GUILHERME ENRIQUE
LUISI LÓPEZ

Phylogenetic analysis of Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) and its position in the superfamily Pentatomoidea, based on morphological studies

Análise filogenética de Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) e seu posicionamento na superfamília Pentatomoidea, com base em estudos morfológicos

Single Volume

SÃO PAULO

2024

GUILHERME ENRIQUE
LUISI LÓPEZ

Phylogenetic analysis of Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) and its position in the superfamily Pentatomoidea, based on morphological studies

Análise filogenética de Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) e seu posicionamento na superfamília Pentatomoidea, com base em estudos morfológicos

Single Volume

Original Version

Dissertation submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Master of Science (Systematics, Animal Taxonomy and Biodiversity).

Advisor: Prof. Dr. Cristiano Feldens Schwertner

SÃO PAULO

2024

Catalogação na Publicação
Serviço de Biblioteca e Documentação
Museu de Zoologia da Universidade de São Paulo

López, Guilherme Enrique Luisi
Phylogenetic analysis of Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) and its position in the surperfamily Pentatomoidea, based on morphological studies. = Análise filogenética de Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) e seu posicionamento na superfamília Pentatomoidea, com base em estudos morfológicos. / Guilherme Enrique Luisi López; orientador Cristiano Feldens Schwertner. São Paulo, 2024.
154 p.

Dissertação submetida ao Programa de Pós-Graduação do Museu de Zoologia Museu de Zoologia da Universidade de São Paulo, em cumprimento parcial aos requisitos para obtenção do título de Mestre em Ciências (Sistemática, Taxonomia Animal e Biodiversidade).

Versão original

Volume único

1. Pentatomoidea - Hemiptera. 2. Phloeidae – Pentatomoidea - filogenética. 3. Pentatomoidea -morfologia. I. Schwertner, Cristiano Feldens orient.; II. Título.

CDU 595.754
CRB-8 3805

LÓPEZ, Guilherme Enrique Luisi

Phylogenetic analysis of Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) and its position in the superfamily Pentatomoidea, basen on morphological studies

Análise filogenética de Phloeidae Amyot & Serville, 1843 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea) e seu posicionamento na superfamília Pentatomoidea, com base em estudos morfológicos

Dissertation submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Master of Science (Systematics, Animal Taxonomy and Biodiversity).

Date approved: _____/_____/_____

COMMITTEE MEMBERS

Prof. Dr._____ Institution:_____

Decision: _____ Signature:_____

Prof. Dr._____ Institution:_____

Decision: _____ Signature:_____

Prof. Dr._____ Institution:_____

Decision: _____ Signature:_____

Dedico este trabalho aos meus pais, Claudia e Fernando, e ao meu tio, Jesus (in memoriam)

ACKNOWLEDGMENTS

Quando comecei a pensar nesses agradecimentos, alguns dias antes do depósito, achei que seria uma lista bastante curta. Depois, percebi que há muita gente que foi (ou que ainda tem sido) essencial, não só para o desenvolvimento deste trabalho, mas também para a vida fora dele (talvez, muito mais para esses momentos). Tenho a certeza de que, depois de revisar essa lista várias vezes, ainda vou ter esquecido de nomes muito importantes. Por isso, agradeço (e me desculpo) desde agora. Realizar um trabalho tão grande e minucioso não teria sido possível sem a contribuição das pessoas listadas nas próximas páginas - cada uma contribuiu de formas diferentes, e por isso sou grato a cada uma delas. É, também por elas, que escrevo os agradecimentos em português, embora todo o trabalho esteja desenvolvido em inglês nas páginas seguintes.

Agradeço, primeiro, ao pessoal da secretaria de apoio acadêmico: Marta, Selma e Sônia. Por toda a ajuda, desde antes do ingresso na pós-graduação, até o depósito deste trabalho. Seja com alguma documentação, relatório, solicitação, ou mesmo alguma dúvida pontual, vocês sempre estiveram disponíveis para ajudar.

Ao pessoal da biblioteca - principalmente à Dione e ao Ricardo, que foram sempre muito solícitos e ajudaram com tanta boa vontade a obter todas as bibliografias, sempre de maneira muito rápida e eficiente.

Aos docentes e pesquisadores que contribuíram para o desenvolvimento desta dissertação e para minha formação durante esses anos de mestrado. Aos professores do MZUSP, em especial à Profa. Eliana Cancello e aos Profs. Aléssio Dátovo e Carlos Lamas que, em um primeiro momento, ainda durante o ingresso, fizeram sugestões muito valiosas para a delimitação do projeto e para as análises dos dados. Ao Prof. Carlos, também, pelas conversas durante os primeiros meses de pós-graduação, quando a situação era bastante incerta (e ficou ainda mais com o início da pandemia). Ao Prof. Silvio Nihei, que ainda no IB - USP me abriu as portas da Entomologia e me apoiou em diferentes momentos, como aluno, monitor ou pós-graduando. A todos os colegas heteropteristas que sempre trouxeram comentários construtivos e palavras de estímulo nas trocas durante os congressos, dividindo parte de sua experiência comigo.

Aos curadores de todas as coleções que emprestaram material ou enviaram fotos que tornaram esse trabalho possível: Birgit Jänicke e Jürgen Deckert (Museum für Naturkunde, Berlin), David A. Rider (North Dakota State University, Fargo), Gerry Cassis e Marcos Roca-Cusachs (University of New South Wales, Sydney), Gunvi Lindberg (Naturhistoriska riksmuseet, Estocolmo), Jeremy Frank (Bishop Museum, Hawaii), Jocélia Grazia (UFRGS, Porto Alegre), Márcio Félix (Instituto Oswaldo Cruz, Rio de Janeiro), María C. Melo e Pablo M. Dellapé (Universidad Nacional de La Plata, La Plata), Mick Webb (Natural History Museum, London), Randall T. Schuh (American Museum of Natural History, New York) e Thomas J. Henry (National Museum of Natural History, Washington DC). Também, à nova curadora de Heteroptera do MZUSP, Dra. Talita Roell, pelo acesso ao material, sem o qual o projeto não seria possível.

Agradeço às inúmeras pessoas que praticam, em seu dia a dia, a ciência cidadã. Suas contribuições nos permitiram desvendar onde se encontram os incríveis percevejos foco deste trabalho, e foram imprescindíveis para o desenvolvimento do primeiro capítulo.

Ao pessoal do Projeto Phasma, Edgar, Phillip e Victor, pela amizade e pelos espécimes coletados e incorporados à coleção do MZUSP, importantes para essa dissertação (e também para outros trabalhos desenvolvidos).

