Entomology in Focus 2

Antônio R. Panizzi
Jocélia Grazia *Editors*

True Bugs (Heteroptera) of the Neotropics

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Editors

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C.W. Schaefer in Antônio's office –
photo by Patrick De Clercq

On April 29, 2015, we were shocked to learn the sad news that our friend and colleague Prof. Carl W. Schaefer had passed away. He will not see his nice chapter on Pyrrhocoridae/Largidae nor the one he co-authored on Alydidae published in this book. However, his legacy as a great heteropterist and as a great man will remain among us. We dedicate this book to Carl's memory for all his contribution to the knowledge we have on true bugs.

Foreword

In entomology, the appearance of group specialists and comprehensive treatments often occurs at very long intervals, and the Heteroptera are no exception. The reasons for this phenomenon are easy to understand: too many insects and too few specialists to study them. This volume represents a real contribution in filling that inevitable gap.

After receiving my PhD in 1971, I had the opportunity to teach in the Brazilian Federal University system for two academic years in the city of Belém, Pará, Brazil. Part of my responsibility was to work with a small group of students—*bolsistas*—on in-depth studies of insects. We often focused on Heteroptera, because that is the group that I knew best, and they served as excellent models for addressing broader questions in entomology. The search for suitable texts and teaching aids led me to two works in particular. On a general level it became clear that the single-volume, 1970 edition of the *Insects of Australia*, recently published by Melbourne University Press, was the reference of choice. It offered far and away the best family-level coverage of the Neotropical fauna because of the many shared faunal similarities of these two tremendously diverse Gondwana fragments. Nonetheless, at a more detailed level discussions of Australian species cited in the work were of little use in understanding the fauna of Brazil in general, or of Amazonia in particular.

The work of recourse for understanding the details of Brazilian Heteroptera was the 351-page 1940 volume on Hemiptera, part of the classical *Os Insetos do Brasil*, a set of 12 volumes authored by Angelo Moreira da Costa Lima. Despite its tremendous popularity among entomologists in Brazil, the volume on Hemiptera (Heteroptera) was of limited utility. This is understandable considering Costa Lima is not a heteropterist per se but rather had a background as an applied entomologist and as a medical sanitarist working at the Instituto Oswaldo Cruz, the center for the study of the triatomine vectors of Chagas disease. He concentrated on few family groups, particularly those of greatest economic and human-health importance, doubtless a sign of the types of entomological studies he conducted and also the main priority at that time. Although it was more comprehensive than the enduring *Hemiptera Argentina* of Carlos Berg from the late 1880s, both works understandably presented far from what we now know to be the actual diversity of the

Neotropical Heteroptera fauna. Also, at the time Costa Lima's work was published, family-level nomenclature in the Heteroptera was in a state of flux as was our understanding of relationships within the suborder; both of these issues inevitably led to the work becoming out of date.

Therefore, I take great pleasure in welcoming the publication of *True Bugs of the Neotropics*, organized and edited by Antônio R. Panizzi and Jocélia Grazia. This impressive volume benefits from events that have taken place since the time of Costa Lima and of which we can now enjoy the full advantage. Standing out prominently is the cadre of young specialists who have contributed to this volume, many from the Neotropical Region and many inspired and trained by coeditor Grazia. Several of them have made real contributions in their own right, and much of that knowledge is summarized as part of their authorship contributions to this volume. The current authors have also had the benefit of contributions made by authorities likely directly influenced by *Os Insetos do Brasil*. Three of those pioneering workers—heteropteran titans—who stand out in my mind are José C. M. Carvalho (Miridae), Herman Lent (Reduviidae, Triatominae), and Pedro Wygodzinsky (Dipsocoromorpha, Reduviidae).

Users of this volume will benefit from the uniformity of treatment across family groups, the digital revolution in photography and photocomposition, and the greatly improved knowledge of the Neotropical fauna that has resulted from extensive field work, local and international collection development, and extensive revisionary work in almost every family of Heteroptera over the last 75 years. The current volume provides the reader with up-to-date knowledge concerning the classification, nomenclature, and biology of Neotropical taxa and offers a solid foundation for specialists, mentors, and students alike in their studies of the true bugs.

My congratulations to the entire team whose knowledge and dedication have brought this volume to fruition.

New York, NY, USA Randall T. Schuh
January 2015

Preface

The idea of making a book on the Heteroptera of the neotropics matured with time. Along the years, the two editors got together in several entomological congresses in Brazil and elsewhere, and, every time they met, they discussed about the need to publish a book on such matter. The initial idea was to publish a text on the stink bugs (Pentatomidae) of Brazil. This is understandable considering the background of the editors, ARP as a biologist and JG as a taxonomist, both working on pentatomids.

Back in 2010, ARP was the president of the Entomological Society of Brazil (SEB), and the society started negotiations with Springer to publish its journal *Neotropical Entomology*. When the agreement was signed, another idea came out, now to start an *Entomology Series Books* with Springer, through the SEB, which would focus on any aspect related to entomology in the neotropics. With that on mind, we editors had a meeting with the senior publishing editor of Springer, Ing. Zuzana Bernhart. She welcomed our plan to publish a more comprehensive book to cover not only the stink bugs but all (most) families of Heteroptera, not only from Brazil but from the whole Neotropical Region.

Not many books have been published recently on true bugs (Heteroptera). Of general interest, two texts are worth of mention: *True Bugs of the World (Hemiptera: Heteroptera) Classification and Natural History* by R. T. Schuh and J. A. Slater, Cornell University Press, 1995, and *Heteroptera of Economic Importance* edited by C. W. Schaefer and A.R. Panizzi, CRC Press, 2000. Fifteen years from this later publication, we believe that it was time to produce a book on Heteroptera from the Neotropical Region, doubtless the most diverse and complex biogeographic zone of the world.

The book is divided in seven parts. Part I is devoted to general aspects, and includes three chapters. Chapter 1 is an introduction to the true bugs of the neotropics; Chap. 2 covers general aspects of the morphology, ontogeny, reproduction, and feeding of true bugs; and Chap. 3 focuses on the classification and biogeography of the Neotropical true bugs. Parts II–VII are dedicated to specific aspects. We decided to divide these parts considering each of the seven infraorders (except the first two that were merged in one part) as follows: Enicocephalomorpha (the unique-headed bugs, Chap. 4) and the Dipsocoromorpha (the minute litter bugs, Chap. 5), Gerromorpha (the semiaquatic bugs, Chap. 6), Nepomorpha (the true aquatic bugs, Chap. 7), Leptopodomorpha (the shore bugs, Saldidae, Chap. 8), Cimicomorpha (minute pirate bugs, Anthocoridae and Lyctocoridae, Chap. 9; plant bugs, Miridae, Chap. 10; damsel bugs, Nabidae, Chap. 11; assassin bugs, Reduviidae excluding Triatominae, Chap. 12; hematophagous bugs, Reduviidae and Triatominae, Chap. 13; and lace bugs, Tingidae, Chap. 14), and Pentatomomorpha (flat bugs, Aradidae, Chap. 15; the big-eyed bugs, chinch bugs, and seed bugs, Lygaeoidea, Chap. 16; the cotton strainers, Pyrrhocoridae, and bordered plant bugs, Largidae, Chap. 17; the broad-headed bugs, Alydidae, Chap. 18; the leaf-footed bugs, Coreidae, Chap. 19; the scentless plant bugs, Rhopalidae, Chap. 20; the burrower bugs, Cydnidae, Chap. 21; the stink bugs, Pentatomidae, Chap. 22; the shield bugs, Scutelleridae, Chap. 23; the negro bugs, Thyreocoridae, Chap. 24, and the less diverse pentatomoid families, Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae, Chap. 25).

The chapters are written mostly by experts on the different taxonomic groups of heteropterans of the neotropics, considering their knowledge of the literature. To elaborate the chapters, we passed to authors a general outline. We asked them to introduce the theme, to provide general characteristics and diagnosis of the representative of the family (group) covered, and to discuss the biology and ecology, eggs and oviposition, nymph feeding and development, adult feeding and reproduction, and classification and diversity. We also asked authors to list the main and secondary species of each family and to highlight their economic importance. Of course, the layout was a suggestion because we did not want to put authors in a "forced frame," and we allowed them some leeway. Most authors followed the original layout, and we believe that the final product met our expectations, and we hope those of the readers interested in the true bugs of the neotropics.

Passo Fundo, RS, Brazil Antônio R. Panizzi
Porto Alegre, RS, Brazil Jocélia Grazia

Acknowledgements

The editing of this book was only possible with the help of many persons. We want to express our gratitude to Zuzana Bernhart, senior publishing editor who coaxed us from the very beginning when the publication contract was signed with Springer to the end of the project. We are also grateful to the editorial assistant Mariska van der Stigchel who reminded us gently of deadlines and other details in the process of having all materials set in time to meet the chronology of the project. We want to thank the gentle manner with which we, editors and authors, were treated by Nagarajan Paramasivam and Rajeswari Sathiamoorthy of Springer, SPi Global, India, in handling proofs of cover, front material, chapters and index. Without their help we surely could not have avoided the many mistakes that usually occur in the production of such a voluminous book.

Special thanks go to the authors of the chapters. Of course, they are the reason by which we ended up with such a nice and complete volume on the true bugs of the neotropics. All of them were very kind and cooperative to meet the deadlines and to follow all the instructions we editors passed to them in the beginning of this endeavour.

Finally, we want to thank Fernando Cônsoli, editor of the Entomology in Focus series, for the invitation to contribute this volume.

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Antônio R. Panizzi is a senior research entomologist at the Wheat Research Center of Embrapa (Brazilian Enterprise of Agricultural Research), in Passo Fundo, Rio Grande do Sul, Brazil. He earned his BS in Agronomy in 1972 from the University of Passo Fundo; his MS in Entomology in 1975 from the Federal University of Paraná, both in Brazil; and his PhD in 1985 from the University of Florida. He is the recipient of the Alexandre Rodrigues Ferreira Prize given by the Brazilian Society of Zoology and editor in chief of the *Annals of the Entomological Society of Brazil* (1993–1998). He served as president of the Entomological Society of Brazil (2008–2012) and in 2014 became Honorary Member of the society. He has been an invited speaker at several congresses and symposia in different parts of the world and an invited scientist at the National Institute of Agro-Environmental Sciences, Tsukuba, Japan (1991). From 2002 to 2004 worked as a visiting scientist at the USDA laboratory at Peoria, IL, Dr. Panizzi coedited *Heteroptera of Economic Importance* (CRC Press, 2000) and *Insect Bioecology and Nutrition for Integrated Pest Management* (CRC Press, 2012) and served as guest coeditor of *True Bugs (Heteroptera) Chemical Ecology of Invasive and Emerging Pest Species* (special issue of Psyche, 2012). He has published extensively on Hemiptera (Heteroptera), over 150 peer-reviewed publications, including an *Annual Review of Entomology* article on wild hosts of Pentatomidae. He teaches a course on insect nutritional ecology at the Federal University of Paraná and is an invited professor at the Universidad de la Republica in Uruguay, where he serves as advisor for MSc and PhD students. His current research focuses on the interactions of heteropterans (mostly Pentatomidae) with their wild and cultivated host plants and the management of pest species on field crops.

Jocélia Grazia is a full professor of the Department of Zoology at the Federal University of Rio Grande do Sul and a researcher of National Research Council of Brazil for the last 50 years. She earned her PhD in Zoology in 1976 from the State University of Campinas (UNICAMP), São Paulo, Brazil, and between October 1994 and April 1995 obtained a postdoc fellowship to develop research at the Heteroptera Laboratory of the American Museum of Natural History, New York, under the supervision of RT Schuh. She is recipient of the Jesus Santiago Moure Prize (2010) and Alexandre Rodrigues Ferreira Prize (2013) given by the Brazilian Society of Zoology for the best paper published in taxonomy and the best book in zoology (senior author of the Hemiptera chapter), respectively. She served as editor in chief of the *Annals of the Entomological Society of Brazil* (1978–1984) and as president of the Entomological Society of Brazil (1984–1990), and in 2014 she received the Edilson Bassoli de Oliveira Prize given by the Brazilian Entomological Society in recognition to the members who have contributed to the development of entomology in Brazil. She served as president of the International Heteropterist's Society (2002–2006). She has published extensively on Hemiptera (Heteroptera), 180 peer-reviewed publications. She advised more than 70 students (undergraduate, MSc, and PhD) in four universities in Brazil (Federal University of Paraná, Federal University of Rio Grande do Sul, State University of Campinas, and Federal University of Alagoas). She was the director of the Natural Science Museum, Zoobotanical Foundation, Porto Alegre, Brazil (1972–1975), and vice rector of graduate courses, Federal University of Rio Grande do Sul (2003–2004). Her current research focuses on the systematic and phylogeny of heteropterans (mostly Pentatomoidea).

Part I
General Aspects

Chapter 1
Introduction to True Bugs (Heteroptera) of the Neotropics

Antônio R. Panizzi and Jocélia Grazia

Abstract True bugs (Heteroptera) are a diverse and complex group of insects, particularly in the neotropics. The fauna of these bugs has been investigated through time, but our knowledge of the species living in the Neotropical Region is limited. In this introductory chapter, we give a general view on true bugs classification and biogeography, with concise comments on their general characteristics and bioecology of each major taxon that comprise each of the seven infraorders of Heteroptera.

1.1 Introduction

The true bugs (Heteroptera) constitute a very interesting widely distributed group of insects, which is greatly diversified in tropical zones. Considered the largest group of insects with incomplete metamorphosis, heteropterans have been studied on both basic and applied aspects worldwide.

Along the years, several books have been published on Heteroptera, the majority on specific aspects, such as certain groups (taxa) of particular areas, and others on more general comprehensive issues. Of more broad interest, two books about the latter were published relatively recently. The first was dedicated to the classification and natural history of true bugs in particular, with insights on the history of the study of Heteroptera, how to collect and preserve true bugs, historical biogeogra-

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phy, and comments of species of economic importance (Schuh and Slater 1995). The second book is a massive review of the world literature on species of economic importance, ranging from pest species of crops to species of medical importance (e.g., transmitters of Chagas disease) and to species that are of "nuisance" to humans (Schaefer and Panizzi 2000).

Considering the Neotropical Region, not a general book devoted to Heteroptera has been published in the last 70+ years. There are texts dealing with Hemiptera (Heteroptera) such as the one by Costa Lima (1940) on the true bugs of Brazil and the one by Berg (1879) devoted to true bugs of Argentina. Recently, Grazia and Fernandes (2012) made an overview of the true bugs of Brazil, updating what was published before on many scattered publications.

In this introductory chapter, we give a concise and fast overview of the true bugs of the neotropics. This includes a general view on their classification and biogeography, with concise comments on their general characteristics and bio-ecology of each major taxon that comprise each of the seven infraorders of Heteroptera.

1.2 Classification, Biogeography, General Characteristics, and Bioecology of Neotropical True Bugs

The order Hemiptera, suborder Heteroptera, is divided into seven infraorders: Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha. These seven infraorders were recognized by Schuh (1979) based on the information on the evolutionary tendencies of heteropterans mouthparts and feeding habits described by Cobben (1978). Recently, Weirauch and Schuh (2011) revised the actual knowledge on the systematics and evolution of the heteropterans.

1.2.1 Enicocephalomorpha

This infraorder, the unique-headed bugs, is divided in two families, Aenictopecheidae and Enicocephalidae. The first family is subdivided into four subfamilies with ten genera and 20 species. These bugs live on or underneath the soil debris or under tree barks showing omnivorous feeding habits (Grazia and Fernandes 2012). The Enicocephalidae has 33 genera and over 400 species divided into five subfamilies. Members of this family show swarming behavior with sexual dimorphism, females being much bigger than males. Wygodzinsky and Schmidt (1991) presented a monography of the fauna of the New World.

1.2.2 Dipsocoromorpha

This infraorder includes the smallest heteropterans with 47 genera and over 200 species, divided into five families, of which Ceratocombidae and Schizopteridae are better studied in the New World. The fauna in the neotropics is greatly diverse and poorly studied (Grazia and Fernandes 2012). Weirauch and Štys (2014) performed a phylogenetic analysis of this infraorder supporting its monophyly.

These small-sized heteropterans, very inconspicuous, live within fallen leaves, in natural small vegetation, or in tree canopy. They are hard to intercept, and many resemble small beetles.

1.2.3 Gerromorpha

Known as the semiaquatic bugs (water striders), the infraorder Gerromorpha comprises over 2,000 species in 11 families, with the majority of species in the neotropics belonging to the families Gerridae, Hebridae, Hydrometridae, Mesoveliidae, and Veliidae (Grazia and Fernandes 2012). The most comprehensive references for Gerromorpha, including morphology, phylogeny, biogeography, and keys for identification, were published by Andersen (1982). Great habitats dominated by freshwater, such as the Amazonia and the Pantanal in the neotropics of mostly Brazil, include a great number of species, many undescribed and waiting to be studied.

The Gerridae include bugs that live mostly on the water surface, with median and posterior legs elongated. Eight subfamilies are recognized (Andersen 1982), of which Trepobatinae contains a greater number of genera, at least in Brazil (Grazia and Fernandes 2012).

The Hebridae are small (1.3–3.7 mm) cryptic bugs living on herbaceous vegetation along waterways. Over 150 species are known and included in seven genera and two subfamilies (Hebrinae and Hyrcaninae) (Andersen 1981, 1982).

The Hydrometridae are long bugs (2.7–22 mm) found on vegetation or on rocks along the side of creeks and rivers. The over 100 species described are included in three subfamilies (Hydrometrinae, Heterocleptinae, and Limnobatodinae) (Andersen 1977).

The Mesoveliidae are small (1.2–4.2 mm), with variable wing development and shape. They live associated with floating vegetation or on open areas over the water. There are about 40 species included in two subfamilies (Mesoveliinae and Madeoveliinae). Very little is known about the Neotropical mesoveliids.

The Veliidae is a fairly large family (38 genera and about 600 species) (Andersen 1982). These bugs posses a truncated body, 1–10 mm long, well adapted to live on the water surface. There are six subfamilies (Ocelloveliinae, Rhagoveliinae, Perittopinae, Veliinae, Microveliinae, and Haloveliinae). They are easily found and captured and a well-studied group in many parts of the world, but not in the Neotropical Region.

1.2.4 Nepomorpha

The Nepomorpha, or true water bugs, comprises about 2,000 species placed on 11 families. Their size varies from 1 mm (Pleidae and Helotrephidae) to 130 mm (Belostomatidae). They are, in general, predators, with some Corixidae feeding on algae and decaying vegetal matter. In the neotropics, Pereira et al. (2007) presented keys for family and genera identification of species occurring in the Central Amazon in Brazil. Species of the following families are found in the neotropics: Belostomatidae, Corixidae, Gelastocoridae, Naucoridae, Nepidae, Notonectidae, Ochteridae, Pleidae, and Potamocoridae. The most speciose families are Naucoridae; Belostomatidae, which include the giant water bugs, *Lethocerus* spp.; Nepidae; and Notonectidae (Grazia and Fernandes 2012).

1.2.5 Leptopodomorpha

About 400 species distributed in four families comprise the infraorder Leptopodomorpha, or shore bugs. The major reference to the literature and classification of the group is by Schuh et al. (1987). In the neotropics only Saldidae is represented. Usually ovoids, these dark fast-moving bugs are found in nearby water in humid open areas. They are predators, even able to dig in order to capture their preys (Grazia and Fernandes 2012).

1.2.6 Cimicomorpha

This infraorder is the largest infraorder of Heteroptera including about 20,000 species in 16 families (Schuh and Slater 1995). The Cimicomorpha is a well-studied infraorder, especially because of its economic and health importance. Of the 16 families referred to by Schuh and Štys (1991), the most common and important ones will be covered in this book.

Minute Pirate Bugs (Anthocoridae)

These small to minute flattened, dark, oval or elongated insects are predaceous, but may feed on pollen and other parts of plants. Schuh and Slater (1995) presented an overview of the family worldwide, presenting a key for the seven tribes, and Carpintero (2002) wrote the first catalog devoted to Neotropical species. Lattin (2000) reviewed the species that are known to occur in managed ecosystems. Apparently, they are important as biological control of pests in agroecosystems. In Brazil there are about 100 species described (Grazia and Fernandes 2012).

Plant Bugs (Miridae)

This is, by far, the most diverse and speciose family within the Heteroptera, with about 1,300 genera and over 11,000 described species worldwide and over 500 genera and more than 3,000 species in the neotropics. In the neotropics, the majority of the species belong to the subfamilies Orthotylinae, Mirinae, and Deraeocorinae. The main taxonomic work for the Neotropical mirids was carried out by José C. M. Carvalho, who described about 400 genera and over 2,000 species and published the world catalog from 1957 to 1960 in a series of five publications (references in Chap. 10).

Mirids, known as plant bugs or capsids, are small- to medium-sized, elongated to ovoid bugs with triangular heads; they show variable coloration, being either phytophagous or carnivorous (predators).

The biology of mirids including habits and hosts has been published in several different publications and were synthesized by Wheeler (2000a, b, 2001). They are important pests in agricultural crops, and the predatory species show potential to be used in biological control programs. Among the most common species, we can cite those in the genera *Lygus*, *Monalonion*, *Pseudatomoscelis*, *Tenthecoris*, *Microtechnites*, and *Pycnoderes* as pests and *Phytocoris*, *Blepharidopterus*, *Campylomma*, *Campyloneura*, and *Engytatus* as potential predators.

Damsel Bugs (Nabidae)

The nabids, known as damsel bugs, are small- to medium-sized, elongated and robust bugs, with pale coloration. They are active predators, found in agricultural and urban areas. Schuh and Slater (1995) presented a key to the two subfamilies, Prostemmatinae and Nabinae. In the neotropics there are about 11 genera and 83 species described, with the genus *Arachnocoris*, *Praecarthasis*, *Hoplistoscelis*, *Nabis*, *Alloeorhynchus*, and *Pagasa* the most speciose (see Chap. 11). The majority of the literature refers to species of the Old World, and the New World fauna is treated by Harris (1930, 1931, 1939) and Kerzhner (1986).

Assassin Bugs (Reduviidae Excluding Triatominae)

The so-called assassin bugs, the reduviids, are voracious terrestrial predators with about 7,000 described species in over 900 genera and 25 subfamilies; it is considered one of the three most abundant in a number of species within the Heteroptera (Forero 2008; Henry 2009). Putchkov and Putchkov (1985) and Maldonado (1990) published catalogs of the species. For the Neotropical Region, over 200 genera and about 1,400 species included in 21 subfamilies are recorded (Forero 2004, and personal communication to JG).

Reduviids show a great morphological diversity with a range in size that varies from few millimeters to very large insects (Schuh and Slater 1995). Excluding the Triatominae that feed on vertebrate blood, all others live on preying.

The most common species belong to the following subfamilies: Chryxinae, Ectrichodiinae (the most abundant in the genus *Brontostoma* Kirkaldy), Elasmodeminae (exclusively from the neotropics, living under tree bark), Emesinae, Hammacerinae, Harpactorinae (with the most speciose genus *Apiomerus* Hahn and the common *Arilus* Hahn and *Zelus* (F.)), Peiratinae, Phymatinae, Reduviinae (which include the most studied genus, at least in Brazil, *Zelurus* Hahn), Saicinae, Sphaeridopinae, and Stenopodaine (Grazia and Fernandes 2012).

Hematophagous Bugs (Reduviidae, Triatominae)

The Triatominae are blood-sucking bugs known in Portuguese as "barbeiros." This subfamily includes about 140 species within 15 genera and five tribes. The actual taxonomic status of this subfamily that recognizes five tribes is based mainly on the revision by Lent and Wygodzinsky (1979), the most important systematic study of the group. This study has been updated by several other inclusions of new taxa (Carcavallo et al. 1998/1999; Schofield and Galvão 2009; see also Chap. 13).

These bugs are fairly big, in general from 20 to 28 mm length in body size, although some species may have about 5 mm or can reach over 40 mm; body color is mainly brownish black with spots in yellow, orange, or red (Jurberg et al. 2012). They can be found living on bird nests, underneath the bark of trees, and in crevices of various species of trees such as bromeliads, palms, and others and feeding on animals.

They are known worldwide as transmitters of the Chagas disease, caused by the flagellate *Trypanosoma cruzi* (Chagas), a major disease affecting human population in several regions of the world, and very important in the neotropics (see Chap. 13 for details). The most common species in the neotropics belong to the genera *Panstrongylus* Berg, *Triatoma* Laporte, and *Rhodnius* Stål, and they have been illustrated by Jurberg et al. (2004, 2014).

Lace Bugs (Tingidae)

The tingids, known as lace bugs, are delicate and small bugs that show outgrowth of the pronotum and forewings with lacy aspect. The family is divided into three subfamilies (Tinginae, Cantacaderinae, and Vianaidinae), all of them represented in the Neotropical Region (Schuh et al. 2006). There are around 300 genera and 2,500 species in this family, with 70 genera and 600 species in the neotropics.

Very few species have been studied in the neotropics with regard to their biology, such as *Corythaica cyathicollis* (Costa) (Kogan 1960) and *Leptopharsa heveae* Drake and Poor (Cividanes et al. 2004), both species of economic importance. The first species is pest of several solanaceous plants, and the second damages rubber plants. Various other genera (over 15) include species of economic importance (see details in Chap. 14). Neal and Schaefer (2000) reviewed the species of economic importance of the world.

1.2.7 Pentatomomorpha

A variable number of superfamilies have been recognized within the infraorder Pentatomomorpha, with five currently accepted: Aradoidea, Coreoidea, Lygaeoidea, Pentatomoidea, and Pyrrhocoroidea (see details in Chap. 3). In this book, we will discuss in details the families most important of this infraorder, as follows.

Flat Bugs (Aradidae)

These bugs, commonly known as “flat bugs” or “bark bugs,” encompass a great number of species worldwide, with over 200 genera and about 1,800 species included in eight subfamilies (Schuh and Slater 1995). For the Neotropical Region, there are 80 genera and 509 species (Coscarón and Contreras 2012).

Aradids are small to medium in length. Many tropical species are wingless and the dorsal surface appears granular or rugose. They have the mouth stylets extremely elongated and coiled; they feed on juices of fungi (mycetophagous) and also can feed on phloem, cambium, and xylem of living trees. Some species might be associated with termites and occasionally can live on bird nests. Detailed information on their biology and ecology and a list of species from the Neotropical Region and their geographical distribution are presented in Chap. 15.

Lygaeoidea Families (Berytidae, Colobathristidae, Lygaeidae, and Piesmatidae)

The Lygaeoidea is the second largest superfamily in the infraorder Pentatomomorpha, with about 700 genera and more than 4,200 species in the world. In the neotropics, there are about 184 genera and 836 species (see Chap. 16). Sweet (2000) made a comprehensive world review of the Lygaeoidea, stating their distribution, life history, biology, and damage and control of the major and minor species of economic importance.

Berytidae

The so-called stilt bugs have a slender elongated body, with long antennae and legs, measuring 2.5–11 mm, dull yellowish or reddish brown; two subfamilies are recognized: Berytinae and Metacanthinae (Schuh and Slater 1995). Berytids are phytophagous, being polyphagous on several species of plants of different families; however, they do have strong predatory tendencies (Henry 2000); he reviewed the most important species of the world, considering their importance either as pests, predators, or pollinators. In Brazil there are over 20 species according to the literature (Grazia and Fernandes 2012).

Colobathristidae

These bugs, elongated with slender legs, 6–20 mm long, feed exclusively on grasses, are well represented in the Neotropical Region; it is divided in two subfamilies, Colobathristinae and Dayakiellinae (Schuh and Slater 1995). In Brazil, there are 13 species (Grazia and Fernandes 2012).

Lygaeidae

These bugs known as "seed bugs," 1.2–12 mm long, are variable in shape and color, brown or black, showing aposematic coloration (red or yellow). Baranowski and Slater (2005) provided the key for the 10 subfamilies, the most important being Lygaeinae, Blissinae, Geocorinae, and Rhyparochrominae. In Brazil, 120 species and 58 genera are registered (Grazia and Fernandes 2012).

Sweet (2000) in his world review of the major and minor species of economic importance pointed out the main pest species, which belong to the following genera: *Blissus*, *Cavalerius*, *Spilostethus*, *Nysius*, *Oxycarenus*, *Chauliops*, and *Elasmolomus*. Of these, species of *Nysius* and *Elasmolomus* (pest of peanuts probably introduced) are of economic concern in the neotropics (see Chap. 16).

Piesmatidae

Called the ash-gray leaf bugs, the piesmatids are small (<5 mm) bugs. Very little is known about these bugs in the neotropics, with about only five species recorded for Brazil (Grazia and Fernandes 2012). Narisu (2000) reviews the world species of economic importance, referring to species of *Piesma* as transmitters of virus to sugar beet.

