INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

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MUSEUM NATIONAL D'HISTOIRE NATURELLE
ÉCOLE DOCTORALE SCIENCES DE LA NATURE ET DE L'HOMME – ED 227

MARCUS RODRIGO GUIDOTI SOARES

SISTEMÁTICA E EVOLUÇÃO DE TINGIDAE (HEMIPTERA, HETEROPTERA)

PORTO ALEGRE/BRASIL – PARIS/FRANÇA
2018

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul e à École Doctorale Sciences de la Nature et de l'Homme, Museum National d'Histoire Naturelle, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biodiversidade

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Prof. Dr. Eric Guilbert (MNHN)

PORTO ALEGRE/BRASIL – PARIS/FRANÇA
2018

CIP - Catalogação na Publicação

Guidoti Soares, Marcus Rodrigo
Sistemática e Evolução de Tingidae (Hemiptera, Heteroptera) / Marcus Rodrigo Guidoti Soares. -- 2018.
109 f.
Orientador: Luiz Alexandre Campos.

Coorientador: Eric Guilbert.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Biologia Animal, Porto Alegre, BR-RS, 2018.

1. Sistemática. 2. Evolução. 3. Tingidae. 4. Vianaidinae. I. Campos, Luiz Alexandre, orient. II. Guilbert, Eric, coorient. III. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

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Aprovada em 28 de novembro de 2018.

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Acknowledgments

To my mother, for being such a wonderful person that words simply can't describe; for teaching and passing me her values, which I care and hold on dearly; for going out of her way supporting me in my dreams, and dealing with me in my difficult moments like no one else could or would; and for being my safe harbor and true example of moral, persistence, and character.

To my brother, always present, comprehensive and supportive when I needed, for his support and understanding in moments of agony and doubt.

To my love Renata, who unexpectedly entered my life to make it better, easier, lighter and more enjoyable, always understanding my moments of struggle with this thesis, the co-tutelle and the uncertainty of the future, and with who I share many, many dreams, plans and goals; and for simply being an awesome person. She rocks.

To both my supervisors who have proven to be more than just academic supervisors but friends to carry for life, and more specifically:

To my supervisor in France, Eric Guilbert, for accepting me as his co-tutelle student, for sharing with me his data, expertise, experience, lessons, and his love for lace bugs, and for being tremendously supportive, understanding and patient, dealing with the worst of my PhD anxiety in the best imaginable way.

To my Brazilian supervisor, Luiz Alexandre Campos, for his lessons and scientific discussions, for allowing my ambitious academic ideas to come to life, for giving me opportunities to teach, to supervise students, and to apply for research grants under his supervision, for his patience and experience to deal with my PhD anxiety and for the many conversations about academia and life we had over the years.

To my former advisor Aline Barcellos, whose support and friendship I carry for life and who assisted me in many moments of doubt, with good advices and incentives not only for my academic pursuits, but also in personal matters.

To Sara Itzel Montemayor, a good friend, colleague, and co-author, who was the first international researcher to believe in my work and potential, and for participating actively in two chapters of this thesis and in many past, present and hopefully, future projects of my academic career.

To Thomas J. Henry, for all the lessons, assistance, motivation, and friendship, and for acting as the mentor I always wanted but never found before, in both professional and personal aspects of my life, and for being someone whose exemplar attitude is a true inspiration that I will always carry with me.

To Dennis Kopp, whose friendship proved to be one of the biggest treasures that my path in Entomology brought to me, and someone that taught and guided me through this process and will always be in my heart.

To my dear friend Felipe Lorenz Simões, whose support, companionship and laughs made this journey lighter, and whose friendship became one of the best gifts from my path in Entomology. To his father and exceptional scientist Jefferson Cardia Simões, who met me only once, but guided me, through his son, in moments of tremendous hardships and doubts.

To my childhood friend Marcus Vinicius Romero Pernez da Silva for the countless conversations and not only moral, but psychological support during my career, support that was pivotal to thrive as a PhD student and candidate as well.

To my great friend Michael Milman, who has been present and witnessing my struggles in this path since the beginning, always helping, being supportive and thus crucial for my moral and motivational levels.

To Vitor Tarli, a good friend that I met during my stay in Paris, who made my PhD journey easier since then with his support and help in crucial moments.

To CNPq (National Council for Scientific and Technological Development) for the assistance and patience when dealing with issues and concerns related to my PhD's fellowships (process number 141467/2014-2) and the Science without Borders fellowship (process number 201352/2015-0), which allowed this co-tutelle and project to happen.

To the Smithsonian Institution for the pre-doctoral fellowship awarded to me, which was an amazing life and academic experience and allowed me to study the world's largest Tingidae collection and for the unlimited access to crucial equipment and material to finish this project.

"For me, there's a lot of strength in knowing that the wandering that I'm doing, that I've done, is normal, and kind of beautiful, and not something I should be stressed out about. You're on a path. You don't know where it's going, and that would be boring if you did."

Hank Green

Abstract

Tingidae (Hemiptera, Heteroptera, Cimicomorpha) is a family of small phytophagous insects comprising about 2500 species distributed in more than 300 genera. The family is commonly known as lace bugs due to the lace-like aspect of thoracic structures, like hood, paranota and hemelytra. In the most-accepted pre-phylogenetic classification Tingidae is divided in three subfamilies, Cantacaderinae with two tribes, Phatnomatini and Cantacaderini, Tinginae with three, Litadeini, Ypsotingini and Tingini, and Vianadinae, with no proposed tribes. Phylogenetic analyses retrieved Vianaidinae as the sister-group of Cantacaderinae + Tinginae, transferring Phatnomatini to Tinginae and disputing the validity of Litadeini, and Ypsotingini. Considering the biogeographical hypotheses available for Tingidae, the fossil record for the family and the sister-group relationship between Vianaidinae and Tingidae *sensu stricto* (Cantacaderinae + Tinginae), the vianaidines are intimately linked to Tingidae origin. Phatnomatini, on the other hand, is also crucial for this question since it presents the oldest known Tingidae fossil. Therefore, this thesis aimed to address Tingidae systematics and evolution by:

i. focusing on Vianaidinae systematics;
ii. contributing on Phatnomatini taxonomy;
iii. and discussing Tingidae classification based on a molecular phylogenetic analysis including the first Vianaidinae sequences.

Pterovianaida duckensis is described as the third macropterous species of Vianaidinae, and a new species of *Zetekella* from Ecuador is also described in a taxonomic review of *Zetekella* and *Minitingis* (Phatnomatini). The Vianaidinae is reviewed on the light of newly collected material and a morphological phylogenetic hypothesis is proposed including macropterous specimens representing undescribed taxa, resulting in the description of nine new species and one new genus. The phylogenetic analysis retrieved all four genera monophyletic, in two clades: the new genus is found sister to *Anommatocoris*, while *Pterovianaida* + *Thaumamannia* form the other clade. Potential synonymies within these two clades are discussed. A molecular phylogeny of Tingidae is presented with all subfamilies included and recovered monophyletic. The main internal relationships were also retrieved, corroborating previous analyses. For Cantacaderinae, all three species included belonged to the tribe Cantacaderini, all from the genus *Cantacader*, therefore, the relationships among the tribes of Cantacaderinae are not addressed. *Ypsotingis sideris*, type-species of the Ypsotingini type-genus, was included and retrieved as the sister-group of the remaining Tinginae (*minus* Phatnomatini). This revived the discussion on this tribe's validity, but its latest accepted composition remains refuted, as Litadeini. Two species of *Leptodictya* were included and recovered as a clade sister to all remaining Tinginae (*minus* Phatnomatini and *Y. sideris*). Thus, a potential new tribe is discussed but not formally proposed due to the small representation of the genus in the phylogeny. In conclusion, the two major topics emphatically addressed in this thesis, the Vianaidinae systematics and Tingidae classification, were discussed and further steps were proposed: for Vianaidinae systematics, molecular data and genital characters are pointed as necessary to improve our knowledge on this taxon, whereas for Tingidae classification, a genomic approach, a more comprehensive terminal sampling and some specific unexplored morphological characters for Tingidae systematics are indicated as potential future steps. Moreover, the new perspective on the Tingidae origin opened by the addition of Vianaidinae sequences on a Tingidae molecular phylogenetic analysis was also highlighted and discussed.

Résumé

Les Tingidae (Hémiptères, Hétéroptères) sont une famille de petits insectes phytophages avec environ 2500 espèces réparties en plus de 300 genres. La famille est communément connue sous le nom de «punaises dentellières» en raison de l'aspect en dentelle des structures thoraciques, comme le capuchon, les carènes latérales et les hémélytres. Dans l'hypothèse de classification pré-phylogénétique la plus acceptée, les Cantacaderinae sont composées de deux tribus, Phatnomatini et Cantacaderini, et les Tinginae sont composés de trois, Litadeini, Ypsotingini et Tingini, et aucune tribu ne compose les Vianadinae. Des analyses phylogénétiques antérieures placent les Vianaidinae en tant que groupe frère des Cantacaderinae + Tinginae, transférant les Phatnomatini dans les Tinginae et contestant la validité des Litadeini et Ypsotingini. Considérant les hypothèses biogéographiques disponibles pour les Tingidae, les archives fossiles de la famille et la relation de groupe-frère entre Vianaidinae + Tingidae *sensu stricto* (Cantacaderinae + Tinginae), cette sous-famille est intimement liée à l'origine des Tingidae. Les Phatnomatini, d'autre part, sont également crucial pour cette question car ils comprennent le plus ancien fossile connu pour les Tingidae. Par conséquent, cette thèse visait aborder la systématique et l'évolution des Tingidae:

i. en se concentrant sur la systématique des Vianaidinae;
ii. en contribuant à la taxonomie des Phatnomatini;
iii. et en discutant de la classification des Tingidae basée sur une analyse phylogénétique moléculaire incluant les Vianaidinae.

Pterovianaida duckensis est décrit comme la troisième espèce macroptère de Vianaidinae, et une nouvelle espèse de *Zetekella* de l'Equateur est également décrit ici dans une étude taxonomique de *Zetekella* et *Minitingis* (Phatnomatini). Les Vianaidinae sont analysés à la lumière de matériel nouvellement collecté et une hypothèse phylogénétique morphologique est proposée incluant des spécimens macroptères représentant des taxons non décrits, neuf nouvelles espèces et un nouveau genre sont ainsi décrits. L'analyse phylogénétique retrouve les quatre genres monophylétiques, séparés en deux clades: le nouveau genre se retrouvé plus étroitement lié à *Anommatocoris*, tandis que *Pterovianaida* + *Thaumamannia* forme l'autre clade. Une phylogénie moléculaire des Tingidae este présentée avec toutes les sous-familles incluses et retrouvées monophylétiques. Les principales relations internes aux Tingidae ont également été retrouvées, corroborant ainsi les analyses précédentes. Pour les Cantacaderinae, les trois espèces incluses appartiennent à la tribu des Cantacaderini et au genre *Cantacader*. Par conséquent, la relation entre les tribus des Cantacaderinae n'a pas été abordée. *Ypsotingis sideris*, espèce-type du genre-type Ypsotingini, est placée comme groupe-frère des Tinginae restant (*sauf* Phatnomatini). Cela a relancé la discussion sur la validité de cette tribu, mais sa dernière composition acceptée reste réfutée, comme Litadeini. Deux espèces de *Leptodictya* sont monophylétiques et groupes-frère de toutes les Tinginae restant (*sauf* Phatnomatini et *Y. sideris*). Ainsi, une nouvelle tribu potentielle est discutée mais pas officiellement proposée en raison de la faible représentation du genre dans la phylogénie. En conclusion, les deux principaux thèmes abordés dans cette thèse, la systématique des Vianaidinae et la classification des Tingidae, ont été discutés et des étapes futures ont été proposées: pour la systématique de Vianaidinae, les données moléculaires et les caractères génitaux apparaissent nécessaires pour améliorer nos connaissances sur ce taxon, tandis que pour la classification Tingidae, une approche génomique, un échantillonnage plus complet des taxons et certains caractères morphologiques inexplorées sont nécessaires pour des étapes futures. De plus, la nouvelle perspective sur l'origine des Tingidae ouverte par l'ajout de séquences de Vianaidinae sur une analyse phylogénétique moléculaire de Tingidae est également été discutée.

Resumo

Tingidae (Hemiptera, Heteroptera) é uma família de pequenos insetos com cerca de 2500 espécies distribuías em mais de 300 gêneros. São conhecidos como percevejos-de-renda devido ao aspecto rendado de algumas das suas estruturas torácicas, como o capuz, o paranoto e os hemiélitros. Na classificação pré-filogenética mais aceita Tigidae é dividida em três subfamílias, Cantacaderinae com duas tribos, Phatnomatini e Cantacaderini, Tinginae com três, Litadeini, Ypsotingini e Tingini, e Vianaidinae sem nenhuma tribo proposta. Análises filogenéticas recuperaram Vianaidinae como o grupo-irmão de Cantacaderinae + Tinginae, transferiram Phatnomatini e questionaram a validade de Litadeini e Ypsotingini. Considerando as hipóteses biogeográficas disponíveis para Tingidae, o registro fóssil da família e a relação de grupo-irmão entre Vianaidinae e Tingidae *sensu stricto* (Cantacaderinae + Tinginae), os vianaidíneos estão intimamente associados à origem de Tingidae. Phatnomatini, por outro lado, também é crucial para esta questão por possuir o fóssil mais antigo conhecido para Tingidae. Portanto, esta tese visa abordar a sistemática e evolução de Tingidae:

i. focando no estudo da sistemática de Vianaidinae;
ii. contribuindo com a taxonomia de Phatnomatini,
iii. e discutindo a classificação de Tingidae com base em uma filogenia molecular incluindo as primeiras sequências de Vianaidinae.

Pterovianaida duckensis é descrita como a terceira espécie macróptera de Vianaidinae e uma espécie nova de *Zetekella* do Equador também é descrita numa revisão taxonômica de *Zetekella* e *Minitingis* (Phatnomatini). Vianaidinae é revisada à luz de novas amostras e uma hipótese de filogenia morfológica é proposta, incluindo espécimes macrópteros representando táxons não descritos, resultando na descrição de nove novas espécies e um novo gênero. A análise filogenética recuperou todos os quatro gêneros como monofiléticos, em dois clados: o novo gênero é grupo-irmão de *Anommatocoris*, enquanto *Pterovianaida* + *Thaumamannia* formam o outro clado. Sinonímias potenciais nestes dois clados são discutidas. Uma filogenia molecular de Tingidae é apresentada com todas as subfamílias incluídas e recuperadas, cada uma, como monofiléticas. As principais relações de parentesco entre estes táxons também foram recuperadas, corroborando os resultados de análises anteriores. Com relação a Cantacaderinae, todas as três espécies incluídas pertencem à tribo Cantacaderini e ao gênero *Cantacader*, portanto as relações entre as tribos desta subfamília não são abordadas. *Ypsotingis sideris*, espécie-tipo do gênero-tipo de Ypsotingini, foi incluída e recuperada como grupo-irmão dos demais tingíneos (menos Phatnomatini). Isto reabriu a discussão sobre a validade da tribo, embora sua composição mais recente continue refutada, assim como Litadeini. Duas espécies de *Leptodictya* foram incluídas e recuperadas como um grupo monofilético, irmão dos demais tingíneos (*menos* Phatnomatini e *Y. sideris*). Assim, uma nova tribo potencial é discutida, mas não formalmente proposta devido à baixa representatividade do gênero na filogenia. No capítulo de conclusão, os dois tópicos mais abordados na tese, a sistemática de Vianaidinae e a classificação de Tingidae, foram discutidos e perspectivas futuras foram sugeridas: para o primeiro, a inclusão de dados moleculares e caracteres morfológicos genitais são apontados como necessários para a melhor compreensão desse táxon, enquanto para a classificação de Tingidae, dados genômicos, uma amostragem de táxons mais ampla e a inclusão de alguns caracteres morfológicos ainda não explorados na sistemática de Tingidae são apontados como possíveis passos futuros. Ainda, a nova perspectiva sobre a origem de Tingidae que se abriu após a obtenção e inclusão das primeiras sequencias de DNA de Vianaidinae em uma análise filogenética molecular também foi discutida e destacada.

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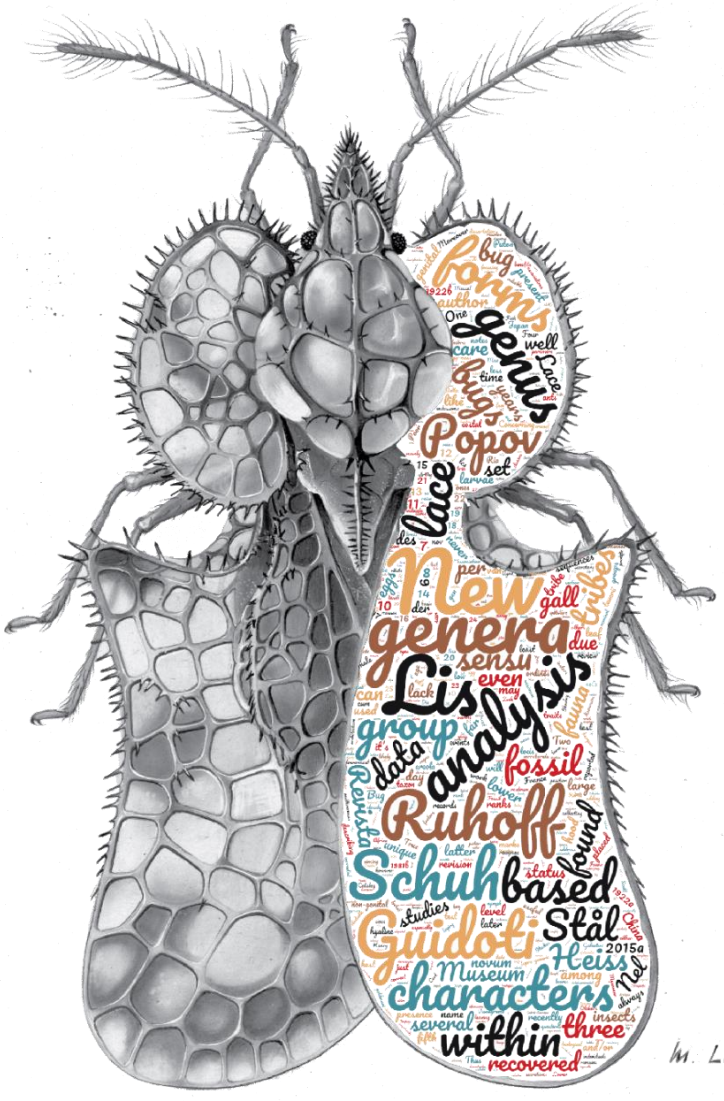
Chapter I

Introduction to Tingidae (Heteroptera, Cimicomorpha) with emphasis on classification, biogeography and Vianaidinae systematics



Corythucha championi dorsal habitus from Drake & Ruhoff (1965).

Chapter I – Introduction to Tingidae (Heteroptera, Cimicomorpha) with emphasis on classification, biogeography and Vianaidinae systematics

Laporte (1833) proposed the family name Tingitidae, 30 years after Fabricius described what would be its type-genus, *Tingis* Fabricius, 1803. However, it was only after a heated discussion in the literature that the grammatically correct name Tingidae was established (Baker, 1922; Holland, 1922a, 1922b; Parshley, 1922a, 1922b), not avoiding, though, misuses that would last for at least 30 years (e.g., Monte, 1940). Tingidae (Hemiptera, Heteroptera, Cimicomorpha) is a group of small phytophagous insects composed by more than 2500 species distributed in about 300 genera (ITIS, 2018). Tingids occur worldwide, being reported in all continents except for Antarctica, and including oceanic islands (Drake & Ruhoff, 1965). They are commonly known as lace bugs due to the remarkable and variable lace-like aspect of the dorsal habitus of most of its species, including the reticulate structure of the hood (when developed), pronotum, paranota and hemelytra (Fig. 1; Drake & Davis, 1960). However, coleopteroid forms with highly modified forewings and reduced or absent hindwings are also present (Drake & Froeschner, 1962; van Doesburg, 1977; Signoret, 1863). Altogether with this interesting morphological variation, tingids are also found in an incredible range of plants, from low grasses to tall woody trees, and in soil or even in caves (Drake & Davis, 1960; Froeschner, 1996; Guidoti *et al.*, 2014), or associated with ants as well (Kormilev, 1955; Drake & Davis, 1960). They are known for being host-specific, but many can be found in several different hosts, including from different botanical families (Drake & Ruhoff, 1965). The host-plant record is generally scant within Tingidae and often misleading due to the lack of reliable documentation of such interactions (e.g., were eggs and nymphs observed in the plant, or just few, scattered and probably accidental adults?), and due to non-specific collecting methods (e.g., beating and sweeping nets). Thus, most species have no host-plant record (Drake & Ruhoff, 1965), and most records are not necessarily reliable. Lace bugs are also considered economically important pests (Guidoti *et al.*, 2015b), and due to this voracious feeding habits of some tingids, a few species were even introduced as biocontrol agents (Neal Jr. & Schaefer, 2000). Tingids are usually found feeding on the abaxial surface of their host-plant leaves, but species are also known for feeding on stems, roots, and allegedly mosses (China, 1945; Henry & Wheeler Jr., 1986). Their feeding behavior causes leaf discoloration, and these discolored marks on leaves surface indicate the exact position where the rostrum was inserted (Moreira *et al.*, 2013). One leaf can present several of these marks, which may be interpreted as a Tingidae footprint in the

field. Depending on the abundance of the tingids they may cause the death of the leaf or of the plant (Guidoti *et al.*, 2015b).

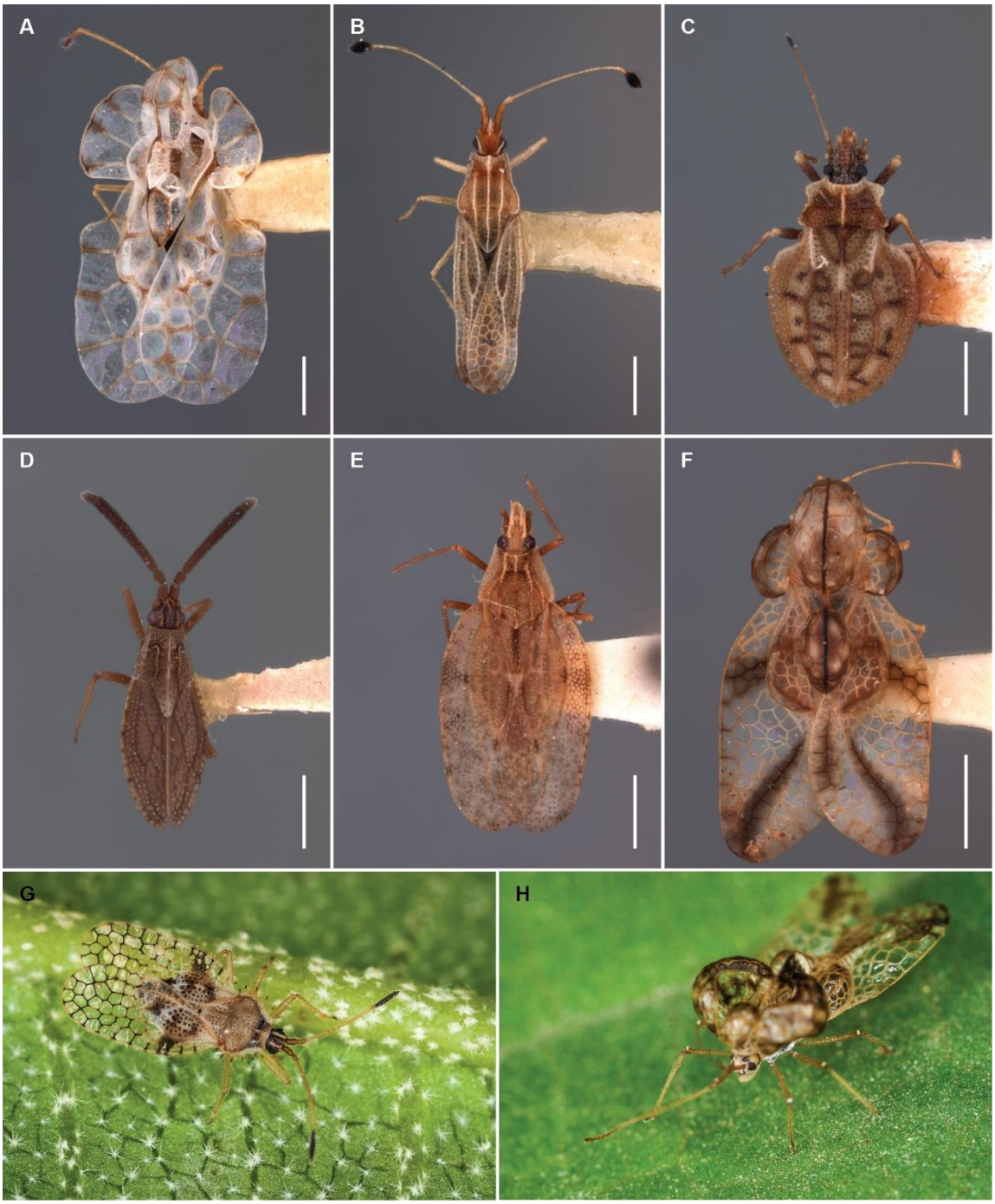


Figure 1. Tingidae morphological variation. A) *Bako dieidis* Drake & Ruhoff, 1961; B) *Campylotingis clavata* Drake & Hambleton, 1939; C) *Eocader vegrandis* Drake & Hambleton, 1934; D) *Hesperotingis mississipiensis* Drake, 1928; E) *Cantacader laratanus* Drake, 1947; F) *Dicysta peruviana* Drake & Poor, 1940; G) *Acanthocheila armígera* (Stål, 1858); H) *Phymacysta magnifica* (Drake, 1922). Photos A-F belong to the National Museum of Natural History, Smithsonian Institution; G-H from Guidoti *et al.* (2015b), taken by C. D'Haese. Scale bars: A-C, 0.5 mm; D-F, 1.0 mm.

Immatures, Behavior and Biology

Tingids infestations are not uncommon. As hemimetabolous insects, the nymphs live and feed in the same substrate as the adults, increasing substantially the number of feeding individuals on the same plant, and in many cases, on the same leaf. Lace bug nymphs are remarkably interesting because of its morphology, behavior, and chemical compounds (Livingstone, 1978; Mason *et al.*, 1991; Guidoti *et al*., 2015a). Morphologically, Tingidae nymphs can exhibit conspicuous outgrowths in forms of tubercles and integumentary projections that can vary in shape, size and type (Fig. 2; Stusak, 1962a; Livingstone, 1968; Guilbert & Montemayor, 2010). These structures, when present, are located on the tergum of thoracic and abdominal segments, either dorsally or laterally inserted (Guilbert & Montemayor, 2010). These outgrowths, or more specifically, the tubercles, are connected to glands and probably have secretory activity (Scholze, 1992). Livingstone (1978) argued that the "sweating" of these structures are associated with osmoregulatory function, and Mason *et al.* (1991) suggested a bird-repellent property on these secretions when studying *Stephanitis pyrioides* (Scott, 1874) nymphs. Tallamy & Denno (1981b) loosely argued that these secretions can also explain the ability of a removed mother to find back its egg-mass even after being moved up to 10 meters away from the original spot. These integumentary outgrowths can also be taxonomically and phylogenetically informative (Guidoti & Montemayor, 2014), which was not the prevalent thought until very recently (Guilbert, 2005; Guilbert & Montemayor, 2010). The sequence of ontogenetic events from the first to the fifth and final instar can also carry important information for the taxonomy and systematics of the group, but if papers describing these immature forms in Tingidae are rare, the ones covering all instars are even rarer (Guidoti & Barcellos, 2013). In addition, comparative papers within the same genus are almost nonexistent (Guidoti & Montemayor, 2014). Most of the information available on nymphs are provided with poor illustrations, and it was only more recently that scanning electron microscopy (SEM) analyses have been applied to nymph descriptions within Tingidae (Guilbert, 2005; Guilbert & Montemayor, 2010; Guidoti & Barcellos, 2013). Moreover, the literature is mainly focused on the Palearctic fauna (e.g., Stusak, 1962b; 1975), leaving much less attention to the remaining biogeographical regions and especially the Ethiopian fauna (Guidoti & Barcellos, 2013; Livingstone, 1962; 1968).

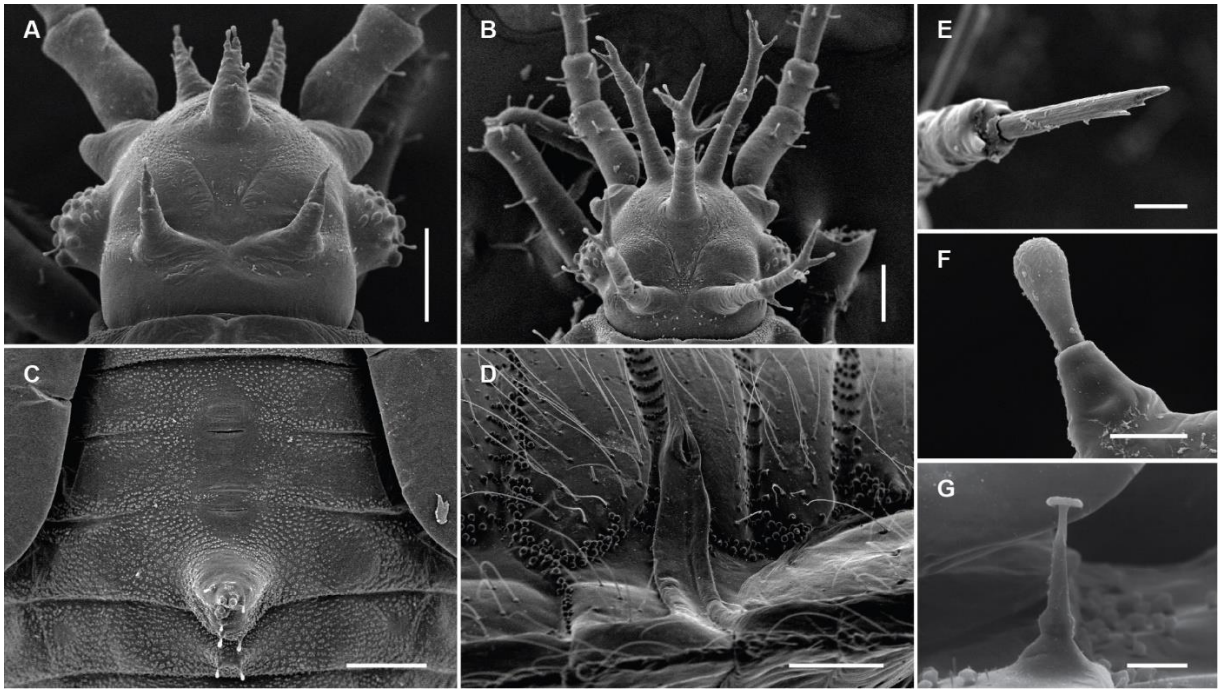


Figure 2. Micromorphology of Tingidae fifth instar nymphs. Head tubercles on A) *Psilobyrsa vriesie* Drake & Hambleton, 1935 and B) *P. aechmeae* Drake & Hambleton, 1935; abdominal scent gland openings dorsally positioned in C) *P. vriesiae*, and laterally positioned in D) *Thaumamannia vanderdrifti* van Doesburg, 1977 (Guidoti *et al.*, 2014); E) tip of a lateral abdominal tubercle on *Leptobyrsa ardua* Drake, 1922; F) integumentary projection on the wing pad of *P. vriesiae*; G) a long-stalked mushroom-shaped projection on *Teleonemia scrupulosa* Stål, 1873. Scale bars: A-D, 0.1 mm; E-F, 0.01 mm; G, 0.05 mm.

Another interesting behavioral feature of the tingids is the presence of maternal care (Tallamy & Denno, 1981a). Strategies and displays as egg-dumping, egg-guarding and/or wing-fanning were reported for several species belonging to the genera *Compseuta* Stål, 1873 (Tallamy & Iglay, 2004), *Corythucha* Stål, 1873 (Sheeley & Yonke, 1977; Faeth, 1989), *Gargaphia* Stål, 1862 (Fink, 1915; Torre-Bueno, 1942; Olckers, 2000) and *Leptobyrsa* Stål, 1873 (Melksham, 1984). In egg-dumping, the female protects her eggs by laying them in egg masses of other females already compromised with egg-guarding (Tallamy, 2005). The egg-dumper benefits from the protection of other female and restart the production of eggs immediately after laying the first batch. Egg-guarders, on the other hand, will have a cluster of younger eggs protecting their own eggs from predators and parasites in the guarded egg masses (Fig. 3; Tallamy and Horton, 1990). Some egg-guarders will guard their eggs until the nymphs become adults, and others, until the fifth instar (e.g., *Leptobyrsa* species). Wing-fanning is usually the aggressive display presented by the guarding female when approached by potential aggressors (Guidoti *et al*., 2015a). Sometimes, the female even climbs on top of the predator in an attempt to scare it away from the egg-mass or the hatched group of nymphs (Tallamy &

Denno, 1981b). Egg-dumping and egg-guarding is not a Tingidae-exclusive feature among insects (Brockmann, 1993; Zink, 2003), which indicates multiple evolutionary origins. However, it's not certain if this is the case in Tingidae evolution because this has never been evaluated in a phylogenetic or evolutionary framework. A complete summary of maternal care in Tingidae was provided by Guidoti *et al.* (2015a).

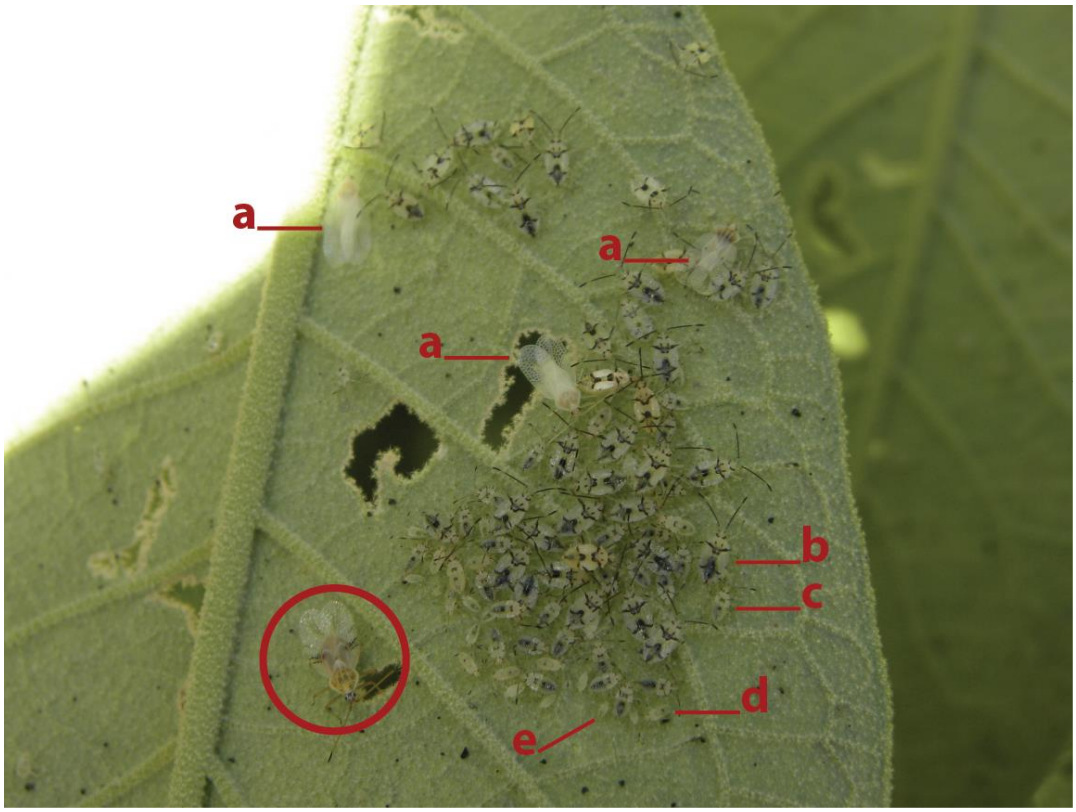


Figure 3. Maternal care behavior displayed by the egg-dumping/egg-guarding species *Gargaphia decoris* Drake, 1931. Circled adult indicates the guarding female. a) recently emerged adults; b) fifth instar nymph; c) fourth instar nymph; d) third instar nymph; e) second instar nymph.

One of the strangest features presented by tingids is the gall-forming behavior of two genera: *Copium* Thunberg, 1922 and *Paracopium* Distant, 1902. These two genera are known from the Paleartic region while the latter is also known from the Ethiopian and Australian regions, and together they are the only gall-inducers within Cimicomorpha (Drake & Ruhoff, 1965). *Copium* and *Paracopium* are composed by eight and 45 species, respectively (ITIS, 2018), and the first report of this behavior was made by the naturalist Réamur (1737) thirty years before the valid description and naming of the observed species, *Copium clavicornis* (Linnaeus, 1767). The galls are induced in flower buds and inflorescences and form a shelter around the immature(s) and/or adult(s), while the insect doesn't present any kind of reduction

on the size of structures like antennae, rostrum or legs (Drake & Ruhoff, 1965). According to Monod & Carayon (1958), the oviposition time and method is adapted and synchronized with the floral cecidogenesis. The gall opens normally when mature revealing the tingid which is often already at the adult stage (Drake & Ruhoff, 1965). Species of *Copium* usually presents one specimen per gall, and the chamber formed by the gall presents a unique architecture and therefore it is taxonomically and phylogenetically informative. This was verified when comparing the gall architecture of *C. teucrii* (Host, 1788) and *C. clavicornis* (Linnaeus, 1758) (Drake & Ruhoff 1965). In *Paracopium*, however, more specimens per gall are found. According to Drake & Ruhoff (1965), a dissection of nine galls induced by *Paracopium hamadryas* (Drake, 1925) presented an average of 5.4 individuals per gall. More recently, an unidentified *Paracopium* species was found infesting *Clerodendrum inerme* in Singapore, but no galls were observed (Murphy, 1989). This could indicate that not all species of *Paracopium* are gall-inducers, but the lack of illustrations of the observed specimens and the lack of voucher specimens deposited in a scientific collection prevents the confirmation of the species identification as well as further considerations on the subject.

Immatures, maternal care, and gall-inducing are intriguing aspects of this remarkable family of true bugs. Despite the interesting evolutionary questions that these aspects of Tingidae may raise, only the immature forms were addressed in an evolutionary and phylogenetic approach (Guilbert, 2004; Guilbert *et al.*, 2008). However, the small number of taxa sampled in both analyses, due to the lack of available high-quality information on Tingidae immature forms, hamper the hypotheses raised in those studies. Still, the presence of a set of any combination of the maternal-care related behaviors in Tingidae species is underreported because the collecting events are usually occasional, and life-history observations are largely missing (Guidoti *et al.*, 2015a). Notwithstanding, even more underreported are the species that clearly do not present this behavior (Guidoti *et al.*, 2015a). The observation of the absence of a behavior is extremely valuable for its analysis in an evolutionary and/or phylogenetic context because it prevents the introduction of missing data. Therefore, maternal care data is also too incipient to be properly analyzed at this point. Likewise, the gall-inducing trait lacks pivotal information to be properly considered in such studies, like the monophyly test and taxonomic review of the genera *Copium* and *Paracopium*, as well as more general information (e.g., on the different and allegedly species-specific gall architectures and the density of bugs per gall for both genera), and their phylogenetic relationship. To this day, only two species belonging to these genera were included in phylogenetic studies, *Copium teucrii* and *P. summervillei*

(Hacker, 1927) were considered individually in two different analysis (Guilbert, 2001; Guilbert *et al.*, 2014). The lack of a solid, comprehensive and corroborated phylogenetic hypothesis for Tingidae is also an important impediment for this and for most of the potential evolutionary studies within this family.

Taxonomy

Historically, Tingidae taxonomy was usually based on external non-genital characters (e.g., Carpintero & Montemayor, 2005; Guilbert, 1999; Lis, 2000; Montemayor & Costa, 2009; Montemayor *et al*., 2011). This is due to the remarkable lace-like structure of the hemelytra and paranota presented by a large number of lace bugs, which always drew the attention of specialists and were largely used for species and genera delimitation (e.g., Drake, 1922; Lis, 2009). Drake & Davis (1960), on the most comprehensive morphological work ever produced on the family, concluded that genital characters are only useful at subfamily level. However, this statement was disputed at least regarding the usefulness of these characters for species, not genera, delimitation, in much less famous contributions. Lee (1969), working with the Asian species of the genus *Stephanitis* Stål, 1873, showed several differences on the pygophore and paramere at species level. Lis (2003), in one of the most important revisionary works available for Tingidae, included genital characters illustrations showing significant differences on female genitalia (e.g., laterotergites, subgenital plates) and on male genitalia (pygophores, parameres and even endosomal sclerites). Carvalho & Costa (1991), described a new *Aristobyrsa* Drake & Poor, 1937 species, *A. uaupesensis* Carvalho & Costa, 1991 and considered some structures on male genitalia as diagnostic characters, which includes substantial differences on the paramere. However, the illustration provided for the endosoma of *A. latipennis* is most likely a mistake: it's possible that a Miridae endosoma was illustrated in place of *A. latipennis* genitalia. Unfortunately, Drake & Davis (1960) misleading ideas regarding genital characters survived and most Tingidae taxonomic contributions lack genital character information. Additionally, the frequently low number of specimens per species in museum collections (safe some exceptions), allied to the difficulty to get authorization to perform dissections in type-material, hamper even more the use of these valuable characters in Tingidae systematics. A summary of the diagnostic characters mentioned in this thesis is presented (Fig. 4), considering the outlines of a Cantacaderinae and a coleopteroid Vianaidinae.

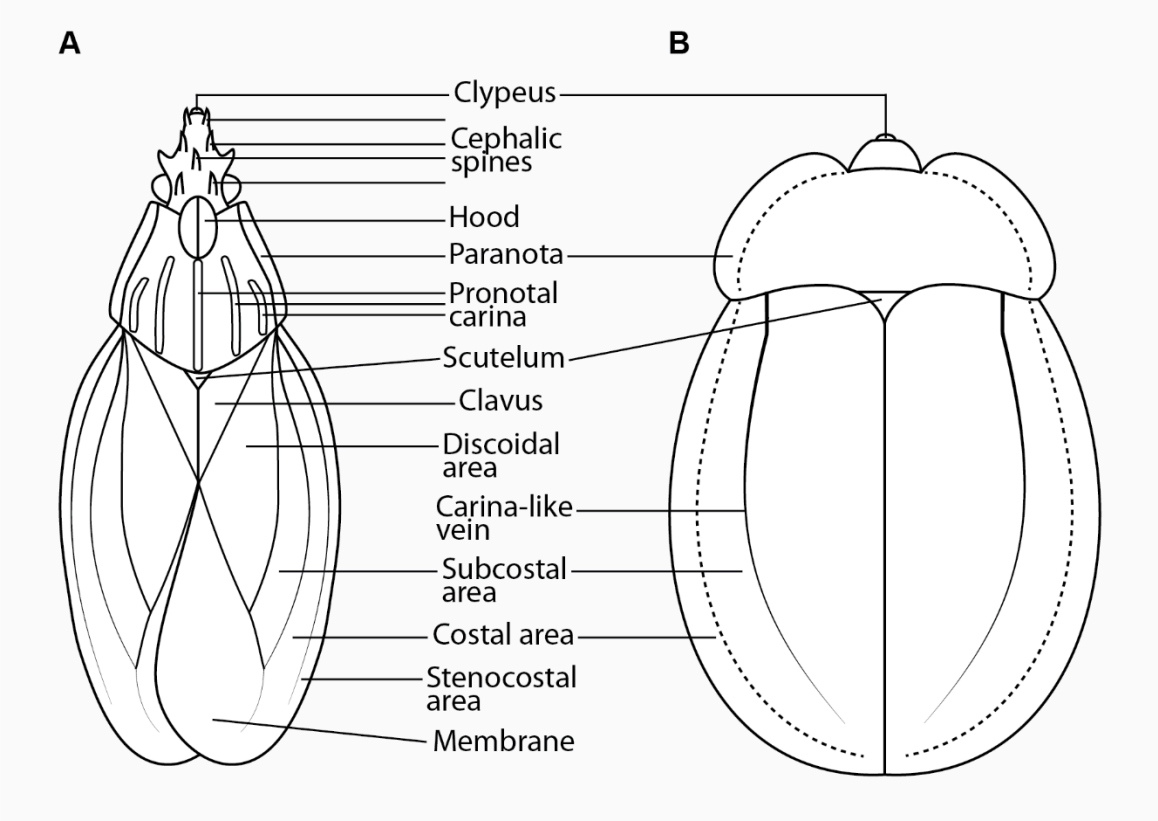


Figure 4. Schematic dorsal habitus of Tingidae. A) generic Cantacaderinae, modified from Froeschner (1996); B) generic *Thaumamannia* (Vianaidinae), modified from van Doesburg (1977).

The most prolific author in the taxonomy of tingids was Carl Drake, publishing actively from 1916 to 1965 and describing roughly 25% of all known species of Tingidae (ITIS, 2018). Drake was also the leading author of the only world catalog of species published to this day (Drake & Ruhoff, 1965). Two more world catalogs were made, both for genera (Monte ,1947a; Drake & Ruhoff, 1960). Drake was also the leading author of the most important morphological work on Tingidae (Drake & Davis, 1960), which set the foundation of Tingidae classification for many years. He worked with the world fauna, being even more active on the New World. Oscar Monte (e.g., 1947) was also a prolific author dealing with Neotropical fauna, and Champion (e.g., 1897) and Stål (e.g., 1873) were the pioneers describing genera and species from the Americas. For North America, Hurd (1946) provided a useful taxonomic summary on the genera reported from that part of the globe. Franz Xavier Fieber, Geza Horváth, Auguste Puton and Jean Péricart contributed significantly for the Paleartic fauna (e.g., Fieber, 1861; Puton, 1886; Horváth, 1906; Péricart, 1983). Pedro Duarte Rodrigues (e.g., Rodrigues, 1977; 1979; 1992) was, perhaps, the most important author for the African fauna, which has an important and very useful catalog made by Ursula Göllner-Scheiding (2004). Choku Takeya (e.g., Takeya, 1962; 1963) and Gerasimos Cassis (e.g., Cassis & Symonds, 2008; Cassis *et al.*,

2017) made strong contributions to the Asian and Australian fauna, respectively. Although many authors have contributed to the taxonomy of the lace bugs, just a few attempted to address the challenge of Tingidae classification.

Classification: pre-phylogenetic hypotheses

Stål (1873) was the first author to provide a classification scheme for Tingidae. The so called "divisions" proposed by Stål was called Tingidaria, Cantacaderaria and Serentharia. In the latter, Stål (1873) included only three genera: *Serenthia* Spinola, 1837 (= *Agramma* Stephens, 1829), *Ceratinoderma* Stål, 1873 and *Solenostoma* Signoret, 1863 (= *Coleopterodes* Philippi, 1864). Distant (1909) created two divisions based mostly on antennae characters to accommodate two newly described monotypic genera, *Aidoneus* Distant, 1909 and *Axiokersos* Distant, 1909. Both remains monotypic to this day (ITIS, 2018). Blatchley (1926), on his notorious catalog, was the first author addressing the classification of Tingidae using family level ranks. He corrected Stål's nomenclature (Tingidaria = Tinginae) and proposed three tribes considering only the fauna of Eastern North America, Galeatini, Acalyptini and Physatocheilini (Blatchley, 1926). These tribes were defined on the basis of external morphological non-genital characters, as such: the presence of large hood and large, hyaline cells on the hemelytra (Galeatini); body oval, hood small and triangular, paranota and costal area only moderately broad, hemelytra usually dimorphic in length (Acalyptini); hood absent, rarely with expanded paranota, hemelytra areola not large nor hyaline (Physatocheilini). Drake & Ruhoff (1960) pointed some taxonomic mistakes on genera delimitation made by Blatchley (1926) to justify suppressing the three aforenamed tribes into Tinginae. The two Distant (1909) divisions, Axiokersoaria and Aidoneusaria, were suppressed within Tinginae as well (Drake & Ruhoff, 1960). These two authors kept Stål's divisions Cantacaderaria and Serentharia treating them as subfamilies, and they followed Drake & Maa (1955), who considered Agrammatinae the correct name for Serentharia. This subfamily was later included in Tinginae by Drake & Davis (1960), which also included Vianaidinae as a subfamily of Tingidae and divided Cantacaderinae into two newly created tribes, Cantacaderini and Phatnomini. Froeschner (1981) corrected the name of the latter to Phatnomatini, which is in current use. The Tinginae tribes Litadeini, Ypsotingini and the nominal tribe Tingini were proposed by Drake & Ruhoff (1965). This classification scheme was followed by most authors since the publication of the world catalog (Drake & Ruhoff, 1965), including the ones addressing Tingidae classification and it will be followed in

the next paragraph. A schematic summary of these pre-phylogenetics classification schemes can be found on Table 1.

Modern Classification: phylogenetic hypotheses

Lis (1999) was the first to apply phylogenetics in an attempt to resolve Tingidae classification. Two different morphological-only data sets aiming different goals were built for these analyses, one using tribes (*sensu* Drake & Ruhoff, 1965) as terminals and one using mainly Cantacaderinae genera (Lis, 1999). The first analysis recovered Phatnomatini as the sister group of Tinginae, leaving Cantacaderinae with only its nominal tribe. The second analysis provided the basis to the proposal of two new suprageneric taxons, Carldrakeaninae and Ceratocaderini. In addition, based on these analyses and on morphological remarks, Lis (1999) suggested the elevation of the taxonomic ranks of Cantacaderidae *status novum*, to hold a reformed Cantacaderinae *sensu novum* and the newly proposed Carldrakeaninae. Yet according to Lis (1999), Tingidae *sensu novum* would hold the newly transferred Phatnomatinae *status novum* and Tinginae, with its three previously proposed tribes: Tingini, Ypsotingini and Litadeini. In two subsequent analyses (Guilbert, 2001; 2004), these groups were not corroborated. Guilbert (2001) performed a morphological cladistic analysis based on external non-genital characters and recovered Vianaidinae as sister-group of Tingidae *sensu* Drake & Ruhoff (1965), but none of the subfamilies or tribes were found to be monophyletic. Later, Guilbert (2004) included immature data into a smaller data set and recovered the relationship Vianaidinae + Tingidae *sensu* Drake & Ruhoff (1965), as well as Cantacaderinae *sensu* Drake & Ruhoff (1965), but with Phatnomatini paraphyletic. Litadeini and Ypsotingini were also non-monophyletic according to Guilbert (2004). In these two studies, Guilbert (2001; 2004) proposed the first evolutionary analyses for the family. In the first, Guilbert (2001) highlighted an evolutionary trend from a simple and less ornamented structure to a more complex set of features, including hood, expanded paranota and large hemelytra with hyaline areola. Guilbert (2004) corroborated this first initial hypothesis. However, the hypotheses raised by these two studies were also hampered by the small number of taxa sampled in both analyses. Schuh *et al.* (2006) rejected Lis (1999) new ranks, but recovered the monophyly of Cantacaderini, Carldrakeanini *status novum* and Ceratocaderini, all three tribes of Cantacaderinae *status novum*, on a morphology-based cladistic analysis focused on the internal

Table 1. Pre-phylogenetic classification hypotheses of Tingidae, according to different authors. Taxa preceded by a "=" sign was considered a junior synonym by the corresponding author. **Bold** represents newly described taxa by the corresponding author. Italic indicates incorporations of previously described taxa into a supra-generic taxon proposed or not by the corresponding author. Underlined indicates valid taxa not described by the corresponding author. Incorporations and synonyms are always shown, regardless if the act was proposed by the corresponding author. (*) Froeschner (1981) later corrected the name Phatnomini to Phatnomatini.

Stål, 1873	**Distant, 1909**	**Blatchley, 1926**	**Drake & Ruhoff, 1960**	**Drake & Davis, 1960**	**Drake & Ruhoff, 1965**
Tingidaria	**Axiokersoaria**	**Tinginae**	**Tinginae**	Tinginae	Tinginae
	Aidoneusaria	= *Tingidaria*	= *Tingidaria*	= *Tingidaria*	= *Tingidaria*
		Galeatini	*Axiokersoaria*	*Agrammatinae*	*Agrammatinae*
		Acalyptini	*Aidoneusaria*	*Axiokersoaria*	*Axiokersoaria*
		Physatocheilini	*Galeatini*	*Aidoneusaria*	*Aidoneusaria*
			Acalyptini	*Galeatini*	*Galeatini*
			Physatocheilini	*Acalyptini*	*Acalyptini*
				Physatocheilini	*Physatocheilini*
					Tingini
					Litadeini
					Ypsotingini
Cantacaderaria			**Cantacaderinae**	Cantacaderinae	Cantacaderinae
			= *Cantacaderaria*	= *Cantacaderaria*	= *Cantacaderaria*
				Cantacaderini	Cantacaderini
				Phatnomini*	Phatnomini*
Serenthiaria			**Agrammatinae**	Vianaidinae	Vianaidinae
			= *Serenthiaria*		

relationships of Cantacaderinae, and on the placement of the first described macropterous species of Vianaidinae. This analysis also used genera as terminals and Phatnomatini was represented by two genera, *Phatnoma* Fieber, 1844 and *Zetekella* Drake, 1944, being recovered paraphyletic within Tinginae. The matrix was mostly based on Lis (1999) matrices, repeating 43 out of its 52 characters with just few taxa added, and thus, the similar results are not completely unexpected. Another similar analysis was conducted six years later (Guilbert, 2012a), with the addition of one newly described genus, *Caledoderus* Guilbert, 2012, and *Afghanoderus* Lis, 2001, and two removed characters from Schuh *et al.* (2006) data set. All three tribes of Cantacaderinae were recovered monophyletic, but in this analysis the sister-group of Ceratocaderini was Carldrakeanini and not Cantacaderini as found in both Lis (1999) and Schuh *et al.* (2006) analyses. Additionally, *Caledoderus* was found as part of Ceratocaderini and *Afghanoderus* was placed in Cantacaderini. The paraphyletic status of Phatnomatini found by Schuh *et al.* (2006) was also recovered in this analysis, with *Zetekella* closer to Tingini than to *Phatnoma* (Guilbert, 2012a). A summary of some of these phylogenetic attempts to resolve Tingidae classification is presented (Fig. 5).

The first and only phylogenetic analysis with molecular data was published by Guilbert *et al.* (2014), with 66 taxa and 30 morphological characters, nuclear (28S rRNA), and mitochondrial (16S, CO1, COII and Leu-tRNA) *loci*, and adopting several different tree search strategies. Among their terminal taxa, only two species belonged to Cantacaderini, two to Phatnomatini, three to Litadeini, two to Ypsotingini, and the rest to Tingini (36 species). No vianaidines were included (Guilbert *et al*., 2014). Despite the apparent low number of species from these tribes, they are proportionally similar to the real distribution of species in the suprageneric Tingidae taxa (*sensu* Drake & Ruhoff, 1965). Moreover, from the thirty morphological characters included in Guilbert *et al.* (2014), at least 20 were proposed by either Lis (1999) or Schuh *et al.* (2006). As a result of these analyses, Phatnomatini was recovered as the sister-group of the remaining Tinginae, as Lis (1999) initially proposed, corroborating with Schuh *et al.* (2006) and Guilbert (2012a). The authors also admitted that the data set was not appropriate to address the Cantacaderinae tribes proposed by Lis (1999) because of the insufficient sampling scheme for these suprageneric taxa. On the other hand, the two and three species included for Ypsotingini and Litadeini, respectively, were considered enough by the authors in order to propose the suppression of these two tribes based on their results (Guilbert *et al.*, 2014). The authors concluded that the next big step in Tingidae systematics would be a

molecular phylogenetic analysis with a bigger data set based on a much more comprehensive sampling scheme including Vianaidinae sequences.

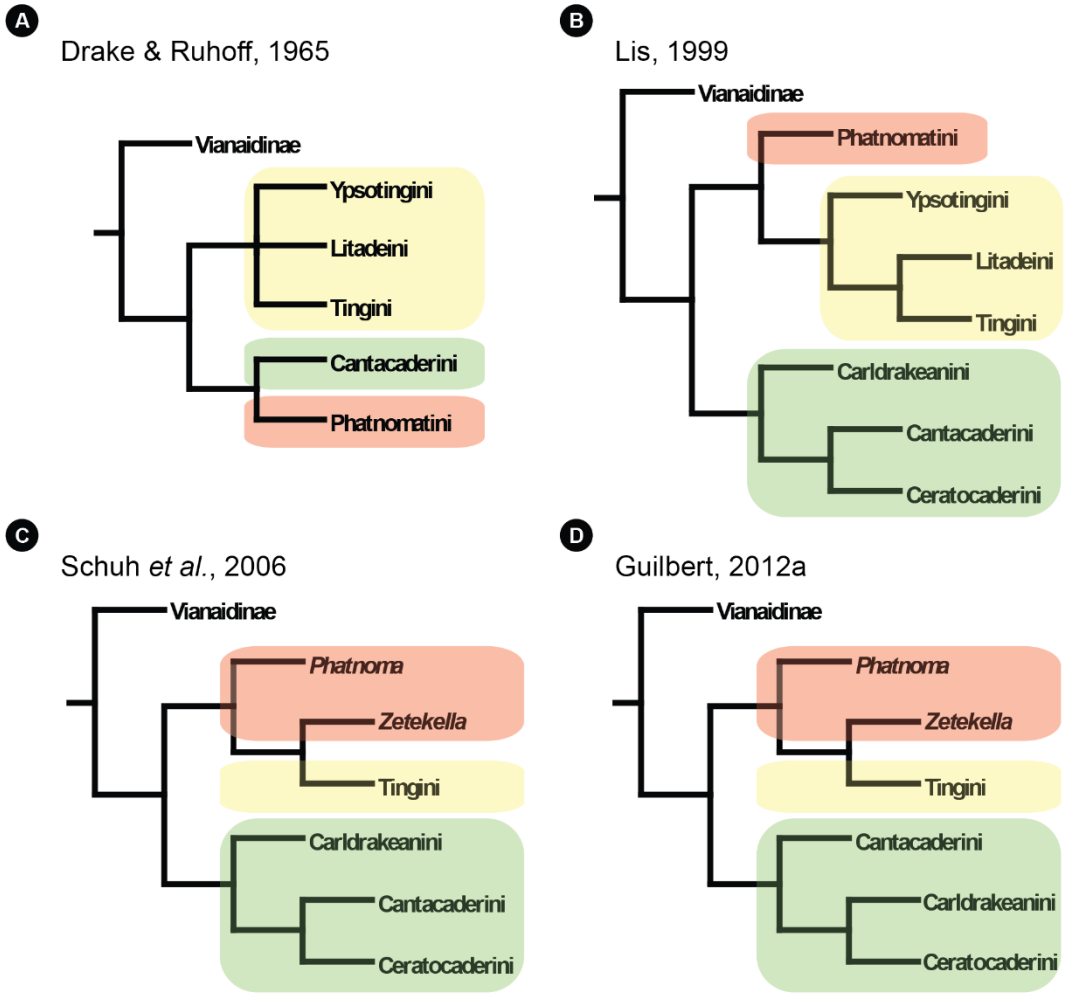


Figure 5. Some of the most important classification hypotheses on Tingidae, based on morphological characters. Colors indicate position and composition of the included supra-generic taxa. B-D are phylogenetic analyses that focused mainly on Cantacaderinae. A) Drake & Ruhoff (1965) proposed the most frequently accepted classification hypothesis based on an alpha-taxonomic approach; B) Lis (1999) was the first phylogenetic analysis to address this question. The taxonomic ranks were elevated by Lis (1999), which is not shown here for the sake of consistency with the other hypotheses; C) Schuh *et al.* (2006) was the first phylogenetic analysis to add a macropterous Vianaidinae specimen; D) Guilbert (2012) added two Cantacaderinae genera on the matrix, one newly described, and based the analysis on both Lis (1999) and Schuh *et al.* (2006).