A todos os amigos e colegas do lab Heteroptera, atuais ou que passaram por lá em outros momentos: Alexandre, Helena, Letícia, Lucas, Maíra, Matheus, Natália, Nicholas e Renan. Obrigado por toda a amizade, companhia e convívio, dentro e fora do laboratório. Sem dúvidas, a colaboração de todos foi essencial para o desenvolvimento deste trabalho. É ótimo poder dividir tantas ideias e projetos com vocês. Ao Lucas, por ter me ensinado sobre as fotos e edição de imagens. Ao Alê, Maíra, Nicholas e Renan pela amizade e convívio quase diário no laboratório e fora dele, dividindo tantos almoços, cafés, angústias, conquistas e trabalhos de campo. À Maíra, também, pela companhia durante a viagem ao congresso de Heteroptera, na Argentina. Um agradecimento especial ao Renan, agora Dr. Carrenho, por ter me acompanhado e ensinado tanto durante meus primeiros meses no laboratório; é ótimo poder colaborar em trabalhos tão legais.

A todos os amigos que estiveram ao meu lado, desde a graduação, apoiando e dividindo tantas coisas na vida acadêmica e fora dela. Em especial, ao Edgar, João Marcus, Leonardo e

Raphael. Dividir tantas coisas com vocês em Itupeva, São Paulo, ou qualquer outro lugar, é sempre muito especial.

À Luiza, com quem em tão pouco tempo já pude construir e dividir tanto. Seu amor, amizade, carinho, companhia e suporte são importantes todos os dias. Obrigado por me acolher e ouvir quando falo sobre meu trabalho, e por me inspirar quando fala sobre o seu. Tenho muito orgulho de poder dividir tanto com você. Agora, um pouco longe. Mas sempre pertinho.

Ao Prof. Cristiano Schwertner, por me receber no laboratório e me orientar por todo esse tempo. Sua amizade, ajuda, conselhos e conversas são essenciais não só para este trabalho, mas também para a minha formação como entomólogo e pesquisador. Obrigado por tantas trocas de ideias, e pela liberdade para desenvolver minhas ideias com outros projetos e permitir que eles resultassem em muito aprendizado e, às vezes, em trabalhos que foram muito prazerosos de desenvolver.

Agradeço, especialmente, à minha família, por todo o amor, apoio e carinho. Aos meus tios, Jesus (in memoriam) e Virgínia, e aos meus primos, Cecília e Emílio, por terem me acolhido e me feito sentir em casa, mesmo tão longe, durante minha visita a Buenos Aires. Por fim, não tenho como agradecer de forma suficiente aos meus pais, Claudia e Fernando, por tanto. Por todo o amor e por todo o apoio, principalmente nos últimos anos. Não poderia ter chegado tão longe sem o apoio de vocês em cada passo da minha trajetória.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001. / This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

ABSTRACT

The family Phloeidae, a.k.a. Neotropical bark bugs, is one of the less speciose families of Pentatomoidea, with three species included in two genera, *Phloea* Spinola and *Phloeophana* Kirkaldy. Distributed in the Neotropics, these bugs are recognized by the large size, flattened body, presence of foliaceous expansions throughout the body, eyes divided into dorsal and ventral portions, and cryptic coloration, camouflaging themselves in the barks of the trees. Despite their larger size, the identity of the three species is not well delimited, their distribution is sparsely known, and their relationships with other Pentatomoidea families is still unknown. Besides that, some authors debate wether the enigmatic genus *Serbana* Distant, described from Borneo, should be included in Phloeidae or not. In this dissertation, we present a morphological review of the family Phloeidae in the Neotropics (considering *Phloea* and *Phloeophana*), providing new diagnoses for the family, genera and species, an identification key for adults and nymphs of the three species, and describing chromatic variation in *Phloea subquadrata* Spinola. We also review the literature and present synonymic lists and updated distribution maps, including unpublished data from collection specimens and citizen science platforms. We also performed a phylogenetic analysis using a morphological approach to investigate two main questions: the relationships between Phloeidae and the other pentatomoids, and wether *Serbana* is included in Phloeidae or not. A morphological matrix with 123 revised characters was assembled, and 71 species in 12 families were included in our analyses. Photographic documentation is provided for most of the morphological characters. Our results corroborated that *Serbana* should be included in Phloeidae, as sister group to *Phloea* + *Phloeophana*. The three genera share many synapomorphies, which are discussed in this study. Our results are dubious regarding the phylogenetic relationships of the Phloeidae (including *Serbana*), suggesting two distinct hypotheses: a sister group relationship between Phloeidae and Scutelleridae, or Phloeidae as sister group of a large clade including Scuteleridae and other four Pentatomoidea families. Finally, we briefly discuss the incongruence between our morphological data and recent molecular evidence supporting *Serbana* as part of the Pentatomidae, and possible morphological convergences as a possible explanation for the incongruences we found.

Keywords: Citizen science. Morphology. Neotropical bark bugs. Neotropical Heteroptera. Phylogenetic analysis.

RESUMO

Os percevejos da família Phloeidae, conhecidos como bichos-casca neotropicais, são uma das famílias menos especiosas de Pentatomoidea, com três espécies incluídas em dois gêneros, *Phloea* Spinola e *Phloeophana* Kirkaldy. Distribuídos na região Neotropical, esses percevejos são reconhecidos pelo tamanho grande, corpo achatado, presença de expansões foliáceas pelo corpo, olhos divididos em porções dorsal e ventral e coloração críptica, se camuflando nas cascas das árvores. Apesar de seu tamanho grande, a identidade das três espécies não é bem delimitada, sua distribuição é pouco conhecida e suas relações com outras famílias de Pentatomoidea são desconhecidas. Além disso, alguns autores debatem se o enigmático gênero *Serbana* Distant, descrito de Bornéu, deveria ser incluído em Phloeidae ou não. Nesta dissertação, nós apresentamos uma revisão morfológica da família Phloeidae na região Neotropical (considerando *Phloea* e *Phloeophana*), fornecendo novas diagnoses para a família, gêneros e espécies, uma chave de identificação para adultos e ninfas das três espécies, e descrevendo variação cromática em *Phloea subquadrata* Spinola. Nós também revisamos a literatura e apresentamos listas sinonímicas e mapas de distribuição atualizados, incluindo dados não publicados de espécimes de coleção e de plataformas de ciência cidadã. Realizamos uma análise filogenética utilizando uma abordagem morfológica para investigar duas questões principais: as relações entre Phloeidae e os outros pentatomóideos, e se *Serbana* está incluído em Phloeidae ou não. Uma matriz morfológica com 123 caracteres revisados foi elaborada, e 71 espécies em 12 famílias foram incluídas em nossas análises. Documentação fotográfica foi fornecida para a maioria dos caracteres morfológicos. Nossos resultados corroboraram que *Serbana* deveria ser incluído em Phloeidae, como grupo-irmão de *Phloea* + *Phloeophana*. Os três gêneros compartilham muitas sinapomorfias, que são discutidas neste estudo. Nossos resultados são dúbios no que diz respeito às relações filogenéticas de Phloeidae (incluindo *Serbana*), sugerindo duas hipóteses distintas: uma relação de grupos-irmãos entre Phloeidae e Scutelleridae, ou Phloeidae como grupo-irmão de um grande clado que inclui Scutelleridae e outras quatro famílias de Pentatomoidea. Finalmente, discutimos brevemente a incongruência entre nossos dados morfológicos e evidências moleculares recentes suportando *Serbana* como parte de Pentatomidae, e possíveis convergências morfológicas como uma possível explicação para as incongruências encontradas.

