

UC Riverside

UC Riverside Electronic Theses and Dissertations

Title

Systematic Research on the Largest Litter Bug Genus Schizoptera Fieber 1860 (Hemiptera: Dipsocoromorpha)

Permalink

<https://escholarship.org/uc/item/6tq7983c>

Author

Leon, Stephanie

Publication Date

2016

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Systematic Research on the Largest Litter Bug Genus, *Schizoptera* Fieber 1860
(Hemiptera: Dipsocoromorpha)

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Entomology

by

Stephanie Leon

March 2016

Thesis Committee:

Dr. Christiane Weirauch, Chairperson

Dr. James Baldwin

Dr. John Heraty

Dr. William Walton

Copyright by
Stephanie Leon
2016

The Thesis of Stephanie Leon is approved:

Committee Chairperson

University of California, Riverside

Acknowledgements

I am extremely grateful for the opportunity to pursue a Master of Science degree in Entomology, with a concentration in systematics and taxonomy, which has granted me with many unimaginable opportunities during the past two-and-a-half years. I am especially thankful to my advisor, Dr. Christiane Weirauch for her never-ending support and mentorship prior to and during the completion of my thesis project. I thank Dr. John Heraty for being an outstanding committee member and also my first-year graduate mentor. I thank Dr. James Baldwin and Dr. William Walton for providing valuable guidance as members of my committee.

I would like to thank every single member of the Heteropteran Systematics lab (previous and current): Dimitri Forero, Michael Forthman, Sarah Frankenberg, Eric Gordon, Rochelle Hoey-Chamberlain, Aleksandr Knyshev, Wei Song Hwang, Paul Masonick, and Guanyang Zhang for their support—thanks guys!! I would like to specially acknowledge the members of our “Dipso Team” Rochelle, Alex and Sarah for always being available when I needed guidance or advice on certain Dipsocoromorpha related issues. I would also like to thank all the undergrads that in one way or another contributed to the Dipsocoromorpha project, especially Christy Hoong, who helped me database hundreds of *Schizoptera* specimens.

I extend my gratitude to all the institutions that loaned material to our lab, without which these three studies would not have been completed. A special thank-you to Dr. Thomas Henry for hosting me during my visit United States National Museum, and Dr. Michael and Donna Ivie for their extreme kindness and accommodation during my visit to the Entomology Collection at the Montana State University.

I would like to thank my parents from their continuous support during my graduate career, my brother Alvin for staying up with me until 3:00 am every night as I finished the last chapter of my thesis, and my sister Jasmine for help with point-mounted specimen sorting and counting. I thank my fiancé Fernando Prillwitz for his support all throughout my undergraduate and graduate career, and for always believing in me. I thank my best friend Kaleigh Russell for being there for me whenever I needed, and for keeping me sane during the last couple weeks of my thesis project.

Financial support for my thesis research has come from the National Science Foundation “ARTS: Litter Bugs: revisionary and phylogenetic research on the least studied true bug infraorder (Insecta: Hemiptera: Dipsocoromorpha)” grant DEB-1257702 (to Christiane Weirauch) and the Department of Entomology at the University of California, Riverside.

ABSTRACT OF THE THESIS

Systematic Research on the Largest Litter Bug Genus, *Schizoptera* Fieber 1860
(Hemiptera: Dipsocoromorpha)

by

Stephanie Leon

Master of Science, Graduate Program in Entomology
University of California, Riverside, March 2016
Dr. Christiane Weirauch, Chairperson

This thesis comprises molecular phylogenetic and morphological studies focusing on the largest genus of litter bugs *Schizoptera* Fieber (Hemiptera: Dipsocoromorpha).

Schizoptera, currently comprises 61 extant species in 4 subgenera. Specimens are abundant in New World bulk and residue samples. *Schizoptera* species showcase stunning morphologies including intricate, asymmetrical genitalia in males that have proven to provide excellent species diagnostic features in the past, and elytrous wings in females of some species. Three research topics are presented: 1) The molecular phylogeny of *Schizoptera* and related taxa, ancestral state reconstruction (asr) of elytrous wings in females of Schizopteridae, and asr of 11 morphological characters used to diagnose *Schizoptera* species. In this study, *Schizoptera* is shown to be polyphyletic, with two subgenera being recovered outside of the *Schizoptera* clade. Elytrous wings in females of Schizopteridae are shown to have evolved at least seven times, three times within *Schizoptera*, and reversed back to macropterous wings twice. ASR of 11 diagnostic characters is used to update generic and subgeneric diagnoses of *Schizoptera* and related taxa. 2) Taxonomic revision of *Orthorhagus* McAtee and

Malloch. Previously a monotypic subgenus of *Schizoptera*, molecular and morphological evidence suggests that *Orthorhagus* is not part of *Schizoptera*. Unlike *Schizoptera*, *Orthorhagus* specimens are rare in samples, and the study is conducted with a total of nine specimens including the holotype. *Orthorhagus* is elevated to generic rank, and five new species from the Neotropics are described in this genus. 3) Taxonomic revision of the subgenus *Schizoptera* (*Odontorhagus*). The molecular phylogeny of *Schizoptera* shows that *S.* (*Odontorhagus*) is monophyletic, without *Kophaegis*, which was previously synonymized with this subgenus. Comprising 10 described species, six from Guatemala and Panama and four from Trinidad, this study results in the description of 20 new species from the Neotropics, increasing the species count in *Schizoptera* to 81. We predict that similar increases in species numbers are to be expected for the remaining subgenera of *Schizoptera*, making this genus and very diverse lineage of minute litter bugs.

Table of Contents

Introduction	1
References.....	5
Chapter 1: Molecular Phylogeny informs generic and subgeneric concepts in the <i>Schizoptera</i> Fieber genus group (Heteroptera: Schizopteridae) and reveals multiple origins of female-specific elytra	7
Abstract.....	7
Introduction.....	8
Materials and Methods.....	13
Results.....	16
Discussion.....	27
References.....	32
Figures and Tables.....	35
Supporting Information.....	42
Chapter 2: Small bugs, big changes: Taxonomic revision <i>Orthorhagus</i> McAtee and Malloch, 1925 (Heteroptera: Dipsocoromorpha)	46
Abstract.....	46
Introduction.....	46
Materials and Methods.....	50
Results.....	53
Discussion.....	68
References.....	73
Figures.....	75

Chapter 3: Scratching the surface? Taxonomic revision of the subgenus *Schizoptera* (*Odontorhagus*) reveals vast undocumented biodiversity in the largest litter bug genus *Schizoptera* Fieber (Hemiptera: Dipsocoromorpha).....80

 Abstract.....80

 Introduction.....81

 Materials and Methods.....84

 Results.....87

 Discussion.....142

 Conclusion.....143

 References.....145

 Figures.....147

CONCLUSION.....154

List of Figures

Figure 1.1. Diagnostic characters historically used to recognized subgenera of Schizoptera and a comparison of the current and proposed classification of genera and subgenera.....	35
Figure 1.2. The best tree derived from the maximum likelihood analysis of <i>Schizoptera</i> and related taxa.....	36
Figure 1.3. Ancestral state reconstruction of female-specific elytra and a summary of the phylogenetic distribution of 11 morphological characters historically used as diagnostic features of <i>Schizoptera</i> and its subgenera.....	37
Figure 1.4. Documentation of characters and character states used in the optimization of the 11 morphological characters.....	38
Figure 2.1. Habitus images of species of <i>Orthorhagus</i>	75
Figure 2.2. Line drawings of dorsal and ventral views of male genitalia and a drawing of female segments VIII and IX in caudal view.....	76
Figure 2.3. Confocal microscopy images of male genitalia of <i>Orthorhagus</i> species.....	77
Figure 2.4. Distribution of <i>Orthorhagus</i> species.....	78
Figure 2.5. Comparison of morphological features of <i>Schizoptera</i> species and <i>Orthorhagus</i>	79
Figure 3.1. Diagnostic features of species of <i>Schizoptera</i> (<i>Odontorhagus</i>) and comparison of <i>Schizoptera</i> (<i>Odontorhagus</i>) and <i>Kophaegis</i>	147
Figure 3.2. Habitus images of <i>Schizoptera</i> (<i>Odontorhagus</i>).....	148
Figure 3.3. Habitus images of <i>Schizoptera</i> (<i>Odontorhagus</i>).....	149

Figure 3.4. Images of select type specimens that were either slide mounted or damaged, with an addition *S. stricklandi* specimen placed next to the damaged type.....150

Figure 3.5. Line drawings of dorsal and ventral views of *S. (Odontorhagus)* male genitalia.....151

Figure 3.6. Line drawings of dorsal and ventral views of *S. (Odontorhagus)* male genitalia.....152

Figure 3.7. Distribution of *S. (Odontorhagus)* species.....153

List of Tables

Table 1. Classification of sampled specimens with ED, USI and GenBank accession numbers for vouches sequenced in this study and numbers for sequences obtained from GenBank.....39

Table 2. Comparison of previous diagnoses presented for *Schizoptera* by McAtee and Malloch (1925) and Emsley (1969) and the updated diagnosis resulting from the present study.....41

INTRODUCTION

The infraorder Dipsocoromorpha (Hemiptera: Heteroptera), or litter bugs, is considered the smallest and least known group of true bugs (Weirauch and Štys 2014). Comprising 5 distinct families and ~380 described species, litter bugs occur worldwide with greatest species diversity in the tropics (Weirauch and Štys 2014). Specimens are minute (~1-2 mm) and are commonly found in forest leaf litter or similar microhabitats (i.e. decaying logs, underneath bark, or in soil [Linnavuori, 1974, Hill 1990, Wygodzinsky 1951]).

Unpublished data gathered by the NSF Litter Bugs ARTS project shows that a myriad of passive and active collecting methods are successful for the acquisition of these miniscule bugs. Consequently, specimens often appear in bulk and residue samples as non-target organisms but are often ignored because of their miniscule size that requires specialized curation (e.g., slide-mounting and genitalic dissections that are challenging because of specimen size). Thus, the current number of described species is a severe underrepresentation of the true diversity of the group.

The largest family, the Schizopteridae comprises 287 diverse species in 57 genera (Linnavuori 1974, Weirauch 2012, Makhan 2013, Weirauch and Štys 2014 Hill 2015, Leon and Weirauch, accepted, Leon and Weirauch, submitted). Schizopteridae are extremely abundant in bulk and residue samples, and are highly attractive due to their bizarre morphologies such as organs of unknown function (Weirauch 2010, Knyshov *et al.*, accepted), asymmetrical male genitalia (Emlsey 1969), and the presence of elytra in several groups (Emsley 1969, Hill 2015).

In genera such as *Corixidea* Reuter, *Glyptocombus* Heideman, and *Hypselosoma* Reuter both males and females can feature macropterous, brachypterous or elytrous wings (Heideman 1906, Emsley 1969). In contrast, only females are either

macropterous or micropterous in *Kokeshia* Esaki and Miyamoto, while males are always macropterous. In the monotypic genus *Ptenidiophyes* Reuter only elytrous females were known prior to the present study (Štys 1975). In *Schizoptera* Fieber, the largest genus of Schizopteridae, all known males are macropterous, but females of several species possess wings that have been modified into elytra (Emsley 1969).

Our lab has assembled more than 10,000 schizopterid specimens from various institutions by sorting bulk samples and loaning point-mounted specimens, in addition to our own field work efforts. About 10% of these specimens belong to *Schizoptera* Fieber (pers. obs.), a genus that is readily identified in mixed samples due to distinctive wing venation and male genitalic morphology (Emsley 1969, Leon and Weirauch, submitted). *Schizoptera* specimens showcase stunning morphological diversity with males possessing an asymmetrical sternite VII, which has been modified into a subgenital plate, and intricate genitalia, including asymmetrical conjunctival appendages (Emsley 1969) and the elytra of females of several species.

The taxonomic history of *Schizoptera* is rich, having been described from a single specimen from Venezuela by Fieber (1860), with subsequent efforts by Poppius and Reuter (Reuter 1882, 1891, Poppius 1910) increasing species the count to six. McAtee and Malloch's (1925) taxonomic revision of Schizopteridae focused mainly on *Schizoptera* specimens from Central America and the Caribbean, describing 27 new *Schizoptera* species and dividing the genus into seven subgenera. China and Wygodzinsky described one species from Trinidad and two from Argentina, respectively (China 1946, Wygodzinsky 1952). Emsley presented what is arguably the most comprehensive taxonomic treatment of Schizopteridae to date (Emsley 1969). In his

monograph, he described 28 new species of *Schizoptera* and also synonymized two subgenera previously described by McAtee and Malloch (Emsley 1969).

The monophyly, subgeneric concepts and relationships of *Schizoptera* have not been tested in a phylogenetic framework. Emsley (1969) hypothesized a close association between *Nannocoris* Reuter and *Schizoptera* based on morphological similarities of head, thorax and hind wing shape. He also noted the similarity in wing venation to species of the New World genus *Ceratocomboides* McAtee and Malloch, but proposed a closer association between *Ceratocomboides* and some Old World Schizopteridae, *Pinochius* Carayon and *Birturinannus* Wygodzinsky, based on tarsal formulae and the structure of the wing-coupling mechanism (Emsley 1969). Weirauch and Štys (2014) tested relationships across Dipsocoromorpha, found high support for a clade comprising the two included species of *Schizoptera*, recovered *Ptenidiophyes* as sister to that clade, and speculated that *Ptenidiophyes* could represent elytrous *Schizoptera* females that had not been matched to their respective macropterous males.

The current thesis integrates molecular phylogenetics and revisionary taxonomy to improve our understanding of this speciose and morphologically attractive genus. The first comprehensive molecular phylogeny of this group is presented, with ancestral state reconstruction of transitions between macropterous and elytrous wings in females of Schizopteridae. The generic and subgeneric diagnoses of this genus are updated through the ancestral state reconstruction of 11 morphological characters historically used to diagnose this genus. Two taxonomic revisions are presented. The revision of *Orthorhagus* McAtee and Malloch, a group of rarely collected schizopterids, results in the elevation of this previous subgenus of *Schizoptera* to generic rank and the description of five new. The revision of *Schizoptera* (*Odontorhagus*) reveals vast

biodiversity in an already speciose group, with the description of 20 new species, and the documentation of extreme morphological diversity in male genitalia of *Schizoptera* species.

References

- China, W. E. (1946) New Cryptostemmatidae (Hemiptera) from Trinidad, British West Indies. *Proceedings of the Royal Entomological Society of London (B)*, 15, 148–154.
- Emsley, M. G. (1969) The Schizopteridae (Hemiptera: Heteroptera) with the descriptions of new species from Trinidad. *Memoirs of the American Entomological Society*, 25, 1–154.
- Fieber, F. X. (1860) Exegesen en Hemiptera. *Weiner Entomologische Monatschrift*, 9, 258-272.
- Hill, L. (1990) Australian *Ogeria* Distant (Heteroptera: Schizopteridae). *Invertebrate Taxonomy* 4, 697–720
- Hill, L. (2015) Three new genera of Schizopteridae from Australia with description of six new species (Hemiptera: Heteroptera: Schizopteridae). *Zootaxa*, 3990, 73–96.
- Knyshov A., Leon S., Hoey-Chamberlain R., Weirauch C. Pegs, pouches and spines: systematics and comparative morphology of the New World genus *Chinannus* Wygodzinsky, 1948, ESA Thomas Say monographs, *accepted*
- Linnavuori, R. E. (1974) Hemiptera of the Sudan, with remarks on some species of the adjacent countries. *Annales Entomologicae Fennicae*, 40, 116–138
- Makhan D (2013) *Soekhnandanius aschne* gen. et sp. nov., Schizopterinae (Hemiptera: Heteroptera: Schizopteridae) from Suriname. *Calodema*, 391, 1–3
- McAtee, W. L., Malloch, J. R. (1925) Revision of bugs of the family Cryptostemmatidae in the collection of the United States National Museum. *Proceedings of the United States National Museum*, 67,1–42.
- Poppius, B. (1910) Neue Ceratocombiden. *Ofversigt Af Finska Vetenskaps societetens Forhandlingar Helsingfors*, 52, 1–14.
- Reuter, O. M. (1882) Sur le genre *Schizoptera* Fieb. *Revue D'entomologie*, 1, 162–164.
- Reuter, O. M. (1891) Monographia Ceratocombidarum orbis terrestris. *Acta Societatis Scientiarum Fennicae*, 19, 1–28.
- Štys, P. (1975). Redescription of *Ptenidiophyes mirabilis* Reuter (Heteroptera: Schizopteridae). *Vestník Československe Spolecnosti Zoologiske*, 39, 154–159.
- Weirauch C. & Štys P. (2014) Litter bugs exposed: phylogenetic relationships of Dipsocoromorpha (Hemiptera: Heteroptera) based on molecular data. *Insect Systematics and Evolution*, 45, 351–370

Weirauch C., & Frankenberg S. (2015) From “insect soup” to biodiversity discovery: taxonomic revision of *Peloridinannus* Wygodzinsky, 1951 (Hemiptera: Schizopteridae), with description of six new species. *Arthropod Systematics and Phylogeny*, 73, 457–475

Wygodzinsky, P. (1951) Descripcion de generos y especies nuevos de “Cryptostemmatidae” Hemiptera. *Revista Brasileira de Biologia*, 11, 259–270.

Wygodzinsky, P. (1952) Sobre algunos Cryptostemmatidae, principalmente de la Argentina (Hemiptera). *Acta Zoologica Lilloana*, 10, 51–74

Chapter 1: Molecular Phylogeny informs generic and subgeneric concepts in the *Schizoptera* Fieber genus group (Heteroptera: Schizopteridae) and reveals multiple origins of female-specific elytra

Abstract

Wing dimorphism occurs in many genera of Schizopteridae, or litter bugs (Heteroptera: Dipsocoromorpha), in both males and females. In the largest litter bug genus, *Schizoptera* Fieber, and closely related taxa, sexual wing dimorphism is observed in several species where males are macropterous, but females possess elytra, or hardened forewings – a feature that is rare outside of beetles and that we here refer to as female-specific elytra. Phylogenetic hypotheses for this group are unavailable, but are essential to reveal if female-specific elytra evolved once or multiple times within the group and to test if elytra can reverse to macropterous wings. In addition, generic and subgeneric concepts of this speciose genus group have not been tested in a phylogenetic framework, and relationships with other schizopterid genera remain largely unknown. Our molecular phylogeny of *Schizoptera* and related groups documents that this genus is currently polyphyletic, and we raise *Kophaegis* to generic rank to render *Schizoptera* monophyletic (*Orthorhagus* was recently elevated to genus). Relationships within *Schizoptera* reveal several well-supported clades with some of them corresponding to currently recognized subgenera. To examine the value of previously used diagnostic features, we optimize 11 morphological characters on the molecular phylogeny and update generic and subgeneric diagnoses. Tracing transitions between macropterous and elytrous wing types, we show that female-specific elytra evolved at least seven times within Schizopteridae, four of them within the *Schizoptera* genus

group, and that elytra reversed to macropterous wings at least twice. We propose that Schizopteridae may be an excellent model to study the selective pressures that have given rise to sexually dimorphic elytra, but also their constraints.

Introduction

The modification of forewings, such as reduction or wing-loss, is a phenomenon observed in almost every insect order (Harrison 1980, Aukema 1995, Zera and Denno 1997). Their reduction and loss, but also their alteration into structures with functions other than flight, have been central to many ecological and evolutionary studies, primarily focusing on the tradeoffs associated with wing reduction or wing loss, and thus the inability to fly or disperse (Harrison 1980, Denno 1994, Aukema 1995, Langelotto et al 2000, Guerra 2011). Wing reduction may be tied to the reallocation of energy resources to other biological functions, such as an increase in the number of eggs developed by females (Roff, 1986, Denno 1994), and is thought to be more prevalent in stable habitats (Slater 1977). Wing dimorphism or polymorphism, the occurrence of different wing types within the same population (Langellotto *et al.* 2000, Braendle 2006), has been thoroughly studied in groups such as aphids (Müller et al 2001, Braendle 2006), crickets (McFarlane 1962, Masaki and Oyama, 1963, Alexander 1968), and delphacid planthoppers (Denno *et al.* 1985, Langellotto 2000) in the context of dispersal capabilities, and has been linked to biotic and abiotic factors including population density, host plant quality, and temperature (Denno et al 1985, Roff 1986, Langellotto 2000, Müller et al 2001, Braendle 2006). In some groups, including certain members of the hemipteran suborder Heteroptera (Sweet 1964, Slater 1977, O'Donnell 1991, Honek 1995), forewing dimorphism can occur in both sexes, where some individuals are

macropterous (with well-developed membrane and hindwings), but others are brachypterous (with reduced membrane, exposing the tip of the abdomen), micropterous (with extremely reduced forewings and no hindwing), elytrous (forewing forms hardened shell) or apterous (wingless) (Slater 1975). In other groups, wing types are sex-dependent and thus expressed as sexually dimorphic features (Desender 1987, Thayer 1992, Keith 2000, Green *et al.* 2013). As an example, males in certain groups of staphylinid beetles (Coleoptera: Omaliinae) can be macropterous or micropterous, but all females are micropterous, suggesting that females inhabit different, possibly more stable microhabitats (Thayer 1992). Similarly, females in some New World Ptininae (Coleoptera: Bostrochidae) are either micropterous or brachypterous and their flightlessness was hypothesized to improve fecundity (Phillips 2000).

Sexual dimorphism of wings is not always restricted to the unequal sizes of wings in males and females. In several diving beetle species, the structure of the dorsal surface of the elytron is sexually dimorphic, with females often having rugose or grooved elytra, and males with smooth elytra (Miller 2003, Green *et al.* 2013). The structure of the female elytra has been linked to a sexual selection “arms race” (Miller 2003), where the corrugation obstructs the adhesion of male tarsal suction cups during mating (Miller 2003, Green *et al.* 2013). A similar pattern of sexual dimorphism in terms of wing surface structure, but additionally also wing shape and size, is observed in several genera of a poorly studied group of true bugs, the Schizopteridae, or minute litter bugs (Hemiptera: Dipsocoromorpha). Schizopteridae are tiny (~1-2mm) and found in diverse, often cryptic microhabitats including forest leaf litter, decaying wood, but also the forest canopy (Emsley 1969, Weirauch and Frankenberg 2015, Leon and Weirauch, accepted). Specimens are fairly common in bulk and residue samples, but often ignored because of

their small size and need of specialized curation. Published notes on their natural history, other than information sometimes associated with insect labels such as microhabitat and collecting method, are restricted to one feeding behavior record by Esaki and Miyamoto (1959) and some observations on oviposition, locomotion, and feeding by Emsley (1969). This lack of biological information for Schizopteridae is unsatisfying, especially because the stunning morphological diversity seen in the group points to intriguing ecological and behavioral adaptations, such as habitat specializations, complex male-female interactions, or sex-specific behaviors and habitat preferences. Among these intriguing morphological features are the complex and diverse male genitalia, male-specific structures of unknown function (Weirauch 2013, Knyshov et al., submitted), pretarsal adhesive structures typically restricted to the males (Emsley 1969), and a prevalence of wing polymorphism across the group (Emsley 1969). In genera such as *Corixidea* Reuter, *Glyptocombus* Heideman, and *Hypselosoma* Reuter both males and females can feature macropterous, brachypterous or elytrous wings (Heideman 1906, Emsley 1969). In contrast, only females are either macropterous or micropterous in *Kokeshia* Esaki and Miyamoto, while males are always macropterous. In the monotypic genus *Ptenidiophyes* Reuter only elytrous females were known prior to the present study (Štys 1975), but we here document congeneric macropterous males. In the largest schizopterid genus, *Schizoptera* Fieber, all known males are macropterous, but females of several species possess wings that have been modified into elytra (Emsley 1969), making this group a good model for the study of the evolution of female-specific elytra. Interestingly, the dorsal surface of the forewing is not uniform across the taxa that feature elytra: the surface fine structure varies from completely smooth (e.g., *Glyptocombus*), punctate (e.g., *Ptenidiophyes*) to rugose with traces of

wing venation (e.g., *Schizoptera*, *Corixidea*, *Nannocoris* Reuter), suggesting that either the elytra or their fine structure may be non-homologous (and possibly tied to different functions). The lack of phylogenetic hypotheses currently precludes investigations into the evolution of female-specific elytra in Schizopteridae.

Specimens of *Schizoptera* are abundant in bulk samples and curated collections including our labs field collections (personal observation). Examination of more than 2,000 specimens of *Schizoptera* assembled in our lab has revealed that this group of litter bugs is both, more morphologically diverse and more speciose than previously assumed. Males possess intricate asymmetrical genitalia that comprise an asymmetrical pair of conjunctival appendages (Emsley 1969), a long and coiled vesica, a pygophore (or genital capsule) that is rotated 90° dextrally, and an asymmetrical subgenital plate (sternite VII). The genus in its current concept comprises 63 extant and two fossil-based described species (Emsley 1969, Poinar 2014), all restricted to the New World and with greatest diversity in the Neotropical region. Fieber (1860) described the genus based on a single specimen from Venezuela and subsequent efforts in the late 19th century increased the number of described species from one to six (Fieber 1860, Reuter 1882, 1891, Poppius 1910, Emsley 1969). McAtee and Malloch's (1925) taxonomic revision of New World Dipsocoromorpha focused greatly on *Schizoptera* from Central America and the Caribbean, resulting in the description of 27 new species and subdivision of the genus into seven subgenera (without providing formal generic or subgeneric diagnoses): *Schizoptera* (*Cantharocoris*) diagnosed by the glabrous, heavily sclerotized region of the metepisternum extending to the midline of the metapleuron (Fig. 1.1A); *S.* (*Kophaegis*) distinguished by the presence of a blunt process (or "tooth") on the propleuron (Fig. 1.1C); *S.* (*Lophopleurum*) recognized by the glabrous, heavily sclerotized region of the

metepisternum extending beyond the midline of the metapleuron (Fig. 1.1B); *S. (Odontorhagus)* distinguished by the lack of ocelli and lack of a blunt tooth on the propleuron (Fig. 1.1C); *S. (Orthorhagus)* diagnosed by the lack of a pronotal collar (Fig. 1.1D); *S. (Schizoptera)* distinguished by the glabrous, “shining” border of the metepisternum (Fig. 1.1E) and *S. (Zygophleps)* recognized by the triangular posterior membranal cell (Fig. 1.1F). The most current synthetic taxonomic treatment of *Schizoptera* was published 44 years later by Emsley (1969), who diagnosed the genus based on the spine-shape of the metepisternum, males possessing asymmetrical conjunctival appendages, and several wing venation characters (Table 2). He also described 28 new species from the continental island of Trinidad, revised existing species and subgeneric concepts, and synonymized the subgenus *S. (Kophaegis)* with *S. (Odontorhagus)*, pointing out that the diagnostic characters used by McAtee and Malloch were not consistent (Fig. 1.1G). Leon and Weirauch (2016) taxonomically revised the subgenus *S. (Orthorhagus)*, added 5 new species, and elevated the subgenus to genus rank, while largely building their arguments for this decision on evidence in the present study.

The monophyly, subgeneric concepts and relationships of *Schizoptera* have not been tested in a phylogenetic framework. Emsley (1969) hypothesized a close association between *Nannocoris* and *Schizoptera* based on morphological similarities of head, thorax and hind wing shape. He also noted the similarity in wing venation to species of the New World genus *Ceratocomboides* McAtee and Malloch, but proposed a closer association between *Ceratocomboides* and some Old World Schizopteridae, *Pinochius* Carayon and *Birturinannus* Wygodzinsky, based on tarsal formulae and the structure of the wing-coupling mechanism (Emsley 1969). Weirauch and Štys (2014)

tested relationships across Dipsocoromorpha, found high support for a clade comprising the two included species of *Schizoptera*, recovered *Ptenidiophyes* as sister to that clade, and speculated that *Ptenidiophyes* could represent elytrous *Schizoptera* females that had not been matched to their respective macropterous males.

The objectives of the present study are threefold. We test the monophyly of *Schizoptera* and its subgenera and examine relationships with putatively closely related taxa using a molecular phylogeny with dense sampling of *Schizoptera* species and outgroups. We optimize characters previously considered to be diagnostic for *Schizoptera* and its subgenera, to examine their evolutionary patterns and guide the reclassification of the *Schizoptera* genus group. Lastly, we investigate the evolutionary history of female-specific elytra in *Schizoptera* and related genera.

Material and Methods

We included 55 terminal taxa in our analyses, 53 of which are Schizopteridae (29 taxa of *Schizoptera* and 24 of non-*Schizoptera* Schizopteridae) and two outgroups representing Ceratocombidae and Dipsocoridae. All three subfamilies of Schizopteridae were represented in our analysis (three taxa of Hypselosomatinae, two Ogeriinae and 48 Schizopterinae). All subgenera of *Schizoptera* were sampled: six representatives of *S.* (*Cantharocoris*), two of *S.* (*Kophaegis*), eight *S.* (*Lophopleurum*), five *S.* (*Odontorhagus*), six *S.* (*Schizoptera*) and four *S.* (*Zygophleps*), and one species of the genus *Orthorhagus* were included. Species were identified using original taxonomic literature and comparison with type specimens, but many species included in the present analysis remain to be described and are listed as “sp.” while denoting their country of origin. Each taxon is represented by a slide-mounted primary voucher and listed in Table 1.

Secondary vouchers, if available were point-mounted and imaged using a GT Vision imaging system (Figs 1-3); the extracted primary voucher was imaged in ethanol (temporarily fixed in KY-Jelly) where no secondary voucher was available. Voucher specimens are deposited at the Entomological Research Museum at the University of California, Riverside or loaning institutions (Table 1). Specimens were labeled with an “ED” number used for tracking sequences and specimens of Dipsocoromorpha in the Weirauch Lab (Table 1) and a Unique Specimen Identifier (USI) matrix code label was also attached to facilitate entry to and retrieval from locality databases. Specimen information was databased in the Arthropod Easy Capture specimen database and is available through the Heteroptera species page website (<http://research.amnh.org/pbi/heteropteraspeciespage>) and Discover Life (<http://www.discoverlife.org>) using the USI information.

DNA extraction, PCR amplification and sequencing

Due to the small size of Dipsocoromorpha specimens, entire specimens were digested in Proteinase K solution for 36 hours. The digested specimens are cleared in this process and can be directly slide-mounted afterward. DNA extractions were performed using a Qiagen DNeasy Blood and Tissue Kit. PCR products were cleaned with Bioline SureClean according to standard protocol. Three regions of two ribosomal genes (18S rDNA, D2 and D3-D5 regions of 28S) and one protein-coding gene (COI) were sequenced. Primer sequences for 18S (18SF, 18Sr, 18S3f, 18SBI) and 28S D2-D5 (28SD3Fa, 28SD5Ra) rDNA are from Weirauch and Munro (2009); 28 D2 (28SD2Fa, 28SD2Ra) primer sequences from Weirauch and Štys (2014); and COI primer sequences (COILCO-1490-J-1514, COIHCOoutout) from Folmer *et al.* (1994), Prendini

et al (2005), and Schwendinger and Giribet 2005, respectively. PCR products were sequenced at the Genomics Core, University of California, Riverside. Sequences were assembled and edited with sequencer 4.8™. Sequences were verified as belonging to Heteroptera or Schizopteridae using BLAST (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>).

Sequencing, alignment and concatenation

Sequences for 18S, 28S and COI were aligned separately using the online MAFFT version 6 (<http://mafft.cbrc.jp/alignments/server/>) (Kato et al. 2005) with default parameters using the E-INS-i algorithm. Gene regions were concatenated in SequenceMatrix v1.7.8. (Vaidya et al. 2011) and exported with external gaps coded as question marks. The alignment resulted in 3785 sites.

Phylogenetic reconstruction

Parsimony (P) analyses were performed using TNT v1.1 (Goloboff et al., 2008) with gaps transformed into missing data. MP tree search was performed using the 'New Technology Search' method in combination with sectorial search, ratchet, drift and tree fusing, all at default settings. The following parameters were specified: initial addseqs = 30, find minimum tree length = 100 times and random seed= 2000. Nodal support was determined by 500 replicates of jackknife resampling (Farris et al. 1996) with 36% character removal probability. A maximum likelihood (ML) analysis was performed using RAxML-HPC2 on XSEDE (Stamatakis, 2006, Stamatakis et al., 2008) version 8.0.24. of the Cyberinfrastructure for Phylogenetic Research (CIPRES) (Science Gateway V.3.1 (http://www.phylo.org/sub_sections/portal)). *Ceratocombus vagans* 247 and *Cryptostemma* sp249 were set as outgroups and 12345 as the random seed. Each partition was analyzed under a GTR+ Γ +I model. Rapid bootstrap analysis (BS) was

performed for 1,000 iterations and followed by a ML best tree search. Default settings were used otherwise.

Ancestral state reconstruction

To examine their transformation on the ML tree, 11 morphological characters comprising features of the thorax, wings and genitalia were coded for all Dipsocoromorpha taxa in our analysis. Several characters (those deemed “diagnostic” for specific subgenera of *Schizoptera*) were coded only for Schizopteridae (Fig. 1.3, characters 3-6). The evolution of these characters was reconstructed in Mesquite using parsimony. Given the diversity of wing modifications observed in species of Dipsocoromorpha (i.e. macropterous, submacropterous, brachypterous, micropterous and elytrous), we only coded the conditions observed in our sampled taxa. Because wing modifications are both dimorphic and polymorphic in *Schizoptera*, we only coded females as either having macropterous or elytrous wings.

Results

New concept of Schizoptera and the Schizoptera genus group

Our ML and P analyses show *Schizoptera* to be polyphyletic, with the subgenus *S. (Kophaegis)* sensu McAtee and Malloch (1925) being recovered as part of the sister clade to *Schizoptera*, and *Orthorhagus* that was formerly treated as a subgenus of *Schizoptera* as sister to *Ceratocomboides* (Figs 2 and 3). *Schizoptera* without *S. (Kophaegis)* and *Orthorhagus* is strongly supported (ML: 100%; P: 100%) and we will subsequently use this new concept of *Schizoptera*, while raising *S. (Kophaegis)* to genus rank (see Fig. 1.1G for proposed changes and Leon and Weirauch [2016] for a

taxonomic treatment of *Orthorhagus*). The sister group to this new concept of *Schizoptera* is a clade comprising *Ptenidiophyes* + *Kophaegis*, with the more inclusive clade comprising these three genera also receiving high support (ML: 97%; P: 83%). We refer to this group of five genera ((*Orthorhagus* + *Ceratocomboides*) + ((*Kophaegis* + *Ptenidiophyes*) + (*Schizoptera*))) as the *Schizoptera* genus group. All other Schizopterinae included in the present analysis (i.e., species of *Nannocoris*, *Pinochius*, members of the *Corixidea* genus group, and *Dundonannus* Wygodzinsky) form the sister clade to the *Schizoptera* genus group, with Schizopterinae as a group receiving 100% BS in the ML analysis.

