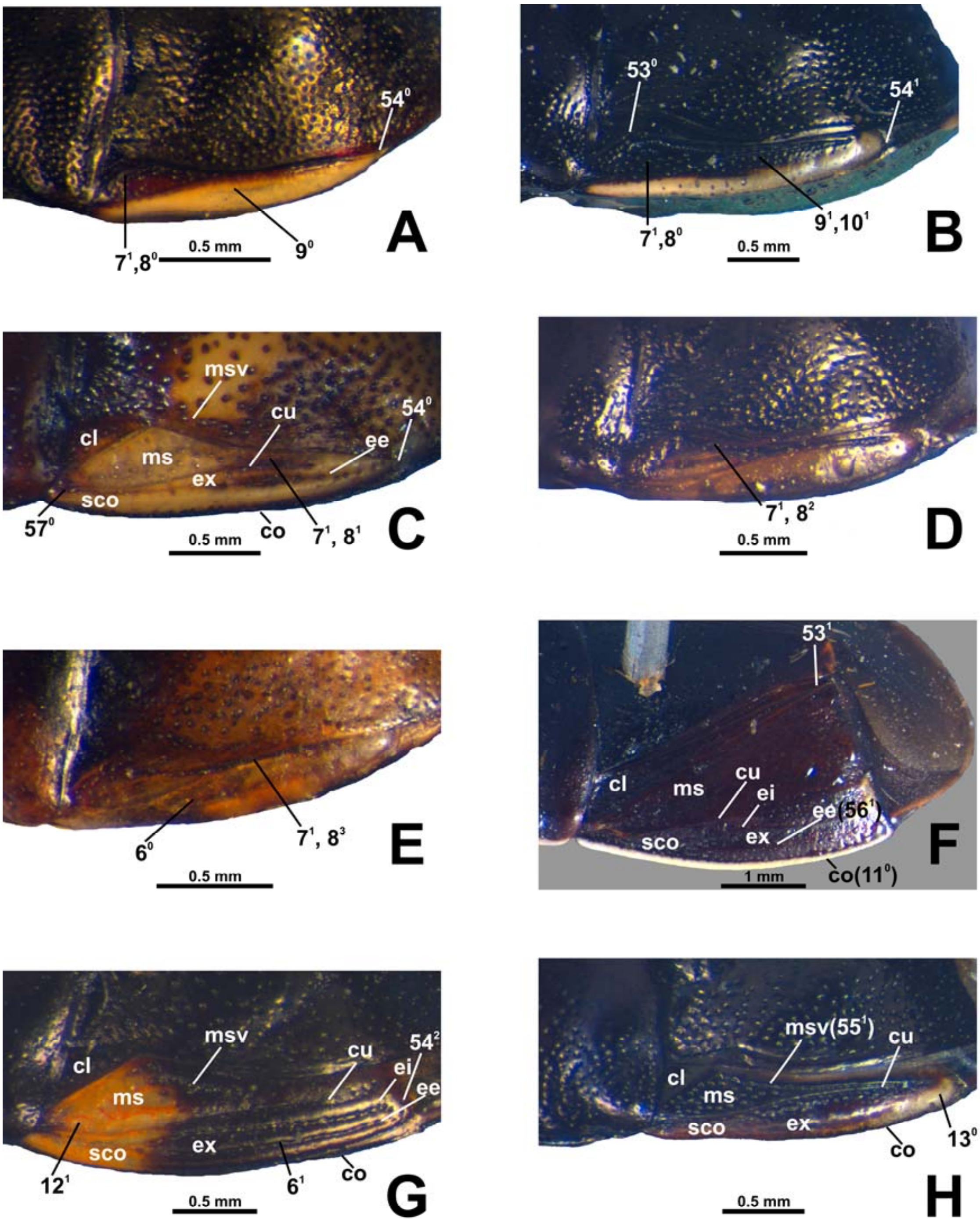

Figure 2. A-H, corium, dorsolateral view: A, *Corimelaena (Corimelaena) harti* Malloch; B, *C. (C.) lateralis* (Fabricius); C, *Pericrepis callosula* Horvath; D, *C. (C.) pulicaria* (Germar); E, *C. (Parapora) parana*; F, *Sehirus cinctus* (Palisot de Beauvois); G, *Galgupha (Euryscytus) difficilis* (Breddin); H, *C. (C.) obscura* McPherson & Sailer. Abbreviations: cl–clavus, co–costa, cu–cubital vein, ee–external branch of the exocorial vein, ei–internal branch of the exocorial vein, ex–exocorium, ms–mesocorium, msv–mesocorial vein, sco–subcostal area.

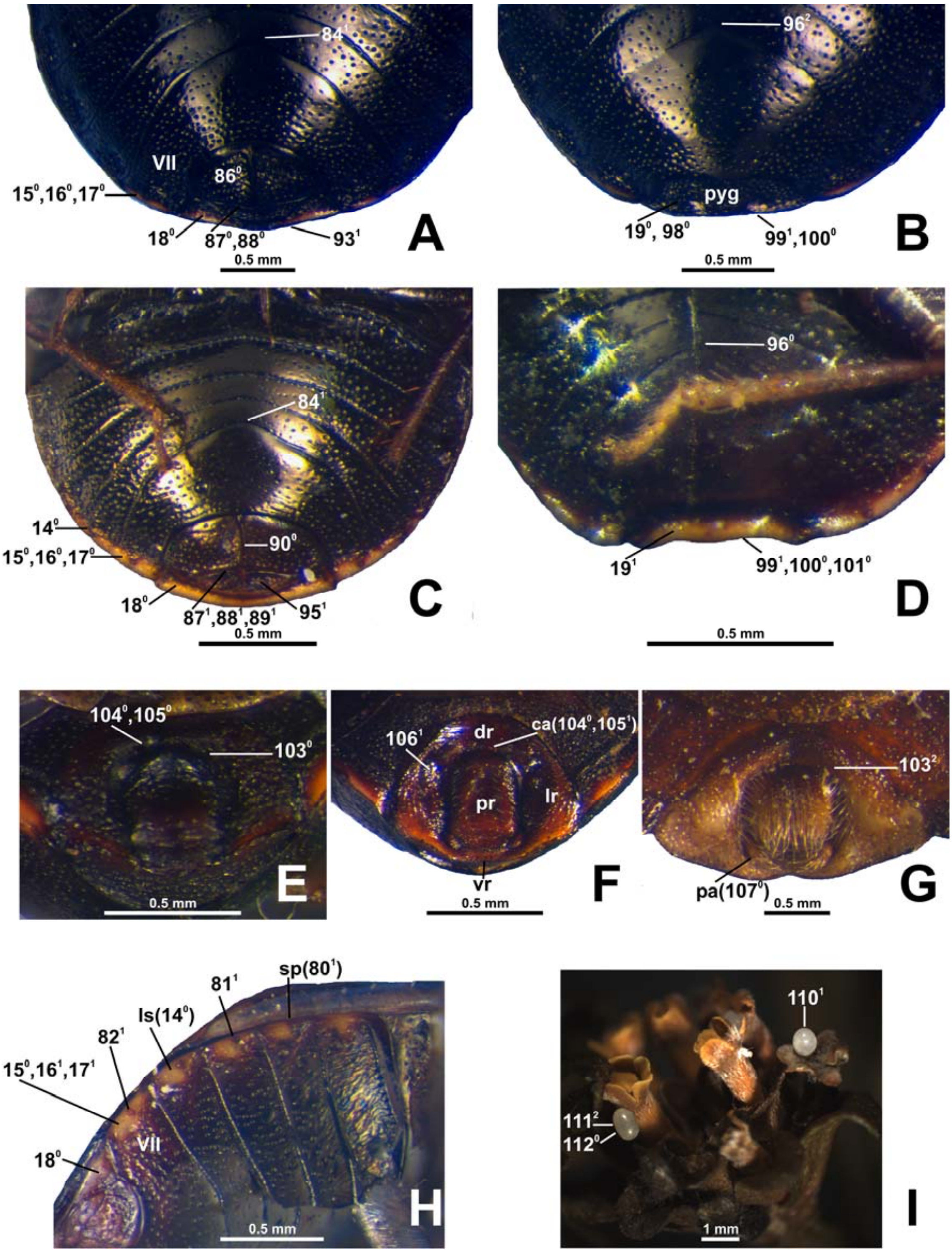

Figure 3. A-B, *Corimelaena (Corimelaena) lateralis* (Fabricius), abdomen, ventral view: A, female; B, male. C-D, *C. (C.) tibialis* (Fabricius), abdomen, ventral view: C, female; D, male. E-G, Pygophore, dorsoposterior view: E, *C. (Parapora) extensa* Uhler; F, *C. (P.) virilis* (McAtee & Malloch); G, *Eumetopia fissipes* Westwood. H, *C. (P.) parana,* female abdomen, ventral view. I, Eggs of *Galgupha (Gyrocnemis) fossata*

McAtee & Malloch attached to inflorescence of *Buddleia brasiliensis* Jacq. ex Spreng. Abbreviations: VII–sternite VII, ca–carina, dr–dorsal rim, lr–lateral rim, ls–lateral spot, pa–paramere, pr–proctiger, pyg–pygophore, sp–spiracle, vr–ventral rim.

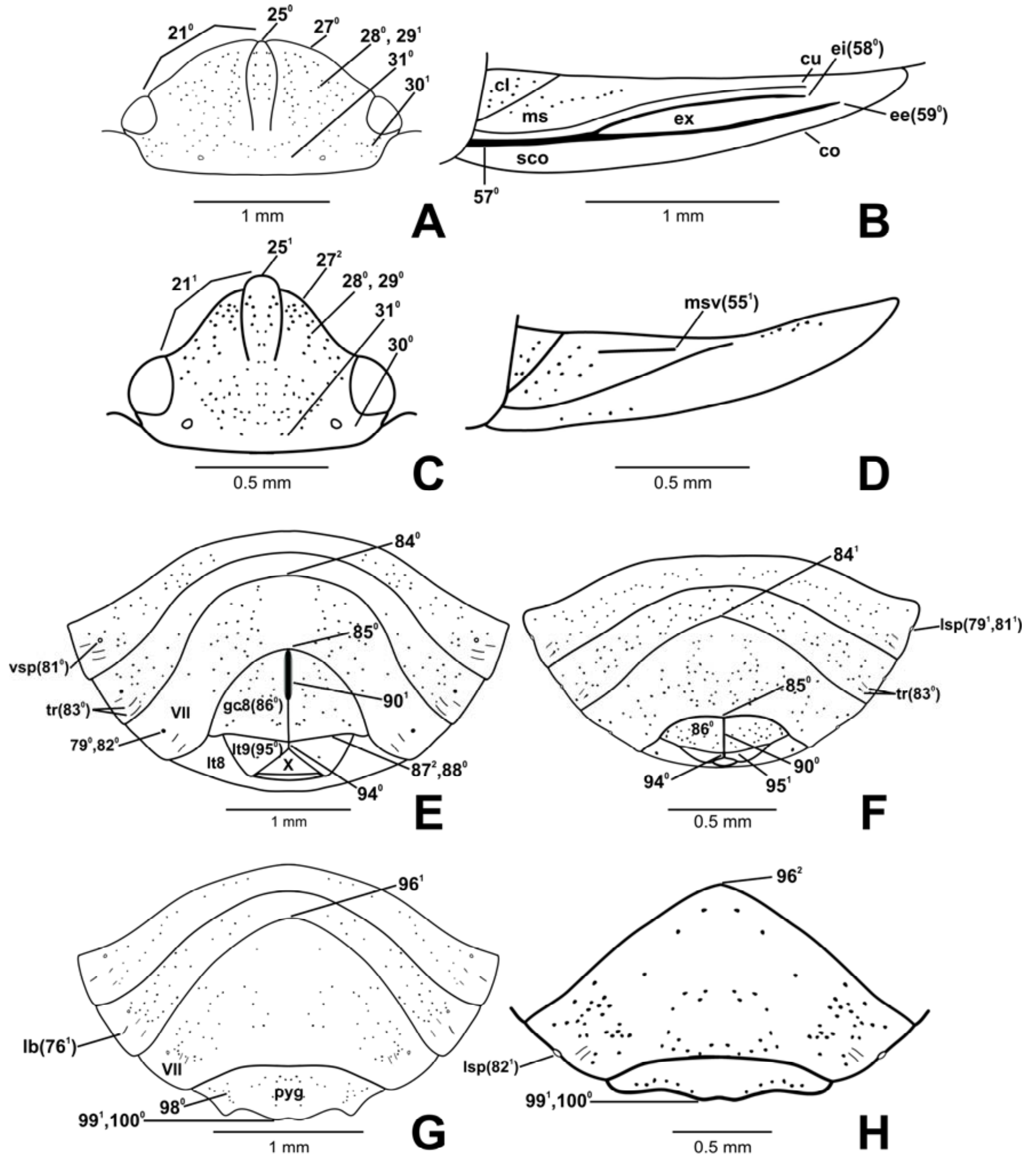

Figure 4. A-B, *Alkindus atratus* Distant: A, head, dorsal view; B, corium, dorsolateral view. C-D, *Corimelaena (Parapora) parana* McAtee & Malloch: C, head, dorsal view; D, corium, dorsolateral view. E, *A. atratus*, female abdomen, ventral view. E, *C. (P.) parana*, female abdomen, ventral view. G, *A. atratus*, male abdomen, ventral view. E, *C. (P.) parana*, male abdomen, ventral view. Abbreviations: VII–sternite VII, X–segment X, cl–clavus, co–costa, cu–cubital vein, ee–external branch of the exocorial vein, ei–internal branch of the exocorial vein, ex–exocorium, gc8–gonocoxite 8, lb–lateral bristle, lsp–lateral spiracle, lt8–laterotergite 8, lt9–laterotergite 9, ms–

mesocorium, msv–mesocorial vein, pyg–pygophore, sco–subcostal area, tr–tricobothria, vsp– ventral spiracle.

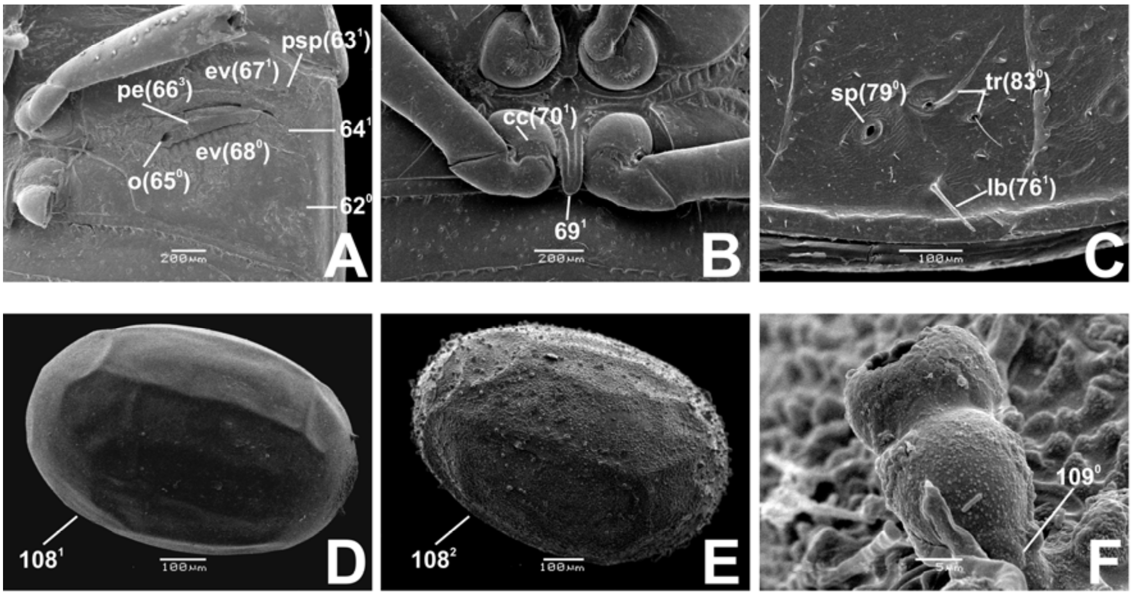

Figure 5. Adult and immature thyreocorid structures under scanning electron microscopy (SEM). A-C, *Alkindus atratus* Distant: A, meso- and metapleuron, showing external scent efferent system; B, metasternum with median projection and coxal combs; C, lateral bristle on abdominal sternite. D-F, eggs: D, *Galgupha (Euryscytus) difficilis* (Breddin); E-F, *G. (Gyrocnemis) fossata* McAtee & Malloch; F, aero-micropylar process. Abbreviations: cc–coxal comb, ev–evaportorium, lb–lateral bristle, o–ostiole, pe–peritreme, psp–pseudoperitreme, sp–spiracle, tr–trichobothria.

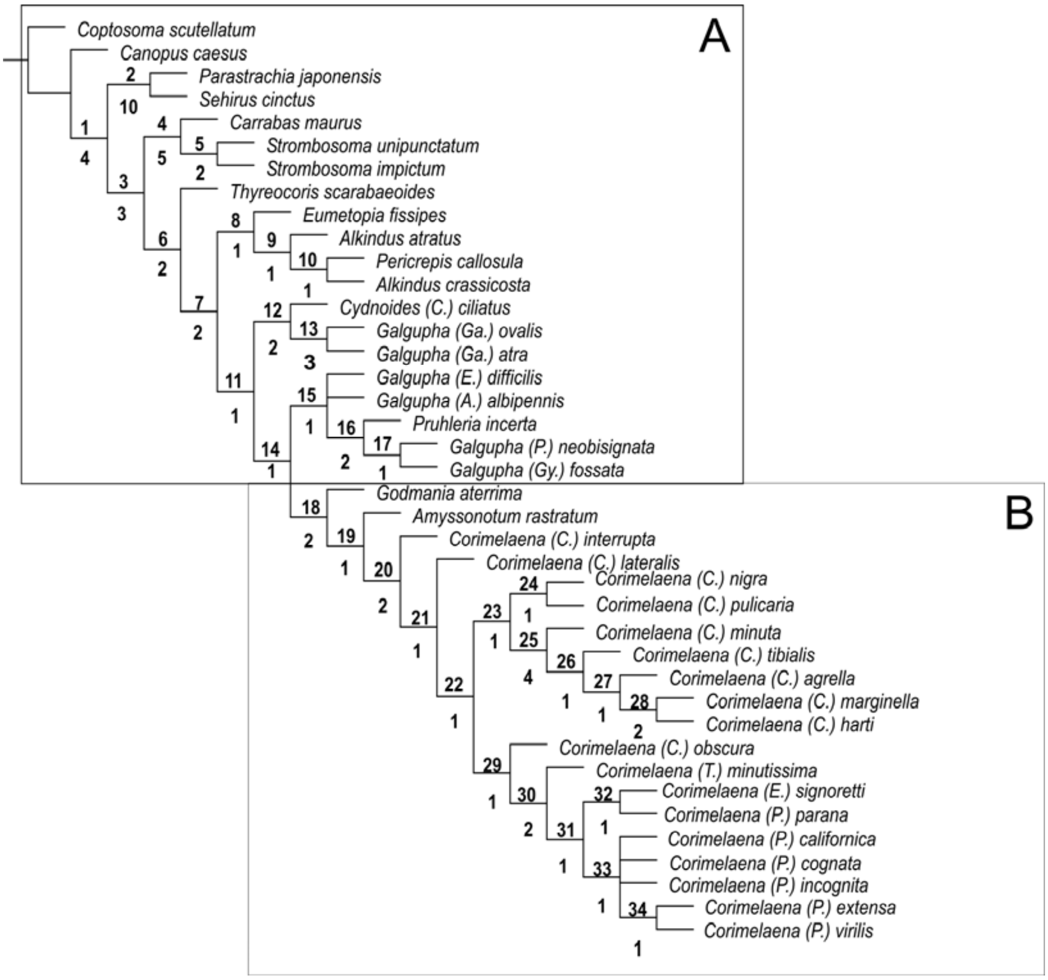

Figure 6. Strict consensus of the six most parsimonious trees found in the analysis (L = 418, CI = 33, RI = 61). The numbers above nodes refer to the nodes mentioned in the text. Bremer support values are indicated below nodes. Parts A and B are detailed in the following figures.