Palavras-chave: Análise filogenética. Bichos-casca neotropicais. Ciência cidadã. Heteroptera neotropicais. Morfologia.

General Introduction

The order Hemiptera (Hexapoda: Insecta) is the fifth largest insect order (Forero, 2008; Grazia et al. 2024) with more than 106,000 described species (Song & Zhang, 2022), thus constituting the largest and most diverse group of non-holometabolous insects (Henry, 2017; Song & Zhang, 2022). The order is included in a clade known as Paraneoptera, which also includes the thrips (order Thysanoptera, sister group of Hemiptera), and the bark and book lices (order Psocodea) (Trautwein *et al*., 2012; Li *et al*., 2015; Johnson *et al*., 2018). Traditionally, four monophyletic suborders are recognized (Forero, 2008): Auchenorrhyncha (e.g. cicadas and leafhoppers), Coleorrhyncha (moss bugs), Heteroptera (true bugs) and Sternorrhyncha (e.g. aphids and scale insects). In the past, the 3 suborders except for Heteroptera were grouped as the "Homoptera" (e.g. Evans, 1963); recent phylogenetic analyses (Li *et al*., 2017; Johnson *et al*., 2018; Song & Zhang, 2022) have, however, demonstrated that "Homoptera" is paraphyletic in relation to Heteroptera. The relationships between the suborders are not completely established. While Sternorrhyncha is usually recovered as the sister clade of all other hemipterans, the position of Coleorrhyncha varies from sister group of Heteroptera (Forero, 2008; Weirauch & Schuh, 2011; Li *et al*., 2017), to sister group of Auchenorrhyncha (Johnson *et al*., 2018) or even nested within this suborder (Li *et al*., 2017, fig. 1 therein).

The suborder Heteroptera comprises the insects commonly known as True bugs. Distributed across all biogeographic realms, their greatest diversity is achieved within the tropical zones of the globe (Panizzi & Grazia, 2015), totaling an impressive number of more than 45,254 described species (Henry, 2017). All this diversity was split into seven monophyletic lineages (Schuh, 1979), recognized as infraorders (Weirauch & Schuh, 2011; Weirauch *et al*. 2019); their interrelationships are not defined as well, but Cimicomorpha and Pentatomomorpha are consistently recovered as sister groups and as the most derived clade within the True bugs (Wheeler *et al*., 1993; Cassis & Schuh, 2010; Li *et al*., 2012; Weirauch *et al*., 2019; de Moya *et al*., 2019). Together, they include ca. 90% of the diversity of the Heteroptera. The infraorder Pentatomomorpha comprises a wide array of ecological and morphological diversity, including mycetophagous, phytophagous, predaceous, and even hematophagous species (Weirauch *et al*., 2019). With more than 14,000 species

(Weirauch & Schuh, 2011), it is divided into 5 (Panizzi & Grazia, 2015) or 6 (Henry, 1997, 2017) superfamilies.

The nominal superfamily, Pentatomoidea comprises more than 1,400 genera and 8,000 species classified in 18 families, two of them fossil (Rider *et al*., 2018). The group is highly supported as monophyletic by multiple lines of evidence (Grazia *et al*. 2008; Liu *et al*. 2019; Weirauch *et al*. 2019; Ye *et al*. 2022), and is diagnosed by i) the five segmented antennae (with some exceptions), ii) an enlarged scutellum, the apex of which typically reaches or surpasses the midpoint of the abdomen, iii) the claval commissure usually obsolete, not surpassing the apex of the scutellum, iv) the presence of 2 + 2 abdominal trichobothria (sometimes 1 + 1) lateral to the spiracle line on abdominal sternites II-VIII; v) abdominal tergite VIII covering abdominal tergite IX in females, vi) the opening of the genital capsule in males directed posteriorly, and vii) the eggs barrel shaped (Grazia et al. 2008; Rider et al. 2018).

Pentatomoids can be found all around the world, and present wide variation in their morphology. Some species are very small, not surpassing a couple millimeters, while many are very large, reaching between 30-40mm, and robust, like some pentatomids and tessaratomids (Rider *et al*., 2018). Except for hematophagy, pentatomoids present all feeding habits described for the Pentatomomorpha. Once again, the phylogenetic relationships within this group are not yet established, and only recently works based on sound phylogenetic methodology have provided some clues as to the classification of the superfamily (e.g. Gapud, 1991; Grazia *et al*., 2008; Lis *et al*., 2017; Bianchi *et al*., 2021; Ye *et al*., 2022). Recently, some works have investigated relationship hypothesis for some of the families within Pentatomoidea, e.g. Dinidoridae (Lis *et al*., 2012a, 2012b), Lestoniidae (Wu *et al*., 2016), and the “cydnoid” complex (Lis *et al*., 2017). Other works have tried to solve some of the internal relationships of some families (Scutelleridae: Wu *et al*., 2018; Pentatomidae: Roca-Cusachs *et al*., 2022; Urostylididae: Duan *et al*., 2023). None of these, however, have focused on the classification of the family Phloeidae and only few of them have included at least one species of it in their analyses (Gapud, 1991, Grazia *et al*., 2008; Bianchi *et al*., 2021; Roca-Cusachs *et al*., 2022).