Monophyly and relationships of Schizoptera subgenera

Within *Schizoptera*, three monophyletic groups that correspond to the subgenera *S.* (*Zygophleps*) and *S.* (*Odontorhagus*) and a clade comprising *S.* (*Cantharocoris*) + *S.* (*Lophopleurum*) were recovered with 100% bootstrap support in our ML analyses and are denoted in different colors in Figure 2. These same three clades were recovered as monophyletic in the parsimony analysis (SM2), but the position of *S.* (*Zygophleps*) and part of *S.* (*Schizoptera*) differed from the ML analysis. Even though the clade comprising *S.* (*Cantharocoris*) + *S.* (*Lophopleurum*) is highly supported, the two subgenera *S.* (*Cantharocoris*) and *S.* (*Lophopleurum*) are not monophyletic. Based on the lack of reciprocal monophyly, but also the ambiguity of the single currently used diagnostic feature (glabrous, heavily sclerotized region of the metepisternum extending to versus beyond the midline of the metapleuron; based on our observations, this feature is gradual and assignment to either subgenus largely arbitrary), we propose the synonymy of the two subgenera as *S.* (*Cantharocoris*) [see below]. In contrast, the last remaining

subgenus in *Schizoptera*, the subgenus *S.* (*Schizoptera*) was recovered as polyphyletic in our analyses (Fig. 1.2). A well-supported clade comprising several *S.* (*Schizoptera*) species from Trinidad is the sister group to *S.* (*Zygophleps*), with the remaining two *S.* (*Schizoptera*) species included in this analysis being treated as sister to *S.* (*Odontorhagus*) and *S.* (*Cantharocoris*), respectively. Relationships between the three strongly supported subgeneric clades and members of *S.* (*Schizoptera*) received somewhat lower support values. The *S.* (*Schizoptera*) [part] + *S.* (*Zygophleps*) is shown as the sister to *S.* (*Odontorhagus*) + *S.* (*Schizoptera*) [part] plus *S.* (*Cantharocoris*) + *S.* (*Schizoptera*) [part].

Optimization of putative generic and subgeneric diagnostic characters

Figure 3 shows the phylogenetic distribution of the 11 morphological characters coded in this analysis and Figure 4 illustrates characters and character states. Parsimony reconstructions for individual characters are available as SM3.

Character #1 Metepisternal Spine (Fig. 1.4): All representatives of *Schizoptera*, the *Ptenidiophyes* + *Kophaegis* clade, and *Orthorhagus* (Fig. 1.3, SM3) possess a postero-lateral spine on the metepisternum, a feature that we did not observe outside the *Schizoptera* genus group. The reconstruction (SM3) of this character is ambiguous. The spine may have evolved independently in *Orthorhagus* and the ancestor of (*Kophaegis* + *Ptenidiophyes*) + *Schizoptera*, or may have been present in the ancestor of these three clades, but was lost in *Ceratocomboides*, where the metepisternum forms a dull lobe instead of spines. In either scenario, the spine is not restricted to species of *Schizoptera*, as proposed by Emsley (1969), and our analysis suggests that the spine found in species of *Ptenidiophyes* is homologous.

Character #2 Ventral margin of metepisternum: shining area surrounding scent gland groove (Fig. 1.4): The cuticle surrounding the groove of the metathoracic glands has been modified to be distinctly glabrous or shining, without setation, and with a faint reticulated pattern in species of *Schizoptera*, *Orthorhagus*, and *Kophaegis*. Emsley (1969) referred to this feature as “narrow shining border”. *Ptenidiophyes* possess what we call a “differentiated” ventral border, which is slightly shining and smoother than the rest of the metasternum, but not as distinct as it is in species of *Schizoptera*, *Kophaegis*, or *Orthorhagus*. Our optimization shows that the shining area evolved in the last common ancestor of the *Schizoptera* genus group, was modified to a more matt surface in *Ptenidiophyes*, and was lost in *Ceratocomboides* where the ventral margin is undifferentiated and punctate as it is in the outgroups (Fig. 1.3, SM3). We treat the shining ventral margin of the metepisternum as a diagnostic feature for the *Schizoptera* genus group.

Character #3 Extent of shining cuticle on metepisternum (Fig. 1.4): The glabrous area surrounding the scent gland groove can either be restricted to the ventral margin of the metepisternum, as seen in species of *S. (Odontorhagus)*, *S. (Schizoptera)* and *S. (Zygophleps)*, or extend to or beyond the midline of the metapleuron, as seen in *S. (Cantharocoris)*. Emsley referred to this feature as “elevated shining area”. Our optimization shows that the expanded condition found in *S. (Cantharocoris)* is derived from a ventral shining border as observed in all other *Schizoptera* species (Fig. 1.3, SM3).

Character #4 Pronotal collar (Fig. 1.4): The lack of a pronotal collar was used by McAtee and Malloch (1925) to distinguish species in their subgenus *S. (Orthorhagus)*, now *Orthorhagus*, from all other *Schizoptera* species. Our observations confirm that all

species of *Schizoptera*, *Kophaegis*, and *Ceratocomboides* within the *Schizoptera* genus group possess a pronotal collar, as do most other genera of Schizopterinae (see Fig. 1.3, SM3). According to our analysis, the pronotal collar was present in the last common ancestor of Schizopterinae and was then lost three times within that clade (Fig. 1.3, SM3), in the *Corixidea* genus group, in *Orthorhagus* and in *Ptenidiophyes*. Given that the pronotal collar is a homologous and common feature across Schizopterinae, its reductions in *Orthorhagus* and *Ptenidiophyes* are good diagnostic features.

Character #5 Blunt tooth on propleuron (Fig. 1.4): A posteriorly directed process or “blunt tooth” (sensu Emsley 1969) on the propleuron (Fig. 1.1C) is a rare feature in Schizopteridae, was used by McAtee and Malloch (1925) to diagnose *S. (Odontorhagus)* and *S. (Kophaegis)* and by Emsley (1969) to synonymize the two subgenera. Our observations and optimization show that these processes in *Odontorhagus* and *Kophaegis* are not homologous; processes found in species of the Old World *Pinochius* Carayon are here treated as a third independent origin (Fig. 1.3, SM3). Given that the pronotal tooth is a fairly rare character across Schizopterinae, it remains a good diagnostic feature for species of *Odontorhagus* among other *Schizoptera* species and for *Kophaegis* amongst species of the *Schizoptera* genus group.

Character #6 Triangular posterior membranal cell (Fig. 1.4): The triangular shape of the posterior membranal cell (Fig. 1.1F) is only found in species of *S. (Zygophleps)*, and has long been used as a diagnostic feature for this subgenus. Our observations and analysis show that this character is restricted to this group and indeed provides an excellent diagnostic feature (Fig. 1.3, SM3).

Character #7 Asymmetrical subgenital plate (Fig. 1.4): Male genitalia of Schizopteridae are complex and asymmetrical (McAtee and Malloch 1925, Emsley 1969, Leon and

Weirauch, accepted, Knyshev *et al.* 2015, submitted), with one of the notable feature being the modification of sternite VII into a subgenital plate (Emsley 1969, Knyshev and Weirauch, in prep). The shape of the subgenital plate ranges from symmetrical to sinistrally asymmetrical, and the plate can be armed with lateral and caudal processes (Fig. 1.4). In *Schizoptera*, the subgenital plate is distinctly asymmetrical with few to many processes on the left and posterior margins. Asymmetrical subgenital plates are also observed in species of *Kophaegis* and *Orthorhagus*. A relatively simpler, more symmetrical subgenital plate without lateral processes is present in males of *Ptenidiophyes* (Fig. 1.3, SM3). Simpler, more symmetrical subgenital plates are observed in Hypselosomatinae (i.e. *Williamsocoris* Carpintero and Dellapé), some Ogeriinae (i.e. *Chinannus* Wygodzinsky and *Kokeshia* Miyamoto) and other Schizopteridae (i.e. *Corixidea* Reuter). Our optimizations allow for two possible scenarios: the ancestor to the *Schizoptera* genus group possessed a simple, symmetrical subgenital plate, and an armed, asymmetrical subgenital plate evolved three times independently within this clade, or the last common ancestor possessed an asymmetrical and complex subgenital plate, with reversals in *Ceratocomboides* and *Ptenidiophyes* (SM 3).

Character #8 Pygophore rotation (Fig. 1.4): In most schizopterids, the pygophore is in-line with the dorsal body plane. In *Schizoptera*, the pygophore is rotated 90° dextrally. This condition is also observed in species of *Orthorhagus* and *Kophaegis*. Our optimization shows the same ambiguity as described for character #7, either treating the rotated pygophores as of independent origins in *Orthorhagus*, *Kophaegis* and *Schizoptera*, or the ancestral conditions in *Ptenidiophyes* and *Ceratocomboides* as reversals.

Character #9 Antler-shaped anophoric process (Fig. 1.4): Species of *Kophaegis* and *Schizoptera* possess many similar morphological features (Fig. 1.3, chars 1-5), among them the two genitalic characters 7 and 8. However, the genitalia also provide features that diagnose the two genera: an “antler” shaped process of the anophore (segments X-XI) is present in *Kophaegis* species, but not in *Schizoptera*. We also found a process that we coded as putatively homologous in species of the Old World genus *Pinochius*, but our analysis indicates that these processes are independently derived in *Kophaegis* and *Pinochius*.

Character #10 Conjunctival appendages (Fig. 1.4): Emsley (1969) documented the diversity of asymmetrical genitalic structures that he called conjunctival appendages in males of *Schizoptera* (that then included species of *Kophaegis* and *Orthorhagus*). Our reconstruction shows that conjunctival appendages are indeed a synapomorphy and good diagnostic feature of *Schizoptera* (Fig. 1.3, SM3), although of the new concept of *Schizoptera* that excludes species now classified in the genera *Kophaegis* and *Orthorhagus*.

Character #11 Discal cell shape (Fig. 1.4): Wing venation homologies remain poorly studied across Dipsocoromorpha (Emsley 1969, Redéi 2008), but certain venation patterns are nevertheless useful in diagnosing and identifying certain groups. Species of the *Schizoptera* genus group possess a discal cell that can be homologized across most other Schizopteridae. In *Schizoptera*, the discal cell is distinctly trapezoidal in shape, whereas this cell is diamond-shaped in *Ptenidiophyes* + *Kophaegis* and *Ceratocomboides* species, and triangular in *Orthorhagus* (Fig. 1.3, Fig. 1.4, SM3). The trapezoidal discal cell is therefore a good diagnostic feature of *Schizoptera*.

Evolution of female-specific elytra

Our reconstruction of female wing type on the ML topology is shown in Figure 3 where blue branches represent elytrous wings and black branches macropterous wings. Given that this analysis focuses on the *Schizoptera* group of genera, sampling of other Schizopterinae, Ogeriinae, and Hypselosomatinae is not comprehensive. Nevertheless, our reconstruction shows that elytrous wings in females have evolved at least seven times within Schizopteridae. Outside of the *Schizoptera* genus group, elytrous wings may have been present in the last common ancestor of all Schizopteridae (node A) or were independently derived in Hypselosomatinae and Ogeriinae and evolved independently within the *Corixidea* group and in *Nannocoris* (nodes B and C). Females of the last common ancestor of the *Schizoptera* genus group are here reconstructed to have had macropterous wings, but elytra evolved four times independently within this clade: in the last common ancestor of *Ptenidiophyes* (node D), where all known females are elytrous and three times within the genus *Schizoptera*. Within *Schizoptera*, females have evolved elytrous wings in an undescribed species from Costa Rica that is currently classified in the subgenus *S.* (*Schizoptera*) and is recovered as the sister group to *S.* (*Odontorhagus*), and twice within the subgenus *S.* (*Cantharocoris*). Our topology and reconstruction also indicate that two reversals from elytrous to macropterous wings occurred within *S.* (*Cantharocoris*), indicating that wing type patterns at least in the females are highly homoplastic and their evolution complicated.

Classification of genera and subgenera in the Schizoptera genus group

Ceratocomboides McAtee and Malloch 1925

Type species: *Ceratocomboides prima* McAtee and Malloch 1925

Updated diagnosis: Recognized amongst other genera in the *Schizoptera* genus group by the lobe-shaped metepisternum (Fig. 1.4, character 1), the undifferentiated ventral margin of the scent-gland groove, the symmetrical subgenital plate of males, and the diamond-shaped discal cell of the forewing (Fig. 1.4, character 11).

Kophaegis (McAtee and Malloch 1925), stat. nov.

Type species: *Kophaegis cubensis* (McAtee and Malloch 1925).

Updated diagnosis: Recognized amongst other genera in the *Schizoptera* genus group by the spine-shaped metepisternum, the glabrous, shining cuticle surrounding the metathoracic scent gland groove, the diamond-shaped discal cell of the forewing (Figs 3 and 4, character 11), the presence of a blunt tooth on the propleuron, and the antler-shaped process of the anophore (s X-XI) (Fig. 1.4, character 9).

Comment: Only two species of *Kophaegis* are known, and only three specimens have been located amongst the >2,000 *Schizoptera* genus group specimens assembled by us. A proper taxonomic revision is necessary to formally diagnose and describe this genus.

Orthorhagus (McAtee and Malloch 1925), stat. nov.

Type species: *Orthorhagus planus* (McAtee and Malloch 1925).

Comment: Leon and Weirauch (2016) raised *Orthorhagus* to generic rank based on several morphological features including male genitalia, lack of a pronotal collar, and eye shape and size.

Ptenidiophyes Reuter 1981

Type species: *Ptenidiophyes mirabilis* Reuter 1981

Updated diagnosis: Recognized amongst other genera in the *Schizoptera* genus group by macropterous males and elytrous females, the punctate structure of the thorax, the spine the slightly differentiated ventral margin of the scent gland groove, the simple, symmetrical subgenital plate in males, and the heavily punctate elytra in females with an explanate wing margin.

Comment: This study resulted in the discovery of male *Ptenidiophyes* specimens. A formal taxonomic revision of this group is necessary for the formal description of male specimens.

Schizoptera Fieber 1860

Type species: *Schizoptera cicadina* Fieber 1860

Updated diagnosis: Recognized amongst other genera in the *Schizoptera* genus group by the spine shape of the metepisternum, the distinctly shining cuticle of the metathoracic scent-gland groove which may be restricted to the ventral margin, or extend up to or beyond the midline of the metapleuron, the sinistrally asymmetrical subgenital plate (s VII), the rotated pygophore, the presence of asymmetrical conjunctival appendages in males, and the trapezoidal shape of the discal cell of the forewing.

Comment: The diagnoses provided by McAtee and Malloch (1925) and Emsley (1969) included characters that are also diagnostic for *Orthorhagus* and *Kophaegis*, and are provided in Table 2. This updated diagnosis is valid for species that fall within the new concept of *Schizoptera* (Fig. 1.2 and 3).

Schizoptera (Cantharocoris) McAtee and Malloch 1925

Type species: *Schizoptera (Cantharocoris) reuteri* McAtee and Malloch 1925.

Updated diagnosis: Recognized among other members of *Schizoptera* by the glabrous, shining cuticle surrounding the scent-gland groove extending to or beyond the midline of the metapleuron.

Schizoptera (Lophopleurum), junior synonym

Comment: We synonymize *S. (Cantharocoris)* (Fig. 1.1A) and *S. (Lophopleurum)* (Fig. 1.1B) based on their position within a strongly supported clade (Fig. 1.2), as well as the lack of reciprocal monophyly for each subgenus. The diagnostic features proposed by Emsley (1969) (Fig. 1.1A and B) appear to be gradual and assignment to either subgenus largely arbitrary, we therefore update the diagnosis for *S. (Cantharocoris)* to encompass both the shining area extending to and beyond the midline of the metapleuron.

Schizoptera (Odontorhagus) McAtee and Malloch 1925

Type species: *Schizoptera (Odontorhagus) bipartita* McAtee and Malloch 1925.

Updated diagnosis: Recognized among other members of *Schizoptera* by the presence of a blunt tooth on the propleuron (Fig. 1.1C, Fig. 1.4).

Comment: The lack of an antler-shaped process of the anophore distinguishes species of *Schizoptera (Odontorhagus)* from those of *Kophaegis*. *Schizoptera (Odontorhagus)* will be revised in an upcoming taxonomic treatment (Leon and Weirauch, in prep), where the dissolution of these two groups will be formalized.

Schizoptera (Schizoptera) McAtee and Malloch 1925

Type species: *Schizoptera (Schizoptera) cicadina* Fieber 1860.

Comment: Emsley (1969) defined this subgenus by the shining ventral margin of the scent gland groove, and the lack of all diagnostic characters of the other subgenera.

Given that our results show that *Schizoptera (Schizoptera)* is polyphyletic, we do not provide an updated diagnosis for this group. Better taxon sampling would clarify potential monophyletic groups within this polyphyletic assemblage. Inclusion of the type species in our analysis would verify whether we can truly designate and diagnose a *Schizoptera (Schizoptera)* clade.

Schizoptera (Zygophleps) McAtee and Malloch 1925

Type species: *Schizoptera (Zygophleps) unica* McAtee and Malloch 1925.

Comment: the triangular shape of the posterior membranous cell remains a good diagnostic feature and synapomorphy (Fig. 1.3) for this subgenus.

Discussion

Female-specific elytra in the Schizoptera genus group

Within the *Schizoptera* genus group, only *Schizoptera* and *Ptenidiophyes* contain species with elytrous females, whereas females in the remaining genera are similar to males in being macropterous. In *Ptenidiophyes*, all known females are elytrous, and also diagnosed from elytrous *Schizoptera* females by the punctuation of the elytra and the expanded wing margin. We conclude that the transition from macropterous to elytrous females therefore occurred in the last common ancestor of *Ptenidiophyes*. *Schizoptera* females present a more complex scenario: elytrous wings have evolved three times independently within this genus, and in all known elytrous morphs, the elytra are rugose,

with traces of wing venation (see habitus images on figs 2 and 3). Compared to the situation in Coleoptera, where elytra evolved only once (Lawrence and Newton 1982), the multiple origins of elytra in this small clade of minute litter bugs are astounding, especially because they are restricted to the female sex.

In the following, we explore two hypotheses that could explain the evolution of female-specific elytra in the *Schizoptera* genus group, one related to mating behaviors that unfortunately remain undocumented for Schizopteridae, the other to ecological preferences. In dytiscid beetles, different modifications of the elytron cuticle in females evolved multiple times within one clade, presumably as a response to the males' enlarged attachment structures on the pro- and mesotarsi (Miller 2003). These modifications are believed to hinder male control over mating by making it more difficult for males to grasp females for mating, showcasing an example of a sexual arms race (Green *et al.* 2013). Based on circumstantial evidence, we speculate that female elytra in species of the *Schizoptera* group may have a similar function. First, the female elytra form a firm cover not only over the dorsal surface of the abdomen, but also obscure at least in part the external female genitalia, which in *Schizoptera* species are strongly reduced. The elytra may therefore limit the males' access to females, and present an additional mechanism for female choice. Second, Emsley (1969) noted the distribution of dorsal arolia (his "empodial vesicles") on the pretarsus of the pro- and mesotarsi of several schizopterid genera, including *Schizoptera*, and realized that this trait only occurs in males. Dorsal arolia are suspected to be attachment structures that facilitate adhesion to surfaces (Beutel and Gorb 2001), and the fact that they only occur in male *Schizoptera* species points to a sexually dimorphic function, e.g., in the context of mating behaviors. Female elytra in Schizopteridae that are both fairly smooth, but also cover the

lateral portions of the thorax and abdomen, possibly make it more difficult for the males to achieve a firm grasp. Direct observation of mating behaviors and more extensive phylogenetic reconstructions that also consider male attachment structures and the complex male genitalia could provide further insights while evaluating this hypothesis. The reversion to macropterous female forms, as seen twice within the subgenus *S. (Cantharocoris)* would appear to remain a puzzle under this “sexual selection hypothesis”.

Alternatively, the modification of wings in females of *Schizoptera* might be tied to different microhabitat preference in males and females. Unpublished data from our lab (Weirauch et al., unpublished data) shows that a significant proportion of specimens sorted from leaf litter sifting samples are elytrous females. In contrast, both males and macropterous female specimens of the subgenus *Odontorhagus* (Fig. 1.3) have been collected in large numbers from UV light traps. Further supporting evidence previously provided by Emsley (1969), this observation suggests that elytrous females are incapable of flight and are restricted to potentially more stable leaf litter habitats. Similar patterns are observed in ptinine beetles, where the females’ inability to fly and occupation of stable leaf litter habitats has been hypothesized to be associated with increased fecundity (Phillips 2000). Elytra in females of *Schizoptera* that occupy forest litter habitats could therefore be beneficial for two reasons. Other than the fragile macropterous forewings found in males and in species with macropterous females, the heavily sclerotized elytra are unlikely to get mutilated in a leaf litter habitat and might provide additional protection against potential predators. In addition, flightless might result in the reallocation of flight energy resources, e.g. to increase egg production (Roff 1986, Denno 1994). Natural history observations on *Schizoptera* and other groups of

Schizopteridae that include elytrous females could shed further light on this hypothesis. This “ecological hypothesis” could also offer an explanation for the reversion to macropterous wings in females, as observed two times independently in *S. (Cantharocoris)*: these macropterous taxa might inhabit less stable microhabitats, where wings are essential.

Phylogenetic relationships of the Schizoptera genus group

This study is the first phylogenetic analysis focusing on relationships within part of the Schizopteridae, and the first study to use molecular tools to investigate generic and subgeneric relationships within the largest subfamily of Schizopteridae, the Schizopterinae. It places the genus *Schizoptera* into the context of several genera that were previously suspected to be close relatives, but also allows for the first time to investigate the monophyly of the genus and its subgenera, informing a re-classification of this genus group. As such, one of the important outcomes of the present study is the subdivision of the *Schizoptera* genus group into more manageable clades and projects that can then be taxonomically revised. *Orthorhagus* was recently raised to generic rank (Leon and Weirauch 2016) and several new species described. A taxonomic revision of the subgenus *S. (Odontorhagus)* is under way and future taxonomic work should focus on *Ptenidiophyes* and subgenera within *Schizoptera*. In addition, the current concept of *Ceratocomboides* is not well defined and the genus is in dire need of systematic revision. Finally, the genus *Kophaegis* with Caribbean distribution and astonishing male genitalic morphology is another intriguing candidate for a taxonomic revision (Fig. 1.4, Char. 9).

Our analyses provide greatly improved insights into relationships amongst Schizopterinae compared to Weirauch and Štys (2014), a study that was focused on testing higher-level relationships amongst Dipsocoromorpha and with insufficient taxon sampling to investigate relationships within Schizopterinae. Nevertheless, Weirauch and Štys (2014) proposed that elytrous *Ptenidiophyes* may in fact be females of *Schizoptera* males not sampled in their analysis. Based on more extensive taxon sampling across the *Schizoptera* genus group, we show that *Ptenidiophyes* is in fact part of the *Schizoptera* genus group, but that males of this genus had simply not been discovered prior to our study. We included two macropterous male specimens that feature a punctate thorax similar to *Ptenidiophyes* females and wing venation similar, but not identical, to *Schizoptera* specimens, and these male specimens (Figs 2 and 3, *Ptenidiophyes* PERU 187 and *Ptenidiophyes* CR 3391) grouped with 100% bootstrap support with three female *Ptenidiophyes* specimens. We conclude that these specimens represent the first report of male *Ptenidiophyes* (male and female habitus images can be seen in Figs 2 and 3). Because we also discovered several undescribed species in this genus, males of *Ptenidiophyes* will be formally described in a separate project.

References

- Alexander, R. D. (1968). Life cycle origins, speciation, and related phenomena in crickets. *The Quarterly Review of Biology* **43**, 1–41.
- Aukema, B. (1995). The evolutionary significance of wing dimorphism in carabid beetles (Coleoptera: Carabidae). *Researches on Population Ecology* **37**, 105–110.
- Beutel, R. G., Gorb, S. (2001) Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. *Journal of Zoological Systematics and Evolutionary Research*, **39**, 177–207.
- Braendle, C., Davis, G.K., Brisson, J.A., and Stern, D.L. (2006). Wing dimorphism in aphids. *Heredity* **97**, 192–199.
- China, W. E. (1946). New Cryptostemmatidae (Hemiptera) from Trinidad, British West Indies. *Proceedings of the Royal Entomological Society of London (B)* **15**, 148–154.
- Denno, R. F. (1994). The evolution of dispersal polymorphisms in insects: The influence of habitats, host plants and mates. *Researches on Population Ecology* **36**, 127–135.
- Denno, R. F., Douglas, L.W., and Jacobs, D. (1985). Crowding and host plant nutrition: environmental determinants of wing-form in *Prokelisia marginata*. *Ecology* **66**, 1588–1596.
- Desender, K. (1987). Distribution, the special case of sex-linked wing dimorphism and phenology of the life cycle in *Trichotichnus laevicollis* and *T. nitens* (Coleoptera: Carabidae). *Deutsche Entomologische Zeitschrift* **34**, 77–84.
- Emsley, M. G. (1969). The Schizopteridae (Hemiptera: Heteroptera) with the descriptions of new species from Trinidad. *Memoirs of the American Entomological Society* **25**, 1–154.
- Fairbairn, D. J. (1994). Wing dimorphism and the migratory syndrome: Correlated traits for migratory tendency in wing dimorphic insects. *Researches on Population Ecology* **36**, 157–163.
- Fieber, F. X. (1860). Exegesen in Hemipteren. *Wiener entomologische Monatschrift* **9**, 257–272.
- Green, K. K., Kovalev, A., Svensson, E.I., and Gorb, S.N. (2013). Male clasping ability, female polymorphism and sexual conflict: fine-scale elytral morphology as a sexually antagonistic adaptation in female diving beetles. *Journal of The Royal Society Interface* **10**, 20130409.
- Guerra, P. A. (2011). Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews* **86**, 813–835.

- Harrison, R.G. (1980). Dispersal polymorphisms in Insects. *Annual Review of Ecology and Systematics* **11**, 95–118.
- Honek, A. (1995). Factors and consequences of a non-functional alary polymorphism in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *Researches on Population Ecology* **37**, 11–18.
- Langellotto, G.A., Denno, R.F., and Ott, J.R. (2000). A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology* **81**, 865–875.
- Lawrence, J. F., Newton, A. F. (1982). Evolution and classification of beetles. *Annual Review of Ecology and Systematics*. **13**, 261–290.
- Masaki, S., and Oyama, N. (1963). Photoperiodic control of growth and wing-form in *Nemobius yezoensis* (Orthoptera : Gryllidae). *Japanese Journal of Entomology* **31**, 16–26.
- McAtee, W.L., and Malloch, J.R. (1925). Revision of bugs of the family Cryptostemmatidae in the collection of the United States National Museum. *Proceedings of the United States National Museum* **67**, 1–42.
- Miller, K.B. (2003). The phylogeny of diving beetles (Coleoptera: Dytiscidae) and the evolution of sexual conflict. *Biological Journal of the Linnean Society* **79**, 359–388.
- O'Donnell, J. E. (1991). A new coleopteroid Lethaeine from Southern South America (Hemiptera: Lygaeidae: Rhyparochrominae). *New York Entomological Society* **99**, 87–96.
- Philips, T.K. (2000). Phylogenetic analysis of the New World Ptininae (Coleoptera: Bostrichoidea). *Systematic Entomology* **25**, 235–262.
- Poinar, G.J., and Brown, A. (2014). New genera and species of jumping ground bugs (Hemiptera: Schizopteridae) in Dominican and Burmese amber, with a description of a meloid (Coleoptera: Meloidae) triungulin on a Burmese specimen. *Annales de La Société Entomologique de France (N.S.): International Journal of Entomology* **50**, 372–381.
- Poppus, B. (1910). Neue Ceratocombiden. *Ofversigt Af Finska Vetenskaps societetens Forhandlingar Helsingfors* **52**, 1–14.
- Reuter, O.M. (1882). Sur le genre *Schizoptera* Fieb. *Revue D'entomologie* **1**, 162–164.
- Reuter, O.M. (1891). Monographia Ceratocombidarum orbis terrestris. *Acta Societatis Scientiarum Fennicae* **19**, 1–28.
- Ribak, G., Pitts, M., L., Wilkinson, G.S., and Swallow, J., G. (2009). Wing shape, wing size, and sexual dimorphism in eye-span in stalk-eyed flies (Diopsidae). *Biological Journal of the Linnean Society* **98**, 860–871.

- Roff, D.A. (1986). The evolution of wing dimorphism in insects. *Evolution* **40**, 1009–1020.
- Roff, D.A. (1994). The evolution of flightlessness: Is history important? *Evolutionary Ecology* **8**, 639–657.
- Schuh, R. T., and Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. (Comstock Publishing Associates, Cornell University Press).
- Slater, J. A. (1975). On the biology and zoogeography of Australian Lygaeidae (Hemiptera: Heteroptera) with special reference to the southwest fauna. *Australian Journal of Entomology* **14**, 47–64.
- Slater, J. A. (1977). The incidence and evolutionary significance of wing polymorphisms in lygaeid bugs with particular reference to those of South Africa. *Biotropica* **9**, 217–229.
- Štys, P. (1975). Redescription of *Ptenidiophyes mirabilis* Reuter (Heteroptera: Schizopteridae). *Vestník Česl Spol Zool* **39**, 154–159.
- Svensson, E. I., Abbott, J.K., Gosden, T.P., and Coreau, A. (2007). Female polymorphisms, sexual conflict and limits to speciation processes in animals. *Evolutionary Ecology* **23**, 93–108.
- Sweet, M. H. (1964). The biology and ecology of the Rhyparochrominae of New England. *Entomologica Americana* **43**, 1–124.
- Zera, A. J., and Denno, R. F. (1997). Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* **42**, 207–230.

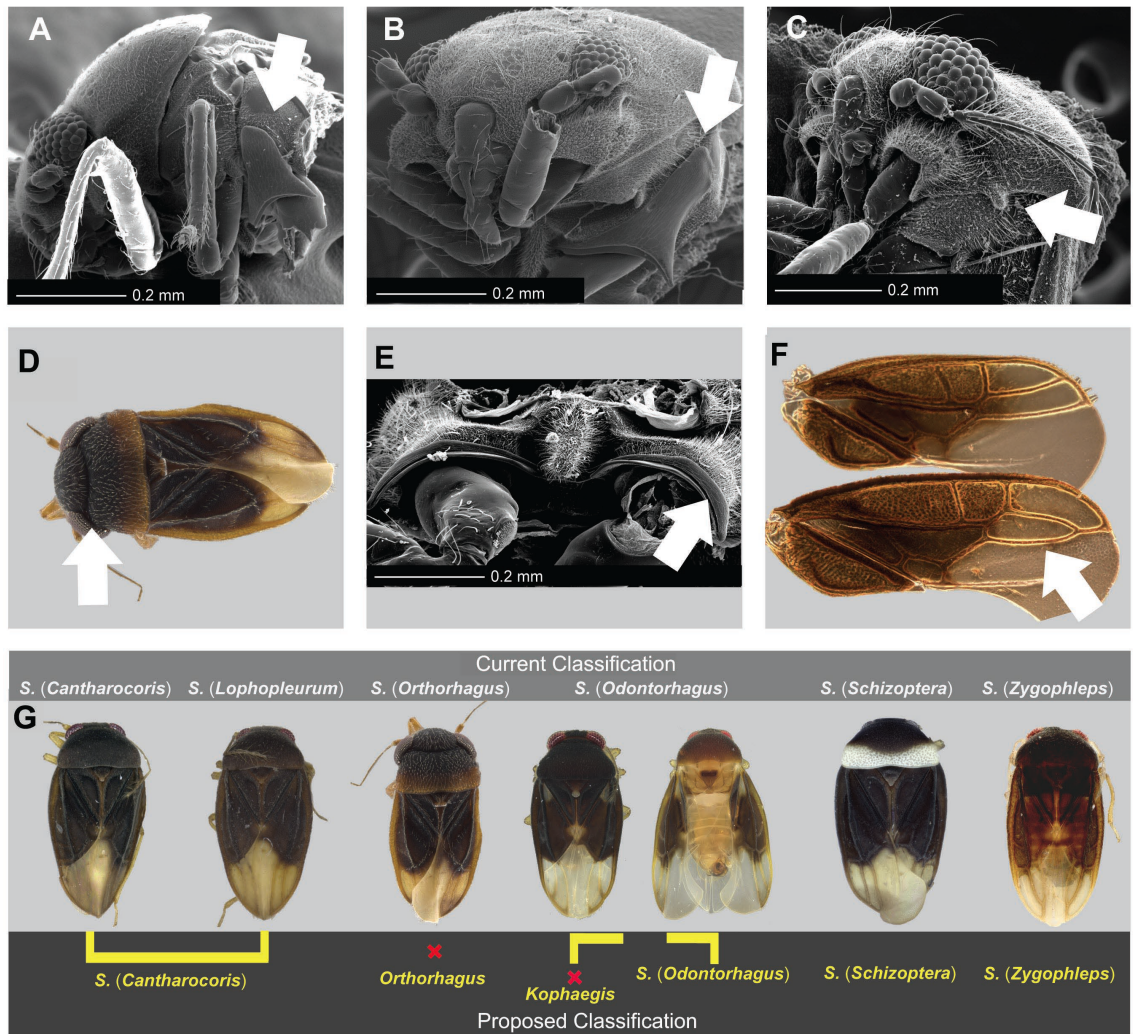


Figure 1.1: Diagnostic characters historically used to recognized subgenera of *Schizoptera* (A-F) and a comparison of the current and proposed classification of genera and subgenera (G). A. subgenus *Cantharocoris* with shining area extending to midline of metapleuron, B. subgenus *Lophopleurum* with shining area extending beyond midline of metapleuron, C. subgenus *Odontorhagus* with blunt tooth on propleuron, D. subgenus *Orthorhagus* without a pronotal collar, E. subgenus *Schizoptera* with shining area restricted to ventral margin, F. subgenus *Zygophleps* with a triangular posterior membranous cell. White arrows indicate the diagnostic feature. G: Habitus images of the six currently recognized subgenera of *Schizoptera*. The current classification is shown in white font and the proposed classification in yellow font. The yellow bracket indicates a proposed synonym of two subgenera, the broken bracket the dissolution of a subgenus, and the red "Xs" symbolize removal from the genus *Schizoptera* and recognition at the genus rank.