Cotton Stainers (Pyrrhocoridae) and Bordered Plant Bugs (Largidae)

The cotton stainers (pyrrhocorids) are medium to large bugs, frequently red or yellow and black. About 30 genera and 300 species are known. They occur in all zoogeographic regions, mostly in tropical and subtropical areas (Schuh and Slater 1995). They feed on fruits and seeds, mostly on Malvales plants. Schaefer and Ahmad (2000) made a world review of the species of economic importance, particularly of those in the genus *Dysdercus*, which include at least 17 species, of which *Dysdercus peruvianus* Guérin-Méneville, *D. maurus* Distant, and *D. ruficollis* (L.) are major pests in the neotropics.

The bordered plant bugs (largids), commonly colored bugs, medium to big size, are divided into two subfamilies, Physopeltinae and Larginae. A key to the subfamilies and tribes of Largidae for New and Old World is presented in Chap. 17. They feed on seeds and on plant extracts. Several species mimic ants. About 60 species included in seven genera were described from South America (Grazia and Fernandes 2012).

Broad-Headed Bugs (Alydidae)

The broad-headed bugs (alydids) are small to medium, slender, with a triangular head. They are divided into two subfamilies, Alydinae and Micrelytrinae, each divided into two tribes, Daclerini and Alydini and Micrelytrini and Leptocorisini, respectively. A key for the two subfamilies, including the tribes for the last presented by Schaefer (2004), is included in Chap. 18, with slight modifications.

The family Alydidae has over 50 genera with about 250 species; in the neotropics there are over 20 genera. The most common species belong to the genera *Neomegalotomus* Schaffner and Schaefer, *Hyalymenus* Amyot & Serville, *Stenocoris* Burmeister, *Cydamus* Stål, and *Trachelium* Herrich-Schäffer (see Chap. 18). The most studied species in the neotropics is the alydine *Neomegalotomus parvus* (Westwood), usually associated with legumes, and may be a pest of soybean. The alydids of economic importance in the world were reviewed by Panizzi et al. (2000b).

Leaf-Footed Bugs (Coreidae)

The coreids, known as leaf-footed bugs or squash bugs, are, in general, medium to very large, strong robust bugs and may be strikingly colorful, showing expansion of femora, tibiae, humeral angles, or antennae. They are distributed worldwide, but are more abundant in the tropics.

The New World Coreidae catalog lists 158 genera with species from the neotropics (Packauskas 2010). The keys to the subfamilies of the Neotropical Region coreids are presented in Chap. 19, adapted from Packauskas (1994). These include the three subfamilies, Pseudophloeinae, Meropachyinae, and Coreinae.

Coreids are polyphagous plant feeders on gymnosperms and angiosperms, monocots and dicots. However, dicots are far more common and few coreid species are exclusively gymnosperms feeders (Schaefer and Mitchell 1983). Mitchell (2000) reviewed the coreids of economic importance of the world. In the neotropics, the most common species include *Crinocerus sanctus* (F.), *Anisoscelis foliaceus* (F.), *Holhymenia histrio* (F.), *Leptoglossus gonagra* (F.), *Leptoglossus zonatus* (Dallas), *Phthia picta* (Drury), *Anasa tristis* (De Geer), and *Spartocera dentiventris* Berg (see details in Chap. 19).

Scentless Plant Bugs (Rhopalidae)

Rhopalidae are plant feeders bugs, mostly associated with reproductive tissues and seeds. The rhopalids are divided into two subfamilies, Rhopalinae and Serinethinae, with about 200 species in over 20 genera (Henry 1988, 2009). Its taxonomy has been studied over time by several authors (e.g., Schaefer 1965; Chopra 1967) and a world catalog was published (Göllner-Scheiding 1983). Several specific catalogs were produced for particular areas of the neotropics (e.g., Froeschner 1981, 1985, 1999; Maes and Göllner-Scheiding 1993; Pall and Coscarón 2012).

Rhopalids are small to medium and have a narrow body that resembles coreids, with brown dull coloration. They are called "scentless" plant bugs, which is an inappropriate name, since they have scent glands that produce volatile compounds (Aldrich et al. 1990).

In the neotropics, the Serinethinae of the genus *Jadera* are the most common species, although little studied regarding their biology and ecology. For example, for Brazil, there are nine species belonging to this genus (Grazia and Fernandes 2012). The species *Jadera choprai* Göllner-Scheiding is an exception, and its biology and its association with the balloon vine, *Cardiospermum halicacabum* L. (Sapindaceae), a weed plant in soybean fields in southern Brazil, have been investigated in detail (Panizzi and Hirose 2002; Panizzi et al. 2002, 2005).

Rhopalids, despite their wide distribution and occurrence in natural vegetation and on cultivated plants, are in general overseen and their role in these habitats is underestimated.

Burrower Bugs (Cydnidae)

The cydnids, called burrower bugs, are small- to median-sized ovoid bugs, black or brown, with flattened head and legs with strong and long spines; tibia and tarsi are modified in species with fossorial habitats that feed on roots. Some cydnids live above ground on vegetation, feeding on falling seeds or plant tissues (Schuh and Slater 1995; Schaefer 2009).

Cydnids are worldwide distributed, being well represented in tropical and temperate regions (Lis 1999, 2002). It includes more than 750 species in 93 genera and is divided into six subfamilies (Grazia et al. 2008). The cydnids in the neotropics are poorly known; Froeschner (1981) presented a key to the subfamily Cydninae of South America, the biggest and more diverse with 90 genera and 300 species.

Lis et al. (2000) made a review of the species of economic importance of the world. In the neotropics, the most common species are *Scaptocoris carvalhoi* Becker, *Scaptocoris castanea* Perty, *Cyrtomenus bergi* Froeschner, and *Pangaeus bilineatus* (Say) (see Chap. 21).

Stink Bugs (Pentatomidae)

The pentatomids, called stink bugs, are in general broad and ovoid, 4–20 mm in length, the fourth largest family in Heteroptera, with about 800 genera and 4,700 species in the world; in the neotropics about 230 genera and 1,400 species are included in seven subfamilies of the world's nine subfamilies (Schuh and Slater 1995; see Chap. 22).

Species in the subfamily Asopinae are predacious and are important as biological control agents. The most common species in the neotropics include those in the genera *Alcaeorrhynchus* Bergroth, *Apateticus* Dallas, *Euthyrhynchus* Dallas, *Brontocoris* Thomas, *Perillus* Stål, *Podisus* Herrich-Schäffer, *Stiretrus* Laporte, *Supputius* Distant, and *Tylospilus* Stål. Two species, *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas), show potential in biological control programs (De Clercq 2000).

The exclusively Neotropical subfamily Cyrtocorinae is small with four genera and 11 species (Packauskas and Schaefer 1998); they are cryptically colored black to brown and are small to medium. Cyrtocorines are rare and of minor economic importance and little is known about their biology. Nymphs and adults of *Cyrtocoris egeris* Packauskas & Schaefer were observed feeding on immature soybean pods in Argentina (Schaefer et al. 2005).

The subfamily Discocephalinae includes two tribes, Discocephalini and Ochlerini, with more than 70 genera and over 300 species; almost all are medium sized and dark colored and restricted to the neotropics. The most known species of Discocephalini belong to the genus *Antiteuchus* Dallas, and in Ochlerini, the genera *Lincus* Stål and *Macropygium* Spinola include species of economic importance by vectoring *Phytomonas* spp. (Trypanosomatidae) in palms in South America (see details in Chap. 22).

The subfamily Edessinae is one of the largest with about 300 species (da Silva et al. 2013) distributed mostly in the Neotropical Region. It includes colored and large stink bugs. They feed on plants and may show economic importance, such as *Edessa meditabunda* (F.), particularly on soybean and on tobacco, and *Edessa rufomarginata* (De Geer) that feeds on Leguminosae and on Solanaceae causing damage to tomato and potato (Panizzi et al. 2000a).

The subfamily Pentatominae is the most diverse with an estimated number between 400 to 600 genera and 2,700 to 3,300 species; the exact number of groups (tribes, genera, and species) is uncertain because the definition of the subfamily is still under discussion (Rider 2013).

They are all phytophagous and many species are economically important as pests of cultivated crops. Main species include *Nezara viridula* (L.), *Piezodorus guildinii* (Westwood), and *Euschistus heros* (F.) and species of *Arvelius* Spinola, *Loxa* Amyot & Serville, *Agroecus* Dallas, *Dichelops* Spinola, and *Chinavia* Orian as important pests of soybean and other crops, and *Mormidea v-luteum* (Lichtenstein), *Oebalus poecilus* (Dallas), *Oebalus ypsilongriseus* (De Geer), and *Tibraca limbativentris* Stål may cause damage to rice and wheat (Panizzi et al. 2000a). Pentatominae are, in general, highly polyphagous, and their life history includes several host plant sequences (Panizzi 1997).

The subfamilies Podopinae and Stirotarsinae are represented by only one species each in the Neotropical Region.

The review of stink bugs of economic importance in the world was carried out by Panizzi et al. (2000a).

Shield Bugs (Scutelleridae)

The scutellerids are known as shield bugs or, sometimes, jewel bugs. These common names are based on their enlarged scutellum that covers the abdomen and their striking vivid color, with body length 5–20 mm long (Schuh and Slater 1995). These bugs are included in 80 genera and about 500 species worldwide (Tsai et al. 2011). In the neotropics, 25 genera and 112 species are registered, although these numbers are much probably underestimated (see Chap. 23).

Scutellerids are included in eight subfamilies, of which three occur in the neotropics, Pachycorinae with 23 genera and Scutellerinae and Elvisurinae with one genus each. The most common species in the neotropics are *Pachycoris torridus* (Scopoli), *Pachycoris klugii* Burmeister, *Augocoris illustris* (F.), *Augocoris gomesii* Burmeister, *Agonosoma flavolineata* (Laporte), *Agonosoma trivittata* (Panzer), *Symphylus deplanatus* (Herrich-Schaeffer), and *Tetyra pinguis* Germar (see details in Chap. 23).

Shield bugs are phytophagous feeding on an array of plants, but they might be necrophagous and be attracted to carrion. Javahery et al. (2000) reviewed the species of economic importance of the world.

Negro Bugs (Thyreocoridae)

The so-called negro bugs, Thyreocoridae Amyot & Serville (Corimelaenidae Uhler), include two subfamilies, Thyreocorinae and Corimelaeninae, this last represented in the Neotropical Region. They are relatively small and dark colored, with oval-elongated body and large scutellum (Grazia and Fernandes 2012). *Galgupha* Amyot & Serville is the most diverse Neotropical genus with 155 species in 15 subgenera; about 160 species are recorded in the neotropics, their biology poorly known (see Chap. 24).

Negro bugs are phytophagous feeding on flowers and on developing or ripe fruits. Despite their occurrence on many crops, they are regarded as minor pests on orchards and flowers and are not mentioned among the Heteroptera of economic importance (Schaefer and Panizzi 2000).

Pentatomoid Families (Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae)

These are pentatomoid bugs that belong to small families, which include less than 70 species in less than 30 genera in the neotropics; species may show maternal care and have cryptic coloration; despite information on their taxonomic status, and on their biology and ecology, in general, they are poorly studied (see Chap. 25).

Acanthosomatidae

These are medium to large bugs, distributed mainly in temperate regions or at high altitudes in the subtropics. They are phytophagous, and some species show maternal care (Tallamy and Schaefer 1997). Few Neotropical species had their biology studied (Faúndez and Osorio 2010a, b). No acanthosomatids with economic importance are recorded from the neotropics (Schaefer et al. 2000).

Canopidae

Exclusively distributed in the neotropics, canopids are small- to medium-sized bugs and are shiny black. Due to their appearance, they are usually mistaken as coleopterans. Eight known species belong to the genus *Canopus* F. Their biology and ecology are less known. They feed on fungi (McHugh 1994).

Dinidoridae

Dinidorids are large, aposematic colored bugs, brown or black with red/yellow stripes, and included in two subfamilies Dinidorinae and Megymeninae, mostly distributed in the Afrotropical and Oriental regions. In the neotropics, only the genus *Dinidor* Latreille is recorded, with six species distributed in South America (see Chap. 25).

Species studied are phytophagous and polyphagous. Schaefer et al. (2000) reviewed the species of economic importance; none were referred to from the neotropics. Few data are available on their biology and ecology in the neotropics; *Dinidor mactabilis* (Dinidorinae) was recorded on *Smilax japecanga* Grisebach (Smilacaceae) in southern Brazil, which deposit large number of eggs in clusters on branches of the host plant (Grazia and Fernandes 2012).

Megarididae

These are small, dark, and shiny bugs and have ovoid and convex shape. They are distributed exclusively in the neotropics, in which 16 extant species are known all in the genus *Megaris* Stål. They are considered phytophagous and their biology and ecology are mostly unknown (see Chap. 25 for more details).

Phloeidae

The phloeids are large, flat depressed bugs with global expansions around the body which makes them look peculiar; they form colonies on the tree trunks where they live, being strongly mimetic (Grazia and Fernandes 2012). They are distributed mostly in the Neotropical Region, with four species in three genera: one species in the genus *Serbana* Distant, which occurs only in Borneo (Leston 1953), two species in *Phloea* Spinola, and one species in *Phloeophana* Leston, the latter two restricted to Brazil (Lent and Jurberg 1965).

Tessaratomidae

Tessaratomids are robust, ovoid-elongated, medium to large bugs; Neotropical species are in general dark green; they are mostly distributed in the Old World tropics with over 40 genera and over 200 species worldwide; the genus *Piezosternum* Amyot & Serville has worldwide distribution and includes three endemic species to the neotropics (see Chap. 25).

The biology and ecology of tessaratomids were studied in the Old World, and few data are available from the neotropics. They are polyphagous on plants; the Neotropical species *Piezosternum subulatum* (Thunberg) was recorded on some cultivated plants in Nicaragua (Maes 1994). However, there are no records on species causing economic damage in the neotropics; the bronze orange bug, *Musgraveia sulciventris* Stål, is referred to as a pest of citrus in the Australian region (Schaefer et al. 2000).

1.3 Concluding Remarks

Heteropterans are indeed a diverse and complex group of insects. They live on several different habitats (terrestrial, aquatic, intertidal and in association with other insects and spiders) as phytophagous (from seed, fruit, leaf, root to mycelia of fungi feeding), or as carnivorous (predators on other insects and arthropods and even feeding on blood of vertebrates); they have great ability to disperse and to adapt to different habitats through mimicry and protective coloration and shape (Schuh and Slater 1995). As a consequence of their success, the clash with humans' interests is inevitable, and many species of heteropterans became with time of economic and/or medical concern. Efforts are focused on research to better understand their biology and ecology in order to develop control strategies to manage pest species to crops or others of medical importance (Schaefer and Panizzi 2000).

Despite the many years of research, heteropterans in the Neotropical Region are still poorly known, as the readers of this book will rapidly verify. However, we hope that the information provided by each chapter will facilitate to learn the knowledge we actually have on the fauna of the heteropterans of the neotropics.

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Chapter 2
Morphology, Ontogeny, Reproduction, and Feeding of True Bugs

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Abstract In this chapter we present an overview of the morphology, ontogeny, reproduction, and feeding of the 28 higher-level categories (infraorder/superfamily/family/subfamily) of true bugs occurring in the neotropical region, which are treated in greater detail in Sect. 2.2.

2.1 Introduction

The Heteroptera can be diagnosed by the presence of mouthparts typically hemipteran with mandibular stylets concentric and surrounding maxillary stylets. The labium is inserted anteriorly on the head and a distinct gular area is always present, often closed behind to form a buccular bridge. Scent-gland structures are often paired, located and exiting ventrally in the metathoracic pleuron; nymphs with paired scent glands which are placed at the junction of one or more of the following abdominal terga: III/IV, IV/V, V/VI, and VI/VII. A detailed description of the adult morphology of heteropterous insects is found in Schuh and Slater (1995). The eggs may be elongate, cylindrical, curved, or barrel-shaped; they are inserted into a plant tissue, cemented to a substratum, or laid free. A distinct operculum may be present, the same applying to a true egg burster. The cephalic pole of the egg of most bugs bears one or two micropyles or aero-micropyles (apparently with gaseous exchange function). Aero-micropylar processes ornament the egg pole; in all bugs except Cimicoidea, the sperm enters the egg during fertilization through the micropyles. There are ordinarily five nymphal instars, which typically resemble adults and live in similar environments. Aside from the lack of ocelli, wings, and genitalia, nymphs are primarily distinguished by the presence of one

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less tarsal segment than those found in adults. Most heteropterous males apparently deposit sperm in the female in the shape of a spermatophore; the sperm is then stored by the female in the spermatheca. Fertilization and oviposition are simultaneous. Plant-feeding species make up the majority of the Heteroptera. The phytophagous habit has been acquired independently at least twice from predatory precursors over the long millennia in which heteropterans have evolved (Schuh and Slater 1995). Phytophagy is found mostly in the Pentatomomorpha and Cimicomorpha. Considering the heteropteran families, the majority are predaceous upon insects and other arthropods. Some heteropterans have also developed the ability to utilize the blood of vertebrates, a characteristic that has arisen at least three and possibly four times independently in the taxon's evolutionary history.

A brief description of the morphology (item 2), ontogeny and reproduction (item 3), and feeding (item 4) of true bugs is presented. Those issues are discussed in more detail in the chapters of Session II. The taxa are listed in alphabetical order, aiming to make more practical the finding of the information.

2.2 Morphology

2.2.1 Alydidae

The Alydidae are 8–20 mm long, usually elongate and slender with disproportionately large heads. The broad-headed bugs as they are known are very often myrmecomorphic, particularly as nymphs. Additional diagnostic characters include: bucculae very short; antennae dorsally inserted with segment 1 not constricted at base; ocelli not placed on elevations; corium elongated on costal margin; metathoracic scent-gland auricles well developed; and tibia nonsulcate (Schuh and Slater 1995).

2.2.2 Anthocoridae

The anthocorids vary from 1.15 to 5 mm long, with a porrect head and ocelli always present in macropterous forms. The labium is four segmented (even though it appears to be three segmented), and the labrum is wide and flap-like. The metathoracic scent gland is deeply bilobed behind with a median accessory gland present. The forewing has an elongate median corial groove, with a short ventral fold, which does not reach the cuneus along the costal margin. The hind wing can have or lack a hamus. Both macropterous and brachypterous forms occur. The tibiae have spongy fossae, either well developed or vestigial; foretibiae in males are, in most of genera, armed with a row of teeth or spines in the inner margin; and the tarsi have three segments. The male genitalia are always asymmetrical. The ovipositor is usually developed or sometimes reduced.

2.2.3 Aradidae

The Aradidae are 3–11-mm-long insects mainly diagnosed by the mandibular and maxillary stylets, which are extremely elongate and coiled within, and the absence of ocelli. Their head is of the prognathous type, highly specialized to accommodate the Mycetophagus sucking mouthparts, and the labium is usually short and stout with 4 distinct segments. The wings, when present, are usually dimorphic, well developed, and exceedingly diverse in development and venation. Metathoracic scent glands are well developed, and the canals and evaporating areas vary in shape with striking development. The legs in Aradidae are considerably variable and sometimes modified for stridulation; the trochanters are commonly and usually distinct from the femora; the front tibiae have an apical or periapical comb on the inner side; and the tarsi are bisegmented. In the abdomen stridulatory structures are present in the ventral surface; the connexivum, even lateroventrally, is morphologically a part of the tergum, since the spiracles are considered to mark the lower limit of the tergum. The connexiva of the first segment or the lateral parts of the first tergite are completely lost. The modification of abdominal segments into reproductive systems begins in the seventh segment for females and in the eighth for males.

2.2.4 Coreidae

Coreids are usually heavy-bodied insects, elongate or elliptical in shape, ranging from 6 to 40 mm. The head is smaller than the pronotum and the antennae have four segments. Their hind femora may be enlarged, with spines and tubercles, and frequently incrassate, while the hind tibiae are curved, with spines or leaflike expansions; apterous, brachypterous, and macropterous forms occur in the family. Abdominal spiracles ventral; three trichobothria on abdominal segments III–VI, two on segment VII; nymphal dorsal abdominal scent-gland openings between terga 4/5 and 5/6. The genital plates are flattened and the spermatheca has only a proximal pump flange. In several coreid tribes, a pronounced sexual dimorphism occurs in the size and armament of the hind femur (Miller and Emlen 2010).

2.2.5 Cydnidae

With ovoid and convex bodies, the cydnids range from 2 to 25 mm. Their head is either quadrate or semicircular, wide, and often explanate; the antennae have five segments. The scutellum never surpasses the middle of the abdomen. The development of wings is variable with the possibility of brachypterous and macropterous forms occurring in the same species; the last three nymphal instars have wing pads, which become more evident in the 5th. The distal margins of the coxae have a row of setae or bristles, known as coxal combs; the tibia has strong and long spines in all extension, and the anterior tibia is usually compressed; and the tarsi have three segments. Female genital plates: Laterotergites 8 fused; gonocoxites 8 large and broad; the spermatheca is relatively small usually with two flanges.

2.2.6 Dipsocoromorpha

Of small size (from 1 to 4 mm) and often strongly declivous head, the Dipsocoromorpha port antennae are with scape and a short pedicel, flagellomeres long, thin and typically with numerous stout setae; the proepisternum is often inflated. One of the most prominent characteristics of the group is wing morphology. While four wing types are found in the taxon (macropterous, submacropterous, brachypterous, and apterous, some of these occurring concomitantly in the same species), wing morphology is even more complex since the forewing is typically not clearly divided into corium and membrane, ranging from completely membranous to entirely elytrous; the hind wing is often seen with deeply separated lobes. The male genitalia are either symmetrical, with appendage-like laterotergites, or strongly asymmetrical.

2.2.7 Enicocephalomorpha

Enicocephalomorpha are small to midsize with body length typically ranging between 2 and 15 mm, are often dull colored, and generally resemble small Reduviidae. Wings are membranous and well developed, but micropterous, brachypterous, and wingless forms, especially in females, also occur (Wygodzinsky and Schmidt 1991). They are characterized by the elongate and porrect head that is subdivided into anterior and postocular lobes by a usually conspicuous postocular constriction (Štys 1995).

2.2.8 Gerromorpha

Semiaquatic bugs are rather diversified in general appearance and structurally very diverse (Andersen 1979), which makes morphologically defining the group somewhat difficult (Nieser and Melo 1997). The head of the gerromorphans is typically elongate, with prominent eyes; contrary to the Nepomorpha, the antennae of Gerromorpha are always long and exposed (Heckman 2011); and the rostrum is typically long and slender. The pronotum is a broad plate with a short anterior lobe, while the scutellum is sometimes reduced. The wings in Gerromorpha are very particular, since pterygopolymorphism is common in the infraorder, with some species showing continuous variation (Schuh and Slater 1995). The forewings are usually not differentiated into the anterior coriaceous and posterior membranous portions; on the other hand, the hind wings are membranous and shorter but much broader than the forewing. Brachypterous and apterous forms also occur, the latter being more common than macropterous. The scent apparatus of semiaquatic bugs belongs to the "type omphalion" of Carayon (1971), with a single median scent orifice on the metasternum. The legs of Gerromorpha generally have modifications that facilitate movement across the surface of the water, so as to stay over the tension layer, and which can even facilitate copulation. The pretarsi have dorsal and ventral arolia (a synapomorphy of the group); the adult tarsus has three segments, but these can be fused sometimes (Andersen 1982). The abdomen has eight dorsal nonreproductive segments in females and seven in males. Nymphs of semiaquatic bugs differ from adults in their usually softer integument; the metathoracic scent apparatus is not formed until the adult stage.

The male genitalia consist basically of a cylindrical abdominal segment eight, a boat-shaped segment nine (the pygophore), and a lid-shaped segment ten (the proctiger), which covers the posterior end of the pygophore. A relatively simple phallic organ is internally attached to the pygophore, and a pair of parameres arises laterally from it. As for the female genitalia, it is formed by the eighth and ninth abdominal segments. The eighth segment has a basal sclerite or first gonocoxa ventrolaterally on either side, and this sclerite carries ventrally and caudally the first gonapophyses. The second pair of gonocoxae is found on segment nine, to which are attached the second pair of gonapophyses. The male genital segments are often more conspicuous than those of females, which may be concealed.

2.2.9 Lygaeoidea

Being the second largest superfamily of Pentatomomorpha, the Lygaeoidea have a plethora of variable morphological characteristics which can hardly be summarized in such a short manner. Nevertheless, the synapomorphies of the taxon can be highlighted: reduced venation nearly always lacking closed cells on the hemelytral membrane and incrassate fore femora found in all basal taxa but lost in a number of distal groups. Also, the Lygaeoidea can be apterous, sub-brachypterous, brachypterous, and macropterous.

2.2.10 Miridae

Mirids can stretch from one to more than 15 mm in ovoid or elongate bodies, although these are variable in adults. The head is triangular and usually prognathous; the eyes are usually large; and the antennae and labium have four segments. Even though most mirids are macropterous, it is common to find submacroptery, brachyptery, microptery, and coleoptery. The hemelytra are distinctive, with the corium divided distally into a triangular cuneus and an apical membrane with one or two unequal cells divided by a short longitudinal vein. Trochanters of all legs are divided. The tarsi are most often three segmented. The metathoracic scent glands are paired and the external efferent or evaporative system is usually well developed. The male genitalia are asymmetrical, with a partially membranous endosoma, often inflatable, and confined by a sclerotized phallotheca. The female ovipositor is laciniate; the sperm-storage organ is a large, saclike structure.

2.2.11 Nabidae

The Nabidae range from 5 to 15 mm with elongate or stout bodies. The head is also more or less elongated, with a cylindrical posterior portion; the labium is flexible and usually curving, reaching onto the pro- or mesothorax, with four distinct segments; antennal prepedicellite is present, although variable in length. Being bell shaped, the thorax itself has no particular features; however, wing polymorphism is common in many species, particularly in those living at higher latitudes; depending on the type of prey, legs can either be simple or enlarged and armed with heavy spines, forming a formidable opposable grasping apparatus. Worth noticing on the abdomen is the presence of trichobothria in some taxa. The male genitalia are usually symmetrical, with eventual asymmetrical parameres or phallus; Ekblom's organ is also usually present. In females, a reduced laciniate ovipositor is found in some cases.

2.2.12 Nepomorpha

The bodies of the nepomorphans can be ovate and flattened dorsoventrally, globular and rounded, convex on the dorsal surface and straight ventrally, elongated, or elongate-ovoid. Besides the variation of forms and colors, aquatic heteropterans are widely diverse in total body length, with some species measuring a little more than 1 mm (Pleidae), whereas others are more than 100 mm long (Belostomatidae). Particularly, the Nepomorpha have reduced antennae (with one to four segments) and a generally small and robust rostrum (three or four segments); the pronotum is long, covering the meso- and metanotum, and the scutellum is always exposed. According to Schuh and Slater (1995), nepomorphans generally have the following six types of wings: micropterous, staphylinid, brachypterous, coleopteroid, submacropterous, and macropterous, although the former five can be grouped into the brachypterous group. The forelegs are generally modified and may be raptorial with the fore femora enlarged or scoop shaped with the fore tarsi unsegmented. The hind legs are generally fringed with golden setae and in some groups can be slightly flattened. The dorsal and ventral arolia are usually present in adults and nymphs

(Schuh and Slater 1995). Sexual dimorphism is observed in some families: the male genital segments vary from symmetrical to asymmetrical, including modifications, and the female ovipositor is generally not developed.

2.2.13 Pentatomidae

The bodies of most pentatomids are of moderate to large size, ranging in length from 4 to 20 mm, and generally ovoid or broadly elliptical. There are, however, some relatively elongate slender species, most of which are associated with grasses. The antennae are usually five segmented, although some species have four. The scutellum is large and usually triangular or subtriangular, in a shield-like form. The forewings are half coriaceous and half membranous, while the hind wings are completely membranous. The tarsi have three segments (two segmented in Cyrtocorinae). Segments VIII, IX, and X of the abdomen are modified into genital structures: whereas the males possess a pygophore with other internal structures like the phallus, ejaculatory reservoir, and spermatheca, females have external plates (laterotergites and gonocoxites) with a generally platelike ovipositor, never truly laciniate.

2.2.14 Pentatomoid Small Families

Acanthosomatidae

Species included in this family resemble median to large pentatomids and may be recognized by the shorter scutellum, two-segmented tarsi, male abdominal segment 8 large and exposed, and most of the females with Pendergrast's organ present.

Canopidae

Species included in this family are medium-sized (5–7 mm), almost rounded, dorsally convex and ventrally flat convex and ventrally flat, totally black, and shiny, with purple and green reflexes. The scutellum is enlarged, covering entirely the abdomen and most part of the hemelytra (Grazia et al. 2012).

Dinidoridae

Adults have large size (10–30 mm), an ovoid and robust body, and a dark brown or black general color, with red/yellow stripes and maculae usually present. The head is carinate laterally, the buccula short and elevated, and the rostrum reaching the meso- and metacoxa. The humeral angles never developed. The scutellum is triangular, almost as wide as long, never covering the corium, and the apex usually blunt. Hemelytral membrane venation is reticulate. *Dinidor* Latreille is the only genus that occurs in the neotropics; it has antennae with five segments and tarsi with three segments.