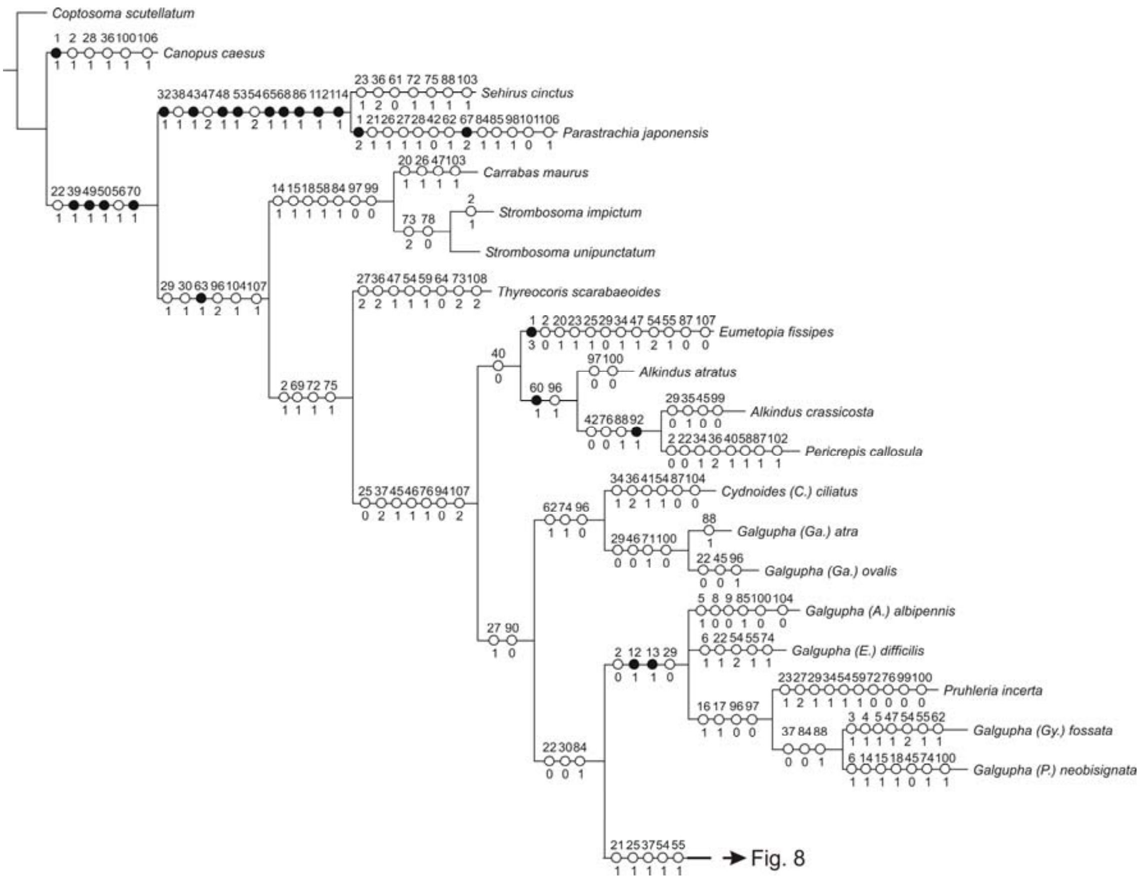

Figure 7. Part A of the strict consensus tree, showing unambiguous characters. Black circles represent non-homoplastic derived states; white circles represent homoplastic derived states. Numbers above circles represent characters; numbers below circles represent character states.

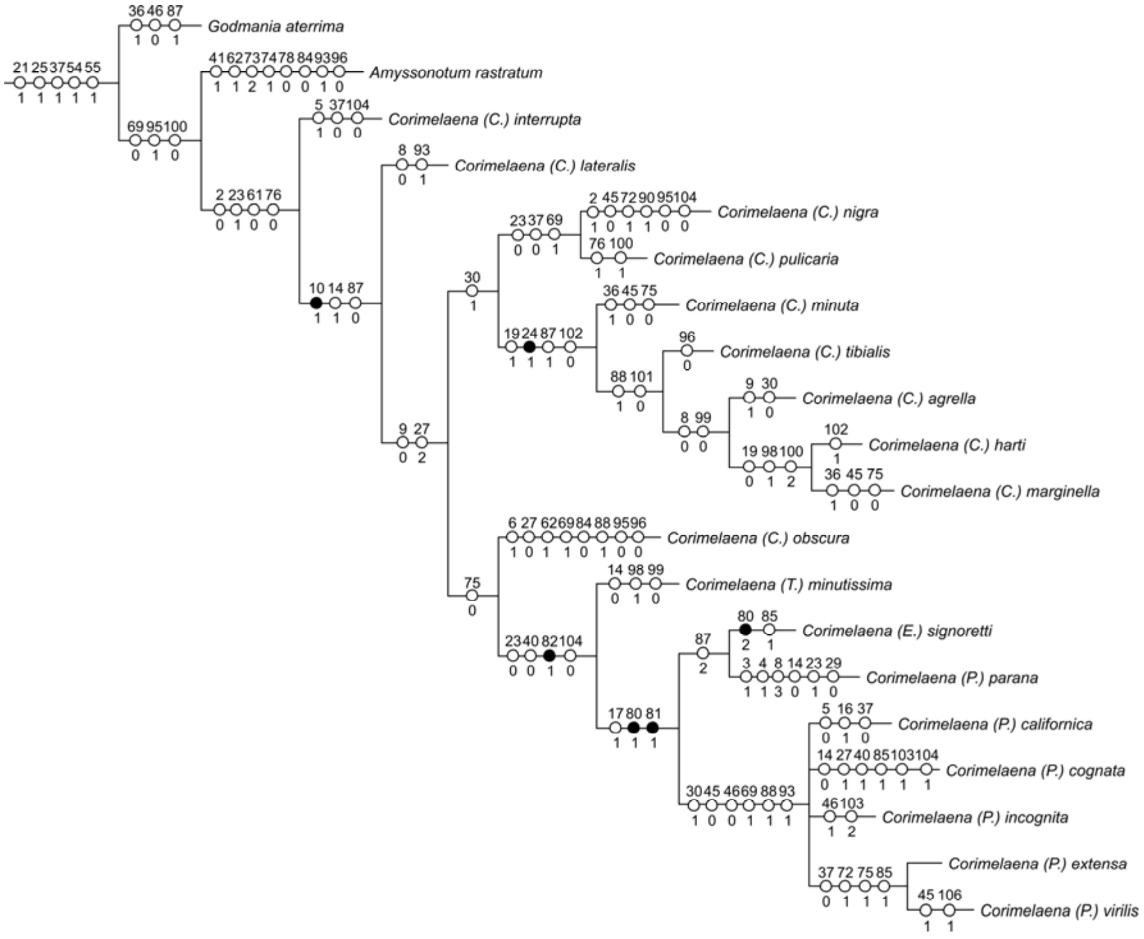

Figure 8. Part B of the strict consensus tree, showing unambiguous characters. Black circles represent non-homoplastic derived states; white circles represent homoplastic derived states. Numbers above circles represent characters; numbers below circles represent character states.

CAPÍTULO 4

External egg structure of the Pentatomidae (Hemiptera: Heteroptera) and the search for characters with phylogenetic importance

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Abstract

The chorionic structure of sixteen pentatomid species is described. Morphological patterns in different taxonomic levels are discussed. In addition, egg characters useful in cladistic analyses are listed, and some of those characters are tested for congruence with two cladistic analyses previously conducted within Pentatomidae. Descriptive studies were conducted with *Banasa induta*, *Capivaccius bufo*, *Catulona pensa*, *Chinavia armigera*, *Chinavia aseada*, *Chinavia brasicola*, *Chinavia runaspis*, *Dichelops furcatus*, *Euschistus heros*, *Euschistus riograndensis*, *Euschistus paranticus*, *Mormidea cornicollis*, *Podisus distinctus*, *Podisus nigrispinus*, *Serdia apicicornis*, and *Thoreyella maracaja*. Adults were collected in southern Brazil and maintained in pots until oviposition. The eggs were examined and photographed under light and scanning electron microscopy. Based on literature data, a list of 40 egg characters with potential phylogenetic importance has been compiled. Some of these characters were included in the cladistic analyses of the genus *Nezara* (six characters) and of the *Chinavia obstinata* group (five characters). Both analyses were performed in TNT with equal weighting of characters. The eggs of most of the Neotropical species studied were barrel-shaped, chorion translucent and spinose, with aero-micropylar processes that were short and clubbed. The patterns of egg morphology could be identified in Carpocorini, Procleticini, and in the genera *Banasa*, *Chinavia*, *Euschistus*, *Mormidea*, and *Podisus*. In the cladistic analyses, the inclusion of egg characters did not affect the topology of the trees shown in the original papers. For the analyses, the egg characters were somewhat informative. At present, a total of 286 Pentatomidae species have their egg stage described.

Key words: Asopinae; Carpocorini; Discocephalinae; Nezarini; Pentatominae; Procleticini

Introduction

The importance of egg structure in defining the status and relationships among heteropteran groups has long been recognized. In the Pentatomoidea, patterns of egg morphology have been identified at different levels (Leston 1955; Southwood 1956; Cobben 1968; Javahery 1994; Matesco *et al.* 2009, 2012). The egg stage has been rarely used in cladistic analyses, although its importance has been widely emphasized. Egg characters usually support groups at high taxonomic levels (Hasan & Kitching 1993; Wheeler *et al.* 1993; Henry 1997; Grazia *et al.* 2008).

The most important list of characters for the eggs of the Pentatomoidea is shown by Javahery (1994), who attempted to conduct a phylogenetic analysis of genera based on the egg stage. The matrix sums 22 characters for 23 pentatomoid genera, with an aim of identifying the characters with phylogenetic value and separating them from characters that are temporary adaptations to a specific environment. Because of several methodological problems in Javahery's analysis (e.g., non-independence of characters, absence of an outgroup and obscure computational analysis), his results are often overlooked despite their relevance to the contribution of the egg stage in phylogenetic studies.

The egg stage remains not described in four of the 15 families of Pentatomoidea (Saileriolidae, Canopidae, Megarididae, and Lestoniidae). For the majority of the families, comprehensive works about the egg stage report only some data (Leston 1955; Southwood 1956; Cobben 1968; Hinton 1981; Javahery 1994). There are also scattered descriptions in the literature, including recent papers with high-quality scanning electron microscopy images, most of them of Scutelleridae (Candan & Suludere 2003, 2006; Williams *et al.* 2005; Candan *et al.* 2007, 2011). Within some families (e.g., Dinidoridae, Tessaratomidae, and Scutelleridae), the morphology of the eggs appears to be relatively well known, but a survey of the number of species studied is still missing. Davidová-Vilímová (1987) reviewed the eggs of the Plataspididae, and more recent studies have been performed (Ren *et al.* 1990; Ren 1992; Candan *et al.* 2012). For the Thyreocoridae *sensu lato* (including Parastrachiinae), a recent review lists descriptions of the egg stage for 13 of the approximately 220 species of the group (Matesco *et al.* 2012).

On the other hand, the eggs of pentatomids have been described for more species than those of any other family in the Heteroptera (Southwood 1956; Hinton 1981; Wolf & Reid 2003), even though it has been considered the least studied developmental stage of the family (Bundy & McPherson 2000). Although some studies were overlooked, Matesco *et al.* (2009) listed 125 species whose eggs have been described by either stereomicroscopy or scanning electron microscopy. We performed a broader search in the literature, and this number has now been raised to 286 species (Table 1). The present revision is by no means exhaustive, but efforts have been made to maximize the available information about the number of species whose eggs have been thus far documented.

Eggs of the Pentatomidae can be easily recognized and bear important characters for the identification of species and genera, such as the color, shape, and size of the egg; the chorion sculpture; and the number, shape, and size of the aero-micropylar processes (Esselbaugh 1946; Hinton 1981; Saini 1984; Javahery 1994; Bundy & McPherson 2000; Candan *et al.* 2001). Patterns at the tribe and subfamily level have also been investigated (Matesco *et al.* 2009). Despite the knowledge available on the egg stage, in terms of diversity of taxa, there are no cladistic analyses at low taxonomic levels within the Pentatomidae including egg characters.

In this paper, the external chorionic structure of sixteen pentatomid species is described, the recognition of morphological patterns at different taxonomic levels is discussed, the egg characters of potential use in cladistic analyses are listed, and some of those characters are tested in two cladistic analyses previously performed within the Pentatomidae.

Material and Methods

Descriptive morphology

Adults of sixteen species of the Pentatomidae were collected in the states of Rio Grande do Sul, Santa Catarina, and Paraná, Brazil (Table 2) and maintained in pots until oviposition. The eggs were examined by stereomicroscopy (SM) and scanning electron microscopy (SEM) and photographed. The egg length and width were measured in millimeters (mean ± standard deviation, minimum and maximum), and the aero-micropylar processes (AMPs) were counted (Table 2). The descriptive terminology used followed Bundy & McPherson (2000), Wolf & Reid (2001), and Matesco *et al.* (2009). For the SEM analyses, two eggs of each species were fixed and prepared according to Bianchi *et al.* (2011). The samples were critical-point dried, mounted on stubs, coated with gold, and analyzed with a JEOL scanning electron microscope, JSM 6060, at the Center of Electron Microscopy of the Federal University of Rio Grande do Sul ("Centro de Microscopia Eletrônica da Universidade Federal do Rio Grande do Sul"–CME/UFRGS), Brazil.

Voucher specimens are deposited at the Entomological Collection of the Zoology Department, Federal University of Rio Grande do Sul ("Coleção Entomológica do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul"–UFRG), Brazil.

Search for characters of phylogenetic importance

A list of egg characters with potential phylogenetic importance was compiled based on the literature. The phylogenetic signal in low taxonomic level analyses within the Pentatomidae was tested for some of these characters: in the analysis of the genus *Nezara* Amyot & Serville (Ferrari *et al.* 2010) and in the analysis of the *Chinavia obstinata* (Stål) group (Genevcius *et al.* 2012). Egg characters were mainly based on Hasan and Kitching (1993) and Javahery (1994), and we searched for character states in the literature about egg morphology and reproductive biology (Whitmarsh 1917; Esselbaugh 1946; Leston 1955; Kobayashi 1959, 1994; Putshkova 1961; Lodos 1964; Rizzo 1968, 1976; Hinton 1981; Ren *et al.* 1990; Brailovsky *et al.* 1992; Ren 1992; Javahery 1994; Candan & Suludere 1999a; Bundy & McPherson 2000; Wolf *et al.* 2002, 2003; Matesco *et al.* 2003, 2007, 2009). Character states were obtained from the literature and from specimens deposited at UFRG. In the analysis of *Nezara*, a "chimera" was created for *Carpocoris purpureipennis* (DeGeer), crossing features from congeneric species with described eggs (Table 1). The preparation of the characters follows Sereno (2007).

In the *Nezara* matrix, six characters were added (Table 3), of which three are discrete (one multistate, treated as non-additive) and three are continuous. In the *C. obstinata* group matrix, five characters were added (Table 4), of which two are discrete (both binary) and three are continuous. Both analyses were performed with TNT (Goloboff *et al.* 2003), following the same parameters used in the original papers and considering only equal weighting of the characters. The continuous characters were normalized in a range between 0 and 1. Continuous characters in the same range prevent the problems associated with the direct use of measures of different scale size. According to Goloboff *et al.* (2006), when continuous characters are treated as such, rather than distorted through discretization, they appear to indeed carry useful phylogenetic information.

Results

Descriptive morphology

Asopinae

Podisus distinctus (Stål, 1860) and *Podisus nigrispinus* (Dallas, 1851)

(Figs. 1, 13–22; Tab. 2)

Eggs barrel-shaped; color prior to embryonic development yellow in *P. distinctus* and golden yellow with black spines in *P. nigrispinus* (Fig. 1); operculum round and convex; chorion translucent and spinose. An eclosion line is evident under SM as a smooth light band delimited by the AMPs (Fig. 1). With the development of the embryo, the eggs become darker, and the red eyes of the nymph become evident through the chorion. The aero-micropylar processes are circularly arranged in a row around the anterior pole, translucent, very long and slender (Fig. 1). Embryonic development has not been followed, so the egg-burster has not been observed. According to Grazia *et al.* (1985), the egg-burster in *P. nigrispinus* (described as *P. connexivus* Bergroth) does not become evident during embryonic development because of its lighter color. The morphological aspects of the eggs have been previously studied under SM for *P. nigrispinus* (Grazia *et al.* 1985; Saini 1994) and more recently under SEM for *P. distinctus*, emphasizing its postdepositional dynamics (Sá *et al.* 2013).

The chorion surface is sparsely spinose under SEM. The lateral wall bears short interconnected spines forming wide polygonal markings (Figs. 13, 15, 18, 20). The operculum is similarly sculptured, but the spines are longer, and the polygonal markings are less evident (Figs. 14, 19), especially in *P. nigrispinus*. The eclosion line is evident as a slightly depressed broad smooth strip (Figs. 16, 21). The aero-micropylar processes are slightly clubbed at apex, and their openings are subapical and outwardly directed (Figs. 16, 17, 21, 22). The surface of the processes is smooth even under higher magnification (Figs. 17, 22).

Discocephalinae

Ochlerini

Catulona pensa Rolston, 1992

(Figs. 23–25; Tab. 2)

Eggs barrel-shaped to subspherical; pearly white prior to embryonic development; operculum broadly round and convex; chorion shiny and smooth. The aero-micropylar processes arranged in an ellipse not coincident to the operculum margin and translucent, short, and clubbed.

The chorion surface is smooth under SEM (Fig. 23). At the posterior pole, there are the remnants of adhesive substances. The operculum may be somewhat granulated, and the eclosion line is evident as a narrow marked strip inward from the AMPs (Figs. 24, 25). The AMPs are strongly clubbed and without evident openings (Figs. 24, 25). Under higher magnification, the surface of those processes is irregular but not spongy (Fig. 25).

Pentatominae

Carpocorini

Dichelops (*Diceraeus*) *furcatus* (Fabricius, 1775)

(Figs. 26–30; Tab. 2)

Eggs barrel-shaped; light green prior to embryonic development; operculum round and convex; chorion translucent and spinose. The eclosion line is not evident under SM; the AMPs are circularly arranged in a row around the anterior pole, translucent, moderately short, and clubbed. Embryonic development has not been followed, but according to Grazia *et al.* (1982), the egg becomes grayish green, and the red eye spots, and the dark T-shaped egg-burster become visible. Morphological aspects of the eggs of this species have been previously studied under SM by Grazia *et al.* (1982).

The chorion surface is densely spinose under SEM. Interconnected spines form polygonal markings at the lateral wall (Figs. 26, 28); the spines display different sizes and can be connected by a short membrane (Fig. 28). The operculum is similarly sculptured, but the spines are longer, and the polygonal markings are somewhat obliterated at the periphery (Fig. 27, 29). The eclosion line is evident as a narrow strip of very short spines inward from the AMPs (Fig. 29). The AMPs are stout and clubbed; their openings are not evident (Figs. 29, 30). Under the magnification used, the AMPs surfaces appear irregular but not spongy.

***Euschistus* (*Euschistus*) *heros* (Fabricius, 1798), *Euschistus* (*Lycipta*) *riograndensis* Weiler & Grazia, 2011, and *Euschistus* (*Mitripus*) *paranticus* Grazia, 1987**

(Figs. 2, 3, 31–42; Tab. 2)

Eggs barrel-shaped; color prior to embryonic development light green (in *E. heros*) or white (in *E. riograndensis* and *E. paranticus*) (Figs. 2, 3); operculum round, with variable convexity, usually slightly convex (Figs. 2, 3), but conspicuously flatter in *E. heros*; chorion translucent and spinose. The eclosion line is not evident under SM; the AMPs are circularly arranged in a row around the anterior pole, white, moderately long and filiform (Figs. 2, 3).

The chorion surface of all species of *Euschistus* Dallas studied here is densely spinose under SEM. The interconnected spines form polygonal markings that are mostly triangular at the lateral wall (Figs. 31, 39). The spines display different sizes, being usually thicker and longer at the triangle vertices (Figs. 33, 37, 38). This pattern may be obscured by traces of adhesive material gluing adjacent eggs (Fig. 39). The operculum is similarly sculptured, with interconnected spines forming triangles (Figs. 32, 36, 40). The spines are shorter at the center of the operculum, and polygonal markings are sometimes obliterated (Fig. 36). The spines display different sizes and are interconnected by a short membrane at the periphery of the operculum (Figs. 34, 41). The eclosion line is not evident. The AMPs are tubular in *E. riograndensis* (Fig. 38) and slightly clubbed in the two other species (Figs. 33, 34, 41). Their openings are circular and apical, and there are fine connector sheets among adjacent AMPs in *E. heros* (Fig. 34). The surface of the AMPs is spongy under higher magnification (Figs. 35, 42).

***Mormidea cornicollis* Stål, 1860**

(Figs. 4, 5, 43–46; Tab. 2)

Eggs barrel-shaped; light yellow prior to embryonic development; operculum round and convex; chorion translucent and spinose (Fig. 4). Eggs darker, with two irregular red stripes and red eyes evident in anterior view after embryonic development (Fig. 5). The eclosion line not evident under SM, and the AMPs are circularly arranged in a row around the anterior pole, white, and moderately long (Figs. 4, 5).

Under SEM, the chorion surface is spinose, and the spines are short. The interconnected spines form faintly distinct polygonal markings at the lateral wall; the sculpture pattern is altered where the eggs were attached to another (Fig. 43). The operculum is similarly sculptured, displaying spines of different sizes, and the polygonal markings are especially apparent (Figs. 44, 45). The eclosion line is not discernible. The AMPs are slender, only slightly clubbed, and bear circular and apical openings (Fig. 46). Their surface is clearly spongy under higher magnification (Fig. 46).