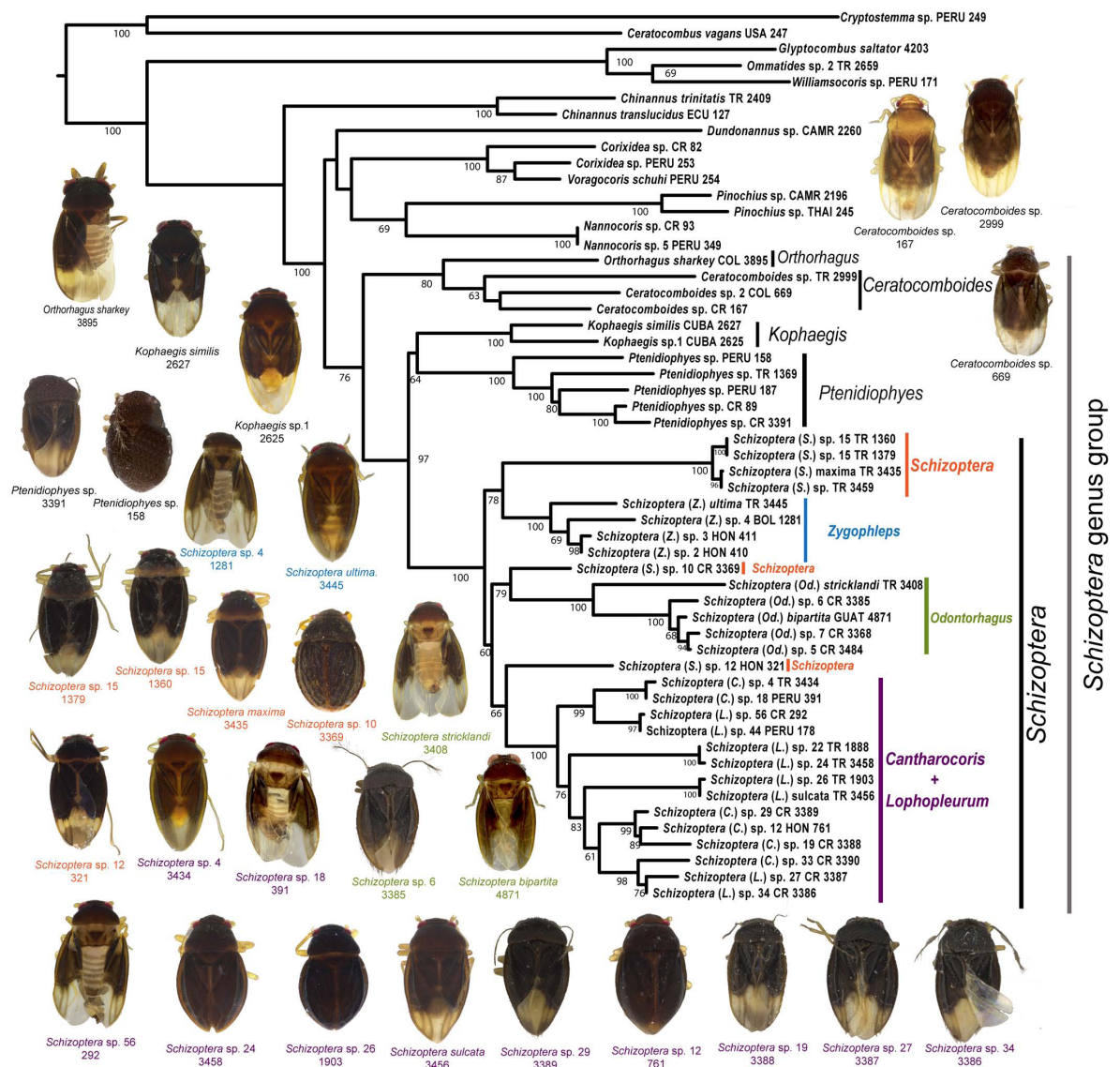


Figure 1.2: The best tree derived from the maximum likelihood analysis of *Schizoptera* and related taxa. Numbers underneath nodes indicate bootstrap values (>60%). The grey line highlights the *Schizoptera* genus group. The monophyletic, new concept of *Schizoptera* (i.e. *Kophaegis* and *Orthorhagus* removed) is highlighted by a black line. Subgenera of *Schizoptera* are highlighted in different colors. Habitus images represent specimens in the *Schizoptera* genus group included in this analysis, the font color corresponds to their respective subgenus, and numbers below taxon names are ED numbers that allow cross-reference with taxa included in the phylogeny.

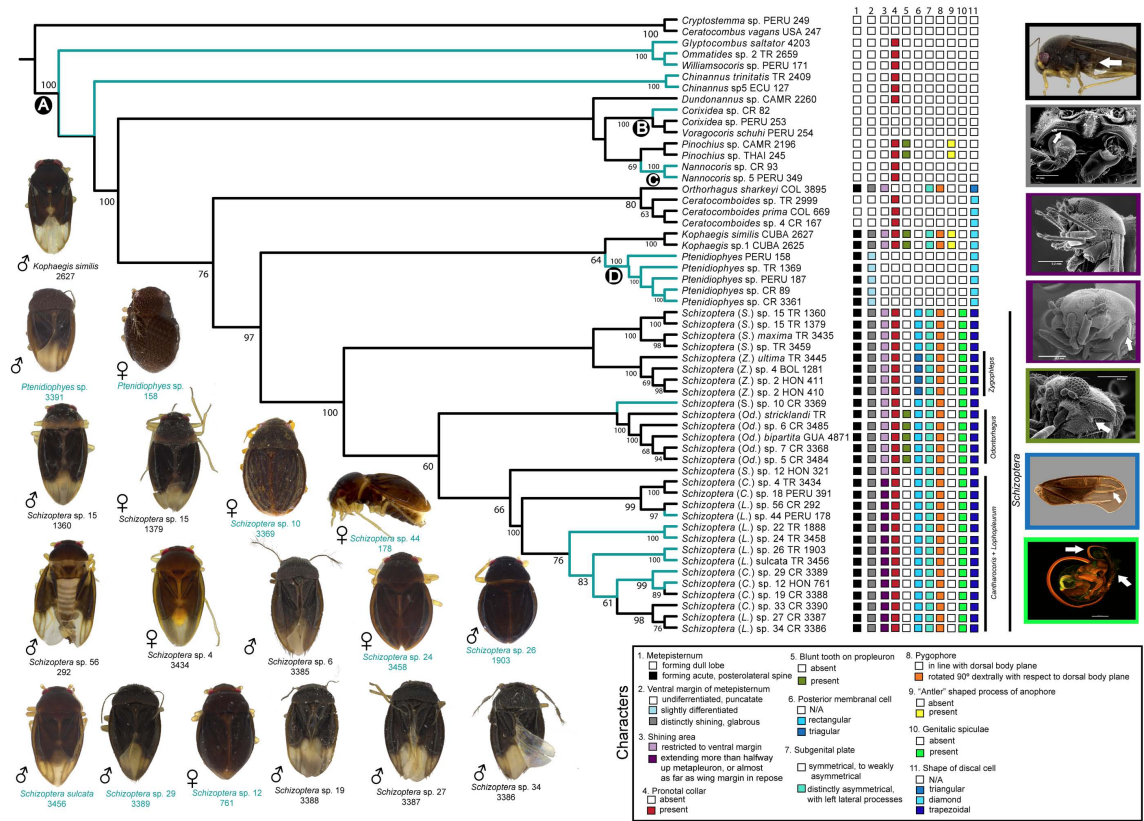


Figure 1.3: Ancestral state reconstruction of female-specific elytra (black branches: macropterous; blue branches: elytrous) and summary of the phylogenetic distribution of 11 morphological characters historically used a diagnostic feature of *Schizoptera* and its subgenera (see supplements for ancestral state reconstructions of individual characters) on the best tree derived from the maximum likelihood analysis. Diagnostic features are shown as colored boxes to the left of the tree, accompanied by thumbnails to illustrate different states (full set of characters and states in Figure 4). Numbers below branches represent bootstrap values (>60%).


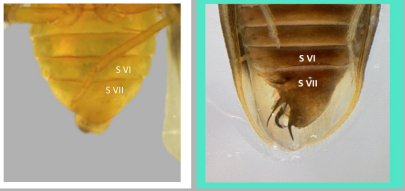
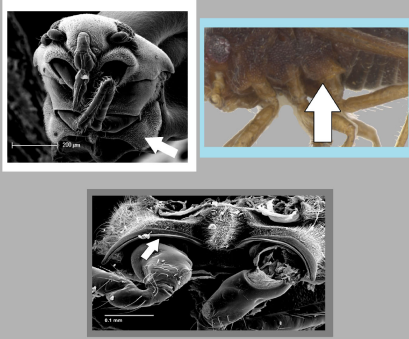
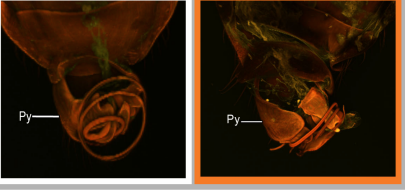
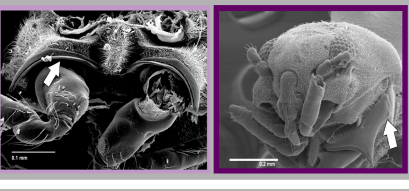
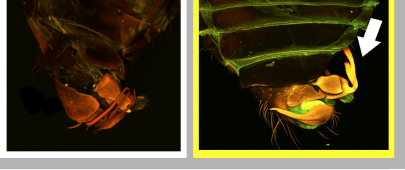

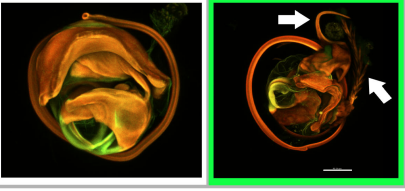


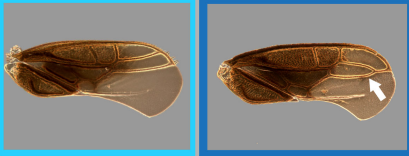
Character	States	Character	States
1. Metasternum <input type="checkbox"/> forming dull lobe <input checked="" type="checkbox"/> forming acute, posterolateral spine		7. Subgenital Plate <input type="checkbox"/> symmetrical, to weakly asymmetrical <input checked="" type="checkbox"/> distinctly asymmetrical, with left lateral processes	
2. Cuticle surrounding scent gland groove <input type="checkbox"/> undifferentiated, punctate <input checked="" type="checkbox"/> slightly differentiated <input type="checkbox"/> distinctly shining, glabrous		8. Pygophore <input type="checkbox"/> in line with dorsal body plane <input checked="" type="checkbox"/> rotated 90° dextrally with respect to dorsal body plane	
3. Shining area <input type="checkbox"/> restricted to ventral margin <input checked="" type="checkbox"/> extending beyond midline of metapleuron, or almost as far as wing margin in repose		9. "Antler" shaped process of anophore <input type="checkbox"/> absent <input checked="" type="checkbox"/> present	
4. Pronotal collar <input type="checkbox"/> absent <input checked="" type="checkbox"/> present		10. Genital spiculae <input type="checkbox"/> absent <input checked="" type="checkbox"/> present	
5. Blunt tooth on propleuron <input type="checkbox"/> absent <input checked="" type="checkbox"/> present		11. Discal cell <input checked="" type="checkbox"/> triangular <input type="checkbox"/> diamond <input type="checkbox"/> trapezoidal	
6. Posterior membranal cell <input checked="" type="checkbox"/> rectangular <input type="checkbox"/> triangular			

Figure 1.4: Documentation of characters and character states used in the optimization of the 11 diagnostic morphological characters shown in Figure 3. Colored borders around images correspond to the character states.

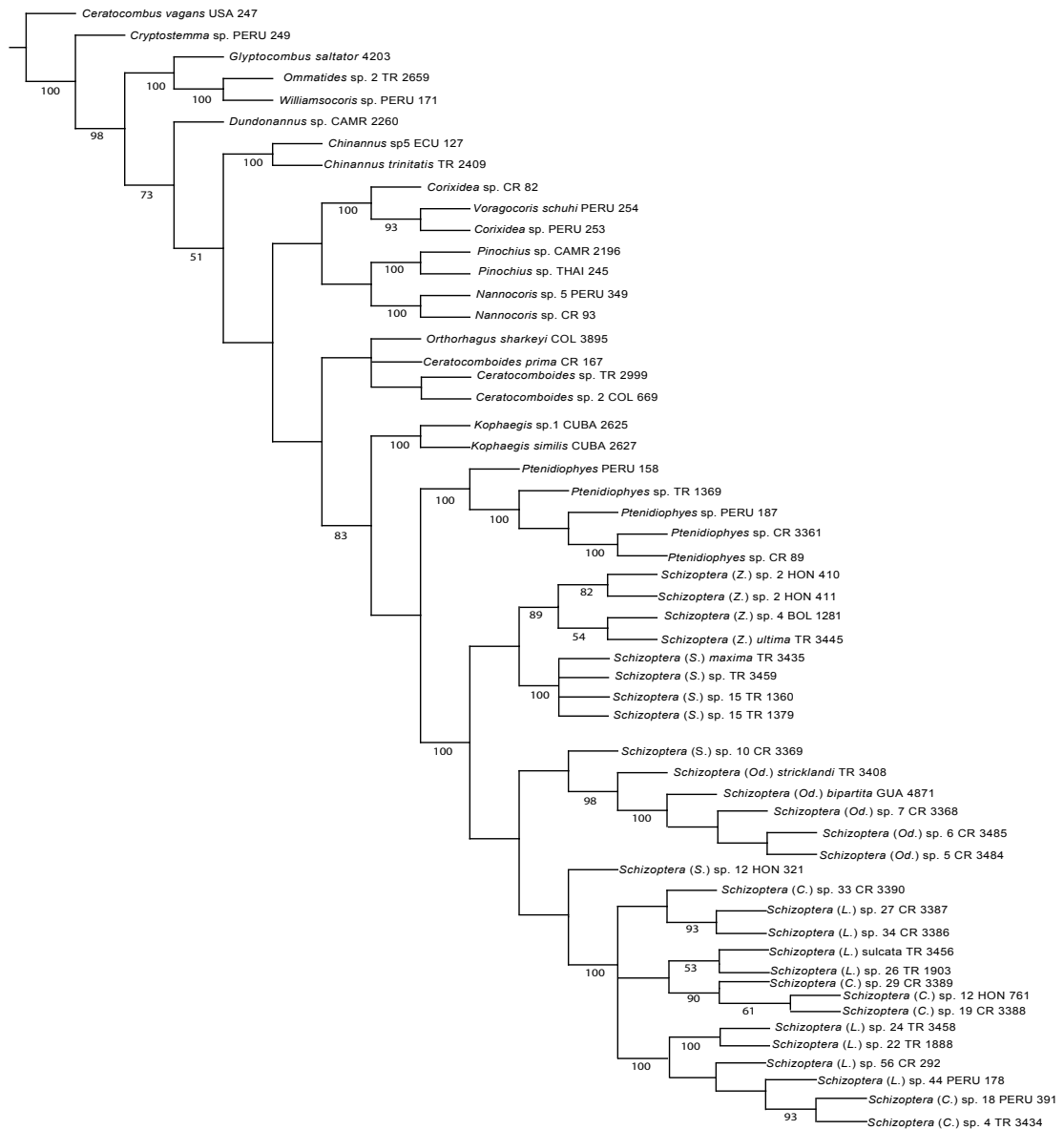
Table 1.1: Classification of sampled specimens with ED, USI and GenBank accession numbers for vouchers sequenced in this study and numbers for sequences obtained from GenBank.

Family	Taxon name in analysis	USI	28S D2 rDNA	28S D3-D5 rDNA	18S rDNA	COI
Ceratocombidae	<i>Ceratocombus vagans</i> USA 247	UCR_ENT 00057521	KF781242	–	KF781210	N/A
Dipsocoridae	<i>Cryptostemma</i> sp. PERU 249	UCR_ENT 00057528	KF781247	–	KF781211	N/A
Schizopteridae	<i>Ceratocomboides</i> sp. 167 CR	UCR_ENT 00078258	TBA	KU315263	N/A	N/A
	<i>Ceratocomboides</i> sp. 2 669 COL	UCR_ENT 00078075	N/A	KU315271	N/A	N/A
	<i>Ceratocomboides</i> sp. TR 2999	UCR_ENT 00093181	TBA	KU315294	KU315247	N/A
	<i>Chinannus trinitatis</i> TR 2904	UCR_ENT 00077712	KT224607	KT272746	N/A	N/A
	<i>Chinannus translucidus</i> ECU 127	UCR_ENT 00078169	KT272746	KT272723	N/A	N/A
	<i>Corixidea</i> sp. CR 82	UCR_ENT 00004790	KF781245	–	KF781209	N/A
	<i>Corixidea</i> sp. PERU 253	UCR_ENT 00057532	KF781246	–	N/A	N/A
	<i>Dundonannus</i> sp. CAMR 2260	UCR_ENT 00077099	TBA	KU315297	N/A	N/A
	<i>Glyptocombus saltator</i> 4203	UCR_ENT 00094273	TBA	KU315295	N/A	N/A
	<i>Kophaegis</i> sp. 1 CUBA 2625	UCR_ENT00088105	TBA	KU315268	KU315244	N/A
	<i>Kophaegis similis</i> CUBA 2627	UCR_ENT 00088107	TBA	KU315269	KU315245	KU315304
	<i>Nannocoris</i> sp. CR 93	UCR_ENT 00004800	KF781246	–	N/A	N/A
	<i>Nannocoris</i> sp.5 PERU 349	UCR_ENT 00077899	TBA	KU315299	N/A	N/A
	<i>Ommatides</i> sp. 2 TR 2659	UCR_ENT 00088130	TBA	KU315296	KU315259	N/A
	<i>Orthorhagus sharkeyi</i> COL 3895	UCR_ENT 00119010	N/A	KU315289	N/A	N/A
	<i>Pinochius</i> sp. CAMR 2196	UCR_ENT 00087540	TBA	KU315298	N/A	N/A
	<i>Pinochius</i> sp. THAI 245	UCR_ENT 00057526	KF781257	–	KF781222	N/A
	<i>Ptenidiophyes</i> sp. CR 89	UCR_ENT 00004805	KF781258	TBA	N/A	N/A
	<i>Ptenidiophyes</i> sp. CR 3391	UCR_ENT 00014874	N/A	KU315281	KU315251	N/A
	<i>Ptenidiophyes</i> sp. PERU 158	UCR_ENT 00004803	KF781259	–	N/A	N/A
	<i>Ptenidiophyes</i> sp. PERU 187	UCR_ENT 00078163	TBA	KU315265	KU315242	N/A
	<i>Ptenidiophyes</i> sp. TR 1369	UCT_ENT 00086209	TBA	TBA	N/A	N/A
	<i>Schizoptera (Cantharocoris)</i> sp. 12 HON 761	UCR_ENT 00077824	TBA	N/A	KU315258	N/A
	<i>Schizoptera (Cantharocoris)</i> sp. 4 TR 3435	UCR_ENT 00100830	TBA	KU315283	N/A	N/A
	<i>Schizoptera (Cantharocoris)</i> sp. 18 PERU 391	UCR_ENT 00086043	TBA	KU315290	N/A	KU315301

	<i>Schizoptera (Cantharocoris)</i> sp. 19 CR 3388	UCR_ENT 00014861	TBA	KU315278	KU315249	KU315306
	<i>Schizoptera (Cantharocoris)</i> sp. 29 CR 3389	UCR_ENT 00014857	TBA	KU315279	KU315250	N/A
	<i>Schizoptera (Cantharocoris)</i> sp. 33 CR 3390	UCR_ENT 00014860	N/A	KU315280	N/A	KU315308
	<i>Schizoptera (Lophopleurum) sulcata</i> TR 3456	UCR_ENT 00100826	TBA	KU315286	KU315253	KU315302
	<i>Schizoptera (Lophopleurum)</i> sp. 22 TR 1888	UCR_ENT 00063158	TBA	KU315266	N/A	N/A
	<i>Schizoptera (Lophopleurum)</i> sp. 24 TR 3458	UCR_ENT 00100828	TBA	KU315287	KU315254	KU315307
	<i>Schizoptera (Lophopleurum)</i> sp. 26 TR 1903	UCR_ENT 00088681	N/A	KU315267	KU315243	N/A
	<i>Schizoptera (Lophopleurum)</i> sp. 27 CR 3387	UCR_ENT 00014880	TBA	KU315277	N/A	N/A
	<i>Schizoptera (Lophopleurum)</i> sp. 34 CR 3386	UCR_ENT 00014879	TBA	KU315276	KU315248	N/A
	<i>Schizoptera (Lophopleurum)</i> sp. 44 PERU 178	UCR_ENT 00078267	TBA	KU315264	KU315241	KU315311
	<i>Schizoptera (Lophopleurum)</i> sp. 56 CR 292	UCR_ENT 00087483	N/A	KU315270	KU315246	N/A
	<i>Schizoptera (Odontorhagus) bipartita</i> GUAT 4871	UCR_ENT 0009170?	TBA	KU315293	KU315257	KU315303
	<i>Schizoptera (Odontorhagus) stricklandi</i> TR 3408	UCR_ENT 00100780	TBA	KU315282	N/A	KU315305
	<i>Schizoptera (Odontorhagus)</i> sp. 5 CR 3484	UCR_ENT 00014845	TBA	KU315274	N/A	N/A
	<i>Schizoptera (Odontorhagus)</i> sp. 6 CR 3385	UCR_ENT 00014485	TBA	KU315275	N/A	N/A
	<i>Schizoptera (Odontorhagus)</i> sp. 7 CR 3368	UCR_ENT00014779	TBA	KU315272	N/A	KU315300
	<i>Schizoptera (Schizoptera) maxima</i> TR 3435	UCR_ENT 00100830	TBA	KU315284	TBA	N/A
	<i>Schizoptera (Schizoptera)</i> sp. 3459	UCR_ENT 00100829	TBA	KU315288	N/A	N/A
	<i>Schizoptera (Schizoptera)</i> sp.10 CR 3369	UCR_ENT 00014845	TBA	KU315273	N/A	N/A
	<i>Schizoptera (Schizoptera)</i> sp. 12 HON 321	UCR_ENT 00077043	TBA	TBA	TBA	N/A
	<i>Schizoptera (Schizoptera)</i> sp.15 TR 1360	UCR_ENT 00086191	N/A	KU315261	N/A	KU315309
	<i>Schizoptera (Schizoptera)</i> sp. 15 TR 1379	UCR_ENT 00086154	TBA	KU315262	N/A	N/A
	<i>Schizoptera (Zygophleps) ultima</i> TR 3445	UCR_ENT 00102132	TBA	KU315285	KU315252	KU315312
	<i>Schizoptera (Zygophleps)</i> sp. 2 HON 410	UCR_ENT 00086122	TBA	KU315291	KU315255	N/A
	<i>Schizoptera (Zygophleps)</i> sp. 3 HON 411	UCR_ENT 00086123	N/A	KU315292	KU315256	N/A
	<i>Schizoptera (Zygophleps)</i> sp. 4 BOL 1281	UCR_ENT 00086525	TBA	KU315260	KU315240	KU315310
	<i>Williamsocoris</i> sp. PERU 171	UCR_ENT 00057523	KF781264	N/A	KF781229	N/A

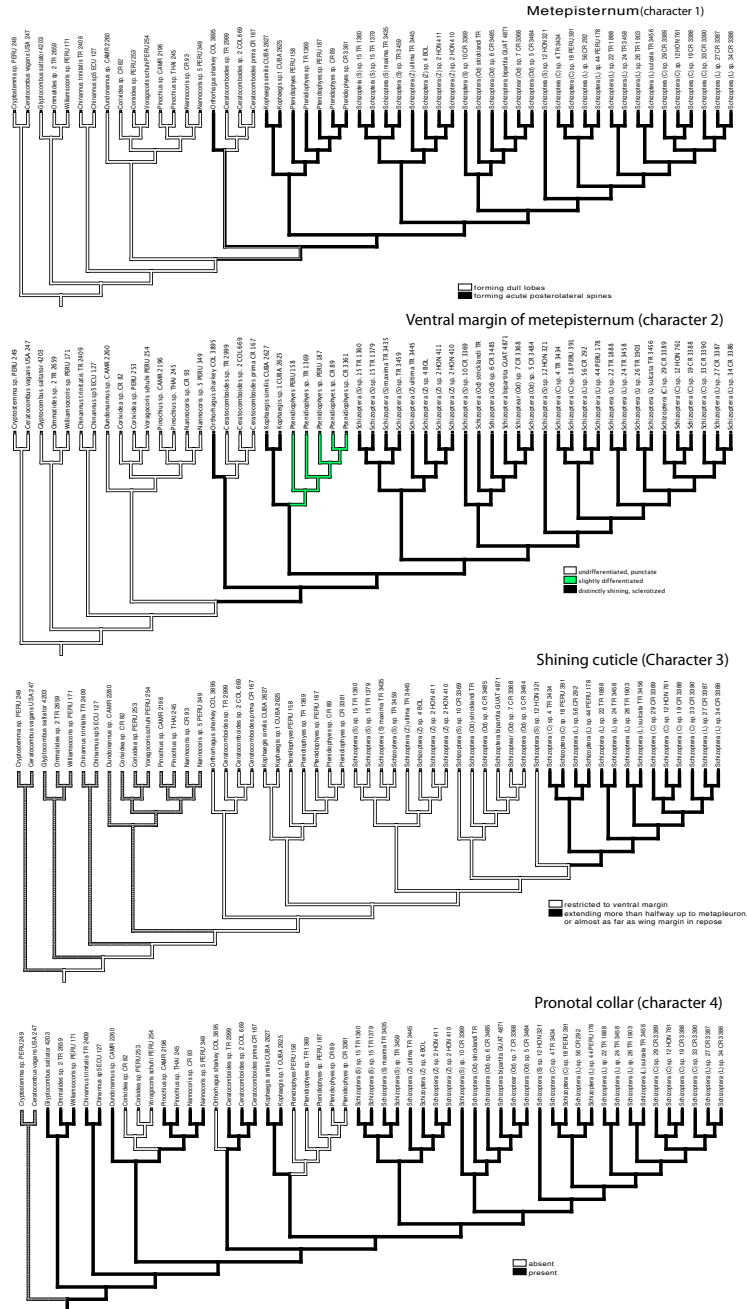
Table 1.2: Comparison of previous diagnoses presented for *Schizoptera* by McAtee and Malloch (1925) and Emsley (1969) and the updated diagnosis resulting from the present study represented in bold lettering.

Authors	Diagnoses
McAtee and Malloch 1925	<ul style="list-style-type: none"> • Metapleuron produced in the form of a prominent spine at inner posterior angle • First costal cell larger than second • Vein bounding apical margin of second costal cell joining costa almost at a right angle
Emsley 1969	<ul style="list-style-type: none"> • Metepisternum has posteroventral angle produced into a sharp, conspicuous spine • Prothorax with collar, except in subgenus <i>Odontorhagus</i> • Forewing with characteristic venation (square cell) • Pair of conjunctival appendages present
Present study	<ul style="list-style-type: none"> • Metepisternum has posteroventral angle produced into a sharp, conspicuous spine, with ventral border differentiated and shining, and sometimes extending to or beyond midline of metapleuron • Prothorax with pronotal collar • Discal cell of forewing trapezoidal • A pair of asymmetrical conjunctival appendages present in males

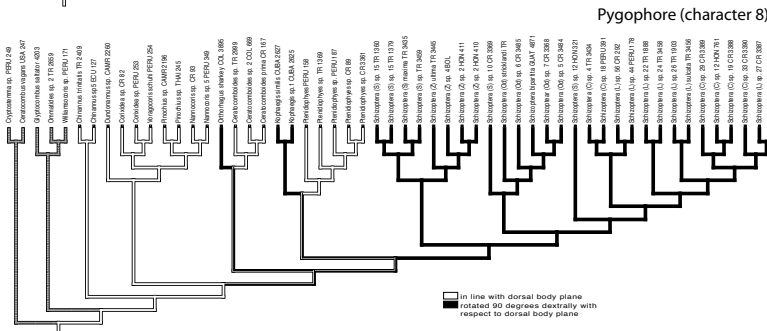
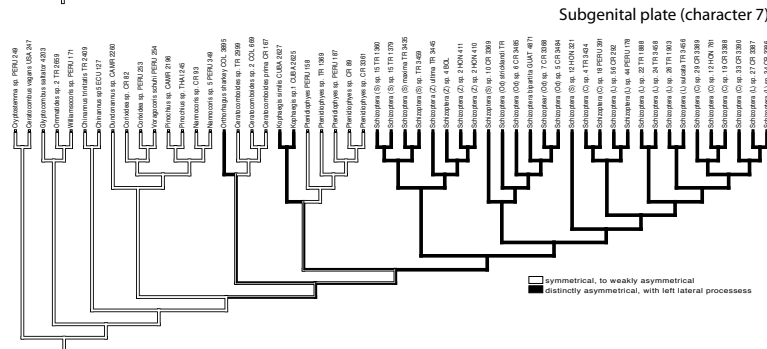
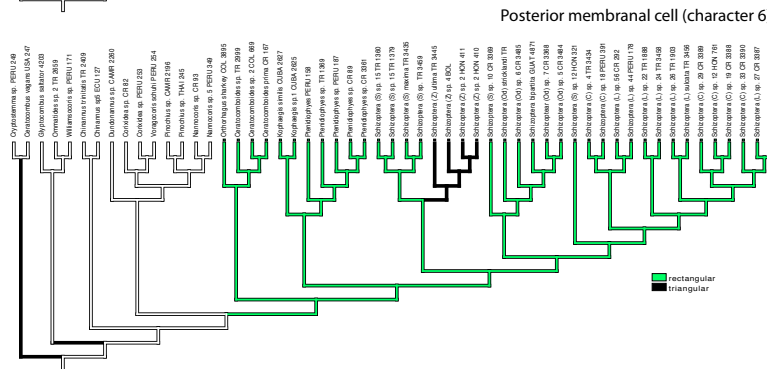
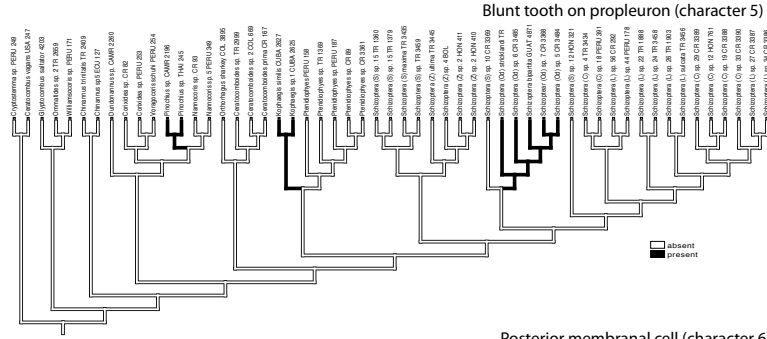


SM1: Strict consensus of the 14 shortest trees of the parsimony analysis of *Schizoptera* and related taxa (L=4182, Ci=53, Ri=62). Numbers below branches indicate jackknife values higher than 50%.

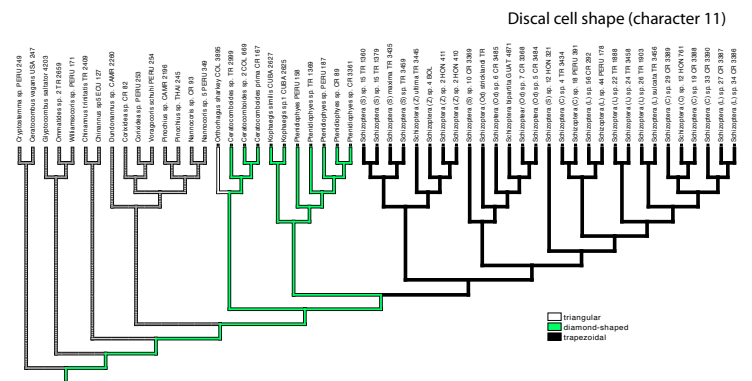
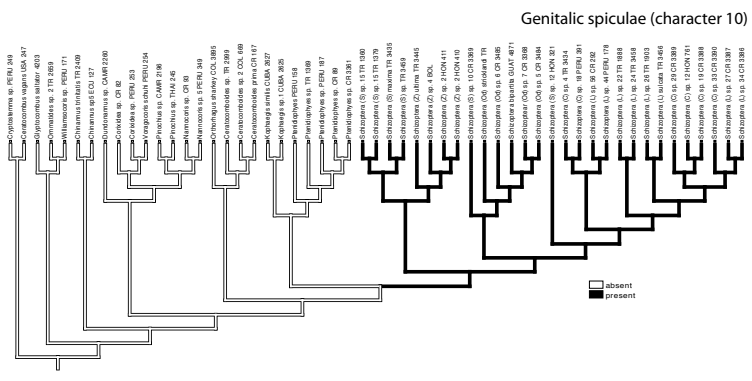
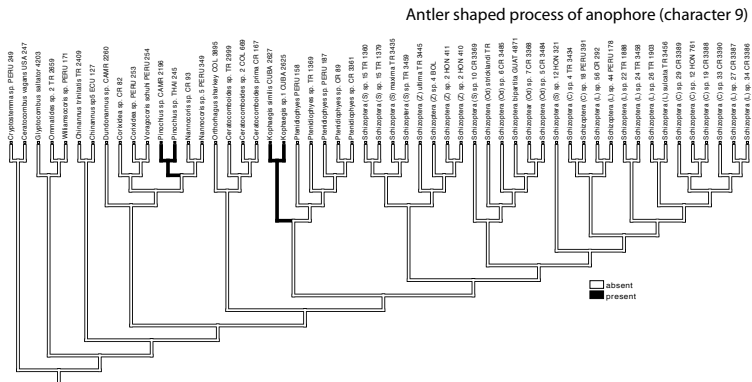
SM2: Individual ancestral state reconstruction using parsimony of characters 1-11 optimized on the ML tree.



SM2: Individual ancestral state reconstruction using parsimony of characters 1-11 optimized on the ML tree.



SM2: Individual ancestral state reconstruction using parsimony of characters 1-11 optimized on the ML tree.



Chapter 2: Small bugs, big changes: Taxonomic revision *Orthorhagus* McAtee and Malloch, 1925 (Heteroptera: Dipsocoromorpha)

Abstract

The Schizopteridae, the largest family of litter bugs (Heteroptera: Dipsocoromorpha), comprises 53 genera of primarily tropical, tiny true bugs. The largest genus *Schizoptera* Fieber, 1860 comprises 64 described species and six subgenera with primarily tropical and subtropical distributions across the New World. *Schizoptera* species are morphologically diverse with extreme asymmetry of male genitalia and sexually dimorphic wing in females of some species. Subgeneric concepts of *Schizoptera* are yet to be evaluated in a phylogenetic context. The subgenus *Orthorhagus* McAtee and Malloch, 1925, was described from a single specimen as part of *Schizoptera* based on similarities of wing venation and other structures. The absence of a pronotal collar was used to separate *Orthorhagus* from other subgenera within *Schizoptera*, but morphological and molecular data show that the differences between *Orthorhagus* species and those of *Schizoptera* extend beyond the lack of a pronotal collar. In this study we elevate the subgenus *Orthorhagus* to generic rank and describe five new species in this genus. We provide morphological documentation including digital habitus images, genitalic drawings, and confocal micrographs for all species. Distribution maps and a key to the species of *Orthorhagus*, stat. nov. are also presented.

Introduction

The infraorder Dipsocoromorpha (Hemiptera: Heteroptera), or litter bugs, is considered the smallest and least known group of true bugs (Weirauch and Štys 2014). Comprising

5 distinct families and ~350 described species, litter bugs occur worldwide with greatest species diversity in the tropics (Weirauch and Štys 2014). Specimens are extremely small (~1-2 mm) and are commonly found in forest leaf litter or similar microhabitats (i.e. decaying logs, underneath bark, or in soil [Linnavuori, 1974, Hill 1990, Wygodzinsky 1951]). Current unpublished data gathered by the NSF Litter Bugs ARTS project shows that an array of passive and active collecting methods, ranging from vegetation beating and litter sifting to canopy fogging and suction traps, are successful for the acquisition of these minute bugs. Consequently, specimens often appear in bulk and residue samples as non-target organisms and are left neglected for years or even decades before proper curation can be employed. Thus, the current number of described species is a severe underrepresentation of the true diversity of the group.

The largest family, the Schizopteridae, comprises 56 genera and over 250 species (Linnavuori 1974, Makhan 2013, Weirauch and Štys 2014, Hill 2015) and is primarily tropical, although some species occur in temperate regions (Hill 1984, 2014). Schizopteridae is divided into three subfamilies, the Schizopterinae, Ogeriinae, and Hypselosomatinae. Representatives of this family showcase remarkable morphologies, with males often displaying extreme genitalic asymmetry, modifications of the pregenital abdomen, and organs of unknown function (i.e. the modified M-vein of the forewing in species of *Chinannus* Wygodzinsky [*Knyshov et al*, submitted]). Despite their morphological allure, Schizopteridae have not received much taxonomic attention for almost five decades. Notable historical works include those of McAtee and Malloch (1925) and Emsley (1969), which augmented previously known records and described new species in the largest schizopterine genus, *Schizoptera* Fieber, 1860.