Fossils and origin

The Tingidae origin was also a question addressed by many different authors and methods through the years (Lis, 1999; Wappler, 2006; Guilbert, 2012b). One important element of the answer is the fossil record. Many family level fossils from lower and upper Cretaceous were

described and tentatively placed closely related to Tingidae: Ignotingidae (Zhang *et al.*, 2005) from the uppermost Jurassic to lowermost Cretaceous; Ebboidae (Perrichot *et al.*, 2006) and Hispanocaridae (Golub *et al.*, 2012) from the lower Cretaceous (Fig. 6D and 6A, respectively); Tingiometrinae (Heiss *et al.*, 2015) from the upper Cretaceous (Fig. 6B). These taxa were never included in a phylogenetic analysis, and thus, their placement was always based entirely on ones' morphological interpretation of both fossil and extant taxa characters. Considering the extant suprageneric groups, the oldest available fossil record thus far is for Phatnomatini: *Sinaldocader drakei* Popov, 1989, from the lower Cretaceous (Fig. 6C; Popov, 1989). In the same contribution, the fossil tribe Golmoniini was described in Cantacaderinae to hold one single species, *Golmonia pater* Popov, 1998 (Fig. 6E). The description was based on a single hemelytron in an uncomplete inverse imprint. However, the placement of the latter within Tingidae was disputed by Lis (1999), who considered Golmoniini to be more closely related to Thaumastocoridae. Golub (2001) defended the classification of this taxon as a Tingidae tribe based on characters that Nel *et al.* (2004) considered weak and shared with many different heteropteran families like Piesmatidae, Berythidae, Thaumastocoridae and others. Nel *et al*. (2004) also disputed the placement of *Sinaldocader* within Phatnomatini. However, Golub & Popov (2008) added a second species to this genus, *Sinaldocader ponomarenkoi* Golub & Popov, 2008 also from the lower Cretaceous. The authors addressed Nel *et al.* (2004) criticism, and a second observation of hemelytral areola in *G. pater* and the description of these structures for *S. ponomarenkoi* were used as arguments against Nel *et al.* (2004) discredit. This debate is particularly important because it changes the minimum age for Phatnomatini, and thus, for Tingidae entirely. Thus, according to Popov (1989) and Golub & Popov (2008), the oldest Phatnomatini record would be from the lower Cretaceous; according to Nel *et al.* (2004), lowermost Eocene based on the description of *Parazetekella eocenica* Nel *et al.*, 2004. Most known Tingidae fossils are from the Cenozoic age, more often from Eocene (e.g., Wappler *et al.*, 2015). The latest compiled list of Tingidae fossils was published by Wappler (2003), but numerous tingid fossils were described later (e.g., Golub, 2007; Golub & Popov, 2008; Golub *et al*., 2008). One of these was the genus *Burmacader* Heiss & Guilbert, 2013 now composed by the species *B. multivenosus* Heiss & Guilbert, 2013 and *B. lativentris* Heiss & Guilbert, 2018, from the upper Cretaceous. The *Burmacader* species are remarkably interesting by their unique set of morphological characters, including a Vianaidine-like scent gland peritreme and hemelytra punctuate to most of their extent bearing tranversal carina-like veins (Heiss & Guilbert, 2018). The phylogenetic position of *Burmacader* is uncertain, being considered two

different scenarios: one as part of the Vianaidinae and another one as part of the Cantacaderinae. This genus is discussed on the Vianaidinae section below.

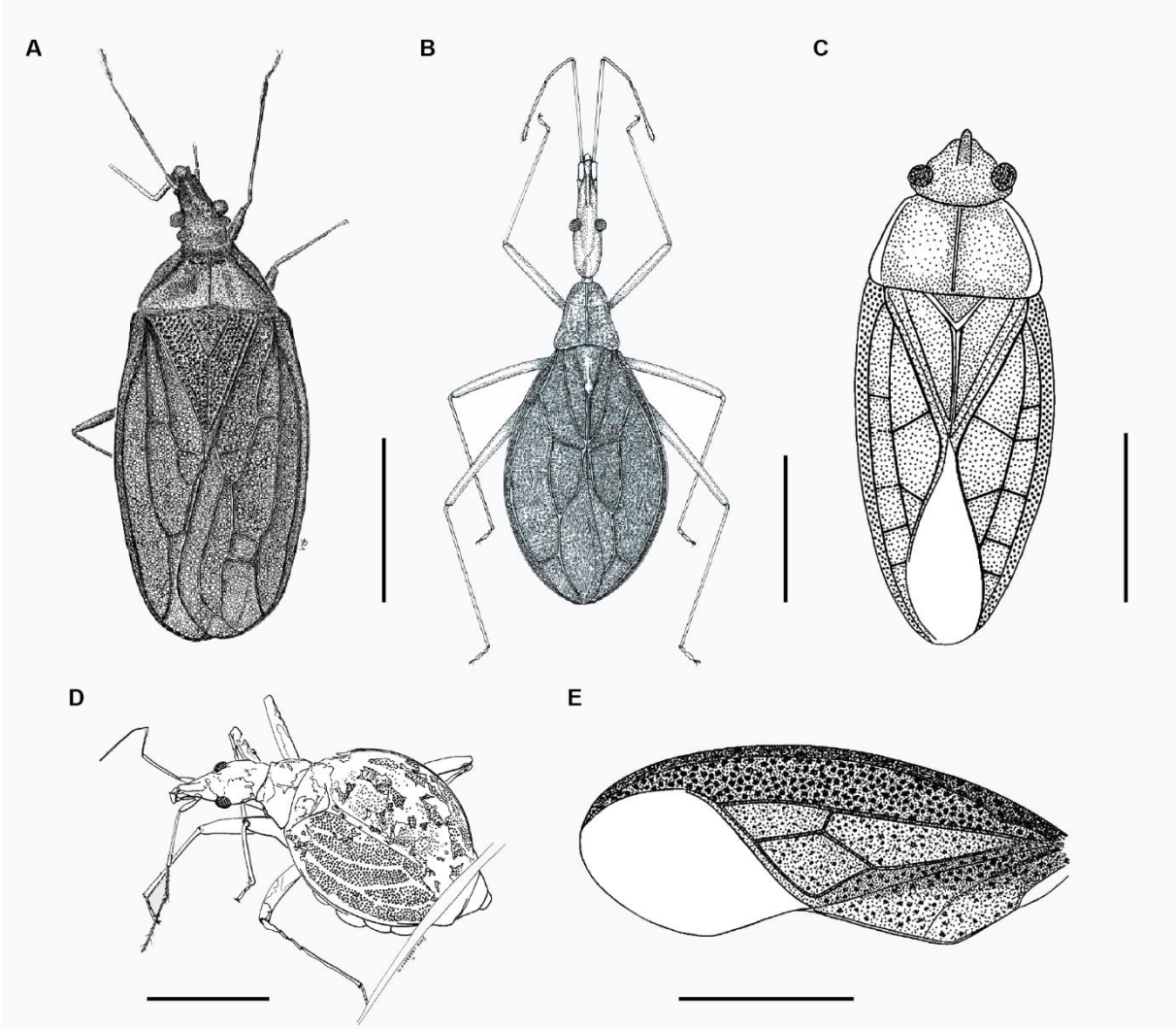


Figure 6. Fossil of Tingoidea: some families closely related to Tingidae and the oldest Phatnomatini fossils, including the uncertain Golmoniini. A) *Hispanocader lisae* Golub, Popov & Arillo, 2012; B) *Tingiometra burmanica* Heiss, Golub & Popov, 2015; C) *Sinaldocader drakei* Popov, 1989; D) *Ebboa areolata* Perrichot, Nel, Guilbert, Néraudeau, 2006; E) *Golmonia pater* Popov, 1989. All images were taken from the original descriptions. Scale bars: 1 mm.

The origin of Tingidae was subject of only three in-depth contributions thus far, two based on analytical methods (Bremer's method: Lis, 1999; BPA and S-DIVA: Guilbert, 2012b) and one historical and discursive approach (Wappler, 2006). Despite the presence of molecular data in Guilbert *et al.* (2014), the origin of the group wasn't addressed in their paper. Lis (1999) was the first to make comments on the Tingidae origin based on the Cantacaderinae phylogenetic analysis presented in the same work. Wappler (2006) included two fossils in the

presented discursive analysis: *Lutetiacader petrefactus* Wappler, 2006 from lower middle Eocene and *Paleocader avitus* (Drake, 1950) from Baltic amber, Eocene, both assigned to Cantacaderini. Lis (1999) and Wappler (2006) proposed somehow similar biogeographical hypotheses, with one major ancient vicariance followed by dispersal events. Guilbert (2012b), based his biogeographical analysis on the phylogenetic analysis of Guilbert (2012a), and found slightly conflicting results, more importantly regarding the origin of Cantacaderini. In Guilbert (2012a) analysis, Vianaidinae origin was also briefly discussed, pointing to an early vicariant event isolating this lineage in South America. Since Vianaidinae was recovered as the Tingidae *sensu stricto* sister group by many authors (Lis, 1999; Schuh & Štys, 1991; Schuh *et al.*, 2006; Schuh *et al*., 2009), understanding its origin may lead to the understanding of all modern tingids origin. Wappler *et al.* (2015) recognized Vianaidinae importance for Tingidae origin and summarized the findings on this question after adding a fossil genus to Schuh *et al.* (2006) dataset, *Gyaclavator* Wappler *et al.*, 2015. Therefore, adding this taxon in molecular phylogenetic analyses will allow not only to corroborate the Vianaidinae + Tingidae *sensu stricto* sister-group hypothesis, but to later estimate the date of the divergence of these two lineages, accessing and perhaps strengthening the available biogeographical hypotheses for the family.

Vianaidinae

Vianaidinae is the rarest group of tingids, composed by eight extant species and one fossil, with both coleopteroid and macropterous forms known to the science (Fig. 7; Montemayor & Carpintero, 2007; López *et al.*, 2016). Among several other differences between the two forms, the first presents coriaceous hemelytra, reduced or absent hindwings, and reduced eyes composed by only few, scattered ommatidia while the latter presents fully-developed compound eyes and hindwings, and hemelytra with clavus, discoidal, subcostal and costal areas, and membrane (Schuh *et al.*, 2006). The group was first placed in Oxycareninae (Pentatomomorpha, Lygaeoidea) by China (1945), and transferred to Cimicomorpha by Komilev (1955), which was the first to recognize its relationship with Tingidae *sensu stricto*. Only after Drake & Davis (1960) the group was considered a Tingidae subfamily. These authors argued that the unique traits within Cimicormopha presented by vianaidines were adaptative features highly dependent on the habitat and behavior of these strange forms and therefore, should not be used as argument to raise the rank of the group to the family level. However, at the time Drake & Davis (1960) made this statement, only coleopteroid forms were known. The

first macropterous form was only formally described in 2006 (*Anommatocoris bolivianus* Schuh *et al.*, 2006), 15 years after their first mention on the specialized literature (Schuh & Štys, 1991). Today, from the eight extant species assigned to the group, two are macropterous: *A. bolivianus* and *Pterovianaida melchiori* Montemayor & Carpintero, 2007. *Anommatocoris* has both forms already described (e.g. for coleopteroid forms, *A. minutissimus* China, 1945), while the monotypic *Pterovianaida* is, thus far, macropterous-exclusive and *Thaumamannia* only known by coleopteroid species. A timeline featuring the taxonomic history of the group is presented (Fig. 8). Although the differences between macropterous and coleopteroid forms are remarkable, the differences between the coleopteroid species of *Anommatocoris* are considerably subtle (López *et al*., 2016). The conserved and highly modified morphology of the coleopteroid forms in this genus is likely to be a consequence of its habitat and behavior.

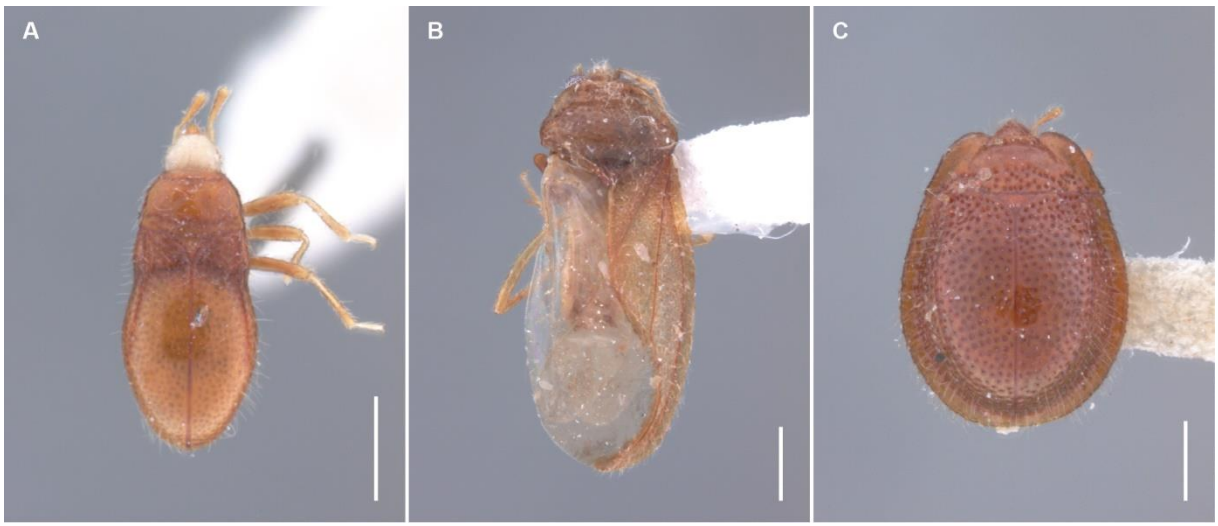


Figure 7. Vianaidinae dorsal habitus with the three extant genera represented, including one macropterous form. A) *Anommatocoris minutissimus* (China, 1945); B) *Pterovianaida duckensis* Guidoti & Montemayor, 2016; C) *Thaumamannia manni* Drake & Davis, 1960. Scale bars: 0.5 mm.

The coleopteroid forms were always collected on soil, and sometimes, associated with ant nests (Drake & Davis, 1960). For this reason, the term “myrmecophilous” has been largely applied for the coleopteroid forms of Vianaidinae. However, this term was often used based on their morphology and not on their association or ecological interaction with ants *per se*, being in some cases, therefore, misused entirely (Drake & Froeschner, 1962). Thus far, two species were collected in ant nests: *A. coleopteratus* and *T. manni* Drake & Davis, 1960 (Kormilev, 1955; Drake & Davis, 1960). *Thaumamannia vanderdrifti* van Doesburg, 1977, which was originally described from Suriname (van Doesburg, 1977) was also found in Brazilian caves

(Guidoti *et al.*, 2014). Only two species out of the nine known extant taxa were collected more than once, *A. coleopteratus* (San Martin, 1966) and *T. vanderdrifti* (Guidoti *et al.*, 2014), indicating the rarity of the group. In terms of immatures, only these two aforementioned species had nymphs described, the latter illustrated by SEM micrographs (Kormilev, 1955; Guidoti *et al.*, 2014). No formal study on their biology, behavior or ecology was conducted to this date and the potential association with ants of those two species remains unexplored. All macropterous species described thus far were collected on light traps (Schuh *et al.*, 2006; Montemayor & Carpintero, 2007), indicating a somehow intense flight activity and thus, a conspicuous behavioral shift considering the coleopteroid vianaidines. Except for *A. minutissimus* and *T. vanderdrifti*, genital characters were not illustrated or described for any other vianaidine. The species delimitation was based mostly on differences on the scent gland peritreme, with the addition of punctuation marks on the hemelytra for coleopteroid forms (Drake & Froeschner, 1962; López *et al.*, 2016), and hemelytra areas and paranota width for macropterous forms (Montemayor & Carpintero, 2007).

Two fossil species from the late Cretaceous New Jersey amber were formally placed within Vianaidinae: *Vianagrama goldmani* Golub & Popov (2000) (Fig. 9A), and *Vianathauma pericarti* Golub & Popov (2003) (Fig. 9B). However, Schuh *et al.* (2006) disputed the relationship of *V. pericarti* due to the holotype condition which hampered the observation of key structures such as the scent gland peritreme. *Vianagrama goldmani*, however, presents the hemelytra extending beyond abdomen, R + M veins distinctly raised, costal vein extending to the apex of the membrane and membrane somehow developed (submacroptery), and, still according to Schuh *et al.* (2006), these characters combined argue for its placement within Vianaidinae. Later, Heiss & Guilbert (2013) described *Burmacader multivenosus* Heiss & Guilbert (2013) (Fig. 9C) with a scent gland peritreme composed by two perpendicular branches, one of the unique features of Vianaidinae. However, several other traits like the lace-like structure of the hemelytra and paranota dispute this hypothetical phylogenetic relationship. Heiss & Guilbert (2018) described a second species of *Burmacader* Heiss & Guilbert, 2013, but no strong claims on the genus relationship with Vianaidinae was made in this contribution as well. To this day, only a few phylogenetic analyses included vianaidines as terminals (Schuh & Štys, 1991; Guilbert, 2001; 2004; Schuh *et al.*, 2006; 2009; Wappler *et al.*, 2015), and none of them included the aforenamed fossils. The goal of such analyses was always to test the relationship of Vianaidinae + Tingidae *sensu stricto*, or the broader relationship within Heteroptera. Lis (1999), in addition, included the group as outgroup of its tribal analysis.

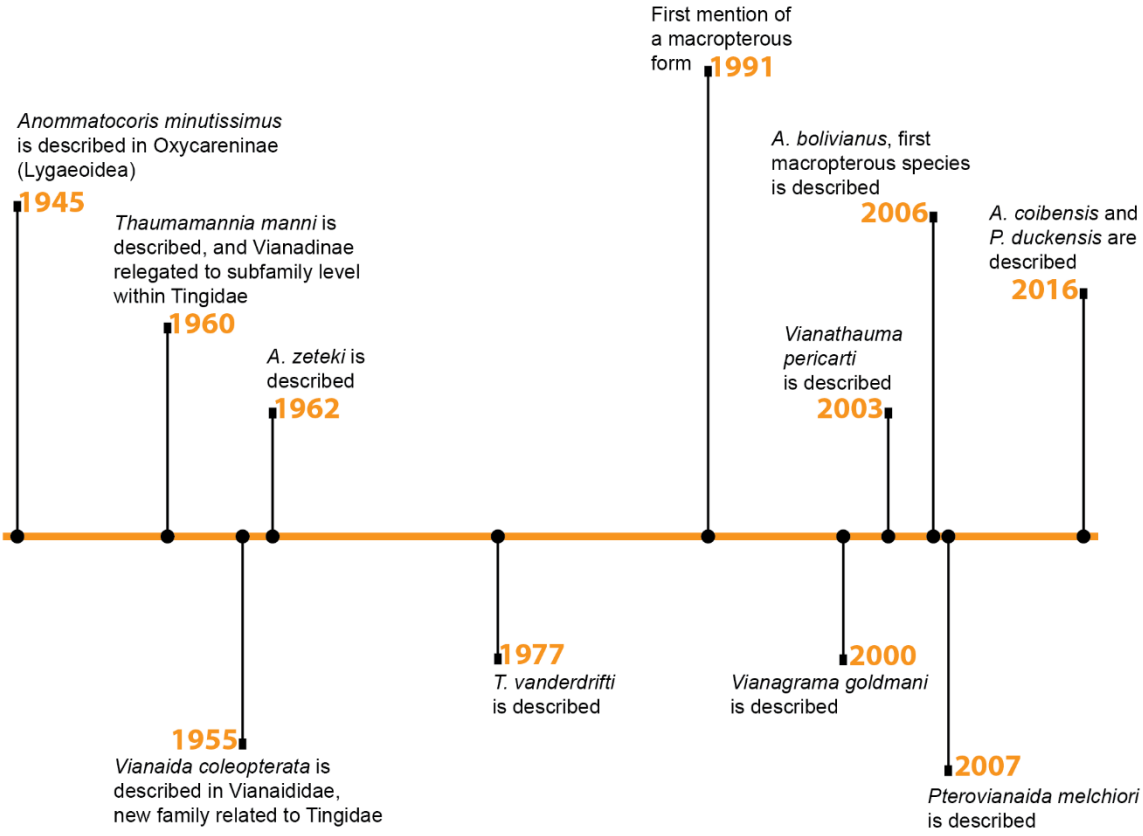


Figure 8. Timeline of taxonomic nomenclatural acts on Vianaidinae, from the first species description to the latest, including the first mention of a macropterous form and the gap between this first mention and the first macropterous description.

Although the relationship Vianaidinae + Tingidae *sensu stricto* was never disputed since Kormilev (1955), the subfamily status of Vianaidinae is not consensual among specialists (Vianaididae: Lis, 1999; Golub, 2001; Montemayor & Carpintero, 2007; Vianaidinae: Drake & Davis, 1960; Drake & Ruhoff, 1965; López *et al.*, 2016). Schuh *et al.* (2006) were the last contribution discussing the rank of the group, and according to them, unnecessary elevation of taxonomic ranks might obscure relationships among sister-groups and these elevations shouldn't be made based on autapomorphies. Additionally, neither the monophyly of the subfamily nor the relationship within the group were addressed in a phylogenetic context to this day. Their monophyly may never have been a concern because of the number of unique characteristics within Cimicomorpha presented by the Vianaidines (Schuh *et al.*, 2006). These "autopomorphies" strongly corroborate the group in a taxonomic approach and thus, its monophyly was never disputed in the literature. However, their internal relationships became more interesting as more species were described, especially new macropterous forms. Due to

the conspicuous morphological differences between coleopteroid and macropterous forms it's basically impossible to recognize two specimens of different morphs as the same species, or even as congeners. However, it might be possible to retrieve monophyletic groups composed by coleopteroid and macropterous forms.

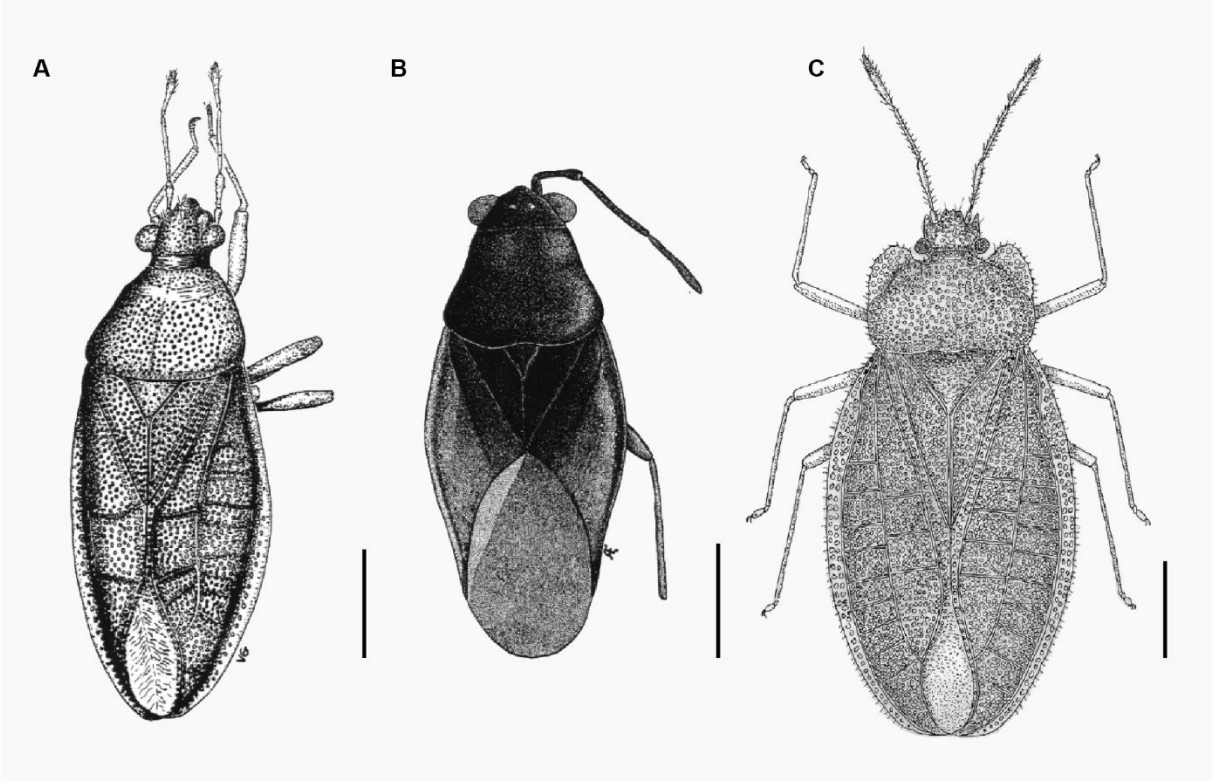


Figure 9. Fossil taxa allegedly related to Vianaidinae. A) *Vianagrama goldmani* Golub & Popov, 2000; B) *Vianathauma pericarti* Golub & Popov, 2003; C) *Burmacader multivenosus* Heiss & Guilbert, 2013. All images were taken from the original descriptions. Scale bars: 0.5 mm.

Justification and Objectives

Considering that the two macropterous Vianaidinae were formally described very recently, a taxonomic review in addition to a phylogenetic hypothesis aiming the internal relationships among the extant Vianaidinae might be crucial to move forward in the knowledge of the subfamily at this point. Moreover, including vianaidine's DNA sequences on a Tingidae phylogenetic analysis could test its close relationship hypothesis with Tingidae *sensu stricto* based on molecular data for the first time, as well as open new perspectives regarding the origin of the family. Taxonomic contributions on the supra-generic taxon with the oldest minimum age, Phatnomatini, could also be crucial to enhance the sampling of this important tribe on this new molecular Tingidae phylogeny. Therefore, this thesis aims to advance the knowledge on

Tingidae systematics and evolution by focusing on Vianaidinae systematics and discussing Tingidae classification based on a molecular phylogeny, with one additional contribution on Phatnomatini taxonomy.

This PhD is a co-tutelle between two institutions, Universidade Federal do Rio Grande do Sul (Porto Alegre, Brazil) and Museum National d'Histoire Naturelle (Paris, France), and several happenings and factors allowed to focus on these aforementioned goals, among them: the finding of a new macropterous Vianaidinae species (chapter 2; presented as the qualification exam for UFRGS) in the Instituto Nacional de Pesquisas da Amazônia (2014); the freshly collected and alcohol-preserved material received after donation (2015), including Vianaidinae samples, which allowed to obtain the first sequences from this subfamily in history (chapters 3-5); the Science Without Borders fellowship (CNPq), which allowed the co-tutelle and the conduction of the molecular bench-work in Paris (chapter 5), alongside with Dr. Guilbert (2016-2017); and the pre-doctoral fellowship from the Smithsonian Institution (Washington, D.C., United States; 2017-2018), obtained only in late 2016, which allowed the taxonomic contribution on Phatnomatini (chapter 3), the revision of Vianaidinae (chapter 4), and the identification of our terminal taxa (chapter 5), all due to the world's greatest Tingidae collection (Drake Collection) housed in that institution.

Therefore, it's the very combination of these chronological factors, happenings, co-tutelle requirements, travels and time abroad, and the academic interest on these relevant questions regarding Tingidae systematics and evolution that divided this dissertation in five additional chapters, including one dealing with the description of a new macropterous Vianaidinae species (chapter 2), one reviewing two small genera of Phatnomatini with also the description of a new species (chapter 3), a taxonomic review and phylogenetic analysis of Vianaidinae (chapter 4), and a Tingidae molecular phylogenetic analysis (chapter 5), including for the first time Vianaidinae sequences and focusing on Tingidae supra-generic classification.

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* presented as the qualification exam to UFRGS

** published in *Zootaxa*, 4150(2): 185-192

Chapter II

A new macropterous species of a rarely collected subfamily (Heteroptera, Tingidae, Vianaidinae)

Hemelytra of *Pterovianaida duckensis* sp. n.

Chapter II – A new macropterous species of a rarely collected subfamily (Heteroptera, Tingidae, Vianaidinae)

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Abstract

Pterovianaida duckensis n. sp., a new macropterous species of the rarely collected subfamily Vianaidinae is here described. The group currently comprises nine species, two of them fossils. *Pterovianaida* Montemayor and Carpintero is a recent monotypic genus described for a macropterous species collected in Peru. Here, a new macropterous species of *Pterovianaida* is described, and characters of the head, pronotum and hemelytra distinguish this species from the type species. This is the first record of a macropterous Vianaidinae for Brazil. A key to all extant species of this subfamily is provided.

Keywords. Brazil, lace bugs, Neotropical, new species, *Pterovianaida*.

Introduction

Vianaidinae (Heteroptera, Tingidae) is a small group of lace bugs composed of nine species, two fossils and seven extant (Drake and Ruhoff 1965, Doesburg 1977, Schuh *et al.* 2006, Montemayor and Carpintero 2007). The three extant genera are Neotropical: *Anommatocoris* China with four species, *A. coleopteratus* (Kormilev, 1955) (Argentina), *A minutissimus* China, 1945 (Trinidad), *A. zeteki* Drake and Froeschner, 1962 (Panama) and *A. bolivianus* Schuh, Cassis and Guilbert, 2006 (Bolivia); *Thaumamannia* Drake and Davis with two species, *T.*

manni Drake and Davis, 1960 (Bolivia) and *T. vanderdrifti* Doesburg, 1977 (Surinam and Guyana; Brazil - Guidoti *et al.* 2014) and *Pterovianaida* Montemayor and Carpintero with one species, *P. melchiori* Montemayor and Carpintero, 2007 (Peru). Both fossil genera are monotypic and belong to the New Jersey Cretaceous amber: *Vianagramma goldmani* Golub and Popov, 2000 and *Vianathauma pericarti* Golub and Popov, 2003; however, the placement of the latter within Vianaidinae was recently revisited (Schuh *et al.* 2006). Five of the recent species were described from coleopteroid specimens and two of them from macropterous forms. The coleopteroid taxa are all from soil samples, sometimes associated with ant nests (Guidoti *et al.* 2014). These highly adapted forms have weakly developed eyes and deeply punctured reduced hemelytra without the typical reticulations and area divisions that characterize the Tingidae. Despite the remarkable differences between macropterous and coleopteroid species, all share the following synapomorphies: peritreme of the scent gland projected, with an anterior and posterior branches and a well-developed evaporatorium; pronotum and hemelytra with punctures similar in size; and the large pedicel, subequal in size with basi- and distiflagellomeres (Schuh *et al.* 2006).

The first species included in this subfamily was *A. minutissimus*, which was originally placed within Oxycarenidae (treated as a Lygaeidae subfamily in the original description of the species). *Vianaida* Kormilev is the type genus of the subfamily, originally described with family status. Drake and Davis (1960) considered *Vianaida* a junior synonym of *Anommatocoris*, yet both species (*A. minutissimus* and *V. coleopterata* Kormilev, 1955) as valid taxa. Also, Drake and Davis (1960) highlighted the morphological characters shared between Tingidae and Vianaididae, changing the status of the latter to subfamily of the former. Since then, this taxon has been considered as a family (e.g. Lis 1999, Golub 2001, Golub and Popov 2003, Montemayor and Carpintero 2007) whereas some authors treated it as a Tingid subfamily (Drake and Davis 1960, Drake and Ruhoff 1965, Doesburg 1977, Schuh and Stys 1991, Schuh and Slater 1995, Guilbert 2001, 2004, 2012a, 2012b, Schuh *et al.* 2006, 2009, Heiss and Guilbert 2013, Guidoti *et al.* 2014). Schuh *et al.* (2006), in their analysis, corroborated the monophyly of Tingidae *sensu* Drake and Davis, and argued that the amount of autapomorphy should not be used to define taxonomic levels, as the relationship within these suprageneric taxa would be clearer without the elevation of their ranks. Therefore, here we follow Schuh *et al.* (2006) considering Vinaidinae as a subfamily of Tingidae.

Pterovianaida was described on the basis of a macropterous specimen collected at light trap in Kirigueti (Ucayali, Peru). This genus is defined by the presence of macrochaetae on the

head, the Y-shaped peritreme, and the hemelytra with the subcostal area distinctly widened at base of membrane (Montemayor and Carpintero 2007). It shares with the other macropterous vianaidine, *A. bolivianus*, well-developed compound eyes and hemelytra and the lack of veins on the membrane. Here we describe a second species of *Pterovianaida*, the third macropterous species of this rarely collected subfamily. This is the first report of a macropterous vianaidine and the second record of the subfamily for Brazil (Guidoti *et al.* 2014). A key for all the extant Vianaidinae is provided.

Methods

The specimen described herein was collected at light traps, in the "Reserva Adolpho Ducke (Manaus, Amazonia, Brasil)" and is deposited in the Instituto Nacional de Pesquisas da Amazônia (INPA). Drawings were made from photographs taken with a digital camera attached to stereomicroscope or compound microscope. Measurements are given in millimeters. Due to the poor condition of the specimen, the total body length was not measured. The distribution map was built using QGIS; the geographical coordinates were obtained from Google Earth. Distributional records for which the only information available was the country where not included (Tab. 1). To construct the key, specimens of *A. coleopteratus* from the American Museum of Natural History, New York, United States (AMNH) and Museu Nacional do Rio de Janeiro, Brazil (MNRJ), *T. vanderdrifti* from the Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCNZ) and *P. melchiori* from the Museo de La Plata, Buenos Aires, Argentina (MLP) were studied. Information regarding the remaining species was obtained from the original descriptions, other literature, and photos of the type specimens.

Results

***Pterovianaida duckensis* sp. n.**

Material examined

Holotype: BRAZIL, Amazonas: Manaus, (Reserva Ducke, km 26 Rodovia AM-010), 1 m#, 06.XII.1977, ["C.D.C. light trap I-I"], Jorge Arias (INPA). Specimen dried up and shriveled, with the head in a position that hampers measurements of total body length and obtaining a full photograph of the habitus.

Table 1. Summary of the known distributional data of extant vianaidines. Country (Ctr) acronyms: ARG, Argentina; BOL, Bolivia; BRA, Brazil; PAN, Panama; PER, Peru; SUR, Suriname; TTO, Trinidad and Tobago.

Species	**Ctr**	**Province**	**Locality**	**Lat**	**Long**
Anommatocoris bolivianus	BOL	Dept. La Paz	Chulumani, Apa-apa	-16.367	-67.500
A. coleopteratus	ARG	Buenos Aires	Tigre	-34.425	-58.579
A. minutissimus	TTO		North of St. Agustine	10.676	-61.402
A. zeteki	PAN	Barro Colorado Isl.		9.152	-79.846
Pterovianaida melchiori	PER	Ucayali		-11.637	-73.001
P. duckensis n. sp.	BRA	Amazonas	Manaus, Reserva Ducke	-2.95	-59.95
Thaumamannia manni	BOL	Santa Cruz		-17.867	-63.000
T. vanderdrifti	SUR	Saramacca	Dirkshoop	5.783	-55.483
	BRA	Pará	Fl. Nacional de Carajás	-6.122	-50.133

Diagnosis

Interocular distance greater than twice the width of eyes in dorsal view; paranota punctate, with three rows of punctures at widest part; anterior branch of metathoracic scent gland not curved downward; distal part of the pronotum greatly elevated; hemelytral margins with scattered scale-like projections.

Description

Body oval-elongate, brownish, antennae brown; posterior half of pronotum and scutellum, reddish brown, covered by long, dense setae. Head (Fig. 1a) unarmed. Punctures and macrochaetae more concentrated on interocular and pre-ocular regions. Interocular distance

almost one half the width of the head, eyes included (Fig. 1a). Rostrum surpassing posterior margin of the metasternum. Antenniferous tubercles visible only in ventral view, very short, about one fourth the length of the scape; inserted ventrally in front of eyes. Scape about one third the length of the pedicel; pedicel, basiflagelomere and distiflagelomere subequal in length. Pedicel claviform, both basiflagellomere and distiflagellomere fusiform. Clypeus well developed; mandibular plates shorter than clypeus, rounded apically. Bucculae subparallel, narrow, with one row of punctures, open in front. Pronotum (Fig 1a) trapeziform, two thirds wider than long, punctures regularly distributed, setae long and curved, less concentrated mesially. Collar glabrous, slightly raised, minutely punctured. Posterior half of the disc conspicuously elevated (Fig 2). Paranota well developed (Fig 1a), subvertical, sinuous, with three rows of punctures at its widest part before pronotal elevation. Scutellum visible; punctures smaller than those of hemelytra, bearing scattered curved setae. Metathoracic scent gland with anterior branch of Y-shapped peritreme longer and more laterally projected than posterior one (Figs 2a–b). Rostral channel narrow; concave at meso- and metasternum, wider in the former, not laminated. Legs light brown; coxae cylindrical, prominent; setae on legs erect, more densely distributed along tibiae. First tarsomere much smaller than second. Claws long, slender, well-developed. Hemelytra (Fig 3) fully developed, much longer than abdomen, with clavus, discoidal, subcostal, and costal areas well delimited, all irregularly punctate. Costal area extending to the apex of membrane, with only one row of punctures; margin with a few, scattered scale like projections, and covered with long, curved setae. Subcostal area widest before the membrane with seven rows of punctures. Discoidal area sub-trapezoidal, longer than half of the hemelytra length; widest after clavus, with six rows of punctures. Clavus two thirds the length of discoidal area, widest at middle, with four rows of punctures. Veins ridge like between subcostal and discoidal areas and between subcostal area and membrane. Membrane slightly longer than half the length of hemelytron; one row of punctures present externally; without veins. Abdomen with scattered, whitish, long, curved setae. Pygophore narrower than abdomen.

Measurements

Head length, 0.35; head width, 0.51; interocular width, 0.21; pronotum length, 0.8; pronotum width, 0.98; scape length, 0.14; pedicel length, 0.34; basiflagellomere length, 0.34; distiflagellomere length, 0.34.

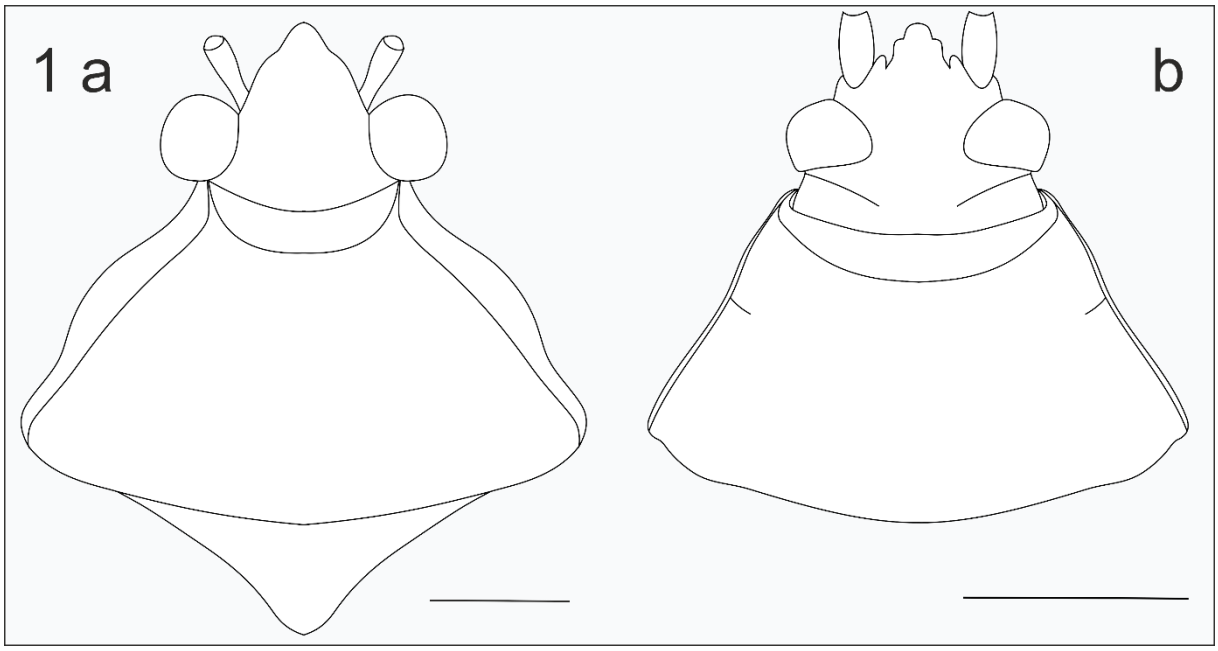

Figure 1. Dorsal view of head and pronotum: a, *Pterovianaida duckensis* sp. n.; b, *P. melchiori.* Scale bar: 0.25 mm.

Etymology

We have named this species for the Reserva Florestal Adolpho Ducke, located nearby Manaus, Amazonas, Brazil, where the specimen was collected in 1977.

Key to the extant species of Vianaidinae

1. Hemelytra reduced, coleopteroid 2

- Hemelytra well developed, with a clearly defined membrane, macropterous 6

2. Body rounded, paranota and costal area of hemelytra widely expanded 3

- Body ovate, paranota and costal area of hemelytra narrow, carinated 4

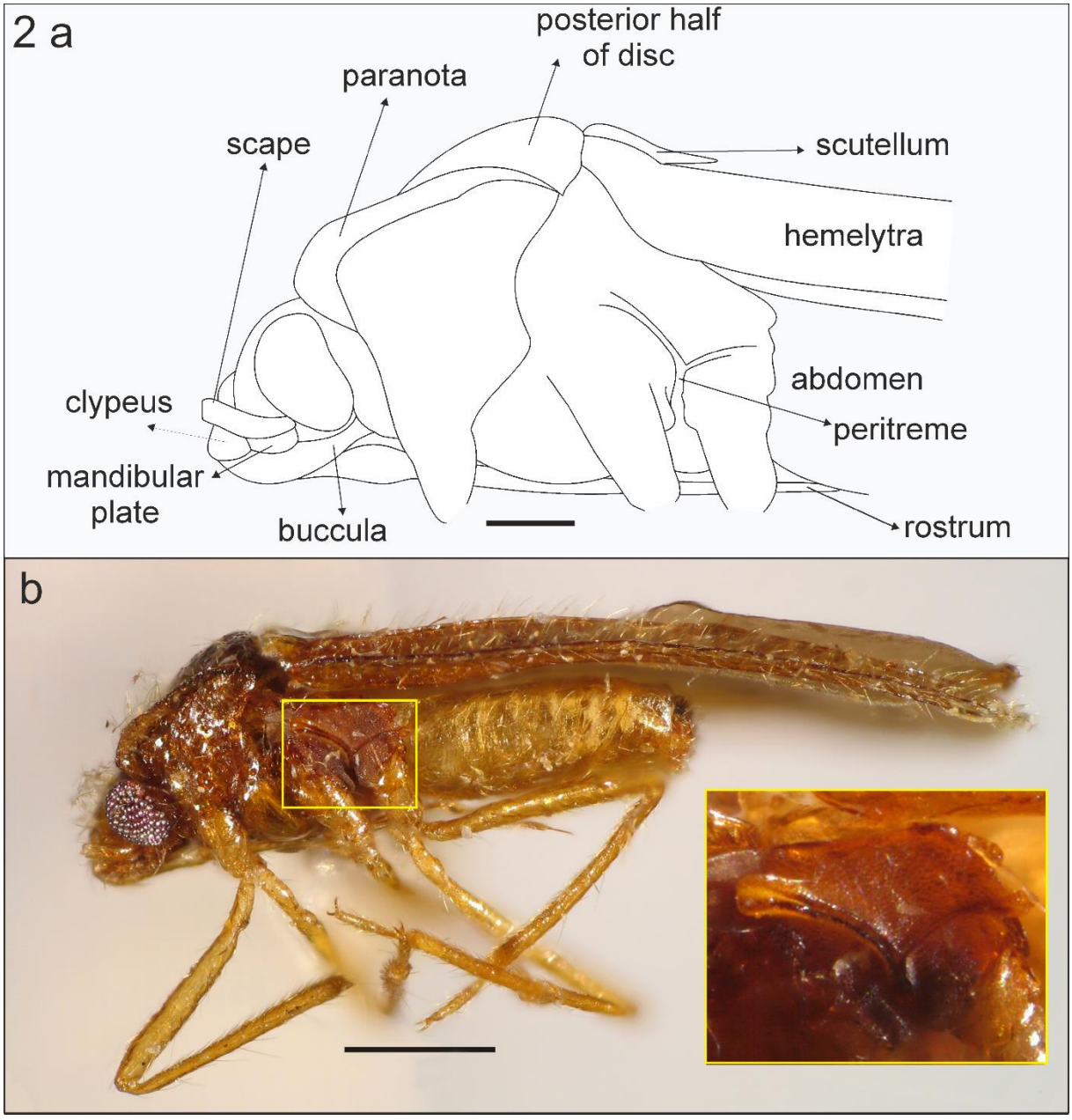

Figure 2. Lateral view of *Pterovianaida duckensis* sp. n.: a, schematic drawing. Scale bar: 0.25 mm; b, photo with focus on the peritreme. Scale bar: 0.5 mm.

3. Pronotum anteriorly and paranota punctate; scent gland extending laterally far beyond the hemelytral margin..... ***Thaumamannia vanderdrifti***

- Paranota and anterior region of pronotum lacking punctures; scent gland not surpassing hemelytral margin.....***T. manni***

4. Transverse branch of peritreme connected anteriorly with the longitudinal branch, dividing metapleura in two conspicuously unequal parts .....***Anommatocoris zeteki***

- Transverse branch of peritreme connected at the middle of the longitudinal branch, dividing metapleura in two subequal parts.....5

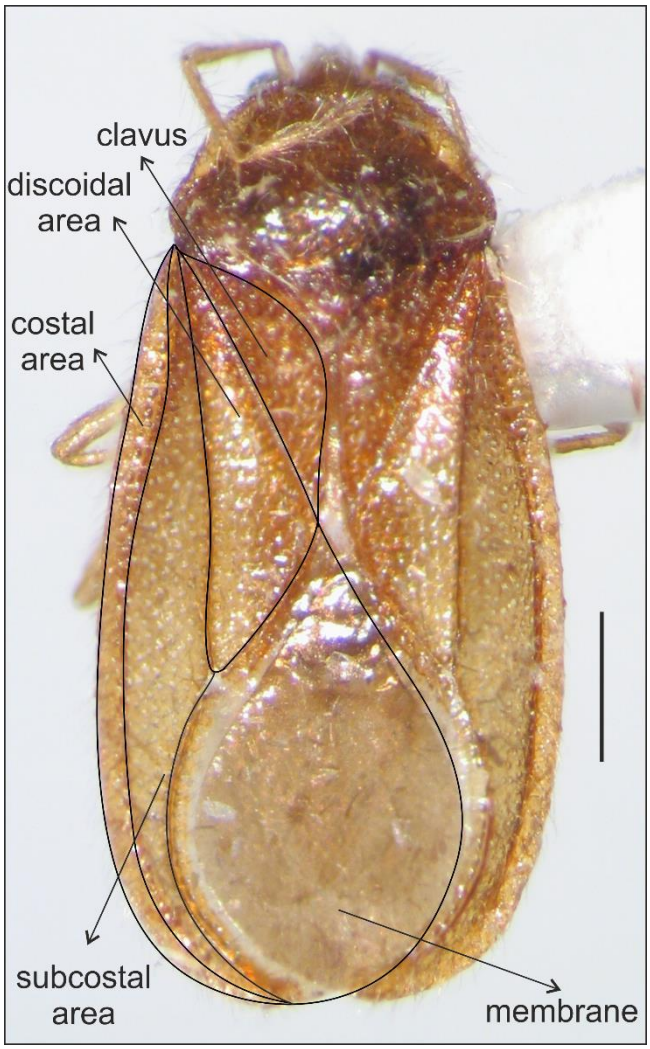

Figure 3. Hemelytra of *Pterovianaida duckensis* sp. n. Scale bar: 0.5 mm.

5. Compound eyes absent, pedicel and basiflagellomere subequal in length.....
.....***A. minutissimus***

- Compound eyes with only a few ommatidia, pedicel slightly shorter than basiflagellomere
.....***A. coleopteratus***

6. Macrochaetae absent on head; costal area and subcostal area subequal in width; membrane without outer row of areolae..... ***Anommatocoris bolivianus***

- Macrochaetae present on head; subcostal area much broader than costal area; membrane with outer row of areolae.....7

7. Paranota expanded laterally, with three rows of areolae at the widest part .... ***Pterovianaida duckensis*** sp. n. (Fig 1a)

- Paranota carinate ..... ***P. melchiori*** (Fig 1b)

Discussion

Pterovianaida duckensis sp. n. differs from *P. melchiori* in having a wider interocular distance; the paranota areolate; the anterior branch of the metathoracic scent gland not curved downward and the hemelytral margins with scattered scale like projections. The remarkable elevation of the distal part of the pronotum in *P. duckensis* sp. n. could not be observed in *P. melchiori* due to the way in which the holotype was preserved (slide-mounted). However, this is a very interesting character since it was not previously observed within the Vianaidinae. To the best of our knowledge, the longer costal area of the hemelytra present in *P. duckensis* sp. n. should not be considered a strong or reliable character because the Pterovianaida species are singletons and this character varies greatly among other Tingidae. The shape of the antennae, head, bucculae, scutellum, peritreme, and hemelytra, as well as the presence of cephalic macrochetae and the outer row of punctures on the membrane are shared between these two congeneric species. The point-mounted holotype of *P. duckensis* sp. n. allowed the complete observation of the male external genitalia of the genus for the first time. The shape and size of the pygophore, as well as the U-shape of its ventral rim and the paramere are similar to those described and/or observed for *A. coleopteratus*, *A. bolivianus* and *T. vanderdrifti* (Kormilev 1955, Doesburg 1977, Schuh *et al.* 2006).

Until now, the only known macropterous Vianaidinae are, the *Pterovianaida* species, *A. bolivianus* (extant) and *V. goldmani* (fossil). Both *Pterovianaida* species share with *V. goldmani* the presence of macrochaetae, the punctated scutellum, the widened subcostal area, and the row of punctures on the membrane. *Pterovianaida* species also share with *A. bolivianus* the large membrane, longer than half of hemelytron. The shape and size of the ventral rim of the pygophore and paramere are shared among *Pterovianaida* species, *A. bolivianus* and *T. vanderdrifti*, the only vianaidines with male genital characters described and illustrated. Within

all Vianaidinae, *Pterovianaida* shares the length of the pedicel subequal with basi- and distiflagellomere; the puncture size on the pronotum and hemelytra and the laterally expanded scent gland. The outstanding morphological difference between macropterous and coleopteroid vianaidines hampers further comparison.

Golub and Popov (2003) hypothezed the evolution of both macroptery and coleoptery within Vianaidinae, where *V. pericarti* plays a crucial role in the evolutionary scenario as its morphology is understood as the first known evidence of preadaptative features towards cryptic myrmecophilous coleopteroid morphologies. Recently, Schuh *et al.* (2006) disagreed with the placement of *V. pericarti* within this subfamily arguing that they could not observe some of the main characters that would support this taxonomic conclusion. Heiss and Guilbert (2013) described a fossil genus from Myanmar Cretaceous amber which shares with all Vianaidinae species the well-developed scutellum and the proportions of the pedicel in relation to the basi- and distiflagellomere. *Burmacader multivenosus* Heiss and Guilbert, 2013 also shares the T-shaped scent gland with *Anommatocoris* and *Thaumamannia* species, and a shorter membrane in the hemelytra with *V. goldmani*. It was proposed that this species could be the sister group of Vianaidinae, but this idea was not based on a phylogenetic approach (Heiss and Guilbert 2013). If this hypothesis is corroborated in further analyses, the type locality of *B. multivenosus* has strong implications in the biogeography of the subfamily as it will be the first record of this lineage outside the New World (Fig 4).

‘ Macropterous specimens of Vianaidinae were first reported by Schuh and Stys (1991). Before the first description macropterous species description (Schuh *et al.* 2006), these forms were mentioned only one more time (Schuh and Slater, 1995). *Pterovianaida duckensis* sp. n. is here described based on a single specimen previously misidentified as Piesmatidae. The lack of information regarding the macropterous forms of this subfamily may also have led to misidentifications in other collections. The authors believe that the observed morphological discontinuity, the slide-mounted type of *P. melchiori* and the rarity of such forms are strong justifications to describe this new singleton. With more information on these rare tingids in the literature, more people will be aware of them and the number of specimens and/or species should increase.

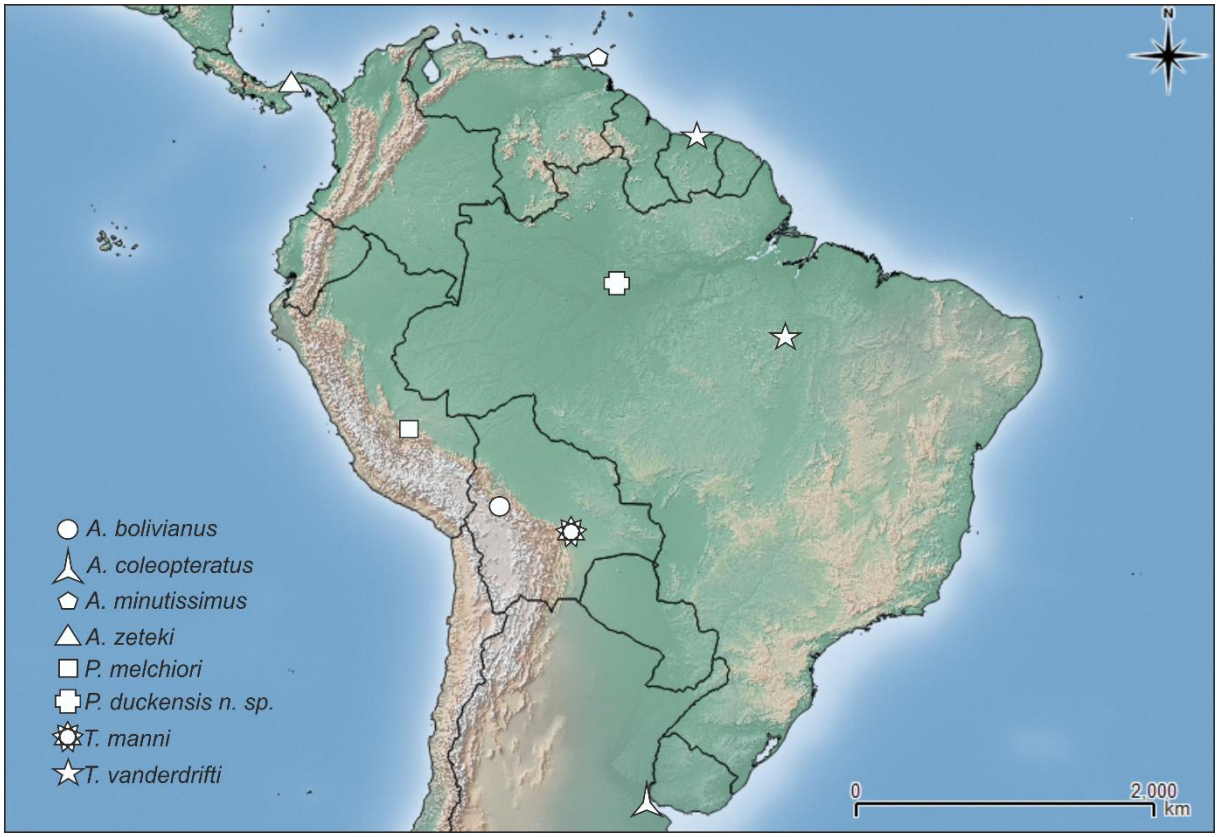

Figure 4. Map of distribution of the Vianaidinae species.

This rarely collected taxon might be extremely important for understanding Tingidae evolution. The monophyly of the family has never been formally tested in a phylogenetic framework. Phylogenetic analyses could also provide hypotheses regarding the relationships between its species, as well as the understanding of the evolution of specific characters (*e. g.*, macroptery). In the absence of comprehensive field observations, molecular data could corroborate or refute the idea of a genus with both macropterous and coleopteroid forms. Efforts towards sampling, ultrastructural morphology studies, and nymphal descriptions could provide important information that will help clarifying the phylogenetic relationships within Vianaidinae.

Acknowledgments

We thank Augusto Loureiro Henriques, curator of the INPA invertebrate collection for having loaned the specimen used in this description. We also thank Thomas Henry (Systematic Entomology lab., USDA at the National Museum of Natural History, Smithsonian Institution, Washington D.C., United States) for providing photos of the *Thaumamannia manni* holotype;

Randall Schuh and Ruth Salas (AMNH) and Luiz Costa (MNRJ) for lending specimens of *Anommatocoris coleopteratus*; and Randal Schuh (AMNH) and Eric Guilbert (MNHN) for their comments on previous versions of this manuscript. Conselho Nacional de Pesquisa e Desenvolvimento (CNPq, Brazil), funded the first author's fellowship and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina) funded the second author.

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* presented as the required publication to MNHN

** accepted for publication in *Zookeys*

Chapter III

A new species of *Zetekella* Drake (Heteroptera, Tingidae) from Ecuador with comments on *Zetekella* and *Minitingis* Barber (Heteroptera, Tingidae)

Head and pronotum of *Zetekella henryi* sp. n.

Chapter III – A new species of *Zetekella* Drake (Heteroptera, Tingidae) from Ecuador with comments on *Zetekella* and *Minitingis* Barber (Heteroptera Tingidae)

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Abstract

Zetekella and *Minitingis* (Heteropera, Tingidae) are morphologically similar genera, each comprising two species. The latter was already considered a junior synonym of the former, but was revalidated on the basis of the number of cephalic spines, projections on the paranotal edge, length of the rostrum, presence of an abdominal groove and distributional pattern. Here, we describe a new species of *Zetekella* from Ecuador, reassess the diagnoses for both genera, report new records for *Z. pulla* and *Z. zeteki* and provide a key to the species of both genera.

Introduction

Zetekella Drake is composed of two species, *Z. zeteki* Drake, 1944 and *Z. pulla* Drake & Plaumann, 1956. After Z. pulla was described, the generic diagnosis was redefined, as follows: head moderately long to long, armed with five spines, bucculae open in front and slightly projected forward, and "rostrum extremely long, extending on venter" (Drake and Plaumann 1956). No macropterous forms are known for this genus, but other characters, such as the proportions of the antennal segments, often have been used in taxonomic studies of the Tingidae *(*excluding Vianadinae).

Zetekella was considered the senior synonym of *Minitingis* Barber by Drake and Ruhoff (1960) without further consideration of morphological characters or generic diagnoses. This

genus was originally proposed to hold *Minitingis minusculus* Barber, 1954 on the basis of the number of pronotal carinae and the lateral acute processes of the paranota. However, the genus was compared with *Phatnoma* rather than *Zetekella*, and the remarkable paranotal acute processes were found to vary by the same author (Barber 1954). Froeschner (1968) reinstated *Minitingis*, described a new species of the genus, and reaffirmed the generic status based on morphological characters and distributional patterns. According to Froeschner (1968), *Minitingis* could be distinguished by the presence of seven cephalic spines, the occipital pair being short and obliquely elevated, and the rostrum reaching the second abdominal segment. The paranotal development and the abdominal groove were also mentioned as diagnostic features of the genus (Froeschner 1968). Both *M. minusculus* and *M. elsae* Froeschner, 1968 are from the West Indies, whereas the known species of *Zetekella* are from Panama and Brazil. This distribution represents different zoogeographical zones and, therefore, corroborates the hypothesis of two genera (Froeschner 1968).

In this paper, we describe a new species of *Zetekella* from Ecuador, report two new records for *Z. pulla* and a new country record for *Z. zeteki*, and re-evaluate the diagnostic characters of both genera.