Nezarini

***Chinavia armigera* (Stål, 1854), *Chinavia aseada* (Rolston, 1983), *Chinavia brasicola* (Rolston, 1983), *Chinavia runaspis* (Dallas, 1851)**

(Figs. 6–9, 47–65; Tab. 2)

Eggs barrel-shaped; light brown prior to embryonic development; operculum round and convex; chorion light brown, reticulated, and usually opaque (Figs. 7–9), shiny in *C. armigera* (Fig. 6). The eclosion line evident under SM and indicated as a smooth band delimited by the AMPs (Figs. 6, 8, 9). With the development of the embryo, the red eyes of the nymph become evident through the chorion (Fig. 6). The aero-micropylar processes are circularly arranged in a row around the anterior pole, clubbed, and translucent (*C. aseada*) to white (remaining species) (Figs. 6–9).

The chorion surface of all species of *Chinavia* Orian studied here is reticulated under SEM, with circular or polygonal cells (Figs. 47, 52, 56, 60). In some species, these cells may be quite regularly hexagonal at the lateral wall (Fig. 49). The cells project inward in a funnel, appearing to bear a hole (Figs. 49, 54, 58). The operculum is similarly sculptured but with smaller cells at center (Figs. 48, 50, 53, 57, 61, 62). The eclosion line is wide and clearly evident, marked by several minute and irregular projections (Figs. 51, 55, 59, 63). The AMPs are moderately short and strongly clubbed, with their openings circular and apical (Figs. 51, 54, 55, 58, 59, 63, 64). Fine connector sheets among adjacent AMPs have been observed in some of the eggs of all species (Figs. 51, 54, 55, 58, 64). Under higher magnification, the AMPs surface is spongy (Figs. 51, 55, 59, 65).

Pentatomini

Banasa induta **Stål, 1860**

(Figs. 10, 66–69; Tab. 2)

Eggs barrel-shaped; brown prior to embryonic development; operculum round and convex; chorion light brown, almost translucent, and reticulated (Fig. 10). The eclosion line is evident under SM, as a smooth paler band delimited by the AMPs (Fig. 10). The aero-micropylar processes are circularly arranged in a row around the anterior pole, white, short, and clubbed (Fig. 10).

The chorion surface is reticulated under SEM, but the sculpture pattern may be obliterated in some portions of the egg (Fig. 66). Remnants of adhesive material are evident at the posterior pole; at the lateral wall, the sculpture pattern is clearly altered in the area where the egg was fixed to another in the egg mass (Fig. 66). Most of the chorion is recovered by shallow cells with irregular edges forming truncated rough masses. The operculum is similarly sculptured (Fig. 67). The eclosion line is evident as a broad depressed band, in which there are smaller rough masses, more widely spaced near the AMPs (Fig. 68). The AMPs are moderately short and distinctly clubbed, with circular and apical openings (Fig. 68). Their surface is clearly spongy under higher magnification (Fig. 69).

Serdia apicicornis **Stål, 1860**

(Figs. 11, 70–73; Tab. 2)

Eggs spherical; light green prior to embryonic development; operculum broadly round and convex; chorion translucent and granulated (Fig. 11). The eclosion line is not evident under SM, and the AMPs are circularly arranged in a row around the anterior pole, slightly displaced posteriorly, translucent, short, and clubbed (Fig. 11).

The chorion surface is granulated under SEM, with perfectly circular projections evenly distributed (Figs. 70, 72). Although the egg may be described as spherical, the posterior pole is flatter than the anterior pole and bears traces of the adhesive material secreted by the female to glue the eggs to the substrate (Fig. 70). The operculum is similarly sculptured (Fig. 71), and the eclosion line is present as a narrow strip very near the AMPs, with smaller granules placed closer to each other (Fig. 72). Except for the eclosion line, the surface of the egg is remarkably uniform. The AMPs are very small, club-shaped, with circular and apical openings (Figs. 72, 73). Under higher magnification, the surface of the processes is slightly spongy (Fig. 73).

Procleticini

Thoreyella maracaja Bernardes, Schwertner & Grazia, 2011

(Figs. 12, 74–76; Tab. 2)

Eggs with flat lateral walls, cross-section of chorion subquadrangular; light green prior to embryonic development; operculum subquadrangular and flat; chorion translucent and granulated, both at the lateral walls (Fig. 12) and at the operculum. The eclosion line not evident under SM, and the AMPs are circularly arranged in a row around the anterior pole, translucent, long, and filiform (Fig. 12).

The chorion surface appears mostly smooth under SEM but is clearly granulated at the lateral wall (Figs. 74, 75). In the micrographs, the eclosion line is obscured, and the AMPs are apparently smooth (Fig. 76).

Unplaced

Capivaccius bufo Distant, 1893

(Figs. 77–81; Tab. 2)

Eggs barrel-shaped; color prior to embryonic development white with a dark spot at operculum and a wide spot at the middle of lateral wall; operculum round, central portion slightly convex; chorion reticulated, light brown with dark brown spots. The eclosion line is not evident, and the AMPs are inconspicuous under SM.

The chorion surface is reticulated and covered by hexagonal cells with fringed edges under SEM (Figs. 77, 78). At the lateral wall, especially near the anterior pole, the cells are delimited by long and filiform chorionic projections (Fig. 78); this confers an aspect far more pilose to the lateral wall than to the operculum (Figs. 77, 79). The operculum is similarly sculptured, except for shorter fringes (Fig. 77, 79); the eclosion line is evident, marked by the absence of hexagonal cells and surrounded by dense irregular laminate chorionic projections (Figs. 80, 81). The AMPs are circularly arranged in a row around the anterior pole, short and clubbed but scarcely visible at lower magnification, except for circular and spaced spots in which the chorionic projections are sparser (Fig. 77). Their opening, if present, is not evident (Figs. 79, 81). Under high magnification, the surface of those processes is at most irregular but not spongy (Fig. 81).

Search for characters of phylogenetic importance

Based on descriptive papers and comprehensive studies of egg morphology in Pentatomoidea, 40 characters of potential phylogenetic importance are mentioned (Table 5). Seven of them could be observed and were used here in two cladistic analyses and are detailed below.

Analysis of *Nezara*

The analysis including three discrete and three continuous egg characters resulted in one most parsimonious tree with 63 steps (Fig. 82). The characters and states for eggs are as follows.

Character 35. Egg, color prior to embryonic development: (0) light brown, (1) yellow

Character 36. Egg, chorion, pigmentation: (0) present, (1) absent

Character 37. Egg, chorion, sculpture pattern: (0) spinose, (1) smooth

Character 38. Egg, length (range, in millimeters) (continuous)

Character 39. Egg, width (range, in millimeters) (continuous)

Character 40. Egg, aero-micropylar processes, number (range) (continuous)

None of the eggs' characters were informative for the analysis. Characters 35 to 37 had ambiguous reconstruction due to missing data. The spinose chorion (character 37, state 0) is plesiomorphic but with uncertain evolution of the apomorphic smooth chorion. All values of egg length (character 38) overlap; the plesiomorphic state ranges from 1.12 to 1.20 mm. The egg width (character 39) values did not overlap, so the plesiomorphic condition for the entire group ranges from 0.95 to 1.00 mm and from 0.84 to 0.95 mm for the genus *Nezara*. The number of AMPs (character 40) also overlaps among species (except in *C. purpureipennis*); the plesiomorphic condition of the clade including *A. chloris* and *Nezara* spp. is 27 to 30 AMPs, whereas the plesiomorphic condition for the entire group is 25 to 30 AMPs. The availability of egg measures and AMPs number for other species of *Nezara* would be interesting to test these assumptions and to minimize the missing data in the analysis. Information on the eggs of *N. yunnana* Zheng would be especially desirable to aid in solving the only polytomy of the cladogram. Ferrari *et al.* (2010) mentioned that a close relationship between *N. viridula* (Linnaeus) and *N. antennata* Scott has been suggested based on different sets of characters (e.g., interspecific mating behavior), but the lack of studies with *N. yunnana* prevented further conclusions. This highlights the importance of searching for the greatest diversity in number and source for characters but is also a reminder that for rare or poorly studied species, information will be missing on several sets of characters.

Analysis of the *Chinavia obstinata* group

The analysis including two discrete and three continuous egg characters resulted in 10 most parsimonious trees with 104.493 steps. Only the strict consensus tree is shown (Fig. 83).

Character 41. Egg, color prior to embryonic development: (0) green, (1) light brown
Character 42. Egg, aero-micropylar process, surface, sculpture: (0) smooth, (1) spongy
Character 43. Egg, length (range, in millimeters) (continuous)
Character 44. Egg, width (range, in millimeters) (continuous)
Character 45. Egg, aero-micropylar processes, number (range) (continuous)

Two of the egg characters were informative for the analysis (characters 43 and 45). Characters 41 and 42 had ambiguous reconstruction due to missing data. The states for *C. hilaris* (eggs green and AMPs smooth, respectively) could be either plesiomorphic or autapomorphic. For the character 43 (egg length), the plesiomorphic condition ranges from 1.49 to 1.56 mm for the entire group. The synapomorphic conditions are the reduction of the egg length in *C. marginata* (Palisot de Beauvois) (1.25-1.30 mm) and its increase (1.64-1.75 mm) in the *C. runaspis* clade. Most values of egg width (character 44) overlap (except for *C. pengue* (Rolston)). The plesiomorphic condition ranges from 1.18 to 1.23 mm for the entire group and from 1.18 to 1.24 mm for the *C. runaspis* clade. The number of AMPs (character 45) overlaps in most terminals, and the plesiomorphic condition ranges from 62 to 63 AMPs; a reduction to 38-58 AMPs is autapomorphic for *C. runaspis*.

Discussion

Descriptive morphology

Including the present study, 286 out of 4721 species described in the Pentatomidae have their egg stage described thus far, covering approximately 6% of the diversity within the family. These species belong to 147 out of 885 genera, 31 out of 53 tribes and represent eight out of nine subfamilies. Only the eggs of the Stirotarsinae remain unknown. A great diversity of morphological features can be observed within the group. It is even possible to recognize patterns within some subgroups of Pentatomidae, whereas for others, especially the less studied ones, some features still appear to be exclusive. Notwithstanding at the present none of the observed morphological characters seem to be exclusive for the eggs of the Pentatomidae.

Asopinae

Within the Asopinae, a morphological pattern is difficult to recognize because few genera besides *Podisus* Herrich-Schäffer have been studied under SEM (Hinton 1981; Ren *et al.* 1990; Ren 1992; Kumar *et al.* 2002). *Troilus luridus* (Fabricius) and *Podisus* spp. are similar. *Eocanthecona furcellata* (Wolff) differs from *Podisus* spp. because of a spherical shape and *Picromerus bidens* (Linnaeus) because of a granulated chorion, with both species displaying shorter and more numerous AMPs (26–28 and 26–34, respectively). Other Asopinae species have been studied, but the original descriptions and illustrations prevent clear recognition of the chorion sculpture. In many of those species, the eggs have dark bands, the AMPs are shorter than in *Podisus* spp., or the sculpture pattern may appear pitted or reticulated [e.g., *Andrallus spinidens* (Fabricius), *Apateticus* spp., *Cantheconidea humeralis* (Distant), *Jalla dumosa* (Linnaeus), *Pinthaeus* spp., *Zicrona caerulea* (Linnaeus)] (Hinton 1981; Saini 1984; Ren 1992; Javahery 1994; Rieger 2000). On the other hand, other species appear to fit the pattern already recognized by Matesco *et al.* (2009) [e.g., *Arma* spp., *Cazira verrucosa* (Westwood)] (Putshkova 1961; Hinton 1981; Ren 1992).

In *Podisus*, the eggs of at least six species have been described, including *P. distinctus* and *P. nigrispinus* (Whitmarsh 1916; Esselbaugh 1946; Hinton 1981; Saini 1984, 1994; Grazia *et al.* 1985; Javahery 1994; Costelo *et al.* 2002), four of them under SEM (Lambdin & Lu 1984; Bundy & McPherson 2000; Wolf & Reid 2004; Sá *et al.* 2013). Egg morphology in this genus is highly conserved as barrel to oval, yellow to dark, usually with metallic reflections, spinose chorion, and AMPs long, clubbed, and few in number (8–20). In *Podisus placidus* Uhler, although other characteristics corroborate the pattern observed, the chorion shows bands of different colors, and the sculpture has been described as rugulose under SM (Oeting & Yonke 1971). However, it is not possible to unequivocally compare the observations made under SM with those made under SEM.

Discocephalinae

Information about the morphology of discocephaline eggs is rare and brief. Cobben (1968) studied the eggs of *Antiteuchus mixtus* (Fabricius) and also refers to the eccentricity of the aero-micropylar processes and the opercular rings, a condition also found in *Edessa* and the Scutelleridae. Miller (1971) illustrated the egg of *Dryptocephala brullei* Laporte. Eggs of *Lincus spurcus* (Rolston) have been described as pearly grey and ornamented on its upper side (Llosa *et al.* 1990), whereas those of *Antiteuchus tripterus* (Fabricius) are merely reported as clear-colored (Panizzi & Grazia 2001). There are no available SEM descriptions for eggs of the Discocephalinae other than *C. pensa* described here. Further studies of this exclusively Neotropical group are urgently needed.

Pentatominae

The Pentatominae comprise the greater diversity within the family, and no pattern could be identified among all species in terms of egg morphology.

With few exceptions (Bundy & McPherson 2000; Pollo *et al.* 2012; Gilio-Dias *et al.* 2013), Carpocorini species share several characteristics, such as the translucent chorion, spinose surface, and AMPs long and only slightly clubbed, varying from 10 to 80 (Matesco *et al.* 2009). The five Carpocorini species here studied fit this pattern, including *D. furcatus* whose eggs have been previously studied only under SM (Grazia *et al.* 1982). The eggs of other species of *Dichelops* Spinola are unknown.

In addition to *M. cornicollis*, seven other species of *Mormidea* Amyot & Serville have been studied, two of them under SEM (Esselbaugh 1946; Martins *et al.* 1986; Weber *et al.* 1988; Brailovsky *et al.* 1992; Javahery 1994; Wolf & Reid 2001). Egg morphology in this genus appears to be constant: eggs white to yellowish prior to embryonic development, rose-colored afterwards; barrel shaped; operculum slightly convex; chorion translucent and spinose; AMPs usually slightly clubbed (but cylindrical in *Mormidea notulifera* Stål), varying from 22 to 47.

Along with *Chinavia*, *Euschistus* is one of the most studied genera in terms of egg morphology. The eggs of at least 14 species are known, 12 of them under SEM (Esselbaugh 1946; McPherson & Paskewitz 1984; Brailovsky *et al.* 1992; Javahery 1994; Munyaneza & McPherson 1994; Bundy & McPherson 2000; Candan *et al.* 2005; Martins & Campos 2006; Matesco *et al.* 2009; Biasotto *et al.* 2013). They fit the Carpocorini pattern, with few exclusive characteristics at the genus or subgenus level. Species of *Euschistus (Euschistus)* are variable: white, yellow or green; AMPs slightly or conspicuously clavate, surface spongy (when described), varying from 25 to 40 in number (Esselbaugh 1946; McPherson & Paskewitz 1984; Brailovsky *et al.* 1992; Javahery 1994; Munyaneza & McPherson 1994; Bundy & McPherson 2000; Candan *et al.* 2005). In both species of *Euschistus (Lycipta)* for which the eggs are known, they are white and the AMPs are tubular and vary from 34 to 52 in number (Matesco *et al.* 2009). In the species of *Euschistus (Mitripus)* the AMPs are slightly clavate and vary from 18 to 47 in number. The eggs of *Euschistus (M.) paranticus* here described are more similar in color to *E. (M.) hansi* Grazia and *E. (M.) grandis* Rolston (white) than to *E. (M.) convergens* (Herrich-Schäffer) (yellow) (Martins & Campos 2006; Matesco *et al.* 2009; Biasotto *et al.* 2013).

In the Nezarini, the eggs reveal a great morphological diversity (Matesco *et al.* 2009), and few intrageneric similarities could be found (e.g., *Chlorochroa* Stål, *Nezara*, and *Palomena* Mulsant & Rey) (Kobayashi 1959, 1994; Putshkova 1961, Hinton 1981; Ren 1992; Javahery 1994). The lack of uniformity in the nomenclature and inaccuracy of illustrations hinder more extensive considerations. As far as is known, *Chinavia* spp. do not share important egg characters with other Nezarini species.

The features observed here in *Chinavia* spp. are compatible with the pattern proposed for the genus: eggs barrel-shaped, chorion brown and reticulate, and AMPs clubbed (Matesco *et al.* 2009). Except for *C. musiva* (Berg) (Matesco *et al.* 2008, 2009), recognition at the species level is difficult. However, *C. armigera* stands out by having glossy eggs, whereas other species exhibit opaque eggs.

The eggs of the Pentatomini under SEM are available for species of nine genera (Hinton 1981; Ren 1992; Candan & Suludere 2001; Matesco *et al.* 2009; Campos *et al.* 2010), and only these are to be considered in the present discussion. As noted previously, it appears that there is no characteristic defining Pentatomini eggs (Matesco *et al.* 2009). The AMPs number may vary between 21 and 59. Tubular AMPs are present in *Loxa deducta* Walker and *Pallantia macunaima* Grazia, whereas cup-shaped ones are present in *Grazia tincta* (Distant) and *Iphiarusa compacta* (Distant), and clavate in *B. induta*, *Banasa maculata* Campos & Garbelotto, *Lelia decempunctata* (Motschulsky), *Pentatoma rufipes* (Linnaeus), *Rhaphigaster nebulosa* (Poda), and *S. apicicornis*. Even the texture of AMP is variable, from rugose as in *L. deducta* and *R. nebulosa* to spongy as in *B. induta*, *B. maculata*, *G. tincta*, and *I. compacta*, appearing smooth in the other species. The chorion surface is likely the most variable characteristic in this tribe, with at least four major observed patterns: apparently smooth in *L. decempunctata* and *P. rufipes*, granulated in *S. apicicornis*, spinose in *I. compacta*, *L. deducta*, and *P. macunaima*, and reticulate in *Banasa* spp., *G. tincta*, and *R. nebulosa*. Eggs with the same major pattern of chorion surface, however, may display great differences when observed in detail.

The eggs of *Banasa* vary from yellow to brown (DeCoursey 1963; Brailovsky *et al.* 1992; Campos *et al.* 2010). The chorion sculpture was described under SM for four species as granulated, punctured or reticulated, and under SEM for *B. maculata* as reticulated with deep cells and truncate rough masses (Campos *et al.* 2010). *Banasa induta* exhibits a similar sculpture but with shallower cells compared to *B. maculata*. Such chorion sculpture bearing rough masses has been so far described only for *Banasa*. The AMPs of *B. induta* show the same shape and spongy surface already observed for *B. maculata* under SEM (Campos *et al.* 2010). Despite these similarities between both species, it is premature to assume a pattern for *Banasa* because this is one of the largest pentatomine genera with 80 species (Campos *et al.* 2010).

Immatures of Procleticini are poorly characterized; only the eggs of *Odmalea basalis* (Walker) have been studied (Matesco *et al.* 2009). Nevertheless, striking similarities between the eggs of *O. basalis* and *T. maracaja* can be outlined in egg shape, size and color, chorion sculpture, and AMP length and number. These set of features are so far unique for species of Procleticini within the Pentatomidae.

Capivaccius Distant has not been included by Rider (2013) in any tribe, remaining unplaced within Pentatominae. Some resemblance can be found with the eggs of *G. tincta* (Pentatomini): egg size, chorion with a striped pattern and reticulated surface with fringed edges, sometimes with long filiform projections delimiting the cells (Matesco *et al.* 2009). This information does not argue for the inclusion of *Capivaccius* in Pentatomini because variegated color patterns have already been described in other pentatomids (Esselbaugh 1946; Brailovsky *et al.* 1992; Javahery 1994; Suludere *et al.* 1999; Panizzi & Grazia 2001), and other features of the eggs of *G. tincta* are aberrant even within the morphologically diverse Pentatomini. A vaguely similar sculpture, displaying reticulated surface with fringes, can be observed in the eggs of *Hoplistodera* spp. (Hoplistoderini) (Ren 1992). The irregular laminate chorionic projections surrounding the operculum are only known for *C. bufo*, although there is some resemblance with the same region of the chorion in the eggs of some species of *Eurydema* Laporte (Strachiini) (Ren 1992; Suludere *et al.* 1999).

Genera that remain unplaced are possibly those whose characteristics of adult morphology prevent their designation to any of the tribes thus far proposed. It is interesting to note that the eggs in those same genera display very peculiar features (e.g., the salebrose chorion in *Thyanta* spp. and the irregular laminate chorionic projections in *C. bufo*), preventing, to some extent, the use of egg morphology as alternative character source for classification purposes.

In this study, some of the patterns previously recognized at the levels of subfamily, tribe, and genus in the Pentatomidae (e.g., Matesco *et al.* 2009) have been corroborated, emphasizing the potential use of egg morphology as an auxiliary tool in classification and phylogenies.