Megarididae

Megaridids are small (5 mm or less in length) and coleopteroid in shape. Strongly convex dorsally, the scutellum is enlarged and covering the abdomen and wings. They are dark in color and polished. The anterior margins of the head and pronotum are carinate and the bucculae undeveloped. The antennae are four segmented, with many setae as long as the diameter of segments in females is much longer than in males. The tibia is without spines, and the tarsi are two segmented.

Phloeidae

Their bodies are depressed; the external margins of juga and pronotum and the base of corium and abdomen broadly foliate. Their eyes are divided into dorsal and ventral portions. Its antenna is three segmented, only partially visible dorsally, and hidden below the expanded juga; segment 1 is very long and segment 3 curved. They have peritreme opening near the lateral margin of the pleuron. Its hemelytral membrane is reticulate. The tarsi are three segmented. The abdominal sterna 3–7 with trichobothria arranged longitudinally to the spiracular line. Spiracle 2 is present and partially exposed.

Tessaratomidae

Piezosternum Amyot and Serville, the only genus representative of the family in the neotropical region, has worldwide distribution and includes three endemic species to the neotropics. Similar to large pentatomids, tessarotomids can be distinguished from them by its very small head; usually four-segmented antenna; short rostrum; metasternum produced anteriorly, generally into a large bladelike projection reaching the anterior coxae; and pronotum extending over the base of the scutellum.

2.2.15 Pyrrhocoridae

As the only known neotropical genus of Pyrrhocoridae, *Dysdercus* serves as the reference in this section (some of the characteristics may be shared with other pyrrhocorids).

The body length of *Dysdercus* range from 8 to 18 mm, with an elongate to oval, somewhat flattened, body. The slender and elongated sucking mouthparts reach the middle of the thorax and occasionally the abdomen. The pronotum is clearly divided into an anterior third and a posterior two-thirds, these sometimes of different colors. As in other heteropterans, the hind wings are membranous, but the forewings are partly sclerotized and partly membranous, the latter porting two closed cells. The fore femora are, at most, slightly swollen (usually slender), and the metathoracic scent gland lacks an auricle.

Pyrrhocoridae can be distinguished from Largidae most readily by the presence in the females of the latter of a median split on the seventh sternum, indicative of an elongate or laciniate ovipositor; the ovipositor of Pyrrhocoridae is platelike, and the female's seventh sternum is entire.

2.2.16 Reduviidae

Most Reduviidae are medium to large bugs and often show elongate or ovoid body shapes. Overall, Reduviidae is one of the most morphologically diverse groups of Heteroptera, ranging from delicate and elongate to large and robust. Reduviidae can also mimic other groups of Heteroptera (Stride 1954), as well as other insects, such as Hymenoptera, with a number of species participating in Müllerian mimicry complexes (Haviland 1931; Hogue 1993). Some of the most distinctive characteristics of the assassin bugs are the necklike shape of the head behind the eyes and the labium, which is short, strongly curved, and inflexible (Schuh and Slater 1995). Other relevant body structures include the membrane of hemelytra, usually with two or three elongated cells; the presence of a fossula spongiosa at the apex of the fore and mid tibiae in many taxa; and the presence of Brindley's glands between the metathorax and the first abdominal segment. The female genitalia have a lateral spermathecae; males with the eighth abdominal segment telescoped largely into the seventh segment and usually with symmetrical genitalia (Schuh and Slater 1995; Weirauch 2008).

Triatominae

The subfamily is diagnosed, among other features, by the slender and straight labium of its members and their blood-feeding habits (Lent and Wygodzinsky 1979; Clayton 1990; Weirauch 2008). Their general appearance is similar to that of other reduviids. The length of most species varies from 20 to 28 mm, but *Dipetalogaster maxima* (Uhler) can reach 44 mm in length, and the smallest species is *Alberprosenia goyovargasi* (Martínez & Carcavallo), with 5 mm. The color pattern varies, with an overall black or piceous color and spotted patterns of yellow, brown, orange, or red (Jurberg et al. 2004, 2012, 2013). Opposite to the females, in which the genital plates are simple and extremely homogeneous, the male genital complex of the Triatominae is composed of approximately 15 features, which are highly variable and can be used for generic and specific differentiation (Singh-Pruthi 1925; Dupuis 1955, 1963; Lent and Jurberg 1969, 1975).

2.2.17 Rhopalidae

With a body length ranging from 4 to 15 mm, rhopalids vary greatly in both shape and color. The main characteristics of the head which can be highlighted are the four-segmented antennae, clypeus that surpasses the mandibular plates, and ocelli based on low tubercles. As for the thorax, it is notable that the metathoracic scent-gland openings are commonly, but not always, obsolete or obsolescent, hence the common name "scentless plant bugs"; the corium frequently has large hyaline areas, and the membrane of the forewings always has numerous slender parallel veins arising from a transverse basal vein. Females have inner laterotergites with a platelike ovipositor, whereas the pygophore in males has lateral, median, and paralateral lobes; internally, the spermatheca consists of a round bulb, small pump, and long, generally coiled duct.

2.2.18 Saldidae

Most shore bugs are typically small, ranging from 2 to 8 mm, with an ovate body covered by fine setae that repel water and bind layers of air to the body, which indicates that these insects are able to adapt to periods of submergence. Usually, the eyes of the Saldidae are very large, occupying the side of the head that is usually relatively short and broad with visible antennae. All three basic wing forms (apterous, brachypterous, and macropterous) have been recorded for Saldidae (Polhemus and Chapman 1979). Its legs are usually relatively short, slender, or longer; the hind coxae are large, transverse, and broad coxal cavity in the thoracic pleurae and adapted for hopping or jumping; the femora sometimes are armed with spines; and all tarsi are usually three segmented with apical claws. The male genitalia are symmetrical, and the parameres are hook shaped with a distinct processus. In females, the valvulae of the ovipositor are developed or reduced and platelike; also, a spermatheca is present.

2.2.19 Scutelleridae

Shield bugs represent a diverse pentatomoid family, which are mainly recognized by the beetle-like appearance, due to the great development of the mesoscutellum (scutellum), which covers almost the entirety of the abdomen. Scutellerids vary greatly in shape, color, and size, but they are usually medium-sized pentatomoids (10–20 mm). The main thoracic characteristics are the well-developed prosternal keel, weakly sclerotized hemelytra, ostiolar peritreme (which can be present or absent), and usually unarmed legs. The external genitalia are either visible or concealed by sternite VII; thus, most of the diagnostic genital characters (apart from the genital plates) are internal, such as in females with the spermathecal bulb with a simple wall and the genital capsule with a ringlike 8th segment. In males, the phallus often has two or three pairs of well-developed conjunctival projections, and the parameres are commonly uncinate (Schuh and Slater 1995; Tsai et al. 2011; Barcellos et al. 2014).

2.2.20 *Thyreocoridae*

Thyreocorids are 3–8-mm-long bugs with oval-elongate, dorsally convex, and ventrally flat bodies, which are characteristically dark colored (usually shiny). The head is declivent and subtriangular in dorsal view, and the antennae are five segmented. The main thoracic features include a strongly convex scutellum, which covers most of the hemelytra, a reduced corium, tibiae with setae, and spines in all their extension and three-segmented tarsi.

2.2.21 *Tingidae*

Tingids range from 2 to 8 mm and are poorly colored, generally varying in shades of brown. The head is armed with up to nine spines, which can be distributed in variable ways; the antennae have four segments. The pronotum is convex or flat; composed by a collar, a pronotal disk with or without carinae, and a pair of lateral expansions (paranota); and can have a posterior projection covering the scutellum. The collar can be developed, forming a hood, which can fully or partially cover the head. An important morphological characteristic of most tingids is the lacelike network of areolae on the wings, which is very often used in species identification. The male genitalia are symmetrical and the phallus has some sclerotized eversible structures (Lee 1969); the parameres are usually directed backward. The ovipositor is laciniate and the connection between the first valvula and first valvifer is lost, as in Miridae (Schuh and Slater 1995). The spermatheca is absent and the pseudospermatheca is present, but it seems to be unrelated with the sperm-storage function (Marchini et al. 2010).

2.3 Ontogeny and Reproduction

2.3.1 *Alydidae*

For the neotropical alydids, not much data is available on their biology, with the exception of a few species with economic interest. *Neomegalotomus parvus* (Westwood) eggs are laid singly or in groups; on soybean, eggs are laid on the upper third of the plant, preferably on the lower side of leaves, close to the midrib (Panizzi et al. 1996). On pigeon pea, *Cajanus cajan* (L.) eggs are laid preferably in-between seeds (crevices) of mature pods (Ventura and Panizzi 2000, 2003). Nymphs mimic ants and are darkish.

2.3.2 Anthocoridae

The duration of embryonic development after spawning depends greatly on the temperature, while the total duration of the hatching takes a few minutes. The nymphs do not differ greatly from the adult stage, and growth after hatching has no metamorphosis; it is only driven by shedding or ecdysis. The last one, called fledging, is accompanied by some structural completions, including the full development of the wings (for winged forms) and sexual organs. The normal number of nymphal stages is five, but it is possible that some species evolve in just four steps. The sexual organs are externally invisible except at the fifth instar, where the ovipositor of the female is apparent.

Insemination is done through “traumatic insemination,” i.e., injection in the hemocoel or in secondarily developed organs and that is not associated with the genital vias, which are only subsequently reached. The way to oviposit varies according to the different development levels of the ovipositor of the females of the different taxa. Fertilization takes place in the vitellarium, where there are two to seven testes follicles.

2.3.3 Aradidae

Aradids generally have one or two generations per year with five nymphal stages: eggs are laid in May, and nymphs hatch in June (the time of incubation depends on temperature and species), reach the fourth instar during the first summer, become adults from July to August, and after which they hibernate. It is not until the following spring that the bugs mate and begin laying eggs.

After copulating (when the male lies beneath the female) in their natural habitats, in fungi, and under tree barks, the eggs are deposited in frass beneath the eggs, and are found partially embedded in softwood in the galleries of termites. A single female can lay 14–45 eggs.

2.3.4 Coreidae

The number of generations per year varies with latitude and as a function of crop cycles, host plant phenology, and host plant specificity. The eggs are cemented to the substrate by the female and laid either in long chains; singly; in small groups, adjacent rows, or large clusters; or even atop one another. Most eggs are laid on host plants, generally on the undersides of leaves, but also along a linear surface or on the backs of males. Five nymphal stadia occur between hatching and adult emergence. Adults live long, reaching more than 50 days (Mitchell 2006).

Courtship and mating involve antennation, touching with the legs, or other body contact prior to copulation (Eberhard 1998; Tatarnic and Spence 2013; Miller 2011), and males and females may mate multiple times for as long as 6–7 h (McLain et al. 1993; Tatarnic and Spence 2013). Mating often occurs on fruits, and feeding by one or both partners during copulation is common. The most frequent mating position is end to end, with the male facing the opposite direction from the female. Copulatory success appears to correlate with the size of the male (McLain et al. 1993; Tatarnic and Spence 2013).

2.3.5 Cydnidae

The females of Cydnidae can lay a single egg underground (García and Bellotti 1980; Riis et al. 2005), egg masses in shallow cracks on the soil surface (Sites and McPherson 1982), or inside the fruits of *Ficus* (Moraceae) (Mayorga and Cervantes 2001). After that, incubation time can vary from 1 to 4 weeks. Newly hatched nymphs measure from 1.0 to 2.5 mm in length (García and Bellotti 1980; Sites and McPherson 1982; Riis et al. 2005), and their development also occurs in five instars, and, even though the time spent in these stages is mostly unknown, studies found they can last from 54 to as much as 180 days.

Although little is known about the reproduction of neotropical cydnids, for species that live in the soil, mating occurs in this habitat. During copulation, males and females remain connected by the genitalia and in opposite directions (Willis and Roth 1962). Whereas Cydnidae present solitary behavior, mating occurs in the soil and finding sexual partners is difficult, since the environment where these bugs live restricts large-scale communication between individuals. Like other Heteroptera, it is likely that copulation in Cydnidae is mediated by chemicals and sound signals.

2.3.6 Dipsocoromorpha

Not much is known about the development and reproduction of neotropical Dipsocoromorpha, with sparse works mentioning, or dealing with, the five nymphal stages and morphology/coupling of the genitalia.

2.3.7 Enicocephalomorpha

Swarming is a biological phenomenon that is rather common in this group and has been documented for species in five genera and both families in the New World (Wygodzinsky and Schmidt 1991). Štys (1981) speculated that all species that are capable of flight might also swarm. Swarms are possibly formed for the purpose of mating and are composed of large numbers of males and much smaller numbers of females (Kritsky 1977; Štys 1981). Some enicocephalids have the unusual ability to autotomize, or shed, their wings. This behavior may be related to the cryptic way of life of most species. In females, it could be important when individuals retreat, after swarming and copulation, into the soil, where wings might be a hindrance, similar to wing shedding in termites and ants (Wygodzinsky and Schmidt 1991).

2.3.8 Gerromorpha

The eggs of gerromorphan bugs are laid in a wide variety of places, such as on moss and algae, in holes of stones, inserted in plant tissue, on floating objects and living or dead leaves, and many other possibilities. One to 500 eggs can be laid at once or through several days, with incubation periods ranging from 6 to 23 days. Only a few works describing the life cycle of nymphs of neotropical Gerromorpha exist, but it is known that they have four to five instars; the development time takes from 14 to 33 days, during which the two wing pairs start developing before the final molt, where the teneral development takes places, hardening and adding pigmentation to the cuticle, resorption of the now useless muscles, and, in macropterous adults, with the growth of the endoskeleton and flight muscles (Andersen 1982).

The reproductive behavior of semiaquatic bugs has been extensively studied, but the vast majority of the experiments are restricted to temperate species. Four basic mating systems have been described among gerromorphans (Spence and Andersen 1994), but it consists of the male jumping on the back of the female and then engaging in the copulation, usually by attaching its legs to the female's thorax subsequently transferring the sperm in a process that can last as quick as minutes or as long as weeks.

2.3.9 Lygaeoidea

As mentioned in the morphology section, lygeoids are a diverse, highly successful group of true bugs and there have been a significant number of important reviews of the habits, life history, and reproduction. For further details on one of the 12 neotropical families of Lygaeoidea, please refer to the respective chapter.

2.3.10 Miridae

The life histories of most Miridae, especially tropical ones, are poorly studied or are unknown (Schuh and Slater 1995; Wheeler 2001). Much of what we know about courtship and oviposition behavior, fecundity, longevity, and voltinism is the result of studies involving species of agricultural importance. However, it is known that they often have life cycles that last no more than 6 weeks. Firstly, the eggs are inserted, usually, into plant tissue. After eclosion, the transition from the first stage to the final, which can be from three to six (Schuh and Slater 1995; Wheeler 2001), takes 15–30 days.

Plant bugs are remarkable for their genitalic evolution (Kelton 1959; Cassis and Schuh 2012), including traumatic insemination and sexual antagonistic coevolution (Tatarnic et al. 2006; Tatarnic and Cassis 2010; Cassis and Schuh 2012). Parthenogenesis occurs in a few mirid species, such as the predatory *Campyloneura virgula* (Herrich-Schaeffer), where males are rare (Wheeler and Henry 1992; Henry 2012).

2.3.11 Nabidae

Most details provided in this section are related to *Nabis capsiformis* (Germar), which is representative of the family (Hormchan et al. 1976), even though some information on other species is also available (however, very little is known about the development of neotropical nabid species).

Generations can be as long lived as 59 days, depending on the conditions provided. After being laid in plant tissue, eggs (more than 110 can be laid) hatch into nymphs after 7–8 days of development. Then, they proceed through the five instars, a process which can last up to 18 days. Adults can live for 21.6 days under laboratory conditions.

Nabidae reproduction is done mainly through vaginal copulation, with fertilization taking place in the mesodermal oviducts near the base of the ovarioles or near the pedicels. The other possibility is through traumatic intravaginal insemination (Carayon 1977).

2.3.12 Nepomorpha

Nepomorphan eggs are deposited individually or grouped, submerged or slightly submerged above the water surface, or even distant from the water. They can be deposited over the substrate (plant and algae masses, rocks, logs, and the hemelytra of males) or inside it (usually plant tissues). After eclosion, the nymphs develop across four to five instars, which have a similar lifestyle of the adults. The development time and number of generations are not known for most neotropical species, but in the tropics and/or subtropics, the species or populations can be multivoltine, with three or more generations annually (Saulich and Musolin 2007).

Reproduction in nepomorphans generally takes place in water and includes various methods across the families of the infraorder. Stridulation is quite common in these bugs and plays an important role in mating. The males generally make use of different leg pairs to hold the female together for copulation; however, the methods are too variable to be explained in this section (please refer to the Nepomorpha chapter for further details).

2.3.13 Pentatomidae

The pentatomid barrel-shaped eggs are laid on the underside of leaves in clusters with tight rows; in early spring, overwintered adult females seek out suitable hosts and typically deposit their eggs on wild host plants. Often, these overwintering populations are found along field borders, particularly along tree lines near their overwintering sites. Later-developing cultivated plants become more attractive when these initial wild hosts dry down, and their proximity allows easy access for stinkbug colonization in crops; emerging nymphs are gregarious and remain on/near the egg mass and then begin to feed and disperse as they grow. Eggs with translucent chorion, through which it is possible to observe their contents, are more common in Pentatomidae than pigmented chorion; the spinose pattern of chorion sculpture seems to be the most frequent, although several studied species show reticulated chorion and a few others a granulated chorion. The number of aero-micropylar processes is rarely used for specific recognition, due to its overlapping in congeneric species; the number varies between 10 and 86. The number of eggs per mass is relatively constant within Pentatomidae species, related to the number of ovarioles in females and the oviposition strategy of each species. Small egg masses are laid, usually with 14 eggs (Matesco et al. 2007), the number of ovarioles more frequently found in Pentatomidae. Among pentatomids, several life history traits are strongly influenced by temperature, humidity, and food quality. The duration in days of the development from the egg to adulthood is about 48–57.

2.3.14 Pentatomoid Small Families

Acanthosomatidae

Faúndez (2007a) gives a brief description of the life cycle of *D. punctiventris*, providing details of the mating behavior (Faúndez 2007a; Faúndez et al. 2009). Females lay eggs in clutches, corresponding more or less with the number of ovarioles. Egg and nymphal development time, prereproductive females, and adult longevity have not been studied in any of the neotropical species. Faúndez and Osorio (2010) described maternal care behavior for the neotropical species *Sinopla perpunctatus* Signoret. The authors also reported coloration change in the female associated to the reproductive period and guard of eggs and nymphs.

Canopidae

The biology of the canopids is poorly known.

Dinidoridae

Eggs or nymphs of any species of the neotropical Dinidoridae have not been formally described up to date. Knowledge is restricted to species from other regions (Malipatil and Kumar 1975; Danielczok and Kocorek 2003). Eggs and nymphs of *D. mactabilis* were illustrated in Schwertner and Grazia (2014). The unique characteristics of the immature include the shape of the eggs and of the aero-micropylar processes, aspect of the chorion surface, and the development of some nymph structures. Eggs are cylindrical, deposited in rows, horizontally positioned to the substrate.

Megarididae

The general body of nymphs is similar to adults in shape and color; they are heavily sclerotized, with abdominal terga not distinguished; and there is no formal description of eggs.

Phloeidae

The life cycle of these bugs occurs entirely on the trunks of the host (Salomão et al. 2012). Females protect eggs and early nymphs; the latter attach themselves to the abdomen of the mother (Lent and Jurberg 1965; Guilbert 2003).

Tessaratomidae

Eggs are spherical, deposited perpendicular to the substrate. The chorion is smooth and thinner than in Dinidoridae. Aero-micropylar processes are reduced, knob-like, and circulating the middle region of the egg, in variable numbers (30–60). The operculum is not apparent, with the line of the operculum dorsolateral extending basally. Nymphs of the 1st, 2nd, and 3rd instars have oval, flattened body; late instars have elongated and more robust body. All species are univoltine and usually use more than one host plant throughout its life cycle (Schaefer et al. 2000; Dzerefos et al. 2009), with biological aspects very similar to Dinidoridae. Depending on the species, females can lay in masses of four rows (3-4-4-3 formula), with an average of 14–28 eggs per clutch. Fertility is considered low (Schaefer et al. 2000). Maternal care has been described for some tessaratomids of the subfamily Oncomerinae in the Australian region (Gogala et al. 1998; Monteith 2006).

2.3.15 Pyrrhocoridae

As mentioned above, *Dysdercus* serves as the model genus for this section. These bugs' biology and ecology remain poorly known.

2.3.16 Reduviidae

Through their mostly platelike ovipositors, reduviids usually glue their eggs to the plant, often in a group, and sometimes cover them a gelatinous material. However, few species are known to guard their eggs. Ground-dwelling species may insert their eggs into the soil, or the eggs may be laid loose. Some reduviines have more well-developed ovipositors, suitable for the insertion of eggs into cracks or crevices.

Triatominae

Triatominae species are found in almost any habitat offering a degree of climatic stability and access to a blood source. Most of them tolerate a range of air humidity between 30 and 80 %, and temperatures of 24–28 °C are satisfactory. Their development is usually slow at temperatures below 16 °C, whereas temperatures above 40 °C are lethal. During the rigorous winters of Patagonia, they undergo lethargy, and on strong summers they increase the number of blood meals in order to compensate the higher loss of water. In general, most triatomines are nocturnal, and during the day they remain in their resting places, although they may sometimes go out to suck blood during the day under adverse conditions. In general, the eggs of the majority of triatomine species are deposited free in the environment, although some species have an adhesive substance that makes the eggs stick to the substrate. The triatomines are parasites with slow development, whose life cycle from egg to adult includes five nymphal stages, ranging from 3 to 4 months in *Rhodnius prolixus* up to 2 years in *Panstrongylus megistus*. This life span can vary considerably according to the temperature to which the bugs are submitted. The first information on copulation in triatomines was published by Neiva (1914), who noted that *Panstrongylus megistus* females appeared to copulate only once, maintaining the eggs fertile throughout their life span. Courting is not complex in this group of insects, and copulation in some species has been observed in the laboratory by some authors. Prior to copulation, the male approaches the female, attempting to immobilize her with the three legs on one side of the body in a dorsolateral position (Abalos and Wygodzinsky 1951; Hack and Bar 1979; Lent and Wygodzinsky 1979; Lima et al. 1986; Rojas et al. 1990; Manrique and Lazzari 1994).

2.3.17 Rhopalidae

Since detailed studies of eggs and oviposition have not been made for most neotropical rhopalids, this section is based mainly in temperate and subtropical congeners and conspecifics. Rhopalids typically lay their eggs on or near host plants, more specifically on sepals, nearby stems, leaf midribs, floral pappi, the undersides of leaves, and flower pedicels, but they can also be buried in the soil or simply dropped to the ground; while as many as 1,000 eggs can be laid by a single female (Wheeler 1977), they require about 8 days to hatch over an average monthlong oviposition period (Yonke and Walker 1970a, b). As with the eggs, not much is known about neotropical rhopalid nymphs, but the relative genera from other regions have a mature period through the five instars that ranges from 22 to 40 days (Yonke and Walker 1970a, b; Paskewitz and McPherson 1983). Adult males have been reported to live for as long as the average life span of 86,6 days, while females lived for up to 47,7 days.

Mostly, what is known of the reproduction of rhopalids focuses on the consequences of low food availability to reproductive life span and diapause; however, this is not the main focus of this section. Apart from that, Carroll (1988, 1991) reported two different mating systems: promiscuous mating, when females are abundant, and a guarding system when males are much more abundant than females.

2.3.18 Saldidae

Even though the life cycles of Saldidae are not yet completely understood, some generalizations can be made. The eggs are laid in over the vegetation or other substrates. Their maturation requires approximately 1 week, and the hatched nymphs will develop across the five instars in around 2–3 weeks (Wiley 1922; Jordan and Wendt 1938). There are some cold-adapted species and others that can overwinter in the egg or adult stages (Wroblewski 1966).

Saldidae usually copulate side by side (Polhemus and Chapman 1979), and according to Cobben (1957) the female's forewing and male abdominal segments show some modifications to facilitate this copulatory position.

2.3.19 Scutelleridae

Even though the length of life cycles in Scutelleridae is quite variable, some model studies do exist, where total cycles lasted for as long as 60 days. Scutellerid eggs are laid in two or more rows, on several parts of a host plant. These egg masses vary in number, averaging from 14 to almost a hundred eggs (around 75–92); the incubation time is not very well known, but a 7-day period has been recorded for one species (Paleari 1992). After eclosion, the nymphs proceed through five instars until reaching the adult stage.

2.3.20 Thyreocoridae

The life cycle of the Thyreocoridae generally corresponds to that of the Pentatomidae (Grazia and Schwertner 2008). They can be uni-, bi-, or multivoltine: in low latitudes, a higher number of generations per year occur, whereas in higher latitudes only one generation per year is possible (McPherson 1972; Lung and Goeden 1982; Bundy and McPherson 1997, 2009). Eggs are laid singly and glued laterally to the substrate, often in the host plants' reproductive parts and less frequently in branches or leaves; the development varies between 8 and 11 days. After eclosion, the first instar nymphs are active, differing from the nymphs of other Pentatomoidea families, feeding and not showing gregarious behavior; the subsequent development through the five nymphal stages takes from 30 to 45 days.

Not much can be said about the reproduction of thyreocorids, but a pre-copulatory behavior has been described by Bundy and McPherson (1997), and it consists on the male standing behind the female and starting the contact through antennation. After the female's acceptance, the copulation takes place with the individuals positioned in opposite directions, just touching genitalic structures; this process can last for hours.

2.3.21 Tingidae

In general, tingid eggs have been relatively poorly studied; thus, not much is known about their egg development. However, some studies delved into the oviposition sites and strategies. Generally, there are one or two generations per year (univoltine or bivoltine), although multivoltine species are known (Neal and Douglas 1990). Oviposition sites are variable, as species drop their eggs on roots, stems, bud flowers, and/or leafs. The eggs can be inserted on the spongy mesophyll, partially inserted in the vegetal tissue (pseudo-endophytic oviposition), or placed at the surface of the vegetal tissue (exophytic oviposition). They are usually oviposited in the abaxial surface of the leaf and can be arranged in small or big groups, or they can be isolated. Although most species have five nymphal instars, four-instar cycles have already been reported (Johnson 1936). Apart from that, tingid nymphs have yet to be further explored, since only recently they started to be featured in the specialized literature (e.g., Guilbert and Montemayor 2010; Guidoti and Barcellos 2013; Montemayor 2009; Montemayor and Dellapé 2010; Montemayor et al. 2011), and their function and evolution were just studied in a few occasions (Guilbert 2004; Scholze 1992).

As with the life cycle, the reproductive behavior of the Tingidae has been seldom explored, with no courtship behavior reported.

2.4 Feeding

2.4.1 Alydidae

The alydids are phytophagous, feeding on noncultivated and cultivated legumes, solanaceas, and other plant families. Research work on their biology, particularly on their life history in nature, to reveal their association with host plants either cultivated or not is needed.

2.4.2 Anthocoridae

Anthocoridae are chiefly predaceous bugs that occur in a variety of habitats where they feed on different arthropods, including mites and insects. Other examples of food source not so often found in Anthocoridae are plants (forbs, shrubs, and trees), ants, and litter.

Nymphal food does not differ substantially from that of adults. The young Anthocoridae, after hatching, are voracious predators of small arthropods and they attack the same prey as that of imagos, preferring only individuals proportional to their size (eggs, young larvae). The number of prey consumed can reach or exceed several hundred mites or a hundred aphids during the nymphal development of a single individual. It seems at least one meal is needed between two molts, and the most hearty meal precedes the ecdysis. Growth is sometimes compatible with a not predatory feeding habitus (Péricart 1972).

2.4.3 Aradidae

Most aradid species are subcortical and mycetophagous, mainly feeding on the bark of dead trees and fungi juices. They are mostly found on branches that have died recently and are not totally dessicated. When the tree becomes too dry, they apparently abandon it for another branch. They have elongated maxillary and mandibular stylets that are coiled within the head; in the resting position, both stylets are coiled up to form a compact double spiral (Weber 1930), and when the bug is feeding, the length of the uncoiled stylets may reach as much as five to six times that of the insect. Nymphs are found with the adults and feed from the same sources.

2.4.4 Coreidae

Coreids are phytophagous, feeding on gymnosperms and angiosperms, through the phloem, buds, fruits, developing seeds, and mature seeds (Mitchell 2000); no coreids feed exclusively from xylem, but hydration from xylem occurs. Opportunistic feeding on fecal matter, carrion, and insect eggs has been reported (Adler and Wheeler 1984; Menezes-Netto et al. 2012) but is never the primary source of nutrients. Plant preference spans a wide spectrum from specialization on a single genus to extreme polyphagy. Nymphs of the first instar often remain in the vicinity of the egg mass and appear to need only a source of water for successful molt to the second stadium (Cook and Neal 1999). Probing into plant tissue may occur, but the tissue selected is always vegetative (tendrils, leaves, terminal buds) (Rodrigues et al. 2007; Wheeler and Miller 1990). The second through fifth instars require a nutrient source and feed similarly to the adults in most cases, although the shorter stylets may prevent access to deeper plant tissues.