Currently, *Schizoptera* comprises 64 extant species (Emsley 1969) and two species known from fossils (Poinar 2014). Fieber described the genus from a single specimen from Venezuela in 1860, and subsequent work by Reuter and Poppius increased the species count from one to six around the turn of the 19th century (Fieber 1860, Reuter 1882, 1891, Poppius 1910, Emsley 1969). McAtee and Malloch's (1925) taxonomic revision largely focused on *Schizoptera* specimens from Central America and the Caribbean collected by Schwarz and Barber in the early 1900s. In their revision, 27 new species were described and subgeneric concepts introduced, dividing the genus into seven subgenera. In the mid-1900s, China described a single species from Trinidad (China, 1946) and Wygodzinsky two new species from Argentina (Wygodzinsky 1952). Following the surge of taxonomic activity focusing on this genus during the first half of the century, almost two decades elapsed before Emsley presented what is arguably the most comprehensive taxonomic treatment of Schizopteridae to date (Emsley 1969). In his monograph, Emsley described 28 new species of *Schizoptera* and also synonymized two subgenera previously described by McAtee and Malloch (Emsley 1969).

Schizoptera species have a wide geographic distribution, ranging from Northern Argentina to the Southern United States. Specimens are extremely abundant in bulk samples and collections; current records from the Heteropteran Systematics Lab at the University of California, Riverside (UCR) indicate that over 2000 ethanol and dry *Schizoptera* specimens have been assembled from multiple collections. Species of *Schizoptera* show striking morphological variation that is useful for species diagnoses: males in all species possess a modified asymmetrical subgenital plate and intricate, asymmetrical spiculae on the aedeagus (Emsley 1969). Extreme sexual dimorphism is expressed in some species, with females being macropterous, brachypterous, or

elytrous and males always being macropterous. Given its rich taxonomic history, wide distribution, abundance in samples and overall morphological attractiveness, *Schizoptera* is likely the best-documented schizopterid genus in terms of species diversity and morphology.

The current subgeneric concepts within *Schizoptera* have recently been evaluated in a phylogenetic context (Leon and Weirauch, in prep). Among the six valid subgenera is the monotypic subgenus *Orthorhagus* McAtee and Malloch, 1925. *Schizoptera (Orthorhagus) plana* McAtee and Malloch, 1925 was described from a single specimen from the highlands of northern Guatemala. The primary morphological difference used by the authors to distinguish *S. plana* from other *Schizoptera* species and subgenera was the absence of a pronotal collar. New morphological evidence suggests that there are a number of additional characters that separate *Orthorhagus* from *Schizoptera*. In addition, recent molecular phylogenetic analyses of *Schizoptera* and related taxa (Leon and Weirauch, in prep) demonstrate that *Orthorhagus* does not fall within the *Schizoptera sensu stricto* clade, prompting the elevation of the subgenus *Orthorhagus*, stat. nov. to genus level in this publication.

Unlike *Schizoptera*, specimens of *Orthorhagus* are scarce in collections: e.g., out of 1215 schizopterids removed from fogging residue samples at the United States Museum of Natural History, only a single *Orthorhagus* specimen was retrieved. Only nine specimens are now recorded in the Arthropod Easy Capture database (<http://research.amnh.org/pbi/databases/locality_database.html>). Specimens were collected from different microhabitats including decaying palm logs, underneath bark, and in subcortical debris. Several other rarely collected groups of Dipsocoromorpha, such as *Peloridinannus* Wygodzinsky, *Ogeria* Distant, and *Trichotonannus* Reuter, have

been collected from, or are associated with similar microhabitats (Wygodzinsky 1951, Linnavouri 1974, Hill 1990, Weirauch and Frankenberg 2015). Focused collecting efforts on these and other specialized microhabitats could dramatically increase species numbers in groups like *Orthorhagus* and eventually allow for a meaningful assessment of their biodiversity.

In this study, we highlight the tremendous morphological diversity within an extremely small subset of schizopterids and elevate the subgenus *Orthorhagus* to genus. With only nine specimens examined, we here increase the number of described species to six. We provide morphological documentation including digital habitus images, genitalic drawings and confocal micrographs for all species. Distribution maps and a key to the species of *Orthorhagus* are also presented.

Material & Methods

Material

We examined five dry, point mounted and four EtOH specimens deposited as seven microscopic slide-mounts and two point-mounted specimens in the following institutions:

FMNH	Field Museum of Natural History, Chicago, Illinois
IAvH	Instituto Alexander von Humboldt, Bogotá, Colombia
INBio	Instituto Nacional de Biodiversidad, San José, Costa Rica
TAMU	Texas A&M University, College Station, USA
USNM	National Museum of Natural History, USA

Several hundred specimens of *Schizoptera* from various institutions have been examined over the past year in order to compare morphological features between *Schizoptera* and *Orthorhagus* for this study. Three specimens of *Schizoptera*

representing three subgenera were also imaged and dissected (UCR_ENT 00077905, 00081350, 00086113) and five additional specimens were imaged to document diagnostic differences between *Schizoptera* and *Orthorhagus* (UCR_ENT 00086123, 00093446, 00093460, 00093580, 00093644).

Methods

Databasing

A matrix-code label with specimen identifier, consisting of a unique combination of prefix and eight-digit number was attached to each specimen, and databased using the PBI instance of the Arthropod Easy Capture database served from the AMNH <<https://research.amnh.org/pbi/locality/>>. Specimens for which geographic coordinates were absent from collecting labels were georeferenced using Google Earth.

Imaging

Dorsal, ventral and lateral habitus images were taken using a Leica DFC 450 C Microsystems system with a Planapo 1.0x objective. Images were stacked using the Leica LAS software or Zerene stacker. Wing photos were acquired on a Zeiss Axioskop 2 compound microscope using GT-vision Archimed v5.4.1 imaging software and images were then stacked using Combine ZP. Confocal images of genitalia were taken on a Leica SP5 Inverted confocal microscope, using 488nm and 543nm lasers and collected by detectors in diapasons of 500-535nm (green in images) and 555-700nm (red in images) at the Institute for Integrative Genome Biology core facility <<http://genomics.ucr.edu/>>.

Dissections

To study genitalia, the male abdomen were separated from the thorax and cleared by immersion into hot 10% KOH. Line drawings were made using a Nikon Eclipse 80i compound microscope with a camera lucida, and edited using Adobe Photoshop CS4 for shading structures.

Species descriptions

A matrix consisting of 43 morphological characters, several of them cloned and modified from other ongoing taxonomic projects on Schizopteridae, was created and coded in mx <<http://mx.phenomix.org>>. Species descriptions were exported using the “export character description” option under the output tab and manually edited. Several characters of the head and thorax were manually added after descriptions had been exported from mx.

Measurements

Specimen total length measurements were taken digitally from habitus images, using the measure function in Adobe Photoshop based on the scale derived from the Leica LAS software stacked image.

Maps

Maps were created using SimpleMappr (<<http://simplemappr.net>>) by importing coordinates for individual species from the PBI database.

Slide mounting

Dissected specimens were permanently slide-mounted following protocols outlined in (Noyes 1982; Platner *et al* 1999).

Terminology

Terminology of genitalic structures follows Štys (1970) and Emsley (1969) and wing venation is treated *sensu* Redei (2008).

Abbreviations

1An – first anal vein; 2An – second anal vein; acc – anterior costal cell; aed s – aedeagal sclerite; ano – anophore; ap – anophoric process; at – anal tube; bp – basal plates; C– costa; Cu – cubitus; dc – discal cell; lp – left paramere; M – media; M1– first branch of media; M2 – second branch of media; pcc – posterior costal cell; py – pygophore; R – radius; rp – right paramere; Sc – subcosta; stVII – subgenital plate consisting of sternite VII; sX – segment X; sIX – segment IX; tc – trapezoidal cell; tVII – tergite VII; tVIII – tergite VIII; v – vesica.

Taxonomy

Orthorhagus McAtee and Malloch, 1925, stat. nov.

Schizoptera (*Orthorhagus*) McAtee and Malloch, 1925

(Figs 2.1-2.5)

Type Species: *Schizoptera* (*Orthorhagus*) *plana* McAtee and Malloch, 1925, by original designation

Diagnosis: Superficially similar to some species of *Schizoptera* in wing venation pattern, large anterior spine of the metapleuron (Fig 2.1 arrow d), and the narrow shining border

of the posterior margin of metasternum, but differs from this genus and other Schizopteridae by the following characters: relatively large body size (1.04-1.4mm); large, conically truncate eyes (Fig 2.5e, white arrow), overlapping the lateral margins of the pronotum; lack of pronotal collar; pronotum with posterior margin undulate except in *O. magnus*, n. sp. (Fig 2.1, arrows b and c); distinct, long, golden setae on head, pronotum and wing veins (Figs 2.1, 2.5b white arrow); subgenital plate with “lobe and blade” processes (Fig 2.2a.1-2.2f.1); tergite VIII often membranous with sclerotized lobes; pygophore rotated 90° clockwise; right paramere Y-shaped and always much larger than left, with short attachment base, short process and a long “leg”, typically holstered between the processes of subgenital plate (Fig 2.2); vesica short and tapering, with a robust, spiked base and a narrow tip (Figs 2.2, 2.3d.1, 2.3f.1). In females, segment VIII is modified with lateral sclerotized lobes, which nearly envelop segment IX (Fig 2.2g).

Redescription: *Male*: Body relatively large, length ranging from 1.05-1.4 mm; body shape oval, broadly oval or almost parallel sided; habitus macropterous. **COLORATION:** General color brown to black with some lighter markings; head, thorax dark brown; pronotum, except in *O. sharkeyi*, with narrow or broad pale band on posterior margin; scutellum uniformly brown; legs light brown to yellow; forewing anteriorly brown to dark brown, posteriorly cream-colored, with fuscous patch; Sc + C either concolorous with remainder of hemelytron (Fig 2.1 *O. gracilis*) or distinctly lighter (Fig 2.1 *O. sharkeyi*); pigmentation of corium slightly extending into wing membrane; abdomen brown. **SURFACE and VESTITURE:** Head and thorax with dense microtrichia; head, pronotum, and wing veins covered with distinct, long, golden setae (Figs 2.1, 2.5b, white arrow);

head with three pairs of long and stout cephalic setae; clypeus and labium without microtrichia and with long stout setae; numerous circular muscle scars on head; subgenital plate densely covered with long setae (Fig 2.3e.1). **STRUCTURE:** HEAD: flat to distinctly inflated in lateral view (Fig 2.1, arrows a and c); vertex straight or distinctly rounded in dorsal view; eyes large, conically truncate (Fig 2.5e, white arrow) with ventral margin straight or notched; width of eyes about 2/3 or as wide as synthlipsis, overlapping lateral margins of pronotum (Fig 2.1, arrow e); ocelli relatively large; labium 3-segmented. THORAX: pronotal collar absent (Fig 2.5e); pronotum trapezoidal, slightly to distinctly undulated (Fig 2.1 arrow b), or uniformly smooth, sometimes with a medial longitudinal depression; posterior margin of pronotum straight or with medial notch; scutellum triangular; lateral margins of scutellum crenulated; tip of scutellum round or oblong with or without medial notch; hemelytron distinctly punctate; Sc+C explanate; posterior costal cell (R-M-M1) trapezoidal, parallel sided or pentagonal (Fig 2.5c); apex of wing membranous with cell-like sculpture; thoracic pleura and sterna distinctly punctate; metapleuron sculpted into large anterior and small posterior spines in lateral view (Fig 2.1 arrow d); metasternum punctate with differentiated, shining posterior border; metasternal spine robust, slightly elongate, tapering, with pointed tip; hind coxa with well-developed adhesive pad; tarsal formula 2-2-3; pretarsus with setiform parempodia; arolia absent; ABDOMEN: with five visible sternites corresponding to segments II-VII; sternite VII modified into asymmetrical subgenital plate, with lateral lobe-shaped process oriented left and a caudal blade-like process, forming holster for right paramere (Fig 2.2e.1, Fig 2.3e.1); tergites of pregenital abdomen membranous except for tergite VII (tVII in subsequent descriptions) and sometimes tergite VIII (tVIII in subsequent descriptions); tVII rectangular or slightly asymmetrical; tVIII rectangular,

rectangular with a single lobe on right side, or partially membranous with a longitudinal fold and lobed process on right side; length of tVIII about 1/2 to 3/4 length of tVII.

GENITALIA: pygophore (py subsequently) rotated 90° to the right; right paramere (rp subsequently) Y-shaped with short base, short process and elongate process (Fig 2.3f); elongate process of rp with various modifications of apex (Fig 2.2); leg of rp folding over py, onto subgenital plate (Fig 2.2c, 2.2c.1, 2.2e.1); left paramere smaller than right; vesica tapering, with robust base, single peak (Fig 3d.1) and narrow tip; with or without aedeagal sclerite; anophore well sclerotized and with lobed process in most species; segment X (sX subsequently) distally forming membranous tube; segment XI (sXI subsequently) uniformly membranous or distinctly sclerotized.

Female: slightly larger than male; general habitus as in male. GENITALIA: segment VIII with lateral sclerotized lobes partially enveloping segment IX (Fig 2.2g); ovipositor vestigial.

Distribution: The distribution of *Orthorhagus* species is Neotropical, ranging from northern Belize and northern Guatemala to northeastern Ecuador (Fig 2.4). There are no current records of *Orthorhagus* species from Honduras, El Salvador or Nicaragua but better sampling in these countries could complement this range.

Etymology: the original authors did not give an etymology for the name, and it is unclear what an appropriate translation might be; however, all of the potential Code Articles which might apply to the name (Art. 30.1.1, 30.1.4.5, or 30.2.4) would lead to the gender being masculine, and it is hereby accepted as such.

Key to the species of *Orthorhagus*:

1. Pronotum with a narrow or broad pale band on distal margin.....2
 - Pronotum uniformly brown without pale band on distal margin.....*O. sharkeyi*, n. sp.
2. Head slightly to distinctly inflated, convex in lateral view (Fig 2.1, arrow a) and rounded in dorsal view.....3
 - Head flat, straight in lateral and dorsal view (Fig 2.1, arrow c).....*O. magnus*, n. sp.
3. Pale band on pronotum broad, head distinctly inflated, convex in lateral view (Fig 2.1, arrow a) greatly surpassing frontal and ventral margins of eye, body elongate, and coloration dark brown.....*O. gracilis*, n. sp.
 - Pale band on pronotum narrow or broad, head slightly inflated, barely passing frontal margin of eye, or in line with frontal margin of eye, body ovoid and small.....4
4. Pronotum slightly undulated with medial longitudinal depression, pale band on pronotum narrow, fuscous patch covering less than half of wing membrane, pigmentation of corium extending to all proximal regions of wing membrane.....*O. planus* (McAtee and Malloch)
 - Pronotum distinctly undulated with deep longitudinal depression, fuscous patch covering more than half of wing membrane, pigmentation of corium extending to proximal regions of cubital and anal regions of wing membrane only.....5

5. Pronotum with narrow pale band in males and broad band in females (Fig 2.1), in males tVIII membranous with deep longitudinal fold and two lobes, apex of long process of right paramere with ventral keel.....*O. subcorticalis*, n. sp.
- Pronotum with narrow pale band, tVIII sclerotized with longitudinal fold and single lobe, apex of long process of right paramere hatchet shaped (Fig 2.3b.1).....*O. lewisi*, n. sp.

Orthorhagus gracilis, n. sp.

(Figs 2.1-2.5)

Diagnosis: Distinguished amongst species of *Orthorhagus* by the elongate body shape, relatively large body size, the distinctly inflated head (Fig 2.1 arrow a), the falcate process of subgenital plate, the presence of an elongate, spatulate aedaegal sclerite (Figs 2.2a, 2.3a.1), the t-shaped apex of the long process of the right paramere, and the pawn-shaped (conical, with rounded apex) spine of the vesica.

Holotype: **ECUADOR: Los Ríos:** Río Palenque, 47 km S. Sto. Domingo, 0.92667°S 79.40833°W, 220 m, 26 Aug 1997, A. R. Gillogly, 1 ♂ (UCR_ENT 00093557) (TAMU) microscopic slide-mount.

Description: *Male*: length 1.37 mm; body elongate oval almost parallel sided.

COLORATION: general color dark brown to black; pronotum with broad pale band on distal margin; scutellum uniformly brown; legs light brown to yellow; fuscous patch covering less than 1/2 of wing membrane; Sc + C distinctly lighter than remainder of hemelytron; pigmentation of corium slightly extending into posterior membranal cell and

anal region of wing membrane. **SURFACE and VESTITURE:** as in generic description. **STRUCTURE:** HEAD: distinctly inflated in lateral view (Fig 2.1, arrow A); vertex flat or distinctly inflated in dorsal view; eyes as in generic description with straight ventral margin; width of eyes about 2/3 of synthlipsis. THORAX: as in generic description; pronotum slightly undulated without longitudinal medial depression; posterior margin of pronotum straight; scutellum as in generic description with oblong tip with medial notch; hemelytron as in generic description; posterior costal cell parallel sided. ABDOMEN: as in generic description; process of subgenital plate falcate, with wide base and tapering tip (Fig 2.2a.1); tVII rectangular; tVIII sclerotized, rectangular with single lobe on right side (Figs 2.2a, 3a); length of tVIII about 1/2 of tVII. GENITALIA: py as in generic description; rp as in generic description with apex of long process T-shaped (Figs 2.2a, 2.2a.1); vesica as in generic description, with single pawn-shaped peak (Fig 2.3a, grey arrow); aedeagal sclerite spatulate (Figs 2.2a, 2.3a.1, white arrow); anophore forming symmetrical tube-like sclerite with prominent dorsal wall; sXI lightly sclerotized; process of anophore lobed.

Female: Unknown.

Distribution: Known from a single locality in the Los Ríos province in Ecuador (Fig 2.3).

Etymology: Named for the slender, elongate shape of the body after the Latin “gracilis” meaning slender. The gender is masculine.

Orthorhagus lewisi, n. sp.

(Figs 2.1-2.5)

Diagnosis: Distinguished among species of *Orthorhagus* by the distinctly undulated pronotum (Fig 2.1 arrow b) with two lateral depressions on the posterior margin and a medial longitudinal depression, parallel sided posterior costal cell, fuscous patch covering more than half of wing membrane, blade-like process of subgenital plate axe-head shaped (Fig 2.2b.1), tVII with a longitudinal fold and single lobe (Fig 2.3b), apex of long process of right paramere hatchet shaped (Fig 2.3b.1), and the conical peak of the vesica.

Holotype: **COSTA RICA: Guanacaste:** Estación Pitilla, 9 km S Santa Cecilia, Parque Nacional Guanacaste, 10.95382°N 85.48493°W, 700 m, Mar 1994, C. Moraga, 1 ♂ (UCR_ENT 00014870) (INBIO) microscopic slide-mount.

Description: *Male*: length 1.33 mm; body ovoid. **COLORATION:** general color brown; pronotum with narrow pale band on distal margin; scutellum uniformly brown; legs light brown to yellow; fuscous patch covering more than 1/2 of wing membrane; Sc + C concolorous with remainder of hemelytron; pigmentation of corium slightly extending into posterior membranal cell and anal region of wing membrane. **SURFACE and VESTITURE:** as in generic description. **STRUCTURE:** HEAD: slightly inflated in lateral view; vertex slightly rounded in dorsal view; eyes as in generic description with notched ventral margin; width of eyes about 2/3 as synthlipsis. THORAX: as in generic description; pronotum distinctly undulated with longitudinal medial depression; posterior margin of pronotum notched; scutellum as in generic description with oblong tip with

medial notch; hemelytron as in generic description; posterior costal cell parallel sided.

ABDOMEN: as in generic description; process of subgenital plate axe-head shaped (Fig 2b.1); tVII rectangular with asymmetrical right side; tVIII sclerotized, rectangular with longitudinal fold and single lobe on right side (Figs 2.2b); length of tVIII about 2/3 of tVII.

GENITALIA: py as in generic description; rp as in generic description with apex of long process hatchet-shaped (Figs 2.2b, 2.2b.1, 2.3b.1, white arrow); vesica as in generic description, with conical peak (Figs 2.2b, 2.3b.1); aedeagal sclerite absent; anophore symmetrical tube-like sclerite with prominent dorsal wall; sXI lightly sclerotized; process of anophore lobed.

Female: Unknown.

Distribution: Known from a single locality in the state of Guanacaste in northern Costa Rica (Fig 2.4).

Etymology: Named after Jim Lewis for providing this single specimen from Costa Rica.

Orthorhagus magnus, n. sp.

(Figs 2.1-2.5)

Diagnosis: Distinguished among species of *Orthorhagus* by the relatively large, broad body, the flat head (Fig 2.1 arrow c), the smooth pronotum without posterior notch, tVIII with sigmoid rim on left side (Fig 2.3c.1), subulate process of subgenital plate, the fluted apex of the long process of the right paramere, the flattened triangular peak of the vesica, and the plate-like anophore (Fig 2.3c.1 white arrow).

Holotype: **ECUADOR: Orellana:** Tiputini Biodiversity Station Co.: nr Yasuni National Park; Erwin transect T/1 Sta 1, 0.63194°S 76.14417°W, 220 m, 26 Oct 1998, canopy fogging, T. L. Erwin *et al.* 1 ♂ (UCR_ENT 00028671) (USNM) microscopic slide-mount.

Description: *Male*: length 1.39 mm; body broadly ovoid. **COLORATION**: general color brown; pronotum with broad pale band on distal margin; scutellum uniformly brown; legs yellow; fuscous patch covering less than ½ of wing membrane; Sc + C lighter than remainder of hemelytron; pigmentation of corium slightly extending into posterior membranal cell and anal region of wing membrane. **SURFACE and VESTITURE**: as in generic description. **STRUCTURE**: HEAD: flat in lateral view (Fig 2.1, arrow c); vertex straight in dorsal view; eyes as in generic description with notched ventral margin; width of eyes about as wide as synthlipsis. THORAX: as in generic description; pronotum flat, without longitudinal medial depression; posterior margin of pronotum straight; scutellum as in generic description with oblong tip with medial notch; hemelytron as in generic description, posterior costal cell pentagonal. ABDOMEN: As in generic description; process of subgenital plate subulate, with very narrow base and tapering tip (Fig 2.2c.1); tVII rectangular; tVIII sclerotized, rectangular with single lobe on right side and sclerotized sigmoid rim on left side (Figs 2.2c. 2.3c, 2.3c.1); length of tVIII about 2/3 of tVII. GENITALIA: py as in generic description; rp as in generic description with apex of long process smooth and rounded, almost flute-like (Fig 2.2c.1); vesica as in generic description with single, triangular, flattened peak (Fig 2.3c.2, grey arrow); aedeagal sclerite absent; anophore consisting of symmetrical tube-like sclerite with prominent plate-like dorsal wall (Fig 3c.2, white arrow); sXI distally membranous; process of anophore lobed.

Female: Unknown.

Distribution: Known from a single locality in the Eastern Ecuadorian Amazon (Fig 2.4).

Etymology: Named for the robust, large body size, after Latin “magnus” meaning large.

The gender is masculine.

Orthorhagus planus, comb. nov.

(McAtee and Malloch 1925)

(= *Schizoptera (Orthorhagus) plana* McAtee and Malloch 1925)

(Figs 2.1-2.5)

Diagnosis: Distinguished among other *Orthorhagus* species by the relatively small body size (Fig 2.1), slightly inflated head, pigmentation of corium extending into all proximal areas of wing membrane, spatulate process of subgenital plate, tVIII membranous with longitudinal fold and a single sclerotized lobe, rounded peak of vesica, plate-like aedeagal sclerite (Figs 2.2d, 2.3d, 2.3d.1, white arrow), and the conical sclerite of sXI (Fig 2.3d.1, grey arrow).

Holotype: **GUATEMALA: Alta Verapaz:** Cacao Trece Aguas, 15.4°N 89.75°W, 11 Apr 1906, Schwarz & Barber, 1 ♂ (UCR_ENT 00028671) (USNM) point-mount.

Redescription: *Male*: length 1.06 mm; ovoid, almost tear-shaped. **COLORATION:**

General color brown; pronotum with narrow pale band on distal margin; scutellum uniformly brown; legs with brown femora and yellow tibiae; fuscous patch covering less

than ½ of wing membrane; Sc + C concolorous with remainder of hemelytron; pigmentation of corium slightly extending into anterior and posterior membranal cells and anal region of wing membrane. **SURFACE and VESTITURE:** as in generic description. **STRUCTURE:** HEAD: slightly inflated in lateral view; vertex slightly rounded in dorsal view; eyes as in generic description with slightly notched ventral margin; width of eyes about 2/3 as wide as synthlipsis. THORAX: As in generic description; slightly undulated, with longitudinal medial depression; posterior margin of pronotum notched; scutellum as in generic description with oblong tip with medial notch; hemelytron as in generic description, posterior costal cell trapezoidal. ABDOMEN: As in generic description; process of subgenital plate spatulate, with rounded tip (Fig 2.2d.1); tVII rectangular; tVIII partially membranous, with longitudinal fold and single sclerotized lobe on right side (Figs 2.2d, 2.3d, 2.3d.1); length of tVIII about 2/3 of tVII. GENITALIA: py as in generic description; rp as in generic description with apex of long process with ventral keel (Figs 2.2d, 2.2d.1); vesica as in generic description with rounded peak (Fig 2.3d.1); aedeagal sclerite plate-like (Fig 2.3d.1, white arrow); anophore not well-developed; sX mostly membranous; sXI heavily sclerotized into conical sclerite (Fig 2.3d.1, grey arrow). *Female:* Total length: 1.15mm; general habitus as in male. GENITALIA: segment VIII with lateral lobes almost enveloping segment IX (Fig 2.2g); ovipositor vestigial.

Distribution: This species is known from a single locality in the highlands of the Guatemalan cloud forest and two localities in the lowland, subtropical forest of northern Belize (Fig 2.4).

Other Specimens Examined: **BELIZE: Orange Walk:** Rio Bravo Conservation Area, La

Milpa Field Station, 17.8°N 88.93333°W, 17 Apr 1995, in subcortical debris, P. W.

Kovarik, 1♂ (UCR_ENT 00093688) (TAMU) microscopic slide. Rio Bravo Conservation Area, off road to La Milpa Archeol. Site, 17.84147°N 89.01818°W, 13 Jul 1996, light trap, P. Kovarik, 1♀ (UCR_ENT 00093694) (TAMU) microscopic slide-mount.

Etymology: no etymology was given by the original authors, but “plana” is clearly adjectival (Latin, meaning “flat”), and following ICZN Code Article 31.2 must change spelling to “planus” to agree in gender with *Orthorhagus*.

Orthorhagus sharkeyi, n. sp.

(Figs 2.1-2.5)

Diagnosis: Distinguished among other species of *Orthorhagus* by the large body size, dark coloration, flat head, small synthlipsis, uniform coloration of pronotum, rounded tip of scutellum, pentagonal posterior costal cell, lanceolate process of subgenital plate (Fig 2.2e.1), rectangular and symmetrical tVIII (Figs 2.2e, 2.3e), hooded apex of long process of right paramere (Fig 2.3e.1), membranous masses in genitalia obscuring the vesica (Fig 2.3e), conical sclerite of sXI.

Holotype: **COLOMBIA: Huila:** PNN Cueva de Los Guácharos, Alto el Mirador, 1.63333°N 76.1°W, 1980 m, 07 Dec 2001 - 21 Dec 2001, Malaise Trap, R. Paramero, 1♂ (UCR_ENT 00119010) (IAvH) microscopic slide-mount.

Description: *Male*: length 1.4 mm; elongate ovoid. **COLORATION:** general color dark brown, almost black; pronotum uniformly dark brown; scutellum uniformly brown; legs with brown femora and yellow tibiae; fuscous patch covering less than 1/2 of wing

membrane; Sc + C concolorous with remainder of hemelytron; pigmentation of corium slightly extending into anterior and posterior membranal cells and anal region of wing membrane. **SURFACE and VESTITURE:** as in generic description. **STRUCTURE:** HEAD: slightly inflated in lateral view; vertex slightly rounded in dorsal view; eyes as in generic description with slightly notched ventral margin; width of eyes about 2/3 as wide as synthlipsis. THORAX: as in generic description; pronotum slightly undulated, with longitudinal medial depression; posterior margin of pronotum notched; scutellum as in generic description with rounded tip; hemelytron as in generic description; posterior costal cell pentagonal. ABDOMEN: as in generic description; process of subgenital plate lanceolate (Fig 2.2e.1); tVII rectangular; tVIII rectangular (Figs 2.2e, 2.3e); length of tVIII about 2/3 of tVII. GENITALIA: py as in generic description; rp as in generic description with long process with hooded apex (Figs 2.2d, 2.2d.1); vesica not seen in dorsal view; anophore not well-developed; sX mostly membranous; sXI forming conical sclerite.

Female: Unknown

Distribution: Known from a single locality in the Andean cloud forest in the department of Huila, Colombia (Fig 2.4).

Etymology: Named after Michael Sharkey for his generous loan of numerous residue samples from which this specimen was removed.

Orthorhagus subcorticalis, n. sp.

(Figs 2.1-5)

Diagnosis: Distinguished among other species of *Orthorhagus* by the relatively small body size, narrow eyes in lateral view, distinctly undulated pronotum, broad posterior

costal cell (Fig 2.5c), blunt axe shaped process of subgenital plate, tVIII membranous a with deep longitudinal fold and two sclerotized lobes (Fig 2.2f), vesica with an acute peak and the triangular aedeagal sclerite (Fig 2.3f.1, white arrow).

Holotype: **PANAMA: Bocas del Toro:** Almirante, at dam on Nigua Creek, 9.25°N 82.65°W, 23 Mar 1959, under bark, H. S. Dybas, 1♂ (UCR_ENT 00090724) (FMNH) microscopic slide. Allotype: **Coclé:** El Valle, trail to Las Minas, 8.60278°N 80.15361°W, 792 m, 21 Feb 1959, collected from subcortical debris, H. S. Dybas, 1♀ (UCR_ENT 00090809) (FMNH) point-mount.

Description: *Male*: length 1.28 mm; ovoid. **COLORATION**: general color brown; pronotum with narrow pale band on distal margin; scutellum uniformly brown; legs light brown; fuscous patch covering more than 1/2 of wing membrane; Sc + C concolorous with remainder of hemelytron; pigmentation of corium slightly extending into posterior membranal cell and anal region of wing membrane. **SURFACE and VESTITURE**: as in generic description. **STRUCTURE**: HEAD: slightly inflated in lateral view; vertex slightly rounded in dorsal view; eyes as in generic description with slightly notched ventral margin; width of eyes about 2/3 as wide as synthlipsis. THORAX: As in generic description; pronotum undulated, with longitudinal medial depression; posterior margin of pronotum notched; scutellum as in generic description with oblong, notched tip; hemelytron as in generic description; posterior costal cell large, parallel sided shaped. ABDOMEN: as in generic description; process of subgenital plate blunt axe head shaped (Fig 2.2f.1); tVII rectangular; tVIII partially membranous, with longitudinal fold, and two sclerotized lobes on right side (Figs 2.2f, 2.3f.1, grey arrow); length of tVIII about 2/3 of

tVII. GENITALIA: py as in generic description; rp as in generic description with long process with ventral keel (Figs 2.2f, 2.2f.2, white arrow); vesica as in generic description, with acute spine; aedeagal sclerite triangular (Fig 2.3f.1, white arrow) anophore not well-developed; sX mostly membranous; sXI forming conical sclerite.

Female: Total length: 1.35 mm; general habitus as in male, with pale band on posterior margin of pronotum slightly broader than in male. GENITALIA: sVIII with lateral lobes seen from ventral view (Fig 2.1, *O. subcorticalis*); ovipositor vestigial.

Distribution: Known from two localities in Panama: the Bocas del Toro province in northern Panama and the southeastern province of Coclé (Fig 2.4).

Etymology: Named after the microhabitat in which both male and female specimens of this species were found. Specimen notes indicated “in subcortical debris” or “underneath bark.” The gender is male.

Discussion: The female allotype for this species was not dissected, to preserve one complete specimen that was to be point-mounted. The sclerotized lobes of sVIII are visible on the habitus images in Fig 2.1.

Discussion

Molecular phylogenetic analyses of *Schizoptera* and related taxa (e.g., *Ptenidiophyes* Reuter and *Ceratocomboides* McAtee and Malloch) show that *Orthorhagus* is not part of *Schizoptera* in the strict sense. Instead, *Orthorhagus* is recovered as sister group to *Ceratocomboides* McAtee and Malloch (Leon and Weirauch, in prep) and that clade as

sister to a monophyletic group comprising *Ptenidiophyes* Reuter and various other Schizopteridae. Morphological differences between *Orthorhagus* and *Schizoptera* provide additional evidence for our decision to raise *Orthorhagus* to genus level. In the following section, we discuss some of the differences and similarities between *Orthorhagus* and *Schizoptera*.

Head and Thorax

At first glance, species of *Orthorhagus* resemble those of *Schizoptera* (Fig 2.5a). The absence of a pronotal collar was originally used to distinguish *Orthorhagus* from other subgenera of *Schizoptera*, and it remains a useful diagnostic character to distinguish between the two genera. In addition, in species of *Orthorhagus*, the eyes are much larger and more conically truncate (or posteriorly expanded; see Fig 2.5e) than they are in species of *Schizoptera*. The long, golden setae on the head, pronotum and hemelytra are another prominent feature unique to *Orthorhagus*. Long and stout cephalic setae occur in *Orthorhagus* as well as other genera of Schizopteridae (i.e. *Voragocoris* Weirauch, 2012), but they are absent in *Schizoptera*. The tip of the scutellum is rounded in *Schizoptera*, but oblong and notched in most species of *Orthorhagus*. Male and female specimens of *Orthorhagus* show a 2-2-3 tarsal formula and do not possess arolia on any pair of legs in either sex, whereas *Schizoptera* males show a 3-3-3 tarsal formula, and have arolia on the tarsi of the fore- and mid-legs.

McAtee and Malloch (1925) used the presence of spines on the metapleuron and characters of the wing venation as diagnostic features for *Schizoptera*. A spine-like process on the metapleuron is present in both *Schizoptera* and *Orthorhagus*, but it is also observed in other Schizopterinae genera. In *Schizoptera*, the border of the posterior

margin of the metapleuron is distinctly “shining” or glabrous, heavily sclerotized, and carries a distinct reticulate pattern. Both, the degree of sclerotization and reticulation are less prominent in species of *Orthorhagus*. These structures may be associated with the scent gland groove, but a more thorough comparative and functional morphological study would be required to fully describe the function and modification of these structures.

The wing venation patterns observed in *Orthorhagus* (Fig 2.5c) are similar not only to those in *Schizoptera*, but also to patterns seen in other genera of the Schizopterinae (i.e. *Ceratocomboides* and *Ptenidiophyes*). In *Schizoptera* species, the posterior costal cell (R-M-M1) always has a fairly equilateral shape, with veins sometimes forming perfect square cells. Veins of the forewing are also more superficially inflated and punctation is not as distinct as it is in species of *Orthorhagus*. In *Orthorhagus*, the posterior costal cell is broader (Fig 2.5c) and more ambiguous in shape (i.e. pentagonal or trapezoidal) and the veins are less prominent than those of *Schizoptera*. Finally, the punctation of the hemelytron and the body is more pronounced in *Orthorhagus* than in *Schizoptera*.