Knowledge about the eggs of Pentatomidae species is still fragmentary, and coupled with the ambiguous use of terminology such as for egg shape, this has led to generalizations and even misconceptions. Comparison among studies using SM and those using SEM suggests that the former were not able to adequately describe all structures comprising the egg. Only the use of SEM enables the review of terminology and the understanding of the differences and similarities between species. We strongly suggest the use of SEM as a standard procedure to describe the egg stage in Heteroptera and to explore details of chorion sculpture and the structure of aero-micropylar processes.

Search for characters of phylogenetic importance

The characters listed in Table 5 should help further phylogenetic studies within the Pentatomoidea. Some of those characters may not be independent from each other (e.g., chorion thickness and degree of sclerotization of the egg-burster), but they are all mentioned because availability of information varies according to the group under study. Some egg structures have been particularly understudied, such as the egg-burster.

Despite of the detailed work of Ren *et al.* (1990) and Ren (1992), few descriptions offer information on this structure because its appearance is related to embryonic development and its visualization under SEM requires hatched eggs. Most of the character states are present in distantly related species among different pentatomoid families. Therefore, their usefulness is dependent on the taxonomic level of analysis. Nevertheless, we strongly encourage those who want to include egg characters in phylogenetic analysis to carefully evaluate the hypotheses of homology in the groups studied.

Egg characters used in both analyses

Egg color prior to embryonic development

Within the Pentatomidae, the egg color is considered to have taxonomic and phylogenetic importance, as well being useful in genus and species identification (Heidemann 1911; Cobben 1968; Hinton 1981; Javahery 1994). This feature has already been included in keys to species in the Pentatomidae (Esselbaugh 1946; Hinton 1981; Saini 1984; Bundy & McPherson 2000). Javahery (1994) included one binary character, "chorion color" [(0) never colored, (1) brownish, blackish, and 2-3 color bands and scattered patches] in his phylogenetic analysis of pentatomoid genera based on the egg stage.

Egg color is related to the egg content and changes during embryonic development due to the emergence of red ocular spots and color changes in other areas of the embryo body (Esselbaugh 1946; Javahery 1994; Candan & Suludere 1999b; Bundy & McPherson 2000). It can vary from white to black, including different shades of yellow, green, brown and grey. This feature is usually conserved within the genera, as in *Carpocoris* Kolenati, *Edessa* Fabricius, and *Nezara*, but there are exceptions, as in *Chinavia* and *Euschistus* (Matesco *et al.* 2009).

Chorion pigmentation

The chorion in most pentatomids is transparent and allows observation of gross embryogenesis after formation of the embryo. Therefore, egg coloration is due to its internal contents (Esselbaugh 1946; Brailovsky *et al.* 1992; Javahery 1994; Candan & Suludere 1999b). However, the chorion is pigmented in few genera (e.g., *Banasa* Stål, *Chinavia*, *Carpocoris*, *Thyanta* Stål), and because of its thickness and microsculpture, observation of the embryo can be prevented. The color that remains after hatching is usually less intense (Esselbaugh 1946; Brailovsky *et al.* 1992; Javahery 1994) but still observable. This feature has also been used in taxonomic keys to species in the Pentatomidae (Esselbaugh 1946; Saini 1984).

Chorion sculpture pattern

The chorion is derived from the maternal secretions deposited before fertilization and displays great diversity in surface morphology (Cobben 1968; Wolf & Reid 2001). It is well accepted that its microsculpture reflects the arrangement of the follicular cells that secrete the chorion (Esselbaugh 1946; Southwood 1956; Margaritis 1985). Chorion sculpture is recognized to bear taxonomic value both at generic and specific levels (Cobben 1968; Candan *et al.* 2005; Matesco *et al.* 2009) and has been used in keys to species in the Pentatomidae (Esselbaugh 1946; Hinton 1981; Saini 1984; Bundy & McPherson 2000). The chorion surface pattern in most pentatomids is smooth, granulated, reticulated, spinose, or salebrose (Heidemann 1911; Esselbaugh 1946; Southwood 1956; Javahery 1994; Bundy & McPherson 2000; Wolf & Reid 2001; Matesco *et al.* 2009). It is well accepted that chorion morphology is conserved at the genus level (Matesco *et al.* 2009).

This feature has been differently explored in two previous cladistic analyses. Hasan and Kitching (1993), in their cladistic analysis of the tribes of the Pentatomidae, included the character "chorionic texture" [(0) smooth, (1) rough]. Javahery (1994) included two related characters entitled "chorion" [char. 10: (0) pitted, (1) hairy; char. 11: (0) without any reticulation and spines, (1) spinose].

In *Carpocoris* spp., the chorion fits the spinose pattern described by Bundy and McPherson (2000). For the eggs of *Aethemenes nigropunctatus* (Signoret) (as *A. chloris* (Dallas) in Ferrari *et al.* 2010), Leston (1955) mentioned an irregular reticulation of the chorion. Although the term reticulation has been used more recently to describe the coarse/foveate/pitted chorion pattern [the "reticulated" pattern mentioned by Bundy and McPherson (2000)], previous authors usually referred to the polygonal figures in spinose eggs (e.g., Esselbaugh 1946). Therefore, we considered the eggs of *A. nigropunctatus* to be most likely spinose.

This appears to be the most common pattern in Pentatomidae (Wolf & Reid 2003), and its function has been speculated to be related with enhanced aeration, fixation or transportation of the eggs or avoidance of desiccation or predation (Hinton 1981; Wolf & Reid 2001). The smooth chorion, as observed in *Nezara* spp., appears to be a less common surface pattern and an explanation of its significance has not been attempted thus far (Wolf & Reid 2003).

Egg length and width

Egg measures (length and width) are used as additional diagnostic features at the species level, especially in keys to the eggs of the Pentatomidae and the Scutelleridae (Esselbaugh 1946; Putschkova 1961; Hinton 1981). Javahery (1994) considered the eggs in Heteroptera differing at the family level in several aspects, including size, and he proposed the character "egg length" [(0) about 1 mm and less, (1) more than 1 mm]. The size of the egg appears to be conserved among lineages and may be proportional to adult body size (Williams *et al.* 2005). On the other hand, Cobben (1968) considered that, among Heteroptera, plesiomorphic species usually have smaller adult body size and proportionally larger eggs, and apomorphic species have a larger adult body size and smaller eggs. Therefore, there would be a generic trend of decrease in relative egg size. The inclusion of those characters in cladistic analysis of low taxonomic levels is interesting for identification of terminals or clades in which egg-size increase or decrease events occurred.

Number of aero-micropylar processes

The presence of the AMPs is considered a synapomorphy of the Pentatomomorpha (Grazia *et al.* 2008). Therefore, they are assumed to be present in all Pentatomidae species, arranged in a circle outside the hatching line, but varying in shape, length, and number, according to the taxa considered (Esselbaugh 1946; Southwood 1956; Javahery 1994). The number of AMPs varies from five to 72 in the Pentatomidae (Esselbaugh 1946; Javahery 1994) and can be used as diagnostic character at the generic level (Bundy & McPherson 2000). It has also been used in keys to species of the Pentatomidae and the Scutelleridae (Esselbaugh 1946; Saini 1984; Bundy & McPherson 2000), but it is of limited value because AMPs number overlaps among congeneric species (Matesco *et al.* 2009).

Esselbaugh (1946) considered the larger number of AMPs (e.g., in *Chinavia* and *Oebalus* Stål) as being an indication of primitive condition. Southwood (1956) also considered the smaller number of AMPs (e.g., in Asopinae) as highly evolved. Cobben (1968) considered a single micropyle on the center of the anterior pole as an ancestral condition in Heteroptera, with a general evolutionary trend represented by multiplication and displacement of the micropyles. Javahery (1994) coded this feature in two characters named “number of micropyles” [char. 3: (0) less than 35, (1) 35 and more; char. 4: (0) less than 11, (1) between 11 and 34]. He considered that the primitive condition would be a single micropylar pore, and within Pentatomidae, some species would have evolved repeatedly toward the higher number or more specialized micropyles.

Aero-micropylar process sculpture

It has been already mentioned that the AMP may display variable morphology. These processes consist of a central channel, for the entry of the sperm prior to fertilization, and a frothy chorionic plastron surrounding it. The latter structure is porous and serves for respiratory interchange (Esselbaugh 1946; Southwood 1956; Cobben 1968; Hinton 1981; Javahery 1994; Wolf & Reid 2003). In most pentatomid species studied under SEM, the AMP surface is spongy (e.g., most *Chinavia* spp., *B. induta*, *M. cornicollis*, *S. apicicornis*), which is compatible with its respiratory function. In some species, however, it is smooth (*Chinavia hilaris* (Say), some *Euschistus* spp., *O. basalis*, *Podisus* spp.) (Bundy & McPherson 2000; Matesco *et al.* 2009), and its significance remains unclear.

Conclusions

Although the eggs of several pentatomid species are already known, this information is disregarded in most cladistic analyses within the family. For analyses of low taxonomic levels, most characters proposed here may be constant or the information may be missing for a high number of terminals. The problem of including missing data in a matrix exists for different groups of characters (e.g., male genitalia, female genitalia, internal genitalia, and immature stages), and those missing entries have a recognized negative effect on the cladistic performance of the matrices (Prevosti & Chemisquy 2010).

Prevosti and Chemisquy (2010) demonstrated that distribution of missing data in most matrices is not random but instead concentrated on some characters, taxa, or both, as would be expected due to the combination of different sources of phylogenetic characters in different taxon sampling. They concluded that the concentration of the missing entries in a few characters (the “character bias,” as observed in our matrices, instead of the “taxa bias” or the “block bias”) produced the least detrimental effect in recovering relationships. In this sense, the inclusion of more characters could make the matrices more robust against the missing data problem. Therefore, it is unwise to exclude characters prior to the analysis because they have missing cells.

On the other hand, minimization of missing data for egg characters in future analyses could be achieved by either choosing the terminals based on the availability of information on the egg stage or preferably by applying efforts to obtain the eggs of terminal species. The latter alternative can be accomplished even by dissecting the abdomen of dry conserved females prior to immersion in KOH for preparation of the genitalia.

Detail descriptions of pentatomid eggs with the use of SEM are still needed. The phylogenetic information contained in the egg stage can only be unraveled by testing the characters suggested here and others for congruence with other sets of morphological and molecular characters in a cladistic framework.

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TABLE 1. List of Pentatomidae species with described eggs complementing Matesco *et al.* (2009).

Subfamily	Tribe[†]	Species	Egg	
			SEM[‡]	SM[‡]
Aphylinae		*Aphylum bergrothi* Schouteden		Cobben 1968
Asopinae		*Afrius yolofa* (Guérin-Menéville) (as *figuratus* Germar)		Cobben 1968
		Andrallus spinidens (Fabricius)	Ren 1992	Miller 1934; Ren 1992
		Arma chinensis (Fallou)	Ren *et al.* 1990; Ren 1992	Ren 1992
		Arma custos (Fabricius)		Putshkova 1961
		Cantheconidea humeralis (Distant)	Ren 1992	Ren 1992
		Cazira verrucosa (Westwood)	Ren 1992	Ren 1992
		Dinorhynchus dybowskyi Jakovlev		Okamoto 1942
		Dorycoris pavoninus (Westwood)		Cobben 1968
		Eocanthecona concinna (Walker)	Ren *et al.* 1990; Ren 1992	Ren 1992
		Jalla dumosa (Linnaeus)		Putshkova 1961
		Perillus bioculatus (Fabricius)		Esselbaugh 1946; Cobben 1968; Javahery 1994
		Picromerus bidens (Linnaeus)	Hinton 1981	Putshkova 1961; Cobben 1968; Javahery 1994
		Picromerus griseus (Dallas)		Zhang 1985

		Picromerus viridipunctatus Yang	Ren 1992	Ren 1992
		Pinthaeus humeralis Horvath	Ren 1992	Ren 1992
		Pinthaeus sanguinipes (Fabricius)		Rieger 2000
		Podisus distinctus (Stål)	Sá *et al.* 2013; this study	
		Podisus nigrispinus (Dallas)	this study	Grazia *et al.* 1985; Saini 1994
		Rhacognathus punctatus (Linnaeus) (as *Eysarcoris*)		Putshkova 1961
		Troilus luridus (Fabricius)	Hinton 1981	Putshkova 1961
		Zicrona caerulea (Linnaeus)		Kobayashi 1951; Putshkova 1961
Cyrtocorinae		*Cyrtocoris egeris* Packauskas & Schaefer	Bianchi *et al.* 2011	Brailovsky *et al.* 1988
Discocephalinae	Discocephalini	*Antiteuchus mixtus* (Fabricius)		Cobben 1968
		Dryptocephala brullei Laporte		Miller 1971
	Ochlerini	*Catulona pensa* Rolston	this study	
Pentatominae	Aeliini	*Aelia acuminata* Linnaeus		Putshkova 1961; Lodos 1964; Javahery 1994
		Aelia fieberi Scott (as *nasuta* Wagner – Ren 1992)	Ren 1992	Kobayashi 1960a; Ren 1992
		Aelia klugii Hahn		Putshkova 1961
		Aelia rostrata Boheman	Candan & Suludere 2006	Putshkova 1961; Javahery 1994

	Aelia virgata (Herrich-Schäffer)		Putshkova 1961; Javahery 1994
	Neottiglossa leporina (Herrich-Schäffer)		Putshkova 1961
	Neottiglossa pusilla (Gmelin)		Putshkova 1961; Javahery 1994
Aeptini	*Aeptus singularis* Dallas		Gillon 1972
Amyntorini	*Bolaca unicolor* (Walker) (as *Amyntor obscurus* Dallas)	Ren 1992	Ren 1992
Antestiini	*Antestiopsis anchora* (Thunberg) (as *Antestia*)		Miller 1934
	Plautia crossota (Fabricius) (as *fimbriata* (Westwood))	Ren 1992	Ren 1992
	Plautia splendens Distant		Kobayashi 1965b
	Plautia stali Scott		Kobayashi 1956 1965b 1994
	Starioides degenera (Walker) (as *Antestia*)		Miller 1934
Cappaeini	*Halyomorpha halys* (Stål) (as *picus* Fabricius – Kobayashi 1956; as *mista* Uhler – Kobayashi 1967)	Ren 1992	Kobayashi 1956 1967; Ren *et al.* 1990; Ren 1992
	Halyomorpha viridescens (Walker)		Miller 1971
	Homalogonia obtusa (Walker)	Ren 1992	Kobayashi 1967; Ren 1992
Carpocorini	*Antheminia lunulata* (Goeze) (as *Carpocoris*)		Putshkova 1961
	Antheminia pusio (Kolenati)	Ren 1992	Ren 1992; Isakov 2000a

Antheminia varicornis (Jakovlev)	Ren 1992	Ren 1992
Caonabo pseudoscylax (Rolston)	Gilio-Dias *et al.* 2013	
Carpocoris coreanus Distant	Ren 1992	Ren *et al.* 1990; Ren 1992
Carpocoris fuscispinus (Boheman)	Candan & Suludere 2000	Javahery 1994
Carpocoris pudicus (Poda)	Candan & Suludere 1999a	Putshkova 1961; Cobben 1968
Carpocoris purpureipennis (De Geer)	Ren 1992	Lodos 1964; Ren 1992
Codophila varia (Fabricius)	Candan *et al.* 2001	Putshkova 1961
Dichelops (*Diceraeus*) *furcatus* (Fabricius)	this study	Grazia *et al.* 1982
Dolycoris baccarum (Linnaeus)	Ren 1992	Kobayashi 1953; Putshkova 1961; Lodos 1964; Ren *et al.* 1990; Ren 1992
Euschistus (*Euschistus*) *heros* (Fabricius)	this study	
Euschistus (*Lycipta*) *riograndensis* Weiler & Grazia	this study	
Euschistus (Mitripus) grandis Rolston	Biasotto *et al.* 2013	Biasotto *et al.* 2013
Euschistus (*Mitripus*) *paranticus* Grazia	this study	
Glyphepomis spinosa Campos & Grazia	Pollo *et al.* 2012	
Holcostethus strictus vernalis (Wolff) (as		Putshkova 1961

	vernalis)		
	Mormidea cornicollis Stål	this study	
	Rubiconia intermedia (Wolff)	Ren 1992	Kobayashi 1951; Putshkova 1961; Ren 1992
	Staria lunata (Hahn)		Putshkova 1961
Catacanthini	*Vulsirea violacea* (Fabricius)		Lopez & Cervantes 2010
Caystrini	*Hippotiscus dorsalis* (Stål) (as *Hippota*)	Ren 1992	Ren 1992
Eysarcorini	*Carbula abbreviata* (Motschulsky) (as *humerigera* Uhler)		Kobayashi 1956
	Carbula crassiventris (Dallas)	Ren 1992	Ren 1992
	Carbula humerigera (Uhler) (as *obtusangula* Reuter)	Ren 1992	Ren *et al.* 1990; Ren 1992
	Carbula putoni (Jakovlev)	Ren 1992	Ren 1992
	Eysarcoris aeneus (Scopoli) (as *parvus* Uhler – Kobayashi 1960b; as *Stollia* – Putshkova 1961)		Kobayashi 1960b; Putshkova 1961
	Eysarcoris annamita Breddin (as *Stollia*)	Ren 1992	Ren 1992
	Eysarcoris fallax Breddin		Kobayashi 1960b
	Eysarcoris guttigerus (Thunberg) (as *Stollia* – Ren *et al.* 1990)	Ren *et al.* 1990	Kobayashi 1953
	Eysarcoris lewisi (Distant)		Kobayashi 1960b

	Eysarcoris ventralis (Westwood) (as *Stollia inconspicua* (Herrich-Schäffer) – Putshkova 1961; as *Stollia* – Ren *et al.* 1990; Ren 1992)	Ren *et al.* 1990; Ren 1992	Kobayashi 1960b; Putshkova 1961; Ren 1992
	Eysarcoris venustissima (Schrank) (as *Stollia*)		Putshkova 1961
	Spermatodes variolosa (Walker) (as *Sepontia)*	Ren 1992	Ren 1992
	Stagonomus amoenus (Brullé)		Putshkova 1961
	Stagonomus bipunctatus (Linnaeus) (as *pusillus* Herrich-Schäffer – Putshkova 1961)		Putshkova 1961; Isakov 2000b
Halyini	*Apodiphus amygdali* (Germar)	Candan & Suludere 2010	Lodos 1964; Javahery 1994
	Apodiphus integriceps Horváth		Isakov 1993
	Dalpada nodifera Walker	Ren 1992	Ren 1992
	Dalpada oculata (Fabricius)	Ren 1992	Southwood 1956; Ren 1992
	Erthesina fullo (Thunberg)	Ren 1992	Ren *et al.* 1990; Ren 1992
Hoplistoderini	*Alcimocoris japonensis* (Scott)		Katsura & Miyatake 1993
	Hoplistodera fergussoni Distant	Ren 1992	Ren *et al.* 1990; Ren 1992
	Hoplistodera incisa Distant	Ren 1992	Ren 1992
Mecideini	*Mecidea lindbergi* Wagner		Isakov 2004
	Mecidea minor Ruckes	Bundy &	

		McPherson 2011	
Menidini	*Actuarius varians* Villiers		Gillon 1972
	Menida disjecta (Uhler) (as *scotti* Puton)	Ren 1992	Ren 1992
	Menida varipennis (Westwood)		Miller 1934
	Menida violacea Motschulsky		Kobayashi 1953; Ren 1992
Myrocheini	*Delegorguella phalerata* Stål		Gillon 1972
	Dymantis grisea Jensen-Haarup		Gillon 1972
	Dymantis plana (Fabricius)		Gillon 1972
	Ennius ater (Dallas)		Gillon 1972
	Ennius morio (Dallas)		Gillon 1972
	Neococalus clausus (Walker)		Gillon 1972
Nezarini	*Brachynema germarii* Kolenati (as *virens* Klug – Lodos 1964)		Lodos 1964; Isakov 2002
	Cellobius abdominalis Jakovlev		Isakov 1990
	Chalazonotum ishiharai (Linnavouri) (as *Brachynema*)		Kobayashi 1965b 1994
	Chinavia armigera (Stål)	this study	
	Chinavia aseada (Rolston)	this study	
	Chinavia brasicola (Rolston)	this study	
	Chinavia runaspis (Dallas)	this study	
	Chlorochroa juniperina orientalis (Kerzhner) (as *Pitedia*)	Ren *et al.* 1990; Ren 1992	Ren 1992