2.4.5 Cydnidae

Cydnid nymphs are typically polyphagous and likely feed on plants closer to the site of hatching. Feeding of host plants through suction, for both nymphs and adults, includes roots, ground pods, aboveground structures, fallen seeds, and fruits. Plants of several families have been reported as hosts (Timonin 1958; Becker 1967; Riis et al. 2005; Mayorga and Cervantes 2001; Chapin et al. 2006), ranging from small-sized plants, such as *A. hypogea*, to larger-sized ones, such as *Eucalyptus* spp. Very often these insects are reported as agricultural pests and, depending on the population level, the symptoms of their occurrence can be checked on the shoots, whose leaves turn yellow and dry (Gallo et al. 2002; Riis et al. 2005; Oliveira and Malaguido 2004; Pereira et al. 2012).

2.4.6 Dipsocoromorpha

Given the small size and cryptic habits of most Dipsocoromorpha, direct observations of their biology are limited. However, it is known that they can feed on chironomid larvae (Esaki and Miyamoto 1959), Collembola, mites, and other Dipsocoromorpha.

2.4.7 Enicocephalomorpha

Enicocephalids are predaceous and appear to feed on soft-bodied insects and other arthropods, but few direct observations are available. In captivity, they were fed with larvae and freshly killed adult flies, symphylids (Symphyla), and campodeids (Diplura), as well as ant larvae and pupae.

2.4.8 Gerromorpha

In general, semiaquatic bugs are intermediate opportunistic stage predators (polyphagous carnivores and scavengers) in the food chains of their communities, normally attacking small invertebrates that fall on the water surface and become trapped or those who swim up to it (Menke 1979). Many species of Gerromorpha are also known to be cannibalistic, feeding upon weaker individuals of their own kind (Butler 1923; Sprague 1956; Andersen 1982). The main sources of food for nymphs and adults are dead or half-dead midges, mosquito larvae and pupae, ostracods, cladocerans, ephemeropterans, and collembolans, while the adults can also feed on pelagic cnidarians, sea anemones, planktonic crustaceans, and fish larvae.

As mentioned above, cannibalism is very common in the infraorder, to the point where some (if not most) experiments with live cultures can be completely lost due to this behavior.

2.4.9 Lygaeoidea

Most lygaeids feed on seeds or plant sap, whereas only a few are predatory. They have piercing-sucking mouthparts, which are made up of the mandibles and maxillae modified to form needlelike stylets lying within a grooved labium (Schuh and Slater 1995). Feeding methods can be divided into two “types”: “stylet-sheath” feeders and “lacerate-flush” feeders (Schuh and Slater 1995; Sweet 2000). The majority of Lygaeoidea are lacerate-flush feeders, a method commonly used by species that feed on portions of the plant rich in nutrients, such as seeds (Schuh and Slater 1995), whereas the families Blissidae, Malcidae, and Colobathristidae are predominantly sap feeders. The lygaeids are often related as pests of agriculture crops (Sweet 2000).

Specific food sources and modified strategies for the neotropical families can be found in the Lygaeoidea chapter in this book.

2.4.10 Miridae

Most plant bugs are oligophagous, occurring on members of one plant family or on plants belonging to a few closely related families (Wheeler 2000), but their piercing-sucking mouthparts and the presence of powerful salivary secretions also allow access to different nutrient resources, such as dried carrion and feces (Wheeler 2001). Even though mirids are often not recognized as predators, specially due to the lack of specialized morphological characteristics for preying, plant bugs are frequently causing severe injuries in crops and have recently invaded several areas across the world due to changes in agricultural practices that lead to the increase of the host range of many plant bugs (Wheeler 2001).

2.4.11 Nabidae

The nabids are usually described as pests of cotton or other important agroecosystems. However, they can get their nutrients from other insects as well. Unfortunately, there's not much information on their feeding sources.

2.4.12 Nepomorpha

Both nymphs and adults are predaceous. They feed on crustaceans, dipteran larvae, and other insects, sometimes even on small vertebrates, such as fishes, tadpoles, salamander and freshwater snakes (Menke 1963), but usually on matter found in deposits on the bottom of the pool and upon the dead leaves that have lodged in its shallow waters, such as diatoms, desmids, *Oscillatoria*, and spores of various algae. Cannibalism is sometimes observed in the taxon, specially from starved individuals feeding on nymphs.

2.4.13 Pentatomidae

The majority of the Pentatomidae is herbivorous, but members of one subfamily (Asopinae) are predaceous on other insects. Both adults and nymphs of plant-feeding species may damage plants, mostly by piercing the plant tissues and thus opening a path for pathogens to enter the plant. Independent of the food source, most species are generalists.

2.4.14 Pentatomoid Small Families

Acanthosomatidae

All known acanthosomatids are phytophagous, usually recorded in more than one host, which includes trees and shrubs (Kumar 1974; Schaefer and Ahmad 1987; Faúndez 2007b, 2009). The feeding sites of acanthosomatids include the young tissues of the host and reproductive parts (Schaefer and Ahmad 1987; Faúndez 2007b, c). Casual records of feeding on decaying organic matter and predation including cannibalism (Miller 1971) are known, probably related to the shortage of suitable host plants (Schaefer and Ahmad 1987). Polyphagy seems to be the rule, but specializations can occur at different levels (Schaefer and Ahmad 1987; Faúndez 2007c, 2009). For instance, *Sinopla perpunctatus* is registered only in *Nothofagus* spp. in Chile and is considered a specialized species (Faúndez 2007c; Osorio 2009). Otherwise, *Acrophyma cumingii* (Westwood) and *Ditomotarsus punctiventris* Spinola are considered generalists (Faúndez 2007a, 2009).

Canopidae

Nymphs and adults of *Canopus* spp. were registered on fungi (McHugh 1994).

Dinidoridae

All species studied so far are exclusively phytophagous, feeding both in reproductive and vegetative parts of their hosts. The data indicate that polyphagy is widespread, but monophagy in some species is likely. Some species may exhibit gregarious behavior during a part of the year, being found in large quantities together on the host, i.e., *Dinidor mactabilis* which was recorded in *Smilax japecanga* Grisebach (Smilacaceae) in southern Brazil (Grazia et al. 2012).

Megarididae

The biology and ecology of the megaridids are completely ignored; it is accepted that all species are exclusively phytophagous.

Phloeidae

The unique cryptic morphology of the phloeids makes these bugs to be confused with the bark of trees where they live (Lent and Jurberg 1965; Grazia et al. 2012). Nymphs and adults feed on the vascular system of the hosts (Bernardes et al. 2005).

Tessaratomidae

All species studied so far are exclusively phytophagous, feeding on both reproductive and vegetative parts of their host. Polyphagy seems to be the rule, but as for Dinidoridae, some species may show host preference [e.g., *Musgraveia sulciventris* (Stål) feeds primarily on plants of the family Rutaceae and is considered pest in the Australian region] (Schaefer and Ahmad 1987; Schaefer et al. 2000).

2.4.15 Pyrrhocoridae

Pyrrhocoridae often feed on the ripening seeds, or secretions on the seeds, of common, fairly low plants (mostly members of the order Malvales). Since they basically feed on a restricted number of sources, some genera or species can be of economic importance, like *Dysdercus* that become serious pests of cotton. Other food sources include wheat, water and energy from the nectar of various flowers and from probing fruits (Myers 1927; Van Doesburg 1966), and even other insects (Schouteden

1912; Kamble 1971). Citrus seems to be such a favored plant (Moizant and Téran 1970, Riley & Howard in Myers 1927), but it may only reflect the likelihood that citrus groves often lay near cotton fields.

2.4.16 Reduviidae

As the common name implies, the assassin bugs are strictly predaceous. Although many Reduviidae appear to feed on a wide variety of arthropods, they sometimes show prey preferences or even prey specializations (see summary in Hwang and Weirauch 2012). Some of these preferences include millipedes (Cachan 1952; Forthman and Weirauch 2012), termite predators (McMahan 1983), ants (Jacobson 1911), spiders (Wignall and Taylor 2008; Jackson et al. 2010), and other reduviids (Bérenger and Pluot-Sigwalt 2009).

Triatominae

Triatomine bugs are obligatory hematophagous insects in all stages of their development and in both sexes, requiring numerous blood meals to complete their development. The amount of blood ingested varies according to the species as well as in relation to the life stage, and generally the 4th and 5th instar nymphs are the ones that feed the most. The vast majority of species feed on the blood of mammals or birds, but some can feed on reptile or amphibian blood (Carcavallo et al. 1998/1999). Coprophagy (ingestion of feces), kleptohematophagy (sucking blood already ingested by another triatomine), and hemolymphagy (sucking hemolymph from other arthropods) have also been reported by various authors (Lafont 1912; Brumpt 1914; Lent and Martins 1940; Wood 1941; Ryckman 1951; Sandoval et al. 2000). Resistance to long periods of fasting and the fact that many species are generalists favor their survival in nature.

2.4.17 Rhopalidae

The rhopalids are exclusively plant-feeding bugs, which specialize on particular host plant taxa as food resources, mainly herbs and woody plants. However, even specialists may take water or nutriment from other sources, including flowers, sweet fruits, and dead insects, which may sometimes lead to confusion about the definitive host on which they depend for growth and reproduction. Usually, Rhopalidae are found hosting on the seeds of plants of the family Sapindaceae. Often, groups of nymphs are found feeding on a single seed, forming a cluster around the seed; feeding on seeds of sapindaceous canopy and light gap lianas in aggregations may exceed a million individuals in number (Carroll and Loye 1987; Wolda and Tanaka 1987). Only some genera, like *Boisea*, have been reported as nuisance pests (e.g., Schowalter 1986).

2.4.18 Saldidae

Most members of Saldidae are predaceous, feeding on small insects (Brooks and Kelton 1967), mainly Diptera larvae, other saldids (Wroblewski 1966), and even their own eggs (Rimes 1951). Some species can adapt to scavenger or carnivore habits (Merritt et al. 2008). After catching the prey, the rostrum is inserted and proteases enzyme are injected to immobilize and liquefy the body contents before they can be sucked up as in several other predaceous Heteroptera (Picado 1937, 1939; Cheng 1967; Pereira and Melo 1998).

2.4.19 Scutelleridae

Scutellerids are generally considered to be exclusively phytophagous, although some authors consider these bugs generalists (Javahery et al. 2000), with extreme examples, such as when some were found feeding on a decomposing snake (Chérot et al. 1998) and on putrefied fish carrion baits (Eger, personal observation). Stems, leaves, and flowers may be used as food although fruit and seeds seem to be most commonly used. Despite their mostly polyphagous habit, several species have been reported to prefer plants from the family Euphorbiaceae. Other known host plant families include Malvaceae and Lamiaceae. The first instar nymphs do not feed, while the other instars feed on the very same plants where their eggs were deposited.

2.4.20 Thyreocoridae

Being exclusively herbivorous, thyreocorids are generally associated to bushes, feeding and living in the reproductive parts of the host plants. Even though most species are restricted to one or two plants (Biehler and McPherson 1982; Bundy and McPherson 1997), up to ten different plant families hosting a single species have been recorded.

2.4.21 Tingidae

These exclusively phytophagous bugs are usually found on the undersides of leaves (with some exceptions), where they feed on the sap of living plants by piercing the epidermis with their very slender stylets. These stylets are protrusile and retractile, and can easily penetrate the cellular tissue to extract the sap. Their feeding activities may cause great injury and plasmolysis of the foliage. Many cultivated and wild plants of prime importance in agriculture and horticulture are seriously affected by the feeding activities of these insects (Drake and Ruhoff 1965). Some non-neotropical genera have been reported to induce galls and feed on pollen and moss (Péricart 1983).

2.5 Concluding Remarks

Morphological studies on the neotropical Heteroptera are increasing in the last four decades specially for the groups with economic interest. Considering the neotropical fauna, the knowledge of the ontogeny, reproduction, and feeding is still incipient.

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Chapter 3
Classification and Biogeography of Neotropical True Bugs

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Abstract A review of Heteroptera classification, biogeography, and phylogeography is presented. The use of molecular data significantly expanded the knowledge of phylogenetic relationships among and within heteropteran infraorders. However, taxa historically less studied continue to receive little attention. Promising, new molecular approaches with increased genetic markers and broader taxon sampling, as well as new morphological approaches (e.g., microtomography), are the future for more stable classifications and a better comprehension of the heteropteran evolutionary history, but their application is still incipient. A non-exhaustive overview of studies about Neotropical heteropteran biogeography is made and discussed, including those about intercontinental connections and regional distribution patterns. The most comprehensible studies, and more promising area, seem to be those focused on distribution patterns, especially employing macroecological methods, and trying to elucidate what are the major factors responsible for the distribution of the group in the Neotropics. Finally, we present an overview of phylogeographic studies involving Neotropical Heteroptera. It is clear that the best biogeographic and phylogeographic studied groups are those with medical and economical importance (e.g., Reduviidae and Pentatomidae).

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3.1 Introduction

The knowledge of the Heteroptera goes back to the eighteenth century, during the 1750s to 1770s. This period was called “Classical” (Slater 1974) and began with C. Linnaeus, followed by J.C. Fabricius and others, which studied the Heteroptera in general and provided the first major higher classifications of the suborder. Carl Stål, from the mid-1850s to the end of the 1870s, represents the watershed of the revisional studies in many heteropteran families (Stål 1870–1876). The appearance of specialized works started in 1870, primarily in Europe, favored by the enrichment of the European museums by major collecting expeditions in all parts of the world. It was a period of dominance for taxonomy, not only with descriptive works but also with faunistic (e.g., Distant 1880–1893) and comprehensive catalogs (e.g., Lethierry and Severin 1893–1896, a general catalog, and Kirkaldy 1909, a Rhynchota catalog). From the seventeenth to the early twentieth centuries, not so many heteropterists were dedicated to describe new taxa in the New World, and mostly faunistic works were done (Mayr 1864, 1866a, b; Uhler 1869, 1894; Berg 1879, 1884 – Hemiptera Argentina; Bergroth 1891, 1893, 1894, 1905, 1908, 1914, 1918; Breddin 1903a, b, c, d, 1904a, b, c, d, 1907, 1908a, b, 1909, 1910, 1912a, b, c, 1914).

Reuter (1910) pioneered in evaluating the classification of Heteroptera, making explicit interpretations of the characters used by previous authors, presenting objective arguments for definition of groups (Schuh 1986), and producing a phylogenetic scheme for the Hemiptera. As in many other works, character polarity was the weakest aspect in Reuter’s work (Schuh and Slater 1995). Although Reuter (1910) proposed subordinal names, most were never consistently adopted, but he already had a close concept of the current Gerromorpha, Nepomorpha, and Cimicomorpha. For a more complete view of Reuter’s work, see Schuh and Slater (1995).

From 1900 to the early 1940s, several workers have devoted to the description of new genera and species. For their influence in the knowledge about classification of Neotropical Heteroptera, worth to mention is the world catalog of part of the families’ currently classified in Pentatomoidea (Kirkaldy 1909) and the world revision of Thyreocoridae (McAtee and Malloch 1933). Other relevant taxonomists in this period were G. Breddin, E.E. Bergroth, R. Jeannel, H.G. Barber, G. Horvath, and E.P. Van Duzee.

From the early 1950s to the beginning of the 1990s, taxonomists focused mainly on the revision and description of taxa within families. Outstanding exceptions are the world catalogs for genera and species of Miridae (Carvalho 1952; Schuh 1995, 2002–2013), Tingidae (Drake and Ruhoff 1960, 1965; Froeschner 1996, 2001), Lygaeidae (Slater 1964; Slater and O’Donnell 1995), and the world classification reviews of Aradidae (Usinger and Matsuda 1959) and Cimicidae (Usinger 1966). Other relevant taxonomists in this period were T. Esaki and H.B. Hungerford for Nepomorpha and Gerromorpha, respectively; D. Leston for Cimicoidea; R. Cobben for Leptopodomorpha; R. Matsuda for Gerridae; P.W. Wygodzinsky for Enicocephalomorpha, Dipsocoromorpha, and Reduviidae; P.D. Ashlock for

Lygaeidae; and R. Ruckes, L.H. Rolston, M. Becker, and A.A. Pirán for Pentatomidae. For an extensive review of the world major taxonomists in Heteroptera, see Schuh and Slater (1995).

In a wider classification approach within the Heteroptera, the work of Leston et al. (1954) was a keystone to heteropteran modern classification. Leston et al. introduced the terms Cimicomorpha and Pentatomomorpha in the first attempt to recognize natural groups within the polyphyletic Geocorisae, based on accumulated evidence from comparative studies of internal anatomy and external morphology of the Heteroptera (Schuh and Slater 1995). The influence of Leston et al. work was widely felt and stimulated other authors into attempting to document the monophyly of higher groups within Heteroptera. As outlined by Štys and Kerzhner (1975), such attempts resulted in the recognition of seven infraorders, which at the time were not proposed based on cladistic analysis: Enicocephalomorpha Stichel; Dipsocoromorpha Miyamoto; Gerromorpha Popov; Nepomorpha Popov; Leptopodomorpha Popov; Cimicomorpha Leston, Pendergrast, and Southwood; and Pentatomomorpha Leston, Pendergrast, and Southwood.

3.2 Phylogenetic Systematics and Modern Higher Classifications of Heteroptera

Hennig's ideas on defining and recognizing monophyletic groups based on shared derived characters (i.e., synapomorphies) took some time to influence the classification of Heteroptera, even after the publication of its English edition (Hennig 1950, 1966). The first studies to apply the concepts proposed by Hennig were approximations of what is now traditionally called "cladistic analysis" – based on characteristics usually employed in taxonomy and comparative morphology, such works aimed to identify equivalence between phylogenetic hypotheses and taxonomic classifications (Schuh 1979, 1986). At higher taxonomic ranks, such hypotheses of relationships were presented as hierarchical branching diagrams, depicting the distributional congruence of attributes (characters) between taxa. At the time of Hennig's work, important aspects of phylogenetic analysis, such as broad sampling of outgroups and questions about rooting, character polarity, and character coding had not yet been developed. Nevertheless, Hennig's legacy laid the foundations to produce a general reference system for biology based exclusively on monophyletic groups and a way to summarize the knowledge contained in classifications and taxa diagnoses (Schuh 1986).

The 1970s and 1980s saw the rapid development of phylogenetic methods and an arising dispute between schools of thought (evolutionary systematics, numerical taxonomy or numerical phenetics, and systematic cladistics) for the establishment of the most suitable classification method (Hull 1988). It was not clear which were the most appropriate methods for assessing phylogenetic relationships neither if this would be a task that could be achieved in the near future.

On his seminal work on adult and immature heteropteran morphology, Cobben (1968, 1978) provided cues for the definition of characters within Heteroptera and enormously expanded the knowledge about features never studied before. Cobben's sampling of the Neotropical fauna was notable, by sampling species from the Antilles, Costa Rica, Brazil, and Chile in its first volume (Cobben 1968), then, on its second volume, by extending the Neotropical sampling to species occurring in Honduras, Paraguay, Peru, and Trinidad (Cobben 1978). Cobben's studies on heteropteran morphology would be later compiled in morphological matrices (Schuh 1979; Mahner 1993; Wheeler et al. 1993), but many characters proposed by Cobben are yet to be coded in a formal cladistic analysis (Weirauch and Schuh 2011).

Cobben (1978) also ventured into proposing phylogenetic relationships within Heteroptera, even though not using formal cladistic analysis. Cobben recognized Gerromorpha as paraphyletic and at the base of Heteroptera. Schuh (1979) reaccessed Cobben's work employing cladistic analyses, proposing the first phylogenetic analysis using parsimony criterion and outgroup comparison to polarize characters, in order to recognize higher-level groups in Heteroptera. Schuh (1979) demystifies wrong concepts implicit in Cobben's work, such as the impossibility to cladistically analyze higher taxa of Heteroptera because of the enormous amounts of parallelisms. Schuh (1979) found the Enicocephalomorpha to be the sister group to the remaining Heteroptera, Dipsocoromorpha as sister group to Neoheteroptera, and Gerromorpha as sister group to Nepomorpha + Leptopodomorpha and Cimicomorpha + Pentatomomorpha.

Since Schuh's reanalysis of Cobben's work, phylogenetic analyses based on morphological and molecular datasets have increasingly influenced the understanding of relationships within Heteroptera, resulting in explicit cladistic hypotheses of relationships among the seven infraorders (Weirauch and Schuh 2011). Wheeler et al. (1993) hypothesis treats the Enicocephalomorpha as the sister group to the remaining Heteroptera, Dipsocoromorpha as sister group to the Neoheteroptera, Gerromorpha as sister group to the Panheteroptera, and Nepomorpha as sister taxon to the Leptopodomorpha (Cimicomorpha + Pentatomomorpha).

Other competing hypotheses, based on morphological data of fossil and extant taxa, include Nepomorpha as the sister taxon to the remaining Heteroptera (Mahner 1993; Scherbakov and Popov 2002), without resolving the relationships among the other infraorders. Li et al. (2012), based on molecular data, agree with the Nepomorpha as sister taxon to the remaining Heteroptera, but find the Dipsocoromorpha + Gerromorpha as sister taxon to Enicocephalomorpha + Leptopodomorpha and Cimicomorpha + Pentatomomorpha. Yet, others agree with Wheeler et al. (1993) with the Enicocephalomorpha as the sister taxon to the remaining Heteroptera, but disagree on the relationships of other infraorders (Xie et al. 2008).

The only sister-group relationship that is not contradicted by any of these hypotheses is the Cimicomorpha + Pentatomomorpha. This clade was also supported in combined morphological and molecular analysis by Schuh et al. (2009) and in morphological analysis focusing on the rhabdom structure of the ommatidia (Fischer et al. 2000).

Spangenberg et al. (2013) provided new data on head morphology (including musculature, tentorium, cephalic nervous system, and alimentary tract) based on serial sectioning and computer-based 3D reconstruction for representatives of the potentially basal heteropteran lineages (Enicocephalomorpha, Dipsocoromorpha, and Gerromorpha). Spangenberg et al. cladistically analyzed 71 cephalic characters scored for 16 heteropteran terminals. Heteropteran monophyly was strongly supported, but some of the recovered relationships between infraorders are not consistent with previous studies, such as the paraphyly of Nepomorpha and Dipsocoromorpha – the authors thus suggest that cephalic features alone are apparently insufficient for a clarification of the relationships of the major lineages of Heteroptera. They also mapped cephalic character data on three alternative hypotheses, being Wheeler et al. (1993) the most parsimonious one, requiring 201 steps for their data. The topologies of Xie et al. (2008) and Mahner (1993) required 202 and 212 steps, respectively.

There has been a recent increase in studies employing DNA data, especially those with a more comprehensive taxon sampling. The availability of new sequencing techniques promises a revolution, by reducing costs and increasing the availability of molecular data. Phylogenomics and proteomics approaches are making possible a better understanding of the relationships within Insecta (e.g., http://www.1kite.org/index.html). At the same time, the availability of molecular data is increasing, as is the refinement of morphology-driven studies with the diffusion of new approaches. New and improved technology for image capture and treatment, such as confocal microscopes and 3D-reconstructions by scanning electron microscopy and X-ray microtomography, are making possible to revisit and investigate underexplored morphological characters (Friedrich et al. 2014). The new challenge will be to integrate new molecular and morphological datasets enabling its combined analysis, as has been recently done by some researchers (Friedrich et al. 2014).

3.2.1 Phylogenetic Relationships Within the Heteropteran Infraorders

Nothing is known about the phylogenetic relationships within Enicocephalomorpha. Therefore, phylogenetic relationships will be presented for the remaining six infraorders of Heteroptera.

Dipsocoromorpha

According to Weirauch and Štys (2014), the Dipsocoromorpha are the least documented heteropteran infraorder, comprising about 300 species in five families. The monophyly of the group has been considered to be controversial because its families show a great morphological variability (Weirauch and Schuh 2011). Weirauch and Štys (2014) were the first authors to comprehensively sample the Dipsocoromorpha and perform a phylogenetic analysis of this infraorder. Their results support a monophyletic Dipsocoromorpha, as well as the families included in the analysis (i.e., Ceratocombidae, Dipsocoridae, and Schizopteridae). However, the position of this infraorder in Heteroptera still needs to be settled, since the dataset alone (ribosomal data) is not sufficient to resolve deep relationships among the Heteroptera.

Gerromorpha

The infraorder Gerromorpha, commonly called the semiaquatic bugs, comprises about 2,100 species in eight families (Damgaard 2008). Although the monophyly of this taxon has been extensively corroborated (Andersen 1982; Damgaard 2008), the monophyly and relationship among its superfamilies have been recently disputed (Damgaard 2012). The pioneerism of Andersen's contributions (Andersen 1981, 1982) is still the most comprehensive comparative study of this infraorder (Damgaard 2012). Damgaard (2008) proposed a phylogenetic hypothesis for Gerromorpha using morphological and molecular data summarized from several studies (Muraji and Tachikawa 2000; Andersen and Weir 2004; Damgaard et al. 2005; Damgaard and Cognato 2003) addressing the systematics of major lineages within Gerromorpha. Damgaard (2008) corroborated the monophyly of the infraorder, as well as the relationship of the Mesoveliidae as the sister group to all other gerromorphan families, and the relationship between Gerridae and Veliidae. Gerroidea, Hydrometroidea, Vellinae, and Cylindrostethinae were recovered as paraphyletic.

Nepomorpha

The Nepomorpha, or true water bugs, comprises about 2,000 species placed on 11 families. The monophyly of Nepomorpha is widely accepted (Wheeler et al. 1993; Mahner 1993; Scherbakov and Popov 2002; Xie et al. 2008), but Hua et al. (2009) found contrasting results, suggesting Nepomorpha was paraphyletic and the Pleidae should be elevated to infraordinal level, i.e., Pleomorpha; given their small taxon sample and lack of a combined effort including morphology, their taxonomic decisions have not been accepted (Weirauch and Schuh 2011).

Within Nepomorpha, there is an agreement in placing the Nepidae+ Belostomatidae as the sister group to the remaining Nepomorpha and in treating the Helotrephidae, Notonectidae, and Pleidae as a clade (Rieger 1976; Mahner 1993; Hebsgaard et al. 2004).

Leptopodomorpha

About 400 species distributed in four families comprise the Leptopodomorpha, or shore bugs. Family-level relationships within the infraorder have not changed since the publication of Schuh and Polhemus (1980) that, based on morphological data, proposed Saldidae+Aepophilidae to represent the sister group to Omaniidae+ Leptopodidae. Recently, Zhang et al. (2014) found the same relationships among the extant leptopodomorphan families, placing the fossil Palaeoleptidae as sister group to Omaniidae+Leptopodidae, and the fossil Archegocimicidae more closely related to Aepophilidae. Other phylogenetic contributions to the Leptopodomorpha are the cladistic revisions of *Saldula* Van Duzee and of *Pseudosaldula* Cobben (Lindskog and Polhemus 1992; Schuh and Polhemus 2009).

Cimicomorpha

Cimicomorpha is the largest infraorder of Heteroptera, comprising about 20,000 species in 16 families (Schuh and Slater 1995). The Cimicomorpha is a well-studied infraorder, especially because of its economic and health importance; however, few studies were concerned with the phylogenetic relationships within the family level (Schuh et al. 2009). Ford (1979) and Kerzhner (1981) were the first to propose hypotheses of phylogenetic relationships within Cimicomorpha, but the phylogenetic relationships proposed by Schuh and Štys (1991) were the most accepted. Since this publication, knowledge about cimicomorphan morphology has increased for many families. Schuh and Slater (1995) made important new observations about the Cimicomorpha morphology; other important contributors to the morphology of the infraorder are Weirauch (2003, 2005, 2006), Schuh (2006), Popov (2008), and Cassis et al. (1999).

Tian et al. (2008) analyzed the phylogenetic relationships of 12 cimicomorphan families based on molecular dataset and different methods of phylogenetic reconstruction, finding small differences from Schuh and Štys (1991), but did not propose taxonomic changes. Analyzing molecular and morphological data, Schuh et al. (2009) found a paraphyletic Cimicomorpha, with the Thaumastocoridae as sister group to the Pentatomomorpha, but the authors avoided taking taxonomic decisions at the infraordinal level because of ambiguities between the datasets results. Within the Cimicomorpha, Schuh et al. (2009) expanded the Cimiciformes to include the Joppeicidae, Microphysidae, Velocipedidae, and Curaliidae; the monophyly of Miroidea, Cimicoidea, Reduviidae, Tingidae, and Miridae were corroborated. At family level or lower levels, families such as the Miridae (Weirauch and Schuh 2010), Reduviidae (Paula et al. 2005, 2007; Weirauch 2008; Weirauch and Munro 2009; Hwang and Weirauch 2012), and Tingidae (Montemayor and Costa 2009; Guilbert 2012a, b; Guilbert et al. 2014) were analyzed phylogenetically, and the Reduviidae has been the focus of studies on comparative morphological and behavioral evolution (Berniker and Weirauch 2012; Weirauch et al. 2011; Zhang and Weirauch 2013).