Genitalia

Apart from similarities in the asymmetrical subgenital plate and the rotated pygophore, male genitalia of *Orthorhagus* species differ dramatically from those in *Schizoptera*, especially with respect to the unique paramere and aedaegal structure in *Orthorhagus*. Females also display features not seen elsewhere such as the sclerotized lobes of sVIII (Fig 2.2g) that allow for unambiguous identification.

Right Paramere Structure

The right paramere of *Orthorhagus* males is unique in being extremely large and y-shaped, with a short base and two bifurcations, one small process and one large “leg”. The short base is attached to the phallobase, the small process can be seen in contact with tVIII in some species (Figs 2.2b, 2.2e, 2.3b) and the long “leg” of the paramere folds under the pygophore, projecting ventrally and being holstered between the processes of the subgenital plate (Figs 2.2e.1, 2.3e.1). We assume that this holstering of the long “leg” occurs when the paramere is at rest. The apex of the long “leg” of the paramere is also highly modified in all species. Unlike *Orthorhagus* species, the right paramere of species of *Schizoptera* is sickle-shaped, does not fold under the pygophore, and has a simple apex.

Aedeagus

The structure of the aedeagus in *Orthorhagus* is complex. Unlike the long, thin, tubular, and coiled (Fig 2.5d) vesica of *Schizoptera* species, the vesica of *Orthorhagus* species is short, robust, spiked and tapering, often wrapping around the anophore (Figs 2.2, 2.3). In addition, membranous areas are associated with the aedeagus (Figs 2.3d.1 blue arrow, 2.3e white arrow), some of which obscure the vesica (i.e. *Orthorhagus sharkeyi*, n. sp.).

Relationships within *Orthorhagus*

Due to the limited number of known *Orthorhagus* specimens, we were unable to include most species of this genus into ongoing molecular analyses. We did not code a formal morphology-based matrix to evaluate phylogenetic relationships in the genus, but

nevertheless, we want to point out some patterns that we have observed. The three Central American species share characteristics that clearly distinguish them from the three South American species. Species from Central America are smaller in body size and their tVIII is modified by a longitudinal fold. In *O. lewisi*, n. sp. (Figs 2.2b, 2.3b) this fold provides a pocket for the short process of the right paramere. Even though this process is upright in *O. planus*, n. sp. and *O. subcorticalis*, n. sp. (Figs 2.2d, 2.2f, 2.3d, 2.3f) (an artifact of the boiling process for dissection), the pocket for this small process also exists in these two species. The South American species share a larger body size and the structure of tVIII is different in all species, but none possess a longitudinal fold. The subgenital plate structure is similar in species from South America, with very acute and tapering processes (Fig 2.2a-1, c.1, e.1).

These characters may prove useful for future evaluation of phylogenetic and biogeographic patterns in this small genus.

References

- China, WE (1946) New Cryptostemmatidae from Trinidad, British West Indies. P Roy Entomol Soc B 15: 148-154
- Emsley, MG (1969) The Schizopteridae (Hemiptera: Heteroptera) with the descriptions of new species from Trinidad. Mem Am Entomol Soc 25:1–154
- Fieber FX (1860) Exegesen en Hemiptera. Wien Ent Monats 4: 257-272
- Hill L (1984) New Hypselosomatinae (Heteroptera: Schizopteridae) from Australia. Aust J Zool 103:1-55
- Hill L (1990) Australian *Ogeria* Distant (Heteroptera: Schizopteridae). Invertebr Taxon 4: 697-720
- Hill L (2014) Revision of *Silhouettanus* with description of nine new species (Hemiptera: Heteroptera: Schizopteridae). Zootaxa 3815:353–385
- Hill L (2015) Three new genera of Schizopteridae from Australia with description of six new species (Hemiptera: Heteroptera: Schizopteridae). Zootaxa 3990: 73-96. Knyshev A, Leon S, Hoey-Chamberlain R, Weirauch C (2015) Pegs, pouches and spines: systematics and comparative morphology of the New World genus *Chinannus* Wygodzinsky, 1948, ESA Thomas Say monographs, submitted
- Linnavuori RE (1974) Hemiptera of the Sudan, with remarks on some species of the adjacent countries. Ann Ent Fenn 40: 116-138
- Makhan D (2013) *Soekhnandanius aschne* gen. et sp. nov., Schizopterinae (Hemiptera: Heteroptera: Schizopteridae) from Suriname. Calodema 391: 1-3
- McAtee WL, Malloch JR (1925) Revision of bugs of the family Cryptostemmatidae in the collection of the United States National Museum. Proc USNM 67: 1-42
- Noyes JS (1982) Collecting and preserving chalcid wasps (Hymenoptera: Chalcididae). J Nat Hist 16:315-334
- Platner GR, Velte RK, Planoutene M, Pinto JD (1999) Slide mounting techniques for *Trichogramma* (Trichogrammatidae) and other minute parasitic Hymenoptera. Ent News 110:56-64
- Poinar G, Brown A (2014) New genera and species of jumping ground bugs (Hemiptera: Schizopteridae) in Dominican and Burmese amber, with description of a meloid (Coleoptera: Meloidae) triungulin on a Burmese specimen. Ann Soc Entomol Fr 50: 372-381
- Poppius B (1910) Neue Ceratocombiden. Ofvers Finsk Vet Soc Föhr 52: 1-42

- Rédei D (2008) First record of *Pinochius* Carayon, 1949 from the Oriental Region, with description of a new species from Vietnam (Heteroptera: Schizopteridae). In: Gozeva S, Simov N (eds) *Advances in Heteroptera Research: Festschrift in honour of 80th anniversary of Michail Josifov*. Pensoft, Sofia pp. 327-337
- Reuter OM (1882) Sur le genre *Schizoptera* Fieb. *Rev Ent Caen* 1: 162-164
- Reuter OM (1891) *Monographia Ceratocombidarum orbis terrestris*. *Acta Soc Sci Fenn* 37: 1-16
- Weirauch C (2012) *Voragocoris schuhi*, a new genus and species of neotropical Schizopterinae (Hemiptera: Heteroptera: Schizopteridae) *Ent Amer* 118: 285-294
- Weirauch C, Štys P (2014) Litter bugs exposed: phylogenetic relationships of Dipsocoromorpha (Hemiptera: Heteroptera) based on molecular data. *Insect Syst Evol* 45:351–370
- Weirauch C, Frankenberg S (2015) From “insect soup” to biodiversity discovery: taxonomic revision of *Peloridinannus* Wygodzinsky, 1951 (Hemiptera: Schizopteridae), with description of six new species. *Arthropod Syst Phylo*, in press
- Wygodzinsky P (1952) Sobre algunos Cryptostemmatidae, principalmente de la Argentina (Hemiptera). *Acta Zool Lilloana* 10: 51-74
- Wygodzinsky P (1951) Descripción de generos y especies nuevos de la familia Cryptostemmatidae (Hemiptera). *Rev Bras Biol* 11: 259–270

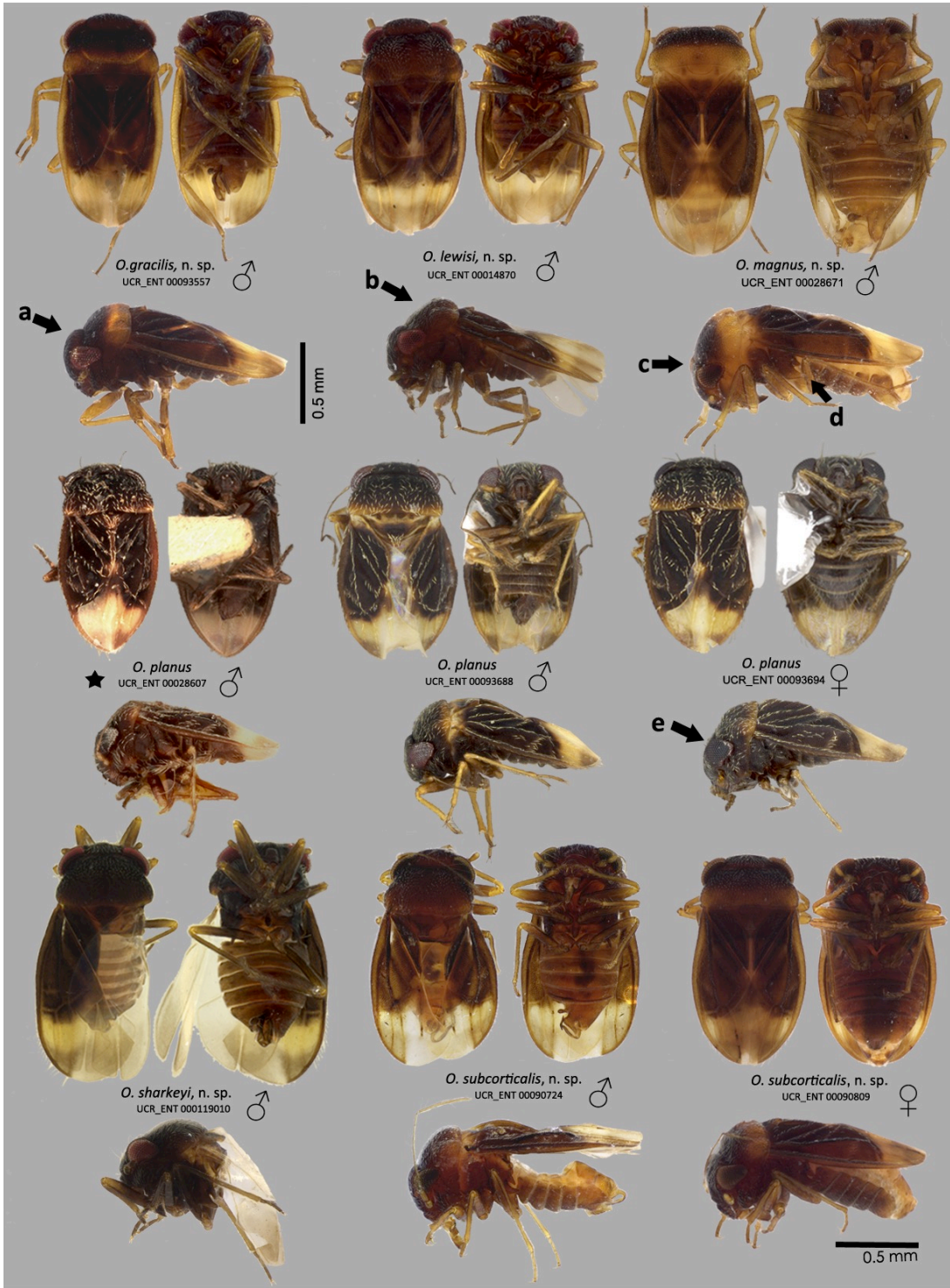


Figure 2.1: Habitus images of species of *Orthorhagus*, arrows with letters indicate diagnostic features mentioned in the text; black star indicates holotype specimen

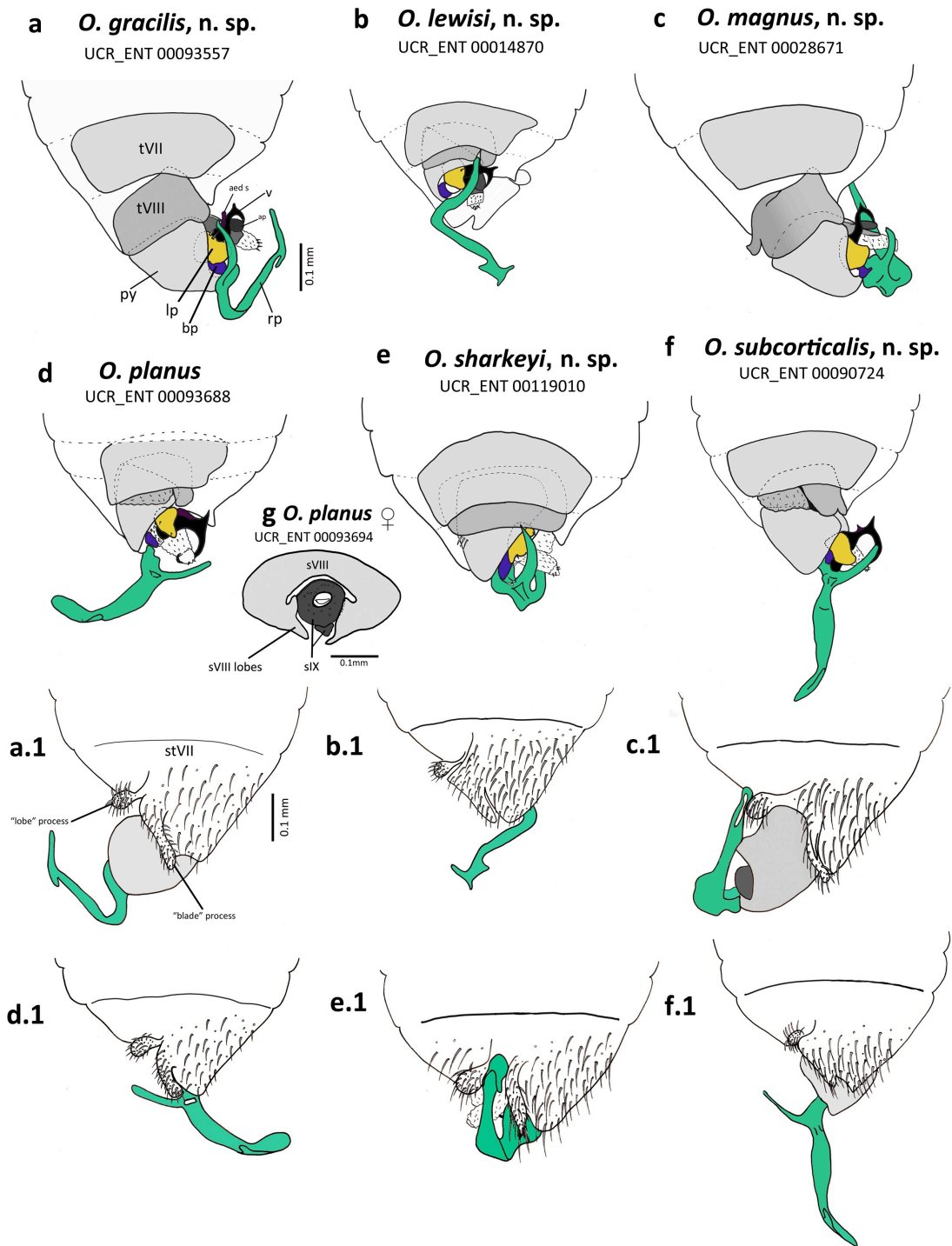


Figure 2.2: a-f line drawings of dorsal view of male genitalia, name of structures indicated in a; g: drawing of female segments VIII and IX in caudal view; a.1-f.1: ventral view of male genitalia.

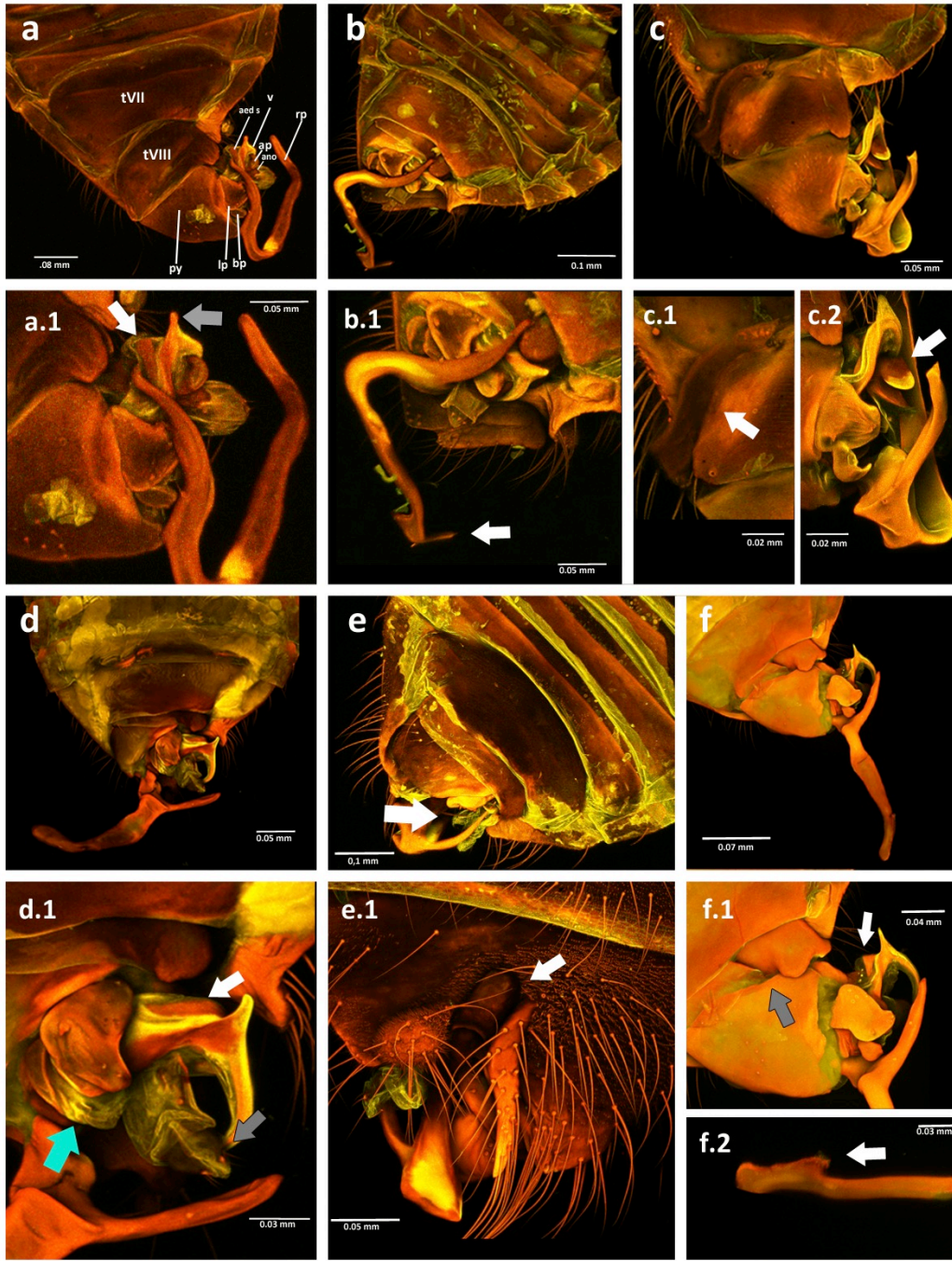


Figure 2.3: Confocal microscopy images of male genitalia of *Orthorhagus* species, a, a.1: *Orthorhagus gracilis*, n. sp.; b, b.1: *Orthorhagus lewisi*, n. sp.; c, c.1, c.2: *Orthorhagus magnus*, n. sp.; d, d.1: *Orthorhagus planus*; e, e.1: *Orthorhagus sharkeyi*, n. sp.; f, f.1, f.2: *Orthorhagus subcorticalis*, n. sp., arrows with letters indicate diagnostic features mentioned the in text.

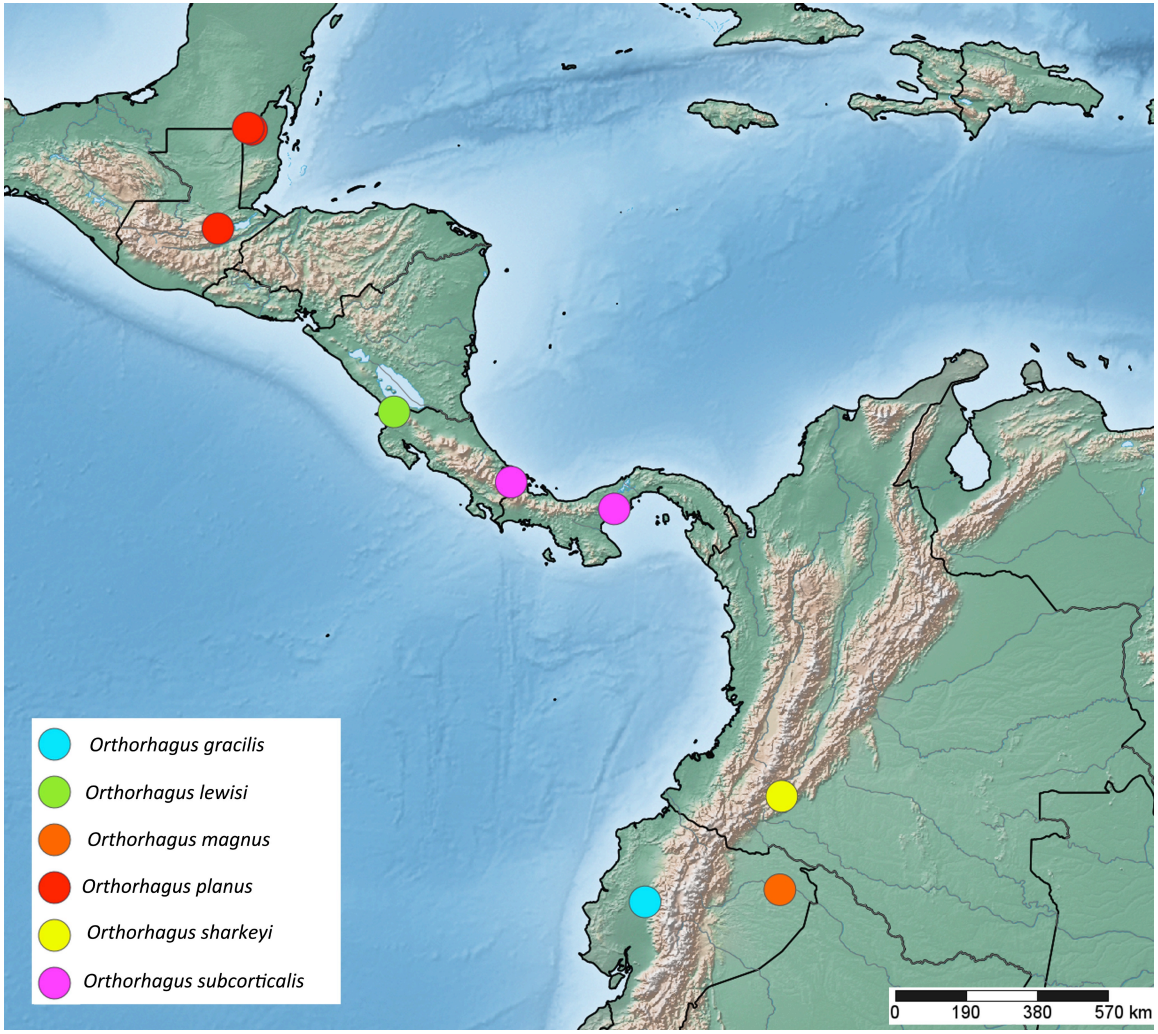


Figure 2.4: Distribution of *Orthorhagus* species.

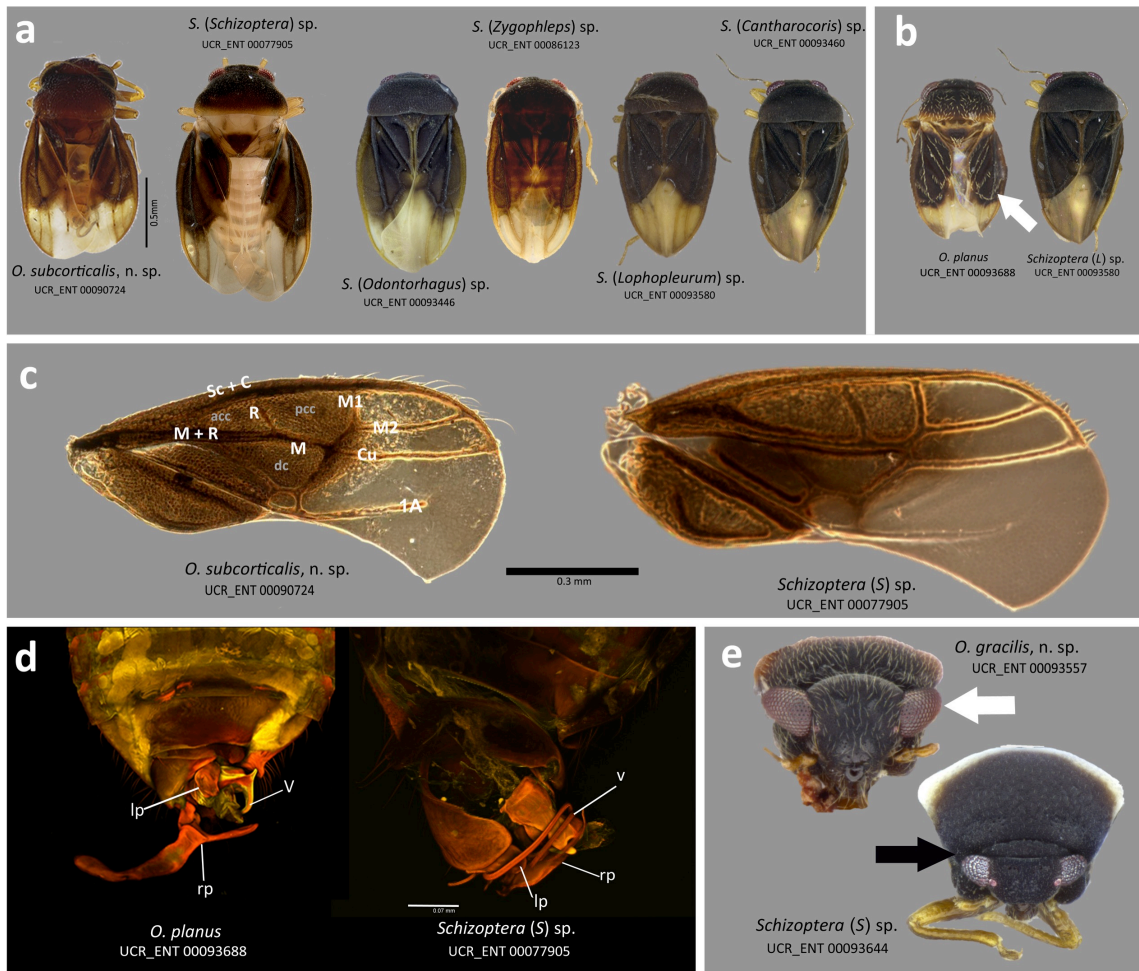


Figure 2.5: Comparison of morphological features of *Schizoptera* species and *Orthorhagus*; a: general dorsal habitus, b: difference in setation, c: comparison of forewing structure, white letters indicate vein names, grey letters indicate cell names, wing vein homology *sensu* Rédei (2008), d: confocal image contrasting genitalia of *Orthorhagus planus* and a species of *Schizoptera*, e: frontal view of head of *Orthorhagus gracilis, n. sp.* and *Schizoptera sp.*, arrows indicate characters mentioned in text.

Chapter 3: Scratching the surface? Taxonomic revision of the subgenus *Schizoptera* (*Odontorhagus*) reveals vast undocumented biodiversity in the largest litter bug genus *Schizoptera* Fieber (Hemiptera: Dipsocoromorpha)

Abstract

Schizoptera Fieber, currently the largest genus of litter bugs (Hemiptera: Dipsocoromorpha), comprises 61 extant species in 4 subgenera. Specimens are abundant in New World bulk and residue samples. *Schizoptera* species showcase stunning morphology including intricate, asymmetrical genitalia in males that have proven to provide excellent species diagnostic features in the past. Recent bulk sample sorting efforts have revealed a vast number of *Schizoptera* specimens from across the New World, with the majority representing undescribed species. We here taxonomically revise the subgenus *Schizoptera* (*Odontorhagus*) that has recently been shown to form a monophyletic group within *Schizoptera*. Characterized by the blunt tooth on the posterior margin of the propleuron, *Schizoptera* (*Odontorhagus*) previously comprised 10 species from Central and the northern part of South America. We here describe 20 new species in *S.* (*Odontorhagus*), increasing the species count of *Schizoptera* to 81. We provide morphological documentation including digital habitus images and genitalic drawings for all new species and document and redescribe existing species where feasible. Distribution maps and a key to the species of *Schizoptera* (*Odontorhagus*) are also presented. We predict that similar increases in species numbers are to be expected for the remaining subgenera of *Schizoptera*, making this genus and very diverse lineage of minute litter bugs.

Introduction

The Dipsocoromorpha, or litter bugs (Hemiptera: Heteroptera) are a poorly studied group of tiny true bugs (~1-2mm), that showcase bizarre morphologies and are suspected to contain a tremendous amount of undocumented biodiversity (Weirauch and Štys 2014). Species of Dipsocoromorpha occur in all biogeographic regions, but are most diverse and prevalent in wet tropical areas, where many species are found in forest leaf litter (Emsley 1969). Ongoing efforts by the Heteropteran Systematics Lab at the University of California, Riverside are starting to transform our understanding of dipsocoromorphan biodiversity, primarily focusing on the New World fauna of the largest litter bug family, the Schizopteridae: three recent taxonomic revisions have resulted in the description of 37 new species (Weirauch and Frankenberg 2015, Knyshev *et al.*, accepted; Leon and Weirauch, accepted), with taxonomic revisions describing additional new species in preparation. The number of species classified as Schizopteridae has increased from 250 to 287 in now 57 genera (Linnavouri 1974; Weirauch 2012; Makhan 2013, Weirauch and Štys 2014; Hill 2015, Leon and Weirauch, accepted; Leon and Weirauch, submitted).

Schizopteridae are extremely abundant in bulk and residue samples but often ignored because of their miniscule size that requires specialized curation (e.g., slide-mounting and genitalic dissections that are challenging because of specimen size). Our lab has assembled more than 10,000 schizopterid specimens from various institutions by sorting bulk samples and loaning point-mounted specimens, in addition to our own field work efforts. About 10% of these specimens belong to *Schizoptera* Fieber (pers. obs.), a genus that is readily identified in mixed samples due to distinctive wing venation and male genitalic morphology (Emsley 1969, Leon and Weirauch, submitted).

Schizoptera currently comprises 61 extant species (Emsley 1969; Leon and Weirauch; accepted; Leon and Weirauch, submitted) and two species known from fossils (Poinar 2014). The genus was described based on a single specimen from Venezuela by Fieber in 1860, and subsequent taxonomic efforts in the late 19th and early 20th centuries by Reuter and Poppius increased the species count from one to six (Fieber 1860; Reuter 1882, 1891; Poppius 1910; Emsley 1969). McAtee and Malloch's (1925) taxonomic revision resulted in 27 new species from Central America and the Caribbean. China (1946) described a single species from Trinidad and Wygodzinsky two new species from Argentina (Wygodzinsky 1952). The peak of taxonomic work focusing on this genus came in 1969 by Emsley, who in his monograph described 28 new species from Trinidad based on his thorough field work across this continental island. This discovery of a large number of new species from a fairly small geographic area suggests that increased sampling efforts in suitable habitats across the New World could lead to a dramatic increase of species numbers in *Schizoptera*.

Given the size of the genus and the fact that groups of species share unique features, attempts were made to subdivide *Schizoptera* into subgenera. McAtee and Malloch (1925) described seven subgenera: *S. (Cantharocoris)*, *S. (Lophopleurum)*, *S. (Kophaegis)*, *S. (Odontorhagus)*, *S. (Orthorhagus)*, *S. (Schizoptera)* and *S. (Zygophleps)*. Emsley (1969) subsequently synonymized *S. (Odontorhagus)* and *S. (Kophaegis)* based on the presence of a blunt process or "tooth" on the posterior margin of the propleuron in species of both subgenera (Fig. 3.1A, white arrow). A recent molecular phylogenetic analysis of *Schizoptera* and related genera tested the monophyly of the genus and monophyly and relationships of its subgenera (Leon and Weirauch, submitted). This analysis showed that *Schizoptera* as defined by McAtee and Malloch

(1925) and Emsley (1969) is polyphyletic. To render *Schizoptera* monophyletic, *Orthorhagus* was elevated to genus rank and taxonomically revised (Leon and Weirauch, accepted) and *Kophaegis* sensu McAtee and Malloch (1925) with two described species also given genus status. Specimens of *S. (Odontorhagus)* and *Kophaegis* may look similar at first glance, but the shape of the discal cell (Fig. 3.1C and E) and the presence of an antler-shaped anophoric process in species of *Kophaegis* distinguish the two groups. Given the lack of reciprocal monophyly based on molecular data, but also the ambiguity of diagnostic characters, *Schizoptera (Lophopleurum)* was synonymized with *S. (Cantharocoris)*. This leaves *Schizoptera* with four valid subgenera: *S. (Cantharocoris)*, *S. (Odontorhagus)*, *S. (Schizoptera)* and *S. (Zygophleps)*.

The 10 currently recognized species of *S. (Odontorhagus)* comprise six species that were described from Guatemala and Panama (McAtee and Malloch 1925) and four from Trinidad (Emsley 1969). Similar to other *Schizoptera* species, males of *S. (Odontorhagus)* possess an asymmetrical sternite VII, which has been modified into a subgenital plate and is species diagnostic, and a pair of asymmetrical conjunctival appendages (Emsley 1969). In species of *S. (Odontorhagus)* both males and females possess macropterous wings. As suggested by their prevalence in malaise trap, light trap, and canopy fogging samples, both sexes are likely to fly (Emsley 1969; personal observation). This pattern is in contrast to other members of *Schizoptera* where females are elytrous, and typically collected from the forest leaf litter (Leon and Weirauch submitted). Specimens of *S. (Odontorhagus)* account for about 1/6 of all *Schizoptera* specimens assembled in our lab and the array of morphological diversity expressed in this subset of specimens indicates the substantial undocumented biodiversity of an already speciose genus.

In the present study, we redescribe and diagnose the subgenus *S.* (*Odontorhagus*) and nine of its 10 described species, and describe 20 species as new. We provide morphological documentation including digital habitus images and genitalic line drawings. Distribution maps and a key to all species of *S.* (*Odontorhagus*) are also presented.

Material & Methods

Material

We examined 378 *S.* (*Odontorhagus*) specimens total, 121 of which were point- or card-mounted and 257 preserved in EtOH. Specimens that are deposited at UCR (University of California, Riverside) were collected during field trips by the Weirauch and Heraty labs, or were donated from several institutions. Other specimens were taken on loan and will be deposited in the following institutions:

AMNH	American Museum of Natural History, New York, New York
FMNH	Field Museum of Natural History, Chicago, Illinois
IAvH	Instituto Alexander von Humboldt, Bogotá, Colombia
INBio	Instituto Nacional de Biodiversidad, San José, Costa Rica
TAMU	Texas A&M University, College Station, USA
USNM	National Museum of Natural History, USA

To document subgeneric diagnostic features, a single *S.* (*Odontorhagus*) specimen (UCR_ENT 00076316) was dissected, mounted on a point with an adhesive carbon sticker, coated with gold-palladium using a Cressington 108 auto sputter coater, and documented using a Hitachi S-4700 electron microscope at the Central Facility for

Advanced Microscopy and Microanalysis at the University of California, Riverside. To compare features between representatives of *Kophaegis* and *S. (Odontorhagus)*, one *Kophaegis* (UCR_ENT 00088107) and one *S. (Odontorhagus)* specimen were dissected and imaged using a Leica SP5 inverted confocal microscope with lasers 488nm and 543nm and detectors set at diapasons of 500-535 and 555-700nm at the Institute for Integrative Genome Biology core facility <<http://genomics.ucr.edu/>>.

Methods

A matrix-code label with specimen identifier, consisting of a unique combination of an eight-digit number and the prefix “AMNH_IZC” or “UCR_ENT” was attached to each specimen, and databased using the PBI instance of the Arthropod Easy Capture database served from the AMNH <<https://research.amnh.org/pbi/locality/>>. Given that the majority of specimens were given “UCR_ENT” USI labels, this prefix was omitted from the material examined section, and only the eight-digit number is shown.