	Chlorochroa pinicola (Mulsant & Rey) (as *Pitedia*)		Putshkova 1961
	Nezara antennata Scott		Kobayashi 1959 1994
	Nezara viridula (Linnaeus)	Ren *et al.* 1990; Ren 1992; Bundy & McPherson 2000	Miller 1934; Kobayashi 1959 1994; Lodos 1964; Rizzo 1968 1976; Ren 1992
	Palomena angulosa (Motschulsky)		Kobayashi 1959
	Palomena prasina (Linnaeus)	Hinton 1981	Putshkova 1961; Javahery 1994
	Palomena viridissima (Poda)	Ren 1992	Ren 1992
Pentatomini	*Banasa induta* Stål	this study	
	Banasa maculata Campos & Garbelotto	Campos *et al.* 2010	
	Iphiarusa compacta (Distant)	Ren *et al.* 1990; Ren 1992	Ren 1992
	Lelia decempunctata (Motschulsky)	Ren 1992	Ren *et al.* 1990; Ren 1992
	Pentatoma metallifera (Motschulsky)		Ren *et al.* 1990; Ren 1992
	Pentatoma rufipes (Linnaeus)	Hinton 1981	Putshkova 1961
	Pharypia nitidiventris (Stål)		Cervantes 2013
	Ramosiana insignis (Blanchard)		Lopez & Cervantes 2010
	Rhaphigaster nebulosa (Poda)	Ren 1992; Candan &	Putshkova 1961; Lodos

		Suludere 2001	1964; Ren 1992
	Serdia apicicornis Stål	this study	
Piezodorini	*Piezodorus hybneri* (Gmelin) (as *rubrofasciatus* Fabricius)		Miller 1934
	Piezodorus lituratus (Fabricius)	Hinton 1981; Candan 1998	Putshkova 1961; Lodos 1964; Javahery 1994
Procleticini	*Thoreyella maracaja* Bernardes, Schwertner & Grazia	this study	
Rhynchocorini	*Rhynchocoris humeralis* (Thunberg)		Hoffman 1931
Sciocorini	*Dyroderes umbraculatus* (Fabricius)		Putshkova 1961
	Menaccarus arenicola (Scholtz)		Putshkova 1961
	Sciocoris capitatus Jakovlev		Isakov 2001
	Sciocoris cursitans (Fabricius)		Putshkova 1961; Cobben 1968
	Sciocoris deltocephalus Fieber		Putshkova 1961
	Sciocoris distinctus Fieber		Putshkova 1961; Cobben 1968
	Sciocoris homalonotus Fieber		Putshkova 1961
	Sciocoris kiritshenkoi Wagner		Isakov 2001
	Sciocoris macrocephalus Fieber.		Putshkova 1961
	Sciocoris sulcatus Fieber		Putshkova 1961

	Sephelini	*Aenaria lewisi* (Scott)		Kobayashi 1958
		Niphe elongata (Dallas) (as *Lagynotomus* – Kobayashi 1960a)	Ren 1992	Kobayashi 1960a; Ren 1992
	Strachiini	*Bagrada stolida* (Herrich-Schäffer) (as *stolata* Horvath)		Putshkova 1961
		Eurydema cyanea (Fieber)		Cobben 1968
		Eurydema dominulus (Scopoli)	Hinton 1981; Ren 1992	Ren 1992
		Eurydema maracandica Oshanin	Ren 1992	Ren *et al.* 1990; Ren 1992
		Eurydema oleracea (Linnaeus)	Suludere *et al.* 1999	Putshkova 1961; Benedek 1968; Javahery 1994
		Eurydema ornata (Linnaeus) (as *festiva* Linnaeus – Putshkova 1961)		Putshkova 1961; Benedek 1968
		Eurydema pulchra (Westwood)		Miller 1934
		Eurydema rugosa Motschulsky		Kobayashi 1958
		Eurydema ventralis Kolenati	Suludere *et al.* 1999	Lodos 1964; Benedek 1968
		Madates limbatus (Fabricius) (as *Cinxia*)		Miller 1934
	Unplaced	*Capivaccius bufo* Distant	this study	
Phyllocephalinae	Megarrhamphini	*Megarrhamphus hastatus* (Fabricius)		Zhang 1985
		Megarrhamphus truncatus (Westwood)		Zhang 1985; Miller 1971
	Phyllocephalini	*Chalcopis glandulosa*	Ren 1992	Ren 1992

		(Wolff) (as *Metonymia*)		
		Dichelorhinus gambiensis (Dallas) (as *vittatus* Signoret)		Gillon 1972
		Gonopsis affinis (Uhler)		Kobayashi 1951
		Gonopsis coccinea (Walker)		Ren 1992
		Gonopsis reuteri Schouteden		Gillon 1972
		Lobopeltista guineensis Schouteden		Gillon 1972
		Macrina juvenca (Burmeister)		Cobben 1968; Gillon 1972
		Tantia striata (Signoret)		Cobben 1968
	Tetrodini	*Gellia dilatata* (Signoret)		Cobben 1968; Gillon 1972
		Gellia punctulata Stål		Gillon 1972
		Tetroda histeroides (Fabricius)	Ren 1992	Miller 1934; Zhang 1985; Ren 1992
Podopinae	Brachycerocorini	*Brachycerocoris camelus* Costa	Ren 1992	Ren 1992
	Graphosomatini	*Ancyrosoma leucogrammes* (Gmelin) (as *albolineatum* Fabricius – Lodos 1964; Cobben 1968)		Putshkova 1961; Lodos 1964; Cobben 1968
		Crypsinus angustatus (Baerensprung)		Putshkova 1961
		Derula flavoguttata Mulsant & Rey		Putshkova 1961
		Graphosoma lineatum Linnaeus	Candan & Suludere 1999b	Putshkova 1961; Lodos 1964
		Graphosoma rubrolineatum (Westwood)	Ren 1992	Kobayashi 1965a; Ren *et al.* 1990; Ren 1992

	Graphosoma semipunctatum (Fabricius)		Putshkova 1961; Lodos 1964
	Leprosoma inconspicuum Baerensprung		Putshkova 1961
	Sternodontus obtusus Mulsant & Rey		Putshkova 1961
	Tholagmus flavolineatus (Fabricius)		Lodos 1964
	Ventocoris halophilum (Jakovlev)		Putshkova 1961
	Ventocoris philalyssum (Kiritshenko) (as *Trigonosoma*)		Putshkova 1961
	Ventocoris trigonum (Krynicki) (as *Trigonosoma*)		Putshkova 1961
	Vilpianus galii (Wolff)		Putshkova 1961
Podopini	*Oncozygidea flavitarsis* Reuter		Gillon 1972
	Podops inunctus (Fabricius)		Putshkova 1961
	Scotinophara horvathi Distant	Ren *et al.* 1990; Ren 1992	Kobayashi 1963; Ren 1992
	Scotinophara lurida (Burmeister)		Kobayashi 1963; Zhang 1985
	Scotinophara scottii Horváth		Kobayashi 1963
	Thoria rontundata Villiers		Gillon 1972
Tarisini	*Dybowskyia reticulata* (Dallas)		Kobayashi 1951 1965a; Ren 1992
	Tarisa pallescens Jakovlev		Putshkova 1961

	Unplaced	*Cyptocoris lundi* Fabricius		Gillon 1972

† Classification for the tribes follows D. A. Rider, available at the website <http://www.ndsu.nodak.edu/ndsu/rider/Pentatomoidea/>, accessed in 14.VIII.2013.

‡ SEM = scanning electron microscopy; SM = stereomicroscopy.

TABLE 2. Measurements of the eggs of species of the Pentatomidae (SD, standard deviation).

Subfamily Tribe Species	Collecting site in Brazil	n	Length (average ± SD) (mm)	Width (average ± SD) (mm)	AMP[†] number (average ± SD) (range)
Asopinae					
Podisus distinctus (Stål)	Criciúma - SC -28,7038; -49,4126	10	1.2 ± 0.04	1.0 ± 0.02	15 ± 1 (13–17)
Podisus nigrispinus (Dallas)	Maquiné - RS -29.541, -50.2523	25	1.2 ± 0.06	1.0 ± 0.04	18 ± 1 (16–20)
Discocephalinae					
Ochlerini					
Catulona pensa Rolston	Caxias do Sul - RS -29.1285, -51.2709	8	1.6 ± 0.02	1.4 ± 0.01	38 ± 4 (33–44)
Pentatominae					
Carpocorini					
Dichelops (*D.*) *furcatus* (Fabricius)	Londrina - PR -23.1139, -51.1040	5	1.1 ± 0.02	0.9 ± 0.03	19 ± 1 (18–21)
Euschistus (*E.*) *heros* (Fabricius)	Londrina - PR -23.1139, -51.1040	10	1.1 ± 0.05	0.9 ± 0.05	35 ± 3 (31–40)
Euschistus (*L.*) *riograndensis* Weiler & Grazia	São Francisco de Paula - RS -29.4266, -50.3962	10	1.3 ± 0.03	1.0 ± 0.02	45 ± 5 (36–52)
Euschistus (*M.*) *paranticus* Grazia	Maquiné - RS -29.541, -50.2523	12	1.3 ± 0.05	1.1 ± 0.05	30 ± 3 (27–34)
Mormidea cornicollis Stål	São Francisco de Paula - RS -29.4281, -50.3903	28	1.0 ± 0.03	0.8 ± 0.04	39 ± 4 (28–47)
Nezarini					
Chinavia armigera (Stål)	Rio Grande - RS -32.5719, -52.5593	11	1.4 ± 0.04	1.2 ± 0.06	55 ± 3 (51–61)
Chinavia aseada (Rolston)	Passo Fundo - RS -28.1546, -53.2424	5	1.4 ± 0.06	1.1 ± 0.07	60 ± 2 (58–62)
Chinavia brasicola (Rolston)	São Francisco de Paula - RS -29.4239, -50.3872	8	1.6 ± 0.04	1.1 ± 0.02	51 ± 3 (47–55)
Chinavia runaspis (Dallas)	Porto Alegre - RS -30.0693, -51.2422	15	1.7 ± 0.06	1.2 ± 0.04	50 ± 6 (38–58)

Pentatomini					
Banasa induta Stål	Maquiné - RS -29.5275, -50.2208	3	1.2 ± 0.05	1.0 ± 0.02	27 ± 2 (24–28)
Serdia apicicornis Stål	Maquiné - RS -29.5199, -50.2209	11	1.5 ± 0.06	1.5 ± 0.07	46 ± 4 (38–51)
Procleticini					
Thoreyella maracaja Bernardes, Schwertner & Grazia	Maracajá - SC -28.8808, -49.4664	2	1.0 ± 0.03	0.9 ± 0.03	21
Unplaced					
Capivaccius bufo Distant	Criciúma - SC -28,7038; -49,4126	8	1.2 ± 0.04	0.9 ± 0.02	22 ± 2 (19–25)

† AMP, aero-micropylar processes.

TABLE 3. Character matrix for the analysis of *Nezara* Amyot & Serville, including only egg characters. Characters 1 to 34 (not shown) as in the original paper (Ferrari *et al.* 2010); characters 38 to 40 treated as continuous, values obtained with *stand 1* in parenthesis. Missing data = ?.

	35	6	7	8	9	40
Carpocoris purpureipennis	0	0	0	1.20-1.40 (0.473-1.000)	1.00-1.05 (0.843-1.000)	20-25 (0.000-0.250)
Pseudoacrosternum cachani	?	?	?	?	?	?
Aethemenes chloris	1	?	0	1.12 (0.263)	0.95 (0.687)	27-31 (0.350-0.550)
N. viridula	1	1	1	1.02-1.26 (0.000-0.631)	0.73-0.84 (0.000-0.343)	26-40 (0.300-1.000)
N. antennata	1	1	1	?	?	30 (0.500)
N. yunnana	?	?	?	?	?	?
N. similis	?	?	?	?	?	?
N. mendax	?	?	?	?	?	?
N. naspira	?	?	?	?	?	?
N. capicola	?	?	?	?	?	?
N. orbiculata	?	?	?	?	?	?
N. soror	?	?	?	?	?	?
N. immaculata	?	?	?	?	?	?
N. robusta	?	?	?	?	?	?
N. niamensis	?	?	?	?	?	?

TABLE 4. Character matrix for the analysis of the *Chinavia obstinata* (Stål) group, including only egg characters. Characters 1 to 40 (not shown) as in the original paper (Genevcius *et al.* 2012); characters 43 to 45 treated as continuous, values obtained with *stand 1* in parenthesis. Missing data = ?.

	4				
	1	2	3	4	5
C. rinapsa	?	?	?	?	?
C. australe	?	?	?	?	?
C. callosa	?	?	?	?	?
C. difficilis	?	?	?	?	?
C. fieberi	?	?	?	?	?
C. geniculata	?	?	?	?	?
C. gravis	?	?	?	?	?
C. hilaris	0	0	1.29-1.49 (0.066-0.400)	1.09-1.23 (0.134-0.343)	45-66 (0.146-0.583)
C. impicticornis	?	?	?	?	?
C. laeta	?	?	?	?	?
C. marginata	1	1	1.25-1.30 (0.000-0.083)	1.00-1.18 (0.000-0.268)	54-74 (0.333-0.750)
C. napaea	?	?	?	?	?
C. nigritarsis	?	?	?	?	?
C. obstinata 1	1	1	1.56-1.84 (0.516-0.983)	1.17-1.43 (0.253-0.641)	63-86 (0.521-1.000)
C. obstinata 2	?	?	?	?	?
C. obstinata 3	?	?	?	?	?
C. obstinata 4	?	?	?	?	?
C. panizzii	?	?	?	?	?
C. pengue	1	1	1.75-1.85 (0.833-1.000)	1.53-1.67 (0.791-1.000)	62-81 (0.500-0.896)
C. runaspis	1	1	1.64-1.76 (0.650-0.850)	1.16-1.24 (0.238-0.358)	38-58 (0.000-0.417)

TABLE 5. List of egg characters of potential use in future cladistic analyses within the Pentatomoidea, mostly based on characters proposed by Hasan and Kitching (1993), Javahery (1994), and Grazia *et al.* (2008). Suggestions are made on the type of data (continuous/discrete). Examples of taxa within Pentatomoidea presenting the proposed states were taken from the literature (Miller 1934, 1971; Esselbaugh 1946; Kobayashi 1953, 1954, 1955, 1958, 1959, 1964, 1965c, 1967; Southwood 1956; Hinton 1981; Saini 1984; Davidová-Vilímová 1987; Javahery 1994; Bundy & McPherson 1997, 2000, 2011; Tallamy & Schaefer 1997; Candan & Suludere 1999a, 1999b, 2003, 2006; Rieger 2000; Wolf & Reid 2003; Bernardes *et al.* 2005; Williams *et al.* 2005; Candan *et al.* 2007, 2011, 2012; Matesco *et al.* 2009, 2012; Bianchi *et al.* 2011; Tsai *et al.* 2011).

Egg

[1] Length (continuous).

[2] Width (continuous).

[3] Shape: **barrel-shaped** [Dinidoridae (*Coridius*, *Megymenum*); Plataspididae (*Brachyplatys*, *Coptosoma*, *Megacopta*); Pentatomidae (*Apodiphus*, *Capivaccius*, *Carpocoris*, *Catulona*, *Chinavia*, *Cyrtocoris*, *Banasa*, *Dichelops*, *Euschistus*, *Grazia*, *Mormidea*, *Pallantia*, *Podisus*, *Thyanta*)], **spherical** [Tessaratomidae (*Piezosternum*, *Pycanum*); Scutelleridae (*Chrysocoris*, *Eucorysses*, *Eurygaster*, *Hotea*, *Odontotarsus*, *Poecilocoris*, *Psacasta*); Pentatomidae (*Edessa*, *Loxa*, *Serdia*)], **cylindrical-elongate** [Urostylididae (*Tessaromerus*, *Urochela*, *Urolabida*, *Urostylis*); Acanthosomatidae (*Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Phloeidae (*Phloea*); Cydnidae (*Sehirus*, *Stibaropus*); Thaumastellidae (*Thaumastella*); Parastrachiidae (*Parastrachia*)].

[4] Color prior to embryonic development: **white** [Acanthosomatidae (*Elasmucha*); Dinidoridae (*Megymenum*); Thyreocoridae (*Corimelaena*, *Galgupha*); Phloeidae (*Phloea*); Cydnidae (*Geotomus*, *Macroscytus*, *Sehirus*); Parastrachiidae (*Parastrachia*); Plataspididae (*Brachyplatys*); Scutelleridae (*Hotea*, *Irochrotus*, *Odontoscelis, Odontotarsus*); Pentatomidae (*Aelia*, *Apodiphus*, *Catulona*, *Euschistus*, *Mormidea*], **yellow** [Urostylididae (*Urostylis*); Plataspididae (*Coptosoma*); Scutelleridae (*Pachycoris*, *Poecilocoris*); Pentatomidae (*Chinavia*, *Cosmopepla*, *Dolycoris*, *Euschistus*, *Graphosoma*, *Mormidea*, *Nezara*, *Podisus*, *Podops*], **green** [Acanthosomatidae (*Acanthosoma*); Tessaratomidae (*Eusthenes*, *Piezosternum*, *Pycanum*); Scutelleridae (*Chrysocoris*, *Eurygaster*, *Psacasta*); Pentatomidae (*Chinavia*, *Dichelops*, *Edessa*, *Euschistus*, *Loxa*, *Odmalea*, *Oebalus*, *Palomena*, *Pentatoma*, *Serdia*, *Thoreyella*], **brown** [Pentatomidae (*Chinavia*, *Banasa*, *Podisus*)], **grey** [Pentatomidae (*Dyroderes*, *Sciocoris*, *Stagonomus*, *Trichopepla*)], **black** [Pentatomidae (*Jalla*, *Oplomus*, *Perillus*, *Picromerus*, *Stiretrus*)].

[5] Color, pattern: **uniform** (most Pentatomoidea), **striped** [Pentatomidae (*Apateticus*, *Arma*, *Bagrada*, *Capivaccius*, *Chlorochroa*, *Eurydema*, *Grazia*, *Murgantia*, *Piezodorus*, *Thyanta*)].

Chorion

[6] Thickness (continuous/discrete): **thin** [Urostylididae (*Urochela*, *Urostylis*); Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Thaumastellidae (*Thaumastella*); Scutelleridae (*Hotea*); Pentatomidae (*Cosmopepla*)], **thick** [Dinidoridae (*Coridius*); Tessaratomidae; Plataspididae (*Brachyplatys*, *Coptosoma*, *Megacopta*); Scutelleridae (*Elvisura*, *Eurygaster*); Pentatomidae (*Aelia*, *Apateticus*, *Aphylum*, *Apodiphus*, *Banasa*, *Brochymena*, *Carpocoris*, *Chinavia*, *Dolycoris*, *Eurydema*, *Mormidea*, *Palomena*, *Piezodorus*, *Podisus*)].

[7] Pigmentation: **absent** (most Pentatomoidea), **present** [Pentatomidae (*Aelia*, *Banasa*, *Capivaccius*, *Carpocoris*, *Chinavia*, *Chlorochroa*, *Cyrtocoris*, *Grazia*, *Holcostethus*, *Pinthaeus*, *Thyanta*)].

[8] Brightness: **shiny** [Urostylididae (*Urostylis*); Acanthosomatidae (*Elasmucha*); Tessaratomidae (*Eusthenes*, *Pycanum*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Plataspididae (*Brachyplatys*); Scutelleridae (*Chrysocoris*, *Eurygaster*, *Poecilocoris*); Pentatomidae (*Catulona*, *Chinavia*, *Cosmopepla*, *Edessa*, *Menaccarus*)], **mat** [Dinidoridae (*Megymenum*); Scutelleridae (*Irochrotus*); Pentatomidae (*Aelia*, *Apodiphus*, *Banasa*, *Brochymena*, *Carpocoris*, *Chinavia*, *Codophila*, *Eurydema*, *Mormidea*, *Neottiglossa*, *Palomena*, *Picromerus*, *Piezodorus*, *Podisus*, *Thyanta*)].

[9] Sculpture, pattern: **smooth** [Acanthosomatidae (*Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Pentatomidae (*Catulona*, *Cosmopepla*, *Nezara*, *Oebalus*)], **granulate** [Thyreocoridae (*Galgupha*); Pentatomidae (*Chinavia*, *Cyrtocoris*, *Edessa*, *Odmalea*, *Picromerus*, *Serdia*, *Thoreyella*)], **reticulate** [Plataspididae (*Coptosoma*); Scutelleridae (*Eurygaster*, *Odontotarsus*, *Pachycoris*); Pentatomidae (*Banasa*, *Capivaccius*, *Chinavia*, *Grazia*, *Mecidea*, *Rhaphigaster*)], **spinose** [Pentatomidae (*Aelia*, *Apodiphus*, *Carpocoris*, *Codophila*, *Dichelops*, *Euschistus*, *Graphosoma*, *Mormidea*, *Loxa*, *Pallantia*, *Palomena*, *Piezodorus*, *Podisus*], **salebrose** [Pentatomidae (*Thyanta*)], **polymorphic tubercles** [Pentatomidae (*Eurydema*)], **mushroom-shaped processes** [Pentatomidae (*Ancyrosoma*)].

[10] Longitudinal carinae: **absent** (most Pentatomoidea), **present** [Thyreocoridae (*Corimelaena*, *Galgupha*); Plataspididae (*Brachyplatys*, *Coptosoma*)].

[11] Eclosion split, direction: **longitudinal** [Urostylididae (*Urochela*, *Urostylis*); Acanthosomatidae (*Acanthosoma*, *Elasmostethus*, *Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Geotomus*, *Sehirus*)], **following the AMP ring** [Scutelleridae (*Eurygaster*); Pentatomidae (*Aelia*, *Apodiphus*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Mormidea*, *Palomena*, *Perillus*, *Picromerus*, *Podisus*, *Trichopepla*)].