Material & Methods

Material studied

The specimen here described was collected in a Berlese trap and had its abdomen removed for DNA extraction. The fixation method of the specimen is unknown, and it was preserved in 75% alcohol before the abdomen was removed and the specimen mounted. The specimen was point-mounted on the left side instead of the right side, to preserve two of its legs that accidentally had come in contact with the glue during the mounting process.

Holotypes of all species (except *M. minusculus*) were studied. For *M. minusculus*, a six-specimen series of paratypes was analyzed. All type material was examined at the National Museum of Natural History (USNM), in Washington, D.C., USA. A total of 15 specimens of *Z. pulla* from the Museu de Zoologia da Universidade de São Paulo, Brazil, was also studied. The remaining specimens are housed in the first author's personal collection.

Species descriptions

Measurements of the holotype were taken from photos using ImageJ and are given in millimeters. The terminology follows the specialized literature (Drake and Davis 1960, Drake and Ruhoff 1965). The taxonomic act here treated was registered in Zoobank (Pyle and Michel 2008).

Images

Photos were taken with a camera attached to a stereoscope and treated in GIMP. Plates were composed in Inkscape. The holotype photos of *Z. pulla*, *Z. zeteki* and *M. minusculus* were kindly provided by Thomas Henry.

Keys

The keys to *Minitingis* and *Zetekella* species provided by Froeschner (1996) were merged, adapted and updated to include new species and new findings.

Occurrence data

Geographic coordinates, when not available on the specimen labels, were obtained using Google Earth. The map was built using SimpleMappr (Shorthouse 2010). This map includes a layer with the Biodiversity Hotspots (*sensu* Conservation International; Mittermeier *et al.* 2004). Additionally, a spreadsheet containing occurrence data extracted from specimen labels was made available at Zenodo; the spreadsheet is organized alphabetically by species and then by the specimen's unique identifiers, when available.

Results

Zetekella henryi sp. n. (Figs 1a, 2a)

Material examined

Holotype: ECUADOR, Orellana: Yasuni Research Station, 228m, 0.67°S 76.40°W, 1-5 Dec 2009, D. Forero, EC09_L5, Berlese. MGPhD-E369. Male, Brachypterous (MPUJ).

Description

Body oval; mostly dark brown, or blackish; collar, paranota and lateral edge of costal area and hemelytral membrane white; tip of cephalic spines, scape and pedicel light brown (basi- and distiflagellomere missing); occipital spines lighter in color. Head with numerous, small, curved hairs and seven spines: clypeal pair non-erect; jugal spine slightly erect; frontal pair divergent; occipital pair short, strongly divergent; frontal and occipital pairs erect. Antenniferous processes spine-like, projected forward, subequal to scape in size. Scape slightly longer than pedicel, basi- and distiflagellomere missing. Interocular distance almost three times width of eye. Rostrum light brown, surpassing posterior margin of metanotum. Bucculae white, areolate; open in front, with an acutely projected antero-inferior edge; widely open posteriorly, width same as anterior region. Pronotum mostly flat, posterior projection absent, leaving small portion of scutellum exposed. Median carinae whitish, uniseriate, composed of small cells, extending throughout pronotum. Collar biseriate and slightly elevated. Paranota slightly reflexed, broad, with four cells at widest part; anterior edge not reaching eyes. Sternal membranes whitish, areolate, uniseriate, and concave. Hemelytra ovate, inner border conspicuously concave posteriorly; clavus large, 2-seriate at widest part, inner vein straight, outer edge convex; discoidal area biseriate; cubitus whitish posteriorly after R+M junction; radius-media (R+M) white for most of length, raised, stout; subcostal area mostly 3-seriate, 4 rows of areolae at widest part; costal area wide, with as many as six rows of areolae, widening posteriorly; membrane shortened (specimen brachypterous); hypocosta dark brown, areolate anteriorly, but light brown, rim-like for most of length, ending at membrane. Scent-gland opening round, auricular-like, dark. Legs light brown, coxae and trochanters stout; longer, spine-like setae at posterior edge of tibiae; second tarsi long and slender. Claws long, slender, well developed. Pygophore conspicuously narrower than abdomen; dorsal rim strongly curved, almost sinuous, forming small depressions laterally and dorsally. Paramere stout at base, abruptly but consistently narrowing to very slender tip, pronounced elbow at base.

Measurements

Body length, 2.01; body width, 1.19; head length, 0.39; head width, 0.31; interocular width, 0.18; pronotum length, 0.35; pronotum width, 0.86; scape length, 0.06; pedicel length, 0.05.

Remarks

Considering the three *Zetekella* species known thus far, *Z. henryi* sp. n. is more morphologically similar to *Z. zeteki* because of the broader paranota and hemelytra, and the long clypeal, jugal and frontal cephalic spines. It differs from *Z. zeteki* by the thinner cephalic spines, the anterior edge of paranota not reaching the eyes, the narrower discoidal and subcostal area, and by its color pattern.

Etymology

This species is named after the outstanding heteropterist and dear friend Thomas Henry, on occasion of his 70th birthday and his remarkable career and countless contributions to the study of Heteroptera.

Key to Zetekella and Minitingis

1. Rostrum conspicuously surpassing posterior edge of metathorax, reaching second or third abdominal segment, abdominal groove present 2

1'. Rostrum surpassing posterior edge of metathorax, or not; not reaching second abdominal segment, abdominal groove absent 3

2. Costal area with alternate, conspicuous black and white quadrate marks, and 4 rows of areolae .....***M. elsae*** (Fig. 1f)

2'. Costal area without alternate black and white marks, and with 2 rows of areolae ....***M. minusculus*** (Figs 1e, 2b, 2c, 3)

3. Paranota wide, with 4 to 5 rows of cells; costal area with at least 4 rows of cells.....4

3’. Paranota narrow, about half as wide as head, with 2 rows and a few cells irregularly placed; costal area with 2 rows of cells..... ***Z. pulla*** (Figs 1b, 1c)

4. Body brownish, anterior edge of paranota reaching eyes, discoidal area mostly 3-seriate; subcostal mostly 4-seriate .....***Z. zeteki*** (Fig. 1d)

4’. Body dark brown or blackish, with collar, paranota, radius-media and lateral part of costal area and elytral membrane white, discoidal area mostly biseriate, subcostal irregularly quadriseriate ..... ***Z. henryi* sp. n.** (Figs 1a, 2a)

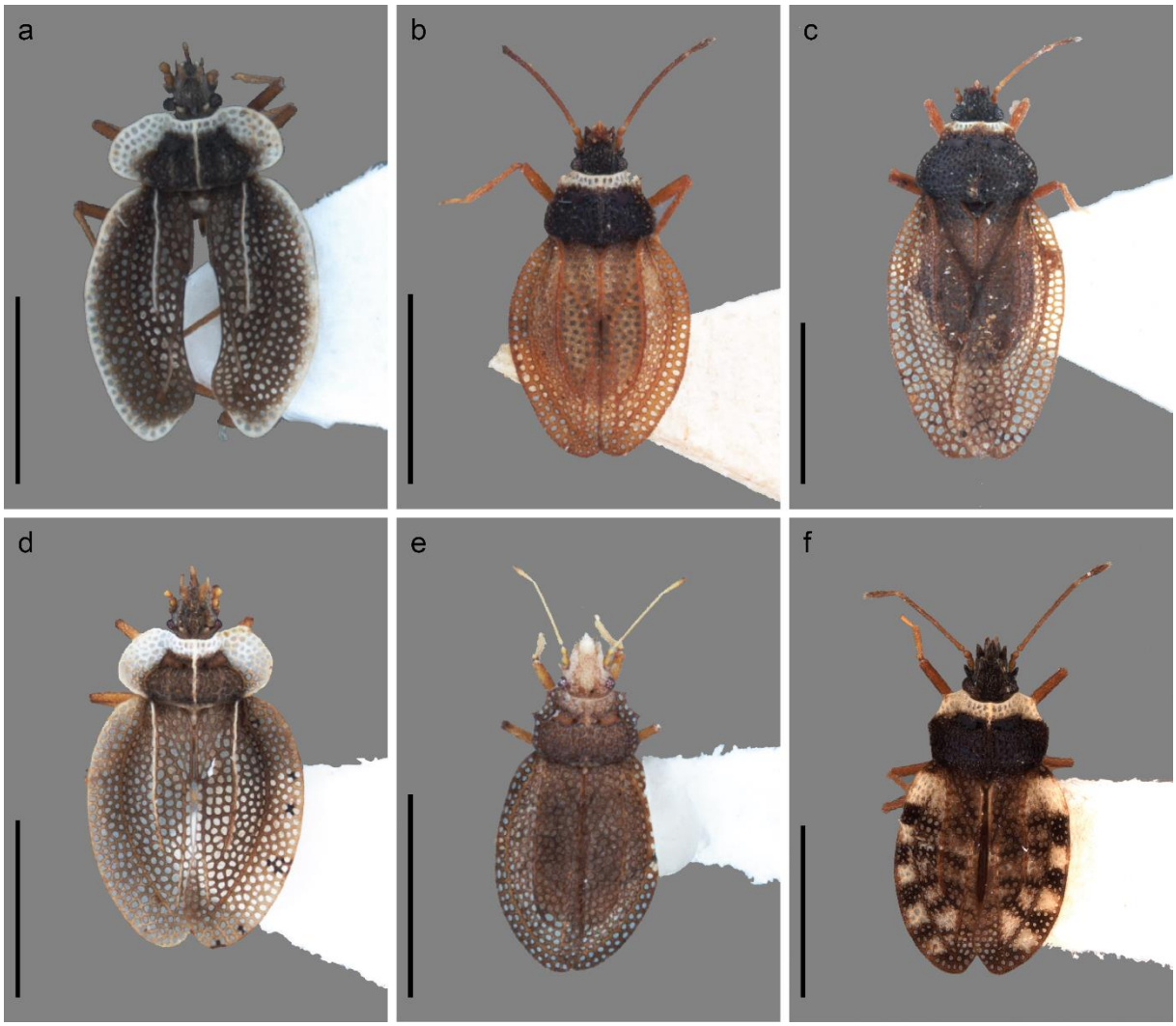

Figure 1. Dorsal habitus of *Zetekella* and *Minitingis* species. a) *Zetekella henryi* sp. n.; b) *Z. pulla*, brachypterous specimen; c) *Z. pulla*, macropterous specimen; d) *Z. zeteki*; e) *Minitingis minusculus*; f) *Minitingis elsae*. Scale bar: 1 mm.

New records (Fig. 4)

Zetekella pulla

BRAZIL. Santa Catarina: Ibicaré, 27º09, 51º18, 600m, F. Plaumann, Set. 1960. DZUP 387511-387515. **New Record**.

BRAZIL. São Paulo: Barueri, 23/VII/1967, K. Lenko - col. **New State Record**.

Zetekella zeteki

COSTA RICA: Heredia: La Selva Biological Station, nr Puerto Viejo, clearing, 59m, 10.426946°N 84.001449°W, 9-15 Aug 2010, OTS Heteroptera course [Berlese]. MGPhD-E290. **New Country Record** (Fig. 1d).

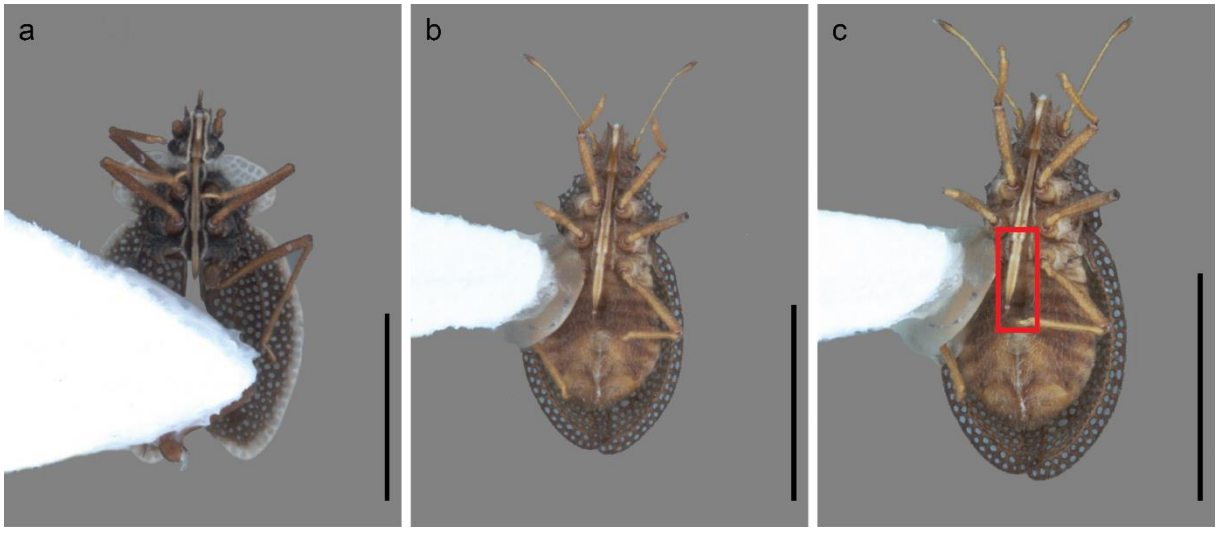

Figure 2. Rostral reach of *Zetekella* and *Minitingis* species. a) *Z. henryi henryi* sp. n.; b) *M. minusculus;* c) *M. minusculus* abdominal groove highlighted with a red square. Scale bar: 1 mm.

Data Resources

- SimpleMappr: http://www.simplemappr.net/map/8595
    - KML: http://www.simplemappr.net/map/8595.kml

- Zoobank: *Zetekella henryi* n. sp.: urn:lsid:zoobank.org:pub:9480B3E7-E726-4718-8EBF-69C58A867887.
- Zenodo DOI: 10.5281/zenodo.1450725.

Discussion

Zetekella henryi sp. n. is described based on morphological differences in characters that have been commonly used to delimit species within Tingidae. The new species resembles *Z. zeteki*, but differs from it by the color pattern, paranota, and discoidal and subcostal areas of the hemelytra. Additionally, the shorter rostrum and the shape of the scent-gland allies these two species with *Z. pulla*. In addition to the description of a new species of *Zetekella*, a macropterous specimen of *Z. pulla* was found and is illustrated. All characters, except the hemelytral membrane, remain virtually the same between the macropterous and brachypterous specimens. Only brachypterous specimens previously have been known for species of *Zetekella* and *Minitingis*. We do not agree with the terminology typically used in the specialized literature to differentiate these two wing forms, but we reserve this subject for a more comprehensive, and illustrated, treatment in a future contribution.

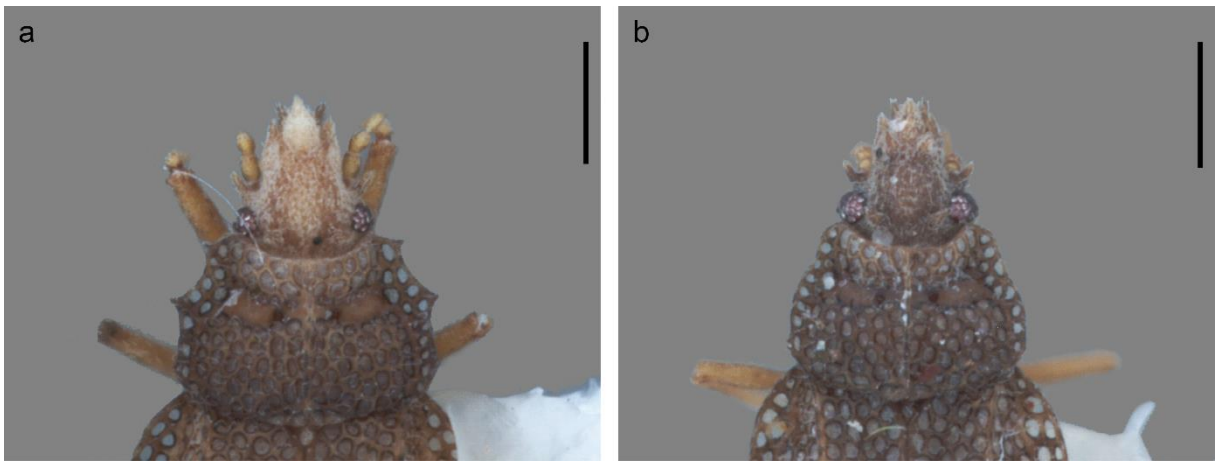

Figure 3. Variation observed in paranota of paratypes of *Minitingis minusculus*. Scale bar = 0.25 mm.

Froeschner (1968) noted that only *Minitingis* and *Gonycentrum* Bergroth have seven cephalic spines in Phatnomatini, assuming that *Zetekella* has only five. Drake (1944), however, in describing the genus and *Z. zeteki*, already observed that "there are indications of a pair of spines on the head behind the eyes and just in front of the collar" and that "as these are very

much atrophied, they are not mentioned in the generic description." Because the type specimen housed at the USNH is missing the head, this statement could not be verified. This feature, however, could be seen in the voucher specimen for the new record. Moreover, these spines were also observed in the new species. Yet, the mistake was perpetuated in the identification keys of Froeschner (1996). Froeschner (1968) also delimited and revalidated *Minitingis* on the basis of the acute processes of the paranota, which, however, can vary (Barber 1954).

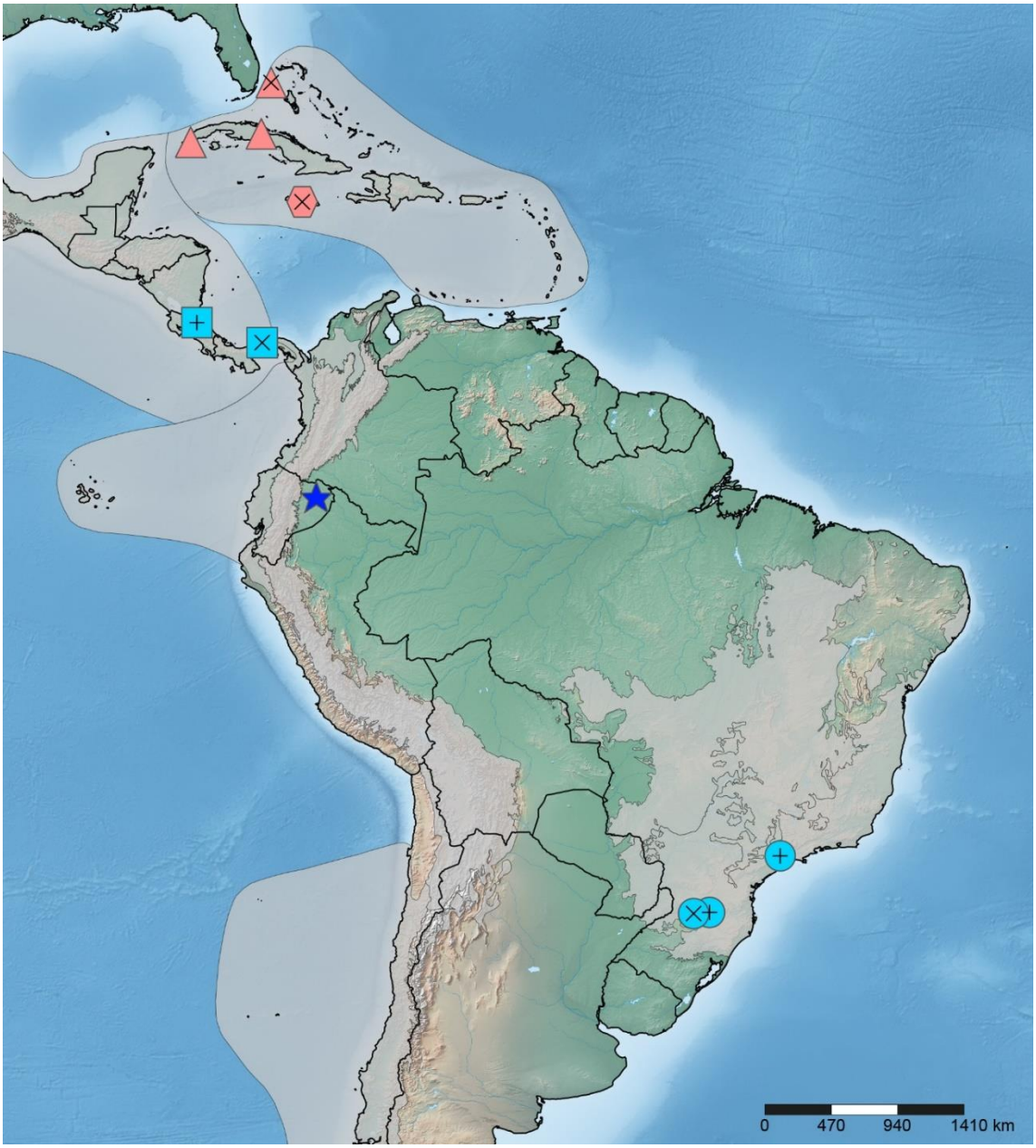

Figure 4. Distributional records for species of *Zetekella* and *Minitingis.* Blue icons = *Zetekella* species; square, circle and star = *Z. zeteki*, *Z. pulla* and *Z. henryi* sp. n. respectively; red icons = *Minitingis* records; triangle = *M. minisculus* and hexagon = *M. elsae*. Internal crosses = holotype localities; internal plus signs = new records.

In addition to cephalic spines and pronotal processes, Froeschner (1968) used rostrum length and presence of an abdominal groove as characters that validate the genus *Minitingis*. These characters were not possible to observe in the holotype (and single known specimen) of *M. elsae* due to the way the specimen is mounted, but they could be seen in all specimens of *M. minusculus* studied. We agree with Froeschner (1968) in regarding these two characters as reliable for distinguishing *Minitingis* from *Zetekella*. Froeschner's (1968) comments on the zoogeographicl significance of the distributional records of both genera remain relevant following our description of a new species of *Zetekella* and report of new distribution records for *Z. pulla* and *Z. zeteki*.

Therefore, we still consider *Minitingis* a valid genus, but we expanded the diagnosis of *Zetekella* to include the occipital cephalic spines and removed the acute processes on the paranota as a reliable character for delimiting *Minitingis*.

Acknowledgments

We thank Thomas Henry for providing the holotype and photos, which enhanced this contribution in his honor. We also thank the Conselho Nacional de Pesquisa e Desenvolvimento (CNPq, Brazil) and the Smithsonian Institution for funding the first author's studies.

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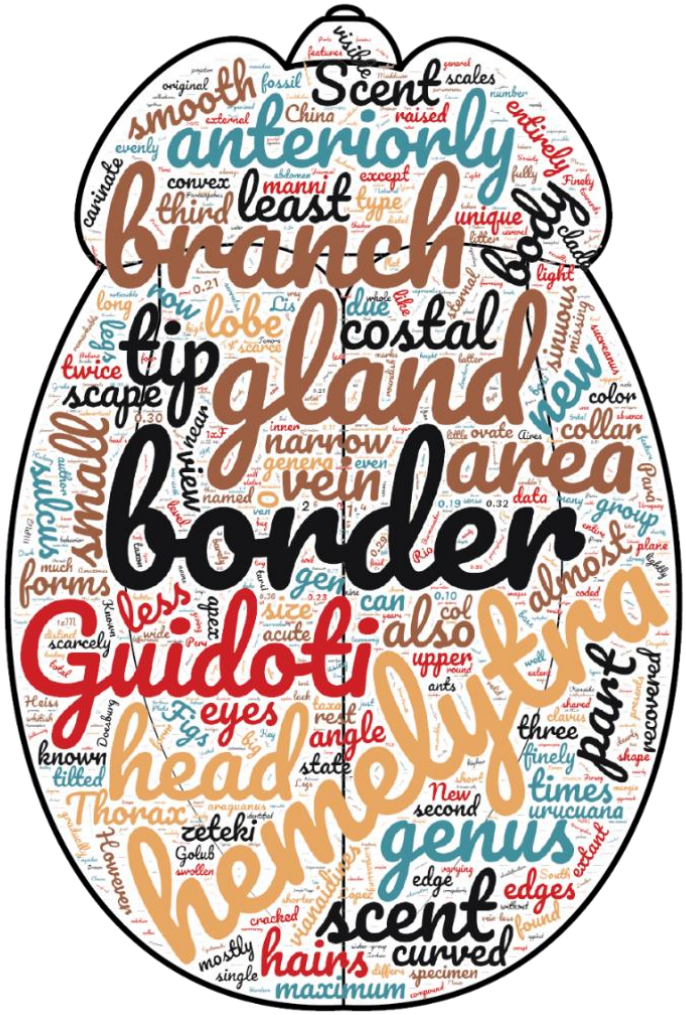
* formatted according to the *Zoological Journal of the Linnean Society*

Chapter IV

Phylogenetic analysis and revision of the strangest lace bug subfamily Vianaidinae (Heteroptera, Tingidae), with the description of nine species and a new genus



Schematic drawing based on *Thaumamannia vanderdrifti*.

Chapter IV – Phylogenetic analysis and revision of the strangest lace bug subfamily Vianaidinae (Heteroptera, Tingidae), with the description of nine species and a new genus

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Abstract

In this study we present a taxonomic review of a rarely collected subfamily of lace bugs (Heteroptera, Tingidae, Vianaidinae) including the description of nine new species and one genus and a phylogenetic analysis targeting its internal relationships. *Anommatocoris araguanus* sp. n., *A. knudsonii* sp. n., *A. schuhii* sp. n., *A. serratus* sp. n., *A. sucreanus* sp. n., *Thaumamannia insolita* sp. n. and *T. urucuana* sp. n. were proposed, in addition to the new genus *Henryianaida* gen. n. and its two macropterous species, *H. colombiensis* sp. n. and *H. machupicchuensis* sp. n. The monophyly of all the vianaidine genera was recovered and their synapomorphies are highlighted. Comments on the fossil forms and insights on the future of Vianaidinae taxonomy and systematics is also included.

Keywords. Cladistics, Coleopteroid, Macropterous, Neotropical, Taxonomy.

Introduction

Vianaidinae (Heteroptera, Tingidae) is a small group of often highly modified and specialized bugs endemic from South America (Drake & Davis, 1960; Schuh et al., 2006; Guidoti & Montemayor, 2016). The first described genus was *Anommatocoris* China, to accommodate one single species, *A. minutissimus* China, 1945. The author originally placed the genus in Oxycareninae (Pentatomomorpha, Lygaeoidea) mostly based on the habitus, similar to some aberrant lygaeids (China, 1945). Ten years later, *Vianaida coleoptera* Kormilev, 1955 was described in a new family, Vianaididae, and placed in Cimicomorpha as a closely-related taxon to Tingidae. Kormilev (1955) placed Vianaididae among cimicomorphans and also recognized the similarity between *Anommatocoris* and *Vianaida*, suggesting that both genera belonged to the newly described family Vianaididae, but he failed to identify both genera as synonymous. Only after Drake & Davis (1960) these two genera were considered to be the same, remaining Vianaididae as the valid family-group name, and *Anommatocoris* as the valid genus name and composed by the two described species, *A. minutissimus* and *A. coleopteratus* (Kormilev, 1955).

The group is currently composed by ten species, nine extant and one fossil (Schuh *et al.*, 2006; Guidoti & Montemayor, 2016). From these, six species are only known from coleopteroid forms: *Anommatocoris coibensis* López *et al.*, 2016, *A. coleopteratus*, *A. minutissmus*, *A. zeteki* Drake & Froeschner, 1962, *Thaumamannia manni* Drake & Davis, 1960, *T. vanderdrifti* van Doesburg, 1977. The three remaining extant species are remarkably different from the previously cited ones by presenting fully-developed hemelytra: *A. bolivianus* Schuh *et al.*, 2006, *Pterovianaida duckensis* Guidoti & Montemayor, 2016 and *P. melchiori* Montemayor & Carpintero, 2007. These macropterous forms were mentioned in the specialized literature 15 years before their first formal description (Schuh & Stys, 1991; Schuh & Slater, 1995; Schuh *et al.*, 2006). Before the description of the first macropterous Vianaidinae, two fossil taxa were proposed: *Vianagrama goldmani* Golub & Popov (2000), and *Vianathauma pericarti* Golub & Popov (2003). Both species were described from amber in the late Cretaceous of New Jersey presenting remarkably different features, and both were placed in Vianaidinae by their original authors (Golub & Popov, 2000; 2003). However, the placement of the latter was disputed by Schuh *et al.* (2006). Two other interesting fossils have been described from the Upper Cretaceous Burmese amber: *Burmacader multivenosus* Heiss & Guilbert, 2013 and *B. lativentris* Heiss & Guilbert, 2018. Despite some strong similarities with

the known vianaidines, Heiss & Guilbert (2013; 2018) only tentatively placed the *Burmacader* Heiss & Guilbert species in between Vianaidinae and the remaining tingids.

Vianaidines are rare and usually absent from scientific collections. To this day, only two species were collected after their original descriptions: *A. coleopteratus* (described from Argentina, reported from Uruguay by San Martin, 1966, and collected in Argentina again by Diego Carpintero, pers. observation), and *T. vanderdrifti* (described from Suriname, reported from Brazil by Guidoti *et al.*, 2014). This rarity also explains the lack of knowledge on their immatures, which are important for Tingidae systematics (Guilbert, 2004) and only described for *A. coleopteratus* (Kormilev, 1955) and *T. vanderdrifti* (fifth instar only, SEM images available on Guidoti *et al.*, 2014). The coleopteroid forms were frequently found on soil or even associated with ants or ants' nests (Drake & Davis, 1960; Drake & Ruhoff, 1965, Guidoti *et al.*, 2014; López *et al.*, 2016). This is the case of *A. coleopteratus*, which type series was collected in the nest of the leaf-cutting ant *Acromyrmex lundi* (Guérin-Méneville, 1838) (Hymenoptera, Formicidae) and apparently was later found associated with the fire ants *Solenopsis richteri* Forel, 1909 and *S. saevissima* (Smith, 1855) (Hymenoptera, Formicidae) (Wojcik, 1990). *Thaumamannia manni* was also found with ants, although, the ant species or the nature of this interaction wasn't cited (Drake & Davis, 1960). López *et al.* (2016) affirmed that *A. zeteki* was also reported associated with ants; however, this is not exactly what Drake & Froeschner (1960) meant and the term "myrmecophilous" in their paper was only implied as a generalization due to the general habitus of the specimens and not an affirmative regarding their ecological behavior. *Anommatocoris minutissimus* and *T. vanderdrifti* were found on soil and not associated with ants (China, 1945; van Doesburg, 1977), which was the case for *A. coibensis* as well (López *et al.*, 2016). *Anommatocoris bolivianus* was not found in soil but in understory vegetation (Schuh *et al.*, 2006;). All the *Pterovianaida* species, on the other hand, were collected on light traps indicating an active flight pattern, different from most tingids (Montemayor & Carpintero, 2007; Guidoti & Montemayor, 2016).

Kormilev (1955) placed Vianadidae as sister-group of Tingidae based on characters like the absence of ocelli, trichobotria, arolio and pseudoarolio; the number of visible sternites (seven); the presence of sternal laminae and the two-segmented tarsi. Drake & Davis (1960) despite the identification of unique characters among all cimicomorphans in this taxon, like the shape of the scent gland peritreme, considered Vianaididae as a subfamily of Tingidae. These authors argued that the unique features presented by the vianaidines were mostly due to their habitat and behavior and therefore not enough to warrant the status of a separate family due to

the character complex shared with Tingidae. Schuh *et al.* (2006) when addressing the relationships between Cantacaderinae + Tinginae, claim that "…elevation of ranks… obscures the sister-group relationships…" and "…and results in the undesirable recognition of taxa of equal rank on the basis of autapomorphies rather than the nesting of taxa on the basis of synapomorphies". Despite these arguments, both status have been observed in the specialized literature (Vianaididae: Lis, 1999; Golub, 2001; Montemayor & Carpintero, 2007; Vianaidinae: Drake & Davis, 1960; Drake & Ruhoff, 1965; Schuh & Stys, 1991; Schuh et al., 2006, 2009).

Schuh & Stys (1991) were the first ones to recover the monophyly of Vianaidinae + Tingidae *sensu stricto* (Cantacaderinae + Tinginae) within a phylogenetic framework, and Schuh *et al.* (2006) included the first macropterous specimens, *A. bolivianus*, in a phylogenetic analysis with similar scope. Other important phylogenetic works on Tingidae failed to include vianaidines (Guilbert, 2012; Guilbert *et al.*, 2014). The monophyletic status of Vianaidinae remains untested, although the set of autopomorphies shared between the species of the group is remarkable. Perhaps more importantly, its internal phylogenetic relationships also remain unclear, including the relationship of the known macropterous species with their coleopteroid congeners. Due to the rarity of this subfamily and the large and unheard amount of Vianaidinae specimens gathered through the years by the first author, we aim with this contribution to describe nine new species, including two macropterous forms and one new genus, accessing the internal phylogenetic relationships of the taxon in a morphology-only analysis, providing comments on potential paths and novelties for future contributions within this taxon.

Material & Methods

Phylogenetic analysis

A total of 32 morphological characters and 20 terminal taxa were included in this phylogenetic analysis. Since the goal of the analysis was to understand the phylogenetic relationships within Vianaidinae and not the monophyly of this subfamily, only two outgroups were included: *Cantacader quinquecostatus* (Fieber, 1844) and *Phatnoma marmorata* Champion, 1897, the root defined in *C. quinquecostatus*. Due to the aforementioned limitations, characters were based solely on external non-genital morphology. Only extant species were included in the analyses, also due to lack of access to the fossil material. Character statements followed Sereno

(2007), and the commented version of the character list is included (Appendix). The matrix was built in Mesquite (Maddison & Maddison, 2018), and is also included (Table 1)

.

Table 1. Character matrix with 32 characters and 20 terminals. Symbols: -, inapplicable; ?, missing data.

	1	2	3
	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1
Cantacader quinquecostatus	0 0 0 0 0 0 ? ? 1 0 1 0 0 1 0 – 0 0 0 0 0 – – – 0 0 0 1 3 0 0 0
Phatnoma marmorata	0 0 0 0 0 0 ? ? 1 0 1 0 0 1 0 – 0 0 0 0 1 – – – 0 0 0 1 3 0 0 0
Anommatocoris araguanus sp. n.	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 1 0 1 2 0 0 0 1 1 1 0 1 1 1 1
Anommatocoris bolivianus	? 0 0 1 1 1 ? 0 0 1 0 1 1 0 0 ? 1 0 0 ? 2 0 0 0 1 ? 1 0 1 1 1 1
Anommatocoris coibensis	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 0 0 1 2 0 0 1 1 0 1 0 1 1 1 1
Anommatocoris coleopteratus	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 0 1 1 0 0 2 1 0 0 1 1 1 0 1 1 1 1
Anommatocoris knudsonii sp. n.	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 0 1 1 0 1 2 0 0 0 1 1 1 0 1 1 1 1
Anommatocoris minutissimus	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 0 1 1 0 0 2 0 0 0 1 1 1 0 1 1 1 1
Anommatocoris schuhii sp. n.	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 0 0 0 2 0 0 1 1 0 1 0 1 1 1 1
Anommatocoris serratus sp. n.	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 1 0 1 2 0 0 0 1 1 1 0 1 1 1 1
Anommatocoris sucreanus sp. n.	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 1 0 0 2 0 0 0 1 1 1 0 1 1 1 1
Anommatocoris zeteki	0 0 0 1 1 1 2 0 0 1 0 1 1 0 0 1 1 0 0 1 2 0 0 1 1 0 1 0 1 1 1 1
Henryianaida colombiensis sp. n.	0 0 1 1 1 1 1 0 1 1 0 0 1 0 0 1 2 0 0 0 2 0 1 0 1 2 1 1 2 1 0 0
Henryianaida machupicchensis sp. n.	0 0 1 1 1 1 1 0 1 1 0 0 1 0 0 1 2 0 0 0 2 0 1 0 1 0 1 1 2 1 0 0
Pterovianaida duckensis	2 1 0 1 1 1 2 0 0 1 1 0 1 1 0 1 2 0 1 0 2 1 1 0 1 2 0 1 2 1 0 0
Pteorvianaida melchiori	2 ? 0 1 1 1 ? ? 0 1 1 0 1 1 0 1 2 0 1 0 2 1 1 ? 1 2 0 1 2 1 0 0
Thaumamannia insolita sp. n.	0 1 0 1 1 1 2 0 1 1 0 0 1 1 0 0 2 2 0 0 2 1 1 1 1 2 0 1 3 1 0 0
Thaumamannia manni	1 1 0 1 1 1 0 1 0 1 1 0 1 1 1 1 2 0 0 1 2 1 1 1 1 2 0 1 3 1 0 0
Thaumamannai urucuana sp. n.	1 1 0 1 1 1 0 1 1 1 1 0 1 1 1 0 2 2 0 0 2 1 1 1 1 2 0 1 3 1 0 0
Thaumamannia vanderdrifti	1 1 0 1 1 1 2 0 1 1 1 0 1 1 1 0 2 2 0 0 2 1 1 1 1 2 0 1 3 1 0 0

Non-applicable characters/states were represented by "-" and made up to 1.25% of the matrix, all of them distributed among the outgroups. Missing data was marked as "?", making only up to 2.19% of the matrix. Five characters were included from the specialized literature (Lis, 1999; Schuh *et al.*, 2006) while 27 were proposed as new based on personal observations and considering the constraint of the lack of accessibility to certain structures on the studied material. The parsimony analysis was conducted on TNT 1.5 (Goloboff & Catalano, 2016), using implicit enumeration due to the small number of terminal taxa which allows an exhaustive search for the most parsimonious trees (Goloboff *et al.*, 2008). All characters were equally weighted and multistate characters were considered non-additive, however, implied weighting

was also attempted (Mirande, 2009). Bremer was the support measure chosen and the equally parsimonious trees were visualized on Winclada (Nixon, 2002). The phylogenetic analysis is here presented before the taxonomic treatments since its results influenced nomenclatural acts and taxonomic decisions.

Taxonomic treatment

More than 60 specimens were studied, which represents almost 99% of the known collected material available in collections to this date. Taxonomic descriptions were made according to the terminology usually applied in recent Tingidae taxonomic descriptions and monographs, which follows, mainly, Drake & Davis (1960). Despite the strong evidence of the importance of genital characters on species delimitation within Tingidae (Lee, 1969; Lis, 2003), the species were delimited solely based on external non-genital characters, due to our lack of authorization to dissect most of species. Holotypes of *Anommatocoris coleopteratus*, *A. zeteki*, *Thaumamannia manni*, and *Pterovianaida melchiori* and *P. duckensis* were consulted. Paratypes of *A. coleopteratus*, *A. minutissimus*, *A. coibensis* and the allotypes of *A. coleopteratus* and *A. zeteki* were also studied. *Anommatocoris bolivianus* type material was reported as lost, and the type material of *T. vanderdrifti* were not available, hence, for these species, the original descriptions and their illustrations were the consulted sources. Types for the new taxa were selected accordingly to the following criteria: 1) preservation state; 2) mounting method (if glued ventrally, the ventral characters wouldn't be visible); 3) sex (traditionally, holotypes were assigned based on male specimens and the defunct term allotype referred usually to a female specimen). Taxa already described were redescribed in an attempted to standardize the terms applied for their descriptions and diagnosis. A unique identifier was assigned to each studied specimen, safe holotypes or allotypes of already described species, in a label as follows: [Guidoti PhD – MNHN 2014-18 – Vianaidinae #unique_number]. The dichotomous identification key was manually constructed after the study of all available material, including types, and their respective original descriptions.

Measurements

A total of 11 measurements were taken with an attached measurement reticle in an eyepiece of a Nikon SMZ645 stereomicroscope, and the results are presented in millimeters as: average

(type measurement; minimum – maximum in males; minimum – maximum in females). The average is always displayed in bold. If a measurement is not available (e.g., distiflagellomere in a species described from a singleton missing this antennae segment) it will simply be missing. If only one specimen of a given sex was available, only one value will be shown and if more than one measurement were taken but they were equal for a given sex, a n-dash will be placed but the value won't be repeated. For males, the characters "xM" was applied; for females, "xF". The following measurements were taken: BL, body length; BW, body width; HL, head length; HW, head width; ID, interocular distance; PL, pronotum length; PW, pronotum width; AS, scape; AP, pedicel; AB, basiflagellomere; AD, distiflagellomere.

Maps and Geographical Data

The geographic coordinates were taken from their label data using Google Earth. SimpleMappr (Shorthouse, 2010) was used to build the maps, which includes a layer with the Biodiversity Hotspots (*sensu* Conservation International — Mittermeier *et al.* 2004) and one with the countries' geopolitical borders. A table with all unique localities per species and their respective geographical coordinates is included (Table 2). The maps per genera is available at the following links:

- *Anommatocoris*: http://www.simplemappr.net/map/10433
- New genus: http://www.simplemappr.net/map/10418
- *Pterovianaida*: http://www.simplemappr.net/map/10198
- *Thaumamannia*: http://www.simplemappr.net/map/10197

Table 2. Geographical data of all extant Vianadinae species. Coordinates were obtained in Google Earth from label data. Identifiers are labels with unique numbers attached to every and each studied specimen, except type material of previously described species. The character "*" was used to indicate which types weren't analyzed for this current work.

Species	**Locality**	**Coordinates**	**Identifier**
Anommatocoris araguanus sp. n.	VENEZUELA: Aragua, Las Tejerias, 12 km N Tiara	10.256719, -67.16845	006-015
Anommatocoris bolivianus	BOLIVIA: La Paz, Chulumani, Apa-apa	-16.366665, -67.500001	Types*
Anommatocoris coibensis	PANAMA: Isla de Coiba, Parque Nacional de la Isla de Coiba	8.216185, -82.181372	061
Anommatocoris coleopteratus	ARGENTINA: Buenos Aires, Tigre, Rio Luján	-34.425087, -58.579658	Types; 039-048
	ARGENTINA: Buenos Aires, Res. Punta Lara	-34.792499, -58.007866	023-035
	URUGUAY: Rocha, 18 de Julio, 4 Km North in Ruta 19	-33.686443, -53.605260	San Martin, 1966
Anommatocoris knudsonii sp. n.	VENEZUELA: Merida, Campo Elias, La Azulita	8.71271, -71.443229	018-021
Anommatocoris minutissimus	TRINIDAD: Saint Augustine, ~ 2 miles N	10.669665, -61.406023	037-038
Anommatocoris schuhii sp. n.	ECUADOR: Tungurahua, El Baños, 12.2 km, 5000 ft	-1.392834, -78.426876	016-017
Anommatocoris serratus sp. n.	COLOMBIA: Boyaca, Santa Maria, Hyca Quye	4.857988, -73.262355	022
Anommatocoris sucreanus sp. n.	VENEZUELA: Sucre, El Pilar, 7 km S.	10.498536, -63.160901	001-005
Anommatocoris zeteki	PANAMA: Barro Colorado Island, Panama Canal Zone	9.152102, -79.84648	Holotype; 036
Henryianaida colombiensis sp. n.	COLOMBIA: Caldas, Villamara	5.042567, -75.514769	059
Henryianaida machupicchensis sp. n.	PERU: Urubamba, Putucusi Trail (Machu Pichu)	-13.155556, -72.536111	058
Pterovianaida duckensis	BRAZIL: Amazonas, Manaus, Res. Ducke, Km 26, AM-010	-3.003803, -59.918714	Holotype
Pterovianaida melchiori	PERU: Ucayali	-11.636944, -73.118889	Holotype
Thaumamannia insolita sp. n.	BRAZIL: Pará	-2.301928, -54.55586	057
Thaumamannia manni	BOLIVIA: Santa Cruz	-17.814582, -63.156085	Holotype
Thaumamannia urucuana sp. n.	AMAZONAS: Petrobras-Urucu	-4.868774, -65.300289	056
	BRAZIL: Pará	-2.301928, -54.55586	055
Thaumamannia vanderdrifti	SURINAME: Saramacca, Dirkshoop Experimental Garden	5.783000, -55.483000	Types*
	BRAZIL: Pará, Parauapebas	-6.068203, -49.90417	049-052
	BRAZIL: Pará, Canaã dos Carajás	-6.532091, -49.851217	053-054

Collections providing specimens

AMNH, American Museum of Natural History (New York, US);

INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil);

MLP, Museo de La Plata (La Plata, Argentina);

MNHN, Museum National d'Histoire Naturelle (Paris, France);

MNRJ, Museu Nacional (Rio de Janeiro, Brazil);

MPEG, Museu Paraense Emilio Goeldi (Belém, Brazil);

MPUJ, Museo Javeriano de História Natural, Pontifícia Unversidad Javeriana (Bogotá, Colombia);

USNM, National Museum of Natural History (NMNH), Smithsonian Institution (Washington D.C., US);

UCDC, University of California (Davis, US), and;

GC, Guidoti's Collection, housed and available at NMNH.

Images

Optical images were obtained at NMNH using an EntoVision Imaging Suite with a JAI Technologies (AT-200GE) digital camera mounted to a Leica Z16 zoom lens via a Leica z-step microscope stand and multi-focus images were mounted using Cartograph 8.0.6 (Microvision Instruments, France) software. Scanning Electron Microscope was conducted in high vacuum conditions and with uncoated specimens in two different systems: the Hitachi Tabletop Microscope TM3030Plus, and the Zeiss EVO MA15. Images were edited on Adobe Photoshop CS5.1 and all the plates were composed with Adobe Illustrator CS5.1, including the map plate and the final phylogenetic tree.

Results

Phylogenetics

The phylogenetic analysis resulted in six equally parsimonious trees of 59 steps (CI = 0.66; RI = 0.87), and the consensus (Fig. 1; 62 steps; CI = 0.62; RI = 0.85) presented one polytomy within the *Anommatocoris* genus, and only four characters are not shown in the consensus tree due to ambiguity: characters 16 (paranota, development), 19 (paranota, posterior region), 25 (hemelytra, anterior region, margins) and 28 (hemelytra, hypocosta, punctuations). The highest observed Bremer support value was in the *Anommatocoris* clade (Br = 7), followed by the *Pterovianaida* and *Henryianaida* + *Anommatocoris* clades (Br = 3). All the other clades had their Bremer support values estimated as Br <= 2. Tests with implied weighting demonstrated to be non-effective in this analysis, probably due to the small size of the matrix and the relative low levels of homoplasy (data not shown).

Two of the new species were found to be monophyletic in *Thaumamannia*, five in *Anommatocoris* and two species formed a clade, sister-group to all *Anommatocoris* species, supported by two synapomorphies and hence proposed here as a new genus.

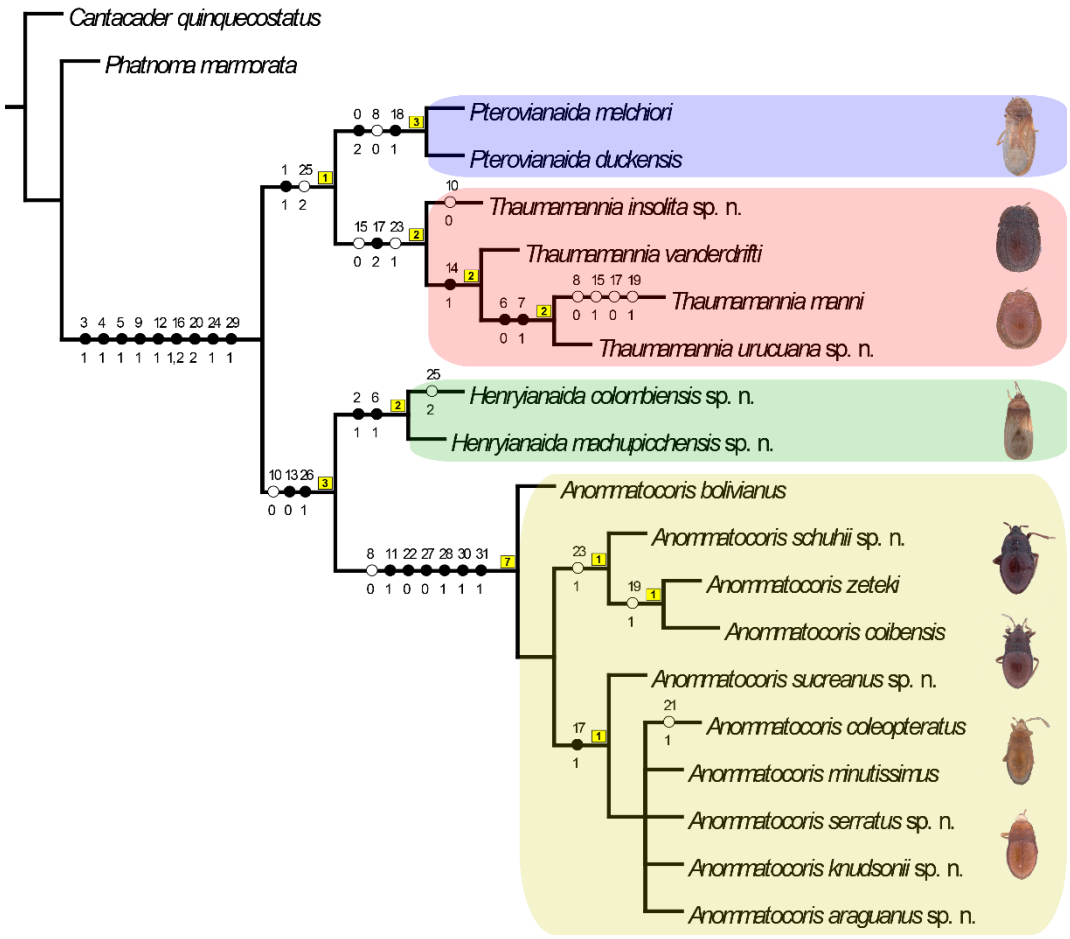

Figure 1. Consensus tree (length = 62 steps; consistency index = 0.62; retention index = 0.85) estimated from 6 equally parsimonious trees (length = 59); unambiguous transformations are the only ones shown. Bremer support indicated in yellow boxes near their respective clades.

Clade Pterovianaida + Thaumamannia

The clade *Pterovianaida* + *Thaumamannia* is supported by one synapomorphy, head position inclined downwards (char 1, state 1 or 1-1 – Fig. 2B), and one homoplastic synapomorphy, the large scales on the anterior region of the hemelytral margins (25-2).

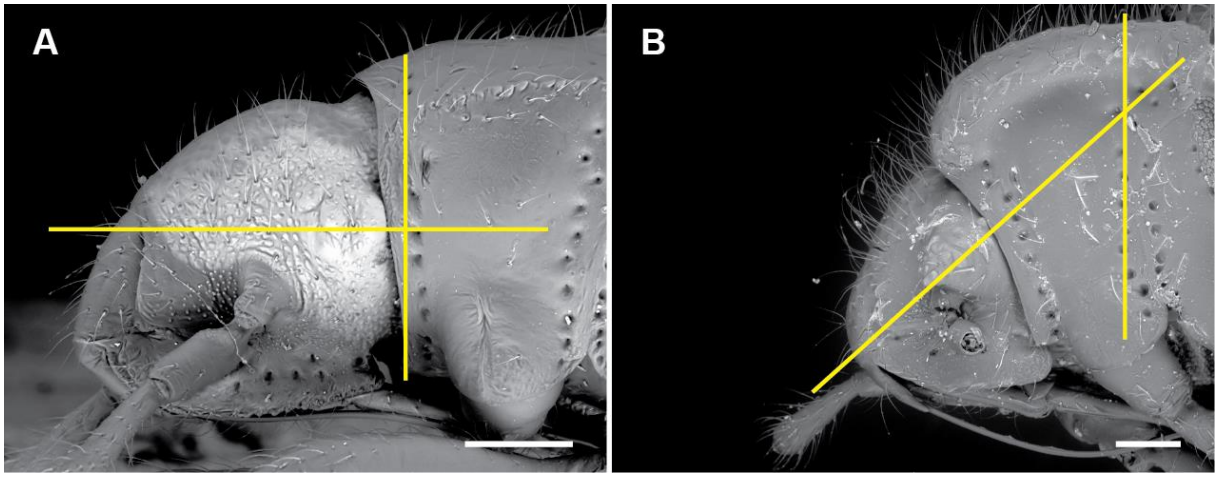

Figure 2. Character 1, head position: A) state 0, straight, as in *Anommatocoris coleopteratus*; B) state 1, declined, considering sagittal plane, as in *Thaumamannia manni*. Character states shown in yellow. Scale bars: 0.1 mm.

Internally to this clade, the *Pterovianaida* genus was recovered monophyletic and is supported by two synapomorphies and one homoplastic synapomorphy: abundant head setae (0-2 – Fig. 3C), presence of a paranota constriction (18-1 – Fig. 4B) and frons at same height as clypeus (8-0), respectively.

Figure 3. Character 0, abundance of head setae: A) state 0, scarce, as in *Anommatocoris coibensis*; B) state 1, moderately abundant, as in *Thaumamannia manni*; C) state 2, abundant, as in *Pterovianaida duckensis*. Character states indicated (arrows) in yellow. Scale bars: 0.1 mm.

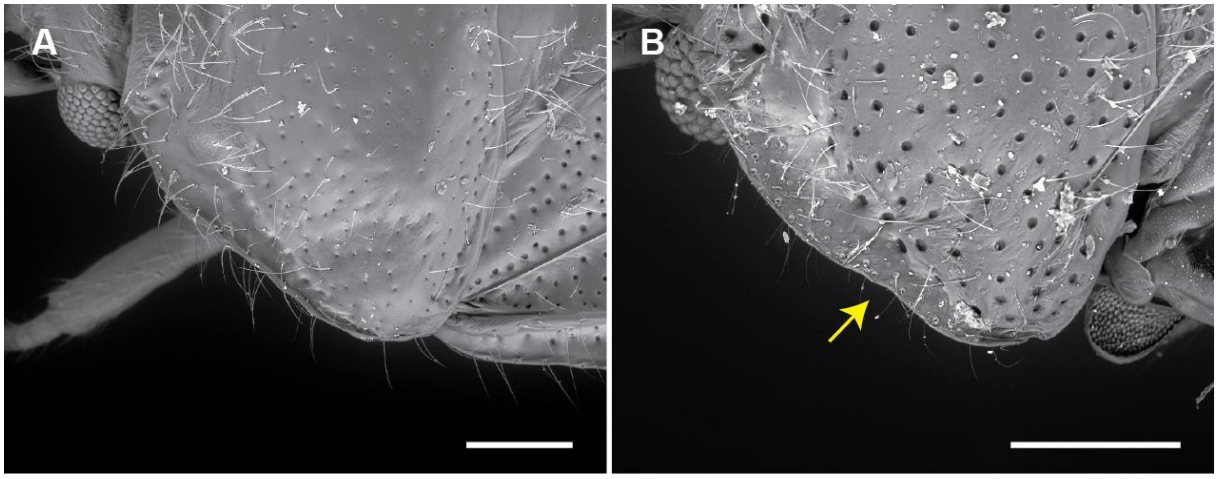

Figure 4. Character 18, lateral constriction of paranota: A) state 0, absent, as in *Henryianaida colombiensis* sp. n.; B) state 1, present, as in *Pterovianaida duckensis*. Character state one indicated in yellow (arrow). Scale bars: 0.2 mm.

Thaumamannia, including the two new species, was also found to be monophyletic, supported by one synapomorphy and two homoplastic synapomorphies as well (presence of large scales on paranota borders, 17-2 – Fig. 5C; scutellum narrower than half of the maximal width of the head, 15-0 and scent gland peritreme with a shorter posterior branch than the upper part of the anterior branch, 23-1, as the homoplastic synapomorphies).

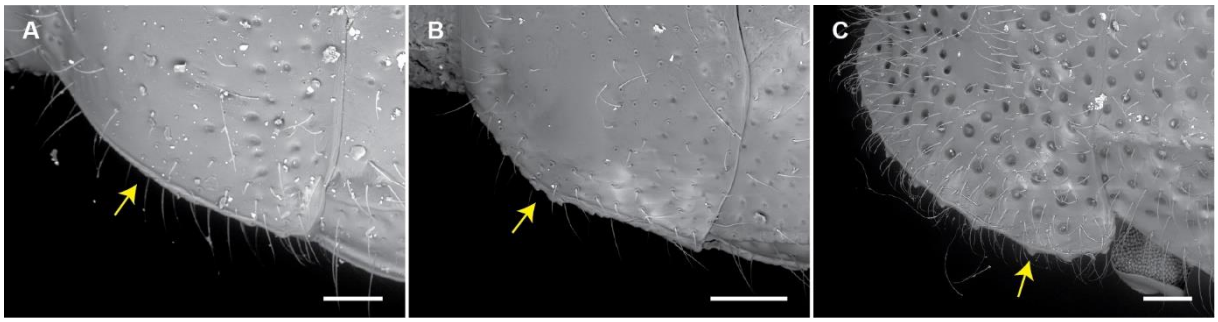

Figure 5. Character 17, paranota borders: A) state 0, smooth, scale-less, as in *Anommatocoris schuhii* sp. n.; B) state 1, with small scales, serrate-like, as in *A. serratus* sp. n.; C) state 2, bearing large scales, as in *Thaumamannia vanderdrifti*. Character states indicated in yellow (arrows). Scale bars: 0.1 mm.

Thaumamannia insolita sp. n. is the sister group of all of its congeners, which clade is supported by only one synapomorphy: pronotum more than two times wider than long (14-1 – Fig. 6B). *Thaumamannia urucuana* sp. n. and *T.* manni was recovered as one clade (two synapomorphies: posterior region of the bucculae round, 6-0 – Fig. 7A; and posterior region of the bucculae wider than anterior half, 7-1), sister-group of *T. vanderdrifti*.

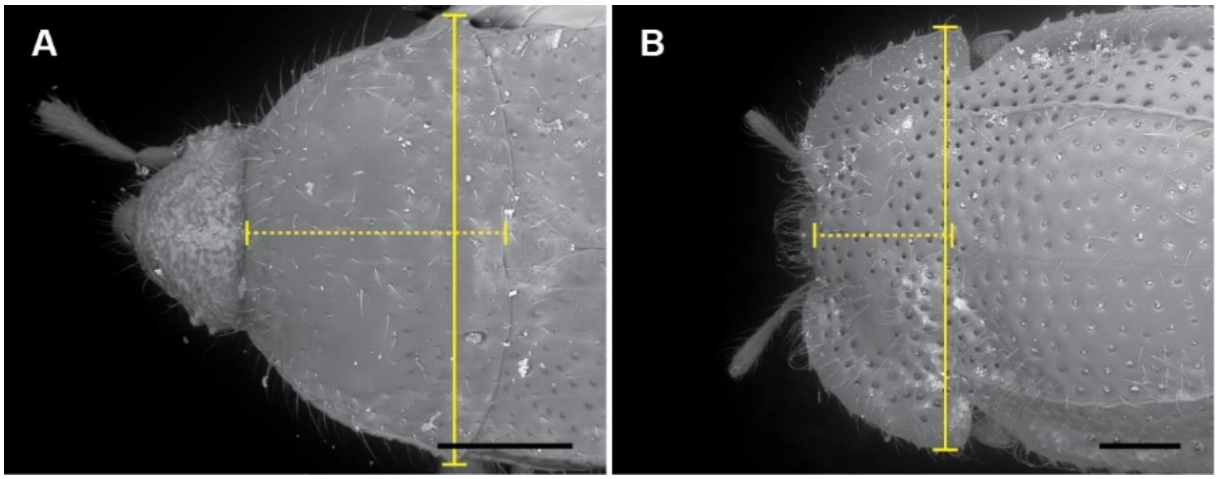

Figure 6. Character 14, pronotum width: A) state 0, approximately two or less times wider than long, as in *Anommatocoris knudsonii* sp. n.; B) state 1, more than two times wider than long, as in *Thaumamannia urucuana* sp. n. Character states shown in yellow. Scale bars: 0.2 mm.