The Phloeidae, popularly known as Neotropical Bark Bugs (Salomão & Vasconcellos-Neto, 2010), are a small family of pentatomoid bugs of very distinctive morphology. Easily

recognizable, they are large bugs (15-30mm), extremely flattened, with cryptic coloration and large foliaceous expansions in their mandibular plates, pronotum, hemelytral corium and connexiva (Rider *et al*., 2018) (figs. 1–14, 82–84). These characteristics, together, allow these bugs to easily blend with the barks of the trees where they live, making it hard to spot them at first glance. Nonetheless, a remarkable morphological characteristic are the compound eyes, divided into dorsal and ventral functional portions, but separated by an annulus without any ommatidia (fig. 17). This characteristic, considered synapomorphic for the family, easily allows its recognition and is found only in another cryptic pentatomoid genus, *Serbana* Distant, 1906. Besides that, the opening of the scent glands is near the lateral margins of the metapleura (fig. 16) (Rider *et al*., 2018), a characteristic that also allows rapid recognition of the family members. The species present gregarious behavior, with large populations being found in tree trunks; nymph density in *Phloea* is usually higher than that of adults, and usually dozens of individuals are found together (Salomão & Vasconcellos-Neto, 2010). In *Phloeophana*, the aggregation behaviour is absent after maternal care ends, shortly after the first nymph moult (Postali, 2009).

The females of all species exhibit strong maternal care, positioning themselves above the eggs they lay, and posteriorly carrying the first instar nymphs, these remaining upside down in the female ventral abdomen. Magalhães (1909) stated that females, when disturbed and moved, always came back to protect their eggs and nymphs, meanwhile Guilbert (2003) reported that disturbed nymphs always came back to re-agregate with the adults. Ecological observations and experimental approaches suggest that the protective behavior of the mothers is not essential to egg hatching, but rather protects the eggs against dissection and natural enemies (Lent & Jurberg, 1966; Bernardes *et al*., 2005; Salomão *et al*., 2012).

Little is known about feeding behaviour of the attached nymphs. Diverging hypothesis have been proposed in the past, such as nymphs feeding from their mothers (Brien, 1930), from excessive sap oozing from the mother's rostrum (Magalhães, 1909; Bequaert, 1935), or from some liquid jets ejected by the females (Leston, 1953), but none of these have been supported by more modern studies (Guilbert, 2003). Indeed, first instar nymphs in related families (e.g. Pentatomidae) usually do not need to feed (e.g. Lockwood & Story, 1986; Chocorosqui & Panizzi, 2008; Eger *et al*., 2015), and that may be the case for phloeids as well.

The function of jets ejected by the adults is also unknown, but Guilbert (2003) observed many individuals ejecting them in intervals of 5–10 minutes. Some authors believe that it could be to eliminate excessive water from the continuous feeding in the tree trunks (Salomão *et al*., 2012). Moreover, they are expelled by both nymphs and adults.

The Phloeidae is among the less diverse families within Pentatomoidea: except for Lestoniidae, which has two described species (Rider *et al*., 2018), Phloeidae is the second less speciose. Usually, three species are recognized in two genera: *Phloea corticata* (Drury, 1773), *Phloea subquadrata* Spinola, 1837, and *Phloeophana longirostris* (Spinola, 1837). The first species was described as *Cimex corticatus*. After that, Lepeletier and Serville (1825) described the genus *Phloea* Lepeletier & Serville, 1825 and proposed an unnecessary new name for *P. corticata*, *P. cassidoides* Lepeletier & Serville, 1825, later recognized as a junior synonym (Amyot & Serville, 1843). Hahn (1834) also proposed an unnecessary new name for *P. corticata*, *Paracoris paradoxus* Hahn, 1834. In the following year, Burmeister (1835) proposed *Phloeocoris* Burmeister, 1835 for *Phloeocoris corticatus* (Drury, 1773) and *Phloeocoris paradoxus* (Hahn, 1834); that resulted in a long-lasting taxonomical problem), and a solution is proposed in the Chapter 1 (section 4.3.) of this dissertation (López & Schwertner, 2024). Spinola (1837) described the remaining two species, *Phloea subquadrata* and *Phloea longirostris* (at the time, included in this genus), totaling the three species known to this day.

Amyot and Serville (1843) were the first authors to recognize the phloeids as a distinct suprageneric group, the Phléides; however, they committed two mistakes: they included in the group *Phloea corticata* and *Phloea paradoxa* sensu Hahn, and considered the later species a junior synonym of *Phloea longirostris*. Besides overlooking the work of Spinola (1837), Amyot and Serville (1843) wrongly attributed authorship of *P. longirostris* to Hahn, when that author had in fact merely described *P. corticata* again (that can be seen in the illustration included in his work). Probably, this was caused by their usage of Burmeister (1835) as a reference.

Amyot and Serville (1843) also included in their Phléides the genus *Coriplatus* White, 1842, a non-related genus of Discocephalini pentatomid. Stål (1872) was the next author to give suprageneric status to the phloeids, as the subfamily Phloeina. Despite not including *Coriplatus*, a few years back (Stål, 1860) he had compared his genus *Glyphuchus* Stål, 1860 to it mainly because of the flat body, expansions of the body, and serrated aspect of the lateral

margins of the abdomen (connexiva), much like Amyot and Serville (1843) had done with *Coriplatus*. Kirkaldy (1908) described the genus *Phloeophana* Kirkaldy, 1908 to accomodate *P. longirostris*, differing the two genera by the shape of the jugae, rostrum and scutellum lengths, and morphology of the coria and membranes. In his works, Kirkaldy (1908, 1909, 1913) always listed Phloeidae as a subfamily of Pentatomidae, a classification followed by other authors (e.g. Costa-Lima, 1940). The first to give family status to Phloeidae was China (1933), but he did not provide much evidence to support his decision. That was posteriorly done by Leston (1953), which presented the following set of characters to confirm his decision on Phloeidae as a distinct family: general body shape, three-segmented antennae, eyes divided into two parts, visible second abdominal spiracle, and the unique genitalia in the males, with complete eighth segment. After Leston (1953), most authors accepted the phloeids at family level (Schuh & Slater, 1995; Schwertner & Grazia, 2015; Rider *et al*., 2018; Schuh & Weirauch, 2020), whith some of them providing phylogenetic support to this decision (Grazia *et al*., 2008; Roca-Cusachs *et al*., 2022).