Pentatomomorpha

Influenced by the work of Tullgren (1918) and Singh-Pruthi (1925) and by their own observations, Leston et al. (1954) coined the Pentatomomorpha to include the Aradoidea and Trichophora. As conceived by Tullgren (1918), the Trichophora gathered the taxa presenting ventral abdominal trichobothria and a certain type of pulvilli (*sic* arolia). As conceived by Leston et al. (1954), the Pentatomomorpha could be recognized by wing venation, pretarsal structure, salivary glands, internal genitalia, and egg morphology; the family composition of Pentatomomorpha little changed after their work, with the exception of the Thaumastocoridae and Saldidae, and Leptopodidae being transferred to Cimicomorpha and Leptopodomorpha, respectively (Štys and Kerzner 1975).

Four to six superfamilies have been recognized within the Pentatomomorpha (Štys 1961; Schaefer 1993; Carver et al. 1991; Schuh 1986; Henry and Froeschner 1988), illustrating the uncertainty of relationships in the infraorder. Currently, five superfamilies are accepted: Aradoidea, Coreoidea, Lygaeoidea, Pentatomoidea, and Pyrrhocoroidea. So far, seven works have addressed the phylogeny of the Pentatomomorpha, all finding the infraorder to be monophyletic and only the Aradoidea and Pentatomoidea are consistently recognized as monophyletic (Henry 1997; Li et al. 2005, 2006; Xie et al. 2005; Grazia et al. 2008; Hua et al. 2008; Tian et al. 2011; Yao et al. 2012). The Aradoidea seems to be the sister group of Trichophora, and the relationships within Trichophora are far from being understood. Some phylogenetic hypotheses agree in Coreoidea and Lygaeoidea probably being polyphyletic (Li et al. 2005, 2006; Xie et al. 2005) and the Pyrrhocoroidea sometimes appearing as sister group to Coreoidea + Lygaeoidea (Henry 1997; Xie et al. 2005; Hua et al. 2009) or as sister group to the Pentatomoidea (Li et al. 2005, 2006) or to the Coreoidea (Tian et al. 2011).

3.3 Biogeography of Neotropical Heteroptera

Since the contributions of Augustin P. de Candolle and Friedrich W. H. A. von Humboldt in the early nineteenth century, the Neotropical region has been the focus of studies on how the geophysical processes influence the distribution of living organisms (Llorente et al. 2000). From the very beginning, naturalists studying the Neotropical biota were amazed by its richness and diversity and were puzzled on how to explain the biogeographical evolution of such a diverse ecosystem. Most of the questions made by the first naturalists remain unanswered: Are there distributional patterns? And how can they be explained? Are distributional patterns similar to all organisms or each taxon responds differently to it? How is the Neotropical biota related to the biota of other biogeographical areas?

Methodological approaches and the understanding of biogeographic patterns were developed concomitantly, resulting in a wide variety of explanations to the current distributional patterns of the Neotropical biota. During the 1850s and 1860s, Joseph Hooker hypothesized the existence of intercontinental land bridges (e.g., between South America and Africa) and posteriorly changed his opinion and accepted the idea of centers of diversity, agreeing with the dispersal views of C. Darwin and A.F. Wallace (Llorente et al. 2000; Morrone 2007). Matthew's (1915) work was the foundation for the, subsequently named, "New York School of Zoogeography" (Croizat 1958; Morrone 2009), a school of thought reconciling biogeography, natural selection, and dispersal theories – a paradigm to neo-Darwinists. In this context, dispersal explanations for distributional patterns state that ancient species live in remote areas, whereas more recently derived species are located in the centers of origin where they speciated. Even though dispersalism was not a unified research program, Simpson (1940), Darlington (1957), and Mayr (1942) followed W.D. Matthew's ideas (Morrone 2002). Simpson (1940) proposed concepts such as *filter bridges* and *sweepstake routes*, stating that any taxon can be originated in a center of origin and expands its distribution in every direction, until it reaches an impassable barrier. Thus, the biota would have random distributions, because the distribution of each taxon would be determined by its dispersal capabilities.

Panbiogeography was developed by L. Croizat to test dispersalist ideas. By comparing the distribution of plant and animal species, Croizat (1958, 1964) found a limited number of distributional patterns (Craw et al. 1999; Morrone 2007), somewhat contrary to the dispersalist assumption of random distribution patterns. Croizat's work had either a low impact or was negatively criticized at its time (Llorente et al. 2000).

The development of cladistics, providing rigorous means of recognizing groups and its relationships and the wide acceptance of plate tectonics, promoted a shift on biogeography, from dispersal, centers of origin, and identification of subregions to the establishment of areas of endemism and degrees of distributional concordance between different taxa and the areas taxa occupy (Schuh and Slater 1995). Biogeographic approaches became methodologically explicit only after Nelson and Platnick's (1981) formalization of the cladistic biogeography method. The method's assumption is that there is evidence of shared common distributional patterns if congruence between phylogenetic and biogeographic patterns of two or more taxa is found.

Biogeographic studies on Heteroptera face old and new impediments, such as limited knowledge on phylogenetic relationship for most groups, limited taxon sampling, lack of dating in phylogenetic hypotheses, and limited knowledge on the distribution of taxa. Most biogeographical discussions are drawn from comparisons between distributional patterns of studied taxa and other taxa, and geological information. Also, biogeographical discussions frequently are neither based on phylogenetic information, nor dating nodes, nor on assumption of ancestral areas from related fossils. Such approaches have serious methodological flaws (Heads 2005), because congruence or incongruence between non-dated biogeographical events may be derived from pseudo-congruence or pseudo-incongruence patterns (Page 1990; Hunn and Upchurch 2001; Donoghue and Moore 2003).

A non-exhaustive overview of studies discussing the biogeography of Heteroptera on the Neotropics, including those about intercontinental connections and local patterns, is presented below. This section is intended as a starting point for new biogeographic studies on Heteroptera occurring in the Neotropics, facilitating literature review, and is organized by infraorder. To avoid the flaws exposed above, we do not assume generalized patterns for the studies discussed.

3.3.1 Continental Biogeographical Connections

Gerromorpha

Andersen (1999) reviewed the phylogenetic, ecological, and geographical aspects of species diversity of the Gerromorpha, finding that about 10 % of the 152 gerromorphan genera are marine and confined to the subtropical and tropical regions of the world. According to Andersen, most marine water striders of the Neotropical region have rather restricted distributional areas, such as the *Rhagovelia* (*Trochopus*) (Carpenter) (Veliidae) and *Rheumatobates* Bergroth (Gerridae), occurring in the Caribbean and Pacific coasts of Central and South America, while other genera, such as *Husseyella* Herring (Veliidae) and *Telmatometroides* Polhemus (Gerridae), are confined to one of these two areas. The fauna of the Atlantic, Caribbean, and East Pacific regions is mainly composed of marine lineages that most likely evolved multiple times from limnic ancestors. Andersen (1999) hypothesized that *Darwinivelia* Andersen and Polhemus, *Rheumatobates*, and *R.* (*Trochopus*) evolved during the Late Pliocene, before the emergence of the Isthmus of Panama. During the Cenozoic, different shallow sea connections (e.g., Atlantic/Caribbean/East Pacific and Indo/West Pacific) were available as dispersal routes for marine water striders and other organisms occurring in the Pacific Ocean, the Tethys Sea, and Southern Africa.

Andersen (2000) described and discussed phylogenetic, paleontological, and biogeographic aspects of eight gerromorphan species from Eocene Baltic amber. Andersen hypothesized that these gerromorphan species seem to have their closest living relatives either in the Palearctic region or in the Neotropical region or belong to an ancestral lineage, which has left few living relict species in the Neotropical region and on isolated islands of the Central Pacific.

Based on two putatively sibling genera, the South American *Mesoveloidea* Hungerford and the West African *Mesovelia* Poisson, Andersen and Polhemus (2003) suggested mesoveliids have had an ancient, wide tropical distribution since the Cretaceous and could, therefore, have diversified in response to global tectonic events. According to Andersen and Polhemus (2003), the restricted distributions of many extant species may be an artifact of the lack of knowledge and sampling effect. Andersen supports his hypothesis on the Neotropical genera *Cryptovelia* Andersen and Polhemus, a monotypic genus known only to Brazil with an allied species found in Borneo, and the *Darwinivelia*, described to contain a species found on the Galapagos archipelago, with other species subsequently recorded from the Atlantic and Pacific coasts of South America.

Polhemus and Polhemus (2008) reviewed the global diversity and taxonomic richness of freshwater aquatic and semiaquatic Heteroptera (Gerromorpha, Nepomorpha, and Leptopodomorpha). Modern gerromorphan lineages can be traced back to the Mesozoic by fossil evidence and can be further supported from Gondwanan distributions, assuming vicariant explanations (South America/Africa, *Platyvelia* Polhemus and Polhemus/*Angilia* Stål (Veliidae); South America/Australasia, *Metrobates* Uhler/*Metrobatoides* Polhemus and Polhemus (Gerridae)).

Based on their own and other colleagues studies, Polhemus and Polhemus (2008) assumed that the main areas of endemicity for aquatic Heteroptera in the world are (1) Madagascar, (2) New Guinea, (3) Indochina, (4) the Malay Archipelago, (5) Australia, (6) tropical Central and Western Africa, (7) the Guiana Shield of northern South America, and (8) the Atlantic rainforests of eastern South America. The northern South American Guiana Shield area is species-rich for aquatic Heteroptera, according to Polhemus and Polhemus (2008) due to its ancient geological age, proximity to the Equator, and topographic complexity. The Guiana Shield has many endemic species, but still most of its genera occur in other areas of tropical South America.

Leptopodomorpha

Before the work of Grimaldi et al. (2013), the Leptosaldinae (Leptopodidae) were known from two Neotropical species, *Leptosalda chiapensis* Cobben, a fossil from Mexican Miocene amber, and the extant *Saldolepta kistnerorum* Schuh and Polhemus, from Ecuador and Colombia. Grimaldi et al. described two new fossil species of *Leptosalda* Cobben from Miocene amber of the Dominican Republic and a remarkable new fossil genus and species, *Archaesalepta schuhi* Grimaldi and Engel, from Early Eocene Cambay amber from western India. They believe *A. schuhi* is the sister taxon to the New World leptosaldines, suggesting leptosaldines were more widespread and that their present-day distribution is relict. Their conclusions should be taken cautiously, since the proposed relationships and biogeographic hypothesis are not based on a phylogenetic analysis.

Cimicomorpha

The understanding of Triatominae (Reduviidae) evolution still puzzles the knowledge about its ancestral areas and its geographical distribution patterns. Trying to answer some biogeographical questions, Schofield (1988, 2000) proposed a polyphyletic origin of triatomines based on biogeographic arguments, with Asian fauna being composed of at least two independent lineages (Hypsa et al. 2002). In a phylogenetic analysis of the New and Old World, including species of the Rhodniini, Linshcosteini, and Triatomini (Reduviidae: Triatominae), Hypsa et al. (2002) found conflicting results (dependent of rooting) for the origin of Triatominae, suggesting either an origin in the northern areas of South America, in Central America, or in southern North America. Hypsa et al. also found a clade of Asian species within the Triatominae.

Studying the Tingidae *sensu stricto* in a phylogenetic framework, Lis (1999) erected the Cantacaderini to family status and applied Bremer's (1992) ancestral areas to explore its biogeography. The ancestral area of Cantacaderidae (*sensu* Lis 1999) was smaller than the current distribution, included the Australian continent, and the taxon probably originated around 140 million years ago (mya). Along a dispersalist narrative, Lis (1999) argues that the sister taxa of the Neotropical genera *Stenocader* Hambleton and *Nectocader* Drake are from New Zealand and Australia, respectively, suggesting the Cantacaderidae colonization of the Neotropics via two dispersal events through a connection between Antarctica and South America, about 50 mya. However, according to Guilbert (2012a), the Vianaidinae (an exclusively South American taxon) is sister to all other Tingidae, including the Cantacaderinae (as a subfamily of Tingidae). This relationship hypothesis would imply that the common ancestor to Vianaidinae and Cantacaderinae could not be restricted to Australia, but should rather have a Gondwanan distribution (Guilbert 2012b). However, this author agrees with Lis (1999) and Wappler (2006) that the Cantacaderinae colonized the Neotropics by ancient vicariance followed by several recent dispersal events.

Pentatomomorpha

Based on evidence of Gondwanan origin to Aradoidea, Sweet (2006) proposed that the Aradidae is an old taxon and its worldwide distribution most likely results from vicariance. The Isoderminae (Aradidae) show an "Antarctic distribution," occurring in Chile, New Zealand, and Australia, while other subfamilies (Aradinae, Calisiinae, Mezirinae, Carventinae, and Aneurinae) have cosmopolitan distributions, more diverse in the tropics.

Mecidea Dallas comprises a group of stink bugs (Pentatomidae) occurring in subtropical and adjacent temperate areas, apparently coinciding with xerophytic or semi-xerophytic environments (Sailer 1952). To Sailer, *Mecidea*'s distribution is similar to countless taxa and is evidence of an ancient faunistic and floristic relationship between the semidesert and desert regions of the Mediterranean Basin, South Africa, southern South America, and southwestern North America. According to a dispersalist point of view, the Ethiopia, Eritrea, and Uganda highlands were suggested as the center of distribution of *Mecidea*, because five of the 14 species of *Mecidea* occur in or are adjacent to this area.

Through Bremer's (1992) ancestral area analysis, Lis (1999) suggests the Cephalocteinae (Cydnidae) originated on the Indian continental block (as part of the Gondwanaland) more than 125 mya. From the absence of paleontological data for the taxa, he assumed that only migratory events could explain distribution patterns and uses Gondwanan age for the group to substantiate the events of migration between land masses without resorting to long-dispersal events.

Scaptocoris Perty (Cydnidae: Scaptocorini) reached the Neotropics through colonization from Antarctica, between 125 and 110 mya (Lis 1999); after, it radiated to South America, giving rise to the endemic *Atarsocori*s Becker in Brazil and dispersing to Central America. The distribution of the single species of Scaptocorini known to Africa (Angola) was explained by dispersion of a "*Scaptocoris* ancestral species," from South America to West Africa, and evolved into a separate genus, which displayed the same evolutionary trends in some characters as those in the South American *Atarsocoris*.

3.3.2 Biogeography of the Neotropical Region

Enicocephalomorpha

Štys (2008) reviewed the geographic distribution of the unique-headed bugs' genera of Aenictopecheidae and Enicocephalidae, emphasizing distributional patterns based on zoogeographic regions. According to Štys, the proposition of historical biogeography hypotheses for the group would be premature, given the lack of knowledge for some faunas, particularly of the islands and archipelagos of the Atlantic and Indian Oceans, and the lack of phylogenies at the generic level.

Five enicocephalomorphan genera have been described for the Neotropical region, occurring from the Caribbean islands and southern Mexico to as south as the Tucuman province and Santa Catarina state, in Argentina and Brazil, respectively. Of these genera, four are assigned to the Enicocephalidae and one to the Aenictopecheidae. About 40 unique-headed bug species have been described to the Neotropical region, but it is estimated that at least 100 more have yet to be described (Štys 2008). Additionally, a monotypic genus, *Gamostolus* Bergroth (Aenictopecheidae), occurs on the South American Subantarctic region in southern Chile (Magallanes and Osorno provinces) and Argentina (Staten Island).

Gerromorpha and Nepomorpha

Based on track analysis of 60 species of Belostomatidae, Corixidae, Micronectidae, and Gerridae from Chaco province, Morrone et al. (2004) found five generalized tracks and three panbiogeographic nodes: Tracks include (1) Bolivia and northwestern and central Argentina (11 spp.); (2) southern Brazil, eastern Bolivia, Paraguay, and northeastern Argentina (four spp.); (3) southeastern Brazil and northeastern Argentina (eight spp.); (4) southeastern Brazil, Uruguay, and central western Argentina (five spp.); and (5) southern Argentina (three spp.). Nodes include (1) northeastern Argentina, (2) central Argentina, (3) and central south Argentina. The authors stated that the Chaco province appears to be a natural biogeographical area that shares taxa with the Amazonian, Parana, and Patagonian biogeographic provinces.

Leptopodomorpha

Trying to answer whether the Andean distribution of *Pseudosaldula* (Saldidae) is part of a broader Austral distributional pattern (including New Zealand, Australia, and part of Antarctica), Schuh and Polhemus (2009) discuss the genus' biogeography based on a morphological phylogenetic hypothesis. Using a qualitative approach to analyze the genus' distribution, they recognized five areas of endemism: Northern Andes, Northern Peru, Puna, Central Chile, and Subantarctic. Using two different cladograms obtained by different optimization criteria (equal weights and implied weighting), area cladograms were constructed, and they found either the Northern and Southern Andes being commingled or a great hierarchical structuring of the Andes, with southern areas basal on the cladogram. The following hypothesis for the biogeography of the group, is proposed (*sic* Schuh and Polhemus 2009): (1) Subantarctic is the basal area on the cladogram; (2) Central Chile is the next area on the cladogram, and either *P. penai* Schuh and Polhemus or *P. pilosa* Schuh and Polhemus are endemic to it; (3) Puna is the next area on the cladogram; and (4) Northern Peru and Northern Andes are sister areas.

Cimicomorpha

Neotropical species of *Rahasus* Amyot and Serville (Reduviidae: Peiratinae) and other three related genera (*Eidmania* Teuber, *Melanolestes* Stål, and *Thymbreus* Stål) were studied by Morrone and Coscarón (1998), using a cladistic biogeographic approach. General area cladograms were constructed using two methods (Component 2.0 by Page 1993 and paralogy-free subtree, Nelson and Ladiges 1996) and resulted in scenarios previously proposed by Morrone and Coscarón (1996): "open vegetated" provinces (Desierto, Caatinga, Cerrado, and Chacoan), found basally on the trees, and "forest" provinces (Caribbean, Amazonian, Paraná, and Atlantic). The general area cladogram was in agreement with the previous scenario proposed by Morrone and Coscarón (1996) and resulted in "open vegetated" provinces (Desierto, Caatinga, Cerrado, and Chacoan) at the base, whereas the "forest" provinces (Caribbean, Amazonian, Paraná, and Atlantic) formed a group. Morrone and Coscarón (1998) relate the formation of the South American arid diagonal with the uplift of the Andes and hypothesized it as a vicariant event that separated the forested areas into two portions (Caribbean + Amazonian and Paranaense + Atlantic) during the middle Miocene. This can be considered one of the most comprehensive cladistic biogeography analyses searching for general patterns on Neotropical Heteroptera.

Abad-Franch and Monteiro (2007) presented an approximation to the historical biogeography and evolution of the main triatomine lineages (*Panstrongylus* Berg and *Triatoma* Laporte) that occur in the greater Amazon. They found the distributional pattern of the Rhodniini in the Amazon forest to be associated with two biogeographically well-defined groups of species ("*pictipes* group" and "*robustus* group," with trans- and cis-Andean distribution, respectively), invoking a basal evolutionary split within the tribe in this area. The origin of Amazonian triatomine species was suggested to be associated with historical, ecological, and anthropogenic ecological disturbances.

Paula et al. (2007) proposed a biogeographic hypothesis to species of Rhodniini (Reduviidae: Reduviinae), based on the historical background of the Neotropical region proposed by Amorim (2009). The authors employed a reconciled tree method to deduce taxon-area associations, implemented in TreeMap (Charleston and Page 2001). Twelve optimal solutions were found to explain Rhodniini biogeographical scenarios, with six vicariance events, 20 duplications (sympatry), at least three dispersals, and one extinction event. However, Paula et al. (2007) decided not to use any of these reconstructions, instead opting to discuss specific scenarios for some lineages that are not necessarily present in all optimal solutions. The main events evoked to explain biogeographic patterns of the group are the uplift of the Central Andes and Andes breakup into three separate cordilleras, emergence of the Isthmus of Panama, and uplift of the Serra do Mar and Serra da Mantiqueira (Brazil). The lack of resolution in the biogeographical history of the group may be the result from poor taxon sampling and inappropriate areas included in the study.

The bee assassin *crassipes* and *pictipes* species groups of *Apiomerus* Hahn (Reduviidae: Harpactorinae) were studied by Berniker and Weirauch (2012). They used the phylogeny to explore biogeographic patterns of 12 species and determine the boundary between Nearctic and Neotropical areas of endemism. Their results support the limits between the Neotropical and Nearctic regions along the Isthmus of Tehuantepec (Mexico), congruent with previous biogeographical analyses for New World insects (e.g., Halffter 1987; Morrone and Marquez 2001). Under a Brooks's parsimony analysis (BPA), Berniker and Weirauch (2012) corroborate the relationship between Chiapan-Guatemalan Highlands, Talamancan Cordillera, and northwest South American areas and together are sister to the remainder of the Neotropics; this pattern was found by previous studies, such as Amorim and Pires (1996) and Amorim (2001). However, this assertion must be taken cautiously, since the authors did not use a BPA area classification with the intent of testing the assumptions of Amorim and Pires (1996) of an Amazonia composed of two distinct biotic components.

Pentatomomorpha

Brochymena Amyot and Serville and *Parabrochymena* Larivière are the only representatives of Halyini (Pentatomidae: Pentatominae) occurring in the New World: *Brochymena* all over North and Central America between 50°N and 15°N and *Parabrochymena* only in the eastern United States, southeastern Canada, and Central America. Generally, Larivière (1994) explains the distribution of both genera based on major geological events and ecological aspects of North America, particularly assumptions concerning climate change. Under a dispersalist framework, he asserts that areas of greatest diversity of *Brochymena* and *Parabrochymena* correspond well with areas occupied by hypothesized oldest lineages of the genera. He speculates there is a general trend of diversity reduction towards northern latitudes, perhaps due to Pleistocene glaciation, but also pinpoint there is an overall pattern observed in pentatomids to not extend far beyond warm temperate conditions.

Grazia (1997) explored the biogeographical relationships of the *Evoplitus* genus group (*Evoplitus* Amyot and Serville, *Pseudevoplitus* Ruckes, and *Adevoplitus* Grazia and Becker; Pentatomidae: Pentatominae). *Evoplitus* occurs on the Atlantic Forest, including Paraguay and northern Argentina, and its sister group, *Adevoplitus* + *Pseudevoplitus*, is distributed in Central America, northern Colombia, and eastern Venezuela and Amazonian Basin. The contact zone between the two clades is along the Amazonas, Madeira, and Mamoré rivers. Under the same reasoning employed by Grazia (1997), the biogeography of the Neotropical *Brachystethus* Laporte was studied by Barcellos and Grazia (2003). In both works, the authors find distributional patterns congruent with the hypotheses of Amorim and Pires (1996) and Amorim (2001) of two distinct Amazonias, the formation of an epicontinental sea in the Maracaibo region, after the Late Cretaceous separated an area in Mesoamerica from the remaining Amazonian elements.

Fortes and Grazia (2005) and Simões et al. (2012) studied *Serdia* Stål (Pentatomidae: Pentatominae), a Neotropical genus distributed from Costa Rica to southern Brazil and northern Argentina, with highest diversity in southern and southeastern Brazil. Reanalyzing the morphological matrix of Fortes and Grazia (2005), Simões et al. (2012) proposed biogeographic hypotheses to *Serdia* based on vicariance analysis (Hovenkamp 1997, 2001), which consists of finding the disjunct (allopatric/vicariant) distributions in the nodes of the cladogram. They identified three nodes sharing disjunct distributions, which might be associated to vicariant events related to the development of the Chacoan subregion (Morrone 2006) that, during the Paleogene and Neogene (former Tertiary), divided the once continuous Amazonian-Parana Forest.

The ancestral area of *Schraderiellus* group (Pentatomidae: Discocephalinae) is the Amazonian subregion, from where the species successively dispersed (Campos and Grazia 2006). The southern distributional limits of the *Schraderiellus* group, the Amazonas, Madeira, and Mamoré river basins, can also be explained by the independent evolution of biota from the northwest and southeast of Amazonia proposed by Amorim (2001). The *Schaefferella* group (Pentatomidae: Discocephalinae), widely distributed in Central and South Americas, is believed to have originated in the Paraná subregion with further expansions to the north, towards southeastern Amazonian subregion, and to the south, towards the Chacoan subregion. The distributions of *Uvaldus* Rolston and *Clypona* Rolston (Pentatomidae: Discocephalinae), restricted to the *Araucaria* Forest and Chaco, respectively, could be the result of vicariant events separating the Parana and Chacoan subregions.

Procleticini (Pentatomidae: Pentatominae) is a small tribe (about 30 species in 11 genera) found only in the New World. According to Bernardes et al. (2009), the group *Lobepomis* Berg + *Neoderoploa* Pennington + *Procleticus* Berg and basal species of *Thoreyella* Spinola are restricted to open vegetation formations of Neotropical region (the Chacoan subregion), and the most apical *Thoreyella* species are more related to forested habitats in the Parana Forest subregion.

3.3.3 Distributional Patterns of Neotropical Heteroptera

Recently, studies of distribution patterns within Heteroptera have increased but are still largely biased towards better-known taxa. In most of those studies, authors point out to the lack of phylogenetic hypotheses and outdated phylogenies for the group and stress their studies are early approaches to the understanding of distributional patterns of the taxa. Macroecological and biogeographic aspects of Heteroptera are hampered from being further understood because of the lack of accessible online databases of biological collections and more research on phylogenetic relationships.

One of the best studied groups of Heteroptera is the Triatominae (Reduviidae). The group has been employed in macroecological studies in attempts to understand its richness and distribution patterns on the Neotropics (e.g., Rodriguero and Gorla 2004; Diniz-Filho et al. 2013; Fergnani et al. 2013).

Rodriguero and Gorla (2004) examined how New World Triatominae species richness responds to latitudinal gradients and explored the relevance of geographical area and available energy. Based on the distribution of 118 triatomine species, the authors found for the first time in obligatory hematophagous organisms an evident increase in the number of species of Triatominae from higher to lower latitudes. Such a pattern is not expected to insects (Rodriguero and Gorla 2004), but is found in some mammalian taxa. Habitable area effect on species richness is different in each hemisphere: on the Southern Hemisphere, an increase in species richness is correlated with an increase in habitable area from the poles towards the Equator, whereas on the Northern Hemisphere, there is an increase of species richness towards low latitudes; habitable area does not affect this relationship. There is a significant correlation of species richness with habitable area, mainly in the Southern Hemisphere and eastern longitudes.

Diniz-Filho et al. (2013) tested different environmental hypotheses to understand geographical patterns of richness and the distribution of 115 Neotropical triatomine species. Testing seven different hypotheses of climatic effects as drivers of species richness, using spatial eigenvector mapping and nonspatial ordinary least squares multiple regression models, they found water, energy, temperature, and temperature seasonality to be the environmental variables with relatively higher explanatory power of species richness and elevation variables having minor effects. The unique effects of these variables are quite difficult to disentangle because of the collinearity among variables and residual autocorrelation and may also be due to low taxonomic sampling.

Fergnani et al. (2013) conducted a complementary study to understand large-scale spatial patterns of morphological diversity and species richness of triatomine species in terms of environmental gradients. Studying 91 species and 12 morphological attributes of Neotropical triatomine, they found the latitudinal gradient of species richness to be in agreement with previous studies (Rodriguero and Gorla 2004; Diniz-Filho et al. 2013). The morphological diversity, by means of Gower index, also followed a latitudinal gradient, suggesting an overall spatial congruence between species richness and morphological diversity. However, the overall correlation pattern between species richness and morphological diversity is not homogeneous throughout taxon distribution (e.g., Brazil and Argentina have regions of high species diversity, but low morphological diversity). According to Fergnani et al. (2013), their's was the first study where this kind of relationship was demonstrated for insects on a continental scale, demonstrating that for the Triatominae, species richness and morphological diversity cannot be considered substitutes for one another.

One of the few studies that looked for distribution patterns exclusively on Neotropical Pentatomidae (Hemiptera) was done by Ferrari et al. (2010), analyzing the distribution of 222 species belonging to 14 genera using analysis of endemicity (NDM – Szumik et al. 2002; Szumik and Goloboff 2004) and identifying hierarchical endemic areas in the Atlantic Forest. The Amazonian region was identified as a single area on the consensus, its southeastern portion share elements with the Chacoan and Paraná subregions, while the Cerrado and the Caatinga were not identified as unique areas of endemism.

3.3.4 Phylogeography

Almost 30 years after Avise et al. (1987) coined the term phylogeography, two major papers reviewed the subject, including works dealing with the Neotropics. As emphasized by Beheregaray (2008), out of the 3049 phylogeographic papers published around the world until 2006, only 15 % explored Southern Hemisphere organisms; the numbers are even lower if we consider only published articles about terrestrial invertebrates on South America (8 % out of 313 papers). Focusing on South America, Turchetto-Zolet et al. (2013) indicate that, from 1987 to 2011, only 29 studies on invertebrates were published, most emphasizing in vectors of human diseases, such as Chagas disease (Hemiptera: Reduviidae) and malaria (Diptera: Culicidae). When compared to other biogeographical regions and continents, phylogeographical studies in South America are still incipient, the same happening in the rest of the Neotropical Region.