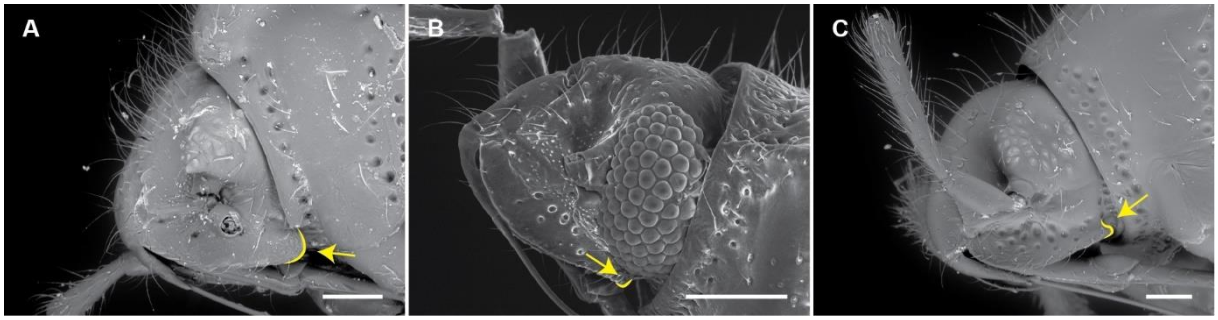

Figure 7. Character 6, form of bucculae's posterior end: A) state 0, rounded, as in *Thaumamannia manni*; B) state 1, straight, as in *Henryianaida machupicchuensis* sp. n.; C) state 2, concave, as in *Anommatocoris schuhii* sp. n. Character states outlined and indicated (arrows) in yellow. Scale bars: 0.1 mm.

Clade Henryianaida gen. n. + Anommatocoris

The clade composed by the *Henryianaida* gen. n. + *Anommatocoris* is supported by one synapomorphy and one homoplastic synapomorphy (pronotum finely punctuate, 13-0 – Fig. 8A; collar not projected towards the head, 10-0, respectively). The new genus is supported as a monophyletic taxon by two synapomorphies: mandibular plates laterally compressed (2-1 – Fig. 9B) and a straight margin on the posterior region of bucculae (6-1 – Fig. 7B).

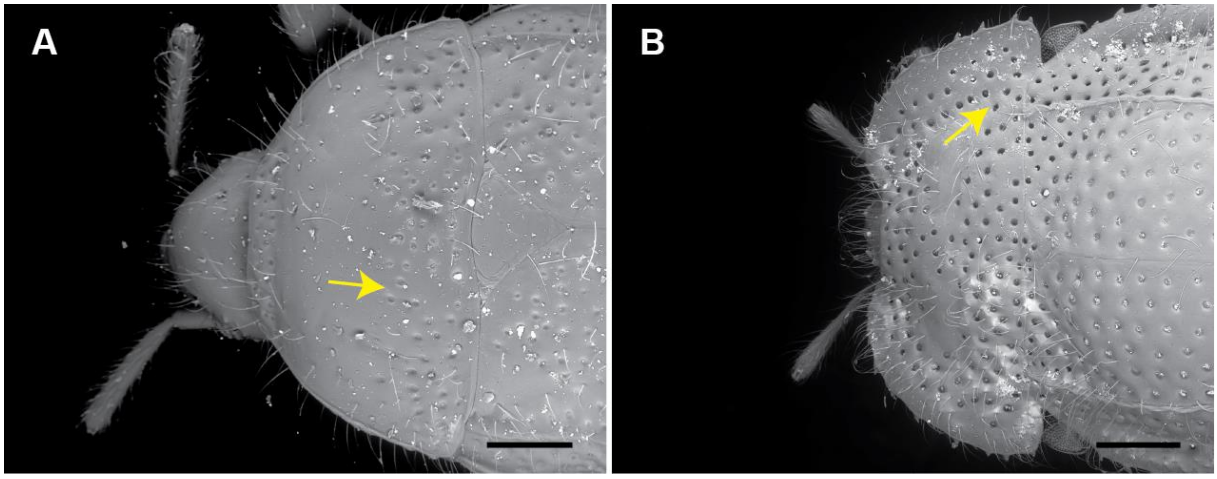

Figure 8. Character 13, punctuations on pronotum: A) state 0, fine, as in *Anommatocoris schuhii* sp. n.; B) state 1, coarse, as in *Thaumamannia urucuana* sp. n. Character states indicated (arrows) in yellow. Scale bars: 0.2 mm.

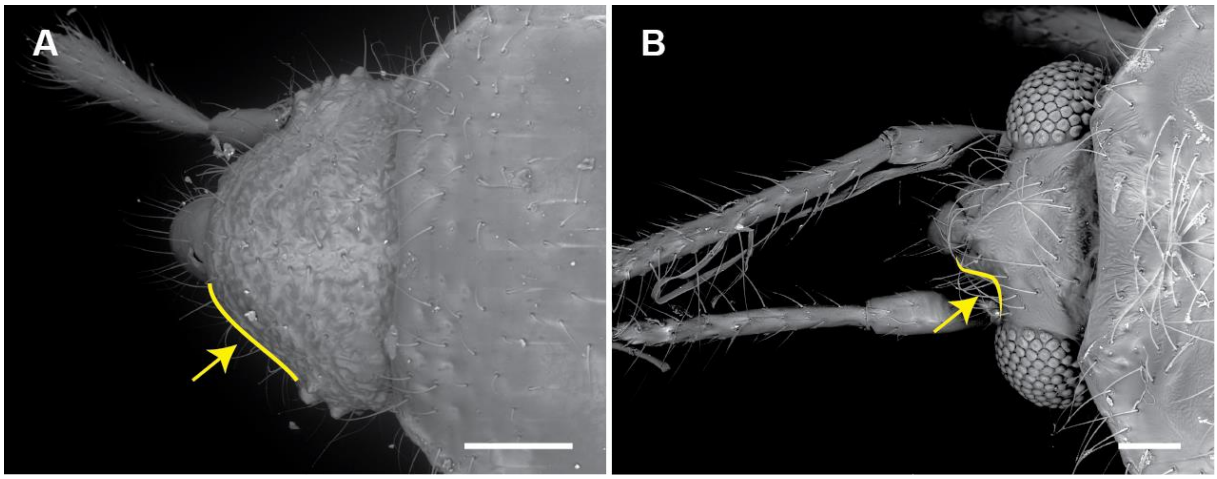

Figure 9. Character 2, mandibular plates: A) state 0, not compressed, as in *Anommatocoris knudsonii* sp. n.; B) state 1, laterally compressed, forming an acute angle with the eyes, as in *Henryianaida colombiensis* sp. n. Character states outlined and indicated (arrows) in yellow. Scale bars: 0.1 mm.

The *Anommatocoris* was recovered with the most number of synapomorphies, seven, in total: a flat posterior region of pronotum (11-1 – Fig. 10B), anterior branch of the scent gland peritreme almost perpendicular to sagittal body plane (22-0), the presence of a constriction on the anterior region of hemelytra (26-1 – Fig. 11B), hypocosta narrow (27-0 – Fig. 12A) and, smooth (28-1 – Fig. 13B), costal area thickened and narrow (30-1 – Fig. 14B), and subcostal area subvertical (31-1 – Fig. 15B).

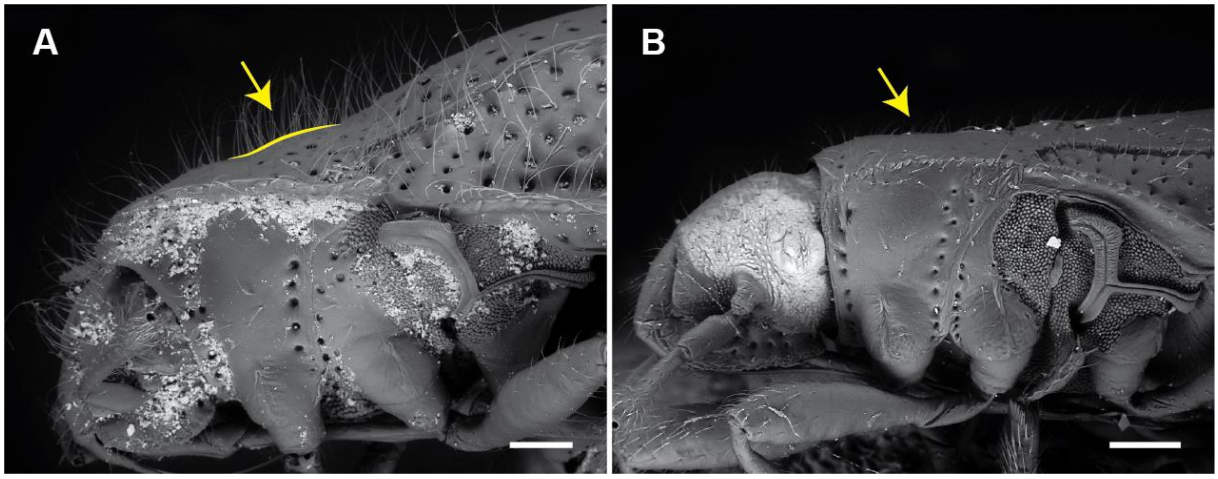

Figure 10. Character 11, pronotum posterior lobe: A) state 0, posterior lobe higher than anterior lobe, as in *Thaumamannia urucuana* sp. n.; B) pronotum flat, as in *Anommatocoris coleopteratus*. Character state zero outlined; both indicated (arrow) in yellow. Scale bars: 0.1 mm.

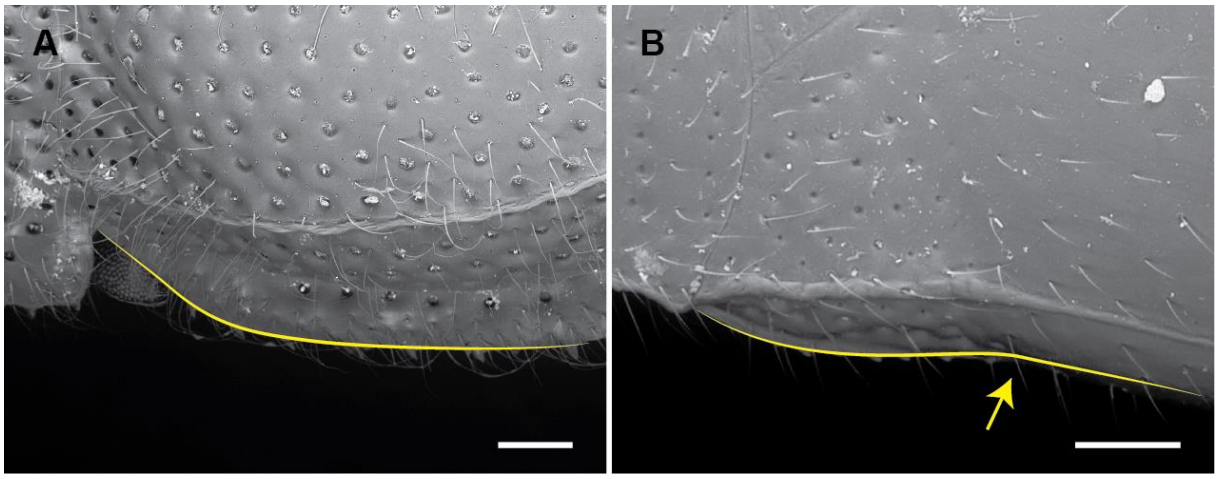

Figure 11. Character 26, lateral constriction of hemelytra: A) state 0, not constricted, as in *Thaumamannia urucuana* sp. n.; B) state 1, slightly constricted, as in *Anommatocoris araguanus* sp. n. Character states outlined in yellow, character state one indicated (yellow arrow) as well. Scale bars: 0.1 mm.

Additionally, one homoplastic synapomorphy also supported the monophyly of this genus: frons at same height as clypeus (8-0). *Anommatocoris bolivianus* is the sister group of the rest of the genus, which then has two different clades: [*A. schuhii* sp. n. + [*A. zeteki* + *A. coibensis*] sustained by one homoplastic synapomorphy (posterior branch of scent gland peritreme shorter than the upper part of anterior branch, 23-1) while the internal [*A. zeteki* + *A. coibensis*] clade is supported by a different homoplastic synapomorphy (posterior region of paranota developed in a small acute humeral angle, 19-1); and *A. sucreanus* sp. n. + the polytomy [*A. coleopteratus*, *A. minutissimus*, *A. serratus* sp. n., *A. knudsonii* sp. n., *A. araguanus* sp. n.], supported by one synapomorphy (paranota borders bearing small scales, 17-1 – Fig. 5B).

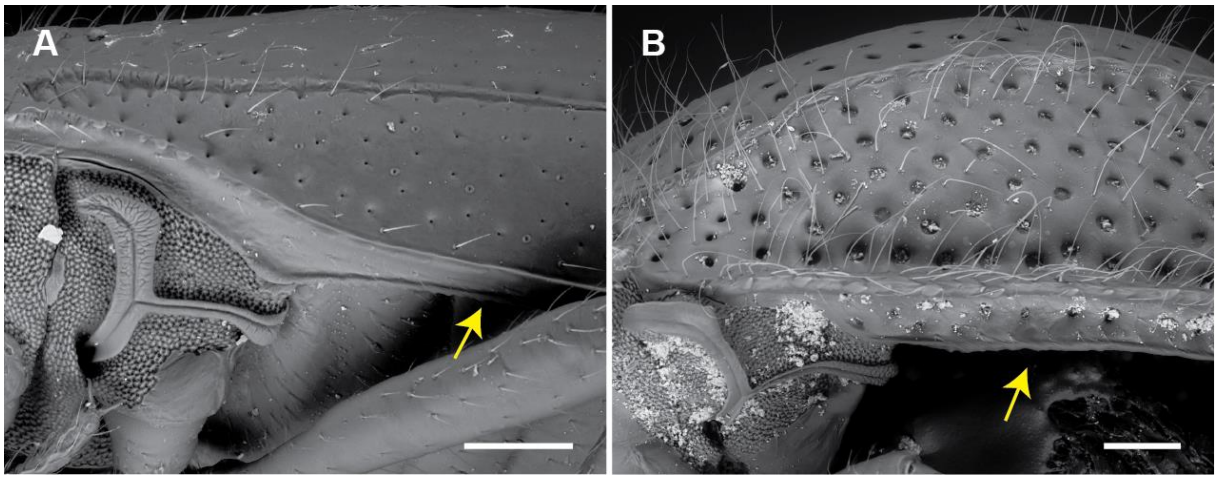

Figure 12. Character 27, hypocosta width: A) state 0, narrow, as in *Anommatocoris coleopterodes* sp. n.; B) state 1, wide, as in *Thaumamannia urucuana* sp. n. Character states indicated (arrows) in yellow. Scale bars: 0.1 mm.

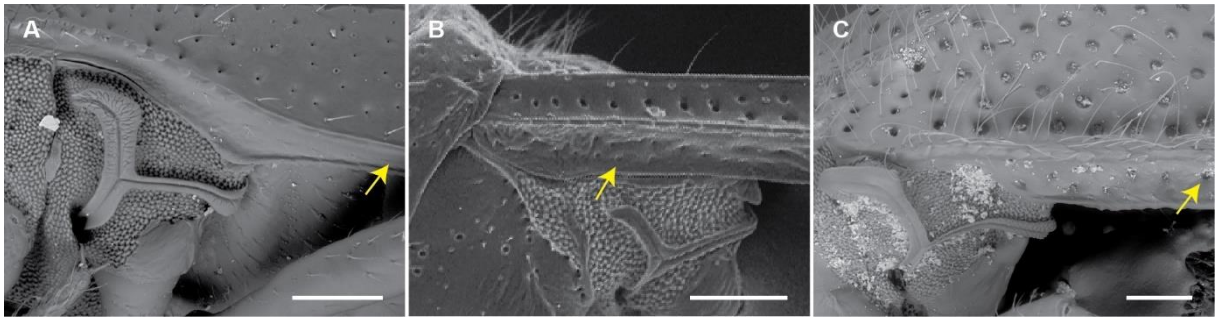

Figure 13. Character 28, punctuations on hypocosta: A) state 1, absent, completely smooth, as in *Anommatocoris coleopterodes*; B) state 2, finely punctuated, as in *Henryianaida machupicchuensis* sp. n.; C) state 3, coarsely punctuated, as in *Thaumamannia urucuana* sp. n. Character states indicated (arrows) in yellow. Scale bars: 0.1 mm.

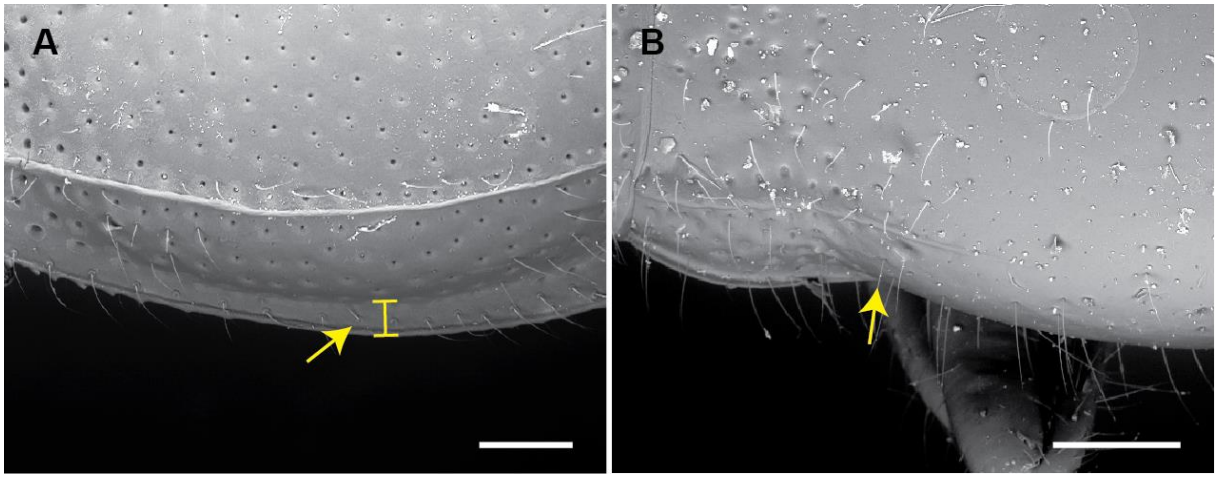

Figure 14. Character 30, costal area: A) state 0, explanate and wide, as in *Thaumamannia insolita* sp. n.; B) state 1, thickened and narrow, as in *Anommatocoris schuhii* sp. n. Character state zero shown in yellow; both indicated by a yellow arrow. Scale bars: A) 0.1 mm; B) 0.2 mm.

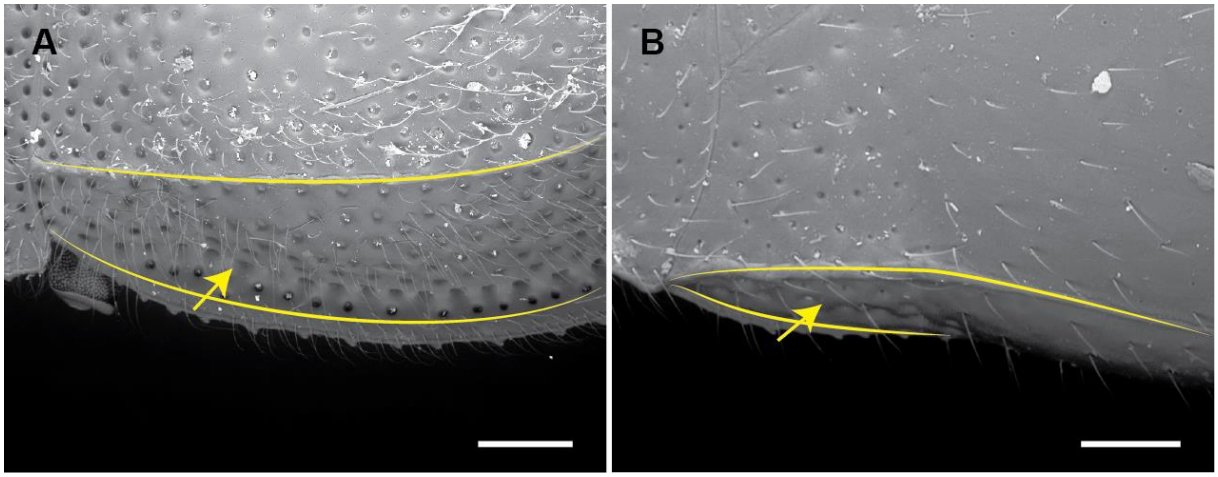

Figure 15. Character 31, subcostal area: A) state 0, subhorizontal, as in *Thaumamannia vanderdrifti*; B) state 1, subvertical, as in *Anommatocoris araguanus* sp. n. Character states indicated in yellow. Scale bars: A) 0.2 mm; B) 0.1 mm.

Taxonomy

Vianaidinae Kormilev

Diagnosis. The subfamily is mainly characterized by its unique scent gland peritreme (Figs. 16-17) composed by an anterior and a posterior branch, the latter transversally connected to the first, forming a sulcus and varying in inclination, curvature and swollenness, giving a T- or Y-shaped aspect. The pronounced clypeus, punctuate pronotum and hemelytra and visible scutellum are also diagnostic characters for the subfamily. It presents both coleopteroid and macropterous forms, which hampers the comparison of hemelytra characters. However, in coleopteroid forms, a carina-like vein extending from its anterior border is always present; and in macropterous forms, a well-defined clavus and vein-less membrane can also be indicated as a diagnostic feature.

Re-description. *Head*. Pubescent, clypeus convex, strongly delimited from vertex, extending beyond mandibular plates; antenniferous process facing downwards; antennae 4-segmented; bucculae strongly developed, extending the entire length of the head ventrally, open anteriorly, divergent posteriorly, punctuate; rostrum 4-segmented always reaching abdominal segments.

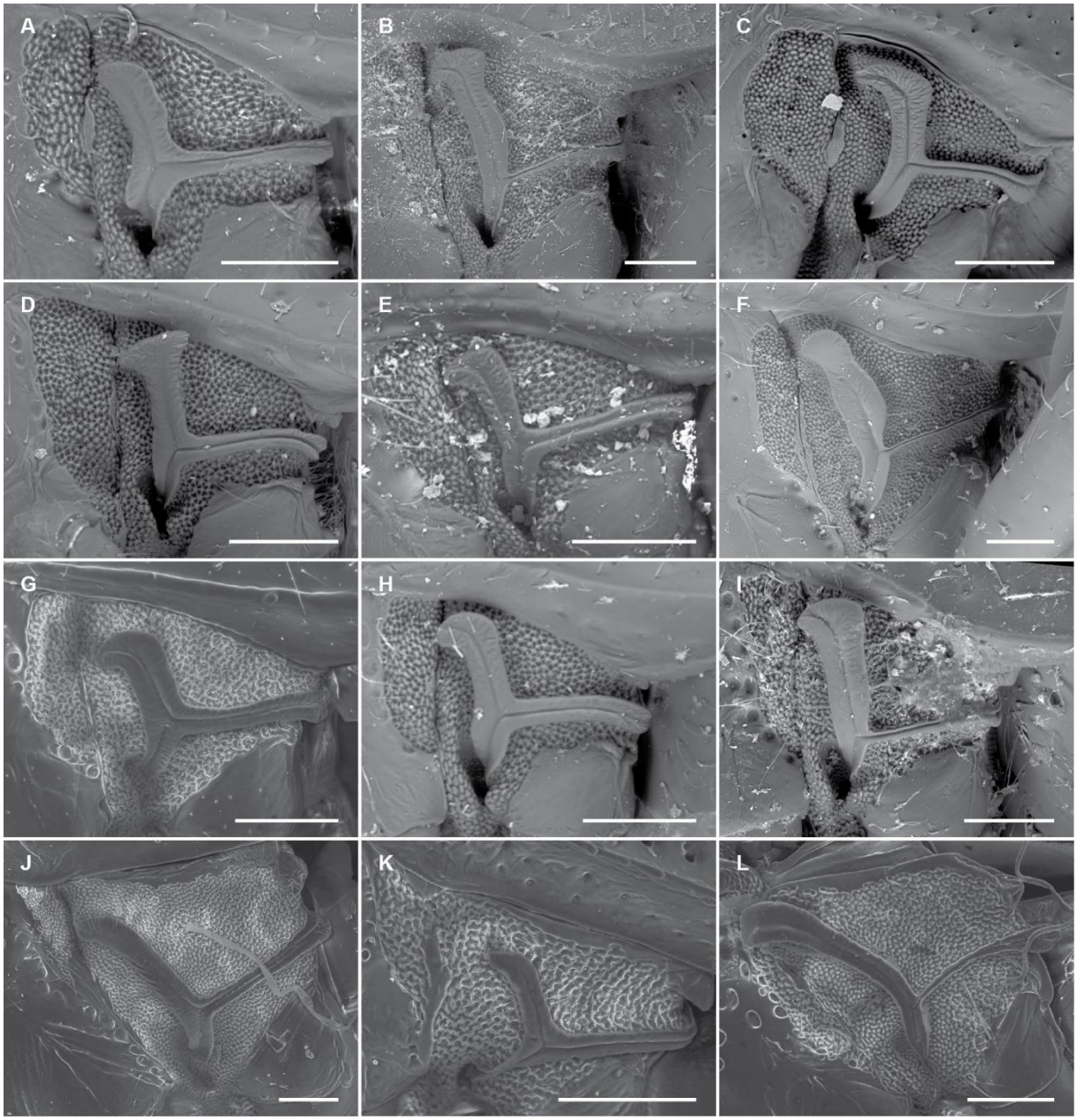

Figure 16. Scent gland system in lateral view, SEM images, of the genera *Anommatocoris*, *Henryianaida* gen. n. and *Pterovianaida*: A) *A. araguanus* sp. n., holotype; B) *A. coibensis*, paratype; C) *A. coleopteratus*; D) *A. knudsonii* sp. n., holotype; E) *A. minutissimus*, paratype; F) *A. schuhii* sp. n., holotype; G) *A. serratus* sp. n., holotype; H) *A. sucreanus* sp. n., paratype; I) *A. zeteki*, allotype; J) *H. colombiensis* sp. n., holotype; K) *H. machupicchensis* sp. n., holotype; L) *P. duckensis*, holotype. Scale bars: 0.1 mm.

Thorax. Pronotum punctuate; pronotal carinae absent; scutellum visible, smooth; sternal laminae present, punctuate, sinuous, widening posteriorly. *Hemelytra*. Coleopteroid or macropterous; in coleopteroid forms, clavus and membrane absent, carina-like vein extending variably from the anterior border; in macropterous forms, clavus and vein-less membrane well-developed in addition to discoidal, subcostal and costal areas, punctuate in coriaceous parts. *Scent gland*. Peritreme very distinct, composed by an anterior and a posterior branch, the latter

transversally connected to the first, these bearing a sulcus and varying in shape, curvature, inclination and swollenness; evaporatorium covering the entire metapleuron and hind mesopleuron, also advancing ventrally; scent gland ostiole conspicuously big. *Legs*. Long, slender, pubescent and unarmed; coxae widely separated; trochanter not fused; femora usually swollen to some degree; tarsi two segmented, second segment many times longer, claws long and slender. *Abdomen*. In coleopteroid forms, completely enclosed in the hemelytra and roundly ovate; in macropterous forms, long, rectangular; spiracles located ventrally near lateral margins of abdominal sternites; usually pubescent.

Type genus. *Vianaida* Kormilev = *Anommatocoris* China.

Distribution. Central and South America (Fig. 18).

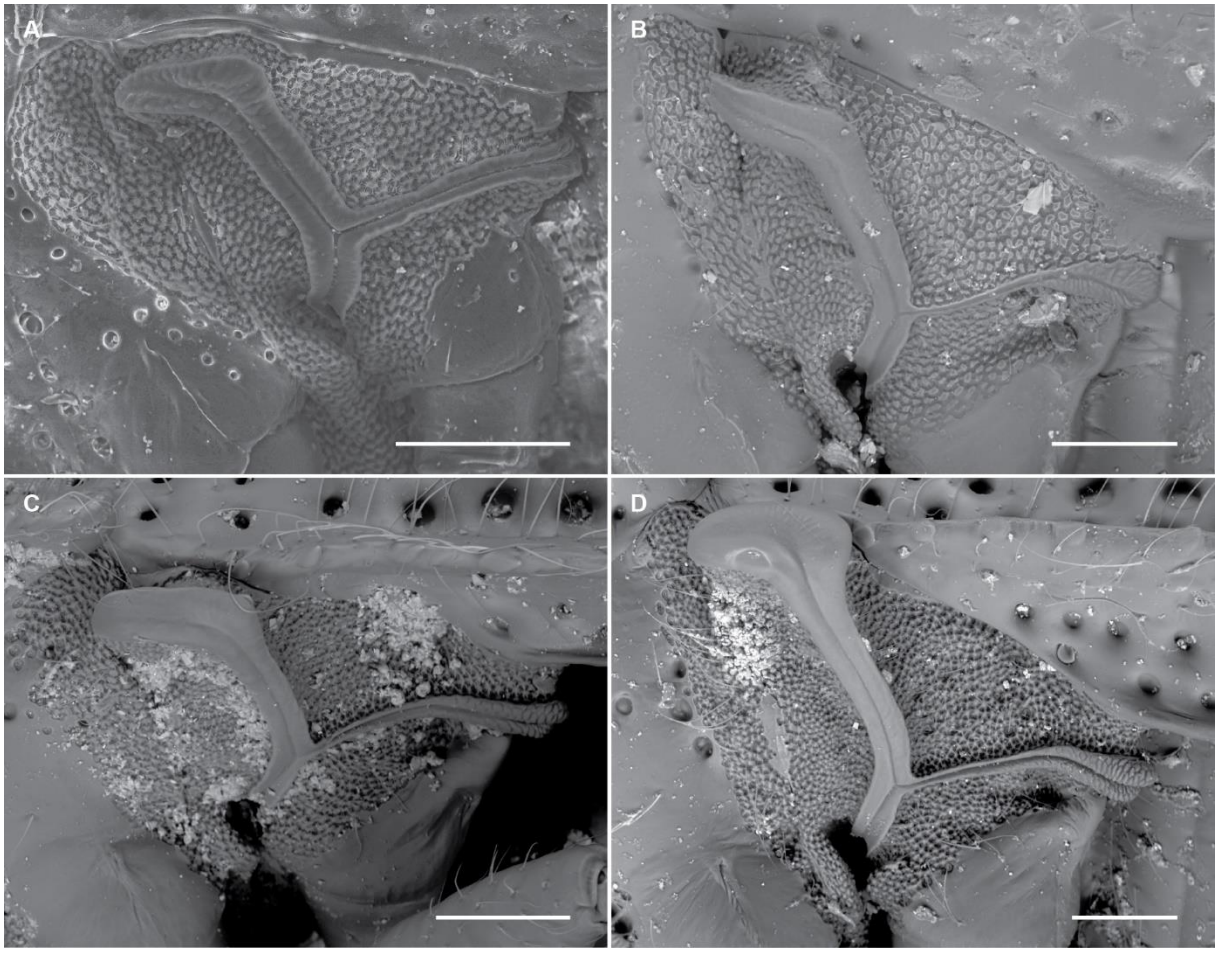

Figure 17. Scent gland system in lateral view, SEM images, of *Thaumamannia* species: A) *T. insolita* sp. n., holotype; B) *T. manni*, holotype; C) *T. urucuana* sp. n., holotype; D) *T. vanderdrifti*. Scale bars: 0.1 mm.

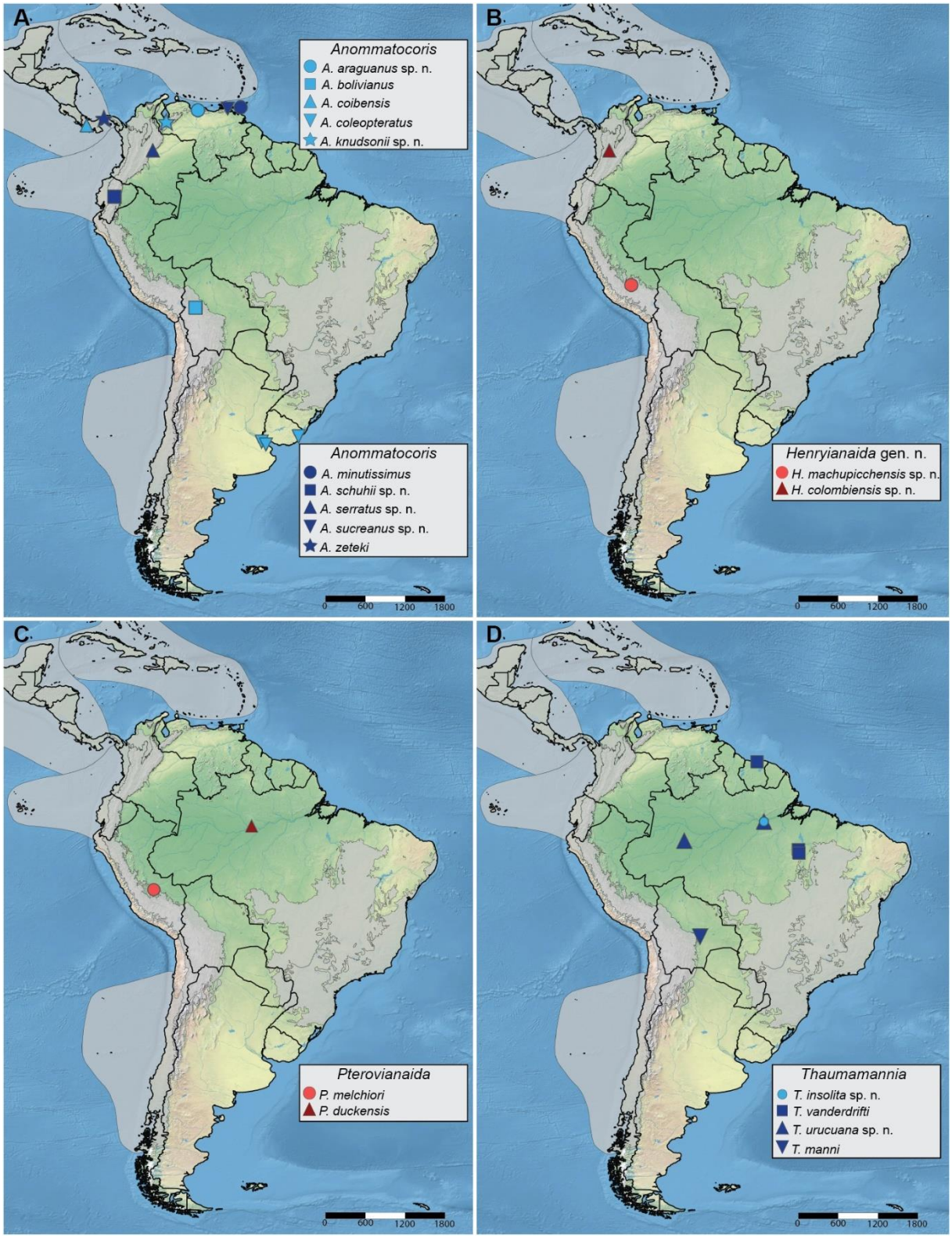

Figure 18. Maps of distribution of the extant vianaidines. A) *Anommatocoris* species; B) *Henryianaida* gen. n. species; C) *Pterovianaida* species; D) *Thaumamannia* species.

Key to the genera of Vianaidinae

1. Hemelytra fully developed, macropterous 2

-. Hemelytra reduced and coriaceous, coleopteroid 4

2. Mandibular plates not constricted; scent gland peritreme somehow laterally projected.. 3

-. Mandibular plates constricted .....***Henryianaida*** gen. n.

3. Head remarkably inclined downwards, with abundant setae on vertex; distal part of pronotum significantly raised; paranota explanate, wider anteriorly; scent gland peritreme strongly laterally projected.....***Pterovianaida*** Montemayor & Carpintero

-. Head mostly straight; pronotum flat; paranota not distinguished explanate; scent gland peritreme only slightly laterally projected.....***Anommatocoris*** China (part)

4. Body ovate; head inclined downwards; paranota and costal area of hemelytra explanate; anterior branch of the Y-shaped scent gland peritreme entirely and strongly laterally projected, tip of anterior branch horizontally extended ....***Thaumamannia*** Drake & Davis

-. Body not ovate, elongate; head straight; paranota carinate, not explanate; costal area of hemelytra only briefly explanate on the anterior region, or entirely carinate; anterior branch of scent gland peritreme not entirely laterally projected..... .....***Anommatocoris*** China (part)

Anommatocoris China, 1945

Diagnosis. This genus can be characterized by the straight position of the head, the flat pronotum, the lack of explanate paranota, the constriction on the anterior part of hemelytra, the mostly carinate costal area, the nearly vertical subcostal area, the narrow and smooth hypocosta, in addition to the almost perpendicular (to the sagittal body plane) anterior branch of the scent gland which is only slightly laterally projected.

Re-description. *Head*. Triangular in dorsal view, pubescent; clypeus usually in different color than head; pedicel subequal to basiflagellomere, both slightly smaller than distiflagellomere and usually twice as big as scape; eyes reduced with none or few scarcely distributed ommatidia or fully developed, compound; bucculae usually with one row of punctures; rostrum reaching at least the first abdominal segment. *Thorax*. Flat, widening posteriorly, sometimes also slightly widened laterally; punctuate, mostly on posterior region of pronotum; collar indistinct, punctuate; anterior border usually straight, posterior usually convex; paranota carinate. *Hemelytra*. Either entirely coriaceous and coleopteroid or macropterous and fully developed; laterally constricted anteriorly; if coriaceous, considerably convex, no clavus nor membrane distinct and vein-less except for one carina-like vein extending variably from the anterior border, punctuate at least up to the hemelytra lateral constriction; subcostal area subvertical; hypocosta narrow and smooth; pubescent at least on the borders. *Scent gland*. Anterior branch varying on shape of tip, sinuosity and inclination, but usually perpendicular to body sagittal plane, slightly but equally laterally projected to its whole extent; posterior branch varying on width of its edges and curvature; evaporatorium varying on the size of its area on mesopleuron. *Legs*. Femora only slightly swollen; tarsi 2-segmented, second segment at least 5-times longer.

Type species. *Anommatocoris minutissimus* China, 1945.

Distribution. Central America: Panama, Trinidad; South America: Argentina, Bolivia, Colombia, Ecuador, Venezuela, Uruguay (Fig. 18A).

Discussion. *Anommatocoris* was firstly described by China, 1945, which placed this eyeless myrmecophilus genus in Oxycareninae (Heteroptera, Lygaeidae). Kormilev (1955) described a new family, Vianaididae, with one new species, *Vianaida coleopterata*. It was only after Drake & Davis (1960) that these two groups were synonymized and Vianadinae recognized as the valid family group name and as a subfamily of Tingidae. Shortly after, *A. zeteki* was described. The other coleopteroid form, *A. coibensis*, was only described in 2016, found in soil litter. Only one macropterous species was described for this genus (*A. bolivianus*) thus far and two species had their immatures studied and described, *A. coleopteratus* and *A. coibensis*, but only the

nymphs of the latter were illustrated (López *et al.*, 2016). The only species of this genus collected in more than one occasion was *A. coleopteratus*, in a very narrow distance from one event to another. Here we propose five new coleopteroid species, three from Venezuela.

Key to the species of Anommatocoris

1. Hemelytra strongly modified, coriaceous, coleopteroid, membrane not entirely developed 2

-. Hemelytra fully developed presenting clavus and, discoidal, subcostal and costal areas, and membrane ..... ***A. bolivianus*** Schuh, Cassis & Guilbert

2. Color of the head is the same as the body; scent gland peritreme unequally divided by the posterior branch, forming an upper part considerably longer than the bottom part on the anterior branch.....3

-. Color of head lighter than the color of the body; anterior branch of scent gland peritreme equally divided by the posterior branch 5

3. Anterior branch of the peritreme with sinuous margins.....4

-. Anterior branch of the peritreme with straight margins..... ..... ***A. zeteki*** Drake & Froeschner

4. Carina-like vein of hemelytra short, fading right after the anterior constriction of hemelytra; paranota humeral angle blunt ..... ***A. schuhii*** sp. n.

-. Carina-like vein of hemelytra somehow long, reaching at least the middle of hemelytra; paranota humeral angle acutely developed..... ***A. coibensis*** López, Costas & Vázquez

5. Scent gland peritreme hidden in dorsal view 6

-. Scent gland peritreme visible in dorsal view .....***A. coleopteratus*** (Kormilev)

6. Carina-like vein of hemelytra long, surpassing the middle hemelytra.....7

-. Carina-like vein of hemelytra short, not reaching the middle of hemelytra 9

7. Anterior branch of scent gland peritreme with roundish tip 8

-. Anterior branch of scent gland peritreme with hammer-like tip.....***A. knudsonii*** sp. n.

8. Carina-like vein of hemelytra slightly surpassing the middle of hemelytra but not reaching the final third ..... ***A. minutissimus*** China

-. Carina-like vein of hemelytra long, reaching the final third of the hemelytra.....
.....***A. sucreanus*** sp. n.

9. Bucculae blunt posteriorly; paranota borders with several scale-like projections giving a serrate aspect to the structure .....***A. serratus*** sp. n.

-. Bucculae concave posteriorly; paranota borders without scale-like projections.....
.....***A. araguanus*** sp. n.

Anommatocoris araguanus Guidoti, Montemayor & Guilbert sp. n. (Fig. 19)

Diagnosis. This species can be recognized by the tiny humeral acute angle on the posterior region of paranota, the short hemelytra carina-like vein not reaching the middle of the hemelytra, the medium-sized scutellum with one-third of the pronotum maximum width, and by the scent gland peritreme, which is short and distant from the hemelytra border and mostly rounded.

Description. Body. Reddish brown; head whitish, antennae, rostrum and legs light brown to yellowish (Fig. 19A). *Head*. Pubescent, with small and well-spaced hairs; clypeus darker than

head; antenniferous process almost half of pedicel length; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and at least twice as big as scape; eyes with few scarcely distributed ommatidia; bucculae rounded, with scarce hairs on its border and few punctures near head insertion, concave posteriorly (Fig. 19E); rostrum reaching up to third abdominal segment (Fig. 19B-C). *Thorax*. Finely punctuate, one row at collar and then only on the posterior lobe of pronotum; anterior border usually straight, posterior sinuous; paranota carinate with few irregularly distributed scale-like projections on its border, culminating in a small humeral acute angle (Fig. 19F); scutellum conspicuously large, a little less than one-third the maximum pronotum width (Fig. 19D). *Hemelytra*. Coriaceous and coleopteroid, evenly pubescent; carina-like vein extending from the anterior border to the middle of hemelytra, fading abruptly; coarsely punctuate anteriorly, up to the hemelytra constriction, smooth posteriorly. *Scent gland*. Anterior branch tip with the same width as the body of the anterior branch; posterior branch straight, with considerably enlarged bottom edge on its entirely extent; sulcus prominent on both branches, more on posterior branch than on anterior branch, fading distally on the latter; evaporatorium with curved border anteriorly, advancing to up to one-third of mesopleuron (Figs. 16A – 19C).

Measurements. BL, **1.84** (1.90; 1.58–1.67 xM; 1.86–1.96 xF); BW, **0.84** (0.87; 0.67–0.72 xM; 0.83–0.95 xF); HL, **0.21** (0.21; 0.17–0.19 xM; 0.19–0.25 xF); HW, **0.30** (0.30; 0.25–0.27 xM; 0.27–0.32 xF); ID, **0.21** (0.19; 0.17– xM; 0.19–0.25 xF); PL, **0.38** (0.36; 0.34– xM; 0.36–0.40 xF); PW, **0.64** (0.67; 0.57–0.59 xM; 0.63–0.70 xF); AS, **0.10** (0.10; 0.10– xM; 0.10–0.11 xF); AP, **0.23** (0.22; 0.27 xM; 0.22–0.24 xF); AB, **0.27** (0.27; 0.27 xM; 0.27–0.28 xF) and AD, **0.38** (0.36; 0.38 xM; 0.36–0.40 xF).

Etymology. This species was name based on its type locality, Aragua state, in Venezuela. We named this species based on its type locality due to its geographical proximity with another *Anommatocoris* coleopteroid species, also named after its type locality, yet to be described in this revision.

Distribution. Described from Venezuela.

Material examined. **Holotype** xF: **VENEZUELA**: Araugua (sic): 1300m, 17km S Las Tejerias, 12km N Tiara, 8.VIII.87, S&J. Peck, cloud forest litter [Guidoti PhD — Vianaidinae 010] (AMNH). **Paratypes**: **VENEZUELA**: Araugua (sic): 1300m, 17km S Las Tejerias, 12km N Tiara, 8.VIII.87, S&J. Peck, cloud forest litter [Guidoti PhD — 2xM, Vianaidinae 006–007; 7 xF, Vianaidinae 008-009 and 011-015] (AMNH).

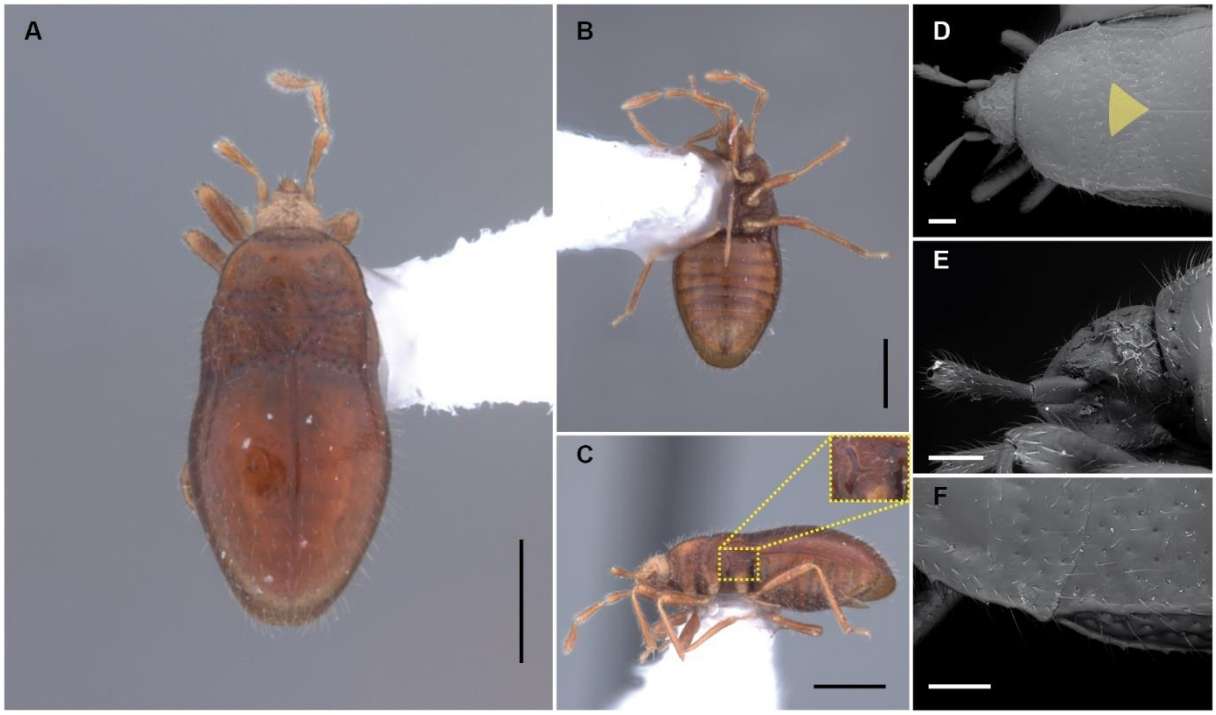

Figure 19. *Anommatocoris araguanus* sp. n. in A) dorsal, B) ventral an C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head in lateral view; F) humeral angle. Holotype illustrated in A and C-F. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Anommatocoris bolivianus Schuh, Cassis & Guilbert, 2006 (Fig. 20)

Diagnosis. This species is the only macropterous species described in the *Anommatocoris* genus, and the discussion provided by Schuh *et al.* (2006) only highlighted characters that are related to this wing polymorphism, like the compound eye (Fig. 20A-B) and forewings (Fig. 20A, C). Since the type material were reported to be lost by the original authors we couldn't study the species and neither improve its diagnosis or access the species validity.

Measurements. BL, **2.33** and BW, **1.33** (Schuh *et al.*, 2006).

Distribution. Known only from Bolivia, La Paz department (Schuh *et al.*, 2006).

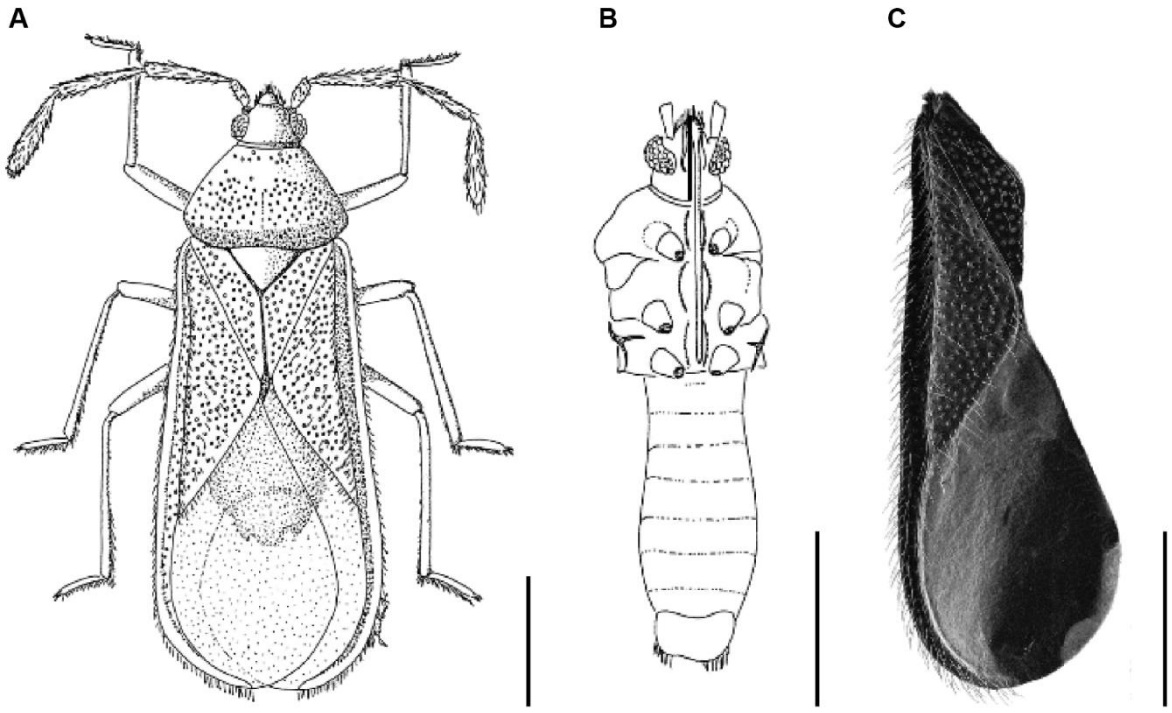

Figure 20. *Anommatocoris bolivianus* modified from Schuh *et al.* (2006). A) habitus view; B) ventral view; C) hemelytra in scanning electron microscopy, dorsal view. Scale bars: 0.5 mm.

Anommatocoris coibensis López, Costas & Vázquez, 2016 (Fig. 21)

<u>*Diagnosis*</u>. This species presents a pronotum broader than the anterior region of the hemelytra, which is unique among the species of *Anommatocoris*. The humeral angle acutely developed, and the conspicuously large scutellum are diagnostic features of this species as well. The scent gland peritreme is unequally divided by its posterior branch, like in *A. zeteki*, but presents a constriction before the tip of the anterior branch, with a nearly straight upper edge, and a very narrow sulcus on the posterior branch, which has an enlarged bottom edge at its posterior region.

<u>*Re-description*</u>. *Body*. Dark brown; head as body; antennae, rostrum and legs lighter (Fig. 21A). *Head*. Pubescent, with small and well-spaced hairs (Fig. 21E); clypeus slightly lighter than head; antenniferous process slightly bigger than one-third of pedicel length; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and at least twice as big as scape; eyes with few scarcely distributed ommatidia; bucculae rounded, with scarce hairs on its border, concave posteriorly; rostrum reaching at least the fourth abdominal segment (Fig. 21B-C). *Thorax*. Finely punctuate, one row at collar and then only on the posterior lobe of pronotum;

anterior border usually straight, posterior sinuous; paranota carinate, culminating is a small humeral acute angle (Fig. 21F); scutellum conspicuously large, a little less than one-third the maximum pronotum width (Fig. 21D). *Hemelytra*. Coriaceous and coleopteroid, pubescent; carina-like vein extending from the anterior border to the middle of hemelytra; coarsely punctuate anteriorly, up to the hemelytra constriction; punctures marks, but not punctures, on the rest of the structure. *Scent gland*. Anterior branch tip enlarged distally, edges sinuous; posterior branch curved distally, with considerably enlarged bottom edge of the tip, upper edge very narrow; sulcus prominent on both branches, more on posterior branch; evaporatorium with straight border anteriorly, advancing to up to one-fourth of mesopleuron (Figs. 15B – 20C).

Measurements. BL, 2.30; BW, 1.11; HL, 0.22; HW, 0.35; ID, 0.23; PL, 0.47; PW, 0.91; AS, 0.12; AP, 0.28 and AB, 0.30.

Distribution. Known only from Panama.

Material examined. **Paratype**: PANAMA: Parque Nacional de la Isla de Coiba, Punto 2, 80 meters, 1998-07-20, J. Pérez Zasallos Log. [Guidoti PhD — 1xF, Vianaidinae 061] (USNM).

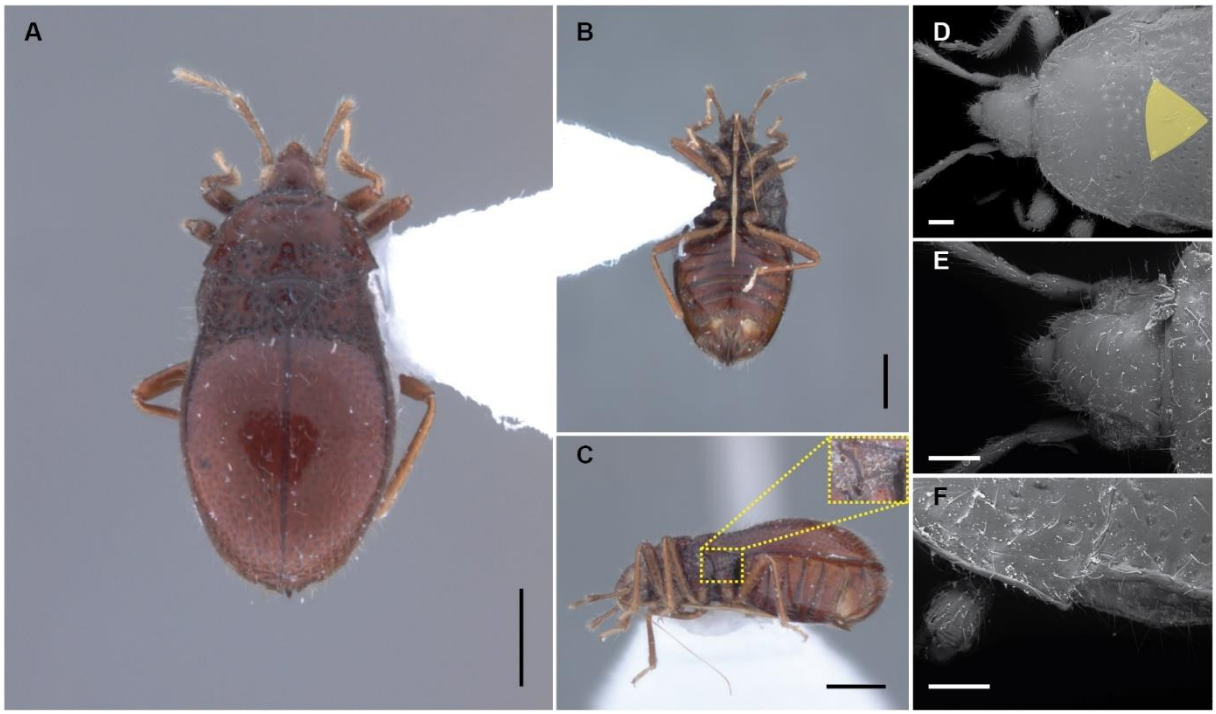

Figure 21 *Anommatocoris coibensis* paratype in A) dorsal, B) ventral an C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head; F) humeral angle. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Anommatocoris coleopteratus (Kormilev, 1955) (Fig. 22)

Diagnosis. This species is the only *Anommatocoris* species with a visible scent gland in dorsal view. It also presents an unusually large tip of the anterior branch of the peritreme for the genus and a long carina-like vein on the hemelytra, reaching its posterior region.

Re-description. *Body*. Light brown; head whitish; antennae, rostrum and legs yellowish (Fig. 22A). *Head*. Pubescent, with small and well-spaced hairs; clypeus darker than head, same color as body; antenniferous process length more than half of pedicel; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and at least twice as big as scape; eyes with few scarcely distributed ommatidia; bucculae rounded, with scarce hairs on its border and deeply impressed punctures near head insertion, concave posteriorly (Fig. 22E); rostrum reaching at least second abdominal segment (Fig. 22B-C). *Thorax*. Punctuate, with small punctures, one row at collar and then only on the posterior lobe of pronotum; anterior border straight, posterior sinuous; paranota carinate with hairs and few irregularly distributed small scale-like projections on its border (Fig. 22F); scutellum large, a little less than one-fifth the maximum pronotum width (Fig. 22D). *Hemelytra*. Coriaceous and coleopteroid, evenly pubescent; laterally constricted anteriorly; carina-like vein extending from the anterior border to the posterior third of hemelytra, fading abruptly; finely punctuate entirely, punctures small, larger anteriorly, up to the hemelytra constriction. *Scent gland*. Anterior branch tip tilted horizontally, large, same size as the rest of the anterior branch, presenting a cracked texture; posterior branch slightly curved, with considerably enlarged bottom edge on its tip; sulcus prominent on both branches; evaporatorium with curved border anteriorly, advancing to most of the upper part of the mesopleuron (Figs. 16C – 22C).

Measurements. BL, **1.78** (1.87; 1.55–1.87 xM; 1.74–1.96 xF); BW, **0.74** (0.84; 0.51–0.84 xM; 0.74–0.89 xF); HL, **0.25** (0.25; 0.21–0.27 xM; 0.23–0.29 xF); HW, **0.32** (0.37; 0.27–0.37 xM; 0.32–0.36 xF); ID, **0.23** (0.29; 0.17–0.29 xM; 0.23–0.25 xF); PL, **0.34** (0.36; 0.29–0.36 xM; 0.32–0.40 xF); PW, **0.55** (0.57; 0.46–0.68 xM; 0.53–0.61 xF); AS, **0.11** (0.10; 0.10–0.11 xM; 0.10–0.11 xF); AP, **0.23** (0.23; 0.22–0.24 xM; 0.22–0.26 xF); AB, **0.24** (0.24; 0.21–0.24 xM; 0.23–0.27 xF) and AD, **0.34** (0.32; 0.32–0.34 xM; 0.34–0.38 xF).

Distribution. Described from Argentina, Buenos Aires province (Kormilev, 1955) and reported from Uruguay, Rocha province (San Martin, 1966).

Material examined. **Holotype** xM: **ARGENTINA**: Buenos Aires: Tigre, Rio Luján, 25-III-1955, M. J. Vianna col. (USNM). **Allotype** xF: **ARGENTINA**: Buenos Aires: Tigre, Rio Luján, 25-III-1955, M. J. Vianna col. (USNM). **Paratypes**: **ARGENTINA**: Buenos Aires: Tigre, Rio Luján, VI-1955, M. J. Vianna col. [Guidoti PhD — Vianaidinae 039–046 and 048, 9 glued to card boards and thus, gender undefined] (039-046 USNM; 048 MNRJ); **ARGENTINA**: Buenos Aires: Tigre, Rio Luján, VII-1955, M. J. Vianna col. [Guidoti PhD — Vianaidinae 047, 1 glued to card board and thus, gender undefined] (USNM). **Other Specimens**: **ARGENTINA**: Buenos Aires: Res. Punta Lara, III-2001, Carpintero col. [Guidoti PhD — 6xF, Vianaidinae 023 and 026-030; 7xM, Vianaidinae 024-025 and 031-035] (MNHN).