Besides the three species mentioned, some authors consider a fourth species, *Serbana borneensis* Distant, 1906 to be part of the family (Kirkaldy, 1909, 1913; Costa-Lima, 1940; Grazia *et al*., 2008; Schwertner & Grazia, 2015; Schuh & Weirauch, 2020). Distant (1906) originally described this species as a phloeid, and indeed it presents many morphological similarities with them: the body is extremely flattened dorsoventrally, and presents foliaceous expansions in the mandibular plates, pronotum, hemelytral coria and connexiva, as well as the compound eyes divided into two portions. There are, however, some differences between *Serbana* and the species of *Phloea* and *Phloeophana*: whilst *Serbana* has four-segmented antennae, it is three-segmented in the other two genera; it is dark brown in color, almost black, while the other neotropical genera are generally yellowish, grayish or greenish, with many iridescent punctures throughout the body; finally, adult females of *S. borneensis* are brachypterous, whereas all individuals are macropterous in *Phloea* and *Phloeophana*. Leston (1953) argued in favor of *Serbana* as a separate subfamily within Pentatomidae, the Serbaninae, in which was followed by Lent and Jurberg (1966) and Rider et al. (2018). Grazia et al. (2008) recovered *Serbana* within Phloeidae using morphological and molecular data, with high Bremer support values. Recently, Roca-Cusachs et al. (2022) brought molecular evidence that Serbaninae belongs in the Pentatomidae; their

support, however, was moderate at best, and they did not discuss morphological synapomorphies that supported this decision.

The inclusion of *Serbana* in Phloeidae remains doubtful. The only works including both *S. borneensis* and at least one species of the neotropical genera in their analyses presented very distinct results (Grazia *et al*., 2008; Roca-Cusachs *et al*., 2022). Moreover, the relationships between Phloeidae and the other families in Pentatomoidea is still unknown (Grazia *et al*., 2008; Rider *et al*., 2018). Each topology presented in Grazia et al. (2008) presents Phloeidae in different positions whithin the Pentatomoidea, for example: 1) in a huge politomy with several other families (fig. 42 therein); 2) in a clade with Lestoniidae, Plataspididae and the "cydnoid complex" (Cydnidae, Parastrachidae, Thaumastellidae and Thyreocoridae) (fig. 43 therein); 3) as sister group of Pentatomidae, Plataspididae, "Scutelleridae", and the "cydnoid complex" (fig. 44 in there); 4) in a clade with Canopidae, Cydnidae, Dinidoridae and Tessaratomidae (fig. 51 in there); etc. One topology even presented Phloeidae as polyphyletic (Grazia *et al*., 2008, fig. 53). Roca-Cusachs et al. (2022) recovered Phloeidae as sister group of Plataspididae + Scutelleridae, but their support was not high. Thus, the question of whom they are most closely related to remains open to investigation.

Nonetheless, the distribution of the family did not receive much attention in the literature in the last decades. The three genera have a disjunct distribution, with *Serbana* being endemic to Borneo and the two remaining genera restricted to South America. Amyot and Serville (1843) cited *P. longirostris* for Chile, but this record has not been confirmed. Kirkaldy (1909) cited *P. corticata* from Argentina and Chile, and Magalhães (1909) cited some specimens of Phloeidae from French Guiana. Since the work of Lent and Jurberg (1965), however, the distribution of the neotropical Phloeidae has not been addressed anymore, except for Salomão et al. (2012), who compiled this information, but did not add much to it. Indeed, the work of Salomão et al. (2012) presented an incorrect distribution record for *Phloea corticata* in the Bahia state, northeastern Brazil (see discussion on chapter 1, section 4.4). Elsewhere in the literature, the distribution of Phloeidae was always presented very generally (e.g. tropical America, Brazil, etc.). Most modern authors accept that the family is restricted to Brazil (Lent & Jurberg, 1965; Salomão *et al*., 2012). Lent and Jurberg (1965), however, mentioned the unconfirmed records in Argentina (Kirkaldy, 1909), Chile (Amyot & Serville, 1843; Kirkaldy, 1909) and French Guiana (Magalhães, 1909). Information on the

distribution of the family remains, therefore, sparse, with many distributional gaps in Brazil, and with three countries unconfirmed, only cited in the literature and generally deemed as invalid or doubtful. An updated distribution map, including precise locality records, was never presented for the family, making it difficult to understand the distribution of the species in a wider context.

Three main questions remain open to investigation when taking all these information into account. Together, they compose the three main goals investigated in this dissertation. The first question is concerning the classification of *Serbana borneensis*, whether it should be included in Phloeidae, in Pentatomidae, or in any of the other pentatomoid familes, or if it is a distinct lineage, included in its own clade within the Pentatomoidea. The second question pertains to which group is most closely related to the phloeids; as presented above, several competing hypotheses have been proposed in the past, and it is urgent to address the classification of Phloeidae in the context of the superfamily. Finally, the third question is about where to find these bugs: their distribution is sparsely known, mainly derived from old records (many of which unconfirmed), and possibly including other countries besides Brazil. If we are to investigate and understand Phloeidae diversity, ecology, natural history, and even the identity of the species included, it is mandatory to summarize their distribution, adding as many new records as possible, and taking into account all sources of information. On Chapter 1, we addressed the third question, focusing on the identity, nomenclature, taxonomic history, and distribution of Phloeidae in South America, reviewing the literature, studying specimens from several collections and checking and compiling records obtained from a citizen science database. On Chapter 2, we addressed questions one and two using a morphological approach, performing a phylogenetic analysis comprehending for the first time the four putative species of Phloeidae and representatives of eight families of Pentatomoidea and three families of Pentatomomorpha (not Pentatomoidea). The analysis represents a tentative to assess the position of *Serbana* and establish which groups are the most closely related to Phloeidae within the Pentatomoidea. For this, an extensive comparative morphological study was carried out, and the positions of *Serbana* and Phloeidae, the resulting synapomorphies/homoplasies, as well as a classification hypothesis focused on Phloeidae were discussed.

General Conclusions

In this dissertation, we provided a morphological review of the family Phloeidae and the three species included in it so far: *Phloea corticata*, *P. subquadrata* and *Phloeophana longirostris*. So far, the taxnomy of the species was dealt with only twice, both more than 50 years ago. Even after these taxonomic treatments, the identity of the species remained unclear. This was observed when visiting other collections or analyzing photos of Phloeidae material from large collections (e.g. National Museum of Natural History, Washington DC, USA): it was very common to find specimens misidentified or with no identification besides family level (even at the MZUSP). In the first chapter of this work, we thoroughly examined hundreds of specimens and photos of Phloeidae from the three species, and provided new diagnoses and updated identification keys, for both adults and nymphs. While studying material from the MZUSP collection, we found and described, for the first time, chromatic variation in the family (more precisely, in *Phloea subquadrata*). We reviewed all relevant literature information, provided extensive synonymic lists for all three species, and proposed two nomenclatural corrections. Finally, we also reviewed the distribution of the three species combining all published data so far, available material, and data from the citizen science website 'iNaturalist'. We were able to corroborate, after more than 100 years, Argentina and French Guiana as countries with occurence of the phloeids. All distributional data was synthesized both as tables with geographical coordinates and as distributional maps.