[12] Operculum: **absent** [Urostylididae (*Tessaromerus*, *Urochela*, *Urolabida*, *Urostylis*); Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Tessaratomidae (*Piezosternum*, *Tessaratoma*); Thyreocoridae (*Corimelaena*, *Galgupha*, *Thyreocoris*); Phloeidae (*Phloea*)], **present** [Dinidoridae (*Coridius*, *Eumenotes*, *Megymenum*); Plataspididae (*Coptosoma*); Scutelleridae (*Hotea*); Pentatomidae (*Aelia*, *Aphylum*, *Apodiphus*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Mormidea*, *Palomena*, *Perillus*, *Picromerus*, *Podisus*, *Trichopepla*)].

[13] Operculum, position: **at anterior pole** [Scutelleridae (*Eurygaster*); Pentatomidae (*Chinavia*, *Euschistus*, *Mormidea*, *Podisus*), **at lateral side** [Dinidoridae (*Coridius*, *Eumenotes*, *Megymenum*)].

[14] Operculum, convexity: **convex** [Pentatomidae (*Aelia*, *Banasa*, *Catulona*, *Chinavia*, *Dichelops*,

Edessa, *Euschistus*, *Grazia*, *Neotiglossa*, *Podisus*, *Serdia*, *Thyanta*, *Trichopepla*)], **flat** [Tessaratomidae (*Pycanum*); Plataspididae (*Brachyplatys*, *Coptosoma*); Pentatomidae (*Codophila*, *Crypsinus*, *Euschistus*, *Holcostethus*, *Nezara*, *Odmalea*, *Oebalus*, *Pallantia*, *Piezodorus*, *Thoreyella*)].

[15] Operculum, shape: **circular** [Plataspididae (*Coptosoma*); Scutelleridae (*Eurygaster*, *Odontotarsus*); Pentatomidae (*Banasa*, *Capivaccius*, *Catulona*, *Chinavia*, *Cyrtocoris*, *Dichelops*, *Euschistus*, *Grazia*, *Loxa*, *Mormidea*, *Odmalea*, *Podisus*, *Serdia*, *Thyanta*)], **elliptical** [Pentatomidae (*Edessa*, *Piezodorus*)], **subquadrangular** [Pentatomidae (*Odmalea*, *Thoreyella*)].

[16] Sealing bar: **absent** [Acanthosomatidae (*Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Scutelleridae (*Eurygaster*)], **present** [Pentatomidae (*Aelia*, *Apateticus*, *Aphylum*, *Apodiphus*, *Banasa*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Eurydema*, *Mormidea*, *Neottiglossa*, *Palomena*, *Perillus*, *Picromerus*, *Piezodorus*, *Podisus*, *Trichopepla*)].

[17] Eclosion line, position during hatching: **following the AMP ring** [Plataspididae (*Coptosoma*); Pentatomidae (*Banasa*, *Chinavia*, *Dichelops*, *Euschistus*, *Graphosoma*, *Mormidea*, *Pallantia*, *Podisus*, *Thyanta*)], **traversing the AMP ring** [Scutelleridae (*Agonosoma*, *Eurygaster*, *Odontotarsus*, *Symphylus*); Pentatomidae (*Antiteuchus*, *Catulona*, *Edessa*, *Loxa*)].

[18] Eclosion line, sculpture pattern: **indistinguishable from the rest of the chorion** [Pentatomidae (*Euschistus*, *Loxa*, *Mormidea*, *Pallantia*)], **clearly different** [Scutelleridae (*Odontotarsus*); Pentatomidae (*Banasa*, *Capivaccius*, *Carpocoris*, *Catulona*, *Chinavia*, *Codophila*, *Dichelops*, *Edessa*, *Nezara*, *Odmalea*, *Podisus*, *Serdia*)].

Aero-micropylar processes (AMPs)

[19] Number (continuous).

[20] Length or ratio AMP length/egg length (continuous/discrete): **small** [Acanthosomatidae (*Elasmucha*); Dinidoridae (*Coridius*, *Eumenotes*); Tessaratomidae (*Piezosternum*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Scutelleridae (*Calidea*, *Chrysocoris*, *Eurygaster*, *Hotea*, *Odontotarsus*, *Psacasta*); Pentatomidae (*Aphylum*, *Banasa*, *Brochymena*, *Capivaccius*, *Catulona*, *Codophila*; *Dichelops*, *Edessa*, *Eurydema*, *Murgantia*, *Neottiglossa*, *Nezara*, *Palomena*, *Serdia*, *Thyanta*)], **long** [Urostylididae (*Urostylis*); Plataspididae (*Ceratocoris*, *Niamia*, *Platycephala*); Pentatomidae (*Apateticus*, *Apodiphus*, *Chinavia*, *Euschistus*, *Grazia*, *Loxa*, *Mormidea*, *Pallantia*, *Pentatoma*, *Piezodorus*, *Podisus*, *Raphigaster*, *Stagonomus*, *Trichopepla*, *Thoreyella*)].

[21] External projection: **absent** [Thaumastellidae (*Thaumastella*)], **present** (most Pentatomoidea).

[22] Internal canal: **absent** [Scutelleridae (*Psacasta*); Pentatomidae (*Ancyrosoma*, *Antiteuchus*, *Aphylum*, *Carpocoris*, *Edessa*, *Eurydema*, *Perillus*, *Picromerus*, *Sciocoris*)], **present** [Urostylididae (*Urochela*); Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Dinidoridae (*Coridius*); Tessaratomidae (*Agapophyta*); Thyreocoridae (*Corimelaena*, *Galgupha*, *Thyreocoris*); Cydnidae (*Sehirus*); Thaumastellidae (*Thaumastella*); Plataspididae (*Ceratocoris*); Scutelleridae (*Elvisura*, *Eurygaster*, *Hotea*)].

[23] Position: **near anterior pole** (most Pentatomoidea), **displaced posteriorly** [Tessaratomidae (*Siphnus*)].

[24] Number of rings: **one** (most Pentatomoidea), **two** [Parastrachiidae (*Dismegistus*); Scutelleridae

(*Chrysocoris*)] **three** [Pentatomidae (*Cyrtocoris*)].

[25] Insertion: **sessile** [Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Tessaratomidae (*Agapophyta*, *Siphnus*); Cydnidae (*Sehirus*); Scutelleridae (*Eurygaster*, *Odontotarsus*)], **pedunculated** [Urostilydidae (*Urostylis*); Thyreocoridae (*Corimelaena*, *Galgupha*); Plataspididae (*Coptosoma*); Pentatomidae (*Aelia*, *Chinavia*, *Coenus*, *Edessa*, *Eurydema*, *Neottiglossa*, *Picromerus*, *Piezodorus*, *Podisus*)]

[26] Shape: **like tubercle** [Scutelleridae (*Eurygaster*, *Odontotarsus*, *Psacasta*); Pentatomidae (*Edessa*)], **tubular/filiform** [Pentatomidae (*Coenus*, *Euschistus*, *Loxa*, *Pallantia*, *Piezodorus*, *Thoreyella*, *Trichopepla*)], **slightly clavate** [Pentatomidae (*Euschistus*, *Mormidea*, *Odmalea*, *Podisus*)], **clavate** [Urostylididae (*Urochela*, *Urostylis*); Tessaratomidae (*Piezosternum*); Pentatomidae (*Banasa*, *Capivaccius*, *Catulona*, *Chinavia*, *Chlorochroa*, *Dichelops*, *Holcostethus*, *Mecidea*, *Oebalus*, *Serdia*, *Thyanta*)], **cup-shaped** [Pentatomidae (*Grazia*, *Iphiarusa*)], **clover-shaped** [Plataspididae (*Coptosoma*)].

[27] Surface, sculpture: **smooth** [Thyreocoridae (*Corimelaena*, *Galgupha*); Pentatomidae (*Chinavia*, *Euschistus*, *Mecidea*, *Odmalea*, *Piezodorus*, *Podisus*, *Thoreyella*)], **irregular/rugose** [Pentatomidae (*Capivaccius*, *Catulona*, *Dichelops*, *Loxa*)], **spongy** [Pentatomidae (*Banasa*, *Chinavia*, *Euschistus*, *Grazia*, *Mormidea*, *Nezara*, *Oebalus*, *Serdia*, *Thyanta*)].

Egg-burster

[28] Shape: **H-shaped** (Tessaratomidae), **Y-shaped** [Acanthosomatidae (*Elasmucha*); Thyreocoridae (*Galgupha*); Cydnidae (*Sehirus*)], **T-shaped** [Tessaratomidae (*Pycanum*); Plataspididae (*Brachyplatys*, *Coptosoma*, *Niamia*, *Platycephala*); Scutelleridae (*Eurygaster*, *Odontotarsus, Pachycoris*, *Psacasta*); Pentatomidae (*Apodiphus*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Graphosoma*, *Mormidea*, *Neottiglossa*, *Palomena*, *Perillus*, *Picromerus*, *Podisus*, *Trichopepla*)].

[29] Degree of sclerotization: **weakly sclerotized** [Acanthosomatidae (*Elasmucha*); Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Sehirus*); Pentatomidae (*Banasa*, *Mormidea*, *Neottiglossa*, *Trichopepla*)], **strongly sclerotized** [Dinidoridae (*Coridius*); Plataspididae (*Coptosoma*); Scutelleridae (*Eurygaster*, *Odontotarsus*, *Psacasta*, *Poecilocoris*); Pentatomidae (*Apateticus*, *Apodiphus*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Eurydema*, *Mecidea*, *Palomena*, *Perillus*, *Picromerus*, *Piezodorus*, *Podisus*)].

[30] Location on the anterior pole: **at the center** [(Acanthosomatidae (*Elasmucha*); Dinidoridae (*Coridius*); Thyreocoridae (*Galgupha*); Cydnidae (*Sehirus*)], **beneath the AMP circle line** [Scutelleridae (*Eurygaster*); Pentatomidae (*Apodiphus*, *Brochymena*, *Carpocoris*, *Chinavia*, *Coenus*, *Cosmopepla*, *Dolycoris*, *Mormidea*, *Neottiglossa*, *Palomena*, *Podisus*, *Trichopepla*)].

[31] Pigmentation: **practically absent** [Scutelleridae (*Irochrotus*, *Odontoscelis*, *Phimodera*); Pentatomidae (*Podisus*)], **present** [Plataspididae (*Coptosoma*); Scutelleridae (*Eurygater*, *Odontotarsus*, *Pachycoris*, *Poecilocoris*, *Psacasta*); Pentatomidae (*Chinavia*, *Euschistus*, *Mormidea*)].

Oviposition

[32] Egg mass, number of eggs (mode) (continuous).

[33] Degree of aggregation: **singly** [Thyreocoridae (*Corimelaena*, *Galgupha*); Cydnidae (*Macroscytus*, *Stibaropus*); Scutelleridae (*Irochrotus*, *Odontoscelis*); Pentatomidae (*Proxys*, *Sciocoris*)],

in masses (most Pentatomoidea).

[34] Position of the eggs in relation to the substrate: **upright** [Urostylididae (*Urochela*); Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Tessaratomidae (*Piezosternum*); Phloeidae (*Phloea*); Plataspididae (*Brachyplatys*, *Coptosoma*); Scutelleridae (*Eurygaster*, *Hotea*, *Odontotarsus*, *Pachycoris*), Pentatomidae (*Apodiphus*, *Banasa*, *Carpocoris*, *Chinavia*, *Edessa*, *Euschistus*, *Mormidea*, *Podisus*)]; **lengthwise** [(Acanthosomatidae (*Elasmostethus*); Dinidoridae (*Coridius*, *Eumenotes*); Thyreocoridae (*Corimelaena*); Plataspididae (*Brachyplatys*); Pentatomidae (*Sciocoris*)], **unstructured** [Cydnidae (*Adomerus*, *Canthophorus*, *Sehirus*); Parastrachiidae (*Parastrachia*)].

[35] Upright position, relation of the eggs to each other: **side by side** [Acanthosomatidae (*Elasmucha*); Phloeidae (*Phloea*); Plataspididae (*Brachyplatys*, *Coptosoma*); Scutelleridae (*Eurygaster*, *Odontotarsus*, *Pachycoris*); Pentatomidae (*Chinavia*, *Cosmopepla*, *Euschistus*, *Mormidea*, *Neottiglossa*, *Podisus*)], **in chains** [Dinidoridae (*Coridius*, *Eumenotes*, *Megymenum*)].

[36] Upright position, eggs side by side, anterior pole, direction: **upwards** (most Pentatomoidea), **toward the outside** [Urostylididae (*Urostylis*); Plataspididae (*Brachyplatys*, *Coptosoma*)].

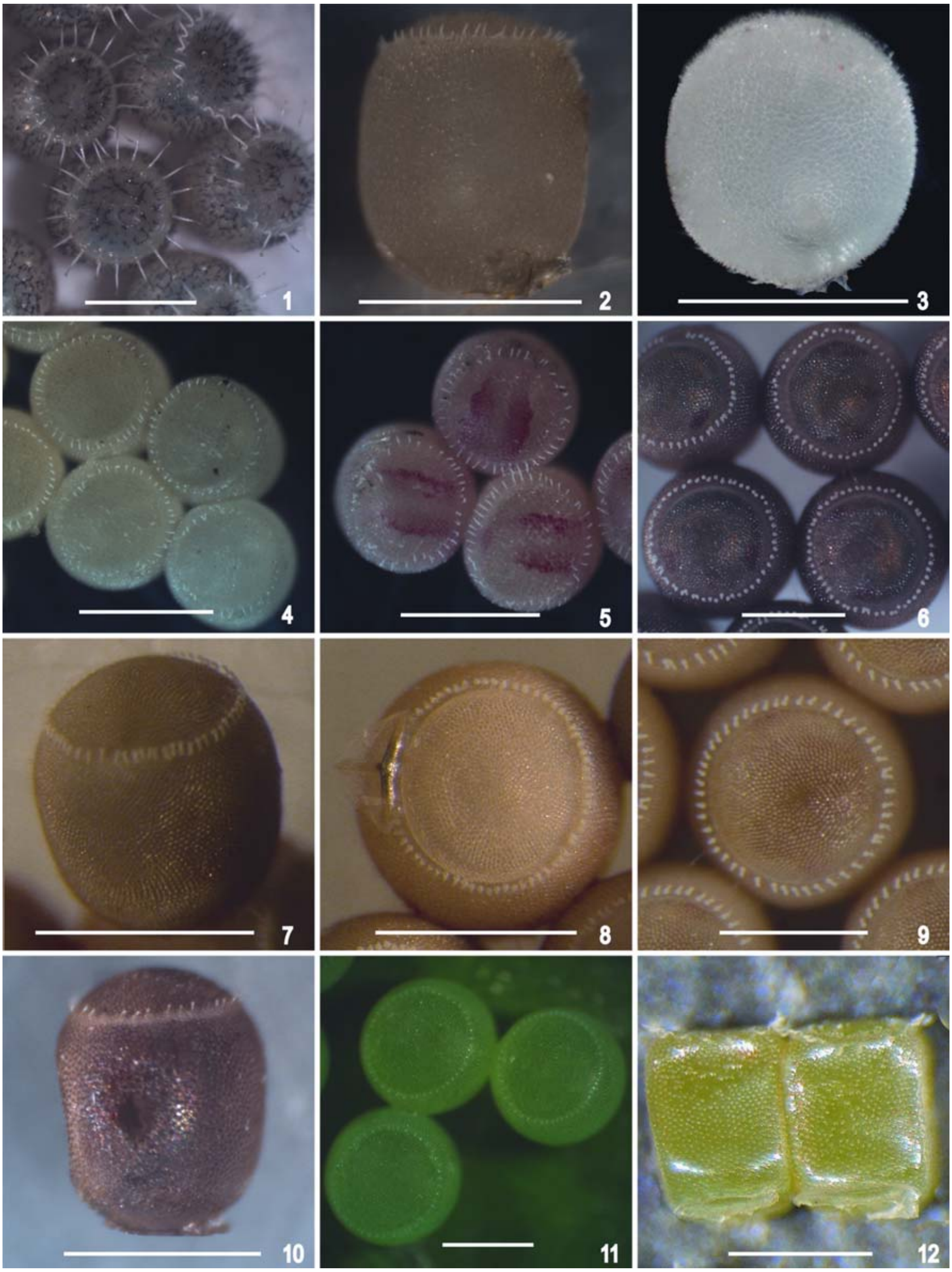
[37] Embryonic orientation: **toward one direction** [Scutelleridae (*Eurygaster*, *Pachycoris*)], **reversed** [Pentatomidae (*Aelia*, *Apateticus*, *Cosmopepla*, *Coenus*, *Eurydema*, *Mormidea*, *Neottiglossa*, *Piezodorus*, *Trichopepla*)].

[38] Spumaline: **absent** (most Pentatomoidea), **present** [Urostylididae (*Urostylis*); Plataspididae (*Ceratocoris*, *Niamia*, *Platycephala*); Scutelleridae (*Irochrotus*, *Phimodera*)].

[39] Location: **in the soil** [Cydnidae (*Geotomus*, *Sehirus*, *Stibaropus*); Parastrachiidae (*Parastrachia*); Scutelleridae (*Irochrotus*, *Odontoscelis*)], **on plants** [Urostylididae (*Urochela*, *Urostylis*); Acanthosomatidae (*Acanthosoma*, *Elasmucha*); Tessaratomidae (*Eusthenes*, *Piezosternum*); Thyreocoridae (*Corimelaena*, *Galgupha*); Plataspididae (*Coptosoma*); Scutelleridae (*Chrysocoris*, *Eucorysses*, *Eurygaster*, *Pachycoris*, *Poecilocoris*, *Tectocoris*); Pentatomidae (*Aelia*, *Apodiphus*, *Carpocoris*, *Chinavia*, *Cosmopepla*, *Dolycoris*, *Euschistus*, *Pinthaeus*, *Podisus*)], **in crevices in the bark of trees** [Urostylididae (*Urostylis*); Phloeidae (*Phloea*)].

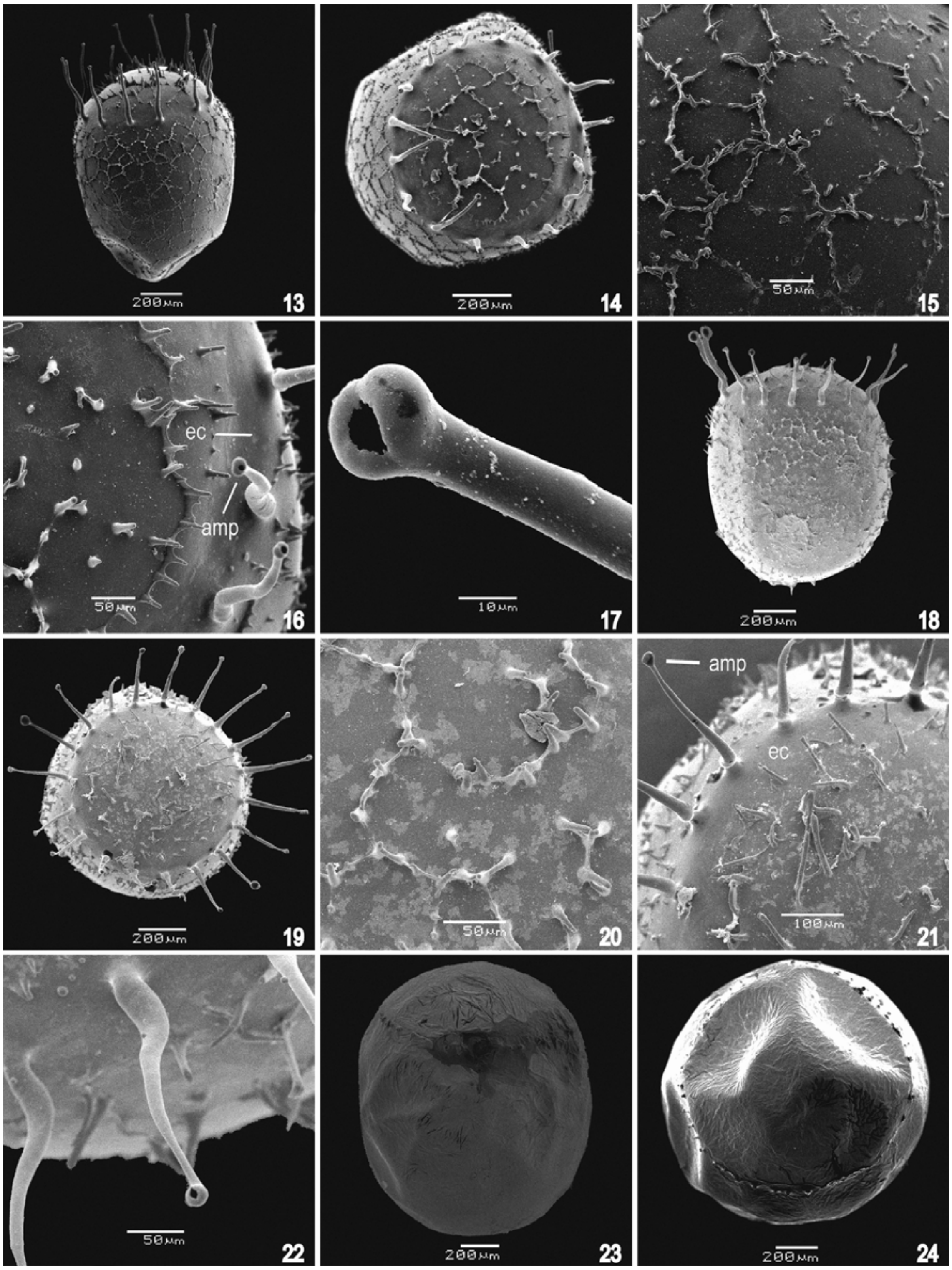
Maternal behavior

[40] Maternal care: **absent** (most Pentatomoidea), **present** [Acanthosomatidae (*Acanthosoma*, *Anaxandra*, *Elasmostethus*, *Elasmucha*); Dinidoridae (*Cyclopelta*); Tessaratomidae (*Erga*, *Pygoplatys*); Phloeidae (*Phloea*, *Phloeophana*); Cydnidae (*Adomerus, Canthophorus*, *Cydnus*, *Sehirus, Tritomegas*); Parastrachiidae (*Parastrachia*); Scutelleridae (*Cantao*, *Pachycoris*, *Tectocoris*); Pentatomidae (*Antiteuchus*, *Chlorocoris*, *Dinocoris*, *Edessa*, *Mecistorhinus*, *Poecilometis*, *Scotinophora*)].