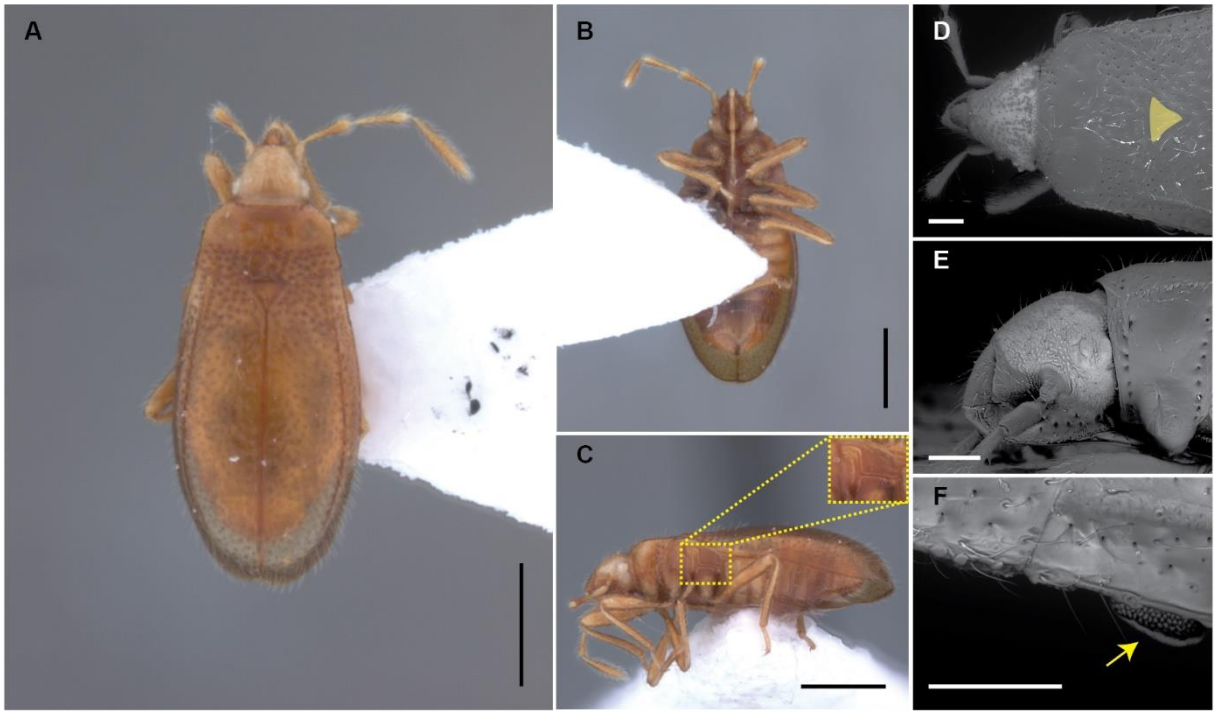

Figure 22. *Anommatocoris coleopteratus* paratypes in A) dorsal, B) ventral an C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head in lateral view; F) humeral angle, and scent gland visible in dorsal view indicated in yellow (arrow). Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Anommatocoris knudsonii Guidoti, Montemayor & Guilbert sp. n. (Fig. 23)

Diagnosis. This species resembles *A. araguanus* sp. n. but differs from it on the more pronounced humeral angle, the narrower relative width of scutellum with pronotum, the thicker and longer carina-like vein on the hemelytra and the scent gland peritreme, which has a

hammer-like tip on the anterior branch, unique among the species of the genus, and a posterior branch inclined downwards.

Description. *Body*. Light brown, same as antennae, rostrum and legs; head whitish (Fig. 23A). *Head*. Pubescent, with small and well-spaced hairs; clypeus darker than head, same color as body; antenniferous process half of pedicel length; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and at least twice as big as scape; eyes with few scarcely distributed ommatidia; bucculae rounded, widest anteriorly, with scarce hairs on its border and finely punctuation organized in a single complete row and few above it near head insertion, concave posteriorly (Fig. 23E); rostrum reaching at least second abdominal segment (Fig. 23B-C). *Thorax*. Finely punctuate, with tiny punctures on collar, small ones on the posterior lobe of pronotum; anterior border straight, posterior sinuous; paranota carinate, culminating is a small humeral acute angle (Fig. 23F), with hairs and few irregularly distributed and small scale-like projections on its border; scutellum large, a little less than one-sixth the maximum pronotum width (Fig. 23D). *Hemelytra*. Coriaceous and coleopteroid, evenly pubescent; laterally constricted anteriorly; carina-like vein extending from the anterior border to the posterior third of hemelytra, fading abruptly; punctuate anteriorly up to the hemelytra constriction, these the biggest punctures on body, smooth posterior to the hemelytra constriction but marked by puncture marks. *Scent gland*. Anterior branch tip projected both front and backwards providing a hammer-like aspect, large, almost the same size as the rest of the anterior branch, presenting a slightly cracked texture; posterior branch curved, with evenly enlarged edges; sulcus prominent on posterior branch, almost unnoticeable on anterior branch; evaporatorium with straight border anteriorly, advancing to more than half of the mesopleuron on its upper part, and one-third on its bottom part (Figs. 16D – 23C).

Measurements. BL, **1.81** (1.79; 1.67 xM; 1.79–1.92 xF); BW, **0.84** (0.86; 0.78 xM; 0.86–0.87 xF); HL, **0.22** (0.19; 0.21 xM; 0.19–0.24 xF); HW, **0.33** (0.32; 0.32 xM; 0.32–0.34 xF); ID, **0.24** (0.23; 0.25 xM; 0.23–0.25 xF); PL, **0.38** (0.38; 0.38 xM; 0.38 xF–); PW, **0.62** (0.61; 0.59 xM; 0.61–0.65 xF); AS, **0.11** (0.11; 0.10 xM; 0.11 xF–); AP, **0.22** (0.21 xM; 0.21–0.23 xF); AB, **0.26** (0.25 xM; 0.27 xF–) and AD, **0.34** (0.32 xM; 0.34–0.36 xF).

Etymology. This species was named after Alexander Knudson, a young American entomologist who kindly left the four specimens of this species to the leading author at the NMNH, after identifying them as a new species of the genus *Anommatocoris*.

Distribution. Described from Venezuela.

Material examined. **Holotype** xF: **VENEZUELA**: Merida: Campo Elias, La Azulita, R. W. Brooks, A. A. Grigarick, J. Mcl.aughlin, R. O. Schuster col. [Guidoti PhD — Vianaidinae 019] [DAVIS] (UCDC). **Paratypes**: **VENEZUELA**: Merida: Campo Elias, La Azulita, R. W. Brooks, A. A. Grigarick, J. Mcl.aughlin, R. O. Schuster col. [Guidoti PhD — 1xM, Vianaidinae 018; 2xF, Vianaidinae 020-021] [DAVIS] (UCDC).

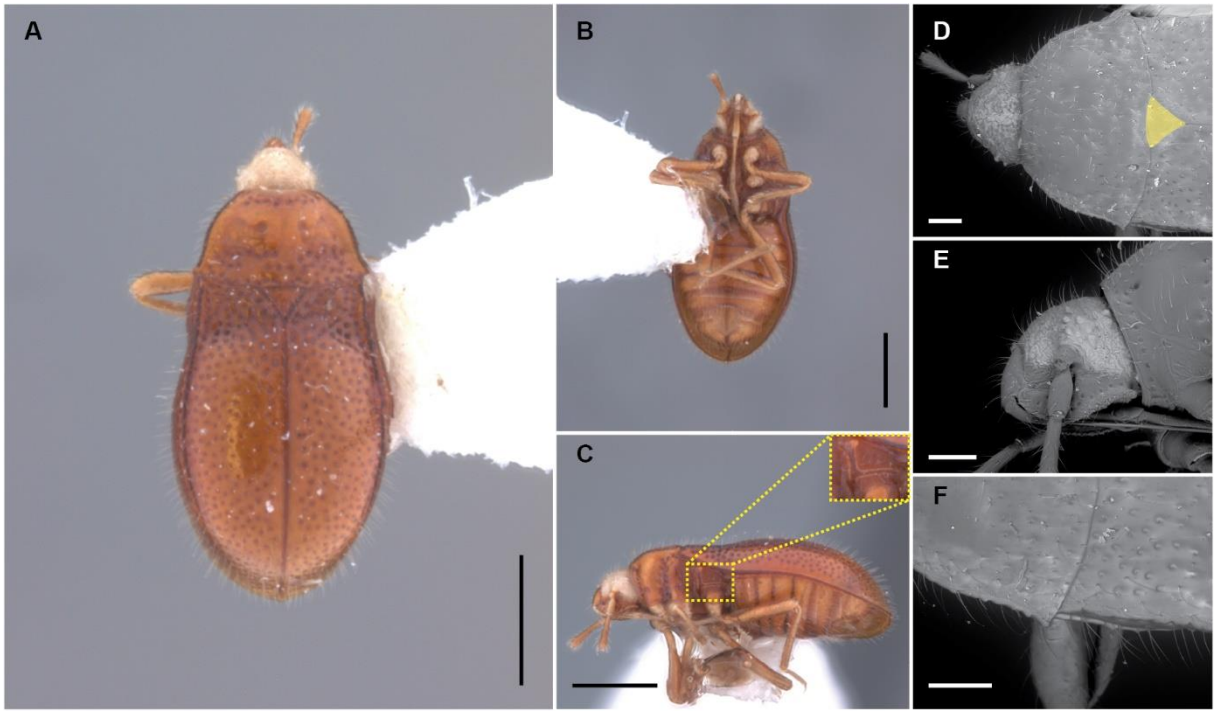

Figure 23. *Anommatocoris knudsonii* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) humeral angle. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Anommatocoris minutissimus China, 1945 (Fig. 24)

Diagnosis. This species is distinguishable from the other *Anommatocoris* species by the lack of acute humeral angle, the lightly pronounced punctuations on pronotum, the narrow scutellum and the scent gland peritreme, which is similar to the one presented by *A. coibensis* due to the almost straight upper part of the anterior branch, but it is equally divided by the posterior branch and lacks a sinuous margin.

Re-description. *Body*. Light brown; antennae, rostrum and legs even lighter; head whitish (Fig. 24A). *Head*. Pubescent, with small and well-spaced hairs; clypeus darker than head, same color

as body; antenniferous process half of pedicel length; pedicel twice the size of scape; eyes with just a few scarcely distributed ommatidia; bucculae rounded, widest anteriorly, with scarce hairs on its border and fine marks of punctures organized in a single complete row in the middle, concave posteriorly (Fig. 24D); rostrum reaching at least second abdominal segment (Fig. 24B). *Thorax*. Finely punctuate, with tiny punctures on collar and on the posterior lobe of pronotum; anterior border concave, posterior only slightly sinuous; paranota carinate with hairs on its border (Fig. 24E); scutellum large, a little less than one-sixth the maximum pronotum width (Fig. 24C). *Hemelytra*. Coriaceous and coleopteroid, pubescent mostly on subcostal and costal areas; laterally constricted anteriorly; carina-like vein extending from the anterior border to the middle of hemelytra, fading abruptly; finely impressed by punctures anteriorly up to the hemelytra constriction, smooth posteriorly to the hemelytra constriction, bearing punctures marks but not punctures. *Scent gland*. Anterior branch tip tilted horizontally, large, slightly smaller than the rest of the anterior branch, presenting a lightly cracked texture; posterior branch straight, with evenly enlarged edges through its whole extant; sulcus much more prominent on posterior branch than in anterior branch; evaporatorium with curved border anteriorly, advancing to up to one-third of the mesopleuron on its upper part (Figs. 16E – 24B).

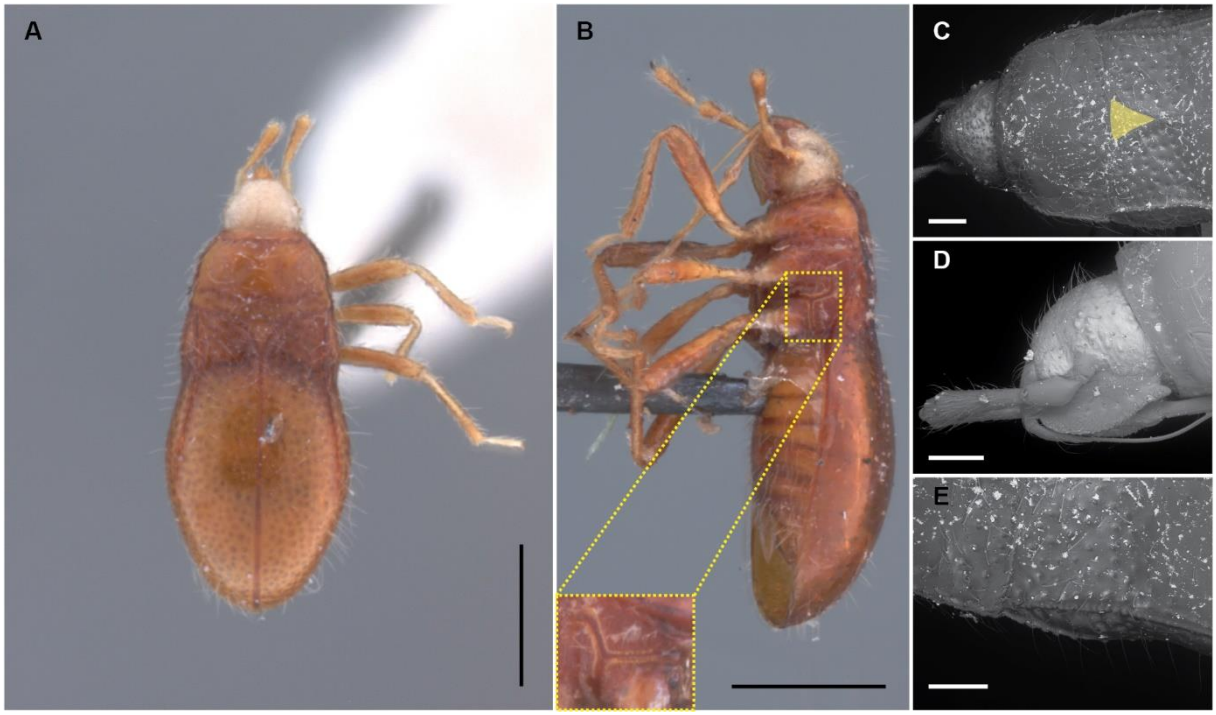

Figure 24. *Anommatocoris minutissimus* paratypes in A) dorsal and B) lateral views, with scent gland in detail and SEM photographs of: C) head and thorax, scutellum roughly highlighted; D) head in lateral view; E) humeral angle. Scale bars: A-B) 0.5 mm; C-E) 0.1 mm.

Measurements. BL, **1.64** (1.58 xM; 1.71 xF); BW, **0.70** (0.67 xM; 0.74 xF); HL, **0.19** (0.19 xM; 0.19 xF); HW, **0.30** (0.30 xM; 0.30 xF); ID, **0.21** (0.21 xM; 0.21 xF); PL, **0.32** (0.32 xM; 0.32 xF); PW, **0.50** (0.49 xM; 0.51 xF); AS, **0.10** (0.10 xM; 0.11 xF) and AP, **0.20** (0.19 xM; 0.21 xF).

Distribution. Known only from Trinidad.

Material examined. **Paratypes**: **TRINIDAD**: B. W. I., St. Augustine, in litter soil, Cacao Plantation, 11.1943 – 2.1944, A. H. Strickland. [Guidoti PhD — 1xF, Vianaidinae 037; 1xM, Vianaidinae 038] (USNM).

Anommatocoris schuhii Guidoti, Montemayor & Guilbert sp. n. (Fig. 25)

Diagnosis. This species resembles the most *A. coibensis* by its darker coloration, larger size, increased number of ommatidia on the eyes and general shape of the scent gland peritreme. It differs from this species by the even darker aspect of its habitus, and by the short hemelytra carina-like vein, which seems to be unique among its congeners. The unequally divided peritreme also differs from *A. coibensis*, and *A. zeteki*, the other species bearing such unequally divided peritreme. The sinuosity of the anterior branch is more pronounced, and the tip of the anterior branch is rounded and not acutely defined as in *A. coibensis*, and the posterior region of the posterior branch is not enlarged like in *A. coibensis* and *A. zeteki*.

Description. *Body*. Dark brown; head same as body; antennae, rostrum and legs brown (Fig. 25A). *Head*. Pubescent, with well-spaced hairs; clypeus slightly lighter than head; antenniferous process less than one-fourth of the pedicel length; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and more than twice as big as scape; eyes with few scarcely distributed ommatidia, more than what is usually observed among its congeners; bucculae rounded, widest anteriorly, slightly concave posteriorly; with scarce hairs on its border, at least three rows of punctures not so deeply impressed, concave posteriorly (Fig. 25E); rostrum reaching at least the third abdominal segment (Fig. 25B-C). *Thorax*. Punctuate, one row at collar and then only on the posterior lobe of pronotum; anterior border usually straight, posterior sinuous; paranota carinate, with hairs on its border (Fig. 25F); scutellum conspicuously large, about one-third the maximum pronotum width (Fig. 25D). *Hemelytra*. Coriaceous and coleopteroid, pubescent almost entirely, glabrous only on the middle of the

hemelytra; laterally constricted anteriorly; carina-like vein extending from the anterior border to only the first third of hemelytra, smoothly fading; coarsely punctuate anteriorly, up to the hemelytra constriction, completely smooth thereafter. *Scent gland*. Anterior branch edges sinuous and considerably enlarged if compared to posterior branch; posterior straight, edges conspicuously narrow, even narrower than sulcus; sulcus prominent on posterior branch, weakly impressed on anterior branch, fading entirely way before the tip; evaporatorium with curved border anteriorly, advancing to up to one-fourth of mesopleuron (Figs. 16F – 25C).

Measurements. BL, **2.91** (2.82; 2.82–3.00 xF); BW, **1.49** (1.48; 1.48–1.50 xF); HL, **0.32** (0.29; 0.29–0.36 xF); HW, **0.55** (0.55; 0.55– xF); ID, **0.35** (0.34; 0.34–0.36 xF); PL, **0.57** (0.57; 0.57– xF); PW, **1.17** (1.16; 1.16–1.18 xF); AS, **0.15** (0.15; 0.15– xF); AP, **0.44** (0.42; 0.42–0.46 xF); AB, **0.39** (0.36; 0.36–0.42 xF) and AD, **0.51** (0.51; 0.51 xF).

Etymology. This species was named after the great American entomologist Dr. Randall T. Schuh, who identified these specimens as *Anommatocoris* sp. and already made an important contribution to Vianaidinae (Schuh *et al.*, 2006); not to mention the countless contributions to Miridae and Heteroptera in general throughout his entire very fruitful career.

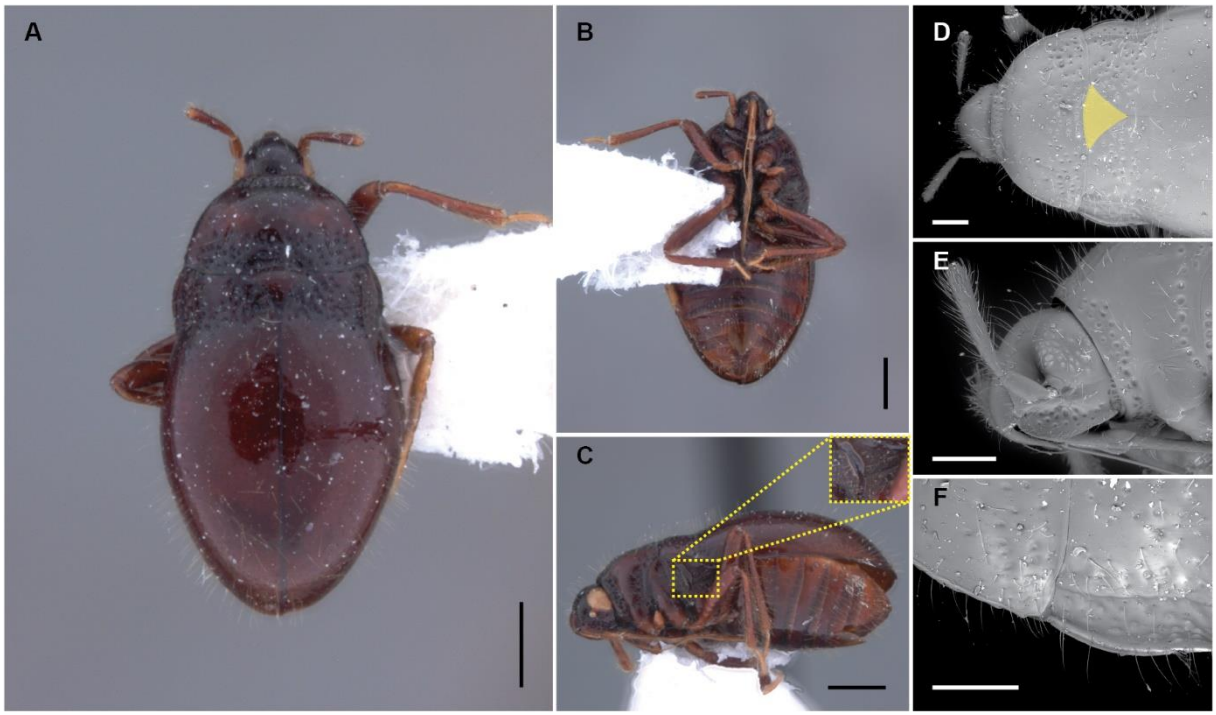

Figure 25. *Anommatocoris schuhii* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) humeral angle. Scale bars: A-C) 0.5 mm; D-F) 0.2 mm.

Distribution. Described from Ecuador.

Material examined. **Holotype** xF: **ECUADOR**: Tungurahua Prov., 12.2 km E Baños, 5000 ft, V-22-93, L. Herman col., #2736, litter near stream [Guidoti PhD —Vianaidinae 017] (AMNH). **Paratype**: **ECUADOR**: Tungurahua Prov., 12.2 km E Baños, 5000 ft, V-22-93, L. Herman col., #2736, litter near stream. [Guidoti PhD — 1xF, Vianaidinae 016] (AMNH).

Anommatocoris serratus Guidoti, Montemayor & Guilbert sp. n. (Fig. 26)

Diagnosis. This species can be recognized by the serrate aspect of the anterior region of the paranota, which is unique among its congeners. The humeral angle slightly pronounced, the hemelytra carina-like vein reaching the middle of the hemelytra, and the tip of the anterior branch of the peritreme resemble *A. zeteki*; but it differs from that species by the larger distance between this tip and the hemelytra border and by the even division of the anterior branch by the posterior branch of the peritreme. From *A. araguanus* sp. n., it differs by the angled posterior branch of the peritreme and the higher position of the anterior branch tip, which is near the hemelytra.

Description. *Body*. Reddish brown, pronotum the darkest; head, antennae, rostrum and legs yellowish (Fig. 26A). *Head*. Pubescent, with well-spaced hairs; clypeus darker than head; antenniferous process almost half of pedicel length; pedicel subequal to basiflagellomere, both smaller than distiflagellomere and at least twice as big as scape; eyes with few scarcely distributed ommatidia; bucculae rounded, widest anteriorly, with a serrate aspect on its border and few scarcely distributed punctures, slightly concave posteriorly (Fig. 26E); rostrum reaching mostly to the second abdominal segment (Fig. 26B-C). *Thorax*. Finely punctuate, one row at collar and then only on the posterior lobe of pronotum; anterior border usually straight, posterior sinuous; paranota carinate, culminating is a small humeral acute angle (Fig. 26F), with small scale-like projections on its border giving an obvious serrate aspect; scutellum conspicuously large, a little less than one-third the maximum pronotum width (Fig. 26D). *Hemelytra*. Coriaceous and coleopteroid, evenly pubescent; laterally constricted anteriorly; carina-like vein extending from the anterior border to the middle of hemelytra, fading abruptly; coarsely punctuate anteriorly, up to the hemelytra constriction, smooth posteriorly. *Scent gland*. Anterior branch slightly inclined frontwards, tip with the same width as the body of the anterior

branch, tilted horizontally, almost same size of the rest of the anterior branch; posterior branch mostly straight, with slightly enlarged upper edge distally; sulcus prominent on both branches; evaporatorium with curved border anteriorly, advancing to up to one-third of mesopleuron (Figs. 16G – 26C).

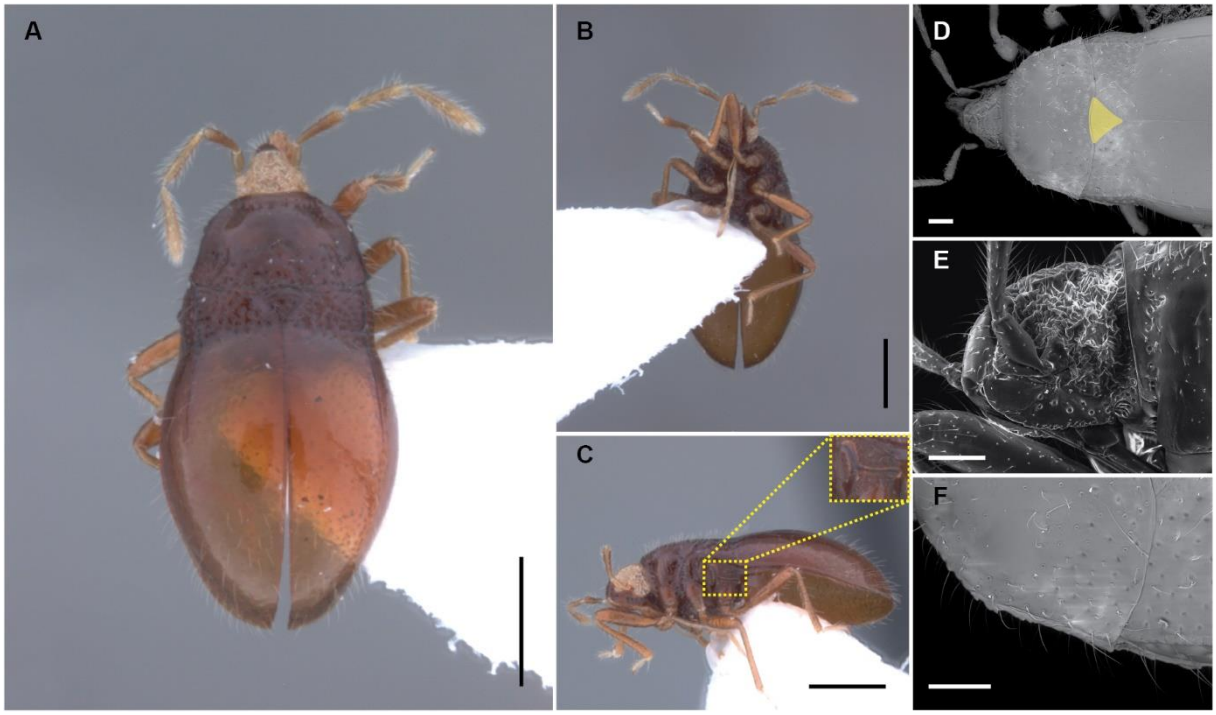

Figure 26. *Anommatocoris serratus* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) humeral angle. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Measurements. BL, 1.92; BW, 0.97; HL, 0.21; HW, 0.29; ID, 0.21; PL, 0.38; PW, 0.74; AS, 0.10; AP, 0.24; AB, 0.27 and AD, 0.34.

Etymology. This species was named after the remarkable serrate aspect of the paranota border, which seems to be unique among its congeners.

Distribution. Described from Colombia.

Material examined. **Holotype** xF: **COLOMBIA**: Boyacá: Sendero Hyca Quye, ~5.5 km NW de Santa Maria, 4.89811ºN 73.29344ºW, 900m, 7-11 Mar 2016, D. Forero col. [MPUJ_ENT 0046245] [Guidoti PhD — Extraction #274] [Guidoti PhD — Vianaidinae 022] (MPUJ).

Anommatocoris sucreanus Guidoti, Montemayor & Guilbert sp. n. (Fig. 27)

Diagnosis. This species can be recognized by the scent gland, which is very similar to the one presented by *A. minutissimus*. However, it distinguishes from *A. minutissimus* by the wider peritreme in both anterior and posterior branches, the longer carina-like vein on the hemelytra and the absence of punctures or punctures marks on the hemelytra.

Description. *Body*. Reddish brown; antennae, rostrum and legs lighter; head whitish (Fig. 27A). *Head*. Pubescent, with small and well-spaced hairs; clypeus darker than head, same color as antennae; antenniferous process less than half of pedicel length (Fig. 27E); pedicel twice the size of scape; eyes with just a few scarcely distributed ommatidia; bucculae rounded, widest anteriorly, with scarce hairs on its border and punctures organized in a single row in the middle; rostrum reaching at least third abdominal segment (Fig. 27B-C). *Thorax*. Finely punctuate, with tiny punctures on collar and on the posterior lobe of pronotum; anterior border straight, posterior only slightly sinuous; paranota carinate with hairs and few scattered scale-like projections on its border (Fig. 27F); scutellum large, about one-fourth of the maximum pronotum width (Fig. 27D). *Hemelytra*. Coriaceous and coleopteroid, evenly pubescent; laterally constricted anteriorly; carina-like vein extending from the anterior border to the final third of hemelytra, fading abruptly; finely impressed by punctures anteriorly up to the hemelytra constriction, completely smooth posteriorly to the hemelytra constriction. *Scent gland*. Anterior branch presenting a lightly cracked texture, tip tilted horizontally, slightly longer than half of the rest of the anterior branch; posterior branch lightly curved, with evenly enlarged edges through its whole extant and the same cracked texture observed on the anterior branch; sulcus more prominent on posterior branch than in anterior branch; evaporatorium with curved border anteriorly, advancing to up to one-third of the mesopleuron on its upper part (Figs. 16H – 27C).

Measurements. BL, **1.59** (1.62; 1.56– xM; 1.62–1.65 xF); BW, **0.72** (0.80; 0.67–0.70 xM; 0.76–0.80 xF); HL, **0.22** (0.19; 0.21–0.25 xM; 0.19–0.25 xF); HW, **0.29** (0.29; 0.27–0.30 xM; 0.29– xF); ID, **0.20** (0.19; 0.19–0.21 xM; 0.19–0.21 xF); PL, **0.31** (0.30; 0.29–0.32 xM; 0.30–0.32 xF); PW, **0.54** (0.55; 0.51–0.55 xM; 0.55–0.57 xF); AS, **0.10** (0.10; 0.10–0.11 xM; 0.10– xF); AP, **0.21** (0.21; 0.19–0.21 xM; 0.21– xF); AB, **0.20** (0.21; 0.19–0.21 xM; 0.19–0.21 xF) and AD, **0.31** (0.30; 0.30–0.32 xM; 0.30– xF).

Etymology. This species was named after the Sucre state, in Venezuela, its type locality. Due to *A. araguanus* sp. n., which was initially considered to be a very similar species and found in a very near location, we decided to name these two species after their type localities.

Distribution. Described from Venezuela.

Material examined. **Holotype** xF: **VENEZUELA**: Sucre: 4m, 7km S El Pilar, 29.VII.87, S. & J. Peck, rainforest remnant, leaf&log litter [Guidoti PhD — Vianaidinae 004] (AMNH). **Paratypes**: **VENEZUELA**: Sucre: 4m, 7km S El Pilar, 29.VII.87, S. & J. Peck, rainforest remnant, leaf&log litter [Guidoti PhD — 3xM, Vianaidinae 001–002, 005; 1xF, Vianaidinae 003] (AMNH).

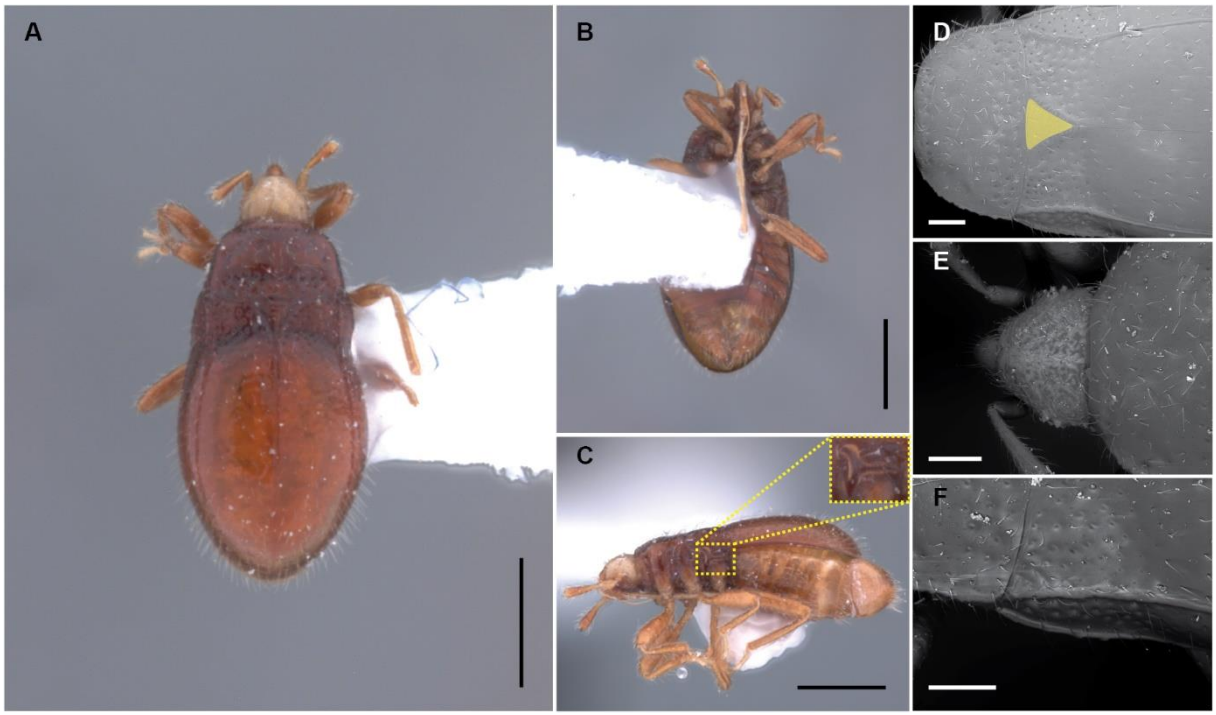

Figure 27. *Anommatocoris sucreanus* sp. n. in A) dorsal, B) ventral an C) lateral views, with scent gland in detail and SEM photographs of: D) thorax, scutellum roughly highlighted; E) head in dorsal view; F) humeral angle and hemelytral constriction. Holotype illustrated in A-B and D. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Anommatocoris zeteki Drake & Froeschner, 1962 (Fig. 28)

Diagnosis. *Anommatocoris zeteki* can be identified by the color of the head, the lightly pronounced humeral angle, the relatively large scutellum, the carina-like vein reaching the middle of the hemelytra, and the scent gland unequally divided as in *A. coibensis* and *A. schuhii* sp. n. It differs from these two species on the degree of development of such traits, on the body length and width remarkably smaller, and by the almost straight and with enlarged edges anterior branch of the peritreme.

Re-description. *Body*. Brown; head, same as the body; antennae, rostrum and legs lighter (Fig. 28A). *Head*. Pubescent, with small and well-spaced hairs; clypeus lighter than head, same color as antennae; antenniferous process about one-third of pedicel length; pedicel more than twice the size of scape; eyes with just a few scarcely distributed ommatidia; bucculae rounded, widest anteriorly, with scarce hairs on its border and punctures organized in a single row in the middle with a couple of extra punctures above, slightly concave posteriorly (Fig. 28E); rostrum reaching at least third abdominal segment (Fig. 28B-C). *Thorax*. Finely punctuate, with fine punctures on collar and on the posterior lobe of pronotum; anterior border straight, posterior sinuous; paranota carinate culminating in a small humeral acute angle (Fig. 28F), with hairs on its border; scutellum large, less than one-third of the maximum pronotum width (Fig. 28D). *Hemelytra*. Coriaceous and coleopteroid, pubescence apparently concentrated on subcostal and costal area, with some few scattered hairs in the middle of the hemelytra; laterally constricted anteriorly; carina-like vein extending from the anterior border to the middle of hemelytra, fading abruptly; punctures on anterior part up to the hemelytra constriction, completely smooth posteriorly to the hemelytra constriction. *Scent gland*. Anterior branch with slightly sinuous edges, these considerably enlarged if compared to posterior branch, tip slightly tilted horizontally; posterior straight, edges conspicuously narrow, bottom edge three times as wide as upper edge; sulcus prominent on posterior branch, weakly impressed on anterior branch; evaporatorium with straight border anteriorly, advancing to slightly less than one-third of mesopleuron (Figs. 16I – 28C).

Measurements. BL, **1.85** (1.77; 1.77 xM; 1.94 xF); BW, **0.86** (0.78; 0.78 xM; 0.95 xF); HL, **0.22** (0.23; 0.23 xM; 0.21 xF); HW, **0.32** (0.30; 0.30 xM; 0.34 xF); ID, **0.19** (0.17; 0.17 xM; 0.21 xF); PL, **0.34** (0.32; 0.32 xM; 0.36 xF); PW, **0.58** (0.55; 0.55 xM; 0.61 xF); AS, **0.11** (0.11; 0.11 xM; 0.11 xF) and AP, **0.25** (0.25; 0.25 xM; 0.25 xF).

Distribution. Known only from Panama, Canal Zone.

Material examined. **Holotype** xM: **PANAMA**: Barro Colorado Island: Panama Canal Zone, VII.VIII.42, J. Zetek col. (USNM). **Allotype**: **PANAMA**: Barro Colorado Island: Panama Canal Zone, VII.VIII.42, J. Zetek col., No. 4988. [Guidoti PhD — Vianaidinae 036] (USNM).

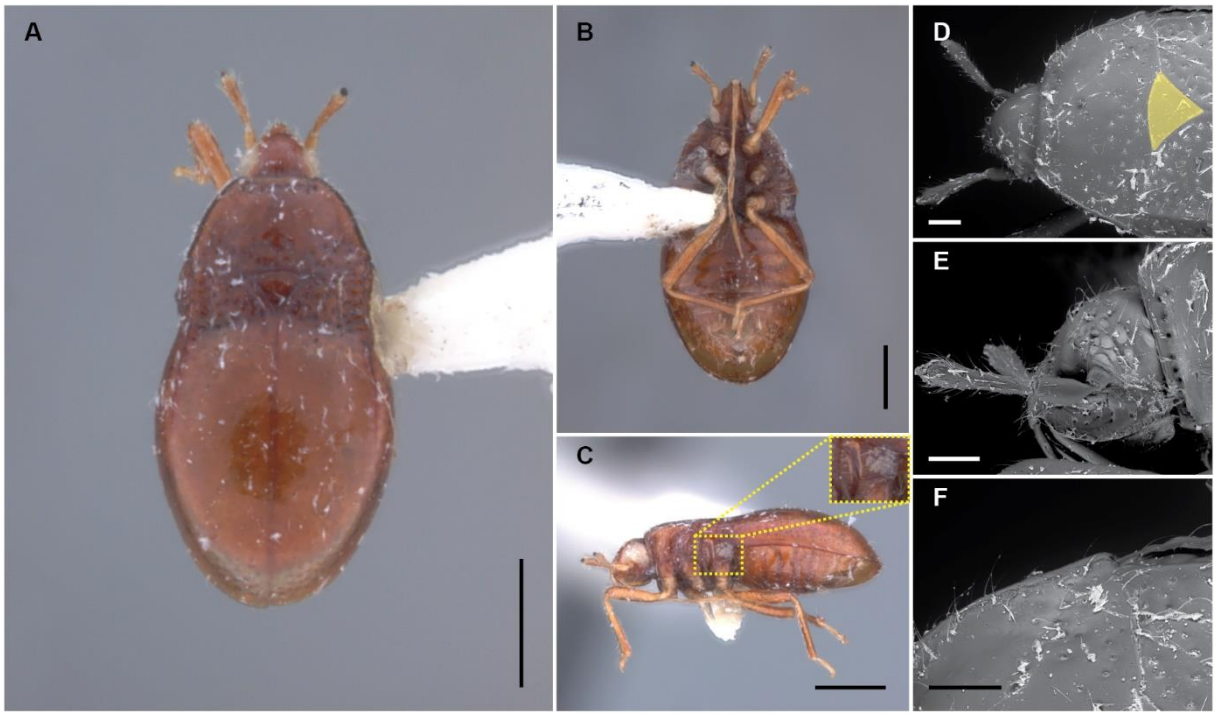

Figure 28. *Anommatocoris zeteki* allotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) humeral angle. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Henryianaida Guidoti, Montemayor & Guilbert gen. n.

Diagnosis. This genus can be easily identified by the constricted mandibular plates, which is unique among the known extant vianaidines. There are only macropterous forms known for this genus but the presence of an anteriorly expanded paranota, the large scutellum, the constriction on the anterior part of the hemelytra, the narrow subcostal area less than half of the width of the discoidal area in its widest part, and the scent gland peritreme clearly Y-shapped and not laterally expanded appears to be diagnostic characters for the genus and possibly not affected by the possible and perhaps expected wing polymorphism.

Description. *Head*. Triangular in dorsal view, pubescent, with hairs on vertex; mandibular plates constricted; pedicel three times the length of scape, other segments missing; eyes fully developed, compound; bucculae posterior border straight; rostrum reaching abdomen. *Thorax*. Posterior lobe raised, barely punctuate on most of its extant, but strongly punctuate near posterior border; collar somehow distinct, punctuate; anterior border convex, passing posterior edge of the eyes; posterior border usually convex; paranota explanate, smooth, expanded anteriorly. *Hemelytra*. Macropterous, clavus and vein-less membrane well-defined; constricted

anteriorly; punctuate on coriaceous parts; subcostal area subvertical; costal vein not very noticeable; costal area explanate, punctuate; hypocosta broad and finely punctuate. *Scent gland*. Anterior branch not laterally projected, strongly inclined forward; posterior branch usually straight; evaporatorium barely projected on mesopleuron, occupying a slightly curved and inclined area. *Legs*. Femora swollen; tarsi two segment, second segment many times the length of the first. *Abdomen*. Rectangular, covered with hairs; spiracles located ventrally near lateral margins of abdominal sternites, these straight.

Etymology. This genus was named after a great friend and wonderful American entomologist, Dr. Thomas J. Henry. Dr. Henry helped the leading author on his PhD by serving as a member on his annual evaluation committee and as his sponsor on a pre-doctoral fellowship awarded by the Smithsonian Institution. Besides this close relationship with this project, Dr. Henry has a remarkably productive career, contributing greatly with Heteroptera and specially, Miridae. His enthusiasm and passion are extremely contagious and left a good mark on the leading author after this year working side-by-side at the NMNH.

Type species. *Henryianaida colombiensis* sp. n.

Distribution. South America: Colombia and Peru (Fig. 18B).

Discussion. *Henryianaida* gen. n. is proposed here based on two macropterous singletons, both described as new species in this contribution. The difference in size of these two species is unique among Vianaidinae genera to this date. The genus presents at least one unique feature among all known extant species of Vianaidinae, which is the constricted mandibular plate. The general habitus of both species resembles *A. bolivianus* but it was impossible to compare the newly described taxa with this species due to its holotype situation. However, features like the presence of an anteriorly explanate paranota, a subhorizontal subcostal area and an anterior branch of peritreme more inclined forward, altogether with the aforementioned constricted mandibular plates, put these two species apart of this macropterous *Anommatocoris*. Following the results of our analysis, these two species are here proposed as a new genus.

***Key to the species of Henryianaida* gen n.**

1. Hemelytra border bearing scale-like projections anteriorly; subcostal area less than two times wider than costal area; total body length not surpassing 2.5 mm..... ..... ***H. machupicchuensis*** sp. n.

-. Hemelytra border smooth throughout its whole extent; subcostal area more than two times wider than costal area; total body length surpassing 4 mm..... .....***H. colombiensis*** sp. n.

Henryianaida colombiensis Guidoti, Montemayor & Guilbert sp. n. (Fig. 29)

<u>Diagnosis</u>. *Henryianaida colombiensis* sp. n. can be easily distinguished from the other *Henryianaida* species by its size: it's almost twice as long and at least twice as large. Additionally, its wider paranota, costal area and consequently hemelytra are also important diagnostic differences among these two species.

<u>Description</u>. *Body*. Head, pronotum, hemelytra brown (Fig. 29A); antennae, rostrum, legs and abdomen light brown, yellowish. *Head*. Pubescent; eyes fully-developed, length at least half of head's length; antenniferous process small; pedicel three times longer than scape, basi- and distiflagellomere missing; bucculae roundish, narrower posteriorly, border pubescent and slightly serrate, few fine punctuate present, posterior border straight (Fig. 29E); rostrum reaching first abdominal segment (Fig. 29B-C). *Thorax*. Pubescent, finely punctuate, except for middle of posterior lobe; paranota explanate, narrowing posteriorly, border sinuous, pubescent; scutellum large, less than one-third the maximum width of pronotum (Fig. 29D); sternal laminae narrow, punctuate. *Hemelytra*. Clavus coarsely punctuate; discoidal, subcostal and costal area only finely punctuate; discoidal area about three times subcostal area at its widest; subcostal area wider at middle, extending to the apex of membrane; costal area broadening posteriorly, widest at middle; membrane without inner row of punctuation (Fig. 29F). *Scent gland*. Anterior branch strongly inclined forward, tip curved horizontally, short and not swollen, sulcus barely present, fading distally; posterior branch tip swollen and curved, sulcus prominent through its entire length (Figs. 16J – 29C).

<u>Measurements</u>. BL, 4.19; BW, 1.88; HL, 0.27; HW, 0.59; ID, 0.29; PL, 0.70; PW, 1.16; AS, 0.25 and AP, 0.76.

Etymology. This species was named based on the country of its type locality, Colombia, becoming the third Vianaidinae macropterous species, out of four, to be named based on its type locality.

Distribution. Described from Colombia.

Material examined. **Holotype** xM: **COLOMBIA**: Caldas Prov.: Villamaria, 2015, D. Forero col. [MPUJ_ENT_0046225] [Guidoti PhD — Extraction #374] [Guidoti PhD — Vianaidinae 059] (MPUJ).

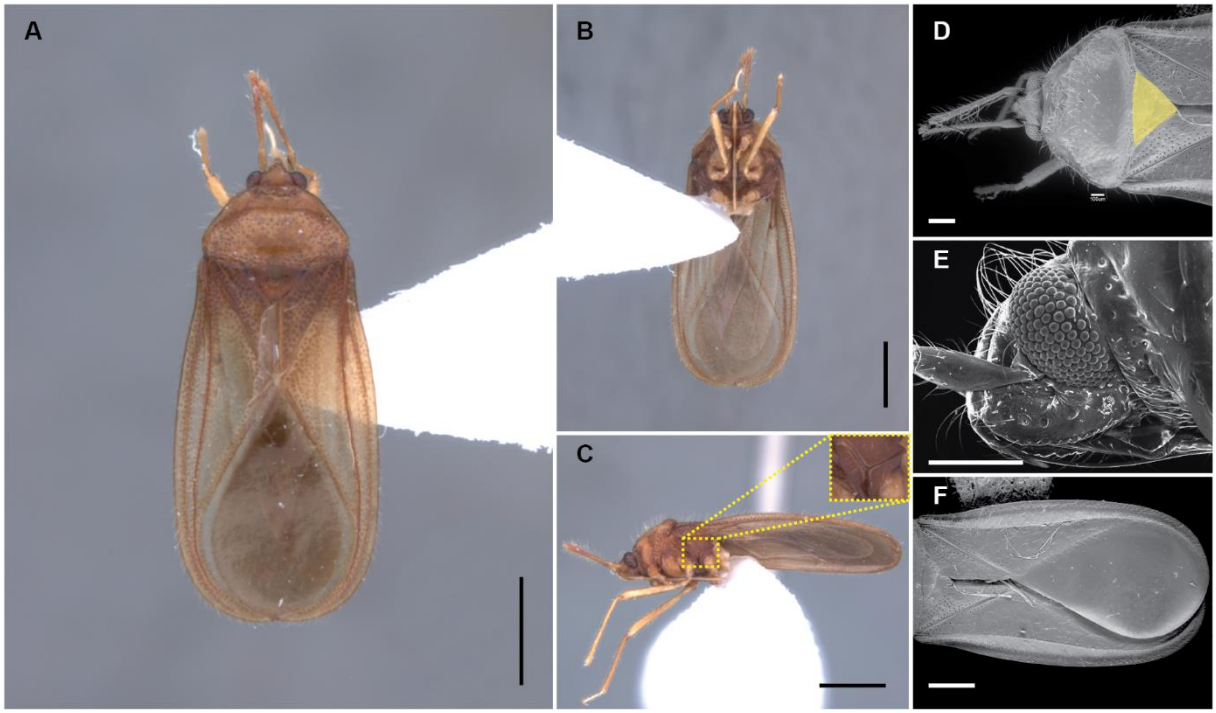

Figure 29. *Henryianaida colombiensis* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) hemelytra macropterous. Scale bars: A-C) 1 mm; D-E) 0.2 mm; F) 0.5 mm.

Henryianaida machupicchuensis Guidoti, Montemayor & Guilbert sp. n. (Fig. 30)

Diagnosis. This species presents scale-like projections on the anterior part of the hemelytra border, and also differs from *H. colombiensis* sp. n. by the anterior branch of the scent gland peritreme, more curved and shorter, and by the entirely enlarged edges on the posterior branch, and by its subcostal area, only less than twice wider than the costal area in its widest part.

Description. *Body*. Head, pronotum, hemelytra light brown (Fig. 30A); antennae, rostrum legs and abdomen even lighter, yellowish. *Head*. Pubescent; eyes fully-developed, length less than half of head's length; antenniferous process small, less than one-eighth of pedicel length; pedicel less than three times longer than scape, basi- and distiflagellomere missing; bucculae roundish, narrower posteriorly, border pubescent, few coarse punctuations near junction with head, a second-row compound by three smaller punctuates present, posterior border straight (Fig. 30E); rostrum only reaching first abdominal segment (Fig. 30B-C). *Thorax*. Hairs mostly anteriorly, finely punctuate, except for middle of posterior lobe; paranota explanate, narrowing posteriorly, border sinuous, lightly pubescent (Fig. 30F); scutellum large, less than one-third the maximum width of pronotum (Fig. 30D); sternal laminae narrow, punctuate.

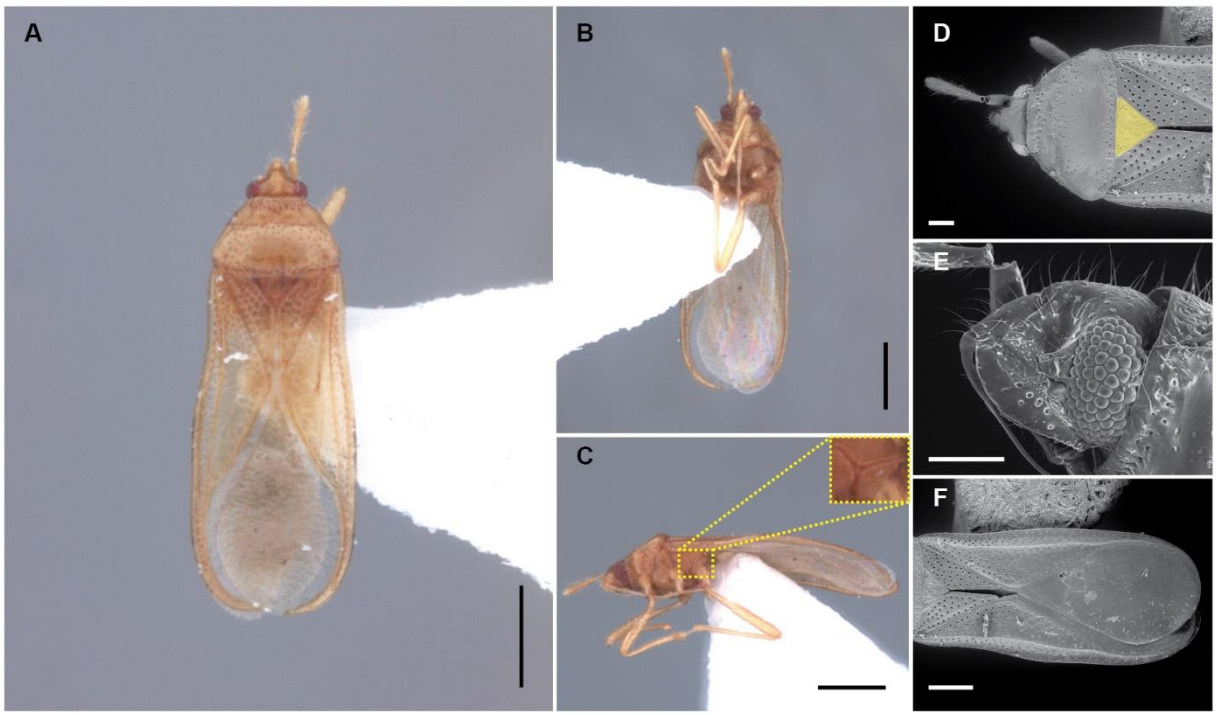

Figure 30. *Henryianaida machupicchensis* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) head and thorax, scutellum roughly highlighted; E) head, in lateral view; F) hemelytra macropterous. Scale bars: A-C) 0.5 mm; D-E) 0.1 mm; F) 0.25 mm.

Hemelytra. Margins with scale-like projections anteriorly; clavus coarsely punctuate; discoidal, subcostal areas coarsely punctuate anteriorly, then fading to become only finely punctuate; discoidal area about two and a half times subcostal area at its widest; subcostal area wider at middle, extending to the apex of membrane; costal area broadening posteriorly, widest at middle; membrane without inner row of punctuation. S*cent gland*. Anterior branch strongly inclined forward, tip curved horizontally and distant from hemelytra border, short and not

swollen, sulcus barely present, fading distally; posterior branch tip curved, sulcus prominent through its entire length (Figs. 16K – 30C).

Measurements. BL, 2.19; BW, 0.78; HL, 0.19; HW, 0.30; ID, 0.17; PL, 0.36; PW, 0.51; AS, 0.13 and AP, 0.32.

Etymology. This species was named based on its type locality, the Putucusí trail, in Peru. This trail is in a mountain with one of the most famous views of Machu Picchu, the prestigious and world-wide famous Inca citadel.

Distribution. Described from Peru.

Material examined. **Holotype** xM: **PERU**: Urubamba Prov.: Putucusí trail, 2104m, 13º09'11.5"S 72º31'38.9"W, 1 Jan 2010, J. Heraty, cloud forest [H10-178] [Guidoti PhD — Extraction #370] [Guidoti PhD — Vianaidinae 058] (GC).

Pterovianaida Montemayor & Carpintero, 2007

Diagnosis. This genus can be characterized by the abundant long hairs in the head, which is remarkably inclined downwards, by the presence of paranota constricted in the middle and a conspicuously raised distal part of the pronotum, and by the scent gland, which is laterally projected with the edges of the tips of both anterior and posterior peritreme branches enlarged.

Re-description. *Head*. Triangular in dorsal view, pubescent, with large long hairs on vertex once referred as macrochetae; pedicel subequal to basiflagellomere and to distiflagellomere, each one of these more than twice the length of scape; eyes fully developed, compound; rostrum reaching at least the second abdominal segment. *Thorax*. Posterior lobe strongly raised, pubescent; entirely punctuate; collar distinct, punctuate; anterior border straight, posterior convex; paranota explanate, smooth, constricted in the middle, between the anterior and posterior lobes. *Hemelytra*. Macropterous, clavus and vein-less membrane well-defined; scale-like projections on hemelytra border; punctuate on coriaceous parts; membrane with one inner row of punctuations; hypocosta broad and finely punctuate. *Scent gland*. Anterior branch gradually projected laterally, tip much more projected than base; tip tilted horizontally, large, conspicuously inclined frontwards; posterior branch usually curved, with enlarged tip. *Legs*. Femora same width of the other segments; tarsi two segment, second segment remarkably

longer and many times the length of the first. *Abdomen*. Rectangular, covered with hairs; spiracles located ventrally near lateral margins of abdominal sternites, these straight.

Type species. *Pterovianaida melchiori* Montemayor & Carpintero, 2007.

Distribution. South America: Brazil and Peru (Fig. 18C).

Discussion. *Pterovianaida* was described by Montemayor & Carpintero (2007) based on a single slide-mounted specimen. Additionally, it is clear the authors were not aware of Schuh *et al.* (2006) macropterous species when proposing the genus. However, the genus gained its second species almost 10 years after its original description based on a single specimen found at INPA, confirming its identity and enhancing the differences between *Pterovianaida* and the only known macropterous *Anommatocoris*. Moreover, in this review, several shared characters between this genus and *Thaumamannia* were observed, and among them is the head inclination and the general shape of the scent gland peritreme. Both specimens were collected on light traps, suggesting an active flight behavior at night. These are the only two specimens known for this genus.

Key to the species of Pterovianaida

1. Paranota explanate, clearly wider anteriorly; a conspicuously raised distal part of pronotum; subcostal area of hemelytra reaching the apex of membrane .... ***P. duckensis*** Guidoti & Montemayor

-. Paranota thin, barely explanate; distal part of pronotum not remarkably raised; subcostal area of hemelytra not reaching the apex of memebrane..... ..... ***P. melchiori*** Montemayor & Carpintero

Pterovianaida duckensis Guidoti & Montemayor, 2016 (Fig. 31)

Diagnosis. *Pterovianaida duckensis* can be easily distinguished from *P. melchiori* by the wider paranota and the longer subcostal area reaching the apex of the membrane.

Re-description. *Body*. Head, pronotum dark brown, scutellum even darker; hemelytra, antennae, rostrum, legs and abdomen yellowish (Fig. 31A). *Head*. Eyes fully-developed, at least half of head's length; antenniferous process small, less than one-sixth of pedicel length; pedicel, basi- and distiflagellomere subequal and more than two times the size of scape; bucculae roundish, widest anteriorly, bearing hairs on its border and few punctuations displayed in a row, these big, almost the size of an ommatidia, posterior border concave (Fig. 31F); rostrum reaching middle of abdomen (Fig. 31B-C). *Thorax*. Projected towards head, covering part of the posterior region of the eyes; posterior lobe considerably raised; paranota always explanate, narrowing posteriorly; scutellum less than one-fourth the maximum width of pronotum (Fig. 31E); sternal laminae narrow, punctuate.