The first effort on phylogeography of Heteroptera was populational studies about species of economic or medical importance (e.g., Monteiro et al. 1999; Sosa-Gomez et al. 2004), triggering studies which focused on Triatominae vectors of *Trypanosoma cruzi* (Chagas), a parasitic euglenoid protozoan that causes Chagas disease. The Triatominae (Reduviidae), known as kissing bugs due their hematophagous feeding habit, are distributed from Argentina to the United States, between the latitudes 46°S and 46°N (García et al. 2013). Of the 15 known genera of Triatominae, 14 occur in the New World (Gourbière et al. 2012), and almost all of the 145 species recognized for Triatominae (Gonçalves et al. 2013) seem to be potential vectors of trypanosomatids. Three species are of greatest epidemiological relevance: *Triatoma infestans* Klug, *Triatoma brasiliensis* Neiva, and *Triatoma dimidiata* (Latreille).

Triatoma infestans is the most studied species because, alone, it is responsible for half of the Chagas disease cases in the Neotropics. The evolutionary lineage of *T. infestans* originated between 2.7 and 1.0 mya as a derivation from *T. platensis* Neiva (Bargues et al. 2006). Bargues et al. (2006) suggest *T. infestans* originated from Bolivian highlands, and the current lineages allows the identification of clear differences between Andean and non-Andean populations. Two initial dispersal routes of *T. infestans* were hypothesized, one through the Andean highlands of Bolivia and Peru and another through the lowlands of Argentina, Paraguay, Uruguay, Brazil, and Chile. Both these primary lineages are corroborated by independent nuclear, mitochondrial, and multilocus microsatellite studies (Monteiro et al. 1999; Piccinali et al. 2009; Pérez-de-Rosas et al. 2011). Torres-Pérez et al. (2010) suggested that *T. infestans* would have originated outside of Bolivia, but they also recognized the Andean and non-Andean lineages with estimated divergence time around 0.388–0.588 mya, agreeing globally with the estimate dates found by Bargues et al. (2006). On the other hand, the widespread distribution of *T. infestans* in South America is attributed to its domiciliation, a probable recent event following the New World colonization by humans around 12,000 years ago (González-José et al. 2003) and main range expansion in post-Colombian times, after the seventeenth century until today (Panzera et al. 2004).

It is believed that the contemporary population structure has been dramatically influenced by human-vector interactions, as indicated by the complex biogeographic pattern of *T. infestans*, at both local and regional scales (Torres-Pérez et al. 2010). The relationship between human dwellings and *T. infestans* has elicited studies aiming to understand: insecticide effectiveness through haplotype diversity/persistence, the fine-scale migration ability, offspring viability between populations/morphs, capability of house infestation, and reinfestation of sylvatic and peridomestic populations (e.g., Marcet et al. 2008; Pérez-de-Rosas et al. 2008, 2013; Piccinali et al. 2009, 2011), as resources for developing rational vector control strategies (Piccinali et al. 2009).

In Northeastern Brazil, *T. brasiliensis* is the most important Chagas disease vector. Monteiro et al. (2004) analyzed the populations of *T. brasiliensis* across its distribution and indicated that each chromatic form is genetically different from each other, suggesting the existence of a species complex: the forms *juazeiro*, *melanica*, and *brasiliensis* + *macromelasoma* should be treated as separate species. Nowadays, *T. juazeirensis* Costa & Felix and *T. melanica* Neiva & Lent are considered species of the *T. brasiliensis* complex. The population structure of *brasiliensis* does not show strong geographic segregation, suggesting recent range expansion. The divergence time between *brasiliensis* and *melanica* is estimated to have occurred around 5.2 mya, which would place their common ancestor in the early Pliocene. On the other hand, *brasiliensis* + *macromelasoma* population structure does not show strong geographic segregation, suggesting recent range expansion.

Triatoma dimidiata is the main vector of *T. cruzi* throughout Central America to Ecuador. The diversity of habitats explored by *T. dimidiata* involves domestic and peridomestic dwellings and non-domiciliated and sylvatic populations, act as sources of reinfestation. Along the distribution of *T. dimidiata*, some populations/subspecies are suggested by phenotypical, genotypical, and ethological traits. Bargues et al. (2008) analyzed its intraspecific variability, finding high haplotypic diversity supporting three groups: group 1, widespread (Colombia, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, and Panama) and highly variable; group 2, geographically restricted to Guatemala and Mexico; and group 3, occurring in Guatemala, Honduras, and Mexico. The high haplotypic variability found in *T. dimidiata* seems to be remarkably outside the limits of the intraspecific variability range known for *Triatoma* species (Bargues et al. 2008; Monteiro et al. 2013).

Monteiro et al. (2013) refined the analyses of Bargues et al. (2008) by adding different molecular markers and finding four genetic groups for *T. dimidiata*. Both groups of authors found a complex of monophyletic cryptic species including the subspecies of *T. dimidiata* plus *T. hegneri* Mazzotti. The *Triatoma dimidiata* species complex is believed to have originated 5.9–10.5 mya. Hypotheses to each population/subspecies origin, expansion, and distribution are explored on the literature (Bargues et al. 2006; Monteiro et al. 2013; Gómez-Palacio and Triana 2014) and include distributional expansions by relatively recent human activity, mountain uplifts, and the connection of South and North Americas through the Isthmus of Panama during the Pliocene (3–5 mya).

Other Neotropical reduviid genera have been studied under phylogeographical approaches. On the Amazonian region, the phylogeography of *Rhodnius prolixus* Stål and *R. robustus* Larrousse was studied by Monteiro et al. (2003), sampling in seven Latin American countries. Five clades were found, being *R. prolixus* homogeneous. *Rhodnius robustus* is represented by four paraphyletic clades, one of them (*R. robustus* Clade I) more closely related to the *R. prolixus* clade. The *R. prolixus* and *R. robustus* Clade I is believed to have originated around 1.4 mya, when an ancestral stock was spread in different refugia at the Orinoco lowland forest (Venezuela). The other *R. robustus* clades are from the Amazon forest region. Extremely low nucleotide diversity of *R. prolixus* suggests a recent bottleneck and posterior dispersion facilitated by human activity. The clade *R. prolixus*+*R. robustus senso lato* suggests an origin in between 3.7 and 2.4 mya. Dating within the Pleistocene, the pattern of phylogenetic discontinuity with geographical distribution of haplotypes could involve long-term biogeographical barriers to gene flow (Avise et al. 1987) and could be explained by the refugium theory (Monteiro et al. 2003).

Maia-da-Silva et al. (2007) compared the phylogeny of *Rhodnius* with *Trypanosoma rangeli* Tejera, 1920 populations, showing a significant overlap in the distribution and demographic correspondence between the *Rhodnius* spp. and *T. rangeli* lineages. The pattern is consistent with a hypothetical long parasite-vector coexistence with and is supported by a high congruence between the phylogeographical analysis of both *T. rangeli* lineages and *Rhodnius* species.

Mepraia Mazza, Gajardo, and Jörg, comprised by three species, is an important endemic Chilean vector of *T. cruzi* in the sylvatic cycle. Campos et al. (2013) found three lineages of *Mepraia*, congruent with the current recognized species. All populations tested were highly structured, suggesting that they have not been affected by strong bottlenecks and/or experienced sudden demographic changes due to repeated climatic fluctuations. The origin of *Mepraia* is suggested to have occurred around 3.6 mya, during the pre-Pleistocene. *Mepraia spinolai* (Porter) is recognized as the oldest lineage, followed by *M. gajardoi* Frias, Henry, and Gonzales (originating 0.99 mya) and *M. parapatrica* Frías-Lasserre (originating 0.66 mya).

The southern green stink bug *Nezara viridula* (L.) (Pentatomidae) is a polymorphic and worldwide pentatomid pest, causing economic damage to many crops (Panizzi et al. 2000). To elucidate its origin and dispersion routes, Karvar et al. (2006) sampled specimens from four continents (Africa, America, Europe, and Asia), and Li et al. (2010) added populations from China and Iran, both agreeing in a basal phylogeographic position of *N. viridula* from Africa and suggesting a deep division between African and non-African populations. Using different molecular clocks, Karvar et al. (2006) suggested the division of African and non-African populations of *N. viridula* since the Pliocene, while Li et al. (2010) suggested the split during the Miocene. Both groups of authors concluded that the New World populations of *N. viridula* are more closely related to European populations. Karvar et al. (2006) hypothesize different routes for the American colonization: one from the eastern Mediterranean (Greece, Italy) to Central America and from there to eastern United States and the western coastal areas of South America and another originating in the western Mediterranean (Iberian Peninsula) and dispersing to the eastern coastal areas of South America. The relationships among Neotropical populations should be better investigated, as well as recent human activity-mediated dispersion.

As showed above, most phylogeographic studies are biased to species with medical relevance and economic impact, and the aim of these studies are often intertwined with applied interests. Nevertheless, as side results, speciation hypotheses, taxa coalescence, population demography, and geographical processes have been improved to those taxa on the Neotropical region. Furthermore, the integrative nature of phylogeography and increased access to molecular evidences are helping elucidate intraspecific relationships, influencing phylogenetic hypotheses and taxonomic decisions.

Phylogeographic studies on the Neotropics are incipient, especially to terrestrial invertebrates (Turchetto-Zolet et al. 2013), and most Neotropical biomes, such as the Amazonia, Cerrado, Atlantic Forest, Pampa, and Caribbean islands, are poorly known. The current systematic, ecological, and distributional knowledge about Neotropical heteropterans make them a useful source to phylogeography. The phylogeography could support the identification of refugia and contact zones, enlightening the biogeographical processes and improving the understanding of lineages history and processes of diversification.

3.4 Concluding Remarks

Much remains to be studied regarding the systematics and biogeography of Heteroptera, especially on the Neotropics. Despite the high diversity of true bugs, most families occurring in the Neotropical region are neglected. In fact, the best known taxa are those of economical or medical importance (e.g., Reduviidae, Pentatomidae), although Pentatomidae lacks an updated Neotropical catalog. In the last decades, though, the training of new systematists has improved the knowledge on some families, as will be presented in the following chapters. However, it is time to expand the scope of revisionary, systematic, and biogeographic studies.

There is a general and global lack of phylogenetic studies for Neotropical taxa, especially with those taxa of broad taxonomic coverage and consistent out-group sampling. The search for heteropteran biogeographic patterns is hampered by the lack of phylogenies and a clear use of biogeographic methodologies. Phylogeographic studies are incipient, focused on taxa of economic importance, even though the integrative nature of the subject can help elucidate the evolutionary history on the Neotropics.

Overall, future works should incorporate new techniques for data gathering and new methodologies for data analysis and become taxonomically broader and comprehensive. All of it would facilitate the understanding of the evolutionary history of the different groups.

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Part II

Infraorders Enicocephalomorpha and Dipsocoromorpha

Chapter 4
The Unique-Headed Bugs (Enicocephalomorpha)

José Antônio Marin Fernandes and Christiane Weirauch

Abstract Enicocephalomorpha, the unique-headed bugs, is one of the more basal taxa within Heteroptera. The small size, unique morphology, and cryptic habits of most unique-headed bugs are the main reasons that most genera and species are poorly known from a biological and taxonomical point of view. Few experts have focused on this group in recent times and the boundaries of several taxa from species to family level are still unclear. In the Neotropical Region, Enicocephalidae and Aenictopecheidae are represented by ca. 70 described species in seven genera, but the true diversity is certainly much larger than these numbers would indicate.

4.1 Introduction

The infraorder Enicocephalomorpha, the unique-headed bugs, has long been considered to be the most basal clade of Heteroptera and the sister group of the Euheteroptera (Schuh 1979; Štys 1995). However, recent analyses have questioned this basal position (Li et al. 2012) and additional phylogenetic investigation is required to firmly establish the sister group of the Enicocephalomorpha. This taxon comprises only two small and still severely understudied families with little more than 320 described species (Štys 2008). The present classification of the taxon was proposed by Štys (1989), in which Aenictopecheidae were raised from the level of a subfamily to family status (see also Štys 1970; Wygodzinsky and Schmidt 1991). The suprageneric classification of both families is in flux. However, Štys (2008) indicated that a cladistic analysis is in preparation that together with the description of new genera will likely change the present suprageneric classification. Aenictopecheidae and Enicocephalidae occur worldwide, but most of the genera

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and described species are restricted to the Old World (Štys 2008). Identification of the described Neotropical genera is possible using the key to New World taxa by Wygodzinsky and Schmidt (1991) or the one to the world genera by Štys (2002b). All Enicocephalomorpha are small to midsized with body length typically ranging between 2 and 15 mm, often dull colored, and generally resemble small Reduviidae. Wings are membranous and well developed, but micropterous, brachypterous, and wingless forms, especially in females, also occur. Some species in both families swarm, a behavior that is rare among true bugs. Also unusual is the fact that swarms may contain more than one species (e.g., Wygodzinsky and Schmidt 1991).

The greatest species diversity is seen in humid tropical and subtropical forests, but species also occur in cool-temperate climates and arid zones where they are found in cryptic microhabitats with high humidity (Wygodzinsky and Schmidt 1991; Štys 1995).

4.2 General Characteristics and Diagnosis

According to the most recent and comprehensive diagnosis (Štys 1995), Enicocephalomorpha are characterized, among other features, by: the elongate and porrect head that is subdivided into anterior and postocular lobes by a usually conspicuous postocular constriction (Fig. 4.1); the ocelli, if present, on the posterior lobe and well removed from the eyes; the long gula; the four-segmented labium short and straight to arcuate, never exceeding the length of the head; the moderately long antennae flagelliform to cylindrical or slightly tapering; the forewings always completely membranous, i.e., without a distinct corium and wing only subdivided into a remigium and clavus; the ambient vein (the vein encircling the margin of the wing) in the remigium marginal or submarginal, if venation reduced, then the vein represented by a row of macrotrichia; the forewing sometimes reduced or absent, occasionally prone to autotomy; the medial fracture located anterior to R; basal crossvein connecting marginal veins (C, Sc, and/or R) with M + Cu; foreleg usually with enlarged femur and tibia, thus presumably raptorial; tibia usually with disto-ventral process carrying one or two clusters of spiniform setae; opposing ventral

Fig. 4.1 A species of Enicocephalidae of the genus *Enicocephalus* (Courtesy of F Carvalho-Filho)

surface of one- or two-segmented foretarsus typically also with spiniform setae; the symmetrical male genitalia either with typical heteropteran phallus (Aenictopecheidae) or with paired genital plates that can be fused into a racquet-shaped guide (Enicocephalidae); parameres small, either movable (Aenictopecheidae) or not (Enicocephalidae); ovipositor present (Aenictopecheidae) to strongly reduced or absent (Enicocephalidae); and subgenital plate of males formed by sternum 8 rather than sternum 7 as in other Heteroptera.

4.3 General Biology and Ecology

The small size and cryptic habits of Enicocephalomorpha make direct observations of their biology and ecology rare events. Biological information is therefore typically scattered in the taxonomic literature. Wygodzinsky and Schmidt (1991) summarized and cited most of the relevant literature. Most sources indicate that Enicocephalomorpha are found in leaf litter, under bark, in rotten logs, under stones at the edges of streams, in superficial but probably also deeper layers of soil, in moss and liverwort mats, suspended leaf litter and soil, and in nests of pack rats (e.g., Wygodzinsky and Schmidt 1991; Usinger 1939, 1945; Schuh 1970; Villiers 1961; Kritsky 1976, 1977). Villiers (1960) reported that species of *Systelloderes* Blanchard may also be collected in bee tunnels and associated with ants.

Enicocephalids are predaceous and appear to feed on soft-bodied insects and other arthropods, but few direct observations are available. In captivity, they were fed on larvae and freshly killed adult flies, symphylids (Symphyla) and campodeids (Diplura), as well as ant larvae and pupae.

Swarming is a biological phenomenon that is rather common in Enicocephalomorpha and has been documented for species in five genera and both families in the New World (Wygodzinsky and Schmidt 1991). Štys (1981) speculated that all species that are capable of flight might also swarm. Swarms are possibly formed for the purpose of mating and are composed of large numbers of males and much smaller numbers of females (Kritsky 1977; Štys 1981). As an example, Schuh (1970) counted 441 males and only seven females in a swarm of *Systelloderes* in Costa Rica. Interestingly, swarms that comprise more than one species of Enicocephalidae are fairly common (Wygodzinsky and Schmidt 1991). Swarming is a complex phenomenon and its behavioral and morphological aspects in Enicocephalomorpha are poorly documented, making this a wide open field for future research.

Some enicocephalids have the unusual ability to autotomize, or shed, their wings. This behavior may be related to the cryptic way of life of most species. In females, it could be important when individuals retreat, after swarming and copulation, into the soil, where wings might be a hindrance, similar to wing shedding in termites and ants (Wygodzinsky and Schmidt 1991).

4.4 Classification and Diversity

Both families Aenictopecheidae and Enicocephalidae are known to occur in the New World. Their taxonomic history and classification, with emphasis on the Neotropical fauna, is outlined below. Štys (1989) proposed the classification used today (Štys 1995). Wygodzinsky and Schmidt (1991) taxonomically revised the New World fauna of Enicocephalomorpha with exception of the speciose genus *Systelloderes* that in the New World alone contains more than 40 described and undescribed species, with many more that await discovery. This monograph also includes substantial morphological information including many scanning electron micrographs and line drawings as well as biological data and a phylogenetic scheme of relationships that could serve as a basis for future cladistic investigations into the group. Štys (2002b) presented a key to world genera and subgenera and a list of valid names and synonymies. Additional information on the two families is found in Štys (1981, 1989, 1995, 2002b, 2008).

4.4.1 Aenictopecheidae

Aenictopecheids are small (2.6–10 mm long) and rarely collected true bugs. Worldwide, they comprise four subfamilies, 11 genera, and about 20 extant species (Štys 1995, 2002b). The four subfamilies show fairly divergent morphologies and the family is mostly diagnosed by the absence of presumably derived characters that occur in the Enicocephalidae. In addition, some species have been reported to display characters commonly found in Auchenorrhyncha but not normally seen in other Heteroptera, a situation that further complicates homology assessment and systematic conclusions (Štys 1995).

According to Štys (1995), Aenictopecheidae are most easily distinguished from Enicocephalidae by the fairly typical heteropteran genitalia in both males and females compared to the strongly modified and reduced genitalia in Enicocephalidae. In the males, these include a typical heteropteran phallus, movable parameres, and a pygophore that is never subdivided into tergum, laterotergites, and sternum; females are characterized by a well-developed ovipositor. Other characters to differentiate this family from the Enicocephalidae include the poorly demarcated posterior lobe of the pronotum, a short costal fracture (absent in Enicocephalidae), and nymphs with wing pads that are not contiguous along the midline.

Among the four subfamilies, only Aenictopecheinae that are subdivided into two tribes are represented in the Neotropical Region. Aenictopecheini with the two monotypic genera *Aenictipechys* Breddin and *Lomagostus* Villiers are restricted to the Oriental Region and Madagascar. Gamostelini comprises four genera, only two of which occur in the Neotropical Region: *Gamostolus* Berg with a single described species, *G. subantarcticus* (Berg), was described from Southern Argentina and Chile. Wygodzinsky and Schmidt (1991) examined nymphs from Venezuela and

Colombia that they classified as *Gamostolus*, but Štys (2008) indicated that these nymphs likely belong to an undescribed genus. *Gamostolus* is diagnosed by the distinct arrangement of fore tibial spines, the foretarsus with four spines, as well as several genitalic features (see Wygodzinsky and Schmidt 1991 for details).

In addition, the Neotropical fauna comprises the genus *Tornocrusus* Kritsky with eight described, and several undescribed, species that are distributed in Central and South America. Among other New World Aenictopecheinae, *Tornocrusus* is most readily identified by the reduced proepimera and the apical mid- and hind tibial armature consisting of only one large spine and one bristle comb (illustrated in Wygodzinsky and Schmidt 1991). Comprehensive diagnoses, drawings, and a key the species can be found in Wygodzinsky and Schmidt (1991). Species of *Tornocrusus* are difficult to identify due to intraspecific variation and similarity among species. Štys (2008) reported the discovery of two new genera from the New World, but both remain undescribed.

4.4.2 Enicocephalidae

This family contains the great majority of described enicocephalomorphan genera and species and the bulk of specimens deposited in natural history collections. Species are small (2–15 mm long) and mostly dull colored, ranging from uniformly yellow or brown to blackish (Štys 1995). Worldwide, Enicocephalidae comprises about 300 described extant species that are classified into 47 genera and five subfamilies (Štys 1995, 2002b). Štys (2008) indicated that at least 30 genera and hundreds of new species have so far remained undescribed. A key to the subfamilies of Enicocephalidae was provided by Štys (1995).

According to Štys (1995), Enicocephalidae are distinguished from Aenictopecheidae by the pronotum that is usually subdivided into three distinct lobes (except in *Alienates* Barber), the common occurrence of wing polymorphism featuring macropterous males and brachypterous to apterous females, the absence of a costal fracture, the strongly modified male and female genitalia, and the large and contiguous wing pads of later nymphal instars large that are sometimes slightly overlapping along the midline. The most prominent feature of the male genitalia is a distally perforated "guide" of uncertain homology that is associated with the ventral margin of the posterior foramen of the pygophore. The parameres are always immobile, fused at the bases or reduced to flat sclerites. The external female genitalia are absent or retained as remnants in the Systelloderini and the female genital opening is covered by an extensive subgenital plate formed by the sternum 8.

In the Neotropical Region, Enicocephalidae are represented by two subfamilies, the Alienatinae and the Enicocephalinae. Alienatinae only contain the genus *Alienates* that can be recognized by very distinctive characters such as the small body size, the one-segmented tarsi of the adult, the males with the posterior pronotal lobe virtually absent, the strongly reduced forewing venation, and the females being largely desclerotized, apterous, and with strongly reduced eyes (Wygodzinsky and

Schmidt 1991; Štys 1995). Species in the genus occur in the Southwestern United States, Central America, and the Caribbean, with 12 out of 13 species being Neotropical (Wygodzinsky and Schmidt 1991). Štys (2008) indicated that about ten species await description. Wygodzinsky and Schmidt (1991) pointed out that morphological variation among examined specimens renders the formulation of species hypotheses difficult.

Enicocephalinae are represented in the Neotropical Region by 48 described species that are classified in six genera. These taxa are divided in two tribes: Systelloderini with the single genus *Systelloderes* and the Enicocephalini that contain the five genera *Chiricocoris* Wygodzinsky and Schmidt, *Enicocephalus* Westwood, *Hymenocoris* Uhler, *Neoncylocotis* Wygodzinsky and Schmidt, and *Xenicocephalus* Wygodzinsky and Schmidt. Three additional genera of Enicocephalini occur in the New World but are restricted to the Nearctic Region (*Brevidorus* Kristsky, *Lysenicocephalus* Wygodzinsky and Schmidt, and *Urnacephala* Wygodzinsky and Schmidt).

Two publications are fundamental for the identification of Neotropical Enicocephalidae: Wygodzinsky and Schmidt (1991) diagnosed and described or redescribed all genera except *Systelloderes*, and Štys (2002b) added diagnostic characters for several genera in his key. *Chiricocoris* is known only from a few female specimens collected in Panama, which represent the single known species *C. dybasi* Wygodzinsky and Schmidt. This genus is distinguished from other New World Enicocephalidae by the very robust overall aspect, the extremely thick forelegs, the great length of the pronotal midlobe and reduction of the hind lobe, the posteriorly closed anterior coxal cavities, and the presence of a large conical projection at the anteroventral angle of the foretarsus. The forewings lack basal and discal cells.

Enicocephalus is diagnosed by features that include the extremely small or obsolete outer claw of the foreleg, one of the foretarsal spines being half-moon shape, and the tibia with five apical spines, with the innermost spine being long, slender, and curved toward the remaining spines. Males are winged and females are either winged or capable of autotomizing their wings. This genus comprises 17 species, keyed by Wygodzinsky and Schmidt (1991), which range from Southern Mexico to Southern Brazil, but undescribed species were mentioned by Wygodzinsky and Schmidt (1991) and Štys (2008).

Males of *Hymenocoris* are delicate and have foretarsal claws that are nearly equal in length, simple setae on the dorsal surface of the abdomen, and apices of the mid- and hind tibiae with two spines, and they frequently display a red forewing stigma. Females are wingless and possess a membranous abdomen and closed foreacetabula, the spine VI of the foretibia is shaped like a molar, and their forefemur features a basal projection. Among the three known species, only *H. hintoni* occurs in the Neotropical Region, with the remaining two species being Nearctic. The delineation of species is considered to be problematic due to substantial intraspecific variation and overlapping species-diagnostic characters (Wygodzinsky and Schmidt 1991).

Neoncylocotis can be identified by the scale-like setae on the abdominal dorsum, the subequal foretarsal claws, the conical to peg-shaped foretarsal spines, the emarginated posterior margin of the pronotum, and the presence of at least a few macrotrichia within the forewings cells. Among New World genera, *Neoncylocotis* is most similar to *Enicocephalus* but can be distinguished by the above characters. All 17 species are Neotropical and range from Southern Mexico to Southern Brazil and Northern Argentina.

Xenicocephalus is recognized by the large body size of the adults (at least 8 mm) and the dense tuberculation on much of the cuticular surface. In addition, distinctive foreleg characters include a heavily sclerotized, ridgelike projection ventrally on the trochanter; the inner apical angle of the tibia shaped into a pointed, strongly sclerotized projection with 3–5 straight and slender, subapically inserted spines; and the foretarsus bearing only one stout claw. This genus was described based on one damaged female and a few nymphs; the male is unknown. The authors acknowledge that this is not an ideal situation but decided to describe this genus based on the unique characteristics, especially the size of the specimens. The single species, *X. giganteus* Wygodzinsky and Schmidt, is known from Colombia, and nymphs were collected in Costa Rica, Panama, and Guyana.

Systelloderes is diagnosed by the autapomorphic fusion of the ninth and tenth abdominal terga, which form the roof of the pygophore, and is most easily distinguished by the presence of a well-developed supradistal plate. Additional diagnostic features comprise: the moderately sized eyes; the distinctly trilobate pronotum; the posterior margin of the pronotal midlobe entire, without Y-shaped impressions and the lateral parts of the midlobe at most with a pair of pits; the apex of the foretibia with none of its spiniform setae spatulate; and the fore claws normally developed and subequal. This genus comprises 11 Neotropical described species ranging from Southern Mexico to Northern Argentina. *Systelloderes* spp. occur in moderate to high altitudes and have small endemic ranges and apparently low mobility. Consequently, dozens or hundreds of undescribed species await discovery and/or description (Wygodzinsky and Schmidt 1991; Štys 2008). Wygodzinsky and Schmidt (1991) suggested that *Systelloderes* is likely not monophyletic and that the Neotropical and Old World species are not congeneric. Štys (1970) divided the genus into three groups: the *moschatus* group from the Americas, the Ethiopian Region, Australia (except New Zealand), and the Asiatic Archipelago; the *maclachlani* group from New Zealand; and the *uvarovi* group from the Ethiopian Region and the Middle East. Štys (2002a) more recently reexamined the latter group and divided it into four new genera.

4.5 Concluding Remarks

Enicocephalomorpha, the unique-headed bugs, is a basal clade of Heteroptera comprising only two families and little more than 320 species. Species are small and usually dull colored resembling small reduviids. Biological and ecological data are scarce due to their cryptic habits, also responsible by the small number of specimens deposited in entomological collections. Better sampling technics, dedicated to soil and suspended soil, will improve considerably the number of species captured in the Neotropical Region. Descriptions of new species and genus will contribute to more robust suprageneric definitions, helping to better characterize families and subfamilies. This suprageneric taxonomical arrangement certainly will be influenced or changed by future cladistic analyses of the infraorder.

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Chapter 5
The Minute Litter Bugs (Dipsocoromorpha)

Christiane Weirauch and José Antônio Marin Fernandes

Abstract Dipsocoromorpha, the minute litter bugs, are the putatively least known infraorder of true bugs. Despite their astounding morphology, the small size and cryptic habits of Dipsocoromorpha have resulted in limited curated museum collections. Few specialists have focused on this group. In the Neotropical and elsewhere region, Ceratocombidae, Dipsocoridae, and Schizopteridae are represented by ca. 120 described species in 22 genera. The true diversity in the Neotropics, but also the tropics of the Old World, is clearly much larger than this number.