Specimens for which geographic coordinates were absent from collecting labels were georeferenced using Google Earth. Maps were created using SimpleMappr (<<http://simplemappr.net>>) by importing coordinates for individual species from the PBI database.

Dorsal and ventral habitus images were taken using a Leica DFC 450 C Microsystems system with a Planapo 1.0x objective. Images were stacked using the Leica LAS software. Specimen total length measurements were taken digitally from habitus images, using the measure function in Adobe Photoshop based on the scale derived from the Leica LAS software stacked image. To study genitalia, the male abdomen were separated from the thorax and cleared by immersion into hot 10% KOH.

Line drawings were made using a Nikon Eclipse 80i compound microscope with a camera lucida, and edited using Adobe Photoshop CS4 for shading structures. Dissected specimens were permanently slide-mounted following protocols outlined in (Noyes 1982; Platner *et al* 1999). A matrix consisting of 39 morphological characters, several of them cloned and modified from other ongoing taxonomic projects on Schizopteridae, was created and coded in mx <<http://mx.phenomix.org>>. Species descriptions were exported using the “export character description” option under the output tab and manually edited. Several characters of the head and thorax were manually added after descriptions had been exported from mx.

Terminology

Terminology of genitalic structures follows Štys (1970) and Emsley (1969) and wing venation is treated *sensu* Redei (2008).

Abbreviations

acc – anterior costal cell; ano – anophore; ap – anophoric process; at – anal tube; C– costa; Cu – cubitus; dc – discal cell; lca– left conjunctival appendage; lp – left paramere; M – media; M1– first branch of media; M2 – second branch of media; pcc – posterior costal cell; py – pygophore; R – radius; rca– right conjunctival appendage; rp – right paramere; Sc – subcosta; stVII – subgenital plate consisting of sternite VII; sX – segment X; sXI – segment XI; tc – trapezoidal cell; tVII – tergite VII; tVIII – tergite VIII; v – vesica.

Taxonomy

Schizoptera (Odontorhagus) McAtee and Malloch, 1925

(Figs 1-7)

Type species: ***Schizoptera (Odontorhagus) bipartita*** McAtee and Malloch 1925

Diagnosis: Distinguished from other Schizopteridae by the relatively large size, the spine-shape of the metepisternum, the glabrous ventral margin of the metepisternum, the trapezoidal shape of the discal cell, the 90° rotation of the pygophore to the right of the dorsal body plane, and the presence of two asymmetrical conjunctival appendages. Distinguished from all other *Schizoptera* species by the blunt tooth on the posterior margin of the propleuron (Fig. 3.1A), the narrow, glabrous ventral margin of the metepisternum (Fig. 3.1B), and the presence of a single process of the subgenital plate (except in *S. (Odontorhagus) enigmatica*, n. sp.).

Re-description: *Male*: Body relatively large, length ranging from 1.19-1.59; body shape ovoid, broadly oval or amygdaliform; habitus macropterous. **COLORATION**: General color light to dark brown with some lighter markings; head and thorax brown; pronotum and scutellum uniformly brown; legs uniformly yellow (except in *S. (Odontorhagus) ansata*, n. sp. and *S. (Odontorhagus) aspera*, n. sp.); forewing anteriorly light to dark brown, posteriorly cream colored, with or without a fuscous patch; Sc + C either concolorous with or distinctly lighter than remainder of hemelytron; pigmentation of corium slightly extending into wing membrane; abdomen brown. **SURFACE and VESTITURE**: Head and thorax with dense microtrichia; head, pronotum and wing veins covered with short, light brown setae; clypeus and labium without microtrichia and with long setae; numerous circular muscle scars on head; abdomen densely covered with

elongate, light brown setae (e.g., Fig. 3.2: *S. (Odontorhagus) dentatis*, n. sp.).

STRUCTURE: HEAD: flat, rounded or slightly concave in ventral view; width of eyes ranging from 1/3 as wide or 1 1/2 wider than synthlipsis; ocelli present, roughly equal in size to one compound eye ommatidium, and closely positioned to margin of compound eye; labium 3-segmented and tapering. THORAX: pronotal collar present and pronounced, about 1/7 length of pronotum; pronotum trapezoidal and smooth, with a medial notch on the posterior margin; propleuron with a distinct, blunt tooth on posterior margin (Fig. 3.1A); scutellum triangular; lateral margins of scutellum smooth; tip of scutellum small and round; hemelytron distinctly punctate; Sc + C explanate; posterior costa cell (R-M-M1) squared; margins of wing veins outlined with small areoles; apex of wing membranous with distinct cell-like sculpture; metepisternum sculpted into a spine; ventral margin of metepisternum differentiated into a narrow, glabrous shining groove (Fig. 3.1B); metasternal spine robust, elongate and tapering with a pointed tip; hind coxa with well-developed adhesive pad; tarsal formula 3-3-3; pretarsus with setiform parampodia; arolia present in all fore- and meso-tarsus. ABDOMEN: with five visible sternites corresponding to segments II-VII; sternite VII weakly asymmetrical with a rounded, or almost rounded, apex (e.g., Figs 5A, C, D) or distinctly asymmetrical, with longitudinal margin fused with base of lateral process forming a distinct, angular incision (e.g., Figs 5B, 5K, 6M), or with large, irregular incisions (Figs 5J, 6N); subgenital plate with a single left lateral process (except in *S. (Odontorhagus) enigmatica*, n. sp.); tergites of pregenital abdomen membranous except tergite VII (tVII in subsequent descriptions) and tergite VIII (tVIII in subsequent descriptions); tVII rectangular or weakly trapezoidal; tVIII weakly rectangular or trapezoidal; length of tVIII about 1/4 to 3/4 length of tVII. GENITALIA: pygophore (py subsequently) rotated 90° to the right; right paramere (rp

subsequently) sickle shaped, with a robust base and elongate stem or ladle-shaped with a rounded base and thin stem; left paramere (lp subsequently) smaller than right; vesica uniformly thin and forming more than one to 4 coils, or short and tapering with or without serrations at apex; anophore well sclerotized and with a prominent dorsal fold forming a slit-like aperture in most species, or forming a half-pipe sclerite in *S. (Odontorhagus) ansata*, n. sp..

Female: slightly larger than male; general habitus as in male; eyes smaller than in males. GENITALIA: segment VII symmetrical; ovipositor vestigial.

Key to the species of *Schizoptera (Odontorhagus)*.

This key includes all new species as well as those species for which re-descriptions of the genitalia were available (*S. decius*, *S. commodus*, and *S. stricklandi*), and *S. trinitatis*, for which the microscopic slide mount image sufficed for species-level diagnostic features of the subgenital plate.

- 1 Subgenital plate distinctly asymmetrical with longitudinal margin forming an angular incision with posterior margin of left lateral process (Figs 5B, 5K), or with a large, irregular incision (Fig. 3.5J)2
- 1' Subgenital plate weakly asymmetrical with rounded, or almost rounded tip.....9
- 2 Subgenital plate with two processes, a club-shaped anterior and a jagged tab-like posterior process, left inner margin of pygophore with long, curving process (Fig. 3.5J) *S. enigmatica*, n. sp. 5
- 2' Subgenital plate with a single lateral process.....3
- 3 stVII with a small process on posterior margin.....4
- 3' stVII without small process on posterior margin.....5

- 4 Subgenital plate short, with posterior with left side reduced, forming an angular incision >90°, right conjunctival appendage large and serrated, body small (Fig. 3.5E).....*S. brevis*, n. sp.
- 4' Subgenital plate lateral process with a straight posterior margin forming a 90° angle with longitudinal margin of subgenital plate (Fig. 3.5B) 6
- 5 Lateral process of subgenital plate small and balde-like, with a straight posterior margin forming a 90° angle with longitudinal margin of subgenital plate (Fig. 3.5V), general coloration dark brown, with SC+C distinctly lighter than remainder of hemelytra (Fig. 3.2, *S. trivialis*, n. sp)*S. trivialis*, n. sp.
- 5' Lateral process of subgenital plate formed by a slit-like lateral and triangular caudal incisions, lateral process of subgenital plate broad and lobe shaped, right paramere with a bifurcating process (Fig. 3.6N), right conjunctival appendage with trifurcating tip, vesica short, forked and serrated (Fig. 3.6N).....*S. monstrosa*, n. sp.
- 6 Lateral process of subgenital plate thumb-shaped, with notch on anterior margin, forming a “key and lock” appearance with process of stVI (Figs 5K, 6N)7
- 6' Lateral process of subgenital plate blade-shaped, without a notch on anterior margin.....8
- 7 Head slightly concave in ventral view (Fig. 3.3, *S. exacta*, n. sp.), body coloration uniformly light brown, right paramere thin, right conjunctival appendage needle-like..... *S. exacta*, n. sp.
- 7' Head flat in ventral view (Fig. 3.3, *S. insidiosa*, n. sp.), body coloration dark brown, with SC+ C distinctly lighter, right paramere large, vesica uniformly thin forming at least four coils, anophore with fingerlike process on dorsal wall and a wide dorsal aperture (Fig. 3.6M).....*S. insidiosa*, n. sp.

8	M2 vein distinctly curving, forming a wedge-shaped anterior membranal cell (Fig. 3.4, <i>S. trinitatis</i>), process of stVI small, and tooth-like.....	<i>S. trinitatis</i>
8'	M2 vein straight (Fig. 3.2, <i>S. angularis</i> , n. sp.), forming a triangular anterior membranal cell, body small, vesica uniformly long and thin (Fig. 3.5B).....	<i>S. angularis</i> , n. sp.
9.	stVI with process on posterior margin.....	10
9'	stVI without process on posterior margin.....	13
10	Process of posterior margin of stVI triangular, and tooth-like.....	11
10'	Process of posterior margin of stVI blunt, tab-like.....	12
11	Tooth-like process of stVI large, about 1/3 length of stVI with jagged edges (Fig. 3.5H), lateral process of subgenital plate tooth-shaped with a serrated posterior margin, subgenital plate lateral margin distinctly curving and sclerotized (Fig. 3.5H).....	<i>S. dentatis</i> , n. sp.
11'	Tooth-like process of stVI small, about 1/10 length of stVI (Fig. 3.5D), lateral process of subgenital plate thumb-like, lateral margins of subgenital plate distinctly jagged, general coloration dark brown (Fig. 3.2, <i>S. aspera</i> , n. sp.), eyes small, about 1/3 width of synthlipsis.....	<i>S. aspera</i> , n. sp.
12	Tab-like process of stVI large, about 1/3 length of stVI, process of subgenital plate blunt and rectangular, pointing apically (Fig. 3.5G), body coloration dark brown, with fuscous patch covering 1/2 of wing membrane (Fig. 3.2, <i>S. decius</i>).....	<i>S. decius</i>
12'	Tab-like process of stVI small, about 1/6 length of stVI, process of subgenital plate blunt, not fully differentiated from subgenital plate (Fig. 3.6P), general coloration dark brown (Fig. 3.3, <i>S. quasicompleta</i> , n. sp.).....	<i>S. quasicompleta</i> , n. sp.

13	Process of subgenital plate uniform, without bifurcation.....	14
13'	Process of subgenital plate bifurcating.....	22
14	Process of subgenital plate relatively large, well-differentiated from subgenital plate.....	15
14'	Process of subgenital plate small, not well-differentiated from subgenital plate.....	16
15	Process of subgenital plate thick straightly projecting to the left.....	17
15'	Process of subgenital plate thin and slightly projecting caudally.....	18
16	Subgenital plate process rounded, projecting apically.....	20
16'	Subgenital plate process triangular, or with jagged margins.....	21
17	Process of subgenital plate elongate, smooth and handle-shaped (Fig. 3.5C), vesica long and forming almost two coils, anophore forming a half-pipe, body size large (~1.53-1.59mm), general body coloration dark brown (Fig. 3.2, <i>S. ansata</i> n. sp.) <i>S. ansata</i> , n. sp.	
17'	Process of subgenital plate stout, with rectangular base, and modified tip.....	19
18	Process of subgenital plate hook-shaped, curving and projecting caudally, right paramere large, right conjunctival appendage large, curving and serrated, left conjunctival appendage prong-shaped (Fig. 3.6F), body coloration light brown (Fig. 3.3, <i>S. commodus</i>) <i>S. commodus</i>	
18'	Process of subgenital plate thin and needle-shaped (Fig. 3.5A), almost projecting caudally, right conjunctival appendage flat, with serrations on ventral margin, body coloration uniformly dark brown (Fig. 3.2, <i>S. acuta</i> , n. sp.)..... <i>S. acuta</i> , n. sp.	

- 19 Process of subgenital plate shaped like a fishtail (Fig. 3.6O), right conjunctival appendage tapering with a serrated tip (Fig. 3.6O), left conjunctival appendage with blunt and finshaped processes, body coloration light brown (Fig. 3.3, *S. piscicaudata*, n. sp.)*S. piscicaudata*, n. sp.
- 19' Process of subgenital plate uniformly rectangular (Fig. 3.6T), apex of subgenital plate almost conical, right paramere with a large, serrated process, left conjunctival appendage cashew-shaped (Fig. 3.6T), body coloration dark brown (Fig. 3.3, *S. singularis*, n. sp.)*S. singularis*, n. sp.
- 20 Body size broadly ovoid, coloration light brown with large eyes (Fig. 3.3, *S. simpla*, n.sp.), process of subgenital plate small and tab-like, left lateral margin of subgenital plate slightly curving and sclerotized (Fig. 3.6S)*S. simpla*, n. sp.
- 20' body ovoid, coloration light brown with prominent fuscous patch on wing membrane (Fig. 3.2, *S. dolosa*, n. sp.), process of subgenital plate simple and tab-like, left inner-lateral margin of pygophore distinctly sclerotized (Fig. 3.5I), vesica short, tapering and with serrations on apex, anophore with two distinct dorsal keels (Fig. 3.5I).....*S. dolosa*, n. sp.
- 21 Process of subgenital plate short, jagged and thumb shaped (Fig. 3.5 L), left conjunctival appendage with three visible processes (Fig. 3.5L), anophore with short, blunt process on dorsal wall, body ovoid, coloration light brown, eyes large, wider than synthlipsis (Fig. 3.3, *S. gorgonensis*, n. sp.)*S. gorgonensis*, n. sp.
- 21' Process of subgenital plate small, almost triangular (Fig. 3.6U), anophore with a heart-shaped dorsal fold, body ovoid, coloration dark brown (Fig. 3.4, *S. stricklandi*)*S. stricklandi*

- 22 Bifurcating process of subgenital plate without serration on margins of anterior or posterior bifurcations.....23
- 22' Bifurcating process of subgenital plate with blade-shaped anterior and lanceolate posterior bifurcations, anterior margin of lanceolate bifurcation of subgenital plate process with distinct serrations (Fig. 3.6R), right paramere with a long, thin and serrated process, apex of right conjunctival appendage serrated, body amygdaliform, coloration dark brown (Fig. 3.3, *S. serrata*, n. sp.).....*S. serrata*, n. sp.
- 23 Bifurcating process of subgenital plate shaped like a claw, with larger anterior and shorter posterior bifurcations (Fig. 3.6W).....*S. unguolata*, n. sp.
- 23' Bifurcating process of subgenital plate root-shaped, with a stem and bifurcating tip, body coloration dark brown (Fig. 3.2, *S. radicata*, n. sp.)*S. radicata*, n. sp.

***Schizoptera (Odontorhagus) acuta*, n. sp.**

(Figs 2, 5, and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the elongate ovoid body shape, the dark brown coloration, the single, needle-shaped process of the subgenital plate (sVII), the flat right conjunctival appendage with a serrated ventral margin, the distinctly curving and sharp tip of the right paramere, and the large, uniformly round left paramere.

HOLOTYPE: **COSTA RICA: Heredia:** La Selva Biological Station, nr Puerto Viejo;

10.43086, -84.00647; 52 m; 16 Apr 1998; INBio-OET-ALAS; L/15/354. 1♂ (0010943)

(microscopic slide mount). PARATYPES: **COSTA RICA: Alajuela:** Costa Rica: Alajuela

San Antonio de los Chiles Hacienda R y R, 10.01667°N 84.21667°W, 30 Dec 1994, 1♂
(00091496) (FSCA).

Description: *Male*: length: 1.25-1.30 mm; body elongate ovoid. **COLORATION**: general coloration dark brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C concolorous with remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: flat in ventral view (Fig. 3.2); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein slightly curving anteriorly toward wing margin, anterior membranous cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate needle-shaped (Fig. 3.5A); tVII rectangular; tVIII weakly trapezoidal and distinctly sclerotized; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with curving stem and sharp tip; lp as in subgeneric description, uniformly rounded in dorsal view (Fig. 3.5A); rca flat and sickle-shaped with serrated ventral margin; lca small, about less than 1/4 length of rca, with hanging tubular process; vesica uniformly cylindrical and thin, forming a single coil; anophore forming asymmetrical tube with prominent dorsal fold.

Female: Unknown.

Distribution: Known from the northern region of Costa Rica, from the provinces of Alajuela and Heredia (Fig. 3.7).

Etymology: Named for the needle-like process of the subgenital plate after the Latin “acutus” meaning sharpened. The gender is feminine.

***Schizoptera (Odontorhagus) angularis*, n. sp.**

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by small body size, ovoid body shape, the dark brown coloration, the rounded process on the posterior margin of sVI, the angular shape of the subgenital plate, the blade-shaped lateral process of the subgenital plate, the small and blunt-tipped right paramere, and the claw-shaped left conjunctival appendage.

HOLOTYPE: **Colombia: Cauca:** PNN Gorgona, Alto el mirador, 2.96666°N

78.18333°W, 180 m, 30 Nov 2000 - 18 Dec 2000, H. Torres 1♂ (00106862) (microscopic

slide mount). PARATYPES: **COLOMBIA: Amazonas:** PNN Amacayacu Matamata [m2],

3.68333°S 70.25°W, 150 m, 12 Mar 2001 - 02 Apr 2001, D. Chota, 1♂ (00077490)

(UCR); 17 Sep 2001 - 01 Oct 2001, D. Chota, 1♂ (00099872) (UCR). **Cauca:** PNN

Gorgona, Alto el Mirador, 2.96666°N 78.18333°W, 180 m, 30 Nov 2000 - 18 Dec 2000,

H. Torres, 2♂ (00106837, 00106862) (UCR). **ECUADOR: Napo:** Waorani, 1km S.

Onkone Gare Camp, 0.63333°N 76.6°E, 220 m, 15 Jan 1994, T. L. Erwin et al., 1♂

(00028361) (USNM); 18 Jan 1994, 1♀ (00028382) (USNM); 20 Jan 1994, 1♂

(00028362) (USNM); 20 Jan 1994, 1♀ (00028383) (USNM); 22 Jan 1994, 1♀

(00028385) (USNM); 22 Jan 1994, 1♂ (00028363), 1♀ (00028384) (USNM); 24 Jan

1994, 3♂ (00028364- 00028366) (USNM); 25 Jan 1994, 1♀ (00028386) (USNM); 25 Jan

1994, 2♀ (00028387, 00028388) (USNM); 21 Jun 1994, 1♂ (00028372) (USNM); 21 Jun 1994, 1♂ (00028371) (USNM); 21 Jun 1994, 1♀ (00028390) (USNM); 21 Jun 1994, 1♂ (00028373), 1♀ (00028393) (USNM); 21 Jun 1994, 1♀ (00028389) (USNM); 21 Jun 1994, 1♀ (00028391) (USNM); 21 Jun 1994, 1♀ (00028395) (USNM); 21 Jun 1994, 2♂ (00028374, 00028376), 1♀ (00028394) (USNM); 21 Jun 1994, 1♀ (00028392) (USNM); 21 Jun 1994, 1♂ (00028377), 1♀ (00028396) (USNM); 21 Jun 1994, 1♂ (00028368) (USNM); 25 Jun 1994, 1♀ (00028397) (USNM); 25 Jun 1994, 1♂ (00028378) (USNM); 25 Jun 1994, 1♀ (00028398) (USNM); 29 Jun 1994, 2♂ (00028380, 00028381) (USNM); 29 Jun 1994, 1♂ (00028379), 1♀ (00028400) (USNM); 29 Jun 1994, 1♀ (00028401) (USNM); 29 Jun 1994, 1♀ (00028399) (USNM); 03 Jul 1994, 1♀ (00028402) (USNM). **Orellana:** Tiputini Biodiversity Station nr Yasuni National Park, 0.63194°N 76.14417°E, 220 m, 21 Oct 1998, T. L. Erwin et al., 1♀ (00026842), 1♂ (00026843) (USFWS).

Description: *Male*: length: 1.22-1.29 mm; body ovoid. **COLORATION:** general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra. **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: rounded in ventral view (Fig. 3.2); eyes about 1/2 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight, anterior costal cell triangular. ABDOMEN: as in subgeneric description; stVI with rounded process on posterior margin; subgenital plate distinctly asymmetrical, with posterior margin lateral process forming a right angle with longitudinal margin of subgenital plate; process of subgenital plate of blade-like (Fig. 3.5B); tVII rectangular; tVIII parallel-sided; length of tVII about 3/4 length of tVII.

GENITALIA: py as in subgeneric description; rp as in subgeneric description with a short, curving stem and rounded tip; lp as in subgeneric description, tab-shaped in dorsal view (Fig. 3.5B); rca thin and curving; lca small, about less than 1/4 length of rca and claw-shaped; vesica uniformly cylindrical and thin, forming more than three coils; anophore as in generic description.

Female: length: 1.27-1.29 mm; general habitus as in male.

Distribution: Known from two localities in Colombia: Gorgona National Park in the Cauca department and the Amacayacu National Park in Amazonas, and from one locality in the Orellana province in Ecuador.

Etymology: Named for the right angle formed by the lateral process and the longitudinal margin of the subgenital plate after the Latin “angularis” meaning angular.

***Schizoptera (Odontorhagus) ansata*, n. sp.**

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the broadly ovate body shape, the dark brown coloration, the “pan-handle” shaped process of the subgenital plate, the robust and serrated right conjunctival appendage, the toothed hood of the left paramere, and the half-pipe shape of the anophore.

HOLOTYPE: **Guatemala: Baja Verapaz:** Quetzal Res, Los Ranchitos; 15.21549°N – 90.21925; 11-16 Oct 2011; 1♂ (0009170) (FSCA) (microscopic slide mount).

PARATYPES: **GUATEMALA: Baja Verapaz:** Quetzal Res, Los Ranchitos, 15.21549°N 90.21925°W, 11 Oct 2011 - 16 Oct 2011, 37♂ (00091590, 00091695, 00091567, 00091628, 00091703, 00091654, 00091652, 00091697, 00091621, 00091622, 00091639, 00091716, 00091682, 00091708, 00091667, 00091678, 00091704, 00091593, 00091669, 00091619, 00091632, 00091643, 00091693, 00091670, 00091625, 00091692, 00011870, 00091640, 00091684, 00091683, 00091577, 00091564, 00091638, 00091630, 00091657, 00091627, 00091589, 00091681, 00091658) (FSCA).

Description: *Male*: length: 1.53-1.59 mm; body broadly ovate; **COLORATION**: general coloration dark brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: slightly convex in ventral view (Fig. 3.2); eyes about 1/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein nearly straight. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate distinctly asymmetrical, almost forming a right angle with posterior margin of lateral process; process of subgenital plate pan-handle shaped (Fig. 3.5C); tVII rectangular; tVIII rectangular, symmetrical and lightly sclerotized; length of tVII about half length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long stem and blunt tip; lp as in subgeneric description, with elongate dorsal process and toothed anterior hood; rca long and robust with distinctly serrated margin; lca large, about 3/4 size of rca, and lanceolate (Fig. 3.5C); vesica uniformly cylindrical and thin,

forming almost two coils; anophore forming asymmetrical half-pipe with prominent dorsal fold.

Female: Unknown.

Distribution: Known only from type locality (Fig. 3.7).

Etymology: Named for the “pan-handle” shape of the process of the subgenital plate after the Latin “ansa” meaning handle. The gender is feminine.

Schizoptera (Odontorhagus) aspera, n. sp.

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* broadly ovoid body shape, the dark brown coloration, the rounded head, the small, tooth-like process on the posterior margin of sVI, the single, jagged, hitch-hikers thumb-like process of the subgenital plate, the needle-shaped right conjunctival appendage, and the bifurcating left conjunctival appendage.

HOLOTYPE: **COSTA RICA: San Jose: Moravia Co.:** Zurqui de Moravia, 10.04808°N 84.01394°W, 1600 m, Jun 1993 - Jul 1993, P. Hanson, 1♂ (00102951) LACM, (microscopic slide mount). PARATYPES: **COSTA RICA: San Jose: Moravia Co.:** Zurqui de Moravia, 10.04808°N 84.01394°W, 1600 m, Jun 1993 - Jul 1993, P. Hanson, 1♂ (00102949) (LACM); 2♂(00014769, 00014501) (INBIO); **COSTA RICA: Limon: Pococi Co.:** R.F. Cordillera Volcanica Central, Las Minas, 10.18467°N

83.91361°W, 400 m, 09 May 2012 - 16 May 2012, W. Porras, 5♂(00014789, 00014778, 00014780, 00014770, 00014779), 4♀ (00014783, 00014768, 00014772, 00014766) (INBIO).

Description: *Male*: length: 1.43-1.49 mm; body broadly ovoid. **COLORATION**: general coloration dark brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C concolorous with remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: distinctly rounded in ventral view (Fig. 3.2); eyes about 1/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein slightly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with a small, tooth-like process on posterior margin; subgenital plate weakly asymmetrical, with jagged margins a single lateral process; process of subgenital plate jagged, and shaped like a hitch-hiker's thumb (Fig. 3.5D); tVII rectangular; tVIII weakly trapezoidal and distinctly sclerotized; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with curving stem pointed tip; lp as in subgeneric description, with a funnel-shaped dorsal process (Fig. 3.5D); rca needle-shaped; lca small, about less than 1/4 length of rca, with with a rounded base and two sharp bifurcations; vesica uniformly cylindrical and thin, forming a single coil; anophore as in subgeneric description.

Female: length: 1.47-1.49 mm; general habitus as in males.

Distribution: Known from two localities in northern Costa Rica in the provinces of Limon and San Jose (Fig. 3.7).

Etymology: Named for the jagged appearance of the subgenital plate after the Latin “asper” meaning rough or coarse. The gender is feminine.

Schizoptera (Odontorhagus) bipartita McAtee and Malloch, 1925

(Figs 2 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* ovoid body shape, the lack of a fuscous patch, and the leaf-like lateral process of the subgenital plate.

HOLOTYPE: **GUATEMALA: Izabal:** Livingston, 15.8333°N 88.75°W, 12 May 1906, Barber and Schwarz, 1♂ (00028601) (USNM).

Description: *Male*: length: 1.25 mm; body ovoid. **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.2).

SURFACE AND VESTITURE: as in subgeneric description. **STRUCTURE:** HEAD:

slightly rounded in dorsal view (Fig. 3.2); eyes about 1/2 as wide as synthlipsis;

THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2

vein slightly curving anteriorly toward wing margin, anterior membranal cell wedge-

shaped. ABDOMEN: as in subgeneric description; stVI with a rounded process on

posterior margin; subgenital plate distinctly asymmetrical; process of subgenital plate

robust and leaf-like.

Female: length: 1.25; general habitus as in males.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No additional specimens examined matched the description of this species or the holotype, and ventral images of the holotype are unavailable; therefore our re-description is solely somatic. For an illustration of the subgenital plate of this species see McAtee and Malloch (1925) Figure 59.

***Schizoptera (Odontorhagus) brevis*, n. sp.**

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the relatively small size, the light brown coloration, the small finger-like process of the subgenital plate, the large, curving and serrated right conjunctival appendage and the slender, needle-like left conjunctival appendage.

HOLOTYPE: PANAMA: Canal Zone: Barro Colorado Island, 9.16667°N 79.85°W, 13 Jan 1959, H. S. Dybas, 1♂ (00090738) (FMNH). (microscopic slide mount).

PARATYPES: PANAMA: Bocas del Toro: 8.8 km W Rambala, Rio La Gloria, 8.98444°N 82.2325°W, 08 Jan 2001, M. Yoder & J. B. Woolley, 1♀ (00093443) (TAMU). **Colon:** Rio Guanche, 5 km S Portobelo, 9.50337°N 79.66505°W, 30 m, 18 Jul 1999, J. B. Woolley, 1♂ (00093571), 1♀ (00093570) (TAMU)

Description: *Male*: length: 1.15-1.19 mm; body ovoid. **COLORATION**: general coloration light brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.2), pigmentation of corium slightly extending into cubital cell and anal region of membrane; **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: **HEAD**: flat in ventral view (Fig. 3.2); eyes about 1/2 as wide as synthlipsis; **THORAX**: as in subgeneric description; hemelytron as in subgeneric description; M2 vein slightly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. **ABDOMEN**: as in subgeneric description; stVI with a small, tab-like process on posterior margin; subgenital plate distinctly asymmetrical, with left side reduced (Fig. 3.5E); process of subgenital plate smooth, and finger-like; tVII weakly trapezoidal, almost hemispherical; tVIII weakly trapezoidal and distinctly sclerotized; length of tVII about 1/2 length of tVIII. **GENITALIA**: py as in subgeneric description; rp small, obscured by rca; lp as in subgeneric description, with a bilobed dorsal process (Fig. 3.5E); rca large, robust and distinctly serrated at apex and wrapping around anophore; lca small and thin, about less than 1/4 length of rca, with a tapering, needle-like apex; vesica short and tapering, forming a single coil; anophore as in subgeneric description.

Female: 1.19 mm; general habitus as in male, with head slightly broader than in males.

Distribution: Known from three localities in Panama, the Canal Zone, the costal province of Bocas del Toro and the Colon province (Fig. 3.7).

Etymology: Named for the small body size, and the small process of the subgenital plate after the Latin "brevis" meaning small or short.

Schizoptera (Odontorhagus) clodius McAtee and Malloch, 1925

(Figs 2 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* ovoid body shape, the lack of a fuscous patch, and the tapering lateral process of the subgenital plate.

HOLOTYPE: **PANAMA: Canal Zone:** Paraiso, 9.03333°N 79.625°W, Apr 11, E.A. Schwarz, Holotype, 1♂ (00028602) (USNM).

Re-Description: *Male*: length: 1.38 mm; body ovoid. **COLORATION:** general coloration dark brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly rounded in dorsal view (Fig. 3.2); eyes about 1/2 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein slightly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with small process on posterior margin; subgenital plate distinctly asymmetrical with a u-shaped incision; process of subgenital plate spine-like and point caudally.

Female: Unknown.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No additional specimens examined matched the description of this species or the holotype, and ventral images of the holotype are unavailable; therefore our re-description is solely somatic. For an illustration of the subgenital plate of this species see McAtee and Malloch (1925) Figure 62.

Schizoptera (Odontorhagus) commodus (McAtee and Malloch 1925)

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* elongate, ovoid body shape, flat head, the small, the single hook-like process of the subgenital plate (sVII), the tapering and serrated right conjunctival appendage, and the pronged left conjunctival appendage.

HOLOTYPE: **GUATEMALA: Izabal:** Livingston, 15.8333°N 88.75°W, 09 May 1906, Barber and Schwarz, 1♂ (00028603) (USNM). PARATYPES: **BELIZE: Cayo:** British Honduras: Cayo Dist Mile 66, Western Highway, 17.20228°N 88.64395°W, 30 Jun 1969, 1♂ (00091587) (FSCA); 03 Jul 1969 1♂ (00091739) (FSCA); 07 Jul 1969, 2♂ (00091618, 00091601), 1♀ (00091620) (FSCA); 06 Jul 1970, 1♂ (00091719) (FSCA).

Re-description: *Male*: length: 1.22-1.31 mm; body elongate ovoid. **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: flat ventral view (Fig. 3.2); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2

vein straight, anterior membranal cell triangular-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate hook-shaped, pointing caudally (Fig. 3.5F); tVII trapezoidal; tVIII weakly trapezoidal and distinctly sclerotized; length of tVII about 1/2 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a tapering stem and pointed tip; lp crescent shaped in dorsal view (Fig. 3.5F); rca elongate, with smooth base and serrated tip; lca about 1/3 length of rca, with two visible thick prongs; vesica uniformly cylindrical and thin, forming a single coil; anophore as in subgeneric description with a triangular process on dorsal wall (Fig. 3.5F).

Distribution: Known from the department of Izabal in northeastern Guatemala and the Cayo district in central Belize (Fig. 3.7).

Schizoptera (Odontorhagus) decius (McAtee and Malloch 1925)

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* elongate, ovoid body shape, flat head, the small, the blunt, upward curving process of the subgenital plate (sVII), the robust and curving right paramere, and the pronged left conjunctival appendage.

HOLOTYPE: **PANAMA: Canal Zone:** Gatún, 9.31646°N 79.80035°W, 07 Apr 1911, E.A. Schwarz, 1♂ (00028604) (USNM). PARATYPES: **PANAMA: Canal Zone: Barro**

Colorado Island Co.: Barro Colorado Island, 9.15472°N 79.84806°W, 16 Jan 1959, H. S. Dybas, 2 ♂ (00090804, 00090806) (FMNH). **Cocle: Antón District Co.:** Panama: Cocle Rio Indio Lodge, N El Valle, 8.6008°N 80.1303°W, 24 Feb 2012 - 27 Feb 2012 1♂ (00091641), 1 juv (00091722) (FSCA).

Re-description: *Male:* length: 1.22-1.27 mm; body ovoid. **COLORATION:** general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C concolorous distinctly lighter than remainder of hemelytra (Fig. 3.2), pigmentation of corium slightly extending into cubital cell and anal region of membrane. **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly rounded ventral view (Fig. 3.2); eyes about 1/2 as wide as synthipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein slightly curving, anterior membranous cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with large rounded process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate blunt and rectangular, pointing apically (Fig. 3.5G); tVII rectangular; tVIII rectangular and distinctly sclerotized; length of tVIII about 1/2 length of tVII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a curving tapering stem and pointed tip; lp triangular in dorsal view; rca elongate and needle-shaped; lca about 1/4 length of rca, with two prong-like processes in dorsal view; vesica uniformly cylindrical and thin, forming almost two coils; anophore as in subgeneric description.
Female: Unknown.

Distribution: Known from three localities in southern Panama (Fig. 3.7).

***Schizoptera (Odontorhagus) dentatis*, n. sp.**

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the broadly ovate body shape, the small eyes, the large tooth-like process of sVI, the tooth-shaped lateral process of the subgenital plate, and the spatulate lca.

HOLOTYPE: COSTA RICA: Alajuela: Guatuso Co.: P.N. Volcan Tenorio, Punto 1:

Catarata Rio Buenavista, 10.70466°N 84.99094°W, 800 m, J. A. Azofeifa, 1♂

(00014763) (INBio) (microscopic slide mount). **PARATYPES: COSTA**

RICA: Alajuela: Guatuso Co.: Cote. Fca. Justo Robles, 10.59187°N 84.85917°W, 494 m, 13 Jul 2010 - 07 Aug 2010, J. A. Azofeifa, 1♀ (00014540) (INBIO). P.N. Volcan

Tenorio, Punto 1: Catarata Rio Buenavista, 10.70466°N 84.99094°W, 800 m, 02 Jul

2008 - 04 Jul 2008, 2♂ (00014747,00014748) (INBIO); 13 Jan 2010 - 30 Jan 2010, 4♂

(00014476,00014502,00014525,00014762) (INBIO); P.N. Volcan Tenorio, Punto 2:

Falda N Cerro Montezuma, 10.69665°N 85.01652°W, 1160 m, 05 May 2008 - 07 May

2008, 4♂ (00014749,00014750,00014856,00014759), 2♀ (00014496,00014495)

(INBIO). P.N. Volcan Tenorio, Punto 4: Cerro Montezuma, 10.69369°N 85.02565°W,

1510 m, 05 May 2008 - 07 May 2008, 1♂ (00014494), 2♀ (00014480,00014481)

(INBIO); 30 Aug 2008 - 01 Sep 2008, 1♀ (00014753) (INBIO). P.N. Volcan Tenorio.