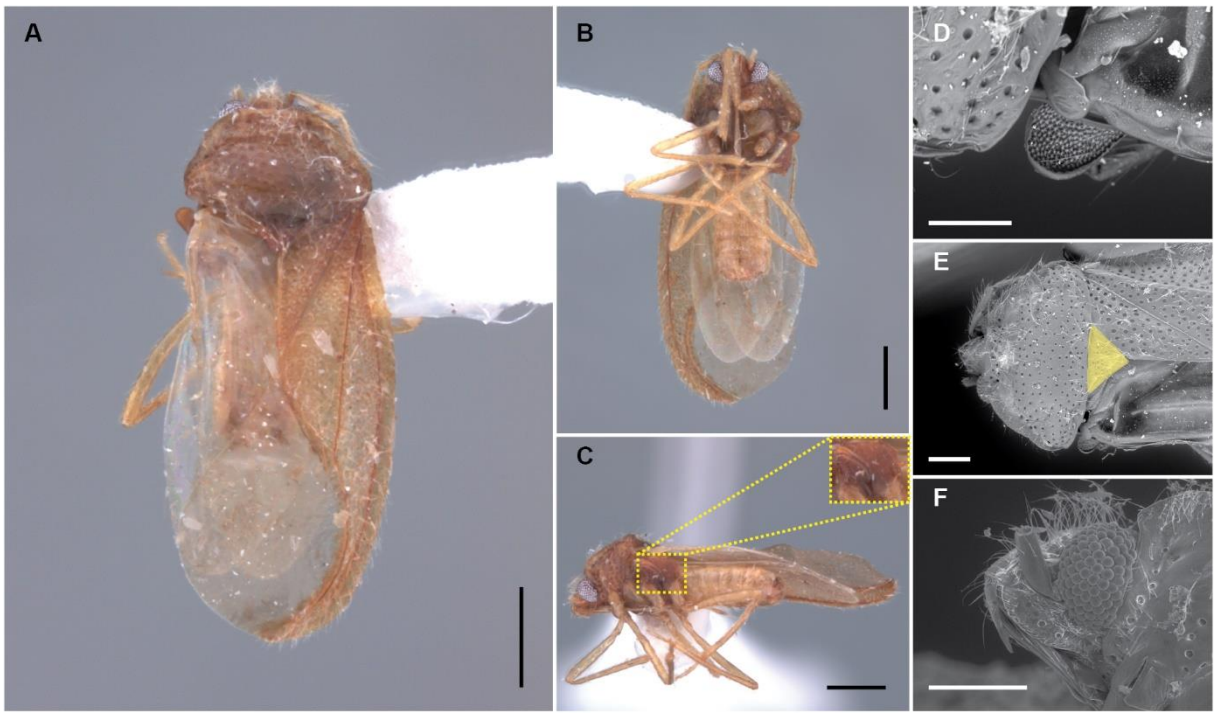

Figure 31. *Pterovianaida duckensis* holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) scent gland, dorsal view; E) head and thorax, scutellum roughly highlighted; E) head, in lateral view. Scale bars: A-C) 0.5 mm; D) 0.1 mm; E-F) 0.2 mm.

Hemelytra. Clavus almost as wide as discoidal area, this, subequal to subcostal area; subcostal area extending to the apex of membrane, at least four times wider than costal area; costal area equally wide on its whole extent; all coriaceous regions equally and coarsely punctuate; membrane with one inner row of punctures. *Scent gland*. Anterior brand gradually projected laterally, tip considerably projected, visible dorsally (Fig. 31A, D), and tilted horizontally and enlarged, strongly inclined forward; posterior branch curved and enlarged on its tip; sulcus

fading on anterior branch and deeply marked on posterior branch; evaporatorium barely projected on mesopleuron, occupying a straight, rectangular area (Figs. 16L – 31C).

Measurements. BL, 2.77; BW, 1.30; HL, 0.35; HW, 0.51; ID, 0.21; PL, 0.80; PW, 0.98; AS, 0.14; AP, 0.34; AB, 0.34 and AD, 0.34 (updated from Guidoti & Montemayor, 2016).

Distribution. Known only from Brasil, Amazonas state.

Material examined. **Holotype** xM: **BRAZIL**: Amazonas: AM 010, Km 26, Reserva Ducke, 06.XII.1977, Jorge Arias col. [C.D.C. Light Trap 1-1] [Piesmatidae (sic)] [INPA (51) — Guidoti, 2012 — Loan] (INPA).

Pterovianaida melchiori Montemayor & Carpintero, 2007 (Fig. 32)

Diagnosis. The only known specimen of this species was slide-mounted, hampering the correct observation of many valuable structures. However, despite the aforementioned differences on the paranota and subcostal area, it seems to also differ from *P. duckensis* by its anterior branch of the peritreme, which apparently is inclined downwards, and by the distal part of the pronotum, which is likely to be much less elevated than in *P. duckensis*.

Re-description. *Body*. Mostly inaccessible due to the preservation method of the only known specimen (Fig. 32E). *Head*. Pubescent; apparently strongly declined (Fig. 32A); eyes fully-developed, slightly less than half of head's length; antenniferous process apparently close to half of pedicel length; pedicel, basi- and distiflagellomere subequal and three times the size of scape; bucculae also inaccessible; rostrum reaching only up to the first two abdominal segments. *Thorax*. Apparently not projected towards head (Fig. 32C); posterior lobe considerably raised; paranota narrow but explanate with a constriction at the posterior lobe anterior region; scutellum inaccessible; sternal laminae narrow, punctuation uncertain. *Hemelytra*. Clavus slightly narrow than discoidal area, this, one and a half times wider than subcostal area; subcostal area extending to the apex of membrane, at least three times wider than costal area; costal area equally wide on its whole extent; all coriaceous regions equally and coarsely punctuate; membrane with one inner row of punctures (Fig. 32B, D). *Scent gland*. Mostly inaccessible, however, anterior branch is clearly inclined forward, with a tilted horizontally and enlarged tip; evaporatorium also inaccessible.

Measurements. BL, 2.45; HL, 0.23; HW, 0.30; ID, 0.09; AS, 0.11; AP, 0.31; AB, 0.33 and AD, 0.37 (Montemayor & Carpintero, 2007).

Distribution. Known only from Peru.

Material examined. **Holotype** xM: **PERU**: Ucayali: Kirigueti (light trap), 11º38'13"S 73º07'08"W, August 2004, J. Williams coll. (MLP).

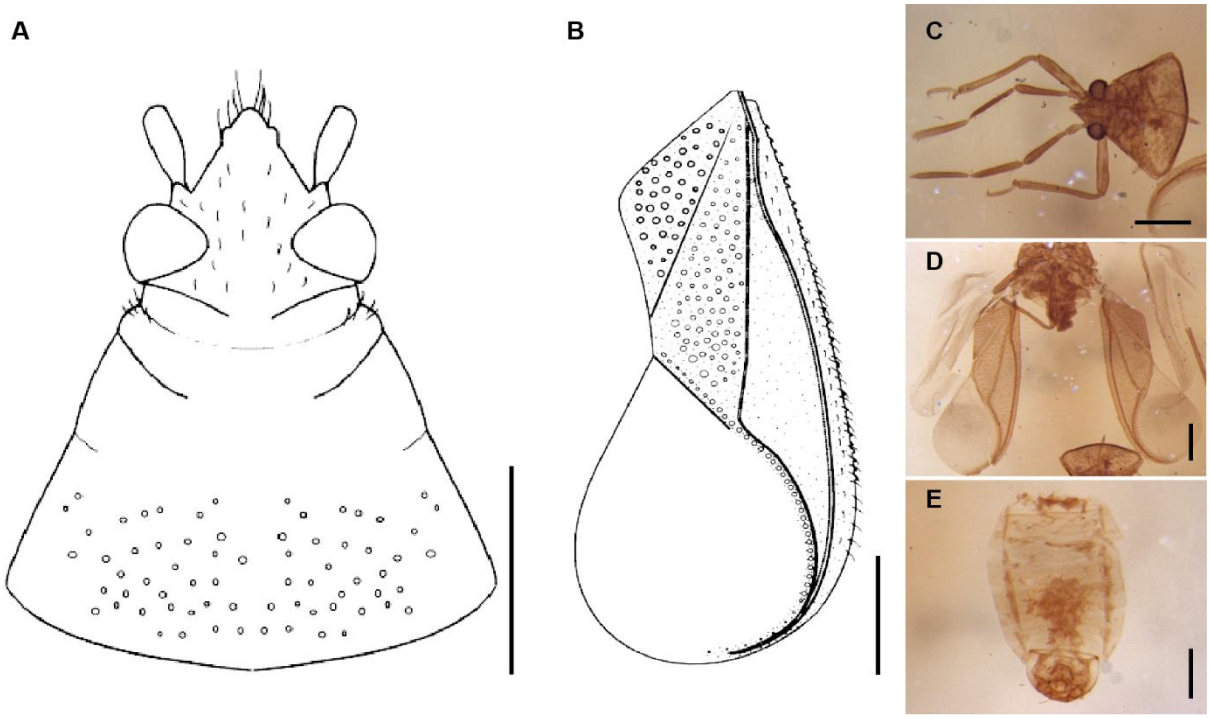

Figure 32. *Pterovianaida melchiori* holotype in A) head and pronotum and B) hemelytra, both in dorsal view and modified from Montemayor & Carpintero (2007); C) head and pronotum; D) meso- and metanotum, with legs and wings and; E) abdomen of the slide-mounted holotype and single known specimen of this species. Scale bars: A) 0.2 mm; B-E) 0.25 mm.

Thaumamannia Drake & Davis, 1960

Diagnosis. Characterized by the inclined head, the presence of explanate paranota and costal area, the relatively small scutellum, conspicuously concave hemelytra, and the laterally projected scent gland, strongly Y-shapped with enlarged tips in both anterior and posterior branches of the peritreme.

Re-description. *Head*. Inclined downwards, usually with most of its length hidden in dorsal view, heavily pubescent; clypeus usually in different color than head; pedicel subequal to

basiflagellomere, both smaller than distiflagellomere and usually twice as big as scape; eyes reduced with none or few ommatidia, triangular in shape; rostrum reaching at least the third abdominal segment. *Thorax*. Posterior lobe slightly raised; coarsely punctuate, mostly on collar and posterior lobe, collar indistinct; anterior border usually concave; posterior usually straight; paranota explanate, smooth, usually projected forwards. *Hemelytra*. Entirely coriaceous and coleopteroid, ovate, pubescent; remarkably convex, no clavus nor membrane distinct; carina-like vein extending variably from the anterior border, deeply punctuate; costal area explanate, with one inner row of punctuations only; hypocosta broad and coarsely punctuate. *Scent gland*. Anterior branch gradually projected laterally, tip much more projected than base; varying in height, conspicuously inclined frontwards; tip tilted horizontally, large; posterior branch usually curved, with enlarged tip. *Legs*. Femora only slightly swollen; tarsi two segment, second segment at least 5-times longer.

Type species. *Thaumamannia manni* Drake & Davis, 1960.

Distribution. South America: Brazil, Bolivia and Suriname (Fig. 18D).

Discussion. The genus was described by Drake & Davis (1960), and the second species, *Thaumamannia vanderdrifti* van Doesburg (1977) was only described 17 years later. From these two species, only *T. manni* was collected associated with ants (Drake & Davis, 1960). The broadly ovate body, which was considered a strong diagnostic feature of the genus is now challenged with the description of a new species herein described. However, the conspicuously Y-shaped scent gland remains as an important diagnostic character for the genus, now currently composed by a total of four species, including the two species described below. *Thaumamannia vanderdrifti* was the first Vianaidinae reported from Brazil (Guidoti *et al.*, 2014), and now both *T. insolita* sp. n. and *T. urucuana* sp. n. are also reported from that country. *Thaumamannia insolita* sp. n. and one specimen of *T. urucuana* sp. n. had its locality data reported as lost and we only know the state where they came from (Pará state, Brazil). The only species with immature forms described is *T. vanderdrifti*, which had its fifth instar described and analyzed in SEM (Guidoti *et al.*, 2014).

Key to the species of Thaumamannia

1. Body broadly ovate; head with the same color as the body, strongly inclined downwards 2

-. Body only ovate; head color significantly lighter than the body, not strongly inclined downwards..... ***T. insolita*** sp. n.

2. Scent gland visible in dorsal view; widest part of the body about as wide as pronotum. 3

-. Scent gland not visible in dorsal view; widest part of the body considerably wider than pronotum ..... ***T. manni*** Drake & Davis, 1960

3. Anterior branch of peritreme without laterally projected edges, bottom edge not visible in dorsal view ..... ***T. urucuana*** sp. n.

-. Anterior branch of peritreme with laterally projected edges, bottom edge visible in dorsal view ..... ***T. vanderdrifti*** van Doesburg, 1977

Thaumamannia insolita Guidoti, Montemayor & Guilbert sp. n. (Fig. 33)

<u>*Diagnosis*</u>. *Thaumamannia insolita* sp. n. is a very interesting new species found to be sister group with the other *Thaumamannia* species while presenting quite a few traits shared with *Anommatocoris* species as well. The inclination of the head, the differences in color between the head and body, the enlarged edges of the tips in the anterior branch of the peritreme, and the slender body are characters that distinguish this species from its congeners.

<u>*Description*</u>. *Body*. Brown, with scutellum and paranota borders light brown; head, antennae, rostrum and legs yellowish, except for clypeus, which is as brown as the body (Fig. 33A). *Head*. Slightly inclined downwards, pubescent; antenniferous process almost half the scape length; pedicel subequal to basiflagellomere, these slightly bigger than scape and smaller than distiflagellomere; eyes reduced with few ommatidia, somehow triangular; bucculae roundish, border serrate, widest in the middle, two rows of small punctures, posterior border concave (Fig. 33F); rostrum reaching at least the fourth abdominal segment (Fig. 33B-C). *Thorax*.

Pubescent; coarsely punctuate, except for the callus region; anterior border straight; posterior convex; paranota explanate, smooth, not projected frontwards, with scale-like projections on its border giving it a serrate-like aspect; scutellum narrow, less than one-sixth of pronotum maximum width (Fig. 33E); sternal laminae considerably narrow, punctuate. *Hemelytra*. Entirely coriaceous and coleopteroid, ovate, pubescent; remarkably convex; carina-like vein extending from the anterior border to the posterior third of the hemelytra; deeply and entirely punctuate, these bigger at anterior region, small at posterior third and even smaller at middle; costal area not punctuate, anterior border round. *Scent gland*. Anterior branch gradually projected laterally, tip tilted horizontally, large, only slightly shorter than the rest of anterior branch, much more projected than base (Fig. 33D), edges equally thick throughout its length; posterior branch straight, with only a slightly enlarged tip with a weak aspect of a cracked texture; sulcus prominent on both branches, fading only distally on the anterior branch tip; evaporatorium curved anteriorly, projected up to half of mesopleuron (Figs. 17A – 33C).

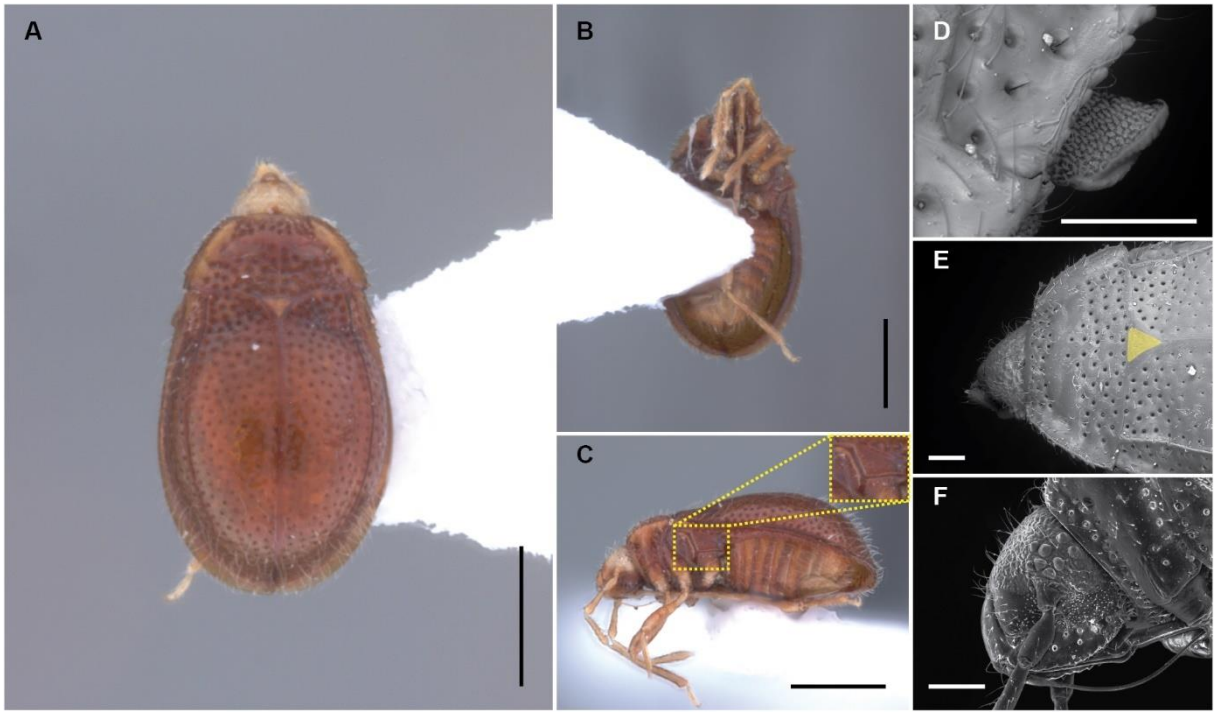

Figure 33. *Thaumamannia insolita* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) scent gland, dorsal view; E) head and thorax, scutellum roughly highlighted; E) head, in lateral view. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Measurements. BL, 1.52; BW, 0.86; HL, 0.15; HW, 0.29; ID, 0.19; PL, 0.30; PW, 0.62; AS, 0.11; AP, 0.17; AB, 0.21 and AD, 0.30.

Etymology. This species confused the authors and could only be placed in a genus after the phylogenetic analysis. Due to its puzzled nature we considered this species "*insolitus*", which means unusual, uncommon, strange.

Distribution. Described from Brazil.

Material examined. **Holotype** xF: **BRAZIL**: Pará state. [Hemiptera 6º P8 (E)] [GCLBN27] [Guidoti PhD — FR056] [Guidoti PhD — Vianaidinae 057] (GC).

Thaumamannia manni Drake & Davis, 1960 (Fig. 34)

Diagnosis. This species is the only *Thaumamannia* species where the scent gland is not visible in dorsal view. Additionally, the body format is remarkably different in *Thaumamannia manni*, with a larger difference between the pronotum width and the widest part of the body, and this is the only *Thaumamannia* species with a slightly acute humeral angle.

Re-description. *Body*. Brown to reddish; antennae, rostrum and legs light brown (Fig. 34A). *Head*. Strongly inclined downwards (Fig. 34F), pubescent; antenniferous process almost half the scape length; pedicel almost twice the scape length, basi- and distiflagellomeres missing; eyes reduced with few ommatidia; bucculae roundish, smooth on its border, widest posteriorly, with only few small punctures near the insertion with the head, posterior border rounded; rostrum reaching at least the third abdominal segment (Fig. 34B-C). *Thorax*. Pubescent; collar punctuate; posterior lobe coarsely punctuate; anterior border straight to slightly concave, posterior straight to slightly convex; paranota explanate, smooth, projected frontwards to up middle of the eyes, and in a small humeral angle posteriorly (Fig. 34D); scutellum large, less than one-fourth of pronotum maximum width (Fig. 34E); sternal laminae narrow, punctuate. *Hemelytra*. Coriaceous, coleopteroid, ovate, pubescent and remarkably convex; carina-like vein extending from the anterior border to the posterior third of the hemelytra; deeply and entirely punctuate; costal area with one row of punctures, anterior border round. *Scent gland*. Anterior branch gradually projected laterally, tip tilted horizontally, large, same size as the rest of the anterior branch, much more projected than base of anterior branch, edges thicker on the tip; posterior branch curved, with considerably enlarged tip with a cracked texture; sulcus prominent on both branches, fading only distally on the anterior branch tip; evaporatorium curved anteriorly, projected up to half of mesopleuron (Figs. 17B – 34C).

Measurements. BL, 1.96; BW, 1.44; HL, 0.11; HW, 0.42; ID, 0.25; PL, 0.40; PW, 0.99; AS, 0.11 and AP, 0.21.

Distribution. Known only from Bolivia.

Material examined. **Holotype** xF: **BOLIVIA**: Mulford Biol. Expe. 1921-1922, W.M. Mann coll., 1954. [USNMENT 00871151] (USNM).

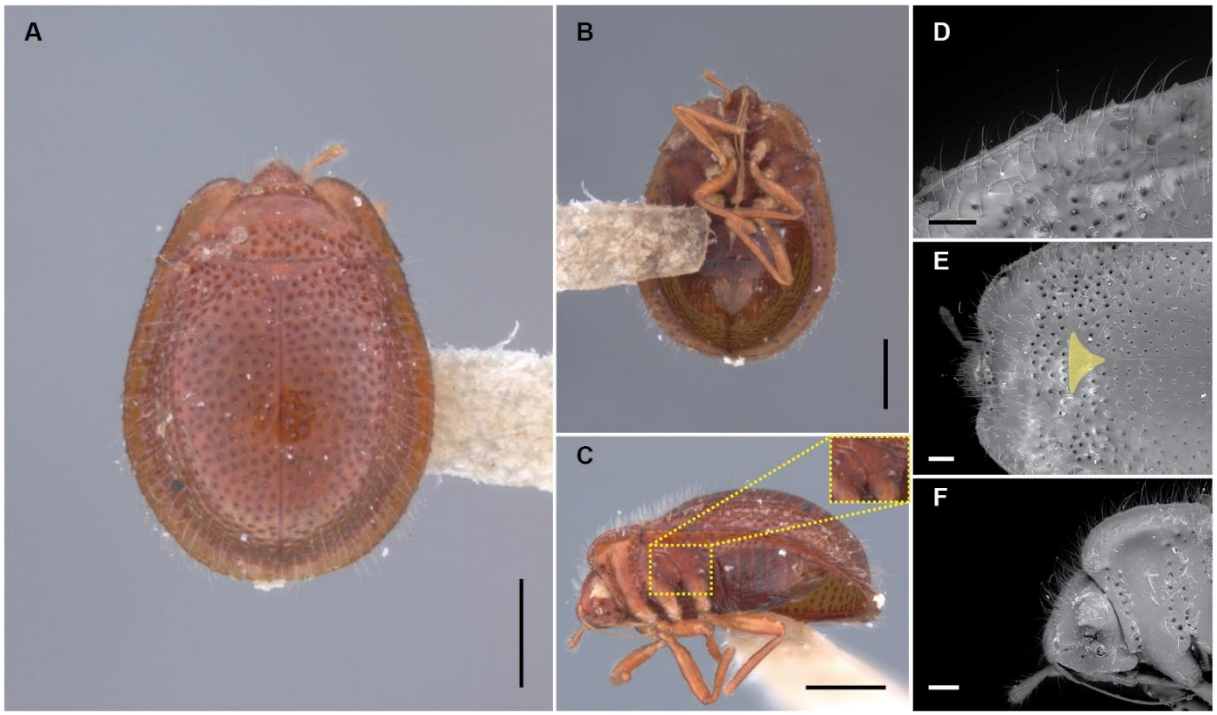

Figure 34. *Thaumamannia manni* holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) humeral angle; E) head and thorax, scutellum roughly highlighted; E) head, in lateral view. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Thaumamannia urucuana Guidoti, Montemayor & Guilbert sp. n. (Fig. 35)

Diagnosis. This species resembles the most *T. vanderdrifti* but can be recognized by the straight border of hemelytra on its anterior part at the scent gland level and by the tip of the anterior branch of the peritreme, which doesn't reach the hemelytra border like in *T. vanderdrifti*.

Description. *Body*. Dark brown, lighter on paranota and costal area; antennae, rostrum and legs yellowish (Fig. 35A). *Head*. Strongly inclined downwards, pubescent; antenniferous process about one-third of the scape length; pedicel almost three times the scape length, basi- and distiflagellomeres missing; eyes reduced with few ommatidia; bucculae round, smooth and

pubescent on its border, widest in the middle, with only few punctures in the middle of the bucculae, posterior border rounded (Fig. 35F); rostrum reaching at least the third abdominal segment (Fig. 35B-C). *Thorax*. Pubescent; coarsely punctuate except for the callus region; anterior and posterior border straight; paranota explanate, not punctuate, bearing scale-like projections on its border, projected frontwards surpassing most of the eyes; scutellum large, less than one-eighth of pronotum maximum width (Fig. 35E); sternal laminae narrow, punctuate. *Hemelytra*. Coriaceous, coleopteroid, ovate, densely pubescent and remarkably convex; carina-like vein extending from the anterior border to the posterior third of the hemelytra; deeply and evenly punctuate; costal area with scale-like projections on its border, with one row of inner punctures, anterior border straight, revealing scent gland dorsally. *Scent gland*. Anterior branch gradually projected laterally, tip tilted horizontally, large, same size as the rest of the anterior branch, much more projected than base of anterior branch (Fig. 35D), edges thicker on the tip; posterior branch curved, with considerably enlarged tip with a cracked texture; sulcus prominent on both branches, fading only distally on the anterior branch tip; evaporatorium more straight than curved anteriorly, projected up to half of mesopleuron (Figs. 17C – 35C).

Measurements. BL, **1.77** (1.79; 1.79 xM; 1.75 xF); BW, **1.23** (1.24; 1.24 xM; 1.22 xF); HL, **0.12** (0.10; 0.10 xM; 0.15 xF); HW, **0.34** (0.32; 0.32 xM; 0.36 xF); ID, **0.23** (0.23; 0.23 xM; 0.23 xF); PL, **0.37** (0.40; 0.40 xM; 0.34 xF); PW, **1.03** (1.06; 1.06 xM; 0.99 xF); AS, **0.12** (0.13; 0.13 xM; 0.11 xF) and AP, **0.32** (0.32; 0.32 xM).

Etymology. This species was named based on its type locality.

Distribution. Described from Brazil; holotype locality is in the Amazonas state, in a famous gas pipeline called “Urucu-Coari-Manaus gas pipeline”; paratype locality was reported as missing by the sample’s responsible (J.A.M. Fernandes, personal communication to the leading author).

Material examined. **Holotype** xM: **BRAZIL**: Amazonas: Petrobras-Urucu, 25.X.2006, S. Dias col. [clareira 3, método de Winkler] [SID 103] (MPEG). **Paratype**: **BRAZIL**: Pará state. [Hemiptera 7º P10 (E)] [GCLBN26] [Guidoti PhD — FR057] [Guidoti PhD — Vianaidinae 056] (GC).

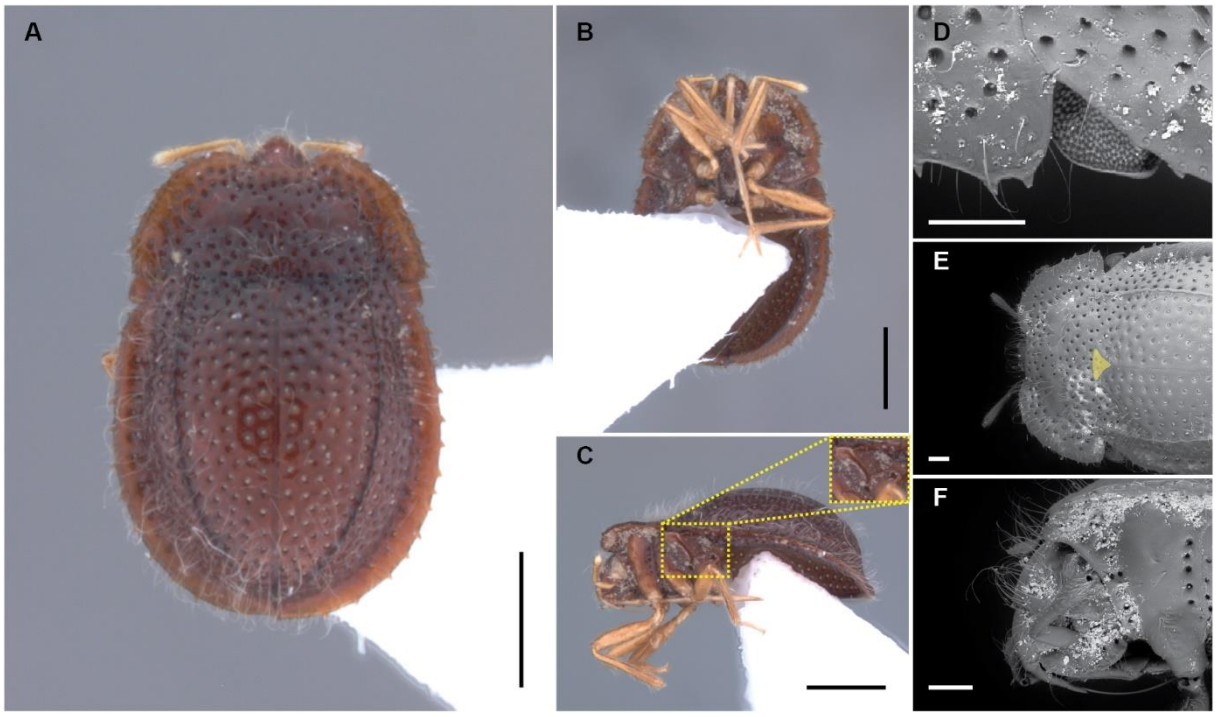

Figure 35. *Thaumamannia urucuana* sp. n. holotype in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) scent gland, dorsal view; E) head and thorax, scutellum roughly highlighted; E) head, in lateral view. Scale bars: A-C) 0.5 mm; D-F) 0.1 mm.

Thaumamannia vanderdrifti van Doesburg, 1977 (Fig. 36)

Diagnosis. This is the largest species of the genus and it's the only known species of *Thaumamannia* to present a laterally projected edge of the peritreme's anterior branch tip, forming a sulcus that is even noticeable in dorsal view.

Re-description. *Body*. Dark brown, slightly lighter on paranota and costal area; antennae, rostrum and legs even lighter (Fig. 36A). *Head*. Strongly inclined downwards, pubescent; antenniferous process about half of the scape length; pedicel mora than two times the scape length, slightly smaller than basiflagellomere, distilagellomere one and a half times the pedicel length; eyes reduced with few ommatidia; bucculae round, smooth and pubescent on its border, widest anteriorly, with few punctures near insertion with the head, these big and deeply impressed, posterior border concave (Fig. 36F); rostrum reaching at least the third abdominal segment (Fig. 36B-C). *Thorax*. Pubescent; coarsely punctuate including few punctuations on the middle of callus region; anterior and posterior border straight; paranota explanate, with few punctuations, bearing scale-like projections on its border, projected frontwards surpassing the eyes; scutellum large, almost one-ninth of pronotum maximum width (Fig. 36E); sternal

laminae narrow, punctuate. *Hemelytra*. Coriaceous, coleopteroid, ovate, densely pubescent and remarkably convex; carina-like vein extending from the anterior border to the posterior third of the hemelytra; deeply and evenly punctuate; costal area with scale-like projections on its border, with one row of inner punctures, anterior border round, revealing scent gland dorsally. *Scent gland*. Anterior branch gradually projected laterally, tip tilted horizontally, large, almost half the size of the rest of the anterior branch, much more projected than base of anterior branch, edges definitely thicker on the tip, these, unevenly laterally projected to the point of being observable dorsally (Fig. 36D); posterior branch strongly curved distally, with considerably enlarged tip with cracked texture; sulcus prominent on both branches, fading only distally on the anterior branch tip; evaporatorium with straight border anteriorly, only slightly projected on mesopleuron (Figs. 17D – 36C).

Measurements. BL, **2.29** (2.16–2.37 xM; 2.30–2.39 xF); BW, **1.51** (1.37–1.48 xM; 1.56–1.65 xF); HL, **0.12** (0.08–0.17 xM; 0.10–0.15 xF); HW, **0.47** (0.42–0.51 xM; 0.46–0.51 xF); ID, **0.27** (0.25–0.30 xM; 0.25–0.29 xF); PL, **0.53** (0.46–0.55 xM; 0.55–0.57 xF); PW, **1.23** (1.06–1.22 xM; 1.27–1.37 xF); AS, **0.13** (0.13– xM; 0.11–0.13 xF); AP, **0.30** (0.29–0.30 xM; 0.29–0.30 xF); AB, **0.39** (0.36–0.42 xM; 0.40 xF) and AD, **0.46** (0.46 xM).

Distribution. Described from Suriname by van Doesburg (1977) and reported in the Brazilian state of Pará by Guidoti *et al.* (2014).

Material examined. **Other specimens**: **BRAZIL**: Pará: Parauapebas, Caverna GEM 1784 (Est. Úmida) [GCLBN5] [Guidoti PhD — FR036] [Guidoti PhD — 1xM, Vianaidinae 049] (GC); **BRAZIL**: Pará: Parauapebas, Gruta S11 D-081 [Guidoti PhD — Extraction #261] [GCLBN8] [Guidoti PhD — FR038] [Guidoti PhD — 1xF, Vianaidinae 050] (GC); **BRAZIL**: Pará: Parauapebas, Gruta S11 D-99 [GCLBN10] [Guidoti PhD — FR042] [Guidoti PhD — 1xF, Vianaidinae 051] (GC); **BRAZIL**: Pará: Parauapebas, D-82 [GCLBN11] [Guidoti PhD — FR043] [Guidoti PhD — 1xF, Vianaidinae 052] (GC); **BRAZIL**: Pará: Canaã dos Carajás, Gruta S11 12 [GCLBN9.2] [Guidoti PhD — FR039] [Guidoti PhD — 1xM, Vianaidinae 053] (GC); **BRAZIL**: Pará: Canaã dos Carajás, Gruta S11 12 [Guidoti PhD — Extraction #262] [GCLBN9.3] [Guidoti PhD — FR041] [Guidoti PhD — 1xM, Vianaidinae 054] (GC).

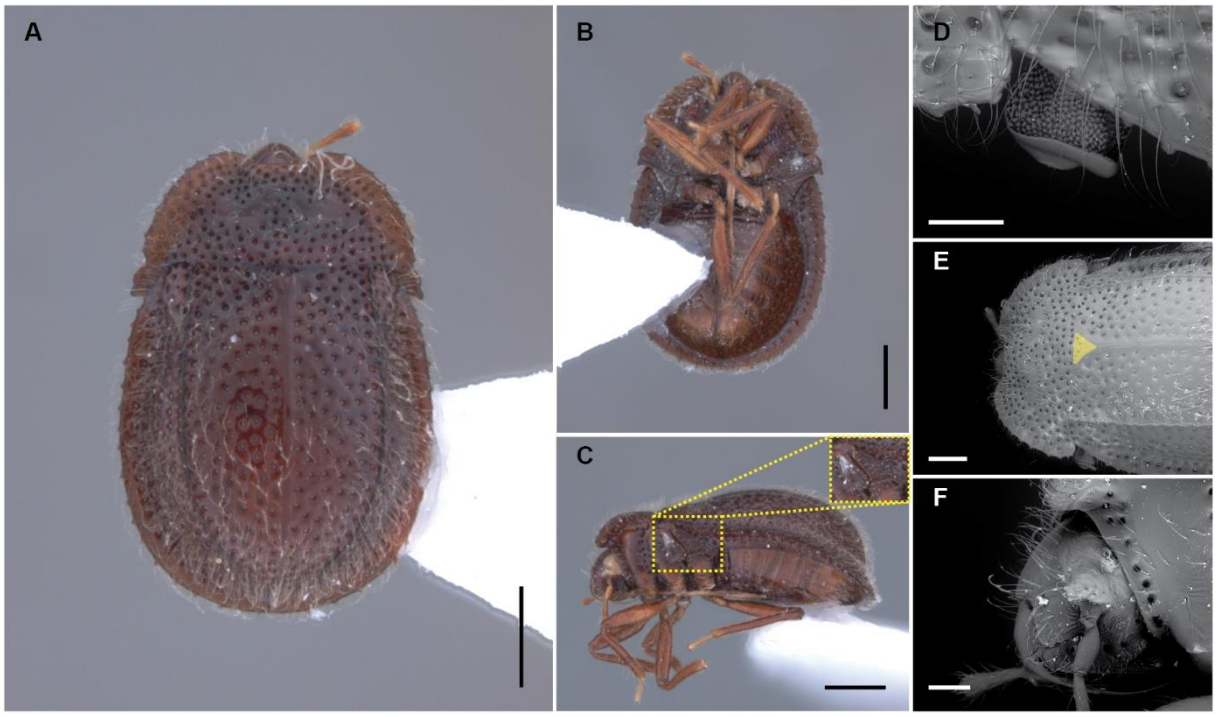

Figure 36. *Thaumamannia vanderdrifti* in A) dorsal, B) ventral and C) lateral views, with scent gland in detail and SEM photographs of: D) scent gland, dorsal view; E) head and thorax, scutellum roughly highlighted; E) head, in lateral view. Scale bars: A-C) 0.5 mm; D, F) 0.1 mm; E) 0.25 mm.

Discussion

The vianaidine species share with each other several remarkable features which are, sometimes, unique among cimicomorphans (e.g., scent gland peritreme). However, they are exceptionally preserved, and the identification process can be arduous. Coleopteroid forms are well-adapted to their habitat and behavior with several reduced or entirely absent structures and they show a high level of similarity among the different species. Macropterous forms of the same genus also present a strong morphological resemblance, with just a handful of taxonomically reliable characters. Despite the argued inefficiency of genital characters in Tingidae taxonomy (Drake & Davis, 1960) has been considered to be misleading (Lee, 1969; Lis, 2003), these characters weren't studied here and hence its usefulness remains unexplored for the species and genera delimitation within Vianaidinae. All species, including the nine new species here proposed, could be recognized and described based on external non-genital characters. Moreover, and due to the high level of morphological similarity among the species, the diagnosis were often proposed based on a combination of the same characters, which includes not exhaustively: the presence of scales on the borders of paranota; and the acute humeral angle on the same structure; the reach of the hemelytral carina-like vein; and the form, inclination and curvature of the anterior and posterior branches of the scent gland peritreme. Generic diagnostic characters

enclosed the inclination of the head, compression of mandibular plates, presence of explanate paranota, constriction on the hemelytra and degree of lateral projection of the scent gland peritreme anterior branch.

However, the challenge of separating similar species, like the *Anommatocoris* coleopteroid species and *Thaumamannia urucuana* sp. n. from *T. vanderdrifti* is not the only challenge regarding Vianaidinae taxonomy. At first glance, the *Anommatocoris* coleopteroids can mislead the identifier to split them in just two or three different species. In the case of *T. urucuana* sp. n. and *T. vanderdrifti*, only a subtle difference on the hemelytra and on the tip of the anterior branch of the scent gland peritreme can safely tell the two species apart. The highly adapted morphology of these coleopteroid forms leads to these high levels of morphological convergence. Withal, the second taxonomic challenge contradicts the first. If it is easy to take a *lumper* approach identifying coleopteroid forms, it seems impossible to identify a macropterous form as the same species of a coleopteroid form if one is using only external non-genital characters. Most of the traits on these two forms are largely non-overlapping (Schuh *et al.*, 2006) and we believe that only molecular data or genital characters, or even same-site collecting events or a combination of two or more of these types of data in an integrative taxonomic approach could bring light to this question. None of these strategies were available to the authors of this contribution, and therefore, all macropterous specimens were considered as different species.

The phylogenetic analysis here presented aimed to unveil the first hypothesis of the internal relationships in Vianaidinae. Although the monophyly of the taxon was purposely not addressed in this study, many well-known autopomorphies of the group within Tingidae *sensu lato* (including Vianaidinae) and Cimicomorpha were recovered as synapomorphies. Examples of the first could be the length of pedicel, the extension of the evaporatorium and the unraised costal vein, and of the latter, the format of the scent gland peritreme. However, since the outgroups and characters chosen focused specifically on the internal relationships and not on the test of the Vianaidinae monophyly, we will not discuss or propose these recovered synapomorphies as valid and relevant synapomorphies for the subfamily. Vianaidinae is considered the basal group of Tingidae *sensu stricto* but the date of this clade within Tingidae remains uncertain due to the absence of sequenced DNA from these species. Additionally, its distribution is restricted to the New World, including the only fossil species currently included in the group, and no biogeographical hypotheses nor analyses have been proposed or conduct to this date.

As stated previously, according to Schuh et al. (2006), only one from the two fossil species described in Vianaidinae (Golub & Popov, 2000; 2003) belong to the subfamily. *Vianagrama goldmani* is a submacropterous species, with the hemelytra extending beyond abdomen, membrane somehow developed, R + M distinct and a costal vein extending to the apex of the membrane (Golub & Popov, 2000). These characters are shared with the extant vianaidines and this species, because of the submacroptery, could be an intermediate between the coleopteroid and macropterous forms observed in the extant fauna. Schuh *et al.* (2006) however, confirmed the presence of pulvilli on this species, which configures an important difference between this species and the remaining vianaidines and could place it outside the group in a phylogenetic framework. Schuh *et al.* (2006) re-observed the type of *Vianathauma pericarti* and noticed "a heavy coating of froth" hampering the observation of the scent gland system and, therefore, they removed this species from the group. This species would be the oldest fully macropterous form registered for the subfamily. In addition to these two fossils, the *Burmacader* species was also suggested as close-related to the vianaidines (Heiss & Guilbert, 2013; 2018). With Vianaidinae the *Burmacader* species share the scent gland peritreme with two perpendicular branches and the relative size of the pedicel. However, many other features like the areolate aspect of paranota and hemelytra might support the placement of these species outside Vianaidinae. Thus, Heiss & Guilbert (2013; 2018) argued that this could be placed in between Vianaidinae and Tingidae *sensu stricto.* All of these hypotheses involving fossil taxa remain untested.

One of the two main clades recovered in the analysis was the *Pterovianaida* + *Thaumamannia* clade. In addition to the synapomorphy and the homoplastic synapomorphy, these two genera share a very similar scent gland peritreme, which is a taxonomically relevant structure for the group at both species and genera levels. The characters supporting the *Pterovianaida* genus could be associated with their habitat and high flight activity, which is supposed because both species were collected on light traps. *Thaumamannia* was supported by weak generic characters as well, like the presence of large scales on paranota borders (character 17-2) and the size of the visible part of scutellum (15-0). Therefore, we do not discard a possible synonymy among these two genera and perhaps, between their species. However, as explained before, the impossibility to identify a coleopteroid form and a macropterous form as the same species based only on external non-genital characters demotivated the authors to take such taxonomic decisions. In addition to the result of the analysis, we decided to remain cautious, at least for now, on these potential synonyms.

The second major clade is composed by the relationship *Henryianaida* gen. n. + *Anommatocoris*. The *Henryianaida* gen. n. species presented a unique feature among Vianaidinae: the laterally compressed mandibular plates (2-1), which was recovered as a synapomorphy for this monophyletic group according to the analysis. In addition to this interesting character, the conspicuously inclined (22-1) and non-laterally projected anterior branch of the scent gland peritreme and the presence of an explanate paranota (16-2) also distinguish these two species from the only known macropterous *Anommatocoris, A. bolivianus*. Since the types of *A. bolivianus* were reported to be missing from the two recipient collections (AMNH and the Australian Museum), we did not have access to the material and therefore, the comparison among *A. bolivianus* and the two aforementioned species is feeble. However, the differences on the scent gland peritreme could be confirmed by a SEM image included on the *A. bolivianus* original description, and the differences on the mandibular plates could be observed on the provided drawing at the same publication (Schuh *et al.*, 2006). Thus, at the light of these characters, we discard any possible synonymy between the newly described genus and the *Anommatocoris* macropterous forms.

Anommatocoris was recovered as a monophyletic genus supported by the most synapomorphies in the analysis. From these, we consider the flat posterior pronotal lobe (11-1), the plane of the anterior branch of the scent gland peritreme compared to the body (22-0) and the hypocosta width (27-0) and texture (28-1) as important genus-level characters. *Anommatocoris bolivianus* was recovered as the most basal taxon of the genus, and that could probably be explained by the overwhelmingly non-overlapping morphology of macropterous and coleopteroid forms which caused some missing data for this species on the character matrix. *Anommatocoris coibensis, A. schuhii* sp. n. and *A. zeteki*, formed an internal monophyletic clade supported by only one HS related to the unequally divided anterior branch of the scent gland peritreme. Additionally, these species present the head with the same color as the body, which was only observed in these three species within *Anommatocoris* but not included in the analysis as a character. *Anommatocoris sucreanus* sp. n. is the basal species of the last subclade of *Anommatocoris*, which is mostly unresolved. This was not a surprise for the authors due to the high morphological similarity among these coleopteroid species. We believe that the external non-genital morphology was not enough to solve this clade, and more data from either genital characters or DNA sequences is required to reach a more desirable result.

The external non-genital morphology was probably explored to its limits in this contribution which almost doubled the number of species and proposed one new genus in

addition to the test of the monophyletic status of all described genera. More species is expected to be discovered, especially considering the small geographical distance among many current valid species. For example, *Anommatocoris* is likely to be present in all over Brazil since several species are reported for the north part of South America and *A. coleopteratus* was found only in Argentina and Uruguay. *Pterovianaida* might be the junior synonym of *Thaumamannia*, but more data is needed to settle this question. The authors believe that after this contribution, molecular data, new collecting events, genital characters, an integrative approach to the taxonomy of the group and the addition of the fossil taxa in a phylogenetic framework are needed to further understand this rarely collected and highly intriguing subfamily of Tingidae.

Acknowledgements

We are grateful to Luiz A. A. Costa (MNRJ), Dr. Randall T. Schuh and Ruth Salas (AMNH), Dr. José A. M. Fernandes (Universidade Federal do Pará, Belém, Brazil), Dr. Augusto Henriques (INPA), Dr. Christiane Weirauch (University of California, Riverside), Dimitri Forero (MPUJ) and Mick Webb (National History Museum, London, UK) for lending a significant part of the analyzed material, to Alexander Knudson (Department of Entomology, North Dakota State University) for sending a series of specimens identified by him as a new *Anommatocoris* species, to Eric Gordon (University of California, Riverside), Filipe Michels and Nathalia Russi (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) and Aline Barcellos (Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil) for helping me prepare and ship samples, to Scott Whittaker (Scanning Electron Microscopy Lab, NMNH) and James N. Zahniser (Animal and Plant Health Inspection Service, United States Department of Agriculture, c/o NMNH) for the crucial help with the scanning electron microscopy, and a special thanks to Thomas J. Henry (Systematic Entomology Laboratory, Agricultural Research Service, United States Department of Agriculture, c/o NMNH), who sponsored the first author in an award received to work for one year as pre-doctoral fellow at the Smithsonian Institution which allowed this project to be concluded. We also thank to CNPq (National Council for Scientific and Technological Development) for the first author's PhD fellowship (process number 141467/2014-2) and science without borders fellowship (process number 201352/2015-0).

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Appendix

Commented list of characters used in the phylogenetic analysis

0. **Head, setae, abundance (Fig. 3):** [0] scarce; [1] moderately abundant; [2] abundant.

Head setae are scarce in all the species of *Anommatocoris*, in *Thaumamannia insolita* sp. n. and in the *Henryianaida* gen. n. species; are moderately abundant in *T. urucuana* sp. n., *T. manni* and in *T. vanderdrifti* and are very abundant and densely distributed in the two species of *Pterovianaida*.

1. **Head, position (Fig. 2):** [0] straight, or [1] inclined downwards, considering sagittal plane.

The head is inclined downwards in all species of *Thaumamannia* and in *Pterovianaida duckensis*. In *P. melchiori* the character was coded as "?" because the character couldn't be observed due to the way the holotype and single known specimen was preserved. The head in *Anommatocoris* and in *Henryianaida* gen. n. species is positioned in a straight line considering the body plane.

2. **Mandibular plates (Fig. 9):** [0] not compressed; [1] laterally compressed, forming an acute angle with the eyes.

The two *Henryianaida* gen. n. species present compressed mandibular plates, and this is noticeable when observing the head in dorsal view. This character state was recovered as a synapomorphy for this genus.

3. **Antennae, pedicel, length (modified from character 3 of the tribal level analysis in Lis, 1999):** [0] not subequal to basi- and distiflagellomere; [1] subequal to basi- and distiflagellomere.

This has been previously recovered as a synapomorphy for Vianaidinae (Lis, 1999).

4. **Cephalic spines:** [0] present; [1] absent.

The absence of cephalic spines was recovered as a synapomorphy for Vianaidinae.

5. **Bucculae, anterior region:** [0] touching, or [1] not touching each other at apex.

The bucculae do not touch each other at the apex in the vianaidines. This character can be easily observed in an antero-ventral view of the head.

6. **Bucculae, posterior region, form (Fig. 7):** [0] rounded; [1] straight or, [2] concave.

In two of the species of *Thaumamannia*, *T. urucuana* sp. n. and *T. manni*, the posterior margin of the bucculae is rounded, in the species of *Henryianaida* gen. n. is straight and in the remaining vianaidines is concave. In three of the studied species this character could not be observed: *A. bolivianus*, *A. sucreanus* sp. n. and *P. melchiori*, thus these were coded as "?".

7. **Bucculae, posterior region, width:** [0] narrower, or [1] wider than anterior half.

In *Thaumamannia urucuana n. sp.* and *T. manni* the posterior half of the bucculae is wider than the anterior half. For the remaining species the posterior half is narrower than the anterior half. In *P. melchiori* the character was coded as "?" because the character couldn't be observed due to the way the holotype and single known specimen was preserved.

8. **Frons, height:** [0] same level, or [1] higher than clypeus (Fig. 1 d).

Three of the species of *Thaumamannia* have the frons dilated: *T. urucuana* sp. n., *T. insolita* sp. n. and *T. vanderdrifti*. Both *Henryianaida* gen. n. species also present the same character state. This character can be observed in lateral view.

9. **Pronotum, carinae (modified from character 5 of the tribal level analysis in Lis, 1999; and from character 20 in Schuh *et al.*, 2006):** [0] present; [1] absent.

The absence of pronotal carinae is shared among all the vianaidines.

10. **Pronotum, collar, disposition:** [0] not projected, or [1] projected towards the head.

The collar is not projected in the species of *Anommatocoris*, *Henryianaida* gen. n. and in *Thaumamannia insolita* sp. n., and in the rest of the species of *Thaumamannia* as well as in the species of *Pterovianaida* the lateral margins of the collar are projected towards the head.

11. Pronotum, posterior region, lobe (Fig. 10): [0] posterior lobe higher than anterior lobe, or [1] flat, at equal heights.

The *Anommatocoris* species have the pronotum flat while the other vianaidines species have the posterior lobe of the pronotum higher than the anterior.

12. Pronotum, posterior region, triangular projection (modified from character 4 of the tribal level analysis in Lis, 1999): [0] present; [1] absent.

The pronotum can be elongated, hiding entirely or partially the scutellum in a posterior pronotal projection; or, as in all vianaidines species and some other tingids, can end shortly after the pronotal posterior lobe exposing the scutellum in its full extant.

13. Pronotum, punctuations (Fig. 8): [0] fine; [1] coarse.

Thaumamannia and *Pterovianaida* species share the presence of coarse punctuations in the pronotum; in the other Vianaidinae genera the pronotal punctuations are finer.

14. Pronotum, width (Fig. 6): [0] approximately two or less times, or [1] noticeable more than two times wider than long.

Three of the *Thaumamannia* species have the pronotum very considerably wider than long; these are *T. urucuana* sp. n., *T. manni* and *T. vanderdrifti*. In the remaining vianaidine species the pronotum is longer but narrower.

15. Scutellum: [-] hidden; [0] less wide, or [1] wider than half of the maximal width of the head.

Three of the species of *Anommatocoris* (*A. coleopterodes*, *A. knudsonii* sp. n. and A. *minutissimus*) as well as three of the *Thaumamannia* species (*T. urucuana* sp. n., *T. insolita* n. sp. and *T. vanderdrifti*) have the scutellum narrow, and in the remaining species the scutellum is much wider than half of the maximal width of the head. This character could not be observed in *A. bolivianus* and therefore, was coded as "?" for this species.

16. Paranota, development: [0] areolate, expanded; [1] not areolate nor expanded; [2] not areolate, expanded.

All the vianaidines have paranota not areolated; *Anommatocoris* species have the paranota not expanded; the rest of the species present the paranota expanded.

17. Paranota, borders (Fig. 5): [0] smooth; [1] with small scales, serrate-like; [2] bearing large scales.

Most species of *Anommatocoris* have the paranota borders serrated (except for *A. bolivianus*, *A. coibensis*, *A. schuhii* sp. n. and *A. zeteki*); *Thaumamannia insolita* sp. n., *T. urucuana* sp. n. and *T. vanderdrifti* have large scales; the remaining species present smooth paranota borders.

18. Paranota, constriction (Fig. 4): [0] absent; [1] present, between anterior and posterior pronotal lobe.

The two *Pterovianaida* species have the paranota constricted between the anterior and posterior lobe, while this constriction is absent in the remaining Vianaidinae species.

19. Paranota, posterior region: [0] not developed, or [1] developed in a small acute humeral angle.

All the species of *Anommatocoris*, except for *A. coleopterodes*, A. *minutissimus, A. schuhii* sp. n. and *A. sucreanus* sp. n., present an acute humeral angle, which is also the case of *T. manni*; the remaining species of the group do not present this feature.

20. Scent gland, peritreme (modified from character 12 of the tribal level analysis in Lis, 1999; **and from character 35 in Schuh *et al.*, 2006):** [0] greatly reduced; [1] auricular-like; [2] T- or Y-shaped.

This character is recovered as a synapomorphy of all vianaidines.

21. Scent gland, peritreme, anterior branch, apex: [-] not developed; [0] not projected or, [1] conspicuously projected laterally.

In most *Anommatocoris* species (except for *A. coleopteratus*), and in the *Henryianaida* gen. n. species, the apex of the anterior branch of the peritreme is not laterally projected; in the *Thaumamannia* and *Pterovianaida* species the apex is so remarkably projected that it can be

observed in dorsal view (except in *T. manni*, which can't be observed in dorsal view, but it is still conspicuously projected).

22. **Scent gland, peritreme, anterior branch, position:** [-] not developed; [0] almost perpendicular to sagittal body plane; [1] clearly inclined forward.

All the *Anommatocoris* species have the anterior branch of the scent gland almost perpendicular to the sagittal body plane giving the gland a "T" shape aspect, and in the rest of the vianaidines the anterior branch is clearly inclined forwards, suggesting a "Y" shape.

23. **Scent gland, peritreme, posterior branch:** [-] not applicable; [0] longer, or [1] shorter than the upper part of the anterior branch.

Most of the species of *Anommatocoris* (except for *A. coibensis*, *A. schuhii* sp. n. and *A. zeteki*) have the posterior branch of the scent gland longer than the upper part of its anterior branch. This is also the case of the *Henryianaida* gen. n. species and *P. duckensis* (*P. melchiori* was coded as "?" because this character couldn't be observed due to the way the holotype and single specimen of this species was preserved). In all the *Thaumamannia* species the posterior branch is shorter than the upper part of its anterior branch.

24. **Scent gland, evaporatorium (modified from character 36 in Schuh *et al.*, 2006):** [0] not covering, or [1] covering the entire metapisternum.

The evaporative area of the metathoracic gland covering entirely the metapisternum is recovered as synapomorphy for Vianaidinae.

25. **Hemelytra, anterior region, margins:** [0] smooth (Fig. 4 b, d); [1] with small scales, serrate-like or, [2] with large scales.

The anterior margin of the hemelytra can be smooth as in *A. coibensis*, *A. schuhii* sp. n. and in *Henryianaida machupicchuensis* sp. n.; or serrated, with small scales as in *A. araguanus* sp. n., *A. coleopterodes*, *A. knudsonii* sp. n., *A. minutissimus*, *A. serratus* sp. n., *A. sucreanus* sp. n. and *A. zeteki;* or have large scales as in *Thaumamannia* and *Pterovianaida* species, and as in *Henryianaida colombiensis* sp. n. This character was coded as "?" for *A. bolivianus* because the authors didn't have access to the specimens and the images in its original description weren't enough to define its state in this character.

26. Hemelytra, anterior region, constriction (Fig. 11): [0] not constricted, or [1] slightly constricted.

All *Anommatocoris* and *Henryianaida* gen. n. species presents the hemelytra slightly constricted at the anterior region.

27. Hemelytra, hypocosta (Fig. 12): [0] narrow; [1] wide.

In all the *Anommatocoris* species the hypocosta is considerably narrower than in the remaining Vianaidinae.

28. Hemelytra, hypocosta, punctuations (Fig. 13): [0] large, areolate; [1] absent, completely smooth; [2] finely punctuated; [3] coarsely punctuated.

In the species of *Anommatocoris* the hypocosta is smooth, whereas in the species of *Pterovianaida* and *Henryianaida* gen. n. is finely punctuated and in the *Thaumamannia* species is coarsely punctuated.

29. Hemelytra, costal area, vein: [0] conspicuously raised; [1] not raised.

The costal vein is a vein that separates the costal from the subcostal area is not raised in all Vianaidinae species.

30. Hemelytra, costal area (Fig. 14): [0] explanate, wide; [1] thickened, narrower.

Thaumamannia, *Pterovianaida* and *Henryianaida* gen. n. species have the costal area explanate and broadened whereas in all species of *Anommatocoris* is not explanate and restricted to a thick margin for most of its extant.

31. Hemelytra, subcostal area (Fig. 15): [0] subhorizontal; [1] subvertical.

In *Anommatocoris*, the subcostal area is nearly vertical to the point that part of it cannot be observed in dorsal view, while in the remaining species of Vianaidinae the subcostal area is inclined and fully observable in dorsal view.

* formatted according to the *Systematic Entomology*

Chapter V

A molecular phylogenetic analysis of Tingidae (Heteroptera, Cimicomorpha), including the first sequences of the subfamily Vianaidinae

Radial representation of the resulting phylogenetic tree.

Chapter V – A molecular phylogenetic analysis of Tingidae (Heteroptera, Cimicomorpha), including the first sequences of the subfamily Vianaidinae

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Abstract

A molecular phylogeny of Tingidae is here proposed using Bayesian inferences and based on the largest dataset to this date. A total of 4309 bp were initially considered in a dataset containing 128 terminals, including the first Vianaidinae sequences from three different species and two genera. All three Tingidae subfamilies were recovered monophyletic and our results corroborate the previous hypotheses concerning their relationships. Vianaidinae was recovered as the sister-group of Tingidae *sensu stricto*, corroborating previous phylogenies. Phatnomatini was corroborated as the sister-group of Tinginae, and its monophyly was retrieved, with the largest number of terminals from this tribe ever considered in a phylogenetic analysis. Additionally, Ypsotingini is re-discussed while the suppression of Litadeini is again suggested. Finally, a potential new tribe composed by the Neotropical and Nearctic genus *Leptodictya* is for the first time considered and discussed. The results as well as the perspectives from our study are discussed in the light of the previous phylogenetic analysis for the family.

Keywords. Bayesian, classification, lace bugs, *Leptodictya*, Ypsotingini.

Introduction

Tingidae (Hemiptera, Heteroptera) is a family of small phytophagous true bugs, ranging from 1.5 to 5 mm, composed by more than 2500 species distributed in about 300 genera (Drake & Ruhoff, 1965; ITIS, 2008). This family is commonly known as lace bugs, mostly due to the

remarkable lace-like aspect of their wings and paranota (Froeschner, 1996). However, coleopteroid forms with highly modified hemelytra and reduced or absent hind wings are also present (e.g., *Coleopterodes* Philippi, *Anommatocoris* China). Tingids are widely distributed, occurring in all continents except for Antarctica but including some oceanic islands (Drake & Ruhoff, 1960). They are also known for being associated with multiple botanical families, and their host-plant can range from small grasses to tall woody trees (Drake & Ruhoff, 1965). The host-plant record is often defective and misleading due to the more frequent occasional collecting events and lack of natural history notes on the literature (e.g., Drake, 1922). It's well-accepted that tingids can be host-specific, but some species are allegedly associated with different species, genera and even different plant families (e.g. *Gargaphia lunulata* (Mayr) – Drake & Ruhoff, 1965). They are usually found feeding on the abaxial surface of leaves, but they have also been found feeding on stems, roots, and putatively, mosses (China, 1945; Henry & Wheeler Jr., 1986). Tingidae nymphs are usually morphologically as remarkable as the adults and can bear integumentary structures named tubercles and projections with taxonomic, phylogenetic and evolutionary value (Guidoti & Barcellos, 2013; Guilbert, 2004; Guilbert *et al.*, 2008). Gall-inducing and maternal-care behaviors were also reported for the family in different genera and for the latter, different faunas as well (e.g., gall-inducing behavior presented by *Copium* Thunberg and *Paracopium* Distant; maternal care in the Neotropical genus *Gargaphia* Stål and the in African genus *Compseuta* Stål – Drake & Ruhoff, 1965; Tallamy & Iglay, 2004; Guidoti *et al*., 2015). Tingidae taxonomy is historically based only on external non-genital characters, but the applicability of both male and female external genital characters on species delimitation was already shown fruitful (Lee, 1969; Lis, 2003).