Once we established the identity and distribution of the Phloeidae in South America, we addressed two very relevant questions for pentatomoidean systematics: the classification of Phloeidae, and wether or not to include the enigmatic Bornean genus *Serbana* in the family. After careful examination of hundreds of specimens amounting to 71 species comprising 12 families, we obtained a morphological matrix of more than 120 morphological characters, most illustrated with high resolution photos; most of them were discussed along chapter two (section 4). All codification done in this work came mainly from original observations, but we also coded information from literature in a handful of cases where not enough specimens were available; even in these cases, we did not code these characteristics exactly like they were in the original works which treated these characters, but instead searched the literature for reliable morphological descriptions. Later, we used

the matrix to perform several analysis using parsimony as the optimality criteria. As a result, we produced one classification hypothesis for Pentatomoidea, with emphasis on Phloeidae. All families included in the analysis were recovered as monophyletic, receiving from moderate to very high support values. *Serbana* was recovered as sister group of the Neotropical Phloeidae, so we propose its classification in this family (currently, it is included in Pentatomidae). We were not able to establish the classification of Phloeidae within the superfamily; instead, two possibilities arose: the Phloeidae are either related to the jewel bugs (Scutelleridae), or to a larger clade of pentatomoids composed of Acanthosomatidae, Cydnidae, Dinidoridae, Pentatomidae, and possibly Scutelleridae.

It is our hope that this work might act as a baseline for morphological phylogenetic analyses in Pentatomoidea in the future by reuniting both large quantities of illustrated morphological information, references, and modern treatment of relevant structures, such as the female genitalia. Finally, we would like to highlight how, in the age of molecular, phylogenomic and 'next generation' methods, morphology can still be an invaluable source of information to comprehend biodiversity, their evolution and general patterns. In the future, integrative works reuniting as much information as possible (including citizen science data) could help elucidate the questions raised here, such as the classification and evolution of such an exceptional group of true bugs, the Phloeidae.

General References

Amyot CJB, Serville A. 1843. *Histoire naturelle des Insectes Hémiptères*. Paris, 675 pp., 12 pls. doi: 10.5962/bhl.title.8471

Bequaert J. 1935. Presocial behavior among the Hemiptera. *Bulletin of the Brooklyn Entomological Society*, XXX (5), 177–191

Bernardes JLC, Grazia J, Barcellos A, Salomão AT 2005. Descrição dos estágios imaturos e notas sobre a biologia de *Phloea subquadrata* (Heteroptera, Phloeidae). *Iheringia, Série Zoologia,* 95 (4), 415–420. doi: 10.1590/S0073-47212005000400012

Bianchi FM, Barão KR, Grassi A, Ferrari A. 2021. A milestone for Pentatomoidea: Grazia *et al*. 2008 – What do we know and where can we go? *Zootaxa*, 4958 (1), 406–429. doi: 10.11646/zootaxa.4958.1.26

Brien P. 1930. Notes sur *Phloea paradoxa* Burm. (1835). *Une mission biologique Belge au Brésil (1922-1923)*, 2, 207–212

Burmeister H. 1835. *Handbuch der Entomologie, 2 (1)*. Berlin, 400 pp. doi: 10.5962/bhl.title.8135

Cassis G, Schuh RT. 2010. Systematic methods, fossils, and relationships within Heteroptera (Insecta). *Cladistics*, 26 (3), 262–280. doi: 10.1111/j.1096-0031.2009.00283.x

China WE. 1933. XIX. - A new Family of Hemiptera-Heteroptera with Notes on the Phylogeny of the Suborder. *Annals and Magazine of Natural History*, 12 (68), 180–196. doi: 10.1080/00222933308673767

Chocorosqui VR, Panizzi AR. 2008. Nymph and Adult Biology of *Dichelops melacanthus* (Dallas) (Heteroptera: Pentatomidae) Feeding on Cultivated and Non-Cultivated Host Plants. *Neotropical Entomology*, 37 (4), 353–360. doi: 10.1590/S1519-566X2008000400001

Costa-Lima AM da. 1940. *Insetos do Brasil. Hemipteros*. Imprensa Nacional, Rio de Janeiro, Tomo 2, capítulo XXII, 351 pp. doi: 10.5962/bhl.title.97953

de Moya RS, Weirauch C, Sweet AD, Skinner RK, Walden KKO, Swanson DR, Dietrich CH, Johnson KP. 2019. Deep Instability in the Phylogenetic Backbone of Heteroptera is Only Partly Overcome by Transcriptome-Based Phylogenomics. *Insect Systematics and Diversity*, 3 (6), 7, 1–14. doi: 10.1093/isd/ixz020

Distant WL. 1906. Oriental Heteroptera. *Annales de la Société entomologique de Belgique*, 50, 405–417

Drury D. 1773. *Illustrations of Natural History, wherein are exhibited upwards of two hundred and forty figures of exotic insects. 2*. London, 90 pp., 50 pls. doi: 10.5962/t.173288

Duan Y, Fu S, Ye Z, Bu W. 2023. Phylogeny of Urostylididae (Heteroptera: Pentatomoidea) reveals rapid radiation and challenges traditional classification. *Zoologica Scripta*, 52 (3), 264–278. doi: 10.1111/zsc.12582

Eger J, Barcellos A, Weiler L. 2015. Shield Bugs (Scutelleridae). *In*: Panizzi AR, Grazia J (Eds.), True bugs (Heteroptera) of the Neotropics, Springer, New York, pp. 757–788. doi: 10.1007/978-94-017-9861-7_23

Evans JW. 1963. The phylogeny of the Homoptera. *Annual Review of Entomology*, 8, 77–94. doi: 10.1146/annurev.en.08.010163.000453

Forero D. 2008. The systematics of the Hemiptera. *Revista Colombiana de Entomología*, 34 (1), 1–21. doi: 10.25100/socolen.v34i1.9244

Gapud V. 1991. A generic revision of the subfamily Asopinae, with consideration of its phylogenetic position in the family Pentatomidae and superfamily Pentatomoidea (Hemiptera-Heteroptera). *Philippine Entomologist*, 8 (3), 865–961

Grazia J, Schuh RT, Wheeler WC. 2008. Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). *Cladistics*, 24, 932–976. doi: 10.1111/j.1096-0031.2008.00224.x