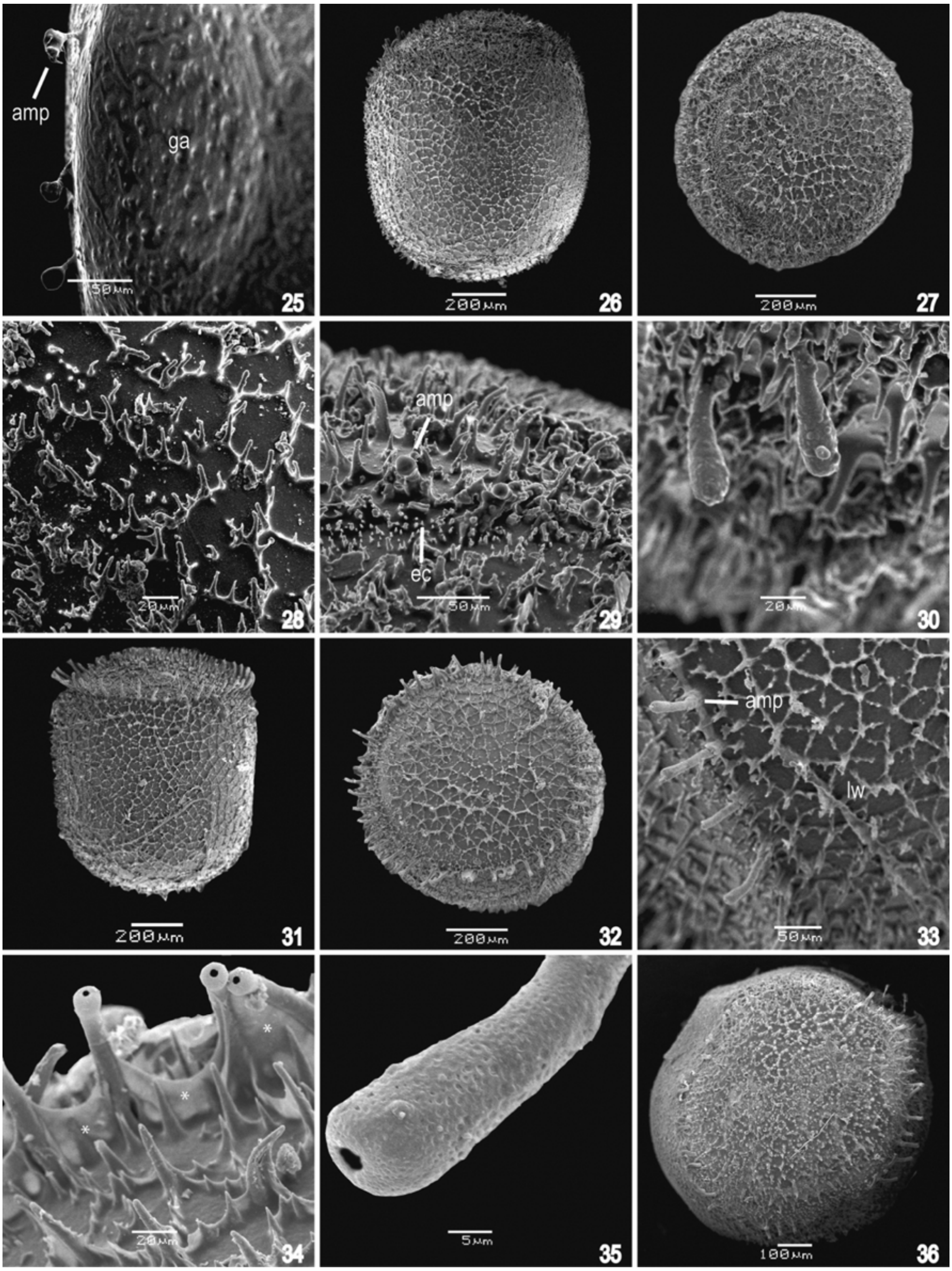
FIGURES 1–12. Eggs of the Pentatomidae viewed with stereomicroscopy. Fig. 1. *Podisus nigrispinus* (Dallas), egg mass, anterior view. Fig. 2. *Euschistus (Lycipta) riograndensis* Weiler & Grazia, lateral view. Fig. 3. *Euschistus (Mitripus) paranticus* Grazia, lateral view. Figs. 4 and 5. *Mormidea cornicollis* Stål. Fig. 4. Newly laid eggs, anterior view. Fig. 5. Fertile eggs, anterior view. Fig. 6. *Chinavia armigera* (Stål),

fertile eggs, anterior view. Fig. 7. *Chinavia aseada* (Rolston), lateral view. Fig. 8. *Chinavia brasicola* (Rolston), anterior view. Fig. 9. *Chinavia runaspis* (Dallas), anterior view. Fig. 10. *Banasa induta* Stål, lateral view. Fig. 11. *Serdia apicicornis* Stål, anterior view. Fig. 12. *Thoreyella maracaja* Bernardes, Schwertner & Grazia, lateral view. Scale bar = 1 mm.



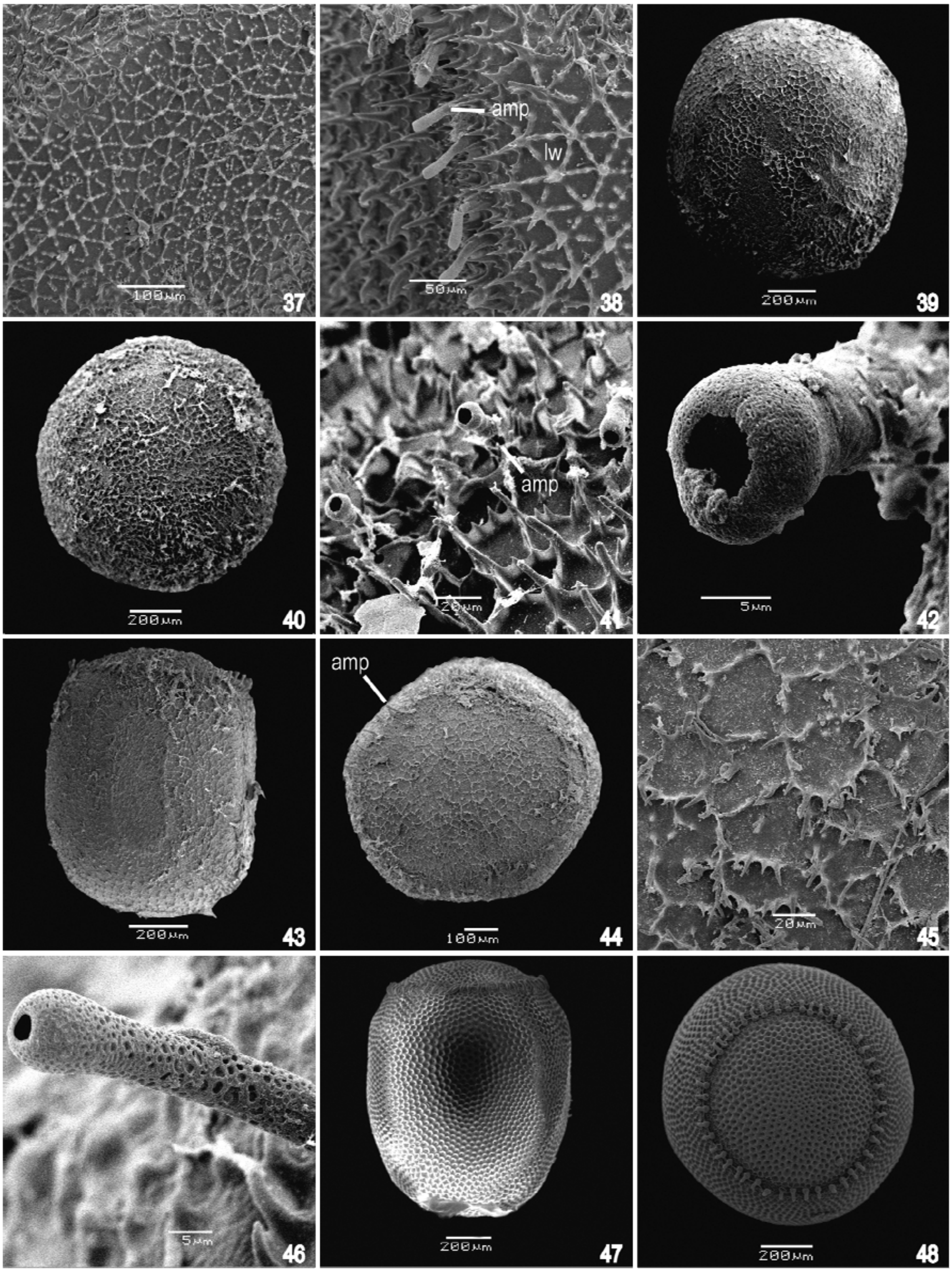
FIGURES 13–24. Eggs of the Pentatomidae viewed with scanning electron microscopy (SEM). Figs. 13–17. *Podisus distinctus* (Stål). Fig. 13. Lateral view. Fig. 14. Anterior view. Fig. 15. Magnification of the lateral wall. Fig. 16. Magnification of anterior pole, showing the eclosion line and the aero-micropylar processes (AMP). Fig. 17. Detail of AMP. Figs. 18–22. *Podisus nigrispinus* (Dallas). Fig. 18. Lateral view. Fig. 19. Anterior

view. Fig. 20. Magnification of the lateral wall. Fig. 21. Magnification of anterior pole, showing the eclosion line and the AMP. Fig. 22. Detail of AMP. Figs. 23 and 24. *Catulona pensa* Rolston. Fig. 23. Lateral view. Fig. 24. Anterior view. Abbreviations: amp–aero-micropylar process, ec–eclosion line.



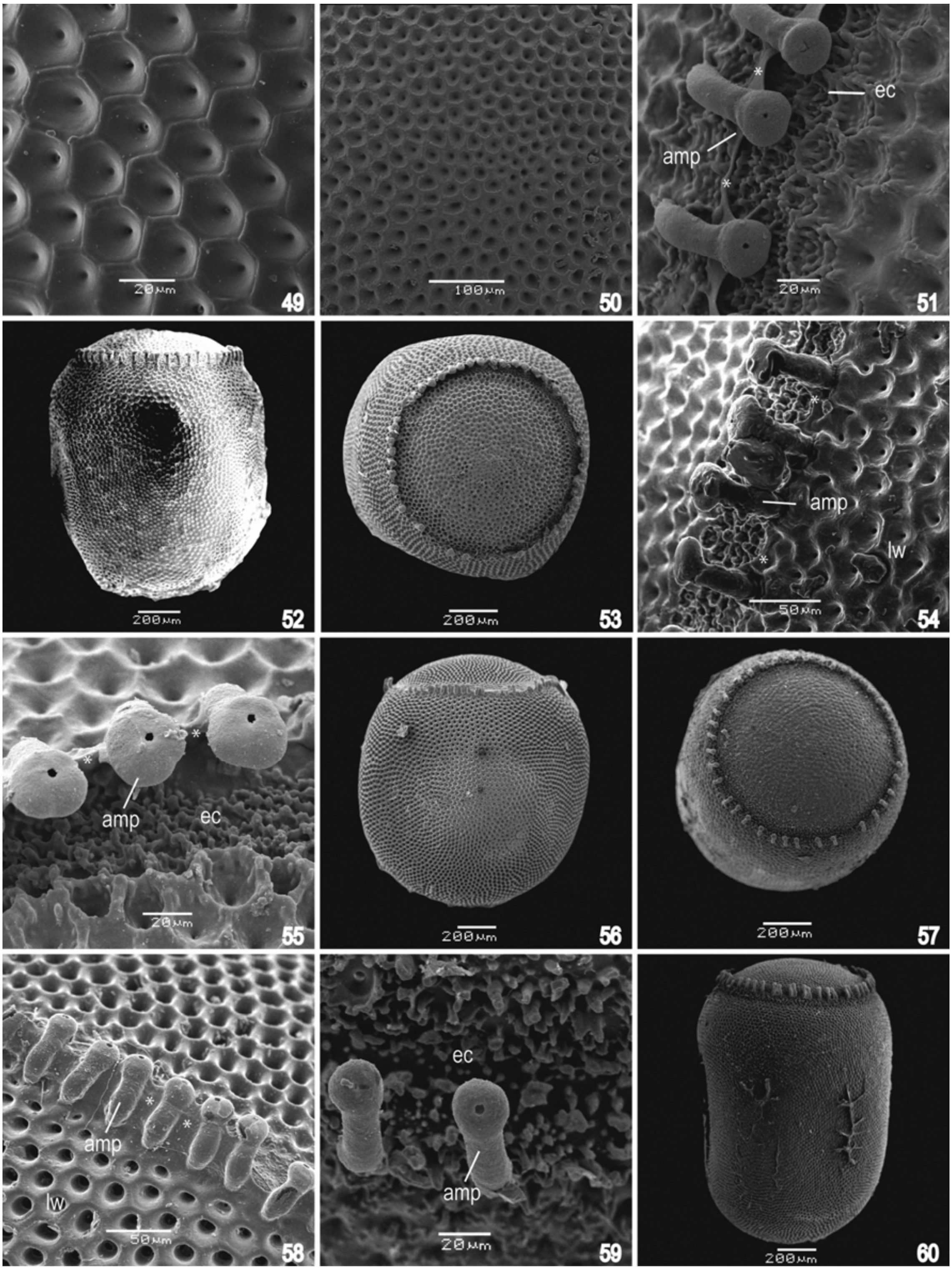
FIGURES 25–36. Eggs of the Pentatomidae viewed with SEM. Fig. 25. *Catulona pensa* Rolston, detail of anterior pole, showing the AMP and the granulated area. Figs. 26–30. *Dichelops (Diceraeus) furcatus* (Fabricius). Fig. 26. Lateral view. Fig. 27. Anterior view. Fig. 28. Magnification of the lateral wall. Fig. 29. Magnification of anterior pole, showing the eclosion line and the AMP. Fig. 30. Detail of AMP. Figs. 31–35.

Euschistus (Euschistus) heros (Fabricius). Fig. 31. Lateral view. Fig. 32. Anterior view. Fig. 33. Magnification of the lateral wall, showing the AMP. Fig. 34. Magnification of AMP, showing connector sheets (asterisks). Fig. 35. Detail of AMP surface. Fig. 36. *Euschistus (Lycipta) riograndensis* Weiler & Grazia, anterior view. Abbreviations: amp–aero-micropylar process, ec–eclosion line, ga–granulated area, lw–lateral wall.



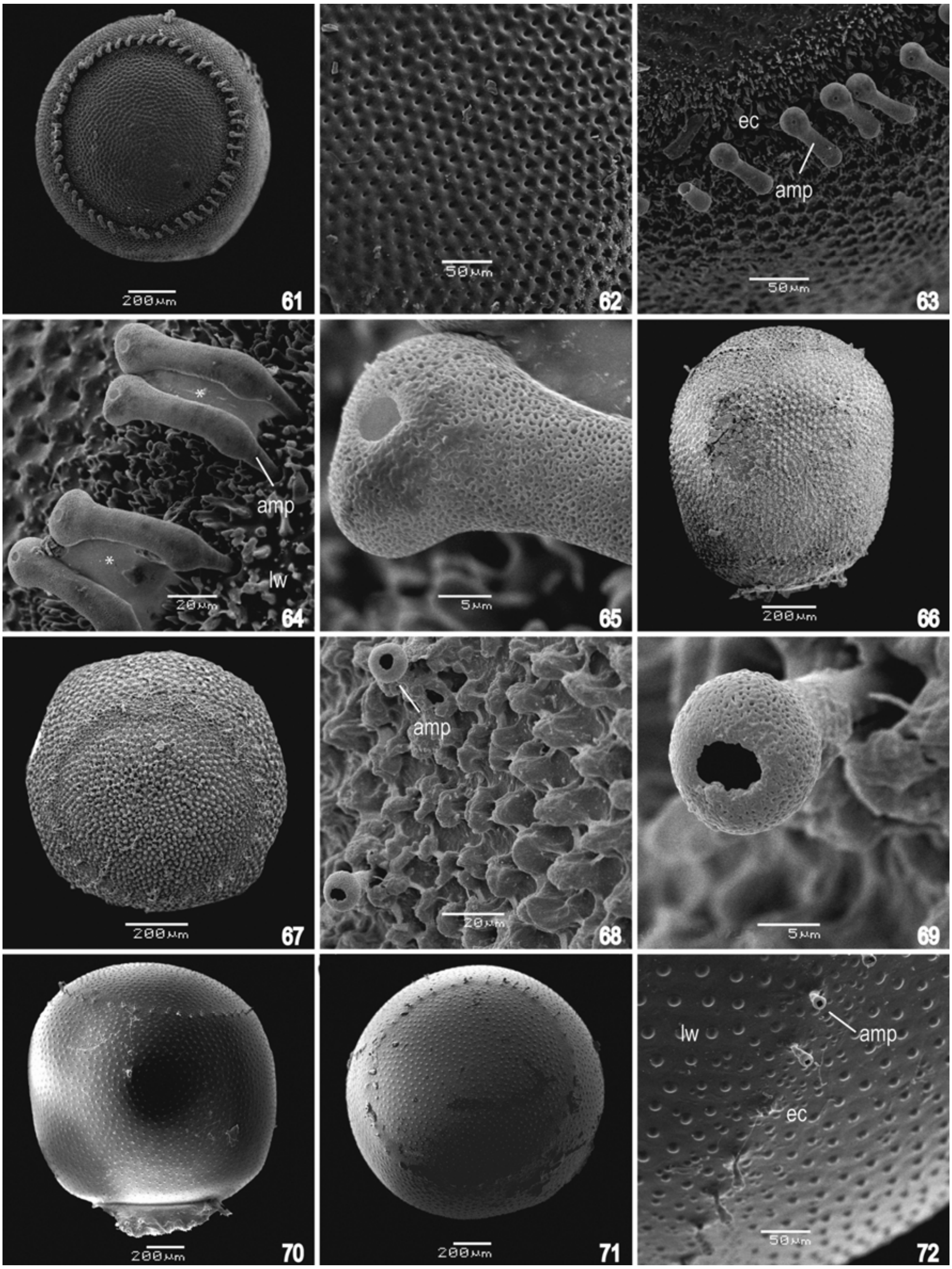
FIGURES 37–48. Eggs of the Pentatomidae viewed with SEM. Figs. 37 and 38. *Euschistus (Lycipta) riograndensis* Weiler & Grazia. Fig. 37. Magnification of the lateral wall. Fig. 38. Detail of the lateral wall, showing the AMP. Figs. 39–42. *Euschistus (Mitripus) paranticus* Grazia. Fig. 39. Lateral view. Fig. 40. Anterior view. Fig. 41. Magnification of anterior pole, showing the AMP. Fig. 42. Detail of AMP.

Figs. 43–46. *Mormidea cornicollis* Stål. Fig. 43. Lateral view. Fig. 44. Anterior view. Fig. 45. Magnification of anterior pole. Fig. 46. Detail of AMP. Figs. 47 and 48. *Chinavia armigera* (Stål). Fig 47. Lateral view. Fig. 48. Anterior view. Abbreviations: amp–aero-micropylar process, lw–lateral wall.