Drake & Ruhoff (1965) proposed the most widely accepted Tingidae classification to this day, based on a taxonomic approach. However, their scheme was strongly influenced by Drake & Davis (1960) who divided Cantacaderinae in two tribes (Cantacaderini and Phatnomini) and considered for the first time Vianaidinae as a Tingidae subfamily. Drake & Ruhoff (1965) additionally divided Tinginae in three tribes: Ypsotingini, Litadeini and the nominal tribe, Tingini. Phatnomini was later amended to Phatnomatini (Froeschner, 1981), due to a new interpretation of the stem of its type-genus, *Phatnoma* Fieber. Lis (1999) was the first author to address Tingidae classification in a phylogenetic framework, in two different analyses: one with tribes as terminals, including all supra-generic taxa in Tingidae *sensu* Drake & Ruhoff; and another one with genera as terminals and considering Cantacaderini only, with the type-genera of Phatnomatini and Tingini, *Phatnoma* and *Tingis* Fabricius, as outgroups.

According to Lis (1999), Phatnomatini was recovered as the sister group of Tinginae. The second analysis focused on Cantacaderini and was used as one of the arguments to raise this tribe to family level, and to divided it in two subfamilies: Carldrakeaninae and the nominal sabfamily, Cantacaderinae *sensu novum*. The latter was additionally divided in two tribes, Ceratocaderini and Cantacaderini *senso novum*. In addition, Lis (1999) considered Tingidae *sensu novum* grouping Phatnomatinae *status novum* and Tinginae, this including its three previously proposed tribes that rested unanalyzed in this work. Lis (1999) also was one of the many authors (e.g., Golub, 2001; Montemayor & Carpintero, 2007) that considered Vianaidinae a family on its own closely related to Tingidae. Guilbert (2001) concentrated the sampling scheme in Tingini, however, this morphological-only analysis did not retrieve any of the suprageneric taxa *sensu* Drake & Ruhoff nor *sensu* Lis. Guilbert (2004), focusing on immature data, presented similar results.

Schuh *et al.* (2006), in an analysis mostly based on Lis (1999) characters, added the newly described first macropterous species of Vianaidinae as a terminal and recovered all supra-generic taxa proposed by Lis (1999). Vianaidinae, represented solely by *Anommatocoris bolivianus* Schuh *et al.*, was retrieved sister to the remainder Tingidae, corroborating previous phylogenetic analyses within Heteroptera and Cimicomorpha (Schuh & Štys, 1991; Schuh *et al.*, 2009). Schuh *et al.* (2006) rejected the new ranks proposed by Lis (1999) arguing that elevation of ranks based on autapomorphic characters might obscure rather than clarify phylogenetic relationships. Therefore, Schuh *et al.* (2006) considered Tingidae composed by three subfamilies, Tinginae, Cantacaderinae (with three tribes: Cantacaderini; Ceratocaderini; Carldrakeanini *status novum*), and Vianaidinae. Although the composition of tribes and their relationships within Tinginae were not addressed, Schuh *et al*. (2006) recovered Phatnomatini sister to the remaining Tinginae. In fact, yet according to this analysis, Phatnomatini was recovered paraphyletic since *Zetekella* Drake was more closely related to other tingines than to the Phatnomatini included, the type-genus, *Phatnoma*. Guilbert (2012a) added two genera and removed two characters from Schuh *et al.* (2006) database to provide another phylogenetic hypothesis for Cantacaderinae. The monophyly of the supra-generic taxa proposed by Lis (1999) were again recovered by Guilbert (2012a) and Wappler *et al.* (2015), but these analyses followed the taxa status defended by Schuh *et al.* (2006). Additionally, Guilbert (2012a) found Carldrakeanini sister to Ceratocaderini, and not to Cantacaderini as Lis (1999) and Schuh *et al.* (2006) previously found.

In the only phylogenetic analysis including molecular data, Guilbert *et al.* (2014) focused on the Tinginae internal relationships. Their dataset also included morphological characters in addition to the four mitochondrial *loci* (16S, CO1, COII and Leu-tRNA) and one nuclear locus (28S rRNA), which was analyzed in a total-evidence approach. Despite their sampling scheme was largely proportional to the genera distribution within Tingidae supra-generic taxa, the Tinginae tribes Litadeini and Ypsotingini, and more expressively Cantaderinae, counted with just a few terminals (three, two and two, respectively). In addition, Vianaidinae was not included in their dataset Guilbert *et al.* (2014). Litadeini and Ypsotingini were not recovered as monophyletic groups and, therefore, the authors suggested their suppression, regardless the representation within their terminal list (Guilbert *et al.*, 2014). Cantacaderinae and Phatnomatini were found to be monophyletic groups, the latter being recovered as the sister-group of Tinginae as in Lis (1999), Schuh *et al.* (2006) and Guilbert (2012a). However, due to the small representation of Cantacaderinae, the supra-generic taxa proposed by Lis (1999) were not assessed nor discussed in Guilbert *et al.* (2014) analyses. Moreover, the authors argued that a more comprehensive analysis would be a key step into a better understanding of Tingidae supra-generic taxa and their internal relationships.

Only Guilbert (2001, 2004) and Guilbert *et al.* (2008) discussed Tingidae evolution in a phylogenetic framework. Guilbert (2001) found an evolutionary tendency from a simpler to a more complex morphology, the latter represented by a well-developed hood, large hemelytra with large hyaline areola, these also present in the paranota. Guilbert (2004) recovered a similar pattern after analyzing immature data, and the tendency went from species with immatures not presenting tubercles to immatures bearing tubercles and other complex integumentary projections. Moreover, Guilbert *et al.* (2008) suggested the presence of both peramorphic and paedomorphic heterochronic events in Tingidae immature ontogeny, after analyzing a small dataset composed by different stages of tingid nymphs. Considering the evolution of Tingidae in space and time, Lis (1999) and Guilbert (2012b) provided biogeographical analyses to address this question based on the phylogenetic analyses in Lis (1999) and Guilbert (2012a), respectively. Most of these authors, in addition to Guilbert *et al.* (2014), argued that a more comprehensive analysis would be a key step into a better understanding of Tingidae internal relationships, its supra-generic classification and evolutionary hypotheses.

The group Vianaidiane + Tingidae *sensu stricto* is strongly corroborated by morphological phylogenetic analyses (Schuh & Štys, 1991; Schuh *et al.*, 2006, 2009; Guilbert, 2012a; Wappler *et al.*, 2015). However, vianaidines were not represented in the only

phylogenetic analysis of Tingidae that included molecular data to this date (Guilbert *et al.*, 2014). Additionally, the internal relationships within Tinginae are still unresolved, hampering the understanding of the evolution of many important behavioral and morphological aspects of the entire family. Therefore, the aim of this contribution is to address Tingidae classification with emphasis in Tinginae, through a molecular analysis that includes the first Vianaidinae sequences, and also to test the monophyly of Vianaidinae + Tingidae *sensu stricto* with a new and unprecedented dataset.

Material & Methods

Taxa Sampling

The dataset includes 128 terminal species including three Vianaidinae, three Cantacaderinae, six Phatnomatini, five Litadeini and five Ypsotingini *sensu* Froeschner (2001). Tingini *sensu* Froeschner (2001) is here represented by 99 different species. A total of 80 genera was included as the ingroup (Appendix). Six terminals were included as outgroups, two from the infraorder Cimicomorpha, including one Miridae (*Europiella albipenis* (Fállen)), and one Thaumastocoridae (*Thaumastocoris petilis* Drake & Slater), two are Pentatomomorpha from the Tessaratomidae (*Erga longitudinalis* (Westwood) and *Lyramorpha parens* Breddin), one is a Dipsocoromorpha, Ceratocombidae (*Ceratocombus australiensis* Gross), and one is Gerromorpha from Macroveliidae (*Macrovelia hornii* Uhler). *Ceratocombus australiensis* is designated as the root, and *Galeatus scrophicus* Saunders is the only species with more than one sequence included in the dataset (two in total).

Character Sampling

Four *loci* were initially sequenced: the nuclear genes 18S rDNA (2090bp) and 28S rDNA (798 bp), encoding the small and large ribosomal subunits, respectively; two mitochondrial *loci* from Cytochrome Oxydase sub-unit I (COI), including the usual barcoding sequence (COI barcode, 590bp) and a *locus* (828bp) nearly located to the former. These two nuclear *loci* were chosen because they are highly variable and have provided phylogenetically useful information for family level divergences in other taxa. The two COI were used since they vary faster than nuclear genes and as such, they can provide useful information for more recent lineages. The

total character set reaches 4309 base pairs. All sequences were obtained by Sanger sequencing method after amplification process through PCR. The primers used in this study are available in Table 1. All the sequencing was done by Eurofins Co., except for *Ceratocombus australiensis* (COI barcode: AY253029.1; 28S D3-D5: AY252547.1; 18S A2.0/9r: AY252300.1), *Macrovelia hornii* (COI barcode: AY252946.1; 28S D3-D5: AY252450.1; 18S A2.0/9r: AY252196.1) and *Thaumastocoris petilis* (COI barcode: AY253123.1; 28S D3-D5: AY252625.1; 18S A2.0/9r: AY252402.1) for which sequences were downloaded from GenBank.

Table 1. Primers used in the DNA amplification. All sequences are 5' → 3' oriented.

Locus	Primer	Sequence	Reference
18S	3F	GTT CGA TTC CGG AGA GGG A	Giribet *et al*. (1996)
	Bi	GAG TCT CGT TCG TTA TCG GA	Whiting *et al*. (1997)
18S	A2.0	ATG GTT GCA AAG CTG AA AC	Whiting *et al*. (1997)
	9R	GAT CCT TCC GCA GGT TCA CCT AC	Giribet *et al*. (1996)
18S	1F	TAC CTG GTT GAT CCT GCC AGT AG	Giribet *et al*. (1996)
	5R	CTT GGC AAA TGC TTT CG C	Giribet *et al*. (1996)
28S	Ai	GAC CCG TCT TGA AAC ACG	Whiting *et al.* (1997)
	D4d5r	GTT ACA CAC TCC TTA GCG GA	Shrubovych *et al.*, 2017
28S	C1n	ACC CGC TGA ATT TAA GCA T	Not published
	Air	CGT GTT TCA AGA CGG GTC	Not published
COI	LCO1490puc_t1-	TTT CAA CWA ATC ATA AAG ATA TTG G	Cruaud *et al*., 2009
	LCO1490Hem1_t1	TTT CAA CTA AYC ATA ARG ATA TYG G	Germain *et al*., 2013
	HCO2198puc_t1	TAA ACT TCW GGR TGW CCA AAR AAT CA	Cruaud *et al*., 2009
	HCO2198Hem2_t1	TAA ACY TCA GGA TGA CCA AAA AAY CA	Germain *et al*., 2013
	HCO2198Hem1_t1	TAA ACY TCD GGA TGB CCA AAR AAT CA	Germain *et al*., 2013
COI	C1-J-2183	CAA CAT TTA TTT TGA TTT TTT GG	Simon *et al*., 1994
	TL2-N-3014	TCC AAT GCA CTA ATC TGC CAT ATT A	Simon *et al*., 1994

DNA Extraction and Amplification

DNA was extracted from abdomens only, which were removed from the individuals in order to preserve most of the voucher specimens. DNAeasy Tissue Kit (Qiagen Inc., Hilden, Germany) was used, and each abdomen was added into a buffer together with proteinase K. The tissues were digested overnight and purified through two chromatographies, culminating in the dilution of the DNA in 200 µl of buffer. The targeted *loci* were obtained by PCR using either Taq Core

Kit (Qiagen) or Taq-&-Load Mastermix (MP Biomedicals Inc., Europe). The PCR cycling program includes an initial denaturation at 94°C for 5 min (2 min only for CO1 C1-J-2183/TL2-N-3014), followed by 35 cycles (except 18S 1F/5R and 28S Ai/d4D5r, which used 40 cycles) composed by one denaturation step of 40s at 94°C, one annealing step for 40s at 45–58°C depending on the primer set, and an extension for 1min at 72°C, with an additional final extension for 10 min at 72°C (except 28S Ai/d4D5r and 28S C1n/Air which the final extension lasted for 7 min). The CO1 Cocktail had two cycles on its program, the first (5x) including a denaturation step of 40s at 94°C, then annealing for 40s at 45°C and extending for 1 min at 72°C, and the second (35x) with denaturation for 30s at 94°C, annealing 40s at 51°C and extension for 1 min at 72°C, followed by the final extension of 10 min at 72°C. The annealing temperatures for the 18S 3F/Bi, A2.0/9R and 1F/5R were 58°C, 52°C and 50°C, respectively. For the 28S Ai/d4D5r and C1n/Air the annealing temperatures were 54°C and 52°C, and for the CO1 C1-J-2183/TL2-N-3014, 45°C. The PCR protocols varied less than the programs, keeping the concentrations of buffer (1x), primers (0.2 µM) dNTPs (200 µM each) as recommended by the Kit instructions. The amount of Taq units used was also the same among all *loci*, 1.25 U/reaction. Both 28S C1n/Air and CO1 Cocktail used an additional 0.5 mM of $MgCl_2$ to the standard 1.5 mM already included in the buffer, and all 18S genes counted with 0.5 µl of DMSO (final concentration, 2%). The standard protocol for the Taq-&-Load Mastermix was applied to the amplification of 28S Ai/d4D5r. PCR reactions included negative controls to detect any possible contamination.

Alignment and Substitution Model Selection

Sequences were cleaned on CodonCode aligner 6.0.2 (https://www.codoncode.com/index.htm) and Geneious 11.0.2 (https://www.geneious.com). Protein-coding sequences of COI were aligned with Muscle 3.8 (Edgar, 2004) under default settings and ribosomal genes 18S and 28S were aligned with MAFFT v7.2015 (Katoh & Standley, 2013) also under default settings. CO1 from "Jerry & Pet" marker was excluded due to the amount of missing data. The three remainder *loci* were partitioned and JModeltest 2 v0.1.10 (Posada & Crandall, 1998; Darriba *et al.*, 2012) was used to define the best-fit models of nucleotide substitution for each *loci*. We applied the Akaike Information Criterium (AIC), and the best model was defined by the lowest criterion value. Thus, the Gamma model was selected for 28S and the Inverse Gamma model was selected for 18S and CO1. This defined the evolutionary model to the GTR substitution model with gamma-distributed (or inverse gamma) rate variation across sites.

Phylogenetic Analysis

Bayesian analysis were conducted using Mr Bayes 3.2.5 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Two runs of two chains each and 20 million generations were carried. Burn-in was set at 25% of the sampled trees. The stability of the distribution was controlled using Tracer v1.5v (Rambaut & Drummond, 2009). Tracer v1.5 (Rambaut & Drummond 2009) was also used to analyse the trace files generated by the Bayesian MCM runs. Posterior probabilities were estimated on the tree topology, and nodes were not collapsed regardless the value of their estimated posterior probabilities. Despite the supporting evidence of the unreliableness of low posterior probabilities in phylogenetic Bayesian inferences (Huelsenbeck *et al.*, 2002; Erixon *et al.*, 2003; Zander, 2004), all major clades were discussed regardless their values. The final tree was initially viewed and edit with FigTree 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/), and a SVG file were extracted to be posteriorly edited on Adobe Illustrator.

Results

The average standard deviation of split frequencies after 20 million generations was 0.067159. It is expected to be under 0.01 (Ronquist & Huelsenbeck, 2003); however, the effective sample size was up to 200 for all statistics while it is expected to be up to 100 (Rambaut & Drummond, 2009).

Considering the supra-generic taxa currently accepted for Tingidae, Vianaidinae, Cantacaderinae, and Phatnomatini were recovered as monophyletic groups (Fig. 1). All these taxa presented high support, with the following posterior probability (pp): 1.00, 0.82 and 1.00, respectively. Vianadinae was represented by three species which includes *Henryianaida colombiensis* Guidoti *et al*. found as the sister-group of the clade *H. macchupichuensis* Guidoti *et al*. + *Anommatocoris serratus* Guidoti *et al*. (pp = 1.00). The relationship Vianaidinae + Tingidae *sensu stricto* presented high support as well (pp = 1.00). *Cantacader* Amyot and Seville was also represented by three species: *Cantacader lethierryi* Scott, *C. quinquecostatus* (Fieber) and *Cantacader* sp. In addition to the relatively high support of the clade composed by the cantacaderid species, the Cantacaderinae + Tinginae clade was recovered with an even higher posterior probability (0.93). Phatnomatini was found composed by two main clades, one

with all *Phatnoma* species included in this study (*Phatnoma marmoratum* Champion + [*P. costalis* Distant + *P. tonkinana* Drake & Maa]) and a second with *Distocader planti* Guilbert & Guidoti, 2018 closely related to *Sinalda helichrysumae* Duarte Rodrigues + *Plesionoma* sp. All clades, with the exception of the latter, presented a high posterior probability (1.00); *S. helichrysumae* + *Plesionoma* sp. was supported with a posterior probability of 0.82, which was the exact same support of the clade Phatnomatini + Tinginae.

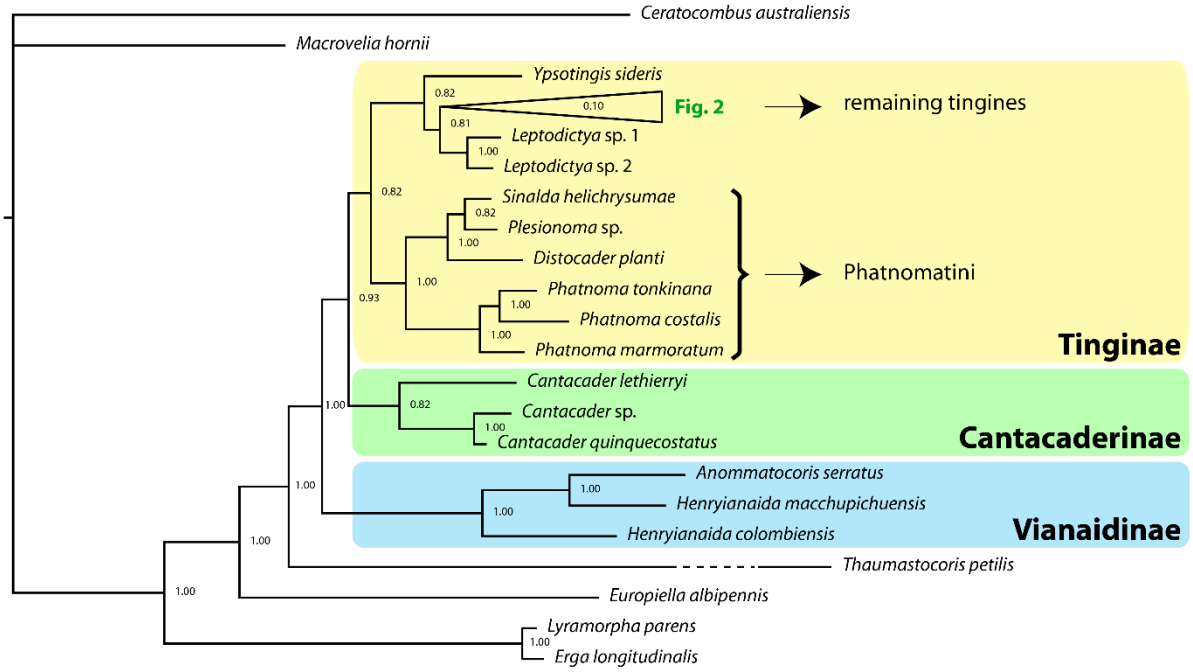

Figure 1. Bayesian analysis resulting tree. Subfamilies and Phatnomatini indicate in the figure. Due to the size of the analysis, the tree was divided and the remaining tingines are shown in the next figure (Fig. 2). Outgroups are not colored, and dotted line was shortened to fit the image aesthetically. Posterior probabilities are indicated next to each node.

Internally in Tinginae, none of the proposed tribes for this taxon were recovered as monophyletic. However, the sister-group of all remaining tingines is *Ypsotingis sideris* Drake, type-species of Ypsotingini's type-genus (pp = 0.82; Fig. 1). Four additional ypsotinginis were included and formed one non-exclusive clade at a different part of the tree (pp = 1.00; Fig. 3): *Kalama tricornis* (Schrank), found as sister-group (pp = 0.70) of *Dictyonota strichnocera* Fieber + *D. phoenica* Seidenstücker (pp = 1.00), and *Derephysia cristata* (Panzer), which was found as sister-group of the *Acalypta* Westwood clade (pp = 1.00), *A. parvula* (Fállen) + *A. pulchra* Štusák (pp = 0.77). These two different branches including Ypsotingini species formed a monophyletic clade, sister-group of *Carvalhotingis visenda* (Drake & Hambleton) (pp = 0.14).

Within Tinginae (*minus Y. sideris*), the monophyletic group formed by the two *Leptodictya* Stål species added to the analyses is the sister-group of the other tingines (Fig. 1).

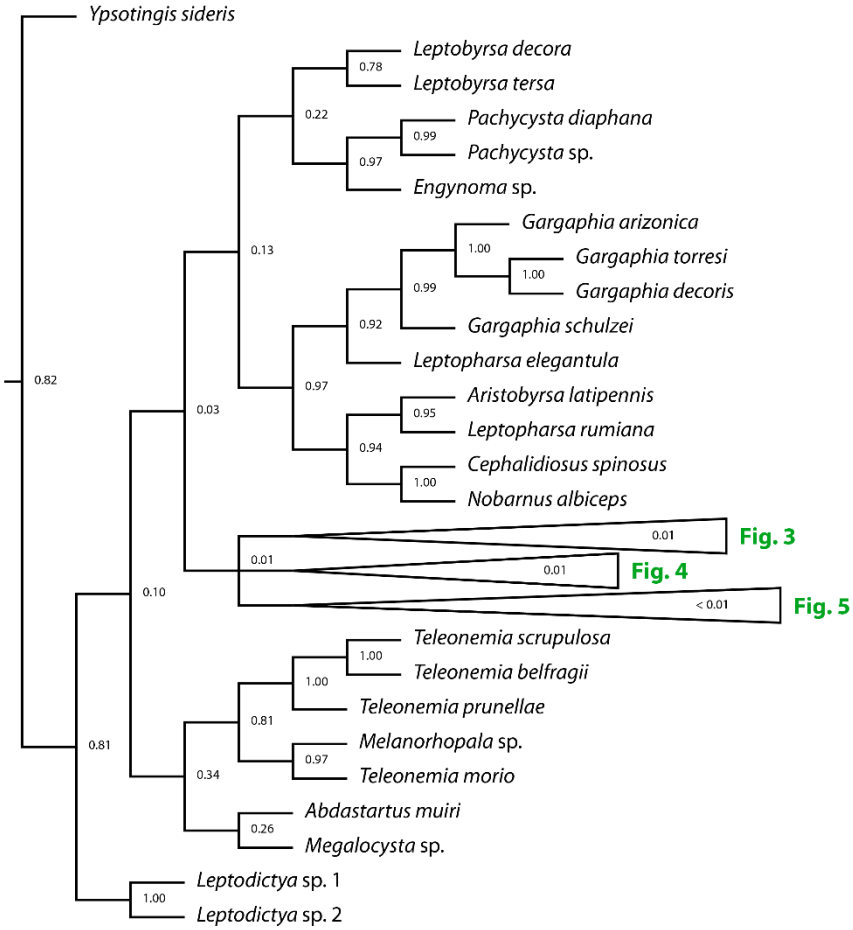

Figure 2. Remaining tingines. Due to the size of the phylogeny, the clades in polytomy are shown in different images (Fig. 3-5). Posterior probabilities are indicated next to each node.

This interesting finding presented a high support level (pp = 0.81). Yet, Litadeini was represented in the dataset by 5 species: *Aristobyrsa latipennis* (Champion), *Cephalidiosus spinosus* Guilbert, *Psilobyrsa aechemeae* Drake & Hambleton, *P. vriesiae* Drake & Hambleton and *Stragulotingis plicata* (Champion). From these, *A. latipennis*, *P. aechemeae* and *S. plicata* are type-species of their respective genera. This tribe was not recovered as a monophyletic group, however, *C. spinosus* and its sister-group *Nobarnus albiceps* Guilbert (pp = 1.00; Fig. 2), were closely related (pp = 0.94) to the clade *A. latipennis* + *Leptopharsa rumiana* Drake & Hambleton (pp = 0.95) while *Psilobyrsa* Drake & Hambleton was recovered as a monophyletic genus (pp = 1.00), but distant, on the topology, from the remaining litadeinis (Fig. 3).

Stragulotingis plicata was found as sister group of *Leptopharsa ornata* Monte (pp = 1.00; Fig. 3), and these two species formed a clade with another *Leptopharsa* Stål species included in the analysis, *L. furculata* (Champion) (pp = 0.65).

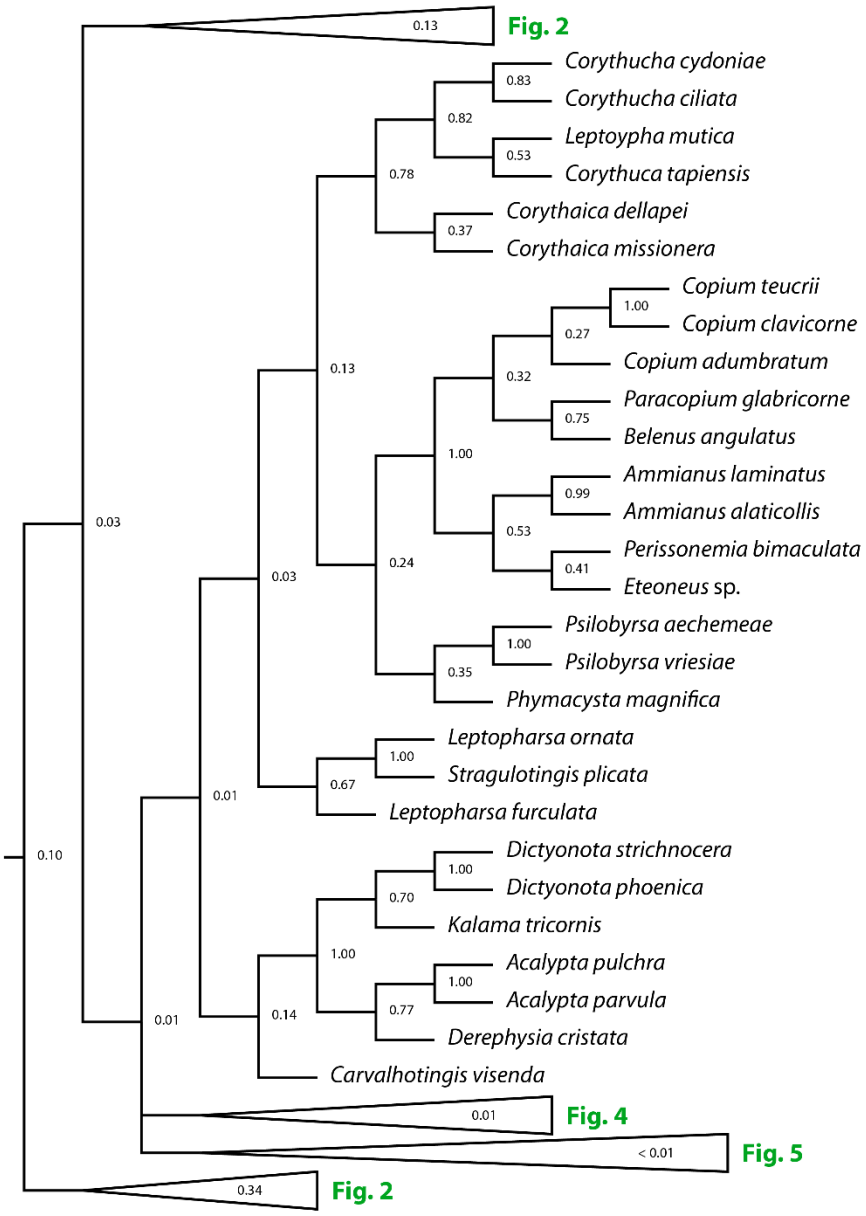

Figure 3. First clade in the polytomy retrieved within Tinginae. The other clades in polytomy are represented in different images (Figs. 4-5). Posterior probabilities are indicated next to each node.

Considering the remaining tingines (*minus Y. sideris* and *Leptodictya* species; pp = 0.10), two main clades with low support were recovered (pps = 0.34 and 0.03; Fig. 2). The first

is composed by *Teleonemia* Costa species, including *T. belfragii* Stål, *T. prunellae* Drake & Hambleton, *T. scrupulosa* Stål, and *T. morio* (Stål), which was found more closely related to *Melanorhopala* sp. than its congeners (pp = 0.97). The *Teleonemia* clade was recovered with high support (pp = 1.00) and related to the *T. morio* + *Melanorhopala* sp. clade (pp = 0.81). *Abdastartus muiri* Drake and *Megalocysta* sp. formed a clade (pp = 0.26) that appears as the sister-group of the aforementioned relationship. The second clade is composed by one weakly supported (pp = 0.13) and another one formed by three subclades in polytomy (pp = 0.01). The former presented two subclades (pp = 0.22), one composed by the monophyletic *Leptobyrsa* Stål (pp = 0.78) and *Pachycysta* Champion (pp = 0.99) genera + *Engynoma* sp. (pp = 0.97), and the second (pp = 0.97) includes the *Gargaphia* species (pp = 0.99) as sister-group of the *Leptopharsa* type-species, *L. elegantula* Stål (pp = 0.92), in addition to the *A. latipennis* clade already reported. The aforementioned polytomy is composed by three clades supported by low posterior probability levels (pps = 0.01, 0.01 and < 0.01; Fig. 3-5).

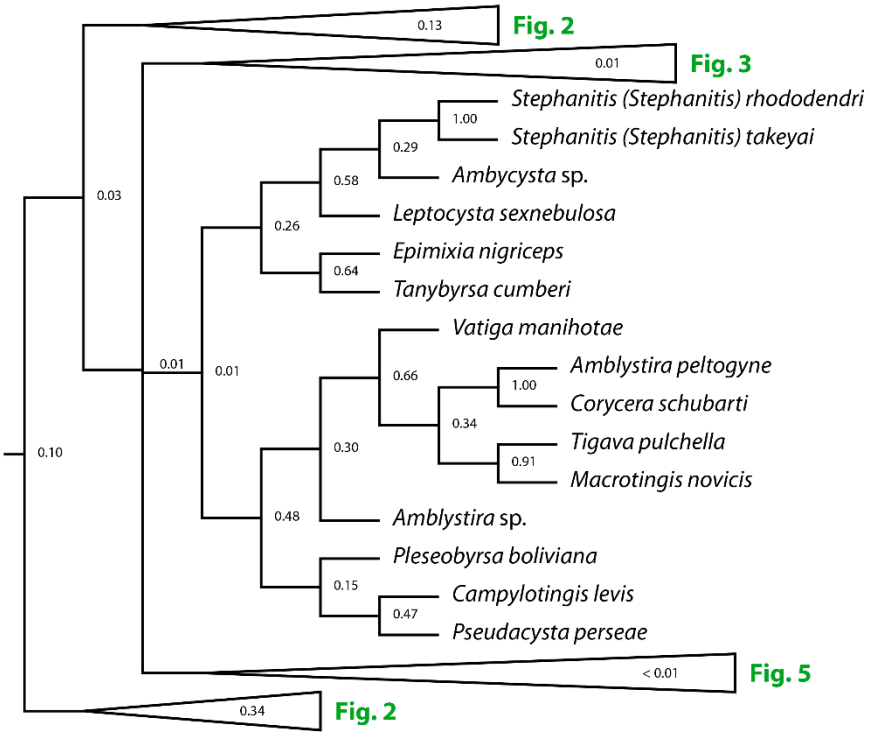

Figure 4. Second clade in the polytomy retrieved within Tinginae. The other clades in polytomy are represented in different images (Figs. 3, 5). Posterior probabilities are indicated next to each node.

Three interesting groups were recovered in subclades of this polytomy: the *Corythucha* Stål clade (Fig. 3), the *Copium* clade (Fig. 3) and the *Dictyla* Stål clade (Fig. 5).

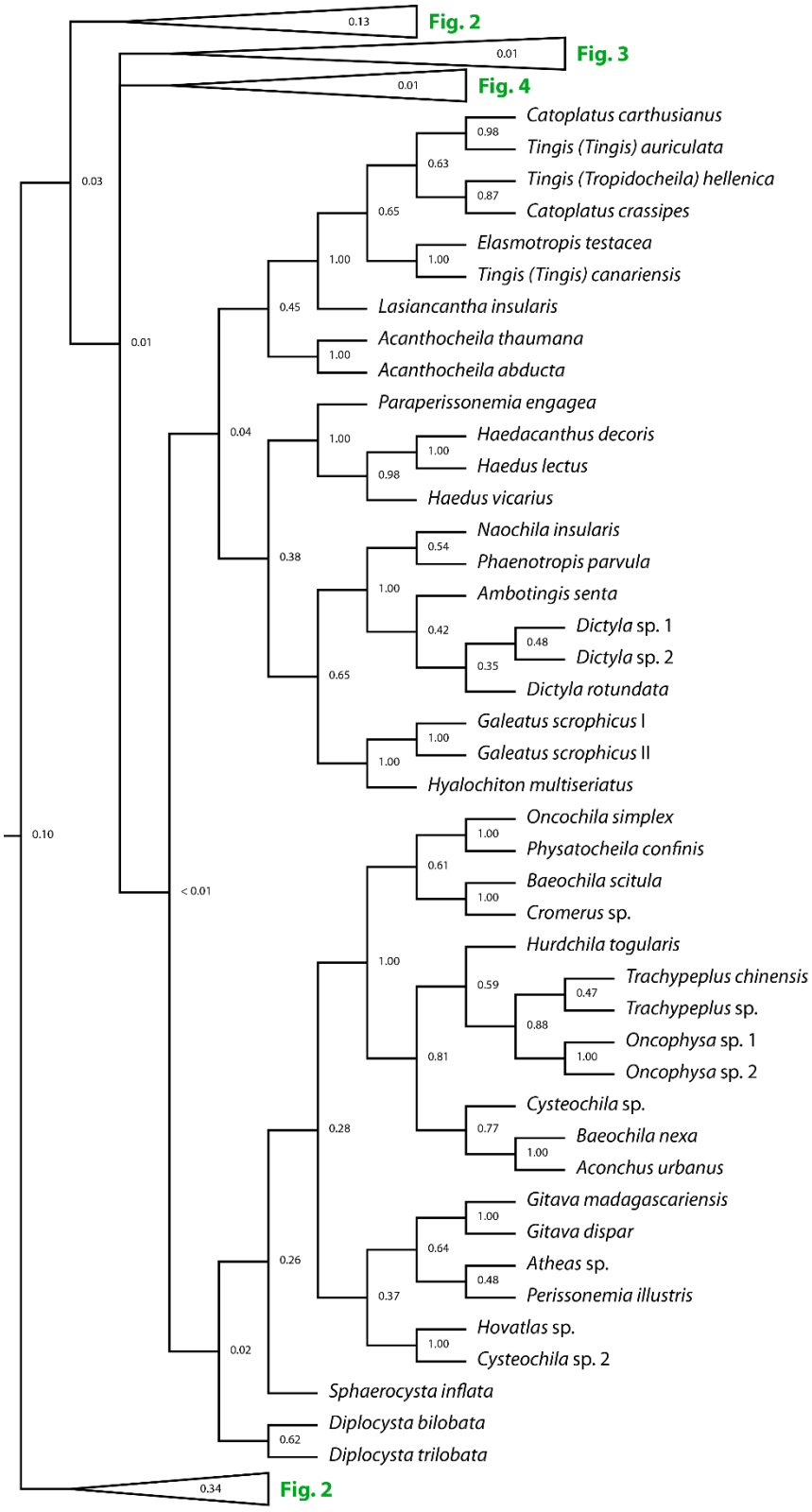

Figure 5. Third and final clade in the polytomy retrieved within Tinginae. The other clades in polytomy are represented in different images (Figs. 3-4). Posterior probabilities are indicated next to each node.

Three *Corythucha* species were added, *C. tapiensis* Ajmat, *C. cydoniae* (Fitch) and *C. ciliata* (Say), and the first was found as sister-group of the only *Leptoypha* Stål species included in the analysis, the type-species *L. mutica* (Say) (pp = 0.53). *Corythucha cydoniae* and *C. ciliata* formed a clade (pp = 0.83), closely related to *C. tapiensis* + *L. mutica* (pp = 0.82). *Copium* was supported by a low posterior probability (0.27) and was the sister-group (pp = 0.32) of the clade *Paracopium glabricorne* (Montandon) + *Belenus angulatus* Distant (pp = 0.75). *Dictyla* (pp = 0.35) was the sister-group to the species of *Ambotingis senta* (Drake & Hambleton) (pp = 0.42), which was then found to be the sister-group (pp = 1.00) of the clade *Naochila insularis* Duarte Rodrigues + *Phaenotropis parvula* (Signoret) (pp = 0.54), the latter being the type-species of the genus *Phaenotropis* Horváth. Additionally, several genera represented by only two species were recovered monophyletic in this analysis: *Corythaica* Stål (Fig. 3); *Ammianus* Distant; *Stephanitis* Stål (Fig. 4); *Acanthocheila* Stål (Fig. 5); *Trachypeplus* Horváth (Fig. 5); *Oncophysa* Stål (Fig. 5); *Diplocysta* Horváth (Fig. 5) and *Gitava* Drake (Fig. 5). On the other hand, *Perissonemia* Drake & Poor, *Haedus* Distant, *Cysteochila* Stål and *Baeochila* Drake & Poor are additional genera that were found paraphyletic in this analysis. *Tingis* and *Catoplatus* Spinola enhanced this list with cross-relationships among the included species, three and two, respectively (Fig. 5). The group formed by *T. auriculata* (Costa) + *C. carthusianus* (Goeze) (pp = 0.98) is the sister-group of *T. hellenica* (Puton) + *C. crassipes* (Fieber) (pp = 0.87) with a relatively high support (pp = 0.63), and this group was found to be the sister-group (pp = 0.65) of *T. canariensis* Péricart + *Elasmotropis testacea* (Herrich-Schaeffer) (pp = 1.00). The other clades were composed by the sole species added for each of the remaining genera, and therefore, with no implications on the monophyly of these taxa. They also have no importance on the composition nor monophyly of any of the current accepted supra-generic taxa, and thus, they were not individually reported here.

Discussion

In our analysis the relationship hypothesis Vianaidinae + Tingidae *sensu stricto* was once again corroborated. This grouping was found in all phylogenetic analyses that included terminals from both taxa and used outgroups from different heteropteran families (Schuh & Štys, 1991; Guilbert, 2001; Schuh *et al.*, 2006, 2009). However, *Henryianaida machupicchuensis* was here retrieved as more closely related to *Anommatocoris serratus* than its congeneric species, *H.*

colombiensis. This is contrary to what was found by Guidoti *et al.* (*in prep*), which proposed *Henryianaida* as a new genus after reviewing the subfamily and discussing the results of the morphological phylogenetic analysis that recovered these two species as a monophyletic group. Guidoti *et al.* (*in prep*) also highlighted the closeness among *Henryianaida* and *Anommatocoris*, not discarding the possible synonymy of both names in the future. However, the authors decided to proceed with the genus proposal due to the hurdles in comparing the macropterous and coleopteroid forms of Vianaidinae, and the lack of access to the type-material of the only known macropterous species of *Anommatocoris* (*A. bolivianus* Schuh *et al.*), which hampered further comparisons. Only three out of the 12 species of this complex (*Henryianaida* + *Anommatocoris*) were included in this current analysis and therefore, we believe that the addition of more taxa is required to assess the status of *Henryianaida* and its phylogenetic relationships within Vianaidinae. The analysis also corroborated the hypothesis of Cantacaderinae + Tinginae, which is the same defended since the last pre-phylogenetic classification hypothesis on Tingidae (Drake & Davis, 1960). This clade was corroborated by all phylogenetic analyses addressing Tingidae to this day (Lis, 1999; Guilbert, 2001, 2004, 2012; Schuh *et al.*, 2006; Guilbert *et al.*, 2014; Wappler *et al.*, 2015). In the current study, only three species belonging to the genus *Cantacader* were included. As such, none of the supra-generic taxa proposed by Lis (1999) and corroborated by Schuh *et al.* (2006), Guilbert (2012a) and Wappler *et al.* (2015) were evaluated. Guilbert *et al.* (2014), the most comprehensive phylogenetic analysis on Tingidae to this date, also did not address these relationships. Therefore, the last study to deal with the relationships between the tribes Cantacaderini, Carldrakeanini and Ceratocaderini remains Guilbert (2012a), which recovered Carldrakeanini and not Cantacaderini as Lis (1999) and Schuh *et al.* (2006) as the sister group of Ceratocaderini.

Phatnomatini was retrieved as a monophyletic taxon, highly supported, and including the largest number of terminals in a phylogenetic analysis to this day. A total of six species were included, three belonging to the type-genus of the tribe. *Phatnoma marmoratum* was found as the sister-group of the clade *P. tonkinana* + *P. costalis*, and the *Phatnoma* clade is sister to the clade *Distocader planti* + [*Sinalda helchrysumae* + *Plesionoma* sp.]. From these, only *P. marmoratum* was considered in previous phylogenetic analyses (Guilbert, 2004; Guilbert *et al.*, 2014), and both Guilbert (2004) and Guilbert *et al.* (2014) included two Phatnomatini species retrieving the tribe as a monophyletic taxon. Schuh *et al.* (2006) included two terminals at genus-level, *Phatnoma* and *Zetekella*, and found *Zetekella* more closely allied

to tingines than to the type-genus of Phatnomatini. This apparent paraphyly was latter corroborated by Guilbert (2012a), who further resolved the initial polytomy that includes *Zetekella* + tingines pointed by Schuh *et al.* (2006). Unfortunately, none of the *Zetekella* species was included in this study, neither from its allegedly closest related genus, *Minitingis* Barber (Guidoti & Guilbert, *in press*). However, the larger sampling scheme and the robust posterior probabilities observed for the Phatnomatini clade in this analysis are strong evidences of the monophyly of the tribe, despite the absence of *Zetekella* in our dataset. Phatnomatini was also found as sister-group of the remaining Tinginae in our results, corroborating a finding observed in most of the previous phylogenetic analyses available for Tingidae (Lis, 1999; Schuh *et al.*, 2006; Guilbert *et al.*, 2014). Therefore, Phatnomatini remains as the strongest supported tribe for Tinginae to this day.

The validity of the Tinginae tribes Ypsotingini and Litadeini were disputed in all analyses that focused the sampling scheme on Tinginae rather than Cantacaderinae, but they were always underrepresented in these datasets (Guilbert, 2001, 2004; Guilbert *et al.*, 2014). In the current analysis, both tribes were slightly more represented than in any of the previous works, comprising five species each, against two and two (Guilbert, 2001), four and one (Guilbert, 2004) and three and two species (Guilbert *et al.*, 2014), respectively for Litadeini and Ypsotingini. These numbers represent about 20% of the described litadeines and less than 10% of ypsotingines according to Froeschner (2001). Both were also found paraphyletic in this study, corroborating the findings of the aforementioned analyses (Guilbert, 2001, 2004; Guilbert et al., 2014). We found a highly supported placement of *Ypsotingis sideris* as the sister-group of the remaining tingines and, considering that this is the type-species of Ypsotingini's type-genus, the question on the tribe validity is revived. *Dictyonota phoenica* and the type-species of the genus, *D. strichnocera*, *Kalama tricornis*, and *Derephysia cristata* were the other Ypsotingini added to this analysis. They were recovered in a clade including two *Acalypta* species, *A. pulchra* and *A. parvula*. The relationship of *D. strichnocera* and *K. tricornis* with *Acalypta* species was already unveiled by Guilbert *et al.* (2014). In Guilbert *et al.* (2014) study, *D. strichnocera* was the sister-group of the clade *A. parvula* + [*A. pulchra* + *A. saturalis* (Puton)], with *K. tricornis* as the more inclusive sister-group. Therefore, the recurrence of a clade with this composition enhances the hypothesis for a close relationship among these taxa, and in addition to the highly supported placement of *Y. sideris*, it seems plausible to consider that if Ypsotingini is a valid supra-generic taxon its composition should most certainly be reviewed.

The sister-group of the remaining tingines (*minus Y. sideris*) was the clade formed by the two unidentified *Leptodictya* species. *Leptodictya* is a genus endemic of the Neotropical region, with only three species occurring in the U.S. (Drake & Ruhoff, 1965), and currently composed by more than 50 species (ITIS, 2018). The genus lacks a more in-depth study with a taxonomic review, a key to species and more importantly to our scope, a test to its hypothesis of monophyly. However, *Leptodictya* is known by one remarkable diagnostic character, the paranota folded on itself, which is unique within Tingidae to the best of our knowledge and its species were only found in Poaceae hosts, frequently on bamboos, which is rarely observed among the remainder tingids. In addition, the support for *Leptodictya* species + Tinginae *minus Y. sideris* and for the *Leptodictya* branch were high, indicating a strong probability for this clade. Since this was the first study to include *Leptodictya* species as terminals and only two were added, an eventual new tribe composed by this genus is a hypothesis to be further discussed on the light of a new phylogenetic analysis with an enhanced representation of this taxon. Five Litadeini species were included in the analysis, among them three type-species, *Aristobyrsa latipennis* (Fig. 6A), *Psilobyrsa aechemeae* (Fig. 6B), *Stragulotings plicata* (Fig. 6C), and the other species of the last genus, *P. vriesiae*. This tribe was disputed several times (Guilbert, 2001; 2004; Guilbert *et al.*, 2014), and our results corroborate the non-monophyly of the latest composition proposed for Litadeini (Froeschner, 2001). However, we did not include the species from its type-genus, the monotypic *Litadea* China, and therefore, it's unsure if its placement would repeat the Ypsotingini situation. In addition, Guilbert (2001) was the only study to include *Litadea delicatula* China in its morphological phylogenetic analysis and found this species in a clade sister to the rest of Tinginae, with the exception of *Eteoneus esakii* Drake, also absent in our study. On contrary to the remaining Ypsotingini species, the included Litadeini were not found in one single clade. *Psilobyrsa* was recovered monophyletic, and *Cephalidiosus spinosus* was retrieved as the sister-group of *Nobarnus albiceps*, also confirming the close relationship of these two genera endemic to New Caledonia, as indicated in previous works (Murienne *et al.*, 2009; Guilbert *et al.*, 2014). Although the placement of *L. delicatula* remains uncertain, the proposed composition for Litadeini (Froeschner, 2001) was refuted, indicating the non-monophyly of the group and suggesting once again, at this point, its suppression into Tingini.

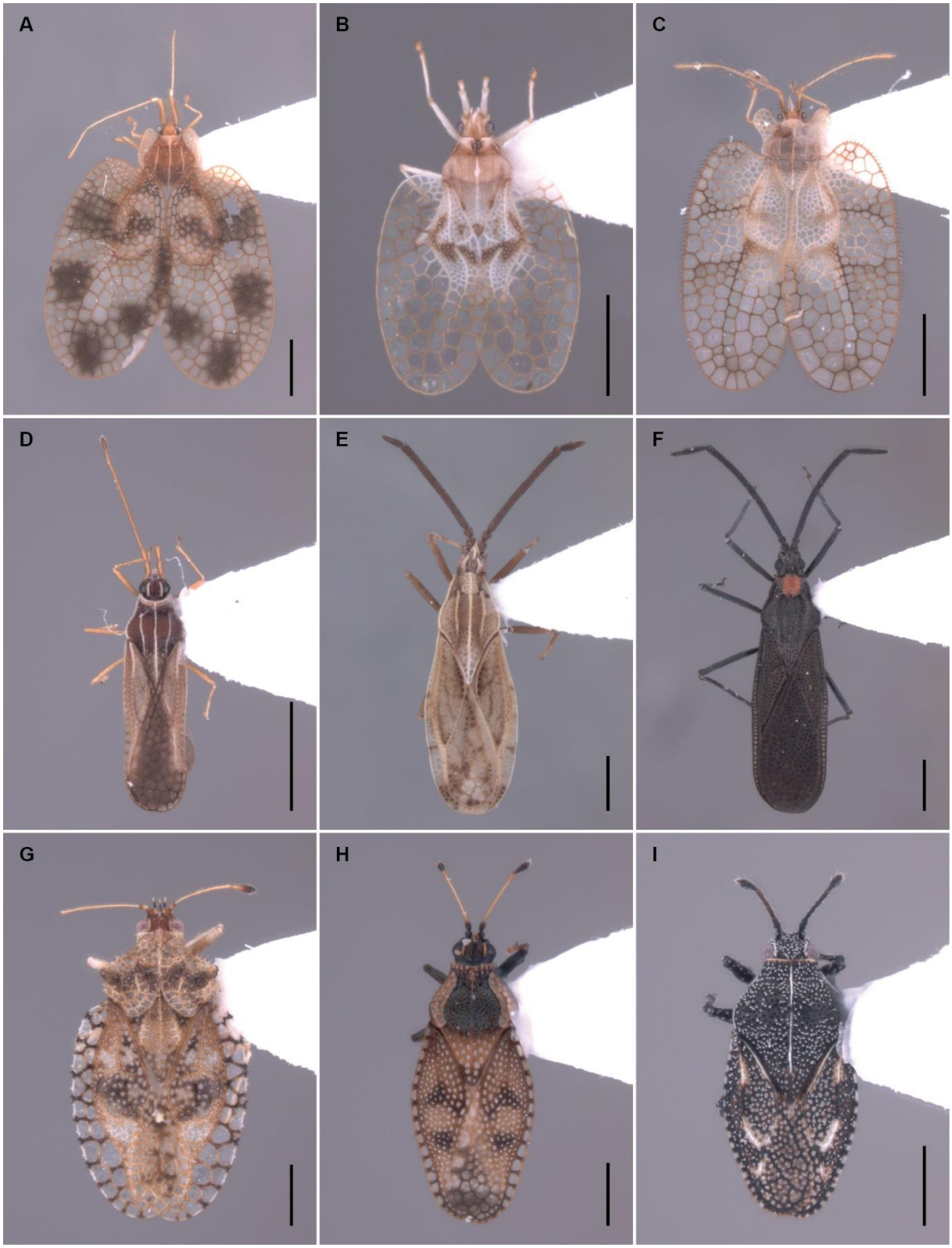

Figure 6. Dorsal habitus of Tingidae. A-C, morphologically similar species but not closely related; D-F, closely related but morphologically different species; G-I, similar morphologically and closely related. A) *Aristobyrsa latipennis*; B) *Psilobyrsa aechemae*; C) *Stragulotingis plicata*; D) *Abdastartus muiri*; E) *Melanorhopala* sp.; F) *Teleonemia morio* (Stål); G) *Ambotingis senta*; H) *Dictyla* sp. 1; I) *Phaenotropis parvula*. Scale bars: A-F) 1 mm; G-I) 0.5 mm.

Within the remaining Tinginae, the *Teleonemia* clade was recovered as sister-group of the remainder species and closely related to *Melanorhopala* sp., *Megalocysta* sp. and *Abdstartus muiri* (Fig. 6D). In fact, the genus *Teleonemia* was recovered paraphyletic, with *T. morio* closer to *Melanorhopala* sp. (Fig. 6E-F) than to its congeners. *Teleonemia* is a large genus composed by more than 80 species (ITIS, 2018), endemic in the Neotropical and Nearctic regions (Drake & Ruhoff, 1965), and morphologically similar to the Nearctic *Melanorhopala* Stål. *Megalocysta* is a monotypic genus from Panama, and the species from Costa Rica here included is yet to be described. This species was retrieved as the sister-group of an Oriental taxon, *A. muiri*, and both are very different morphologically and even more when in comparison with the *Teleonemia* or *Melanorhopala* species (Fig. 6D-F). The narrower basi- and distiflagellomere than the scape and pedicel of the antennae in *A. muiri* and its lack of hood are important differences between this species and the remaining taxa of this clade. *Megalocysta* sp., on the other hand, presents an expanded and inclined paranota and a conspicuously developed hood while the *Teleonemia* and *Melanorhopala* species have thick antennae with equally wide segments, a small and non-projected hood and a narrow, almost vertical, paranota. The clade *Megalocysta* sp. + *A. muiri* was weakly supported as well as the clade including all these taxa. The internal clades of the *Teleonemia* clade + *Melanorhopala froeschneri*, however, were highly supported. We consider the morphological differences and low support combined strong evidence to indicate that the relationship of both *Megalocysta* sp. and *A. muiri* with the *Teleonemia* + *M. froeschneri* clade is in fact misleading and need further analysis. All other phylogenetic analyses included only a single *Teleonema* species, *T. scrupulosa*, as terminal (Guilbert 2001, 2004; Guilbert *et al.*, 2014), and even considering the low representation of the genus and the fact that this analysis was not designed to address its monophyly, this is the first assessment of this hypothesis in a phylogenetic framework.

On the other hand, *Corythucha* was better represented on the latest phylogenetic analysis that focused on Tinginae (Guilbert *et al.*, 2014), which included seven different *Corythucha* species. According to Guilbert *et al.* (2014), the genus was found monophyletic and closely related to *T. scrupulosa*. In the present analysis only three species were included, and the genus was not recovered monophyletic nor closely related to any *Teleonemia* species. *Corythucha tapiensis* was found as the sister-group of the type-species of the genus *Leptoypha*, *L. mutica*. This species was also included in Guilbert *et al.* (2014), but it was retrieved distant from the *Corythucha* clade and as sister-group of *Amblystira pallipes* (Stål). Only two *Amblystira* Stål species were included in our analysis (*A. peltogyne* Drake & Hambleton and *Amblystira* sp.),

and they were found in a clade with *Corycera schubarti* Monte, *Tigava pulchella* Champion, *Macrotingis novicis* Drake and *Vatiga manihotae* (Drake), distant from the *Corythucha* + *L. mutica* clade. *Corythucha* is exclusive from the Neotropical and Nearctic regions (Drake & Ruhoff, 1965), with around 50 species (ITIS, 2018) and a remarkably unique morphology that includes a plane and roundish paranota, a drop-like hood projecting towards the head, and hemelytra with a characteristic basal fold. The only genus with a similar dorsal habitus is the monotypic Oriental *Macrocorytha* Stål, which was not included in any phylogenetic analyses to this day (Drake & Ruhoff, 1965). *Leptoypha* presents a carinate paranota, hood absent and hemelytra with a straight anterior border. Therefore, the morphology of these two genera is conspicuously different, and their relationship is unlikely to the eyes of Tingidae specialists. Additionally, the support for *C. tapiensis* and *L. mutica* was low (pp = 0.53), but the one presented by the entire clade was higher (pp = 0.82). Considering the conflicting results with Guilbert *et al.* (2014), we argue that more data, including the addition of more *Leptoypha* species, must be considered before the acceptance of this relationship. Moreover, even if this analysis was not addressing the monophyly of *Corythucha*, its unexpected paraphyly was noticed and should not be ignored in future studies on this genus.

Dictyla was here represented by three species, the largest number of *Dictyla* species in a phylogenetic analysis to this day. Guilbert (2004) and Guilbert *et al.* (2014) included one species each, *D. rasilis* (Drake & Maa) and *Dictyla* sp., and here we included *D. rotundata* (Herrich-Schaeffer) and two unidentified species. *Dictyla* is a genus distributed world-wide (Drake & Ruhoff, 1965) with more than 80 valid species (ITIS, 2018). The genus was found monophyletic, but with low support and its closest related taxon was *Ambotingis senta*, the type-species of this respective genus. This clade, *A. senta* + *Dictyla* species, is the sister-group of the clade *Naochila insularis* + *Phaenotropis parvula*. All these relationships were weakly supported, although the clade including all of them presented a higher posterior probability (1.00). On the other two analyses, however, the included *Dictyla* species were related to different taxa. According to Guilbert (2004), *D. rasilis* was found in a polytomy that included *Monosteira unicostata* (Mulsant & Rey), *Amblystira peltogyne*, *Kapiriella maynei* (Schouteden), *Cephalidiosus longispinus* Guilbert, *Compseuta ornatella* (Stål) and *Tingis irregularis* (Montrouzier). Guilbert *et al.* (2014) found the single *Dictyla* sp. included in the analysis as the sister-group of *Urentius hysticellus* (Richter). All four genera found related to *Dictyla* in our study present a very similar morphology sharing key diagnostic characters like the lack of hood, the paranota folded on the pronotum (excepted for *P. parvula*, which presents

a narrow, almost carinate paranota), and a curved radius-media vein on the hemelytra, whose degree of curvature varies greatly among these genera and their species (Fig. 6G-I). The geographical distribution of these genera is also somehow similar, with *Naochila* being reported from the Oriental and Ethiopian regions and *Phaenotropis* found in the Oriental, Ethiopian and Paleartic regions (Drake & Ruhoff, 1965). Only *Ambotingis* is exclusive from the Neotropical region (Knudson *et al.*, 2017). The need of a taxonomic review and a phylogenetic analysis of *Dictyla* is self-evident. A large genus never reviewed before with such large distribution might be indeed an interesting case-study for systematics. However, once again, the indication of its monophyly and close relationship with these morphological similar genera revealed in our analysis should not be entirely ignored in future contributions.

Copium and *Paracopium* were found closely related in our analysis. Three species of *Copium* were included, *C. teucrii*, *C. clavicorne* and *C. adumbratum*, against only one species of *Paracopium* Distant, *P. glabicorne*. *Copium* was found monophyletic but not highly supported, and sister-group to the clade *P. glabicorne* + *Belenus angulatus*. This latter species is remarkably different from both genera by the presence of hood and the explanate and frontwards projected paranota, but even more remarkably different by the antennae, which is not thick neither has thicker basi- and disitflagellomeres. However, the support for the clade *P. glabicorne* + *B. angulatus* was high (0.72), but the support for the entire clade was expressively lower than this (0.32), indicating a possible spurious relationship among all these taxa. This was the first study to include species from both genera, *Copium* and *Paracopium*, in a phylogenetic analysis. Guilbert (2001) and Guilbert *et al.* (2014) included one species of one of these genera each, *P. summervillei* (Hacker) and *C. teucrii*, respectively. In the first analysis, *P. summervillei* was found as sister-group of *T. scrupulosa*; in the second, *C. teucrii* formed a clade with *Oncochila simplex* (Herrich-Schaeffer). *Copium* presents eight species in total (ITIS, 2018), all from the Palearctic region (Drake & Ruhoff, 1965), while *Paracopium* is composed by at least 45 species (ITIS, 2018) also from the Palearctic region (Drake & Ruhoff, 1965). The morphological similarity and their biogeographical distribution might add arguments to corroborate the monophyletic relationship found in this study between these two genera. But perhaps more important than the test of their individual and combined monophyletic status is the uniqueness of the gall-making behavior presented exclusively by these two genera. This is only observed within these two genera in Cimicomorpha. Even incipient, the evidence of their relationship here presented might indicate a unique evolutionary event for this feature not only among Tingidae, but in the infraorder as well.