Punto 3: Los Pelados Falda N Cerro Montezuma, 9.6551°N 85.0679°W, 1300 m, 05 May 2008 - 07 May 2008, J. A. Azofeifa, 7♂

(00014755,00014482,00014754,00014744,00014746,00014760,00014758) (INBIO); 02

Jul 2008 - 04 Jul 2008, J. A. Azofeifa, 1♂ (00014752) (INBIO). P.N V. Tenorio. Est.

Pilou, 10.6713°N 85.01254°W, 700 m, 21 May 2009 - 23 May 2009, J. A. Azofeifa, M. A. Zumbado, 1 ♀ (00014765) (INBIO). Upala. Bjugua, San Miguel, Finca Inti - Aura, 10.89792°N 85.01454°W, 300 m, 18 Sep 2011 - 16 Oct 2011, I. Chacon, 1 ♂ (00014542) (INBIO); 24 Feb 2013 - 28 Apr 2013, I. Chacon, 1 ♂ (00014505), 1 ♀ (00014506) (INBIO); 25 Aug 2013 - 06 Oct 2013, I. Chacon, 3 ♂ (00014538,00014530,00014539) (INBIO).

Description: *Male*: length: 1.39-1.44 mm; body broadly ovate; **COLORATION**: general coloration dark brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C concolorous with remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: slightly convex in ventral view (Fig. 3.2); eyes about 1/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 distinctly curving, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with large, tooth-like process posterior margin; subgenital plate weakly asymmetrical, with lateral margin perpendicular to lateral process slightly curving and distinctly sclerotized; process of subgenital plate "tooth" shaped, with small serration on posterior margin; tVII trapezoidal; tVIII oblong and sclerotized; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long, narrow stem and blunt tip; lp as in subgeneric description, with elongate dorsal finger-like process; rca narrow and thin; lca large, about 1/4 size of rca, and spatulate (Fig. 3.5H); vesica uniformly cylindrical and thin, forming almost two coils; anophore forming asymmetrical tube with prominent dorsal fold.

Female: length 1.42-1.44 mm; general habitus as in males, with a broader head.

Distribution: Known from various collection events in the Volcan Tenorio National Park in the Alajuela province in northern Costa Rica (Fig. 3.7).

Etymology: Named for the tooth-like process of the posterior margin of sVI and the tooth-like process of the subgenital plate after the Latin “dentatis” meaning toothed.

***Schizoptera (Odontorhagus) dolosa*, n. sp.**

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the ovoid body shape, the large eyes, the short, tapering and serrated vesica, the two dorsal keels of the anophore, and the distinctly sclerotized tips of the pygophore.

Holotype: **Costa Rica: COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N

84.01667°W, 01 Aug 1995, 1♂ (00086489) (LACM) (microscopic slide mount).

PARATYPES: **COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N 84.01667°W, 01 Aug 1995, 4♂ (00086514,00086529,00086542,00086490)

Description: *Male*: length: 1.41-1.43 mm; body ovoid; **COLORATION**: general coloration light brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: flat in ventral view (Fig. 3.2); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein nearly distinctly curving anteriorly toward wing margin.

ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate simple and tab-shaped (Fig. 3.5I); tVII trapezoidal; tVIII weakly rectangular and distinctly sclerotized; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description, with inner-lateral margins distinctly sclerotized; rp as in subgeneric description with a long, thick stem and fin-like tip; lp as in subgeneric description, with a bi-lobed dorsal process; rca narrow and thin; lca large, about 1/2 size of rca, with a rounded base and a triangular tip (Fig. 3.5I); vesica thick and tapering with distinct serrations at apex, not forming a coil; anophore forming an asymmetrical tube with a prominent dorsal fold and two dorsal keels (Fig. 3.5I).

Female: Unknown.

Distribution: Known only from type locality (Fig. 3.7).

Etymology: Named after the Latin “dolosus” meaning cunning and deceitful because of the deceitfully simple appearance of the subgenital plate, but the extremely intricate and bizarre morphology of the genitalia. The gender is feminine.

Schizoptera (Odontorhagus) drusus McAtee and Malloch, 1925

(Figs 2 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* ovoid body shape, the lack of a fuscous patch, and the cylindrical and tapering lateral process of the subgenital plate.

HOLOTYPE: **GUATEMALA: Alta Verapaz:** Cacao Trece Aguas, 15.4°N 89.75°W, Mar 30, Schwarz & Barber, Holotype, 1♂ (00028605) (USNM).

Re-description: *Male*: length: 1.5 mm; body ovoid. **COLORATION**: general coloration dark brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: flat dorsal view (Fig. 3.2); eyes about 1/2 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight, anterior membranal cell triangular. ABDOMEN: as in subgeneric description; stVI with small, tooth-like process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital cylindrical and tapering.

Female: Unknown.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No additional specimens examined matched the description of this species, and ventral images of the holotype are unavailable; therefore our re-description is solely somatic. For an illustration of the subgenital plate of this species see McAtee and Malloch (1925) Figure 65.

Schizoptera (Odontorhagus) enigmatica, n. sp.

(Figs 2, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the large body size, the dark brown coloration, the distinct, asymmetrical subgenital plate with a large, irregular incision and two process, the elongate, club-shaped anterior process of the subgenital plate, the jagged tab-like posterior process of the subgenital plate, the curving and distinctly sclerotized left process of the pygophore, and the serrated dorsal surface of the anophore.

HOLOTYPE: **PANAMA: Panama: Cerro Campana**, 8.68333°N 79.91667°W, 13 Feb 1959, Henry S. Dybas, 1♂ (00086489) (FMNH) (microscopic slide mount). PARATYPE: **PANAMA: San Blas**: 2 km N. Nusagandi, 9.35806°N 78.97833°W, 400 m, 14 Jan 2001, M. Yoder & J. B. Woolley, 1♂ (00093436) (TAMU).

Description: *Male*: length: 1.51-1.53 mm; body broadly ovate; **COLORATION**: general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.2). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: slightly rounded in ventral view (Fig. 3.2); eyes about 1/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight; anterior membranal cell triangular. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate distinctly asymmetrical, with a large, irregular incision; anterior process of subgenital plate elongate, club shaped and curving (Fig. 3.5J); posterior

process of subgenital plate jagged and tab-like; tVII weakly rectangular; tVIII weakly rectangular with a sharpened posterior margin on the left; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description, with an elongate, curving and sclerotized process on left margin; rp as in subgeneric description with a long, thick stem and fin-like tip; lp as in subgeneric description with two tubular dorsal processes; rca tapering with serrated margin; lca small, about 1/4 size of rca, and y-shaped (Fig. 5J); vesica short and tapering forming almost one coil; anophore forming an asymmetrical tube with a prominent dorsal fold and distinct serrations on dorsal surface (Fig. 3.5J).

Female: Unknown.

Distribution: Known from two localities in Panama: the Altos de Campana National Park in Panama province, and the San Blas region (now Guna Yala) on the northeast coast (Fig. 3.7).

Etymology: Named for the bizarre subgenital plate morphology after the Latin “enigmaticus” meaning mysterious or puzzling. The gender is feminine.

Schizoptera (Odontorhagus) exacta, n. sp.

(Figs 3, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the slightly concave head, the large eyes, the lobed process of the posterior margin of sVII, the distinctly asymmetrical subgenital plate, and the notched lateral process of the subgenital plate.

HOLOTYPE: **COSTA RICA: Heredia:** La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 19 May 1998, INBio-OET-ALAS, 1♂ (00109155) (INBIO). (microscopic slide mount). PARATYPES: **COSTA RICA: Heredia:** La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 02 Feb 1998, INBio-OET-ALAS,(00109233), 1♂ (00109234) (INBIO); 16 Feb 1998, INBio-OET-ALAS, 4♂(00109476, 00109477) (INBIO); 16 Apr 1998, INBio-OET-ALAS, 1♂ (00109475) (INBIO); **PANAMA: Canal Zone: Barro Colorado Island Co.:** Barro Colorado Island, 9.15472°N 79.84806°W, 14 Jan 1959, H. S. Dybas, 1♂ (00090790) (FMNH); 16 Jan 1959, H. S. Dybas, 1♀(00090807) (FMNH); 21 Jan 1959, H. S. Dybas, 1♂ (00090817) (FMNH). Barro Colorado Island, 9.16667°N 79.85°W, 13 Jan 1959, H. S. Dybas, 1♂ (00090739) (FMNH). **Cocle: Antón District Co.:** Cocle Rio Indio Lodge, N El Valle, 8.6008°N 80.1303°W, 24 Feb 2012 - 27 Feb 2012, 5♂(00091591, 00091664, 00091680, 00091592, 00091612) (FSCA).

Description: *Male*: length: 1.39-1.42 mm; body broadly ovate; **COLORATION:** general coloration light brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly concave in ventral view (Fig. 3.3); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with a strout, tab-like process on posterior margin; subgenital plate distinctly asymmetrical, almost forming a right angle with posterior margin of lateral

process; process of subgenital plate thumb-shaped, with an notch on anterior margin, almost forming “key and lock” with process of sVI; (Fig. 3.5K); tVII rectangular; tVIII weakly trapezoidal and sclerotized; length of tVII about 3/4 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long, narrow stem and blunt tip; lp as in subgeneric description, with two visible lobate dorsal processes; rca narrow and thin, mostly obscured by vesica; lca with three finger-like processes (Fig. 5K); vesica uniformly thin and tubular, almost forming three coils; anophore forming an asymmetrical tube with a prominent dorsal fold forming a hollow slit in dorsal view (Fig. 3.5K).

Female: length 1.42 mm; general habitus as in males.

Distribution: Known from one locality in the Heredia province in northern Costa Rica, and two localities in Panama: the Canal Zone and the southern province of Coclé (Fig. 3.7).

Etymology: Named for the “key and lock” appearance of the process of sVI and the notched margin of the lateral process of the subgenital plate after the Latin “exactus” meaning exact because of the knob and tab appearance of the. The gender is feminine.

Schizoptera (Odontorhagus) gorgonensis, n. sp.

(Figs 3, 5 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the slightly concave head, the large eyes, the weakly asymmetrical subgenital plate, and the simple, thumb-like lateral process of the subgenital plate.

HOLOTYPE: COLOMBIA: Cauca: PNN Gorgona, Alto el Mirador, 2.96666°N 78.18333°W, 180 m, 03 Aug 2000 - 16 Aug 2000, H. Torres, 1♂ (00078124) (microscopic slide mount). **PARATYPES: COLOMBIA: Boyacá:** SFF Iguaque La Planada, 5.7°N 73.45°W, 2850 m, 19 Apr 2000 - 06 May 2000, P. Reina, 5♂ (00076293,00076300,00076297,00076275,00076273) (UCR). **Cauca:** PNN Gorgona, Alto el Mirador, 2.96666°N 78.18333°W, 180 m, 10 Jun 2000 - 26 Jun 2000, H. Torres, 5♂ (00081350,00081358,00081357,00081351,00081343) (UCR); 03 Aug 2000 - 16 Aug 2000, H. Torres, 1♂ (00078109), 1♀ (00078101) (UCR); 06 Oct 2000 - 23 Oct 2000, R. Duque, 2♂ (00115605,00115614) (UCR); 30 Nov 2000 - 18 Dec 2000, H. Torres, 1♂ (00106944) (UCR). PNN Gorgona, Antigua Laguna, 2.96667°N 78.18333°W, 70 m, 18 Jan 2001 - 03 Feb 2001, H. Torres, 1♂ (00100667) (UCR). PNN Gorgona, El Helechal, 2.96667°N 78.18333°W, 30 m, 22 Mar 2001 - 13 Apr 2001, R. Duque, 1♂ (00112583) (UCR); 23 Jun 2001 - 15 Jul 2001, H. Torres, 1♂ (00092754) (UCR). **ECUADOR: Napo:** Waorani, 1km S. Onkone Gare Camp, 0.63333°N 76.6°E, 220 m, 19 Jan 1994, T. L. Erwin et al., 1♀ (00028404) (USNM); 22 Jan 1994, 1♀ (00028403) (USNM); 23 Jan 1994, 1♀ (00028405), 1♂ (00028408) (USNM); 23 Jan 1994, 2♀ (00028406,00028407) (USNM); 21 Jun 1994, 1♂ (00028409) (USNM); 21 Jun 1994, 1♀ (00028413) (USNM); 25 Jun 1994, 2♂ (00028410,00028411) (USNM); 03 Jul 1994, 1♂ (00028412) (USNM)

Description: *Male*: length: 1.41-1.46 mm; body broadly ovate; **COLORATION:** general coloration light brown; fuscous patch covering less than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:**

as in subgeneric description. **STRUCTURE:** HEAD: slightly concave in ventral view (Fig. 3.3); eyes wider than synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate short and thumb-shaped (Fig. 3.5L); tVII rectangular; tVIII weakly trapezoidal and sclerotized; length of tVII about 1/2 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long, narrow stem and blunt tip and a medial dorsal flap; lp as in subgeneric description, with two visible triangular dorsal processes; rca narrow and thin, mostly obscured by vesica; lca with three finger-like processes (Fig. 3.5L); vesica with a thick base, and uniformly thin and tubular apex, almost forming two coils; anophore as in subgeneric description, with a short blunt process on dorsal wall (Fig. 3.5L).

Female: length 1.44-1.46 mm; general habitus as in males.

Distribution: Known from the western region of northern South America from two localities in Colombia (Cauca department and Boyacá) and one locality in the Napo province in Ecuador (Fig. 3.7).

Etymology: Named after the Gorgona National Park in Colombia, where the majority of specimens were collected.

***Schizoptera (Odontorhagus) insidiosa*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by flat head, the large eyes, the distinctly asymmetrical subgenital plate, the notched lateral process of the subgenital plate, the tubular and serrated right conjunctival appendage, the supercoiled vesica, and the large aperture of the anophore.

HOLOTYPE: **COLOMBIA: Cauca:** PNN Gorgona El Saman, 2.96667°N 78.18333°W, 5 m, 13 Apr 2001 - 07 May 2001, T. Helmer, 1♂ (00087513) ((microscopic slide mount)).

PARATYPES: **COLOMBIA: Cauca:** PNN Gorgona El Saman, 2.96667°N 78.18333°W, 5 m, 13 Apr 2001 - 07 May 2001, T. Helmer, 2♂ (00087514,00087523)

(UCR). **Putumayo:** PNN La Paya Cabaña Chagra, 0.11667°S 74.93333°W, 320 m, 01 Nov 2001 - 15 Nov 2001, R. Cobete, 1♀ (00076330), 2♂ (00076290,00076316)

(UCR). **ECUADOR: Orellana:** Tiputini Biodiversity Station nr Yasuni National Park Erwin Transect - T/10, 0.63194°N 76.14417°E, 220 m, 05 Feb 1999, T. L. Erwin et al., 4♂xd (00028651,00028652) (USFWS); 05 Feb 1999, 1♂ (00028648) (USFWS); 05 Feb 1999, 2♂ (00028665,00028666) (USFWS). Transect Ent. 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, Onkone Gare Camp, 0.65714°N 76.453°E, 216 m, 25 Jun 1996, 9♂ (00028668- 00028670) (USFWS).

Description: *Male*: length: 1.41-1.44 mm; body broadly ovate; **COLORATION:** general coloration brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description.

STRUCTURE: HEAD: flat in ventral view (Fig. 3.3); eyes about 2/3 wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate short and thumb-shaped (Fig. 3.6M); tVII rectangular; tVIII weakly trapezoidal and sclerotized; length of tVII about 1/2 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long, tapering stem; lp as in subgeneric description, with two lobate dorsal processes; rca narrow and thin with a serrated base; lca large, about 1/2 length of rca with two finger-like processes (Fig. 3.6M); vesica uniformly thin and tubular, forming more than four coils; anophore as in subgeneric description, with a blunt finger-like process on dorsal wall, and a wide dorsal aperture (Fig. 3.6M).

Female: length 1.44 mm; general habitus as in males.

Distribution: Known from the western region of northern South America from the western Colombian district of Cauca and the southwestern district of Putumayo, and from the neighboring province of Orellana in northern Ecuador.

Etymology: Named after the Latin “insidiosus” meaning deceitful because of the superficial similarity between to the subgenital plate of *S. exacta*, n. sp. The gender is feminine.

Schizoptera (Odontorhagus) kirkpatricki Emsley, 1969

(Figs 4 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* ovoid body shape, the lack of a fuscous patch, and the small and notched blade-like process of the subgenital plate.

HOLOTYPE: **TRINIDAD AND TOBAGO: Arima:** William Beebe Tropical Research Station (Simla), 10.68361°N 61.28333°W, 04 Jul 1961, Emsley, M. G., Light Trap, Paratype, 1♂ (AMNH_IZC 00150342) (AMNH).

Re-description: *Male*: length: 1.33 mm; body ovoid. **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.4). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly rounded in dorsal view (Fig. 3.4); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight; anterior membranal cell triangular. ABDOMEN: as in subgeneric description; stVI with a small rounded process on posterior margin; subgenital plate distinctly asymmetrical; process of subgenital elongate, notched anteriorly and with a straight posterior margin.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No additional specimens examined matched the description of this species. Only slide mount type images were available (Fig. 3.4). For an excellent illustration of the subgenital plate of this species see Emsley (1969) Figure 248.

***Schizoptera (Odontorhagus) monstrosa*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by rounded head, the distinctly asymmetrical subgenital plate, with a small slit-like lateral incision and a triangular caudal incision, the broad and lobe-shaped process of the subgenital plate, the bifurcating process of the right paramere, trifurcating right conjunctival appendage, the short, serrated and forking vesica, and the dorsal hump of the anophore.

HOLOTYPE: **PANAMA: Cocolé:** Antón District Co.: Panama: Cocolé Rio Indio Lodge, N El Valle, 8.6008°N 80.1303°W, 24 Feb 2012 - 27 Feb 2012, 1♂ (00091615) (FSCA) microscopic slide mount.

Description: *Male*: length: 1.46 mm; body broadly ovate; **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description.

STRUCTURE: HEAD: slightly rounded in ventral view (Fig. 3.3); eyes about 1/2 as wide as synthipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving anteriorly toward wing margin, anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on

posterior margin; subgenital plate distinctly asymmetrical, with a small lateral and large caudal incisions (Fig. 3.6N) forming the process of subgenital plate; process of subgenital plate broad and round; tVII rectangular; tVIII weakly trapezoidal and sclerotized; length of tVII about 1/2 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a long, tapering stem; lp as in subgeneric description, with two lobate dorsal processes; rca narrow and thin with a serrated base; lca small, about 1/4 length of rca and spatulate with a toothed tip (Fig. 6N); vesica short and serrated with a forked apex, anophore as in subgeneric description, with a dorsal hump (Fig. 3.6N).

Female: Unknown.

Distribution: Known only from the type locality.

Etymology: Named after the Latin “monstruosus” meaning monstrous because of the monstrous morphology of the subgenital plate and the uniquely forked vesica and bifurcating process of the right paramere. The gender is feminine.

Schizoptera (Odontorhagus) piscicaudata, n. sp.

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by rounded head, the weakly asymmetrical subgenital plate, the “fishtail” shaped process of the subgenital plate, and the tapering right conjunctival appendage with a serrated tip.

HOLOTYPE: Holotype: COSTA RICA: Heredia: La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 16 Apr 1998, INBio-OET-ALAS, 1♂ (00109171) (INBIO) microscopic slide mount. **PARATYPE: PANAMA:** Canal Zone: Barro Colorado Island Co.: Barro Colorado Island, 9.15472°N 79.84806°W, 14 Jan 1959, H. S. Dybas, 1♂ (00090791) (FMNH).

Description: *Male:* length: 1.36-1.39 mm; body broadly ovate; **COLORATION:** general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** **HEAD:** slightly rounded in ventral view (Fig. 3.3); eyes about 1/3 as wide as synthlipsis. **THORAX:** as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight; anterior membranal cell triangular. **ABDOMEN:** as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate fishtail shaped (Fig. 3.6O); tVII rectangular; tVIII weakly rectangular and sclerotized; length of tVII about 1/2 length of tVIII. **GENITALIA:** py as in subgeneric description; rp as in subgeneric description with a hook-like stem; lp as in subgeneric description, with two triangular dorsal processes; rca tapering with a serrated tip; lca small, about 1/4 length of rca, with blunt and fin-shaped processes juxtaposed in a twist (Fig. 6O); uniformly thin with a needlelike tip; anophore as in subgeneric description.

Female: Unknown.

Distribution: Known from a single locality in the northern Costa Rican province of Heredia and a single locality in the Canal Zone in Panama (Fig. 3.7).

Etymology: Derived from the Latin “piscis” meaning fish and “caudatus” meaning tailed.

The gender is feminine.

***Schizoptera (Odontorhagus) quasicompleta*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the rounded head, the weakly asymmetrical subgenital plate, the tab-like process of stVI, the small, blunt process of the subgenital plate, the needlelike right conjunctival appendage, and the uniformly thin stem of the right paramere.

HOLOTYPE: **COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N 84.01667°W, 03 May 1993, 1♂ (00109145) (INBio) (microscopic slide mount). PARATYPES: **COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N 84.01667°W, 03 May 1993, UnKnown, 1♂ (00084191) (LACM). La Selva Biol. Sta., 10.43056°N 84.00667°E, 58 m, 13 Feb 2002 - 15 Feb 2002, B. Brown, L. Gonzales, and K. Walker, 1♂ (00096271) (UCR); 14 Aug 2010, J. Mottern, 2♀ (00081614,00082318) (UCR). La Selva Biol. Sta., Arborita trail, 10.43028°N 84.00722°E, 64 m, 10 Aug 2010, J. Mottern, 2♀ (00122238,00122239) (INBIO). La Selva Biological Station, Jaguar trail entrance, 10.43111°N 84.02389°E, 60 m, 21 May 2011, J. Heraty & E. Murray, 1♀ (00084362) (UCR). La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, INBio-OET-ALAS, 4♂ (00109180,00109181) (INBIO); 16 Feb 1998, INBio-OET-ALAS, 4♂xd (00109178,00109179) (INBIO); 16 Apr 1998, INBio-OET-ALAS, 4♂xd

(00109172,00109173) (INBIO); 16 Apr 1998, INBio-OET-ALAS, 4♂ (00109146-00109149) (INBIO); 19 May 1998, INBio-OET-ALAS, 1♂ (00109154) (INBIO); 30 Dec 1999, INBio-OET-ALAS, 2♀ (00109121,00109122), 1♂ (00109123) (INBIO).

Description: *Male*: length: 1.39-1.42 mm; body broadly ovate; **COLORATION**: general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C concolorous with remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: slightly rounded in ventral view (Fig. 3.3); eyes about 1/3 as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with a tab-like process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate blunt, not fully differentiated from subgenital plate (Fig. 3.6P); tVII rectangular; tVIII weakly rectangular and sclerotized; length of tVII about 1/3 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description with a uniformly thin stem; lp as in subgeneric description, with a blunt triangular dorsal process; rca needlelike; lca with a short, about 1/3 length of rca, tapering tip (Fig. 3.6P); vesica uniformly thin with a needlelike tip, forming two coils; anophore as in subgeneric description with a tab-like dorsal flap (Fig. 3.6P).

Female: length 1.42 mm; general habitus as in males.

Distribution: Known from multiple collection events at the La Selva Biological station in Costa Rica (Fig. 3.7).

Etymology: Derived from the Latin “quasi” meaning as if and “completus” meaning completed because of the seemingly “entire” look of the subgenital plate in ventral view. The gender is feminine.

Schizoptera (Odontorhagus) radicata, n. sp.

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the rounded head, the weakly asymmetrical subgenital plate, the bifurcating, root-shaped process of the subgenital plate, the bifurcating right conjunctival appendage, the ladle-shaped right paramere, and the rectangular dorsal process of the left paramere.

HOLOTYPE: **COSTA RICA: Heredia:** La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 16 Apr 1998, INBio-OET-ALAS, 1♂ (00109170) (INBIO) (microscopic slide mount). PARATYPES: **COSTA RICA: Heredia:** La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 16 Apr 1998, INBio-OET-ALAS 1♂ (00109152) (INBIO). **Puntarenas: San Vito Co.:** Las Cruces Biological Station, 8.78556°N 82.96°W, 1214 m, 27 Sep 2014, A. Knyshov, S. Leon and C. Weirauch, 2♂ (00122962,00122977) (UCR).

Description: *Male*: length: 1.36-1.39 mm; body broadly ovate; **COLORATION:** general coloration dark brown; fuscous patch covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly rounded in ventral view (Fig.

3.3); eyes about 1/3 as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital plate stem-like with a bifurcating tip (Fig. 3.6Q); tVII rectangular; tVIII rectangular and sclerotized; length of tVIII about 1/3 length of tVII. GENITALIA: py as in subgeneric description; rp ladle shaped, with a uniformly thin stem and rounded base; lp as in subgeneric description, with an elongate, rectangular dorsal process; uniformly thick, with a bifurcating tip; lca small, about 1/5 length of lca, with a rounded triangular tip (Fig. 3.6Q); vesica uniformly thin with a needlelike tip; anophore as in subgeneric description.
Female: Unknown.

Distribution: Known the northern and southern Costa Rica (Fig. 3.7).

Etymology: Named for the root-like shape of the subgenital plate process after the latin “radicatus” meaning rooted. The gender is feminine.

Schizoptera (Odontorhagus) repetita McAtee and Malloch, 1925

(Figs 3 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* broadly ovoid body shape, the prominent fuscous patch covering more than 1/2 of the wing membrane, and the thin, tomahawk-shaped process of the subgenital plate.

HOLOTYPE: **GUATEMALA: Izabal:** Livingston, 15.8333°N 88.75°W, 04 May 1906, Schwarz & Barber, Holotype, 1♂ (00028606) (USNM).

Re-description: *Male*: length: 1.5 mm; body broadly ovoid. **COLORATION**: general coloration dark brown; fuscous patch absent covering more than 1/2 of wing membrane; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: slightly rounded in ventral view (Fig. 3.3); eyes about 1/3 as wide as synthipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein straight, anterior membranal cell triangular. ABDOMEN: as in subgeneric description; stVI with small, tooth-like process on posterior margin; subgenital plate weakly asymmetrical; process of subgenital thin and tomahawk-shaped.

Female: general habitus as in males.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No specimens examined matched the description of this species, ventral images of the holotype are available, but the pointmout obscures the process of the subgenital plate; therefore our re-description is solely somatic. For an illustration of the subgenital plate of this species see McAtee and Malloch (1925) Figure 61.

Schizoptera (Odontorhagus) serrata, n. sp.

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the flat head, the weakly asymmetrical subgenital plate, the blade-like anterior and serrated posterior bifurcation of the subgenital plate process, the serrated right conjunctival appendage, and the thin and serrated process of the right paramere.

HOLOTYPE: **PANAMA: Colon:** Rio Guanche, 5 km S Portobelo, 9.50337°N

79.66505°W, 30 m, 18 Jul 1999, J. B. Woolley, 1♂ (00093558) (TAMU).

PARATYPES: **PANAMA: Colon:** 2 km S of Sabanitas, 9.32194°N 79.79833°W, 120 m,

04 Jul 1999 - 15 Jul 1999, A. Gillogly & J.B. Woolley, 1♂ (00093561) (TAMU). Rio

Guanche, 5 km S Portobelo, 9.50337°N 79.66505°W, 30 m, 18 Jul 1999, J. B. Woolley,

1♂ (00093560) (TAMU). **San Blas:** 2 km N. Nusagandi, 9.35806°N 78.97833°W, 400 m,

14 Jan 2001, M. Yoder & J. B. Woolley, 1♂ (00093435) (TAMU).

Description: *Male*: length: 1.37-1.39 mm; body amygdaliform; **COLORATION:** general coloration dark brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description.

STRUCTURE: HEAD: flat in ventral view (Fig. 3.3); eyes about 2/3 as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped.

ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; lateral process of subgenital plate bifurcating;

anterior bifurcation of subgenital plate process blade-shaped with a flat posterior margin; posterior bifurcation of subgenital plate process lanceolate with serrated lateral margin (Fig. 3.6R); tVII rectangular; tVIII rectangular and sclerotized; length of tVII about 1/3 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description, with a long and thin serrated process (Fig. 3.6R); lp as in subgeneric description; rca uniformly thick, with a serrated tip; lca small, about 1/5 length of lca, with two processes (Fig. 3.6R); vesica uniformly thin with a needlelike tip; anophore as in subgeneric description with a u-shaped slit.

Female: Unknown.

Distribution: Known from three localities in Panama (Fig. 3.7).

Etymology: Named for the numerous serrated structures on this species after the Latin “serratus” meaning serrated. The gender is feminine.

***Schizoptera (Odontorhagus) simpla*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the flat head, the large eyes, the weakly asymmetrical subgenital plate, small, tab-like process of the subgenital plate, the differentiated left lateral margin of the subgenital plate, the w-shaped left paramere, and the plate-like dorsal fold of the anophore.

HOLOTYPE: **COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N 84.01667°W, 6 Apr 1998, INBio-OET-ALAS, 1♂ (00109150); PARATYPES: **COSTA RICA: Heredia:** Est. Biol. La Selva, 10.43333°N 84.01667°W, 03 May 1993, 2♂ (00088289,00088291) (LACM). La Selva Biological Station, River Station, 10.43°N 84.00472°E, 60 m, 19 May 2011 - 23 May 2011, J. Heraty & E. Murray, 3♂ (00086102,00086114,00086115) (UCR). La Selva Biological Station, nr Puerto Viejo, 10.43086°N 84.00647°W, 52 m, 16 Apr 1998, INBio-OET-ALAS, 1♂ (00109174) (INBIO); 16 Apr 1998, INBio-OET-ALAS, 1♂ (00109151) (INBIO). **Puntarenas:** San Vito Co.: Las Cruces Biological Station, 8.78556°N 82.96°W, 1214 m, 24 Sep 2014, A. Knyshev, S. Leon and C. Weirauch, 2♂ (00122963,00122966), 2♀ (00122964,00122965) (UCR).

Description: *Male*: length: 1.41-1.46 mm; body broadly ovoid; **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: flat in ventral view (Fig. 3.3); eyes about as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical, with left lateral margin differentiated (Fig. 3.6S); lateral process small, stout and tab-like (Fig. 3.6S); tVII rectangular; tVIII rectangular and sclerotized; length of tVII about 2/3 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description; lp as in subgeneric description, w-shaped in dorsal view; rca slender and hook-shaped; lca small, about 1/3 length of rca, with two processes (Fig.

3.6S); vesica uniformly thin with a needlelike tip, forming almost two coils; anophore as in subgeneric description with flat, plate-like dorsal fold (Fig. 3.6S).

Female: length 1.44-1.46 mm; general habitus as in males.

Distribution: Known from Heredia and Puntarenas provinces in Costa Rica (Fig. 3.7).

Etymology: Named for the simple subgenital plate, and relatively simplistic genitalic structures after the Latin “simplus” meaning simple. The gender is feminine.

***Schizoptera (Odontorhagus) singularis*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by rounded head, the large eyes, the weakly asymmetrical subgenital plate, with a conical apex, the robust, rectangular process of the subgenital plate, cashew-shaped left conjunctival appendage, and the broad, serrated process of the right paramere.

HOLOTYPE: **PANAMA: Cocle: Antón District Co.:** Panama: Cocle Rio Indio Lodge, N El Valle, 8.6008°N 80.1303°W, 24 Feb 2012 - 27 Feb 2012, 1♂ (00091644)

(FSCA). PARATYPE: **PANAMA: Cocle: Antón District Co.:** Panama: Cocle Rio Indio Lodge, N El Valle, 8.6008°N 80.1303°W, 24 Feb 2012 - 27 Feb 2012, 1♀ (00091706) (FSCA).

Description: *Male*: length: 1.39 mm; body ovoid; **COLORATION**: general coloration dark brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.3). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: flat in ventral view (Fig. 3.3); eyes about 1/3 as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical, forming a straight line from apex to posterior margin of lateral process (Fig. 3.6T); lateral robust and rectangular (Fig. 3.6T); tVII rectangular; tVIII rectangular and sclerotized; length of tVIII about 3/4 length of tVII. GENITALIA: py as in subgeneric description; rp as in subgeneric description, with a broadly elongate serrated process; lp as in subgeneric description; rca slender and obscured by vesica; lca small, about 1/5 length of rca, and cashew-shaped (Fig. 3.6T); vesica short and tapering with a needlelike tip; anophore as in subgeneric description obscured by rp (Fig. 3.6T).

Female: length 1.42 mm; general habitus as in male.

Distribution: Known only from the type locality (Fig. 3.7).

Etymology: Named for unique morphology of the right paramere after the Latin “singularis” meaning unique.

Schizoptera (Odontorhagus) southwoodi Emsley 1969

HOLOTYPE: **TRINIDAD AND TOBAGO: Arima:** William Beebe Tropical Research Station, 10.68361°N 61.28333°W, 21 Jul 1961, Emsley, M. G., Light Trap, 1♂ (AMNH).

Discussion: Type specimens for this species were deposited in glycerin vials, which have dried out and made it impossible to remove the specimen without destroying it. We do not provide a redescription of this species because we were not able to examine the type specimen. For the description and illustration of genitalia see Emsley (1969) pp. 64-65, and Figure 247.

Schizoptera (Odontorhagus) stricklandi China 1946

(Figs 4, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the flat head, the weakly asymmetrical subgenital plate, the small, undifferentiated triangular process of the subgenital plate, the serrated right conjunctival appendage, the thin and tapering stem of the right paramere, and the heart-shaped dorsal fold of the anophore.

HOLOTYPE: **TRINIDAD AND TOBAGO: Trinidad: Tunapuna-Piarco Regional**

Corporation Co.: St. Augustine, Nov 1943 - Feb 1944, A.H. Strickland, 1♂ (BMNH)

PARATYPES: **BRAZIL: Para: Belem Co.:** 8 km E Belem, Ananindeua, 20 May 1973, R.

T. Schuh, Light Trap, 1♂ (00096382) (AMNH). **TRINIDAD AND**

TOBAGO: Trinidad: Tunapuna-Piarco Regional Corporation Co.: St. Augustine, Nov 1943 - Feb 1944, A.H. Strickland, 1♂ (BMNH).

Redescription: *Male*: length: 1.3 mm; body elongate ovoid; **COLORATION**: general coloration light brown; fuscous patch absent; Sc+C distinctly lighter than remainder of hemelytra (Fig. 3.4). **SURFACE AND VESTITURE**: as in subgeneric description.

STRUCTURE: HEAD: flat in ventral view (Fig. 3.4); eyes about 2/3 as wide as synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped.

ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; lateral process of subgenital triangular, not fully differentiated from subgenital plate; (Fig. 3.6U); tVII rectangular; tVIII weakly rectangular with a distinctly sclerotized posterior margin; length of tVII about 1/3 length of tVIII.