5.1 Introduction

The infraorder Dipsocoromorpha, the minute litter bugs, comprise five small and poorly studied families that together amount to little more than 320 described species (Štys 1995; Henry 2009; Weirauch and Štys 2014). Ceratocombidae, Dipsocoridae, and Schizopteridae are distributed worldwide (Fig. 5.1), whereas Hypsipterygidae (Indo-Pacific, Afrotropics, Baltic amber) and Stemmocryptidae (Oriental) are restricted to the Old World. The greatest species diversity is seen in humid tropical forests, but species occur from temperate rain forests (Scudder 2010) and other cool temperate climates (Hill 1980) to the deserts of the Western United States (Uhler 1904). All Dipsocoromorpha are small (typically 1–2 mm, rarely up to 4 mm), many are dull colored or black, the antennal flagellomeres are typically strongly setose, and male genitalia range from symmetrical to strongly asymmetrical and include appendages not observed in other infraorders of true bugs. Far from being uniform despite their small size, Dipsocoromorpha show tremendous morphological variation in the male genitalia, which frequently expand to abdominal segments considered as "pregenital" in other Heteroptera (Fig. 5.1). The second

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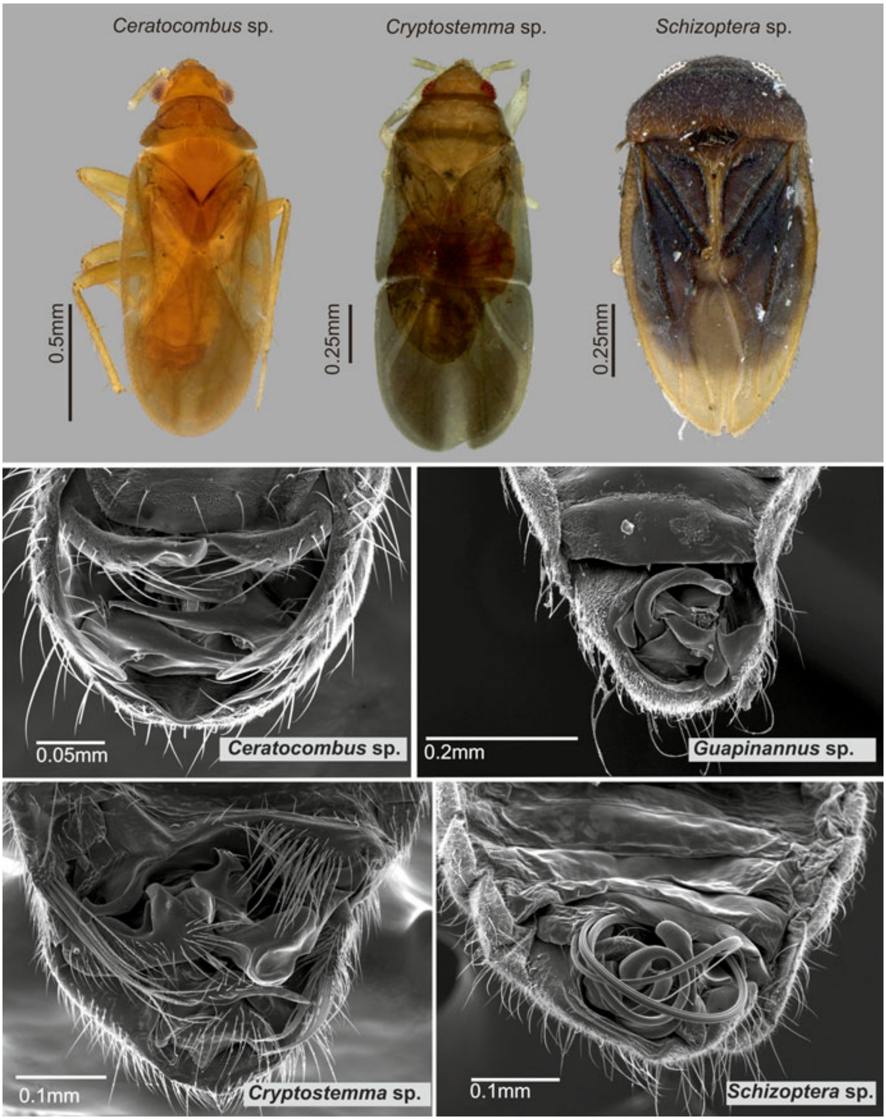

Fig. 5.1 Habitus of species of *Ceratocombus*, *Cryptostemma*, and *Schizoptera*. Scanning electron micrographs showing dorsal views of the distal part of abdomen and pygophore of species of *Ceratocombus*, *Guapinannus*, *Cryptostemma*, and *Schizoptera*

character complex with astounding variation among Dipsocoromorpha is the hemelytra, better referred to as forewings, since a clear division of the corium and membrane is frequently absent. Macropterous, submacropterous, brachypterous, and apterous wing types exist, and sometimes multiple types co-occur in the same species. The most intriguing wings are found among females (and less frequently males) of certain Ceratocombidae and many Schizopteridae: they are shortened, convex, and sclerotized and give these true bugs a beetle-like appearance. This wing type is therefore called “coleopteroid.”

The small size of Dipsocoromorpha, together with their cryptic life style, poses several obstacles to taxonomic and systematic investigations. Dipsocoromorpha occur in leaf litter, among gravel along streams, in low herbaceous vegetation, and even in the tree canopy. However, few specialists are capable of recognizing them in the field, and given the oddly beetle-like appearance of many species, specimens may even be overlooked in samples from passive traps, such as Berlese funnels as well as flight intercept and pan traps. Most natural history collections therefore hold relatively few curated specimens of Dipsocoromorpha. In addition, their small size makes thorough examination for taxonomic and phylogenetic purposes difficult. Taxonomic work before the middle of the twentieth century was therefore often hampered by poor illustrations and the lack of detailed morphological descriptions. Our current understanding of the morphology and systematics of the group is mostly based on the excellent work conducted by P. Štys, P. Wygodzinsky, L. Hill, and M. Emsley and a few other authors who have contributed less comprehensively to the study of Dipsocoromorpha.

5.2 General Characteristics and Diagnosis

According to the most recent and comprehensive diagnosis, by Štys (1995), Dipsocoromorpha are characterized, among other features, by: the small size; the often strongly declivous head; the antenna with short scape and pedicel and long and thin flagellomeres and typically with numerous stout setae; the proepisternum often inflated; the forewing typically not clearly divided into the corium and membrane, ranging from completely membranous to entirely elytrous; the hind wing often with deeply separated lobes; and the male genitalia either symmetrical with appendage-like laterotergites (some Ceratocombidae) or strongly asymmetrical (some Ceratocombidae, Dipsocoridae, and Schizopteridae), with the asymmetry being distinctly different in the three groups.

5.3 General Biology and Ecology

Given the small size and cryptic habits of most Dipsocoromorpha, direct observations of their biology are limited. Esaki and Miyamoto (1959) kept specimens of the schizopterid *Hypselosoma hirashimai* Esaki & Miyamoto in the laboratory and fed them on chironomid larvae. Emsley’s (1969) monograph on the fauna of Schizopteridae also includes some observations of specimens of *Hoplonannus* and *Schizoptera* that he kept in captivity. Lattin (2000) focused on *Ceratocombus vagans* McAtee & Malloch, and this life history study is the most comprehensive account published to date on the biology of any species of Dipsocoromorpha. Specimens were observed to feed on Collembola and mites but also to engage in cannibalism. The sparse knowledge on the ecology of Dipsocoromorpha, including habitats and microhabitats, is mostly derived from specimen records and few published observations. Literature data and some personal observations are summarized in the family accounts below.

5.4 Phylogeny and Evolution

Our current understanding of the phylogeny and evolution of Dipsocoromorpha is mostly based on the comparative morphological studies by Štys (1970, 1982, 1985), supplemented by publications by P. Wygodzinsky and L. Hill. However, Štys also pointed out that the monophyly of the group is far from being well established (Štys 2014; Weirauch and Schuh 2011). Molecular data were virtually unavailable until recently (Wheeler et al. 1993; Schuh et al. 2009) and are still scarce after the first published molecular study focusing on relationships among the three larger families of Dipsocoromorpha (Weirauch and Štys 2014). Weirauch and Štys (2014), based on molecular cladistic analyses of 87 taxa (35 of them Dipsocoromorpha) and two gene regions, found strong support for the monophyly of Dipsocoromorpha and the three included families. The three recognized subfamilies of Schizopteridae were included in the analyses: Hypselosomatinae were supported as the sister taxon to a clade comprising the Ogeriinae and Schizopterinae. More comprehensive molecular analyses clearly need to follow up on this first effort: only one genus was included for both Ceratocombidae and Dipsocoridae; Schizopteridae were represented by ca.15 genera. Combined morphological and molecular analyses will allow for including rarely collected taxa, such as the Hypsipterygidae and Stemmocryptidae, as well as fossil species, and at the same time test diagnostic characters for recognized families.

5.5 Classification and Diversity of Neotropical Dipsocoromorpha

Only the families Ceratocombidae, Dipsocoridae, and Schizopteridae are known to occur in the New World. The taxonomic history for each of the three families, with emphasis on the Neotropical fauna, is outlined below. A summary on the scarce natural history data is provided.

5.5.1 Ceratocombidae

Ceratocombidae contain two subfamilies, the Ceratocombinae with worldwide distribution and the Trichotonanninae that are restricted to the tropics of the Old World. The current classification is based on Štys (1982). Ceratocombinae are further subdivided into two tribes, the Ceratocombini and Issidomimini. Ceratocombini include three valid genera, *Ceratocombus* Signoret and *Leptonannus* Reuter, which are represented in the Neotropical region, and *Feshina* Štys that is only documented from Africa. *Leptonannus* is distinguished from *Ceratocombus*, among other characters, by the trilobed hind wing, although Wygodzinsky (1953) pointed out that the status of the two genera is in need of revision. Issidomimini comprise three valid genera that are restricted to the Old World and not discussed here.

Ceratocombus comprises 25 extant species worldwide, only seven of which were described from the Neotropical region (Reuter 1891; Poppius 1910; McAtee and Malloch 1925; Usinger 1946; Štys 1995). Species are small and typically dull colored (Fig. 5.1), although some species, especially in the Old World, can have striking, contrasting color patterns. Species are difficult to identify, mostly due to the fact that species descriptions by Poppius, Reuter, Usinger, and McAtee and Malloch were rather generic and omitted reference to genitalic features. Based on observations by Štys (1995), hundreds of undescribed species of *Ceratocombus* await description, including dozens of species from the Neotropics (C. Weirauch personal observation). *Ceratocombus cuneatus* McAtee & Malloch that was described from Southeastern Brazil has recently also been reported from Argentina (Dellapé et al. 2010).

The genus *Leptonannus*, first treated as a subgenus of *Ceratocombus* and later raised to genus rank (Reuter 1891; McAtee and Malloch 1925; Wygodzinsky 1953), contains three extant species known from Africa (Reuter 1891; Wygodzinsky 1953), North America (Uhler 1904), and the Caribbean (Uhler 1894) and one Chiapas amber fossil from Mexico (Azar and Nel 2010).

Species of *Ceratocombus* are most commonly associated with leaf litter and moss and therefore frequently collected using Berlese or Tullgren funnels (Štys 1959; Crowson 1972; Lattin 2000). Specimens of *Ceratocombus* can also be abundant in Malaise traps, as recently documented for an Asian species (Jung et al. 2011). Data derived from surveys in 12 countries in the Neotropical region indicate that species of *Ceratocombus* are frequently found in Malaise traps also in the New World, with 244 being the highest number of individuals recorded from a single trap in Amazonian lowland rainforest (C. Weirauch 2014). The Malaise trap data are an indication that, although ground dwelling, species of *Ceratocombus* are also relatively mobile and thus collected in flight intercept traps that rarely sample other Dipsocoromorpha such as Schizopteridae and Dipsocoridae.

5.5.2 Dipsocoridae

Dipsocoridae in the modern sense comprise only the genera *Alpagut* Kiyak (Palaearctic), *Cryptostemma* Herrich-Schäffer (worldwide), and *Pachycoleus* Fieber (Palaearctic) and about 30 described species. According to Štys (1995), *Pachycoleus* that has often been considered as a subgenus of *Cryptostemma* is represented in the Neotropical region by many undescribed species. Nine species of *Cryptostemma* were described from the Neotropical region (Fig. 5.1), five of which from the Caribbean including Trinidad (Uhler 1894; McAtee and Malloch 1925; China 1946; Nieser 1973). *Cryptostemma pratti* Unsiger is known from Puerto Rico (Usinger 1945), *C. haywardi* Wygodzinsky from Argentina (Wygodzinsky 1952), *C. pedunculatum* McAtee & Malloch from Panama (McAtee and Malloch 1925), and *C. uhleri* from Mexico (McAtee and Malloch 1925). Similar to the situation in Ceratocombidae, species are difficult to tell apart partly due to poorly illustrated original descriptions that lack detail on important genitalic features. Wygodzinsky's (1952) exceptionally well-illustrated description of *C. haywardi* is an exception.

Species of *Cryptostemma* are typically found on or underneath gravel and stones along streams (Leston 1954; Hill 1987; Heckmann and Rieger 2001) but have also been collected using suction (Halbert and Brambila 2002) and light traps (Péricart and Matocq 2003). *Pachycoleus* has been collected in moss (Champion 1908; Golub 2004; Whitehead 2005) but is also found in leaf litter extracts (Costas et al. 1993).

5.5.3 Schizopteridae

All three recognized subfamilies of Schizopteridae, the Hypselosomatinae, Ogeriinae, and Schizopterinae, occur in the Neotropical region, although Schizopterinae contribute the greatest proportion of the genus- and species-level diversity (Emsley 1969; Weirauch and Štys 2014). The family comprises about 48 genera and more than 200 described species (Weirauch and Štys 2014). Nineteen of these genera occur in and are restricted to the New World, and all except four are only documented from the Neotropical region. Hypselosomatinae are diagnosed, among other characters, by large eyes, a well-developed ovipositor (Esaki and Miyamoto 1959), and typically a labium with four segments; Ogeriinae and Schizopterinae share a reduced ovipositor and smaller eyes. According to Emsley (1969), Ogeriinae and Schizopterinae can be separated based on wing venation: in Schizopterinae, four free veins originate from the trapezoidal cell; Ogeriinae are characterized by five free veins emanating from the trapezoidal cell.

Genus-level identification of Schizopteridae mostly relies on original literature and reference collections, given that available keys are incomplete. McAtee and Malloch (1925) keyed the nine genera of Neotropical Schizopteridae described at the time, whereas Emsley (1969) provided a key to the four genera that according to his studies occurred in Trinidad, and Weirauch (2012) keyed the five genera that constitute the *Corixidea* genus group.

Hypselosomatinae, the "big-eyed bugs," comprise about 14 genera worldwide that are most diverse in the Old World (Hill 1984, 2013). They are represented in the Neotropical region by described and undescribed species in the genera *Ommatides* Uhler and *Williamsocoris* Carpintero & Dellapé and undescribed species of *Glyptocombus* Heidemann (Fig. 5.2; Hill 1980; C. Weirauch 2014). Uhler created the monotypic genus *Ommatides* to accommodate *O. insignis* Uhler from St. Vincent that based on Emsley's (1969) examination is closely related to species in the genus

Glyptocombus. The monotypic *Williamsocoris* was described from Formosa in Argentina and is distinguished from other Hypselosomatinae by unique paired processes on the third and fourth labial segments. Undescribed Hypselosomatinae are known from Colombia, Ecuador, Peru, and Trinidad (Hoey-Chamberlain and Weirauch 2014) indicating that the actual species-level diversity of this subfamily in the Neotropics is distinctly higher.

The subfamily Ogeriinae was created by Emsley (1969) to accommodate the New World genus *Chinannus* (Fig. 5.2) together with several Old World genera (*Ogeria* Distant, *Pachyplagia* Gross, *Luachimonannus* Wygodzinsky, and *Kokeshia* Miyamoto; *Kaimon* Hill was later included). Given the characters shared between *Chinannus* and the monotypic genus *Itagunannus* Wygodzinsky (outlined by Wygodzinsky 1948), the latter genus is here treated as part of the subfamily Ogeriinae, despite the fact that Emsley (1969) placed it as *incertae sedis*. The two described species of *Chinannus*, *C. trinitatis* (China) and *C. bierigi* Wygodzinsky, are known from Trinidad and Costa Rica, respectively, but undescribed species range as far south as Bolivia (Knyshov 2014). *Itagunannus itaguaiensis*

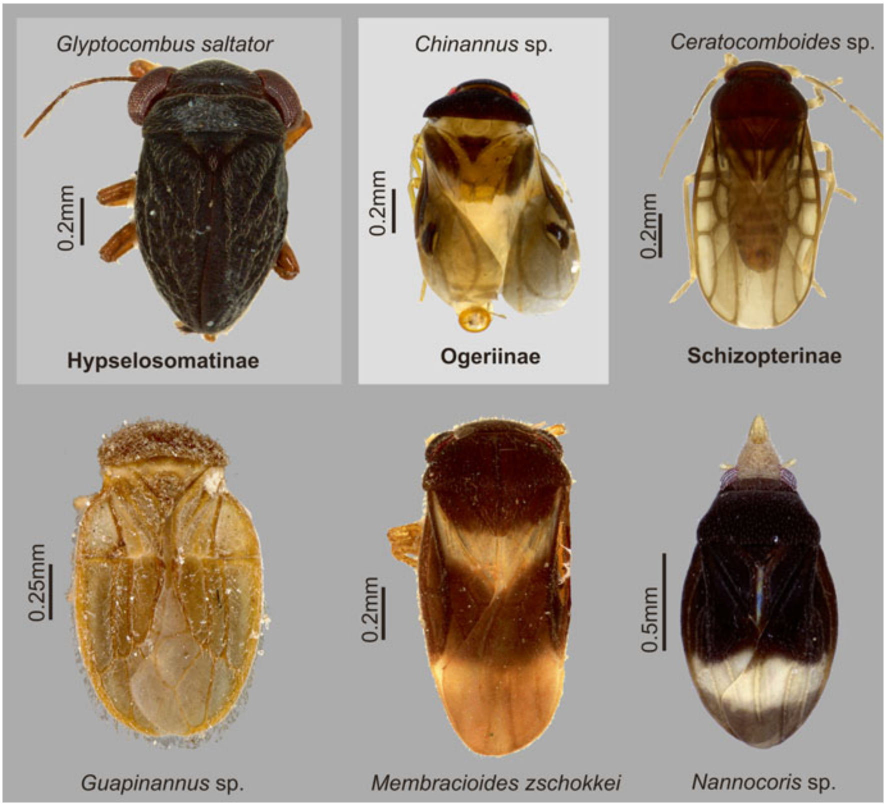

Fig. 5.2 Habitus of selected Schizopteridae: *Glyptocombus saltator*, *Chinannus* sp., *Ceratocomboides* sp., *Guapinannus* sp., *Membracioides zschokkei*, *Nannocoris* sp.

Wygodzinsky, described from the state of Rio de Janeiro in Brazil, is known only from the male holotype. Wygodzinsky (1948) speculated that this species could be sexually dimorphic similar to the situation in *Chinannus*, where males are macropterous, but females coleopteroid.

Emsley (1969) organized Schizopterinae in a number of "associations" of genera that he thought to be closely related. Two of these groups occur in the New World, the *Corixidea* group and the *Biturunannus* group. Emsley recognized the *Corixidea* group of genera based on the uniquely truncate apex of the labium that is shared by *Corixidea* Reuter, *Hoplonannus* McAtee & Malloch, *Membracioides* McAtee & Malloch (Fig. 5.2), *Voccoroda* Wygodzinsky, and the recently described *Voragocoris* Weirauch (Emsley 1969). *Corixidea* includes seven described species from Central America including the Caribbean; *Hoplonannus* three described species from Guatemala and Trinidad; and *Membracioides* two species described from Mexico and Panama. *Voccoroda* is monotypic and only known from Rio de Janeiro State, Brazil. *Voragocoris* now includes two species from Peru and Suriname (Weirauch 2012; Makhan 2013). A key to genera in this group was provided by Weirauch (2012). Numerous undescribed species, some likely representing new genera, that belong to the *Corixidea* group have been collected across the Neotropical region (Knyshov personal communication). McAtee and Malloch (1925) suspected the monotypic genus *Oncerodes* Uhler, described for *O. robustus* Uhler from St. Vincent, to be closely related to *Corixidea*. Given the lack of detail in Uhler's description (coleopteroid black specimen with yellowish legs, sex not specified, labium tapering) and the fact that McAtee's and Malloch's assessment was based on drawings (the head, prothorax, and forewing) provided by China and not on direct observation, *Oncerodes* is here treated as *incertae sedis*.

The *Biturunannus* group comprises the two Old World genera *Bironannus* Wygodzinsky and *Humpatanannus* Wygodzinsky and two genera that are restricted to the Neotropical region: *Biturunannus* Wygodzinsky is monotypic and only known from Parana State, Brazil. *Ceratocomboides* McAtee & Malloch comprises two species from Panama and Rio de Janeiro State, Brazil. The characteristic shape of the clypeus that also bears three long and stout setae ties the three former genera together, but the affinities of *Ceratocomboides* that lacks these features are less clear-cut. Among Neotropical genera, *Ceratocomboides* is most easily recognized by a small cell posterior to the trapezoidal cell (Fig. 5.2).

The remaining six New World genera are not placed in genus groups. In fact, the subfamily placement of *Guapinannus* Wygodzinsky, *Peloridinannus* Wygodzinsky, and *Tropistotrochus* Reuter is tentative at this point. *Schizoptera* Fieber (Fig. 5.1) is the by far largest genus of Schizopterinae. It contains more than 60 species that were mostly described by McAtee and Malloch (1925) and Emsley (1969), with additional species authored by Reuter (1882, 1891), Poppius (1910), China (1946), and Wygodzinsky (1952). McAtee and Malloch (1925) and Emsley (1969) contributed to the subgeneric classification of *Schizoptera*, and six subgenera are recognized. Species of *Schizoptera* are diagnosed by characters of wing venation and male genitalia, especially the uniquely modified and asymmetrical subgenital plate in the males. *Nannocoris* Reuter is likely the most easily recognized and charismatic among all Neotropical schizopterine genera: the majority of species are recognized by the elongate and pointed anteocular head region (Fig. 5.2). Twelve valid species range from Central America and the Caribbean to Argentina. As true for the most Neotropical schizopterine genera, a number of new species await description (Weirauch 2014). *Ptenidiophyes* Reuter is a rather enigmatic monotypic, female-based genus, described by Reuter (1891) for *P. mirabilis* Reuter from Santa Catarina State, Brazil. As speculated by Weirauch and Štys (2014), *P. mirabilis* may represent the female of a sexually dimorphic species. In the molecular analyses by Weirauch and Štys (2014), two specimens tentatively identified as *Ptenidiophyes* grouped with *Schizoptera*.

Some of the most stunning looking Schizopteridae in the New World are found in the genera *Guapinannus*, *Peloridinannus*, and *Tropistotrochus*. The holotype of the monotypic genus *Tropistotrochus*, *T. ampliatipennis* (Santa Catarina State, Brazil), is lost, but Reuter illustrated the wing venation that closely resembles the one seen in *Guapinannus*. *Guapinannus* (Fig. 5.2) was described by Wygodzinsky (1950) to accommodate *G. bierigi* from Costa Rica. The explanate forewings and in particular the very long fracture of the forewing that appears to divide the wing into two sections distinguish *Guapinannus* from other Neotropical Schizopterinae. *Peloridinannus* is also monotypic and was described by Wygodzinsky (1950) for *P. margaritatus* Wygodzinsky from Costa Rica. Its generic name emphasizes the fact that species in this genus resemble Coleorrhyncha in the family Peloridiidae in having flat and explanate wings with a complex pattern of wing venation. Undescribed species of *Peloridinannus* are known from Peru, Ecuador, and Panama, and species of *Guapinannus* also occur in Ecuador and Brazil.

The biology and ecology of Neotropical Schizopteridae are largely unknown, except the information provided by Emsley (1969) and notes on specimen labels recorded in Wygodzinsky's publications. Specimens are typically thought to be best collected using leaf litter extraction methods or light traps (Emsley 1969). Recent data (Weirauch Lab 2014) from sorting Schizopteridae from passive trapping samples show that out of 3,488 schizopterid specimens (35 countries; sampling all biogeographic regions), 822 specimens were collected using leaf extraction methods, only 17 in light traps, but 171 in pan traps and 1,396 specimens in flight intercept and Malaise traps (sampling method unknown for ca. 400; the remainder are other methods including hand collecting, pit fall traps, and canopy fogging). This indicates that many Schizopteridae may be more mobile than typically assumed.

5.6 Concluding Remarks

The minute litter bugs are clearly understudied in the Neotropical region, as they are elsewhere. The existing classification of subfamilies and genera will almost certainly undergo substantial changes as new genera are described and phylogenies produced that will put the current classification to the test. Similarly exciting as these changes above the genus level is the fact that a plethora of new species remain to be discovered and described from the Neotropical region.

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Part III
Infraorder Gerromorpha

Chapter 6
The Semiaquatic Gerromorphans

Felipe F.F. Moreira

Abstract The Gerromorpha comprise a group of mainly semiaquatic predatory bugs that play important roles in freshwater ecosystems. Despite its current low economic importance, there are evidences that certain groups may be utilized in the biological control of mosquitoes and agricultural pests or as potential indicators of biological quality in aquatic habitats. They are rather diversified in general appearance, structurally very diverse, and their two-dimensional habitat makes them ideal subjects for ecological and behavioral analysis. The Neotropical fauna of Gerromorpha is relatively well known, but more than a hundred undescribed species are known to exist. This fact, allied to the existence of large under-collected areas, makes taxonomic and faunistic studies concerning the semiaquatic bugs from tropical America urgent.

6.1 Introduction

Heteroptera constitutes a very interesting worldwide distributed group of insects, which is more diversified in tropical zones (Mazzucconi et al. 2009). Most of the species is terrestrial, but numerous others are aquatic or semiaquatic. Out of the seven infraorders of the suborder, the true aquatic bugs (most of which live in the water) constitute the Nepomorpha, and the mainly semiaquatic species constitute the Gerromorpha (water striders) and Leptopodomorpha (shore bugs) (Nieser and Melo 1997; Polhemus and Polhemus 2008).

Water bugs in general play an important role in freshwater ecosystems, and knowledge about them is essential for the study of water biology and the proper management of aquatic habitats. Furthermore, there is increasing evidence that

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This chapter is dedicated to the memory of Dr. John T. Polhemus (1929–2013), one of the greatest researchers who worked with Gerromorpha and other aquatic Heteroptera.

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certain groups may be utilized in the biological control of mosquitoes (Menke 1979; Armúa de Reyes et al. 2005; Rodríguez-Castro et al. 2006; Shaalan and Canyon 2009) and agricultural pests (Nakasuji and Dyck 1984; Ignacimuthu 2002) or as potential indicators of biological quality in aquatic habitats (Mazzucconi et al. 2009; Cabette et al. 2010).

The Gerromorpha, or semiaquatic bugs, have been recognized as a unique taxonomic entity since the time of Dufour (1833) and were treated for a long period as "Amphibicorisae" due to their ability to walk on the surface of the water, distinctly from the true aquatic bugs "Hydrocorisae" and the terrestrial bugs "Geocorisae" (Schuh and Slater 1995; Damgaard 2008b). The name Gerromorpha itself was proposed only by Popov (1971).

In his view, the Nepomorpha, Gerromorpha, and Leptopodomorpha arose in the Triassic, and the ancestral stocks of the modern superfamilies all had diverged by the end of the Jurassic. However, while Nepomorpha has a very extensive fossil record dating back into the Triassic, the Gerromorpha has by comparison left much fewer fossils (Grimaldi and Engel 2005). So far, only a few more than 30 fossil species belonging to six families have been described or recorded, spanning more than 120 million years of geological history. The evolutionary history of water striders probably began in the early Mesozoic, and the oldest members of the infraorder are Lower Cretaceous age, belonging to the families Mesoveliidae, Veliidae, and Hydrometridae (Andersen 1998; Damgaard 2008b).

As for the extant fauna, the Gerromorpha comprises more than 2,100 species distributed all over the World's continents, except for Antarctica (Andersen 1982; Polhemus and Polhemus 2008). Most of the known species occupy an adaptative zone defined by water surfaces (the pleustonic zone), and their habitats range from the few square centimeters surface area of water accumulated in tree holes to the millions of square kilometers of the world's great oceans (Andersen 1982, 1998). Some species have also become secondarily terrestrial, being found, for example, on forest litter or moss covering fallen trees (Andersen and Polhemus 1980; Malipatil and Monteith 1983).

Some gerromorphans, like most members of the family Gerridae and many of the Veliidae, spend nearly the entire active period of their lives on the water surface (Schuh and Slater 1995), and their two-dimensional habitat makes them ideal subjects for ecological and behavioral analysis, with many northern temperate species being extensively used as model organisms in such studies (Spence and Andersen 1994; Andersen 1998). Studies of the systematics, functional morphology, and ecological diversity of semiaquatic bugs (Andersen 1973, 1975, 1976, 1978) have also demonstrated a striking variation in habitat preference and ways of life among the Gerromorpha.

The Neotropical fauna of Gerromorpha is relatively well known (Polhemus and Polhemus 2007), especially because of the works of Champion (1898), and C. J. Drake, H. M. Harris, and H. B. Hungerford from the 1920s to the 1950s. Taxonomic studies tended to decline since then, with the exception of the studies of N. Nieser on the Caribbean, Suriname, and northern South America, J. T. Polhemus on Mexico, and the monograph on Neotropical *Rhagovelia* Mayr (1865) by D. A.