Another interesting evolutionary question within Tingidae concerns the maternal-care behavior. Several different displays of this behavior have been reported for species belonging to at least four genera, *Compseuta*, *Corythucha*, *Gargaphia* and *Leptobyrsa* (Guidoti *et al*., 2015). In our analysis, four out of the 67 *Gargaphia* species (ITIS, 2018) were included and retrieved as a monophyletic taxon. *Gargaphia schulzei* Drake was found as the sister group of *G. arizonica* Drake and Carvalho + [*G. torresi* Costa Lima + *G. decoris* Drake], and all these nodes presented high posterior probabilities. The sister-group of the *Gargaphia* clade is the type-species of *Leptopharsa*, *L. elegantula*. *Leptopharsa* is a larger genus, composed by more than 100 species, and as *Gargaphia* it's also endemic in the Neotropical and Nearctic regions. In this analysis, three other *Leptopharsa* species were included and therefore, the genus was recovered as a paraphyletic taxon. In previous phylogenetic analyses, *Leptopharsa* counted with one species in both Guilbert (2001) and Guilbert (2004), while *Gargaphia* was considered only in the first, also with one species. However, Guilbert *et al*. (2014) considered three different *Gargaphia* species and one *Leptopharsa*, *L. firma* Drake and Hambleton, recovering them as a monophyletic group as well, with *L. firma* as the sister-group of the *Gargaphia* clade. Both genera need a comprehensive taxonomic review and phylogenetic analysis to test their monophyly properly. *Gargaphia* was the subject of a PhD dissertation, but the main contribution from this dissertation with the proposition of a new genus and three species-groups composed by *Gargaphia* species was never formally published (Smith, 1996). Moreover, that study did not address the monophyly of the group in an appropriate manner due to the outgroup selection. Additionally, *Leptopharsa* is widely considered as a paraphyletic genus, and its future division in many other supra-specific taxa will not be a surprise. However, a genus or genera including species from both *Gargaphia* and *Leptopharsa* is considered unlikely due to the diagnostic character presented exclusively by all *Gargaphia* species: the anteriorly closed metasternal laminae. But now that the relationship between these two genera was once again corroborated, including the *Leptopharsa* type-species, *L. elegantula*, this hypothesis was strengthened. The next step would be a combined analysis with an increased number of terminals from both genera and a comprehensive outgroup sampling scheme, focusing on the relationships among and within these taxa.

Leptobyrsa was the third genus that presents maternal care to be included in this analysis, here represented by two species, *L. decora* Drake and *L. tersa* Drake & Hambleton. They were retrieved as a monophyletic taxon, related to the clade *Engynoma* sp. + *Pachycysta* clade. In other analyses, only one *Leptobyrsa* species was included and likewise in this

contribution, no major hypotheses regarding its status were proposed (Guilbert, 2001; Guilbert *et al.*, 2014). However, the fact that the genera with maternal care does not group in one exclusive clade neither are closely located in the tree might indicate a multiple origin of this intricate behavior. As Guidoti *et al.* (2015) summarized, maternal care in Tingidae is a complex behavior composed by many traits. Egg-dumping, egg-guarding, wing-fanning and variations within every and each of these behaviors were already reported for different species and genera Guidoti *et al.* (2015). Therefore, a multiple-origin scenario as indicated in our results would not be unlikely considering what is known for this behavior in Tingidae at this point. Another interesting evolutionary aspect of Tingidae is represented by *Carvalhotingis visenda*, which was recovered as the sister-group of the clade composed by the remaining Ypsotingini + *Acalypta* species. This genus, *Carvalhotingis* Froeschner, was proposed to accommodate species previously described in *Acanthocheila*. During the revision of the two genera, Froeschner (1995) pointed out what is probably the only mimicry case reported within Tingidae: the cephalic spines of *Carvalhotingis* species are not actual spines, but setae organized in a way to look like spines. Considering this and many other characters discussed in this Froeschner's taxonomic review (1995), the distant relationship among *C. visenda* and the two *Acanthocheila* species was expected, despite the superficial morphological similarity presented by both genera.

Most of the internal clades in Tinginae (*minus Y. sideris* and *Leptodictya* clade) were weakly supported. Additionally, each genus here included counted with four species or less, and thus, their monophyletic status was not properly tested. Therefore, only a few comments on specific genera were drawn in this contribution. Guilbert (2001, 2004) and Guilbert *et al.* (2014) focused their sampling scheme in this subfamily, and more specifically, in Tingini, and also faced similar results: low support and non-corroborated results regarding the internal Tinginae classification among these studies. Sadly, our results don't scape this trend, and, once again, highlighted the need for more data to clarify these relationships within Tinginae. One example of the contradictory results among the different analyses available to this day is the genus *Tingis*. It was included in most analyses (Guilbert, 2001, 2004; Guilbert *et al.*, 2014) but usually represented by different species and retrieved as related to different taxa. *Tingis* is a large nominal genus comprising more than 100 species, world-wide distributed, that lacks a taxonomic review and a proper phylogenetic analysis. Thus, this genus is somehow expected to be paraphyletic among specialists. However, the lack of consistency between the results affected by the differences in the datasets, in both terminals and characters, hampers not only

the understanding of *Tingis* position within Tingidae phylogeny but also the proposal of strongly corroborated supra-generic taxa for this subfamily. Additionally, the remarkable external morphology of Tinginae doesn't seem to carry a strong phylogenetic signal. The supra-generic taxa in Cantacaderinae and the relationship of the subfamilies, on the other hand, are well-understood and highly corroborated in the different available phylogenies (Lis, 1999; Schuh *et al.*, 2006; Guilbert, 2012a; Wappler *et al.*, 2015). The lack of molecular data for all the Cantacaderinae tribes imposes some limits on the exploration of evolutionary hypotheses. One example is the estimation of the date for their clades, and the comprehension of their biogeographical history considering both molecular clock methods and the fossil record on the light of modern biogeographical analyses. Fortunately, this is not the case for Vianaidinae anymore, due to the three terminals here added.

Therefore, we understand that this contribution corroborated the relationship hypotheses among the subfamilies in Tingidae phylogeny. It also includes the first molecular sequences for Vianaidinae, which will allow several further studies in the near future. We also retrieved Phatnomatini as a monophyletic taxon and corroborate its close relationship with Tinginae, with the largest dataset for this tribe presented to this day. Our results also brought some light to Tinginae tribes by reviving Ypsotingini but disputing its composition, corroborating the suppression of Litadeini and by discussion, for the first time, a potential new tribe to accommodate *Leptodictya* species. Further studies should continue to focus the efforts to improve the dataset in terms of both terminals and characters, including the addition of morphological characters as well, and evolutionary and biogeographical analyses since now not only fossil record but molecular data is available for all subfamilies and major supra-generic clades.

Acknowledgments

We would like to thank Dr. Christiane Weirauch (University of California, Riverside), Dimitri Forero (MPUJ) and Marcos Rosa-Cusachs (Universitat de Barcelona) for donating the material used in the DNA extractions; to Eric Gordon (University of California, Riverside), Filipe Michels and Nathalia Russi (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) and Aline Barcellos (Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil) for preparing and shipping samples; to the Smithsonian Institution for the pre-doctoral fellowship awarded to the first author, which allowed the study and

consultation of the world's largest Tingidae collection, and to Thomas J. henry (Systematic Entomology Laboratory, Agricultural Research Service, United States Department of Agriculture, c/o NMNH), who sponsored the first author in this program. We also thank to CNPq (National Council for Scientific and Technological Development) for the first author's fellowships (process number: 141467/2014-2 and 201352/2015-0).

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Appendix

List of terminals included in the analysis.

For Ypsotingini and Litadeini, the supra-generic composition proposed by Froeschner (2001) is followed.

Family	Subfamily	Tribe	Species
Miridae			*Europiella albipennis* (Fállen, 1829)
Thaumastocoridae			*Thaumastocoris petilis* Drake & Slater, 1957
Tingidae	Cantacaderinae	Cantacaderini	*Cantacader lethierryi* Scott, 1874
			Cantacader quinquecostatus (Fieber, 1844)
			Cantacader sp.
	Tinginae	Litadeini	*Aristobyrsa latipennis* (Champion, 1897)
			Cephalidiosus spinosus Guilbert, 2008
			Psilobyrsa aechemeae Drake & Hambleton, 1935
			Psilobyrsa vriesiae Drake & Hambleton, 1935
			Stragulotingis plicata (Champion, 1897)
	Tinginae	Phatnomatini	*Distocader planti* Guilbert & Guidoti, 2018
			Phatnoma costalis Distant, 1909
			Phatnoma marmoratum Champion, 1897
			Phatnoma tonkinana Drake & Maa, 1955
			Plesionoma sp.
			Sinalda helichrysumae Duarte Rodrigues, 1982
	Tinginae	Tingini	*Abdastartus muiri* Drake, 1927
			Acalypta parvula (Fallén, 1807)
			Acalypta pulchra Stusák, 1961
			Acanthocheila abducta Buchanan-White, 1879
			Acanthocheila thaumana Drake and Cobben, 1960
			Aconchus urbanus (Horváth, 1905)
			Amblystira peltogyne Drake and Hambleton, 1935
			Amblystira sp.
			Ambotingis senta (Drake and Hambleton, 1942)
			Ambycysta sp.
			Ammianus alaticollis (Stål, 1855)
			Ammianus laminatus (Horváth, 1911)
			Atheas sp.
			Baeochila nexa (Distant, 1903)

Tinginae	Tingini	*Baeochila scitula* Drake, 1948
		Belenus angulatus Distant, 1909
		Campylotingis levis Drake and Hambleton, 1942
		Carvalhotingis visenda (Drake and Hambleton, 1934)
		Catoplatus carthusianus (Goeze, 1778)
		Catoplatus crassipes (Fieber, 1861)
		Copium adumbratum (Horváth, 1891)
		Copium clavicorne (Linnaeus, 1758)
		Copium teucrii (Host, 1788)
		Corycera schubarti Monte, 1946
		Corythaica dellapei Montemayor and Melo, 2012
		Corythaica missionera Ajmat, 2000
		Corythucha tapiensis Ajmat, 1991
		Corythucha ciliata (Say, 1832)
		Corythucha cydoniae (Fitch, 1861)
		Cromerus sp.
		Cysteochila sp. 1
		Cysteochila sp. 2
		Dictyla rotundata (Herrich-Schaeffer, 1835)
		Dictyla sp. 1
		Dictyla sp. 2
		Diplocysta bilobata Horváth, 1925
		Diplocysta trilobata Drake and Poor, 1939
		Elasmotropis testacea (Herrich-Schaeffer, 1830)
		Engynoma sp.
		Epimixia nigriceps (Signoret, 1881)
		Eteoneus sp.
		Galeatus scrophicus Saunders, 1876
		Gargaphia arizonica Drake and Carvalho, 1944
		Gargaphia decoris Drake, 1931
		Gargaphia schulzei Drake, 1954
		Gargaphia torresi Costa Lima, 1922
		Gitava dispar Schouteden, 1957
		Gitava madagascariensis Schouteden, 1957
		Haedacanthus decoris Duarte Rodrigues, 1992
		Haedus lectus (Drake, 1937)
		Haedus vicarius (Drake, 1927)
		Hovatlas sp.
		Hurdchila togularis (Drake & Poor, 1936)
		Hyalochiton multiseriatus (Reuter, 1888)

Tinginae	Tingini	*Lasiancantha insularis* Schouteden, 1957
		Leptobyrsa decora Drake, 1922
		Leptobyrsa tersa Drake and Hambleton, 1935
		Leptocysta sexnebulosa (Stål, 1858)
		Leptodictya sp. 1
		Leptodictya sp. 2
		Leptopharsa elegantula Stål, 1873
		Leptopharsa furculata (Champion, 1897)
		Leptopharsa ornata Monte, 1940
		Leptopharsa rumiana Drake & Hambleton, 1946
		Leptoypha mutica (Say, 1832)
		Macrotingis novicis Drake, 1928
		Megalocysta sp.
		Melanorhopala froeschneri Henry & Wheeler, 1986
		Naochila insularis Duarte Rodrigues, 1982
		Nobarnus albiceps Guilbert, 1998
		Oncochila simplex (Herrich-Schaeffer, 1830)
		Oncophysa sp. 1
		Oncophysa sp. 2
		Pachycysta diaphana Champion, 1898
		Pachycysta sp.
		Paracopium glabricorne (Montandon, 1892)
		Paraperissonemia engaea Duarte Rodrigues, 1992
		Perissonemia bimaculata (Distant, 1909)
		Perissonemia illustris Drake & Poor, 1937
		Phaenotropis parvula (Signoret, 1865)
		Phymacysta magnifica (Drake, 1922)
		Physatocheila confinis Horváth, 1905
		Pleseobyrsa boliviana Drake and Poor, 1937
		Pseudacysta perseae (Heidemann, 1908)
		Sphaerocysta inflata (Stål, 1858)
		Stephanitis (Stephanitis) rhododendri Horváth, 1905
		Stephanitis (Stephanitis) takeyai Drake & Maa, 1955
		Tanybyrsa cumberi Drake, 1959
		Teleonemia belfragii Stål, 1873
		Teleonemia morio (Stål, 1855)
		Teleonemia prunellae Drake & Hambleton, 1946
		Teleonemia scrupulosa Stål, 1873
		Tigava pulchella Champion, 1897
		Tingis (Tingis) auriculata (Costa, 1847)

	Tinginae	Tingini	*Tingis (Tingis) canariensis* Péricart, 1982
			Tingis (Tropidocheila) hellenica (Puton, 1877)
			Trachypeplus chinensis Drake & Poor, 1936
			Trachypeplus sp.
			Vatiga manihotae (Drake, 1922)
	Tinginae	Ypsotingini	*Derephysia cristata* (Panzer, 1806)
			Dictyonota phoenica Seidenstücker, 1963
			Dictyonota strichnocera Fieber, 1844
			Kalama tricornis (Schrank, 1801)
			Ypsotingis sideris Drake, 1947
	Vianaidinae		*Anommatocoris serratus* Guidoti et al., *in prep*.
			Henryianaida colombiensis Guidoti et al., *in prep*.
			Henryianaida machupicchuensis Guidoti et al., *in prep*.
Ceratocombidae			*Ceratocombus australiensis* Gross, 1950
Macroveliidae			*Macrovelia hornii* Uhler, 1872
Tessaratomidae			*Erga longitudinalis* (Westwood, 1837)
			Lyramorpha parens Breddin, 1900

Chapter VI

Perspectives on Tingidae (Heteroptera, Cimicomorpha) systematics and evolution

Chapter VI - Perspectives on Tingidae (Heteroptera, Cimicomorpha) systematics and evolution

From the first phylogenetic analysis addressing Tingidae classification to this day, very little has advanced on the understanding of the limits and relationships of Tingidae supra-generic taxa, especially within Tinginae *sensu* Drake & Ruhoff, 1965 (Lis, 1999; Guilbert 2001, 2004, 2012a; Schuh *et al.*, 2006; Guilbert *et al.*, 2014). Efforts were made towards this goal, but the small sampling scheme and the hurdles of coding such remarkably varied external morphology (Fig. 1) into strong and reliable phylogenetic characters hampered the authors' intentions (Guilbert 2001, 2004; Guilbert *et al.*, 2014). Still due to recent phylogenetic efforts, the study of immature forms was revived (Guilbert, 2004), and contributions focusing on their descriptions counting on high-quality illustrations, as well as terminological reviews, were produced (e.g., Guilbert, 2005). Evolutionary studies were conducted based on these forms as well, but once again, the lack of data has limited the development of more robust hypotheses on the evolution of the group (Guilbert, 2004; Guilbert *et al.*, 2008). However, Guilbert *et al.* (2008) highlighted the importance of the ontogenetic information on the complete set of nymphs, and since then, highly illustrated contributions concerning all instars were also produced (e.g., Guidoti & Barcellos, 2013). Tingidae presents two very unusual behaviors within Cimicomorpha, one of them being unique for the infraorder: the gall-forming and maternal care (Drake & Rufoff, 1965; Guidoti *et al.*, 2015). These behaviors present faulty data on the literature, which hampers further analyses within a phylogenetic or evolutionary framework. One other aspect of Tingidae evolution has been explored: its biogeographical reconstruction. Lis (1999) was the first contribution to address the subject under an analytical methodology, followed by Guilbert (2012b). Additionally, Wappler (2006) and Wappler *et al.* (2015) made theoretical contributions as well, focusing on the available fossil record rather than a specific methodological approach. However, as discussed below, there are constraints hampering the advance on this subject as well. One of these constraints that is common to all aspects mentioned here (classification, immatures, behaviors and biogeography) is the lack of a strong classification hypothesis for Tingidae based on a comprehensive phylogenetic analysis that deals with supra-generic taxa in all subfamilies, especially in Tinginae. Nonetheless, slowly but somehow firmly the knowledge on these subjects and perhaps more importantly, on Tingidae classification and biogeography, has progressed.

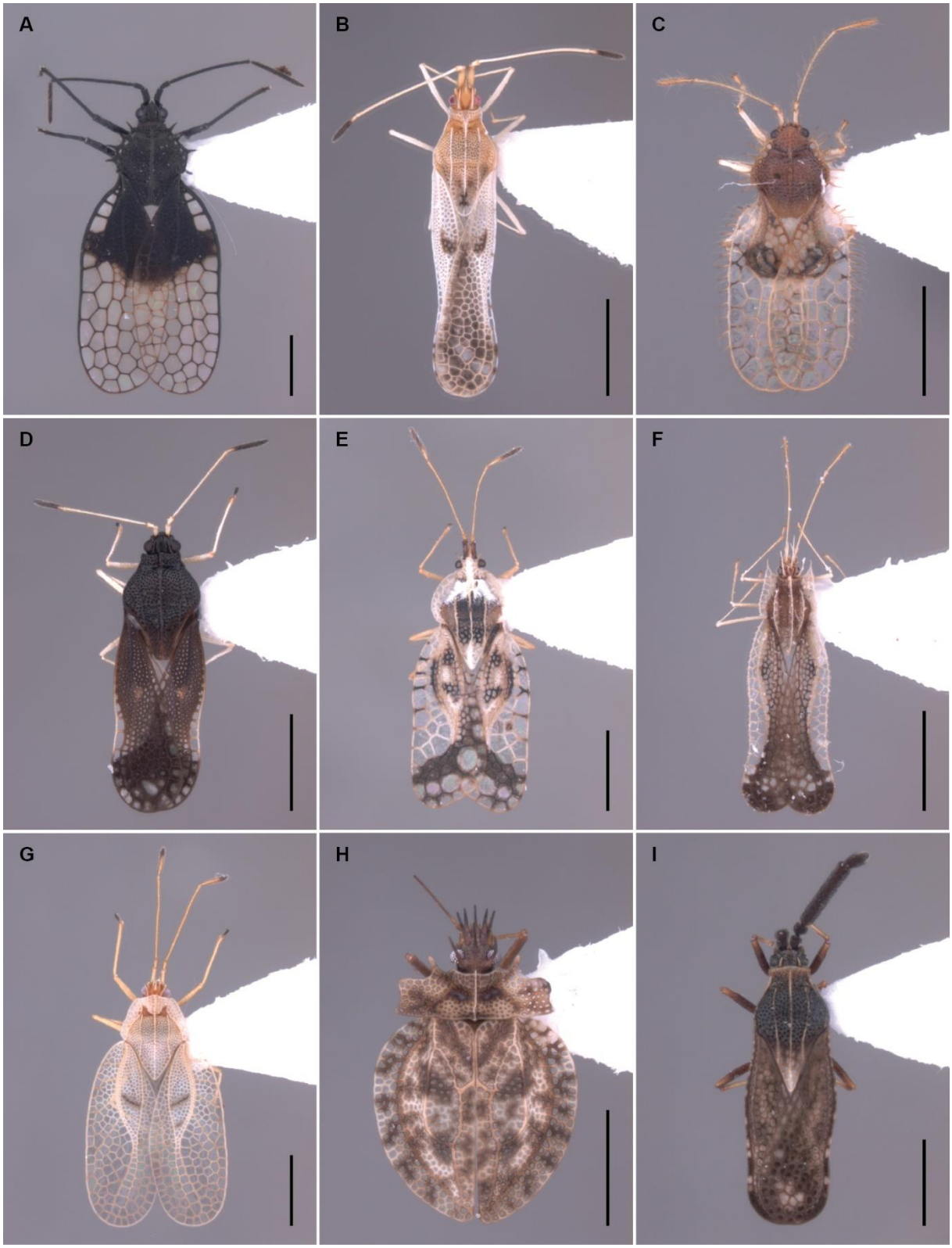

Figure 1. Dorsal habitus of Tingidae. A) *Acanthocheila abducta* Buchanan-White, 1879; B) *Campylotingis levis* Drake & Hambleton, 1942; C) *Carvalhotingis visenda* (Drake & Hambleton, 1934); D) *Corycera schubarti* Monte, 1946; E) *Gargaphia schulzei* Drake, 1954; F) *Haedus vicarius* (Drake, 1927); G) *Leptodictya* sp. 1; H) *Plesionoma* sp.; I) *Teleonemia prunellae* Drake & Hambleton, 1946. Scale bars: 1.0 mm.

If Tingidae classification hasn't changed much in the past 20 years, Tingidae taxonomy remains the same for over a century. The description of new taxa in this family is usually based on external morphology, focusing almost exclusively on non-genital characters. This was established by Drake & Davis (1960), on the most comprehensive morphological work on the family, when they affirmed that genital characters are informative only at subfamily levels. However, Lee (1969) and Lis (2003) showed that some differences on the female genital plates and the shape of paramere and pygophore on males might be used to delimit species in *Stephanitis* Stål, 1873 and *Cantacader* Amyot and Serville, 1843. The revisionary works available for Tingidae genera also tend to follow the same tendency of describing only non-genital morphology, safe some rare exceptions (e.g., Lis, 2003). Therefore, the taxonomic practice within the family remains the same since Drake & Davis (1960) and the most important recent novelty on Tingidae taxonomy was the description of one single species, *Anommatocoris bolivianus* Schuh et al., 2006. This species was the first macropterous species of Vianaidinae to be formally described, although its first mention on the literate came many years before (Schuh & Štys, 1991). It was after this description, the first since *Thaumamannia vanderdrifti* van Doesburg, 1977, that Vianaidinae became a focus of attention of many authors and in many different contributions, culminating in two chapters here included.

In this thesis, I focused on important taxonomic contributions for two key supra-generic taxons, Phatnomatini and more emphatically, on Vianaidinae. With the review, expansion and phylogenetic analysis of Vianaidinae, its external non-genital morphology was explored to its limit. Moreover, the largest molecular phylogenetic analysis of Tingidae was provided, including for the first time Vianaidinae sequences and raising important points of debate on the supra-generic taxa composition of the family, especially within Tinginae. In the next three subsections I discussed in detail the impact of these findings on these three different subjects concerning Tingidae systematics and evolution.

Vianaidinae Systematics

Vianaidinae was retrieved as the sister-group of Tingidae *sensu stricto* (Tinginae + Cantacaderinae *status* Schuh et al., 2006) by many different studies (Schuh & Stys, 1991; Guilbert, 2001; Schuh *et al.*, 2009), and some authors considered it as a closely related family instead of a Tingidae subfamily (e.g., Lis, 1999; Golub, 2001). Schuh *et al.* (2006) were the last authors to address the taxonomic status of Vianaidinae, together with the status of other supra-

generic taxa within Tingidae. According to these authors, elevation of ranks based on autapomorphies might obscure phylogenetic relationships rather than clarify them (Schuh *et al.*, 2006). For this reason, Vianaidinae has been treated as a subfamily of Tingidae since then, safe Montemayor & Carpintero (2007), who apparently missed Schuh *et al.* (2006) paper by not citing it in their contribution. The fact that Vianadinae was considered the sister-group of Tingidae *sensu stricto* always linked this subfamily to the origin of all tingids (Golub, 2001; Guilbert, 2012b). In this thesis, Guidoti & Guilbert (*in prep.*) retrieved Vianaidinae as the sister-group of the remaining Tingidae once again, including the first DNA sequences available for this subfamily. *Henryianaida macchupichuensis* Guidoti *et al.*, *in prep.*, *Anommatocoris serratus* Guidoti *et al.*, *in prep.* and *H. colombiensis* Guidoti *et al.*, *in prep.* were the species included as terminals in the analysis (Fig. 2; Guidoti & Guilbert, *in prep.*). The availability of DNA sequences for this subfamily (Guidoti & Guilbert, *in prep.*), allied to the existence of undisputed fossil record for this subfamily (see below), unlock an important perspective for Tingidae biogeography and the question of the origin of all tingids.

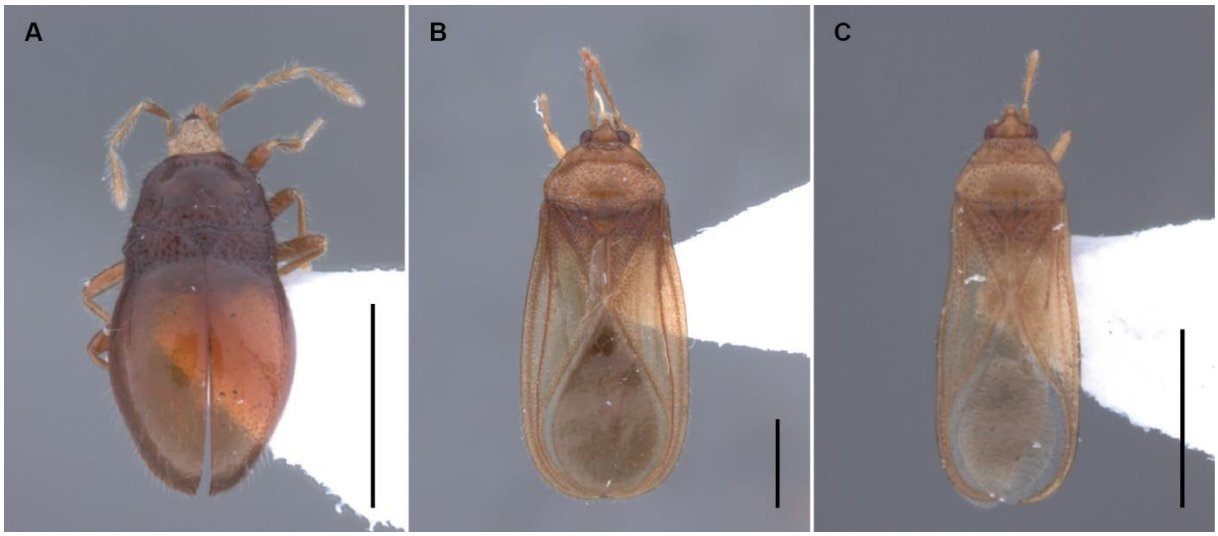

Figure 2. Dorsal habitus of the sequenced Vianaidinae species. A) *Anommatocoris serratus*; B) *Henryianaida colombiensis;* C) *H. machupicchuensis*. Scale bars: 1.0 mm.

In a different contribution from this thesis, Guidoti *et al.* (*in prep.*) provided the first phylogenetic analysis addressing the internal relationship of Vianaidinae, in addition to the description of nine new species and one new genus. After this comprehensive taxonomic review, the subfamily almost doubled its number of taxa. Except for *A. bolivianus* and *T. vanderdrifti*, all previously described species were studied and re-described from type-material

to maintain consistency of the applied terminology. This includes recently described species like *Pterovianaida duckensis* Guidoti & Montemayor, 2016 (chapter 2), which was found at the Instituto Nacional de Pesquisas da Amazonia (INPA) in 2015, and therefore, described first and separately. The other species' material were accumulated from collection loans since 2013, but the two alcohol-preserved macropterous forms from *Henryianaida* Guidoti *et al., in prep.* were obtained only in late 2016. The first key to the genera of Vianaidinae since Drake & Ruhoff (1965) was provided, as well as keys to the species of each genera. Since genital characters were not used due to accessibility issues, all descriptions, identification keys, and phylogenetic characters were based on external non-genital morphology (Guidoti *et al., in prep.*). *Anommatocoris* China, 1945 species are less variable morphologically than the ones in any other genus. The species in *Anommatocoris* were delimited based on characters like the pronotal humeral angle, the extension of the carina-like vein on hemelytra, and more importantly, the shape, size, and curvature of the scent gland peritreme. *Thaumamannia insolita* Guidoti *et al., in prep.* provided the biggest taxonomic challenge and its placement was initially uncertain, being defined only after the phylogenetic analysis. This species shares with *Anommatocoris* the lighter color and straight orientation of the head, and the narrower costal area, but it was retrieved monophyletic with *Thaumamannia* supported by three characters: the narrow scutellum, the large scale-like projections on the paranota border, and the posterior branch of the scent gland peritreme shorter than the upper part of the anterior branch (*Guidoti et al., in prep.*). *Henryianaida* Guidoti *et al., in prep.* species, on the other hand, presented remarkable size differences unnoticed in any other genus of this subfamily (Guidoti *et al., in prep.*).

Although many taxa were described in Guidoti *et al.* (*in prep.*), the discussion on the Vianaidinae internal relationships was perhaps the most interesting contribution from that chapter. *Henryianaida* was found sister to *Anommatocoris*, and this clade was supported by the abundance of the head setae, the fine punctuation on pronotum and the anterior constriction of hemelytra. *Pterovianaida* Montemayor & Carpintero, 2007 was found monophyletic and closely related to *Thaumamannia* (Guidoti *et al., in prep.*). The former genus is composed by two macropterous species, while *Thaumamannia* is still exclusively known from coleopteroid forms. The head inclination and the large scales on the hemelytra borders were the supporting characters. In addition, the scent gland peritreme of both *Pterovianaida* and *Thaumamannia* species presented a very similar shape, inclination and curvature, and even if not pointed as a synapomorphic trait on the analysis, its remarkable resemblance was noticed and discussed (Guidoti *et al., in prep*). However, identifying macropterous and coleopteroid specimens as the

same species based exclusively on external non-genital characters is an improbable task due to the conspicuous differences among these two forms. The scent gland peritreme is believed to be highly conserved among macropterous and coleopteroid specimens of a given species, and no two species in these genera were found with identical peritremes (Guidoti *et al., in prep.*). Therefore, the possibility of *Pterovianaida* as a junior synonym of *Thaumamannia* was not formally proposed, but discussed (Guidoti *et al., in prep.*). This, allied to the lack of access to the type-material of *A. bolivianus* also puts *Henryianaida* in the same situation of not having the possibility of its synonymy with *Anommatocoris* entirely discarded.

After Guidoti *et al.* (*in prep.*) it seems that questions concerning Vianaidinae systematics are now restricted to two topics: whether a single species presents both macropterous and coleopteroid forms, and whether the macropterous-exclusive genera, *Pterovianaida* and *Henryianaida,* are junior synonyms of *Thaumamannia* and *Anommatocoris*, respectively. Since Guidoti *et al.* (*in prep.*) explored the external non-genital morphological characters to the limit and this source of information was not enough to properly address these two issues, they remain to be solved. An integrative approach for Vianaidinae taxonomy, considering data from different origins as, DNA sequences, morphology and distribution, might bring some light to the first issue. The understanding on the morphology of the group would improve if genital characters, both external and internal, could be explored. Geometric morphometrics could bring important data on the subtle differences on the shape of specific structures, including genital characters, among closely-related species, macropterous and coleopteroid congeneric species, or just similar specimens. And these genital characters allied to DNA sequences could be used to test the monophyletic groups and relationships retrieved in Guidoti *et al.* (*in prep.*), addressing with an even more robust dataset the two hypotheses of synonymy raised but not formally proposed in this study. The first step to perform these analyses will be to collect more specimens of this rare and intriguing Tingidae subfamily.

Tingidae Classification

In addition to Vianaidinae, Tingidae is currently composed by two other subfamilies: Cantacaderinae and the nominal subfamily, Tinginae. Lis (1999) focused on Cantacaderinae, in perhaps the most influential phylogenetic analysis concerning Tingidae thus far. Lis (1999) proposed, in addition to the elevation of some taxonomic ranks, two new supra-generic taxa. These were considered tribes of Cantacaderinae by Schuh *et al.* (2006) when rejecting the ranks

proposed by Lis (1999), but more importantly, Schuh *et al.* (2006) recovered the monophyletic status of these newly proposed taxa. Guilbert (2012a) and Wappler *et al.* (2015) using similar datasets also retrieved the same monophyletic taxa. Guilbert (2012a) added two extant genera, *Caledoderus* Guilbert, 2012 and *Afghanoderus* Lis, 2001, and these were retrieved in Ceratocaderini and Cantacaderini, respectively. In addition to these two added genera, Guilbert (2012a) also found Carldrakeanini sister to Ceratocaderini and not Cantacaderini as in Lis (1999) and Schuh *et al.* (2006). Wappler *et al.* (2015) retrieved the three tribes of Cantacaderinae *status* Schuh *et al.* (2006) in a polytomy after the addition of the fossil genus *Gyaclavator* Wappler *et al.*, 2015, which in turn was found in polytomy with Tingidae *sensu stricto* in the strict consensus tree whereas sister to Cantacaderinae in the majority rule consensus tree. Guilbert *et al.* (2014) and Guidoti & Guilbert (*in prep.*), the only phylogenies to include molecular data to this day, added *Cantacader* species from this subfamily on their respective datasets. Therefore, the supra-generic composition of Cantacaderinae remains the one proposed by Lis (1999), and considering the high floatability of *Gyaclavator* in Wappler *et al.* (2015) results, it seems that the internal relationships of Cantacaderinae remain the same recovered by Guilbert (2012a).

Lis (1999) also proposed transferring Phatnomatini to Tinginae, which was corroborated by most subsequent phylogenetic analyses to this day (Schuh *et al.*, 2006; Guilbert, 2012a; Guilbert *et al.*, 2014; Wappler *et al.*, 2015; Guidoti & Guilbert, *in prep.*). After the suppression of Ypsotingini and Litadeini proposed by Guilbert *et al.* (2014), Phatnomatini remained the only valid tribe of Tinginae in addition to the nominal tribe, which is now also composed by the former Ypsotingini and Litadeini. However, Schuh *et al.* (2006), Guilbert (2012a) and Wappler *et al.* (2015) retrieved *Zetekella* Drake, 1944 within the remaining Tinginae and not closely related to the type-genus of its original tribe, *Phatnoma* Fieber, 1844. *Zetekella* is a small genus composed by only three species and, although not based in a phylogenetic hypothesis, it's accepted as closely related to *Minitingis* Barber, 1954, another small taxon (two species) that shares many morphological characters with *Zetekella* (Guidoti & Guilbert, *in press*). As Guilbert *et al.* (2014) added exclusively *Phatnoma* species, the monophyly of Phatnomatini found by Lis (1999) was only corroborated again in Guidoti & Guilbert (*in prep.*). In this contribution, Guidoti & Guilbert (*in prep.*) added six species distributed in four different genera but failed to include any *Zetekella* or *Minitingis* species. Notwithstanding, there was an unsuccessful attempt to extract DNA from the available material (Guidoti & Guilbert, *in press*). Therefore, in Guidoti & Guilbert (*in prep.*) the monophyletic status of the tribe was

corroborated as well as its position within Tinginae, but the *Zetekella* position among Tinginae (+ Phatnomatini) remains unsettled.

As stated before, the two tribes originally proposed by Drake & Ruhoff (1965), Ypsotingini and Litadeini, were suppressed following Guilbert *et al.* (2014). Guilbert (2001) and Guilbert (2004) already had disputed these tribes based on his morphological phylogenetic hypotheses. However, all three analyses included just a few terminals from these taxa and therefore, the suppression was never indeed strongly corroborated. Guidoti & Guilbert (*in prep.*) included the type-genus of Ypsotingini, the monotypic *Ypsotingis* Drake, 1947, and other four species of this tribe. Additionally, five Litadeini species were also considered, including three type-species: *Aristobyrsa latipennis* (Champion, 1897), *Psilobyrsa aechemeae* Drake and Hambleton, 1935 and *Stragulotingis plicata* (Champion, 1897). These represented less than 10% and about 20% of both Ypsotingini and Litadeini, respectively, and was the largest set of terminals from these tribes ever added into a phylogenetic analysis. As a result, *Ypsotingis sideris* Drake, 1947 was found as the sister-group of Tinginae (*minus* Phatnomatini), which revived the discussion on the tribe's validity, but the remaining Ypsotingini species were found in a clade with *Acalypta* Westwood, 1840 species in a different part of the tree and not even remotely related to *Y. sideris* Guidoti & Guilbert (*in prep.*). Litadeini was also retrieved as a paraphyletic group with its included species widely spread in the topology Guidoti & Guilbert (*in prep.*).

In addition, one interesting finding from Guidoti & Guilbert (*in prep.*) deserves to be highlighted. For the first time, *Leptodictya* Stål, 1873 species were included in a phylogenetic analysis. This is a Neotropical and Nearctic genus comprising more than 50 species exclusively occurring on plants of the botanical family Poaceae, and frequently, on bamboos (Drake & Ruhoff, 1965). Its main diagnostic character is the paranota folded on itself which seems to be unique within Tinginae. In Guidoti & Guilbert (*in prep.*) two *Leptodictya* species were included and found monophyletic and sister to the remaining tingines (*minus* Phatnomatini and *Y. sideris*). This relationship was highly supported and considering the uniqueness of its morphology and the strict association with Poaceae, Guidoti & Guilbert (*in prep.*) suggested but not proposed a potential new tribe for Tinginae composed by this genus. In addition, the authors admitted that new analyses including more *Leptodictya* species are needed to strengthen this hypothesis before this new supra-generic taxon can be formally established. Therefore, according to Guidoti & Guilbert (*in prep.*), Phatnomatini remains as a Tinginae tribe, and its monophyly was corroborated, but its relationship with *Zetekella* remains uncertain; the

retrieved position of *Y. sideris* revived the discussion on Ypsotingini, however, its composition *sensu* Froeschner (2001) was once again refuted; Litadeini was also refuted, corroborating previous analyses (e.g., Guilbert *et al.*, 2014); and the hypothesis of a new tribe to hold *Leptodictya* species was raised and discussed, but the taxon wasn't formally proposed and now waits further consideration. Tingidae current classification according to all these phylogenetic analyses here discussed, including Guidoti & Guilbert (*in prep.*), is presented (Fig. 3).

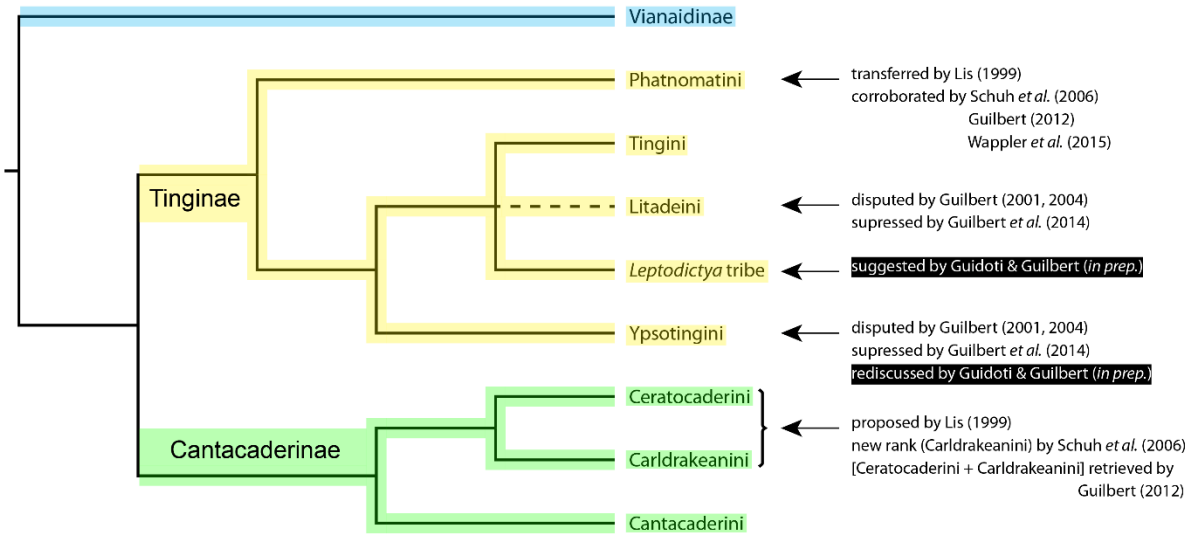

Figure 3. Current Tingidae classification based on different phylogenetic analyses. Original publications of propositions, transfers and suppressions of taxa are indicated. Major contributions by Guidoti & Guilbert (*in prep.*) are highlighted. Dotted line indicated a currently non-valid supra-generic taxon.

Guidoti & Guilbert (*in prep.*) was the first phylogenetic analysis to consider molecular characters exclusively. All the other analyses included morphological characters, which allowed a brief discussion on the synapomorphies of the supra-generic taxa (Lis, 1999; Guilbert, 2001, 2004, 2012a; Schuh *et al.*, 2006; Guilbert *et al.*, 2014; Wappler *et al.*, 2015). Therefore, the characters proposed by Drake & Davis (1960) and Drake & Ruhoff (1965) on their pre-phylogenetics classification hypotheses were tested in these previously available phylogenetic analyses. Moreover, since Lis (1999) dataset was largely used by Schuh *et al.* (2006), and Guilbert (2012a) and Wappler *et al.* (2015) analyses based their datasets on Schuh *et al.* (2006), the results in terms of both relationships and their supportive synapomorphies were basically the same among these four contributions. Lis (1999) considered tribes and genera as terminals, adding only one genus for Tinginae *sensu* Drake & Ruhoff (1965) and one for Phatnomatini in the analysis with genera as terminals. In this analysis, an initial polytomy was observed [*Tingis*

Fabricius, 1803 + *Phatnoma* + Cantacaderinae *status* Schuh *et al.* (2006)], recovering characters as autapomorphies rather than synapomorphies for Tinginae (*Tingis*) and Phatnomatini (*Phatnoma*). For the tribe analysis, Lis (1999) considered eight genera for Phatnomatini, 12 for Tingini, four for Ypsotingini and only the type-genus for Litadeini. Therefore, one can argue that even if the tribes were added as terminals, the retrieved characters for these terminals were not autapomorphies, but synapomorphies. Vianaidinae was firstly considered in a phylogenetic framework as ingroup terminal by Guilbert (2001), which included two species, *Thaumamannia manni* Drake & Davis, 1960 and *Anommatocoris coleopteratus* (Kormilev,1955). These were retrieved monophyletic, but it's not clear which characters supported the clade. Schuh *et al.* (2006), and the subsequent analyses of Guilbert (2012a) and Wappler *et al.* (2015), included *Anommatocoris bolivianus* as the sole Vianaidinae terminal. Therefore, in the context of these analyses, the retrieved characters for *A. bolivianus* were autapomorphies rather than synapomorphies, despite the fact that they were later found to be shared among all vianaidines (Guidoti *et al., in prep.*). All these analyses (Lis, 1999; Schuh *et al.*, 2006; Guilbert, 2012a; Wappler *et al.*, 2015) focused on Cantacaderinae, which was a poorly represented group in Guidoti & Guilbert (*in prep.*). Guilbert (2001, 2004) and Guilbert *et al.* (2014), on the other hand, focused their sampling on Tinginae, but as mentioned before, none of the originally proposed tribes by Drake & Ruhoff (1965) were recovered. Additionally, Guilbert *et al.* (2014) added only *Phatnoma* species for Phatnomatini, and despite that the *Phatnoma* clade was recovered monophyletic and closely allied to Tinginae, the characters supporting the clade itself must then be considered autapomorphies for the genus rather than synapomorphies for Phatnomatini. Although it was not the desired goal aimed by Guidoti & Guilbert (*in prep.*), the lack of morphological characters in their dataset hampered the already somehow vacant comparison between different datasets and phylogenies on the recovered synapomorphies for the aforementioned supra-generic taxa.

On the light of Guidoti & Guilbert (*in prep.*) findings, three different paths to advance the knowledge on Tingidae classification may be proposed. First, the addition of morphological characters to the large molecular dataset presented in this thesis might be a natural future step. However, the hurdles faced by the morphological phylogenetic analyses focusing on Tinginae due to the highly variable non-genital morphology of adults is difficult to overcome (Guilbert, 2001; Guilbert *et al.*, 2014). Structures like the hemelytra and paranota, traditionally used to describe Tingidae species and genera, present a great variability of shapes, inclinations and sizes. Many of the previous phylogenetic analyses, including the ones designed to test the

monophyly of a given genus, attempted unsuccessfully to translate these highly variable structures in reliable and strong phylogenetic characters (Guilbert, 2000, 2001; Montemayor & Costa, 2009; Guilbert *et al.*, 2014). This resulted in high levels of homoplasy and unresolved supra-generic relationships (e.g., Guilbert, 2001). However, structures like tarsi, scent gland peritreme (Fig. 4), scutellum and hind wings, which have been widely applied to characterize the supra-generic taxa in closely related families (e.g., Schuh, 1976) are still waiting to be thoroughly explored in Tingidae systematics. Some of these structures, together with the useful phylogenetic characters based on genitalia already proposed by Lis (1999), require invasive and/or destructive dissection methods or preparation and sometimes there aren't enough specimens, or authorization from museum curators to perform these procedures.

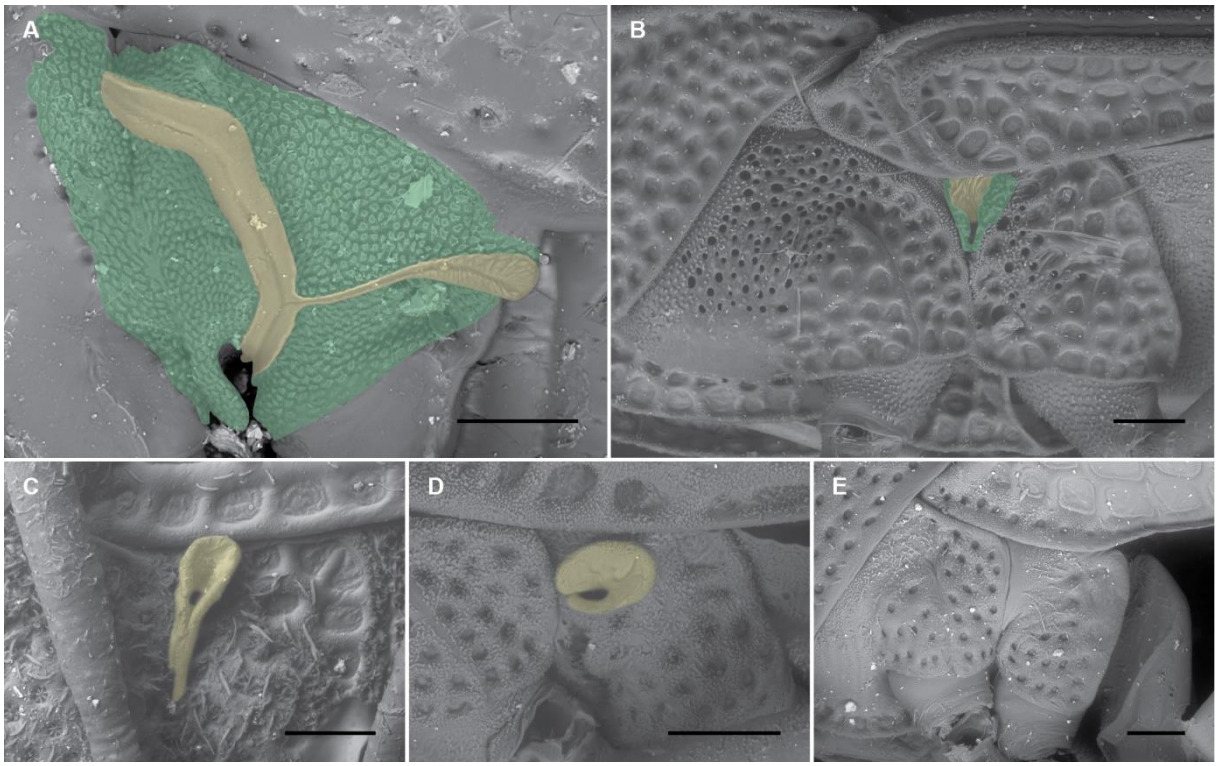

Figure 4. Scent-gland peritreme in different Tingidae. Highlighted in yellow, peritreme; in green, evaporatorium. Supra-generic classification indicated here. A) *Thaumamannia manni* (Vianaidinae); B) *Cantacader afzelli* Stål, 1873 (Cantacaderinae, Cantacaderini); C) *Leptocysta sexnebulosa* (Stål, 1858) (Tinginae, Tingini); D) *Phatnoma marmoratum* Champion, 1897 (Tinginae, Phatnomatini); E) *Pleseobyrsa boliviana* Drake & Poor, 1937 (Tinginae, Tingini). Scale bars: 0.1 mm.

Still considering morphology, another path that could be explored is the design of a morphological phylogenetic analyses targeting type-species only. Because molecular data is more reliably obtained from freshly collected material, which is frequently unavailable and then

imposes limitations on the terminal selection, and because there are many genera in need of a taxonomic review and a dedicated phylogenetic analysis to test their monophyletic status (e.g., *Cysteochila* Stål, 1873, *Gargaphia* Stål, 1862, *Leptopharsa* Stål, 1873), the relationship among type-species recovered from a morphological-only analysis could help define the position of each of the current genera on Tingidae phylogeny, regardless their monophyletic status. Thus, this would elucidate the supra-generic taxa composition of Tingidae, leaving for further and individual consideration the status of each genera. And finally, improving the molecular dataset is the third path here proposed to improve our knowledge on Tingidae classification. In Guidoti & Guilbert (*in prep.*), as well as Guilbert *et al.* (2014), only a handful of selected nuclear and mitochondrial *loci* were included. This could be definitely expanded, on the light of, for instance, the Nextgen sequencing. Efforts on Tingidae phylogenomics are on its way (e.g., Kocher *et al.*, 2015), but the biggest issue hampering this strategy is the sampling scheme. Because of the small size of an average tingid, many specimens from each species are needed to extract enough DNA for these new technologies. Therefore, all three paths have hurdles to overcome but it seems safe to say that the shared one is strictly related with collecting more material.

Tingidae Origin

The most important issue on Tingidae evolution at this moment is, perhaps, its biogeographical origin. Lis (1999) and Guilbert (2012b) provided biogeographical analyses to address this question after the phylogenetic analyses by Lis (1999) and Guilbert (2012a). Wappler (2006), in the other hand, discussed the topic in the light of two fossils from the Eocene, *Paleocader avitus* (Drake, 1950) and *Lutetiacader petrefactus* Wappler, 2006. The biogeographical reconstructions proposed by Lis (1999) and Wappler (2006) are similar, with one major vicariant event followed by several dispersal events, leaving the origin of Cantacaderinae *status* Schuh *et al.* (2006) in the Australia-New Zealand complex. The main difference between these two hypotheses and the one raised by Guilbert (2012b) is the origin of Cantacaderinae *sensu* Schuh *et al.* (2006), which according to Guilbert (2012b) was in the Oriental region. Perhaps more importantly and only briefly addressed in Guilbert (2012b), the Vianaidinae origin was pointed to an earlier vicariant event that potentially isolated this lineage in South America around 132-139 million years ago (Guilbert, 2012b). Regardless the importance of this group highlighted by its close relationship with Tingidae *sensu stricto* (Schuh & Štys, 1991; Schuh *et al.*, 2006, 2009), Guilbert (2012b) was the only one to discuss the origin of Vianadinae in-depth,

which is endemic in South America, in a biogeographical analysis. This proposed Vianaidinae origin is older than the minimum age of the fossil record available for the group. *Vianagrama goldmani* Golub & Popov (2000) and *Vianathauma pericarti* Golub & Popov (2003) were described from the New Jersey amber, which dates to the late Cretaceous (ca. 60-100 Myr). However, Schuh *et al.* (2006), after examination of these two fossils holotypes, disputed the placement of *V. pericarti* in Vianaidinae due to the inaccessibility of some key diagnostic characters, including the diagnostic scent gland peritreme. On the other hand, the placement of *V. goldmani* remains untested and therefore, undisputed.

Wappler *et al.* (2015) affirmed that the New Jersey amber of *V. goldmani* that belongs to the Turonian age (ca. 93 Myr) isn't the oldest fossil record for Tingidae. *Sinaldocader* Popov, 1989 is a genus from lower Cretaceous, whose original placement in Phatnomatini was already disputed by Nel *et al.* (2004). However, Golub & Popov (2008) refuted Nel *et al.* (2004) criticism after re-analyzing *Sinaldocader* type-species and describing a new species, *Sinaldocader ponomarenkoi* Golub & Popov, 2008, also from lower Creteaceous (ca. 125-135 Myr). *Burmacader* Heiss & Guilbert, 2013 is a genus composed by two species from the Burmese amber from earliest Cenomanian (ca. 100 Myr) that shares with Vianaidinae its key diagnostic character: the scent gland peritreme composed by two perpendicular branches (Heiss & Guilbert, 2013). *Burmacader* species also share with Tingidae *sensu stricto* several other characters, which makes their placement uncertain (Heiss & Guilbert, 2013, 2018). However, the possibility of a close relationship between *Burmacader* and Vianaidinae expands the ancestral distribution of the latter, contradicting the hypothesis of a New World origin (Heiss & Guilbert, 2013; Wappler *et al.*, 2015). These, allied to the fossil tribe Golminiini from lower Cretaceous (Popov, 1989) whose closeness to Tingidae was also already disputed (Lis, 1999; Nel *et al.*, 2004), advocate for a much earlier origin of Vianaidinae and consequently, of Tingidae. To this day, none of these fossils were included in phylogenetic analyses in order to test the hypotheses of their placement within Vianaidinae, Phatnomatini or even Tingidae.

One of the biggest contributions of Guidoti & Guilbert (*in prep.*) was the success in obtaining Vianaidinae sequences for the very first time. Although these were available in addition to the extensive fossil record already discussed, Guidoti & Guilbert (*in prep.*) focus was on Tingidae classification and not on Tingidae origin. Therefore, Guidoti & Guilbert (*in prep.*) did not attempt to conduct any calibration analysis within their results. However, efforts were already made in this direction. Guilbert *et al.* (2018) presented on the 8th European Hemipteran Congress a first attempt to calibrate a Tingidae phylogeny. No Vianaidinae

sequences were included, but both Cantacaderinae and Phatnomatini were considered, and two of the aforementioned fossils were added among others in this preliminary analysis: *Lutetiacader petrefactus* and *Sinaldocader ponomarenkoi* (Guilbert *et al.*, 2018). As a result, Tingidae emergence was estimated to 172 Myr, and Cantacaderinae and Phatnomatini to 155 Myr and 140 Myr, respectively (Guilbert *et al.*, 2018). With this, it was hypothesized a Tingidae origin in South America, with further dispersion events to explain the emergence of Cantacaderinae and Phatnomatini (Fig. 5).

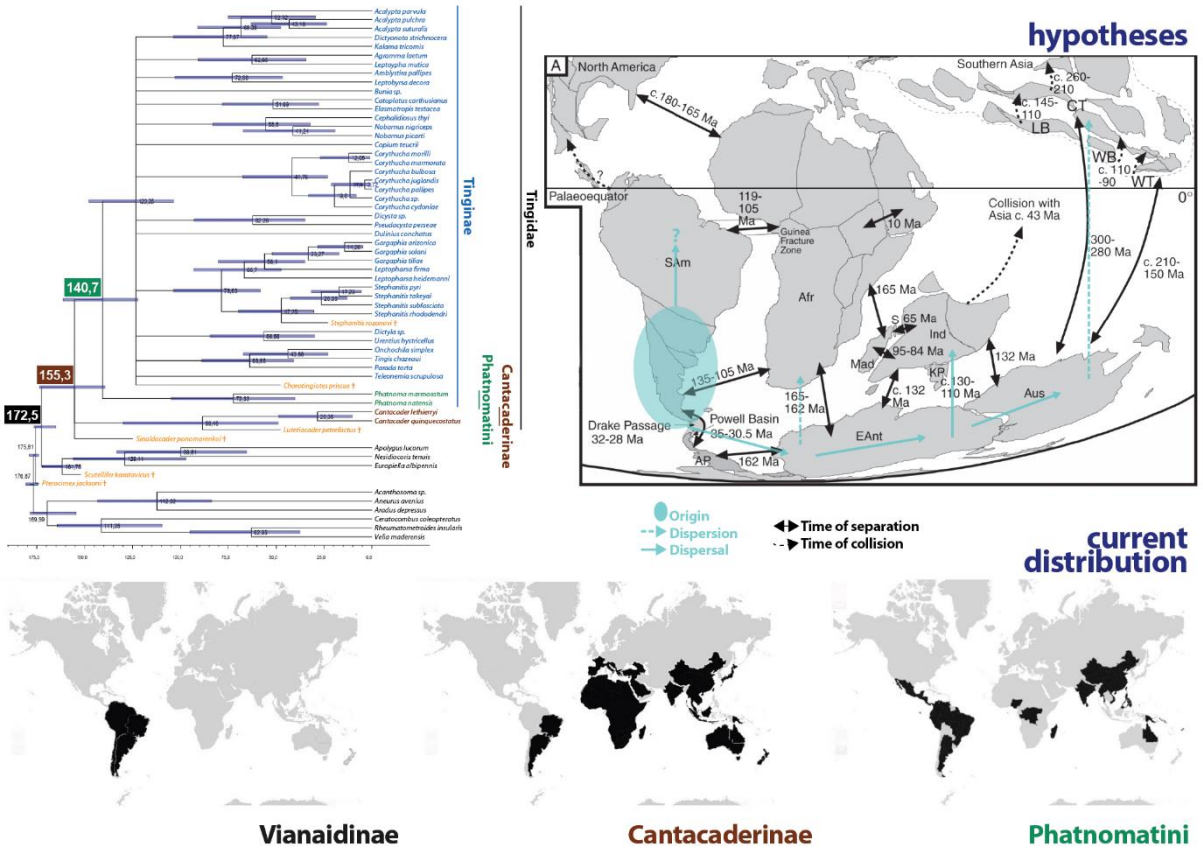

Figure 5. Preliminar results on a biogeographical hypothesis for Tingidae origin based on a calibrated phylogeny, without Vianaidinae sequences. Due to the age of the Tingidae clade, its origin is hypothesized to South America, which corroborates with Vianaidinae distribution, sister-group of Tingidae *sensu stricto*. Dates for the major clades [Outgroups + Tingidae], [Cantacaderinae + Tinginae], and [Phatnomatini + remaining tingines] highlighted on the phylogeny. Major dispersion and dispersal hypothetical events indicated.

However, with the now available Vianaidinae sequences a new effort must be made regarding Tingidae origin. This subfamily is highly corroborated as the sister-group of the remaining tingids, and its exclusive South American distribution in addition to the fossil record in the New Jersey amber, allied to the unexplored potential relationship with the Burmese fossil genus

Burmacader, keep the issue on Tingidae origin alive and as the most interesting evolutionary question to be investigated within the family at this point.

Beyond the Thesis

This thesis dealt with Tingidae classification and evolution with emphasis on the taxa Vianaidinae and Tinginae, specially Phatnomatini. Its two major contributions, on Vianaidinae taxonomy and systematics and Tingidae classification, opened new perspectives on a third subject, the Tingidae origin. All perspectives and future directions suggested in this chapter, however, depends on one basic common step: the availability of more freshly collected, and preferably alcohol-preserved, material. Tingidae has large collections, as any other taxonomic group, in all major museums and institutions around the world. However, they are usually poorly represented taxonomically, and even traditional institutions hold material from regional faunas only. One institution, the National Museum of Natural History (Washington, D.C.), holds the Drake Collection, which is the largest Tingidae collection in the world. But in this important collection most species are represented by only a few specimens as well, frequently collected almost a century ago, and usually badly mounted or damaged through the time. This collection was crucial to the execution of this thesis, but even there faunistic holes were observed. One of these, the Neotropical region, had a recent unrepairable lost: the fire at the Museu Nacional (Rio de Janeiro, Brazil) on September 2nd, 2018. This fire apparently burned the Monte Collection, the largest Tingidae collection in the world for the Neotropical region, holding up to 25% of the type-specimens of the species reported from Brazil. Although not composed by freshly collected material, the Monte collection will be missed in the pursuit of the future projects here suggested, and in many other also necessary projects in Tingidae taxonomy and systematics. Therefore, the advancement achieved here allowed those discussed perspectives to be drawn, and those were directly impacted by this unfortunate happening. As such, the further improvement of Tingidae phylogeny and Vianaidinae systematics, and the future biogeographical analyses on Tingidae origin, should be considered alongside to the reconstruction of this lost reference collection as the next steps for beyond this thesis.

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