Grazia J, Takiya D, Wolff VRS, Schwertner CF, Mejdalani G, Cavichioli RR, Peronti ALBG, Queiroz DL, Burckhardt D, Fernandes JAM, Moreira FFF, Gil-Santana HR, Ferreira PSF, Carrenho R, Brugnera R, Guidoti M. 2024. Cap. 25, Hemiptera Linnaeus, 1758. *In*: Rafael JA, Melo GAR, Carvalho CJB de, Casari S, Constantino R (Eds.), *Insetos do Brasil: Diversidade e Taxonomia*, 2ª ed., Instituto Nacional de Pesquisas da Amazônia, Manaus, pp. 368–456. doi: 10.61818/56330464c25

Guilbert E. 2003. Habitat use and maternal care of *Phloea subquadrata* (Hemiptera: Phloeidae) in the Brasilian Atlantic Forest (Espirito Santo). *European Journal of Entomology*, 100, 61–63. doi: 10.14411/eje.2003.013

Hahn CW. 1834. *Die Wanzenartigen Insecten. 2*. Nürnberg, 142 pp., tab. 37–72. doi: 10.5962/bhl.title.11547

Henry TJ. 1997. Phylogenetic Analysis of Family Groups within the Infraorder Pentatomomorpha (Hemiptera: Heteroptera), with Emphasis on the Lygaeoidea. *Annals of the Entomological Society of America*, 90 (3), 275–301. doi: 10.1093/aesa/90.3.275

Henry TJ. 2017. Biodiversity of Heteroptera. *In*: Foottit RG, Adler PH (Eds.), *Insect Biodiversity: Science and Society*, second edition, Wiley, pp. 279–335. doi: 10.1002/9781118945568.ch10

Johnson KP, Dietrich CH, Friedrich F, Beutel RG, Wipfler B, Peters RS, Allen JM, Petersen M, Donat A, Walden KKO, Kozlov AM, Podsiadlowski L, Mayer C, Meusemann K, Vasilikopoulos A, Waterhouse RM, Cameron SL, Weirauch C, Swanson DR, Percy DM, Hardy NB, Terry I, Liu S, Zhou X, Misof B, Robertson HM, Yoshizawa K. 2018. Phylogenomics and the evolution of hemipteroid insects. *Proceedings of the National Academy of Sciences*, 115 (50), 12775–12780. doi: 10.1073/pnas.181582011

Kirkaldy GW. 1908. Bibliographical and nomenclatorial notes on the Hemiptera - nº. 8. *The Entomologist*, 45, 123–124

Kirkaldy GW. 1909. *Catalogue of the Hemiptera (Heteroptera), vol. 1 - Cimicidae.* Felix L. Dames ed., Berlin, XL + 392 pp. doi: 10.5962/bhl.title.15205

Kirkaldy GW. 1913. Generic tables for the cimicid subfamilies Phyllocephalinae, Phloeinae and Dinidorinae. *The Canadian Entomologist*, 45, 81–84

Lent H, Jurberg J. 1965. Contribuição ao conhecimento dos Phloeidae Dallas, com um estudo sôbre genitália. *Revista Brasileira de Biologia*, 25 (2), 123–144

Lent H, Jurberg J. 1966. Os estádios larvares de "*Phloeophana longirostris*" (Spinola, 1837) (Hemiptera, Pentatomoidea). *Revista Brasileira de Biologia*, 26 (1), 1–4

Lepeletier ALM, Serville JGA. 1825. Encyclopédie méthodique, vol. 10. *In*: Latreille, P., *Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustaces, des Arachnides et des Insectes*. Agasse, Paris, p. 111

Leston D. 1953. "Phloeidae" Dallas: systematics and morphology, with remarks on the phylogeny of "Pentatomoidea" Leach and upon the position of "*Serbana*" Distant (Hemiptera). *Revista Brasileira de Biologia*, 13 (2), 121–140

Li H, Shao R, Song N, Song F, Jiang P, Li Z, Cai W. 2015. Higher-level phylogeny of paraneopteran insects inferred from mitochondrial genome sequences. *Scientific Reports*, 5, 8527. doi: 10.1038/srep08527

Li H, Leavengood Jr JM, Chapman EG, Burkhardt D, Song F, Jiang P, Liu J, Zhou X, Cai W. 2017. Mitochondrial phylogenomics of Hemiptera reveals adaptive innovations driving the diversification of true bugs. *Proceedings of the Royal Society B*, 248, 20171223. doi: 10.1098/rspb.2017.1223

Li M, Tian Y, Zhao Y, Bu W. 2012. Higher Level Phylogeny and the First Divergence Time Estimation of Heteroptera (Insecta: Hemiptera) Based on Multiple Genes. *PLoS ONE*, 7 (2), e32152. doi: 10.1371/journal.pone.0032152

Lis JA, Bulinska-Balas M, Lis P, Ziaja DJ, Kocorek A. 2012a. Systematic position of Dinidoridae and Tessaratomidae within the superfamily Pentatomoidea (Hemiptera: Heteroptera) based on the analysis of the mitochondrial cytochrome oxidase II sequences. *Opole Scientific Society Nature Journal*, 45, 43–53.

Lis JA, Lis P, Ziaja DJ, Kocorek A. 2012b. Systematic position of Dinidoridae within the superfamily Pentatomoidea (Hemiptera: Heteroptera) revealed by the Bayesian phylogenetic analysis of the mitochondrial 12S and 16S rDNA sequences. *Zootaxa*, 3423 (1), 61–68. doi: 10.11646/zootaxa.3423.1.5

Lis JA, Ziaja DJ, Lis B, Gradowska P. 2017. Non-monophyly of the “cydnoid” complex within Pentatomoidea (Hemiptera: Heteroptera) revealed by Bayesian phylogenetic analysis of nuclear rDNA sequences. *Arthropod Systematics & Phylogeny*, 75 (3), 481–496. doi: 10.3897/asp.75.e31918

Lockwood JA, Story RN. 1986. Adaptive Functions of Nymphal Aggregation in the Southern Green Stink Bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae). *Environmental Entomology*, 15 (3), 739–749. doi: 10.1093/ee/15.3.739

López GEL, Schwertner CF. 2024. Synopsis of the remarkable family Phloeidae (Hemiptera: Pentatomoidea): species identification, chromatic polymorphism and updated distribution. *Journal of Natural History*, 57 (45–48), 2083–2113. doi: 10.1080/00222933.2023.2284417

Magalhães PS de. 1909. Contribution à l’histoire naturelle des Phlées. *Mémoires de la Société zoologique de France*, 22, 234–260

Panizzi A, Grazia J. 2015. Introduction to True Bugs (Heteroptera) of the Neotropics. *In*: Panizzi AR, Grazia J (Eds.), *True bugs (Heteroptera) of the Neotropics*, Springer, New York, pp. 3–20. doi: 10.1007/978-94-017-9861-7_1

Postali TC. 2009. História natural e biologia populacional de *Phloeophana longirostris* Spinola, 1847 (Heteroptera: Phloeidae) na Serra do Japi, Jundiaí, SP (Dissertação). Instituto de Biologia, Universidade Estadual de Campinas, Campinas, 76pp.