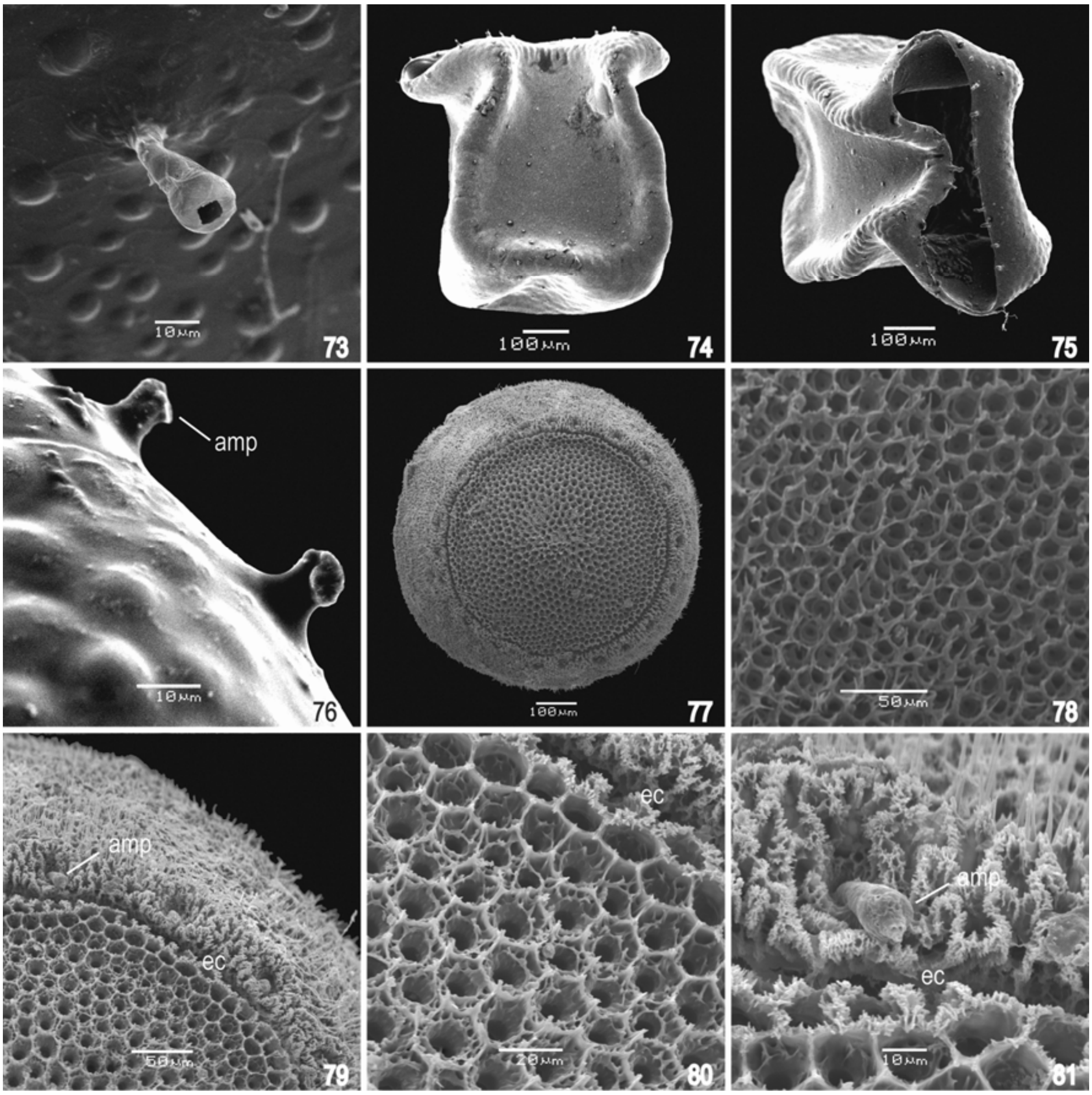
FIGURES 49–60. Eggs of *Chinavia* spp. viewed with SEM. Figs. 49–51. *Chinavia armigera* (Stål). Fig. 49. Magnification of the lateral wall, showing the polygonal cells projected inward in a funnel. Fig. 50. Detail of the anterior pole. Fig. 51. Detail of the anterior pole, showing the eclosion line, the AMP, and the connector sheets (asterisks). Figs. 52–55. *Chinavia aseada* (Rolston). Fig. 52. Lateral view. Fig. 53. Anterior view.

Fig. 54. Magnification of the lateral wall, showing the AMP and the connector sheets (asterisks). Fig. 55. Magnification of anterior pole, showing the eclosion line, the AMP, and the connector sheets (asterisks). Figs. 56–59. *Chinavia brasicola* (Rolston). Fig. 56. Lateral view. Fig. 57. Anterior view. Fig. 58. Magnification of the lateral wall, showing the AMP and the connector sheets (asterisks). Fig. 59. Magnification of anterior pole, showing the eclosion line and the AMP. Fig 60. *Chinavia runaspis* (Dallas), lateral view. Abbreviations: amp–aero-micropylar process, ec–eclosion line, lw–lateral wall.

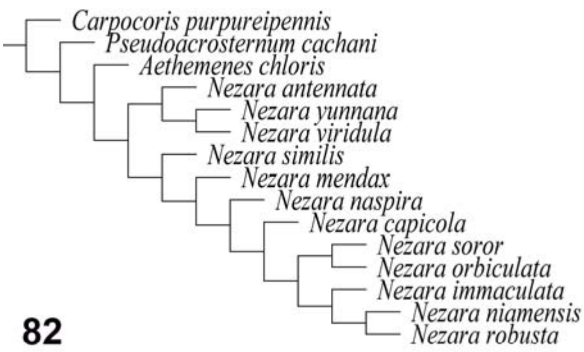


FIGURES 61–72. Eggs of the Pentatomidae viewed with SEM. Figs. 61–65. *Chinavia runaspis* (Dallas). Fig. 61. Anterior view. Fig. 62. Magnification of anterior pole. Fig. 63. Magnification of the lateral wall, showing the eclosion line and the AMP. Fig. 64. Detail of AMP and connector sheets (asterisks). Fig. 65. Detail of AMP surface. Figs. 66–69. *Banasa induta* Stål. Fig. 66. Lateral view. Fig. 67. Anterior view. Fig. 68.

Magnification of anterior pole, showing the AMP. Fig. 69. Detail of AMP surface. Figs. 70–72. *Serdia apicicornis* Stål. Fig 70. Lateral view. Fig. 71. Anterior view. Fig. 72. Magnification of the lateral wall, showing the eclosion line and the AMP. Abbreviations: amp–aero-micropylar process, ec–eclosion line, lw–lateral wall.



FIGURES 73–81. Eggs of the Pentatomidae viewed with SEM. Fig. 73. *Serdia apicicornis*, detail of AMP. Figs. 74–76. *Thoreyella maracaja* Bernardes, Schwertner & Grazia. Fig. 74. Lateral view. Fig. 75. Anterior view. Fig. 76. Magnification of anterior pole, showing the AMP. Figs. 77–81. *Capivaccius bufo* Distant. Fig. 77. Anterior view. Fig. 78. Magnification of the lateral wall. Fig. 79. Magnification of anterior pole, showing the eclosion line and the AMP. Fig. 80. Detail of anterior pole. Fig. 81. Detail of AMP. Abbreviations: amp–aero-micropylar process, ec–eclosion line.



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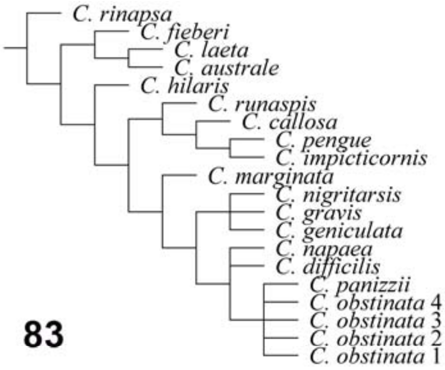

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FIGURES 82–83. Fig. 82. Most parsimonious tree (L = 63) in the analysis of the genus *Nezara* resulting from analysis under equal weighting of characters with 40 characters, six of which were egg characters. Fig. 83. Stric consensus of 10 most parsimonious trees (L = 104.493) of the *Chinavia obstinata* group resulting from analysis under equal weighting of characters with 45 characters, five of which were egg characters.

CONSIDERAÇÕES FINAIS

Frente à escassez de dados em Thyreocoridae no tocante a hipóteses de relacionamento, classificação, morfologia, biologia, estágios imaturos, plantas hospedeiras e distribuição, o presente trabalho consiste em importante contribuição para o conhecimento da família. Entretanto, muitos aspectos da morfologia e classificação do grupo, tais como o estudo comparativo das estruturas da genitália interna de ambos os sexos e as relações evolutivas entre os táxons pertencentes ao "complexo Cydnoidea", ainda precisam ser esclarecidos.

Antes do presente trabalho, nenhum gênero neotropical havia sido revisado, os estágios imaturos eram conhecidos para poucas espécies e não havia nenhuma hipótese de relacionamento entre os gêneros de Thyreocoridae. Com a revisão de *Alkindus*, foi possível caracterizar adequadamente o gênero e suas espécies, inclusive descrevendo pela primeira vez o macho de uma espécie previamente conhecida apenas pela fêmea. Nesse trabalho, descreveram-se, em microscopia eletrônica de varredura, características antes pouco exploradas no grupo de estudo, e a ampliação dos registros de distribuição geográfica permitiu um breve comentário sobre a biogeografia do táxon.

O estudo dos ovos de espécies de *Galgupha* possibilitou não só a caracterização detalhada do estágio de ovo em duas espécies, mas também uma discussão dos padrões de morfologia dos ovos, hábitos de oviposição e cuidado maternal encontrados em todas as espécies de Thyreocoridae e em grupos próximos. Com isso, abriu-se caminho para a exploração de caracteres de ovos na filogenia do grupo, subsidiado pelos resultados obtidos e pelos caracteres propostos na descrição da morfologia dos ovos de 16 espécies de Pentatomidae.

Por último, a análise do gênero *Corimelaena* constitui a primeira contribuição para o entendimento das relações de parentesco entre e dentro dos gêneros de Thyreocoridae. Graças aos avanços aqui relatados, mais informações estão disponíveis para o grupo, facilitando a identificação das espécies, o acúmulo de novas informações sobre as mesmas, bem como sua inclusão em futuros estudos voltados à evolução, ecologia e morfologia do grupo.

Uma amostragem de táxons mais ampla em Thyreocoridae e grupos considerados próximos e conjuntos de dados adicionais e mais completos auxiliarão a esclarecer o status de vários táxons de difícil posicionamento, em particular dentro do “complexo Cydnoidea”.

ANEXO I

Information for authors

Aim and scope

Zootaxa is a peer-reviewed international journal for rapid publication of high quality papers on any aspect of systematic zoology, with a preference for large taxonomic works such as monographs and revisions. *Zootaxa* considers papers on all animal taxa, both living and fossil, and especially encourages descriptions of new taxa. All types of taxonomic papers are considered, including theories and methods of systematics and phylogeny, taxonomic monographs, revisions and reviews, catalogues/checklists, biographies and bibliographies, identification guides, analysis of characters, phylogenetic relationships and zoogeographical patterns of distribution, descriptions of taxa, and nomenclature. Open access publishing option is strongly encouraged for authors with research grants and other funds. For those without grants/funds, all accepted manuscripts will be published but access is secured for subscribers only. All manuscripts will be subjected to peer review before acceptance. *Zootaxa* aims to publish each paper within one month after the acceptance by editors.

Based on length, two categories of papers are considered.

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Research articles are significant papers of four or more printed pages reporting original research. Papers between 4 and 59 printed pages are published in multi-paper issues of 60, 64 or 68 pages. Monographs (60 or more pages) are individually issued and bound, with ISBNs.

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2) **Correspondence**

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- commentary on or additions/corrections to papers previously published in *Zootaxa*(e.g. Zootaxa 1494: 67-68)
- obituary in memory of deceased systematic zoologists (e.g. Zootaxa 545: 67-68)
- taxonomic/nomenclatural notes of importance
- book reviews meant to introduce readers to new or rare taxonomic monographs (interested authors/publishers must write to subject editors before submitting books for review; editors then prepare the book review or invite colleagues to prepare the review; unsolicited reviews are not published)
- and short papers converted from manuscripts submitted as research articles but are too short to qualify as formal research articles.

These short contributions should have no more than **20 references** and its **total length should not exceed four printed pages (except editorials).** Neither an abstract nor a list of key words is needed; major headings (Introduction, Material and methods...) should NOT be used, except for new taxon heading and references. A typical correspondence should consist of (1) a short and concise title, (2) author name and address (email address), (3) a series of paragraphs of the main text, and (4) a list of references if any. For correspondence of 3 or 4 pages, the first or last paragraph may be a summary.

Commentaries on published papers are intended for scholarly exchange of different views or interpretations of published data and should not contain personal attack; authors of concerned papers may be invited to reply to comments on their papers.

Special issues

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Preparation of manuscripts

1) *General.* All papers must be in English. Authors whose native language is not English are encouraged to have their manuscripts read by a native English-speaking colleague before submission. Nomenclature must be in agreement with the *International Code of Zoological Nomenclature* (4th edition 1999), which came into force on 1 January 2000. Author(s) of species name must be provided when the scientific name of any animal species is first mentioned (the year of publication needs not be given; if you give it, then provide a full reference of this in the reference list). Authors of plant species names need not be given. Metric systems should be used. If possible, use the common font New Times Roman and use as little formatting as possible (use only **bold** and *italics* where necessary and indentions of paragraphs except the first). Special symbols (e.g. male or female sign) should be avoided because they are likely to be altered when files are read on different machines (Mac versus PC with different language systems). You can code them as m# and f#, which can be replaced during page setting. The style of each author is generally respected but they must follow the following general guidelines.

2) The **title** should be concise and informative. The higher taxa containing the taxa dealt with in the paper should be indicated in parentheses: e.g. A taxonomic revision of the genus *Aus* (Order: family).

3) The **name(s) of all authors** of the paper must be given and should be typed in the upper case (e.g. ADAM SMITH, BRIAN SMITH & CAROL SMITH). The address of each author should be given in *italics* each starting a separate line. E-mail address(es) should be provided if available.

4) The **abstract** should be concise and informative. Any new names or new combinations proposed in the paper should be mentioned. Abstracts in other languages may also be included in addition to English abstract. The abstract should be followed by a list of **key words** that are not present in the title. Abstract and key words are not needed in short correspondence.

5) The arrangement of the **main text** varies with different types of papers (a taxonomic revision, an analysis of characters and phylogeny, a catalogue etc.), but should usually start with an **introduction** and end with a list of **references**. References should be cited in the text as Smith (1999), Smith and Smith (2000) or Smith *et al.* 2001 (3 or more authors), or alternatively in a parenthesis (Smith 2000; Smith & Smith 2000; Smith *et al.* 2001). All literature cited in the text must be listed in the references in the following format (see a sample page here in PDF).

A) **Journal paper**:

Smith, A. (1999) Title of the paper. *Title of the journal in full*, volume number, page range.

B) **Book chapter**:

Smith, A. & Smith, B. (2000) Title of the Chapter. *In*: Smith, A, Smith, B. & Smith, C. (Eds), *Title of Book*. Publisher name and location, pp. x–y.

C) **Book**:

Smith, A., Smith, B. & Smith, C. (2001) *Title of Book*. Publisher name and location, xyz pp.

D) **Internet resources**

Author (2002) Title of website*,* database or other resources, Publisher name and location (if indicated), number of pages (if known). Available from: http://xxx.xxx.xxx/ (Date of access).

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(2) **journal titles and volume numbers are followed by a ","**

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7) **Tables**, if any, should be given at the end of the manuscript. Please use the table function in your word processor to build tables so that the cells, rows and columns can remain aligned when font size and width of the table are changed. Please do not use Tab key or space bar to type tables.

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1 Seven setae present on tarsus I; four setae present on tibia I; leg I longer than the body; legs black in color ... Genus A

- Six setae present on tarsus I; three setae present on tibia I; leg I shorter than the body; legs brown in color ... 2

2 Leg II longer than leg I ... Genus B

- Leg II shorter than leg I ... Genus C

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3) Number of plates and cited references

4) High taxon name (i.e. taxon section in Zootaxa website) and number of new taxa described in the paper

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ANEXO II

Zoological Journal of the Linnean Society: Instructions for Authors

The Linnean Society publishes four periodicals: the *Biological, Botanical* and *Zoological Journals*, and *The Linnean*, the Society's newsletter and proceedings.

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This should be uploaded as a separate file, designation 'Title Page'. It should include title, authors, institutions and a short running title. The title should be concise but informative, and where appropriate should include mention of family or higher taxon in the form: 'The Evolution of the Brown Rat, *Rattus norvegicus* (Rodentia: Muridae)'. A subtitle may be included, but papers in numbered series are not accepted. Names of new taxa should not be given in titles.

Abstract

This must be on a separate page. The abstract is of great importance as it may be reproduced elsewhere, and is all that many may see of your work. It should be about 100-200 words long and should summarize the paper in a form that is intelligible in conjunction with the title. It should not include references. The abstract should be followed by up to ten keywords additional to those in the title (alphabetically arranged and separated by hyphens) identifying the subject matter for retrieval systems.

Subject matter

The paper should be divided into sections under short headings. Except in systematic hierarchies, the hierarchy of headings should not exceed three. The Zoological Codes must be strictly followed. Names of genera and species should be printed in italic or underlined to indicate italic; do not underline suprageneric taxon names. Cite the author of species on first mention. Use SI units, and the appropriate symbols (mm, not millimetre; µm, not micron., s, not sec; Myr for million years). Use the negative index (m-1, l-1, h-1) except in cases such as 'per plant'). Avoid elaborate tables of original or derived data, long lists of species, etc.; if such data are absolutely essential, consider including them as appendices or as online-only supplementary material. Avoid footnotes, and keep cross references by page to an absolute minimum. Please provide a full English translation (in square brackets) for any quoted matter that is not in English.

References

We recommend the use of a tool such as EndNote or Reference Manager for reference management and formatting. EndNote reference styles can be searched for here: http://www.endnote.com/support/enstyles.asp

Reference Manager reference styles can be searched for here: http://www.refman.com/support/rmstyles.asp

In the text, give references in the following forms: 'Stork (1988) said', 'Stork (1988: 331)' where it is desired to refer to a specific page, and '(Rapport, 1983)' where giving reference simply as authority for a statement. Note that names of joint authors are connected by '&' in the text. **When papers are by three authors, use all names on the**

first mention and thereafter abbreviate to the first name *et al*. For papers by four or more authors, use *et al*. throughout.

The list of references must include all publications cited in the text and only these. Prior to submission, make certain that all references in the text agree with those in the references section, and that spelling is consistent throughout. In the list of references, titles of periodicals must be given in full, not abbreviated. For books, give the title, place of publication, name of publisher (if after 1930), and indication of edition if not the first. In papers with half-tones, plate or figure citations are required only if they fall outside the pagination of the reference cited. References should conform as exactly as possible to one of these four styles, according to the type of publication cited.

Burr FA, Evert RF. 1982. A cytochemical study of the wound-healing proteins in *Bryopsis hypnoides. Cytobios* 6: 199-215.

Gould SJ. 1989. *Wonderful life: the Burgess Shale and the nature of history*. New York: W.W. Norton.

Dow MM, Cheverud JM, Rhoads J, Friedlaender J. 1987b. Statistical comparison of biological and cultural/history variation. In: Friedlaender J, Howells WW, Rhoads J, eds. *Solomon Islands project: health, human biology, and cultural change*. New York: Oxford University Press, 265-281.

Gay HJ. 1990. The ant association and structural rhizome modifications of the far eastern fern genus *Lecanopteris* (Polypodiaceae). Unpublished D. Phil. Thesis, Oxford University.

Other citations such as papers 'in press' [i.e. formally accepted for publication] may appear on the list but not papers 'submitted' or 'in preparation'. These should be cited as 'unpubl. data' in the text with the names and initials of all collaborators. A personal communication may be cited in the text but not in the reference list. Please give all surnames and initials for unpublished data or personal communication citations given in the text.

In the case of taxonomic reviews, authors are requested to include full references for taxonomic authorities.

Give foreign language references in ordinary English alphabetic form (but copy accents in French, German, Spanish, etc.), if necessary transliterating in accordance with a recognized scheme. For the Cyrillic alphabet use British Standard BS 2979 (1958). If only a published translation has been consulted, cite the translation, not the original. Add translations not supplied by the author of the reference in square brackets.

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Keep these as simple as possible, with few horizontal and, preferably, no vertical rules. When assembling complex tables and data matrices, bear the dimensions of the printed page (225 × 168 mm) in mind; reducing typesize to accommodate a multiplicity of columns will affect legibility.

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These normally include (1) half-tones reproduced from photographs, (2) black and white figures reproduced from drawings and (3) diagrams. Use one consecutive set of Arabic numbers for all illustrations (do not separate 'Plates' and 'Text-figures' - treat all as 'Figures'). Figures should be numbered in the order in which they are cited in the text. Use upper case letters for subdivisions (e.g. Figure 1A-D) of figures; all other lettering should be lower case.

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