GENITALIA: py as in subgeneric description; rp as in subgeneric description, with a thin, tapering stem (Fig. 3.6U); lp as in subgeneric description; rca thin and obscured by vesica; lca wedge-shaped (Fig. 3.6U); vesica uniformly thin, forming at least one coil; anophore as in subgeneric description heart-shaped dorsal fold, and a prominent slit.

Female: general habitus as in males.

Distribution: Known from the continental island of Trinidad as well as the northeastern state of Pará, Brazil (Fig. 3.7).

Schizoptera (Odontorhagus) trinitatis Emsley, 1969

(Figs 4 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the relatively small body size, ovoid body shape, the distinctly curving M2 vein, the small process of the posterior margin of stVI, and the blade-like process of the subgenital plate.

HOLOTYPE: **TRINIDAD AND TOBAGO: Arima:** William Beebe Tropical Research Station (Simla), 10.68361°N 61.28333°W, 04 Jul 1961, Emsley, M. G., Light Trap, Paratype, 1♂ (AMNH_IZC 00150342) (AMNH).

Re-description: *Male:* length: 1.25 mm; body ovoid. **COLORATION:** general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.4). **SURFACE AND VESTITURE:** as in subgeneric description. **STRUCTURE:** HEAD: slightly rounded in dorsal view (Fig. 3.4); eyes about 2/3 as wide as synthlipsis; THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving anteriorly toward wing margin; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI with a small rounded process on posterior margin; subgenital plate distinctly asymmetrical; process of subgenital elongate and blade-shaped.

Female: general habitus as in males.

Distribution: Known only from the type locality (Fig. 3.7)

Discussion: No additional specimens examined matched the description of this species or the holotype. Only slide mount type images were available (Fig. 3.4). For an excellent illustration of the subgenital plate of this species see Emsley (1969) Figure 248.

***Schizoptera (Odontorhagus) trivialis*, n. sp.**

(Figs 4, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by the flat head, the large eyes, the small blade-like process of the subgenital plate, the cactus-shaped left conjunctival appendage, and the wide slit of the anophore.

HOLOTYPE: **COLOMBIA: Putumayo:** PNN La Paya Cabaña Viviano Cocha, 0.11667°S 74.93333°W, 320 m, 20 Sep 2001 - 26 Sep 2001, D. Campos, 1♂ (00100849) (UCR). PARATYPES: **ECUADOR: Napo:** Res. Ethnica Waorani, 1 km S. Onkone Gare Camp, 39.16667°N 76.43333°E, 220 m, 21 Jun 1994, T. L. Erwin et al., 1♂ (00028432) (USNM); 21 Jun 1994, 2♀ (00028435, 00028436) (USNM); 21 Jun 1994, 1♂ (00028431) (USNM); 21 Jun 1994, 1♂ (00028430) (USNM); 25 Jun 1994, 1♂ (00028433) (USNM); 25 Jun 1994, 1♀ (00028437) (USNM); 25 Jun 1994, 1♂ (00028434), 1♀ (00028439) (USNM). Res. Ethnica Waorani, 1km S. Onkone Gare Camp, 0.63333°N 76.6°E, 220 m, 15 Jan 1994, 1♀ (00028422) (USNM); 18 Jan 1994, 1♀ (00028424) (USNM); 18 Jan 1994, 2♂ (00028415, 00028416) (USNM); 19 Jan 1994, 1♀ (00028425) (USNM); 19 Jan 1994, 1♀ (00028427) (USNM); 19 Jan 1994, 1♀ (00028426) (USNM); 20 Jan 1994, 1♀ (00028428) (USNM); 22 Jan 1994, 2♂ (00028418, 00028419) (USNM); 24 Jan 1994, 1♂ (00028421), 1♀ (00028429) (USNM);

24 Jan 1994, 1 ♂ (00028420) (USNM). **Orellana:** Tiputini Biodiversity Station, nr Yasuni National Park, 0.63194°S 76.14416°W, 250 m, 24 Oct 1998, T. L. Erwin et al., 1 ♀ (00026867), 9 ♂ (00026868- 00026870) (USFWS). Tiputini Biodiversity Station nr Yasuni National Park, 0.63194°N 76.14417°E, 220 m, 26 Oct 1998, 3 ♂ (00026820- 00026822), 1 ♀ (00026823) (USFWS). Transect Ent. 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, Onkone Gare Camp, 0.65714°N 76.453°E, 216 m, 03 Oct 1996, 1 ♀ (00026846) (USFWS).

Description: *Male*: length: 1.38-1.42 mm; body ovoid; **COLORATION**: general coloration light brown; fuscous patch absent; Sc+C concolorous with remainder of hemelytra (Fig. 3.4). **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: HEAD: flat in ventral view (Fig. 3.4); eyes 1 1/3 times wider than synthlipsis. THORAX: as in subgeneric description; hemelytron as in subgeneric description; M2 vein distinctly curving; anterior membranal cell wedge-shaped. ABDOMEN: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; lateral process of subgenital plate blade shaped; (Fig. 3.6V); tVII rectangular; tVIII weakly trapezoidal; length of tVII about 1/2 length of tVIII. GENITALIA: py as in subgeneric description; rp as in subgeneric description; lp as in subgeneric description with two blunt dorsal processes; rca uniformly thin; lca small, about 1/3 length of rca, and cactus-shaped (Fig. 3.6V); vesica uniformly thin, forming at least three coils; anophore as in subgeneric description with a prominent, elongate slit.

Female: length 1.42 mm; general habitus as in males.

Distribution: Known from three localities in the western region of northern South America: the Putumayo department in Colombia, and the Napo and Orellana provinces in Ecuador (Fig. 3.7).

Etymology: Named for the ordinary, rather non-descript shape of the subgenital plate after the Latin “trivialis” meaning trivial or ordinary.

***Schizoptera (Odontorhagus) ungulata*, n. sp.**

(Figs 3, 6 and 7)

Diagnosis: Distinguished among species of *Schizoptera (Odontorhagus)* by claw-shaped process of the subgenital plate, the sickle-like process of the left paramere, the ladle-shaped right paramere, and the brush-like tip of the right conjunctival appendage.

HOLOTYPE: HONDURAS: Atlantida: San Alejo Co.: Honduras: Dept. Atlantida, San Alejo Farm, United Fruit Co., 15.35°N 87.43333°W, 04 Jun 1964, 1♂ (00091829) (microscopic slide mount)(FSCA).

Redescription: *Male*: length: 1.41 mm; body ovoid; **COLORATION**: general coloration light brown. **SURFACE AND VESTITURE**: as in subgeneric description. **STRUCTURE**: **HEAD**: flat in ventral view (Fig. 3.3); eyes about 1/2 as wide as synthlipsis. **THORAX**: as in subgeneric description. **ABDOMEN**: as in subgeneric description; stVI without process on posterior margin; subgenital plate weakly asymmetrical; lateral process of subgenital plate claw-shaped with a long anterior and short posterior processes (Fig. 3.6W); tVII

rectangular; tVIII weakly rectangular; length of tVII about 1/3 length of tVIII. GENITALIA: py as in subgeneric description; rp ladle-shaped with a large rounded base, and elongate stem; lp as in subgeneric description a sickle-shaped dorsal process; rca uniformly tapering with a distinct, brush-like tip; lca large, about 1/2 length of rca, and tapering (Fig. 3.6W); vesica uniformly thin, forming at one coil; anophore as in subgeneric description with a pawn-shaped process on the dorsal wall.

Female: Unknown.

Distribution: Known only from the type locality (Fig. 3.7).

Etymology: Named for the claw shaped process of the subgenital plate after the Latin “ungulatus” meaning having hoofs or claws. The gender is feminine.

Discussion

Relationships within S. (Odontorhagus)

Molecular phylogenetic analyses of *Schizoptera* reveal the monophyly of this subgenus (Leon and Weirauch, submitted) and suggest two potential clades within *Schizoptera* (*Odontorhagus*): a South American and a Central American clade. This hypothesis is also consistent with the pattern of certain morphological features observed in species in this group. South American species are smaller in total body size, and have fairly simple genitalic structures. For example, all South American species described in this study possess simple, needle-like right conjunctival appendages (Figs 5B, 5L, 6M, 6U), uniformly thin and long vesicae (Figs 5B, 6M) and rather simple lateral processes of the subgenital plates (Figs 5L, 6U). This is contrasted by the extremely variable genitalic

morphology, often with strongly modified components, of most Central American species, where the right paramere can have one or multiple processes (Figs 6N, 6R, 6T), the right conjunctival appendage can be bifurcated (Fig. 3.6N), serrated (Figs 5C, 5E), or brush-tipped (Fig. 3.6W), and the vesica can range from uniformly thin (Fig. 3.5C) to short and forked (Fig. 3.5I).

Distribution patterns

Species of *S. (Odontorhagus)* display intriguing distributional patterns. In Costa Rica, seven different species (Fig. 3.7) have been collected from the same locality (La Selva Biological Station), and several of those species have also been collected in other regions in Costa Rica (Las Cruces Biological Station) or in Panama. *Schizoptera angularis*, n. sp. and *S. insidiosa*, n. sp. are found along both the western and eastern slopes of the Andes in Colombia and Ecuador and *S. gorgonensis*, n. sp. is found on both sides of the Andes, as well as in the mountain ranges in northern Colombia. Similar distribution patterns are observed in other Schizopteridae, namely species in the genus *Chinannus* Wygodzinsky, where male specimens of *C. communis* have been collected on either side of the Andes in Colombia (Knyshov et al., accepted). These patterns, in conjunction with collection data (i.e. malaise traps, light traps and canopy fogging) suggest that *S. (Odontorhagus)* species may be extremely active fliers, and thus comparatively strong dispersers.

Conclusions

Our taxonomic revision of *Schizoptera (Odontorhagus)* led to a threefold increase of species numbers in this subgenus. Assuming that the situation is similar for the

remaining three subgenera, we predict that a significant portion of the biodiversity of *Schizoptera* is yet to be described. We found that several morphological characters, particularly the shape and structure of the subgenital plate (Figs 5 and 6), provide excellent species-diagnostic characters for species in the subgenus *Schizoptera* (*Odontorhagus*) and we expect that these features will also be useful for future taxonomic revisions of the remaining three subgenera.

References

- China, W. E. (1946) New Cryptostemmatidae (Hemiptera) from Trinidad, British West Indies. *Proceedings of the Royal Entomological Society of London (B)*, 15, 148–154.
- Emsley, M. G. (1969) The Schizopteridae (Hemiptera: Heteroptera) with the descriptions of new species from Trinidad. *Memoirs of the American Entomological Society*, 25, 1–154.
- Fieber, F. X. (1860) Exegesen en Hemiptera. *Weiner Entomologische Monatschrift*, 9, 258-272.
- Hill L (2015) Three new genera of Schizopteridae from Australia with description of six new species (Hemiptera: Heteroptera: Schizopteridae). *Zootaxa* 3990, 73-96.
- Knyshov A., Leon S., Hoey-Chamberlain R., Weirauch C. Pegs, pouches and spines: systematics and comparative morphology of the New World genus *Chinannus* Wygodzinsky, 1948, ESA Thomas Say monographs, *accepted*
- Linnavuori RE (1974) Hemiptera of the Sudan, with remarks on some species of the adjacent countries. *Annales Entomologicae Fennicae*, 40, 116-138
- Makhan D (2013) *Soekhnandanius aschne* gen. et sp. nov., Schizopterinae (Hemiptera: Heteroptera: Schizopteridae) from Suriname. *Calodema* 391, 1-3
- McAtee, W.L., & Malloch, J.R. (1925) Revision of bugs of the family Cryptostemmatidae in the collection of the United States National Museum. *Proceedings of the United States National Museum*, 67, 1–42.
- Noyes J. S. (1982) Collecting and preserving chalcid wasps (Hymenoptera: Chalcidoidea). *Journal of Natural History*, 16, 315-334.
- Poinar, G.J. & Brown, A. (2014) New genera and species of jumping ground bugs (Hemiptera: Schizopteridae) in Dominican and Burmese amber, with a description of a meloid (Coleoptera: Meloidae) triungulin on a Burmese specimen. *Annales de La Société Entomologique de France (N.S.): International Journal of Entomology*, 50, 372–381.
- Poppus, B. (1910) Neue Ceratocombiden. *Öfversigt Af Finska Vetenskaps-societetens Forhandlingar Helsingfors*, 52, 1–14.
- Rédei, D. (2008) First record of *Pinochus* Carayon, 1949 from the Oriental Region, with description of a new species from Vietnam (Heteroptera: Schizopteridae). In: Gozeva, S., Simov, N. (eds) *Advances in Heteroptera Research: Festschrift in honour of 80th anniversary of Michail Josifov*. Pensoft, Sofia pp. 327-337.
- Reuter, O.M. (1882) Sur le genre *Schizoptera* Fieb. *Revue D'entomologie*, 1, 162–164.

Reuter, O.M. (1891) Monographia Ceratocombidarum orbis terrestris. *Acta Societatis Scientiarum Fennicae*, 19, 1–28.

Weirauch C. & Štys P. (2014) Litter bugs exposed: phylogenetic relationships of Dipsocoromorpha (Hemiptera: Heteroptera) based on molecular data. *Insect Systematics and Evolution*, 45, 351–370

Weirauch C., & Frankenberg S. (2015) From “insect soup” to biodiversity discovery: taxonomic revision of *Peloridinannus* Wygodzinsky, 1951 (Hemiptera: Schizopteridae), with description of six new species. *Arthropod Systematics and Phylogeny*, 73, 457-475

Wygodzinsky, P. (1952) Sobre algunos Cryptostemmatidae, principalmente de la Argentina (Hemiptera). *Acta Zoologica Lilloana*, 10, 51-74

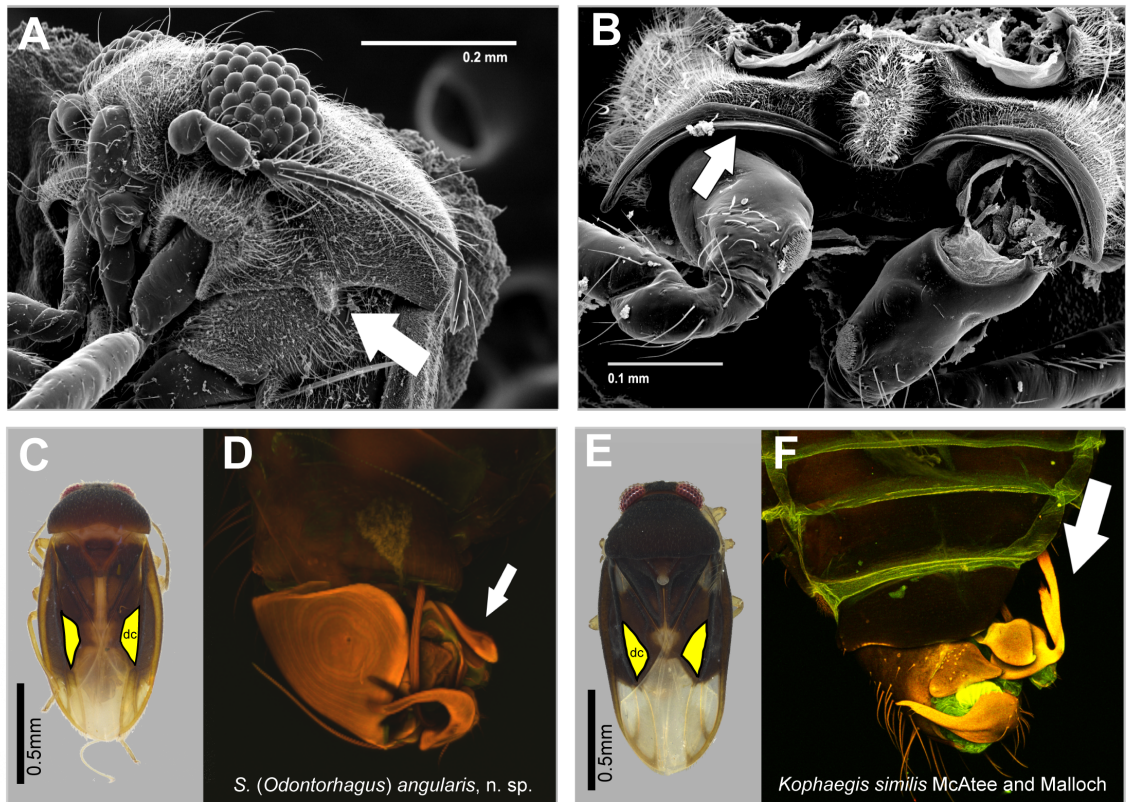


Figure 3.1: A, B Diagnostic features of species of *Schizoptera* (*Odontorhagus*). A. The white arrow points to the blunt tooth on the propleuron; B. The white arrow points to the narrow, glabrous margin of the metepisternum. C-F Comparison of *Schizoptera* (*Odontorhagus*) and *Kophaegis*; C. Dorsal habitus of *S. (Odontorhagus) angularis*, n. sp. male, region in yellow on hemelytra outlines the trapezoidal shape of the discal cell; D. Confocal micrograph of male genitalia of *S. (Odontorhagus) angularis*, n. sp., white arrow points to anophore; E. Dorsal habitus of *Kophaegis similis* male, region in yellow outlines the triangular shape of the discal cell; F. Confocal micrograph of genitalia of *Kophaegis similis* male genitalia, white arrow point to antler-shaped anophoric process.



Figure 3.2: Habitus images of *S. (Odontorhagus)* species.

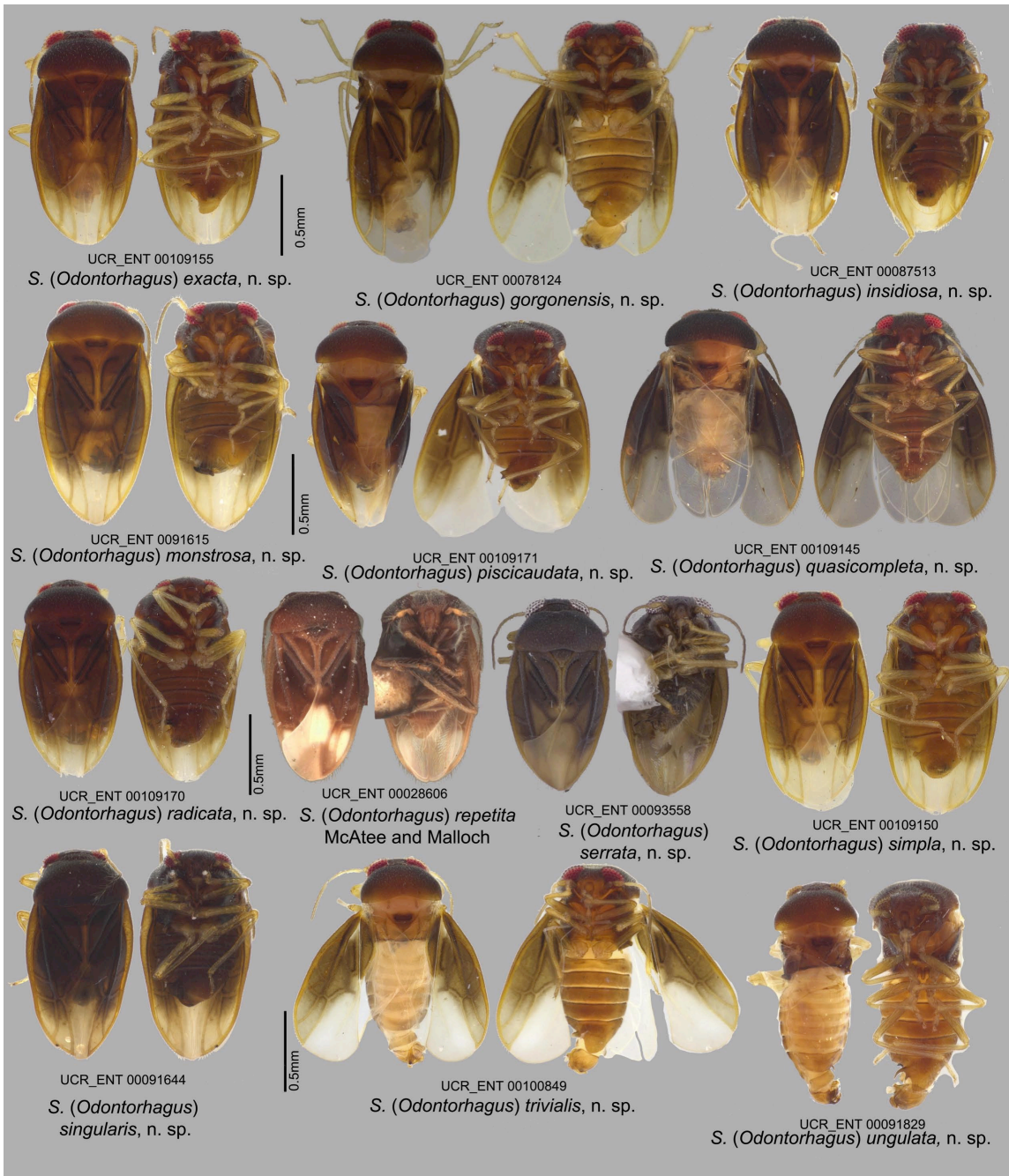


Figure 3.3: Habitus images of *S. (Odontorhagus)* species.

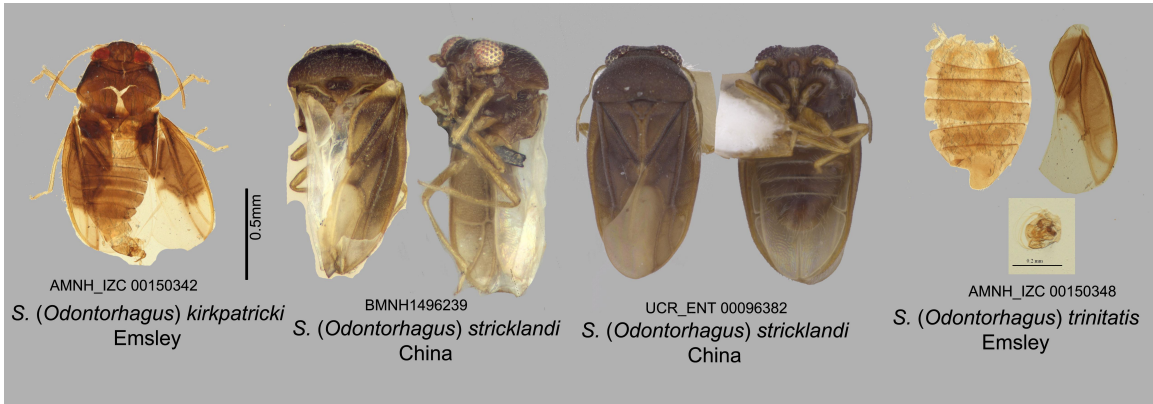


Figure 3.4: Images of select type specimens that were either slide mounted or damaged, with an additional *S. stricklandi* specimen placed next to the damaged type for comparison.

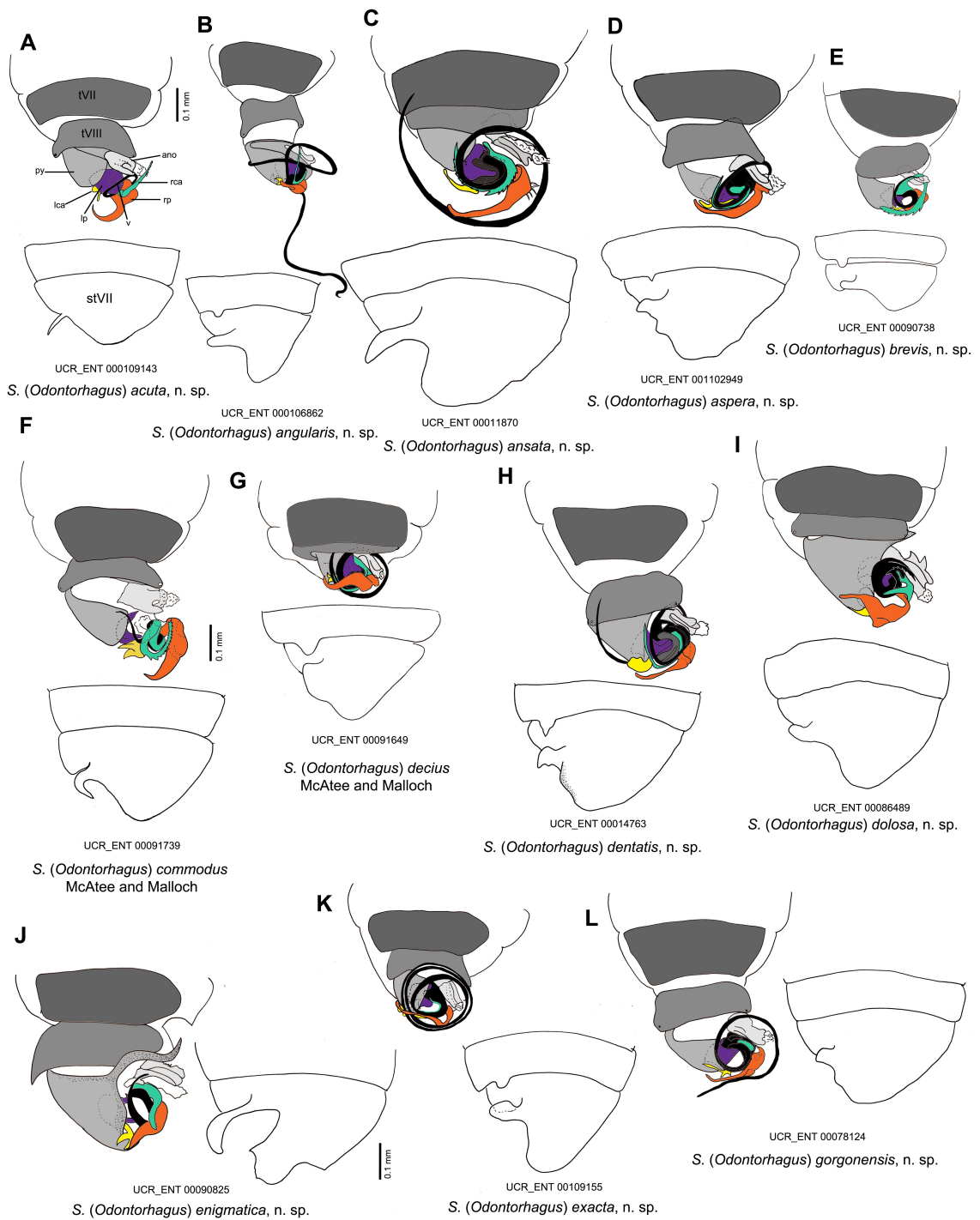


Figure 3.5A-L: Line drawings of dorsal (above) and ventral (below) views of male genitalia, different colors correspond to different structures labeled on *S. (Odontorhagus) acuta*, n. sp.

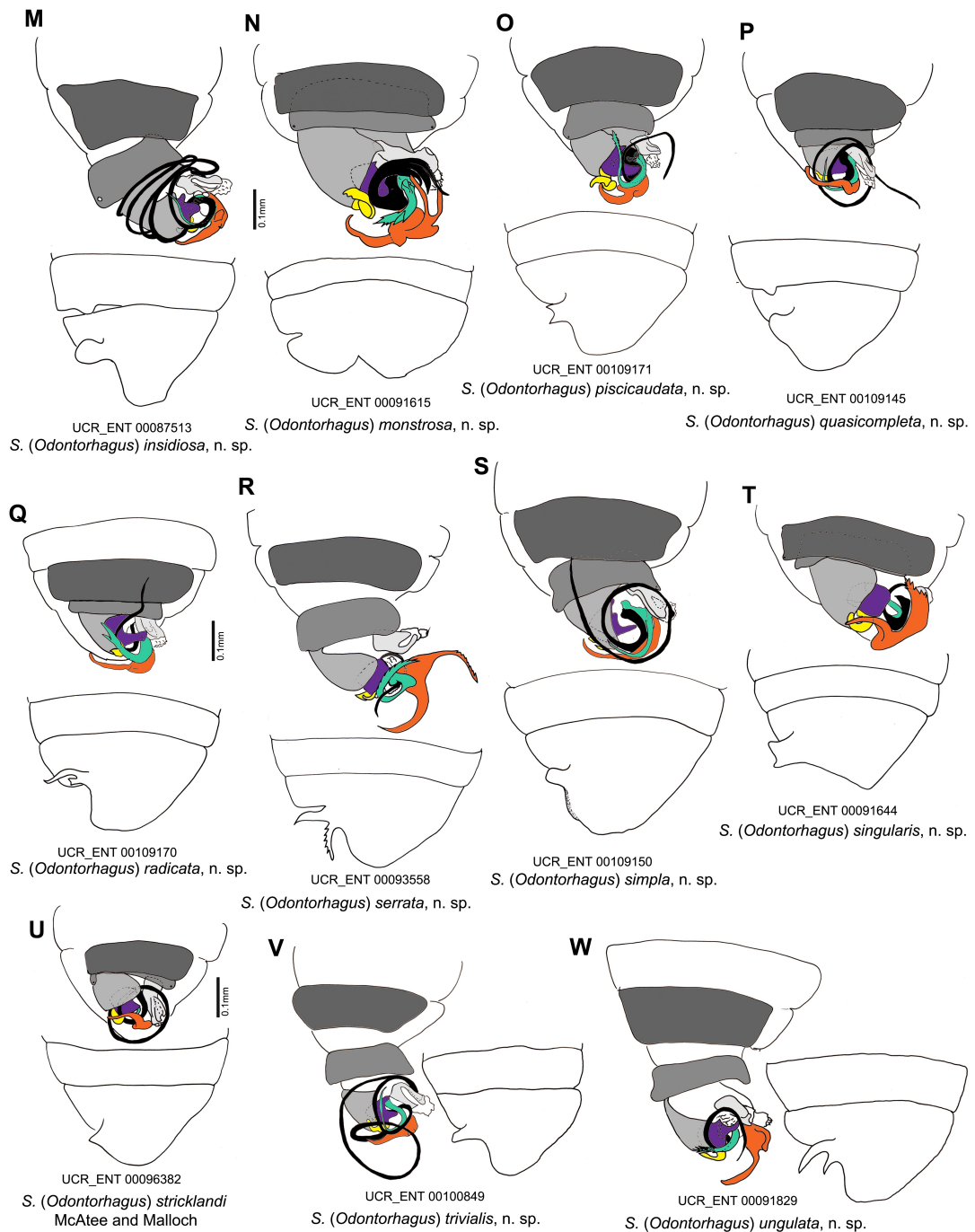


Figure 3.6M-W: Line drawings of dorsal (above) and ventral (below) views of male genitalia, different colors correspond to different structures labeled on *S. (Odontorhagus) acuta*, n.sp. (Fig. 3.5A).

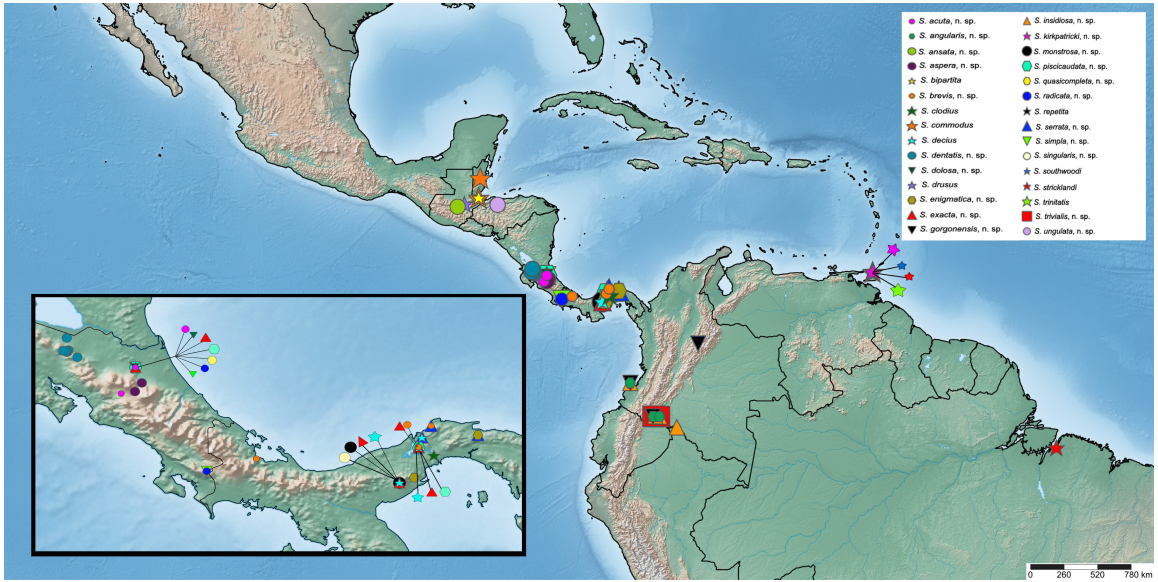


Figure 3.7: Distribution of *S. (Odontorhagus)* species.

CONCLUSION

This thesis contributes to the knowledge of the biodiversity, systematics, taxonomy and evolution of one of the least studied groups of true bugs, the Dipsocoromorpha, with focus on the largest genus *Schizoptera*.

In the first chapter, the first molecular phylogeny of *Schizoptera* was presented. The genus was recovered as polyphyletic, the elevation *Orthorhagus* and *Kophaegis* to generic rank resulted in a monophyletic *Schizoptera*. Within the *Schizoptera*, three monophyletic groups were recovered: *S. (Cantharocoris)* + *S. (Lophopleurum)*, *S. (Odontorhagus)* without *Kophaegis*, and *S. (Zygophleps)*. *Schizoptera (Schizoptera)* was recovered as polyphyletic. *Schizoptera (Cantharocoris)* + *S. (Lophopleurum)* were synonymized based on monophyly, lack of reciprocity and ambiguity of their respective diagnoses. A clade comprising *Kophaegis* species and representatives of *Ptenidiophyes* was recovered as the sister to *Schizoptera*.

Ancestral state reconstruction of elytrous wings in females of Schizopteridae showed that elytrous wings have evolved seven times separately within the family. In *Schizoptera* alone, elytrous wings have evolved four separate times, and reversed back to macropterous wings twice within the same clade. These results were discussed in the context of two potential hypotheses: the “sexual selection” hypothesis or the “ecological” hypothesis.

The second chapter was a taxonomic revision of *Orthorhagus*. Specimens of *Orthorhagus* are extremely rare in bulk samples, primarily due to their specialized habitats, such as decaying wood or subcortical debris. Nonetheless, nine specimens sufficed to conduct a thorough morphological study of males of this group, resulting in the description of five new species from the Neotropics. Additionally, comparative

morphology of *Schizoptera* and *Orthorhagus* species was presented to complement molecular data (presented in chapter 1).

The last chapter was a taxonomic revision of the subgenus *Schizoptera* (*Odontorhagus*), which prior to this study comprise 10 described species. Examination of over 300 specimens resulted in the description of 20 new species in this group. Observation of collection method notes, in addition to intriguing geographic distribution patterns, suggest that both males and females of *Schizoptera* (*Odontorhagus*) may be active fliers, and strong dispersers. The modified sternite VII, or subgenital plate proved to be an excellent species-level diagnostic feature for males of *Schizoptera*. This revision increased the species count of *Schizoptera* from 61 to 81. We predict that similar increases in species numbers are to be expected for the remaining subgenera of *Schizoptera*, making this genus and very diverse lineage of minute litter bugs.