Rider DA, Schwertner CF, Vilímová J, Rédei D, Kment P, Thomas DB. 2018. Higher Systematics of the Pentatomoidea. *In*: McPherson JE (Ed.), *Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management*, CRC Press, Boca Raton, Florida, pp. 25–201. doi: 10.1201/9781315371221-2

Roca-Cusachs M, Schwertner CF, Kim J, Eger J, Grazia J, Jung S. 2022. Opening Pandora's box: molecular phylogeny of the stink bugs (Hemiptera: Heteroptera: Pentatomidae) reveals great incongruences in the current classification. *Systematic Entomology*, 12514, 1–16. doi: 10.1111/syen.12514

Salomão AT, Vasconcellos-Neto J. 2010. Population Dynamics and Structure of the Neotropical Bark Bug *Phloea subquadrata* (Hemiptera: Phloeidae) on *Plinia cauliflora* (Myrtaceae). *Environmental Entomology*, 39 (6), 1724–1730. doi: 10.1603/EN09282

Salomão AT, Postali TC, Vasconcellos-Neto J. 2012. Bichos-cascas na Serra do Japi: história natural dos percevejos Phloeidae (Hemiptera). *In*: Vasconcellos-Neto J, Polli PR, Penteado-Dias AM (Eds.), *Novos olhares, novos saberes sobre a Serra do Japi: ecos de sua biodiversidade*, Editora CRV, Curitiba, pp 321–337

Salomão AT, Postali TC, Vasconcellos-Neto J. 2012. Bichos-cascas na Serra do Japi: história natural dos percevejos Phloeidae (Hemiptera). *In*: Vasconcellos-Neto J, Polli PR, Penteado-Dias AM (Eds.), *Novos olhares, novos saberes sobre a Serra do Japi: ecos de sua biodiversidade*, Editora CRV, Curitiba, pp 321–337

Schuh RT. 1979. Evolutionary Trends in Heteroptera. Part II. Mouthpart-structures and Feeding Strategies. *Systematic Biology*, 28 (4), 653–656. doi: 10.2307/sysbio/28.4.653

Schuh RT, Slater JA. 1995. Chapter 74: Phloeidae. *In:* Schuh, R. T. & Slater, J. A. (Eds.), *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History*, Cornell University Press, Ithaca, New York, pp. 234–235

Schuh RT, Weirauch C. 2020. Chapter 100: Phloeidae. *In:* Schuh RT, Weirauch C (Eds.), *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History (Second Edition)*, Siri Scientific Press, London, pp. 498–500

Schwertner CF, Grazia J. 2015. Less diverse pentatomoid families (Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae). *In*: Panizzi AR,

Grazia J (Eds.), *True bugs (Heteroptera) of the Neotropics*, Springer, New York, pp. 821–862. doi: 10.1007/978-94-017-9861-7_25

Song N, Zhang H. 2022. A comprehensive analysis of higher-level phylogenetic relationships of Hemiptera based on transcriptome data. *Journal of Systematics and Evolution*, 61 (4), 572–586. doi: 10.1111/jse.12855

Spinola M. 1837. *Essai sur les genres d'insectes appartenants à l'ordré des Hémiptères. Lin. ou Rhyngotes, Fab. et à la section des Hétéroptères, Dufour*. Genova, 383 pp. doi: 10.5962/bhl.title.65481

Stål C. 1860. Bidrag till Rio Janeiro-Traktens Hemipter-Fauna. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 2, 1–84

Stål C. 1872. Enumeratio Hemipterorum. Bidrag till en forteckning ofver alia hittils kanda Hemiptera. Pt. 2. *In*: *Kungl. Svenska Vetenskapsakademiens Handlingar*, 10, 3–159

Trautwein MD, Wiegmann BM, Beutel R, Kjer KM, Yeates DK. 2012. Advances in Insect Phylogeny at the Dawn of the Postgenomic Era. *Annual Review of Entomology*, 57, 449–468. doi: 10.1146/annurev-ento-120710-100538

Weirauch C, Schuh RT. 2011. Systematics and Evolution of Heteroptera: 25 years of Progress. *Annual Review of Entomology*, 56, 487–510. doi: 10.1146/annurev-ento-120709-144833

Weirauch C, Schuh RT, Cassis G, Wheeler WC. 2019. Revisiting habitat and lifestyle transitions in Heteroptera (Insecta: Hemiptera): insights from a combined morphological and molecular phylogeny. *Cladistics*, 35 (1), 67–105. doi: 10.1111/cla.12233

Wheeler WC, Schuh RT, Bang R. 1993. Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets. *Entomologica scandinavica*, 24 (2), 121–137. doi: 10.1163/187631293X00235

Wu Y-Z, Yu S-S, Wang Y-H, Wu H-Y, Li X-R, Men X-Y, Zhang Y-W, Rédei D, Xie Q, Bu W-J. 2016. The evolutionary position of Lestoniidae revealed by molecular autapomorphies in the secondary structure of rRNA besides phylogenetic reconstruction (Insecta: Hemiptera: Heteroptera). *Zoological Journal of the Linnean Society*, 177 (4), 750–763. doi: 10.1111/zoj.12385

Wu Y-Z, Rédei D, Eger Jr J, Wang Y-H, Wu H-Y, Carapezza A, Kment P, Cai B, Sun X-Y, Guo P-L, Luo J-Y, Xie Q. 2018. Phylogeny and the colourful history of jewel bugs (Insecta: Hemiptera: Scutelleridae). *Cladistics*, 34 (5), 502–516. doi: 10.1111/cla.12224

Ye F, Kment P, Rédei D, Luo J-Y, Wang Y-H, Kuechler SM, Zhang W-W, Chen P-P, Wu H-Y, Wu Y-Z, Sun X-Y, Ding L, Wang Y-R, Xie Q. 2022. Diversification of the phytophagous lineages of true bugs (Insecta: Hemiptera: Heteroptera) shortly after that of the flowering plants. *Cladistics*, 38 (4), 403–428. doi: 10.1111/cla.12501