Polhemus (1997). During the last two decades, however, there has been increasing interest concerning Neotropical Gerromorpha and their taxonomy and diversity, especially by workgroups from Colombia, Brazil, and Argentina. However, detailed studies on ecology, behavior, genetics, and evolution are still very scarce when compared to those based on Palearctic and Nearctic species.

6.2 General Characteristics and Diagnosis

Semiaquatic bugs are rather diversified in general appearance and structurally very diverse (Fig. 6.1) (Andersen 1979), which makes morphologically defining the group somewhat difficult (Nieser and Melo 1997). Besides that, pterygopolymorphism is common in the infraorder, with some species showing continuous variation, whereas others are known only from the macropterous and/or micropterous or apterous morphs (Schuh and Slater 1995). Nevertheless, Andersen (1982) gives an excellent account of the structural features common to all or at least most of the families of Gerromorpha.

Out of the characters mentioned by him, the following, among others, are considered synapomorphies of the group: presence of three pairs (rarely four) of cephalic trichobothria inserted in deep cuticular pits in the adult; epipharynx with a long, narrow, external projection; mandibular levers quadrangular; maxillary levers absent; forewings usually not differentiated into anterior coriaceous and posterior membranous portions; pretarsus with dorsal and ventral arolium, the ventral one being sometimes modified; body covered by a 2-layered hair pile; and female gynatrial complex with long, tubular, entirely glandular spermatheca and secondary fecundation canal (Fig. 6.2) (Schuh and Slater 1995).

The cuticular surface of semiaquatic bugs is covered by dense hair layers, which makes these insects appear dull or velvety, with a silvery or golden sheen in certain angles of illumination (Andersen 1982). The greater part of the head and body of most species is covered by hair layers which have the same basic structure: a macro-hair layer of long, tapering and pointed macrotrichia, flexibly inserted in sockets, and a micro-hair layer of much smaller, stiff, usually filiform cuticular outgrowths or macrotrichia (Fig. 6.3). The surface of the antennae, rostrum, and leg segments, however, has only a layer of macrotrichia interspersed with other setae. These elaborate surface structures comprise without a doubt a system designed to prevent wetting and also function secondarily as protection against UV radiation from the sun (Cheng et al. 1978).

Another peculiar characteristic of the body surface of gerromorphans is the presence of peg-plates or “sieve-pores” (Fig. 6.4) (Cobben 1978). Under the stereomicroscope, they appear as minute, shiny dots, and in the scanning electron microscope, they are seen as ovate or circular plates bordered by a rim surrounding minute subconical pegs. Peg-plates are distributed all over the surface of the head, thorax (except posterior lobe of pronotum), and abdomen, but they are usually more numerous on the pleural and ventral parts of the body. They are commonly absent

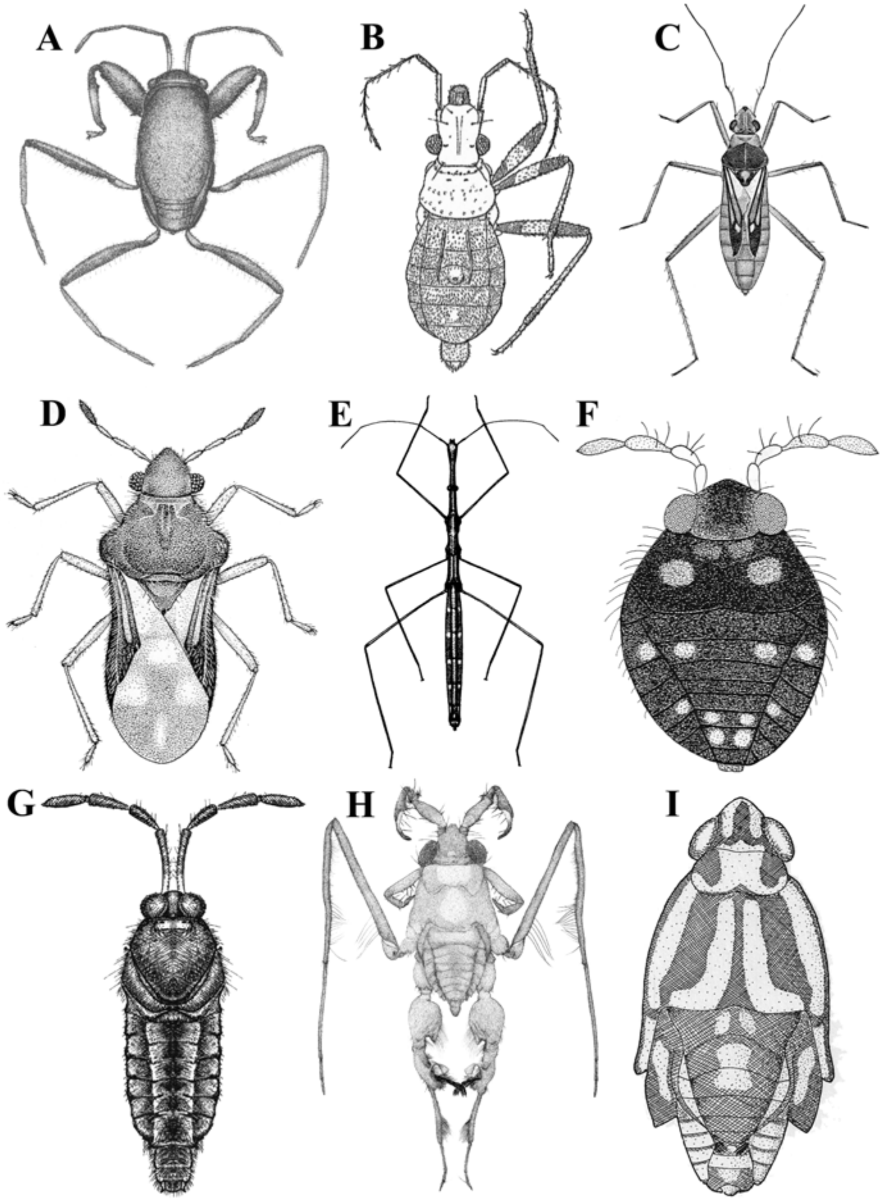


Fig. 6.1 Morphological diversity among the Gerromorpha. (**a**) *Hermatobates* (Hermatobatidae). (**b**) *Chepuvelia* (Macroveliidae). (**c**) *Mesovelia* (Mesoveliidae). (**d**) *Merragata* (Hebridae). (**e**) *Hydrometra* (Hydrometridae). (**f**) *Euvelia*, legs omitted (Veliidae). (**g**) *Rhagovelia*, legs omitted (Veliidae). (**h**) *Rheumatobates* (Gerridae). (**i**) *Halobatopsis*, antennae and legs omitted (Gerridae) (Modified from **a** – Andersen and Weir 2000; **b** – China 1963; **c** – Cobben 1960; **d** – Drake and Cobben 1960; **e** – Menke 1979; **f** – Polhemus and Polhemus 1984a; **g** – Moreira and Ribeiro 2009; **h** – Padilla-Gil and Pacheco-Chaves 2012; **i** – Nieser and Melo 1999)

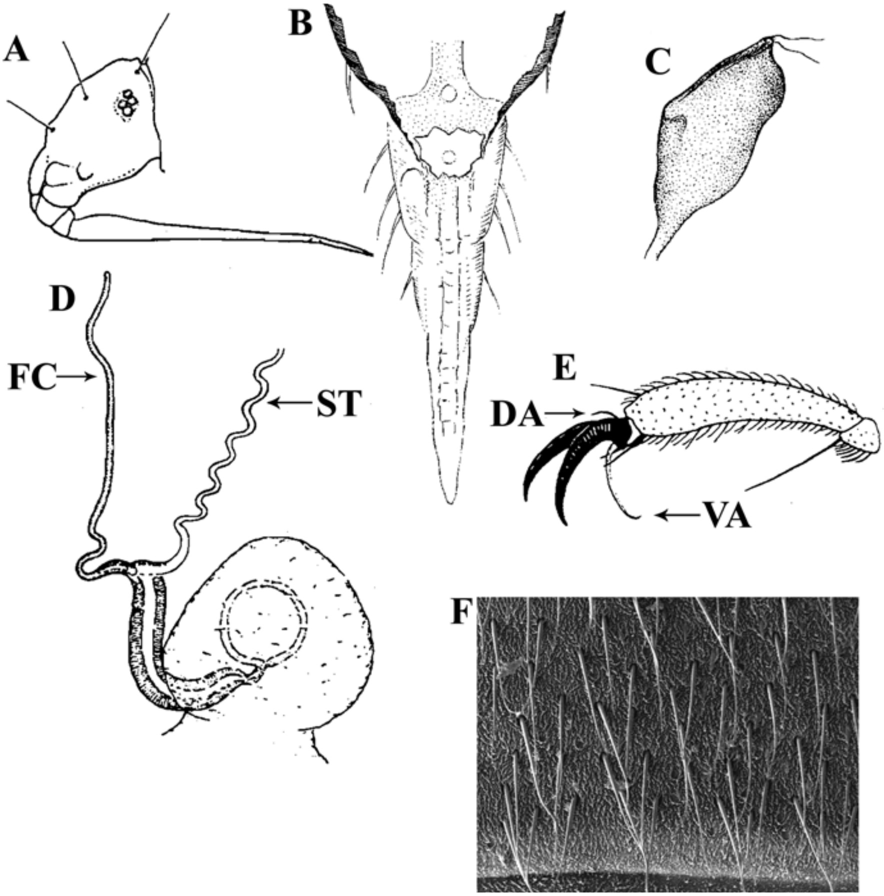


Fig. 6.2 Some of the synapomorphies of the Gerromorpha. (**a**) *Cryptovelia* (Mesoveliidae), head in lateral view showing three cephalic trichobothria. (**b**) *Hydrometra* (Hydrometridae), epipharynx in ventral view. (**c**) *Hydrometra* (Hydrometridae), quadrangular mandibular lever in plane view. (**d**) *Hyrcanus* (Hebridae), female gynatrial complex (*FC* fecundation canal, *ST* spermathecal tube). (**e**) *Hyrcanus* (Hebridae), fore tarsus (*DA* dorsal arolium, *VA* ventral arolium). (**f**) *Velia* (Veliidae), hind portion of fourth abdominal sternite showing layers of macro- and micro-hairs (Modified from **a**, **d**–**e** – Andersen 1982; **b, c** – Cobben 1978; **f** – Cianferoni and Santini 2013)

from leg segments (except coxae) and have been recorded in all families of semiaquatic bugs except Hermatobatidae and Gerridae (Andersen 1982).

As mentioned above, water striders also typically bear three pairs of cephalic trichobothria, which were first noticed by China (1955) and that are very likely to be mechanoreceptors (Andersen 1976). The distribution of these long setae on the dorsal head surface is practically the same in all semiaquatic bugs, with the posterior pair inserted at the base of the head and usually quite close to the hind corners of the eyes and the two anterior pairs inserted on the frontal surface of the head. An additional pair of trichobothria is inserted laterally to the two anterior pairs in most

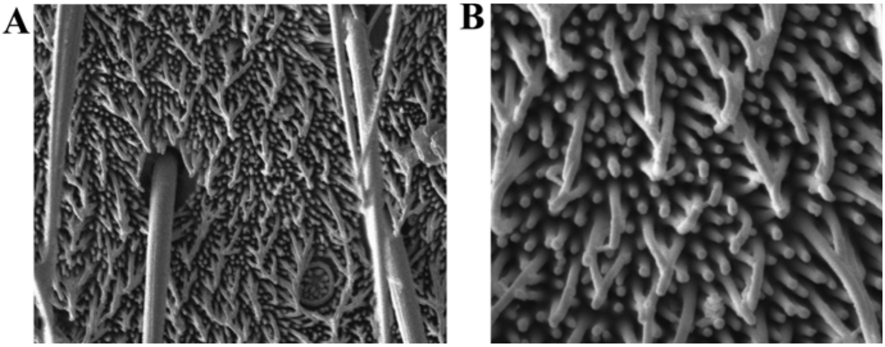
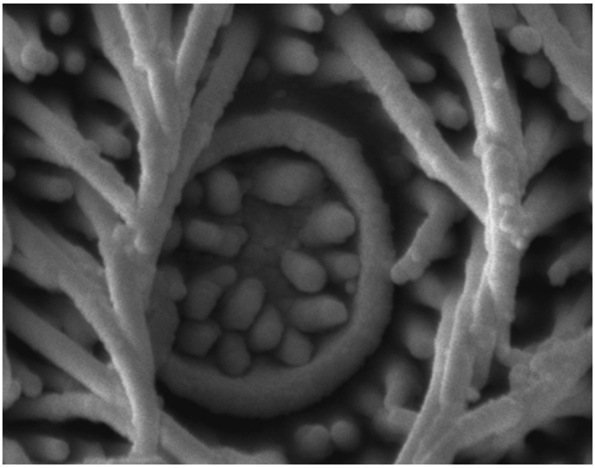


Fig. 6.3 Cuticular hair layers of the gerromorphans. (**a**) *Velia* (Veliidae), fourth abdominal sternite, detail of the socket of a macro-hair (micro-hairs also visible). (**b**) *Velia* (Veliidae), fourth abdominal sternite, double layer of micro-hairs (Modified from Cianferoni and Santini 2013)

Fig. 6.4 *Velia* (Veliidae), fourth abdominal sternite, peg-plate (Modified from Cianferoni and Santini 2013)



Gerridae. While cephalic trichobothria-like setae are recorded in several Heteropterans, the type of insertion found in semiaquatic bugs is unique. The long and slender seta arises from a deep pitlike depression in the cuticle, and this socket is located on a domelike elevation (Andersen 1982).

The head of the gerromorphans (Fig. 6.5) is typically elongate, with prominent eyes, usually with a pair of ocular setae. A pair of ocelli can be found near inner eye margins, but is reduced along with wing reduction in polymorphic species and totally lost in some Hydrometridae, most Veliidae, and all Gerridae. The surface of the head has very few sutures and is usually longitudinally impressed or has longitudinal rows of shiny punctures. A pair of dorsal indentations is also commonly present (Andersen 1982).

Contrary to the Nepomorpha, the antenna of Gerromorpha is always long and exposed (Heckman 2011). They are inserted medio-dorsally on the antennal tuber-

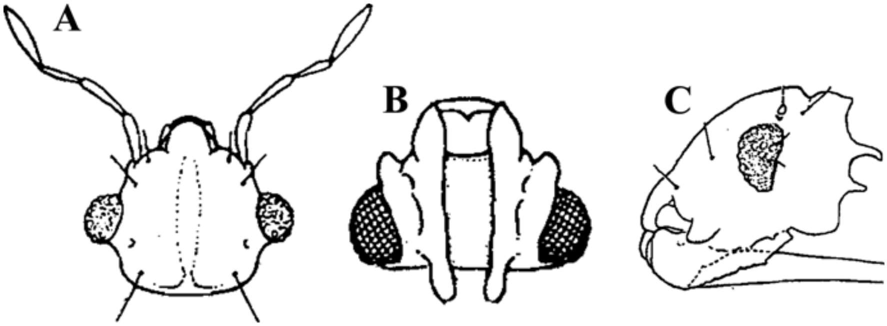


Fig. 6.5 General aspect of the head of the gerromorphans. (**a**) *Merragata* (Hebridae), dorsal view. (**b**) *Timasius* (Hebridae), ventral view. (**c**) *Hebrus* (Hebridae), lateral view (Modified from Andersen 1982)

cles, usually well in front of eyes, and always have four articles, besides short intersegmental pieces which are usually found between antennomeres II–III and III–IV. A superficial ring on antennomere IV of some genera of Hebridae gives the impression of a five-segmented antenna, which was misinterpreted in the past. The rostrum of semiaquatic bugs is typically long and slender, reaches far backward beneath the body when not in use, and is always four-segmented (Andersen 1982).

Most of the externally visible parts of the prothorax of gerromorphan bugs are composed of marginal evaginations or lobes. The pronotum is a broad plate with a short anterior lobe that surrounds the postocciput of the head, sometimes forming a narrow anterior collar. The lateral and, in particular, the posterior margin of the pronotum are expanded into a large posterior lobe, which in most semiaquatic bugs with winged adults extends far behind as the level of the wing bases, covering the whole mesonotum and usually also the median part of the metanotum (Andersen 1982).

The mesonotum is always the largest part of the pterothorax tergum in semiaquatic bugs. It consists of a broad anterior scutum and, in Mesoveliidae and Hebridae only, of a posterior scutellum. A large triangular scutellar lobe, typically found in other Heteroptera, is only present in *Mesoveloidea* Hungerford and *Madeovelia* Poisson of the family Mesoveliidae. In all other gerromorphan bugs, the scutellum is reduced (*Mesovelia* Mulsant & Rey), rudimentary (Hebridae), or absent (other families) (Andersen 1982).

The above notes on the thoracic skeleton apply only to the macropterous adult form (Fig. 6.6a). Most semiaquatic bugs commonly occur in a form which has more or less reduced wings (brachypterous or micropterous) or without recognizable wings (apterous). In these forms, the posterior lobe of the pronotum is usually reduced in length and width or completely absent, the mesonotum is thickened and sclerotized, and the pterothoracic endoskeleton is more or less reduced (Fig. 6.6b) (Andersen 1982).

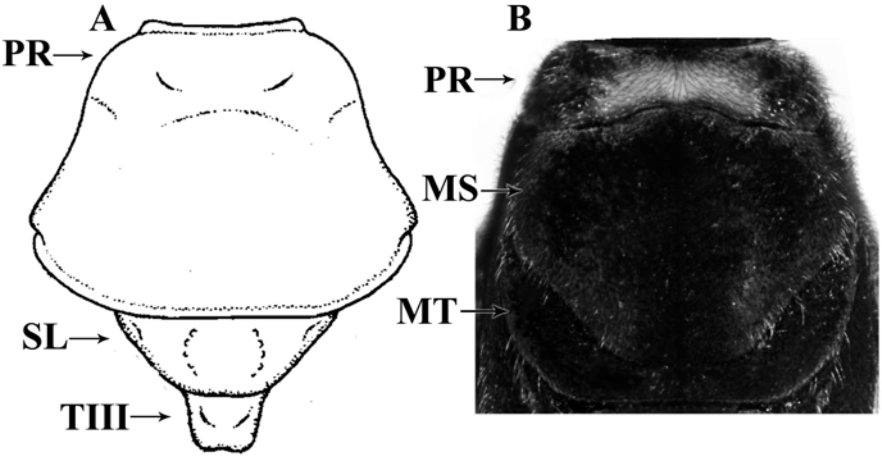


Fig. 6.6 Variation of the structure of the thorax in Gerromorpha. (**a**) *Mesovelia* (Mesoveliidae), macropterous thorax in dorsal view. (**b**) *Rhagovelia* (Veliidae), apterous thorax in dorsal view (*MS* mesonotum, *MT* metanotum, *PR* pronotum, *SL* scutellum, *TIII* metanotal lobe; modified from: **a** – Andersen 1982; **b** – Moreira et al. 2010)

There is a great diversity within the Gerromorpha concerning the functional morphology of the legs (Andersen 1976). In the Mesoveliidae, they are inserted close to the ventral midline of the body, and the long metacoxae almost touch each other, whereas in most other semiaquatic bugs, the coxae of each thoracic segment are widely separated (Andersen 1982). The plesiomorphic state of the inclination of the coxal axis in Gerromorpha is oblique in all legs, but it can range from a vertical inclination on fore and middle legs of *Hydrometra* Latreille to an almost horizontal inclination on middle and hind legs of Gerridae (Andersen 1976).

Members of some genera of the families Veliidae and Gerridae show very long legs with characteristic modifications that facilitate movement across the surface tension of the water. Others, like the Hydrometridae, have legs that do not appear markedly different from those of terrestrial bugs, but which nevertheless easily support the insect on the surface tension layer (Andersen 1976; Heckman 2011).

The trochanter of the Gerromorpha has proximal groups of cuticular sense organs, which are most likely proprioceptive and more or less uniform in constitution and number among most families, except for Gerridae and Veliidae, in which they are more numerous (Andersen 1982). Some or all of their tibiae have distal grooming structures composed by modified macrotrichia, usually arranged in combs, and used as cleaning devices to keep the hair layers of the legs and body tidily arranged and free of dust or water drops (Andersen 1976). In most families of Gerromorpha, the adult tarsus has three segments, whereas in Hebridae, some Veliidae, and all Gerridae, the number of tarsomeres is reduced due to the fusion of articles (Andersen 1982).

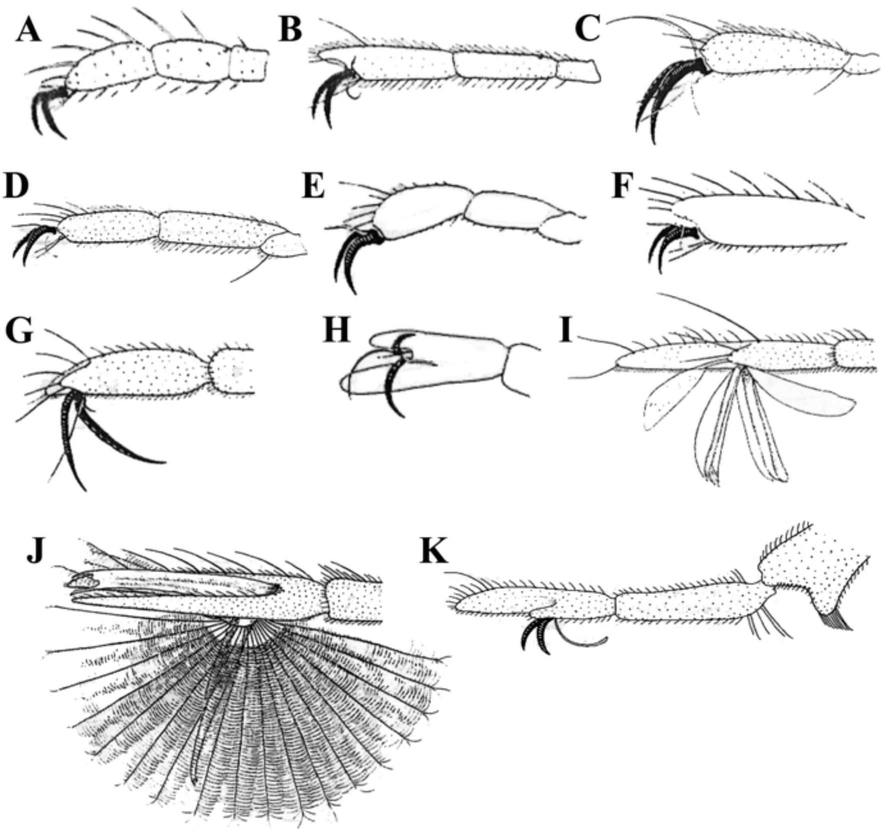


Fig. 6.7 Variation of the structure of the pretarsus in Gerromorpha. (**a**) *Cryptovelia* (Mesoveliidae). (**b**) *Mesoveloidea* (Mesoveliidae). (**c**) *Timasius* (Hebridae). (**d**) *Macrovelia* (Macroveliidae). (**e**) *Veliometra* (Hydrometridae). (**f**) *Limnobatodes* (Hydrometridae). (**g**) *Platyvelia* (Veliidae). (**h**) *Oiovelia* (Veliidae). (**i**) *Veloidea* (Veliidae). (**j**) *Rhagovelia* (Veliidae). (**k**) *Halobates* (Gerridae) (Modified from Andersen 1982)

The pretarsus structure in Gerromorpha is complex and highly variable (Fig. 6.7) (Cobben 1968, 1978). On the plesiomorphic condition, it consists of two long, thick, and hook-shaped claws articulating to the tarsus and connected to a small posterior plate, the unguiractor, which extends to the distal part of the last tarsal segment. From the distal end of the unguiractor arises a pair of setiform parempodia, and between the claws originate two vertically oriented arolia, one dorsal and one ventral (Andersen 1982). The dorsal arolium is typically setiform, but may be horizontally flattened like the ventral arolium, which is usually the longer (Andersen 1976).

The position of the point of articulation between the pretarsus and the tarsal segments varies within semiaquatic bugs, being apical or preapical. The apical type is undoubtedly the plesiomorphic condition among the Gerromorpha, being found in almost all species of the basal families. The preapical type is typical of the Veliidae and Gerridae, produced by a prolongation of the anterior part of the last tarsal segment, and with parempodia usually modified, asymmetrically developed or reduced (Andersen 1982).

The gerromorphan fore wing is not divided into a leathery basal part (corium and clavus) and membranous apical part (membrane) like the typical hemielytron of Heteroptera. Most of the wing is sclerotized but relatively thin, and only the proximal parts of the longitudinal veins are thickened. The hind wing, on its turn, is membranous and shorter but much broader than the fore wing. The two wings of each side of the thorax are coupled during flight, and the hind wing is moved passively. The coupling apparatus consists of a hook-shaped protuberance on the lower side of the fore wing and an upturned fold along the anterior margin of the hind wing. The number of muscles in the pterothorax of gerromorphan bugs is much reduced as compared with other Heteroptera, and in adults with reduced wings, all muscles involved in their operation are reduced or lost (Andersen 1982).

The scent apparatus of semiaquatic bugs belongs to the "type omphalien" of Carayon (1971), with a single median scent orifice on the metasternum, which is a feature shared with Dipsocoromorpha, Enicocephalomorpha, Leptopodomorpha, and Nepomorpha. The scent orifice is overgrown by integument, so that the secretion has to flow each side through two short channels, and a distinct evaporative apparatus as found in terrestrial bugs is not present. Some Gerridae and Veliidae, however, have a more complex apparatus than other families, with prolonged lateral channels that reach the pleural regions of the metathorax. An abdominal scent gland is found in nymphs and adults of all semiaquatic families except for some Hydrometridae, the Veliidae and the Gerridae, and is situated between tergum III and IV (Andersen 1982).

An abdomen with eight plate-shaped segments on the abdominal dorsum of the female and seven on the male is the plesiomorphic condition among the Gerromorpha (Fig. 6.8). The eighth segment of females is divided ventrally along the midline, and in males it is cylindrical and usually withdrawn into the pregenital abdomen. A typical gerromorphan abdominal segment is divided dorsally into mediotergites and a pair of laterotergites, with endotergites being present in some females. The laterotergites form the abdominal connexives, with usually six segments, and the pleural and sternal parts of the abdominal segments are fused to each other to form a sternopleuron. The first abdominal sternopleuron is fused with the metasternum, except in the subfamily Rhagadotarsinae of the Gerridae, where it is secondarily retained (Andersen 1982).

The male genitalia of Gerromorpha were considered the most plesiomorphic among the Heteroptera by Cobben (1968, 1978). It consists basically of a cylindrical abdominal segment eight, a boat-shaped segment nine (the pygophore), and a lid-shaped segment ten (the proctiger), which covers the posterior end of the pygophore (Fig. 6.9). A relatively simple phallic organ is internally attached to the pygophore, and a pair of parameres arises laterally from it. The phallus is typically composed of two parts: the sclerotized proximal phalloteca and a membranous dis-

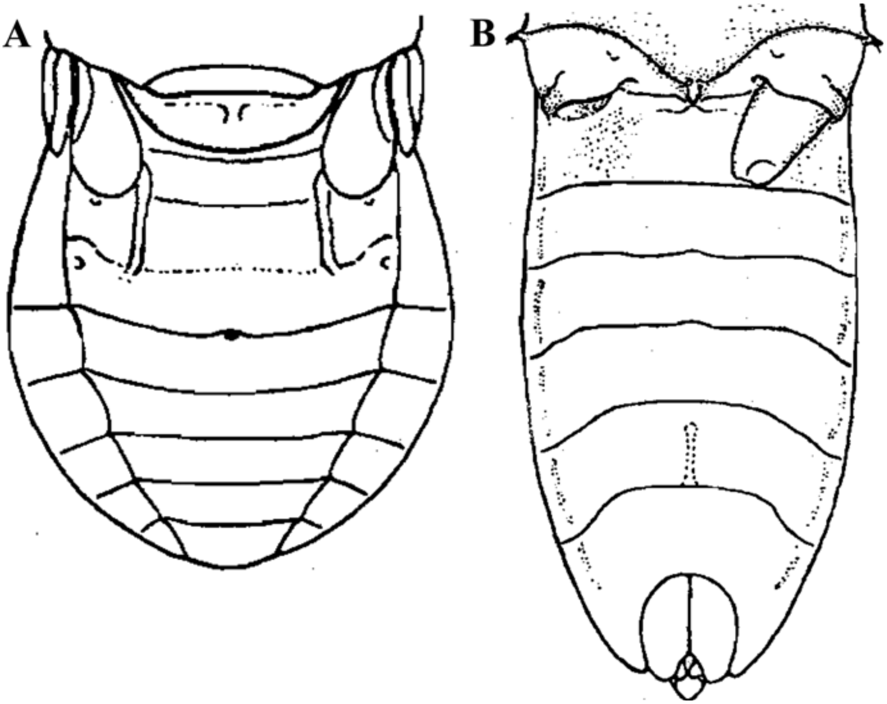
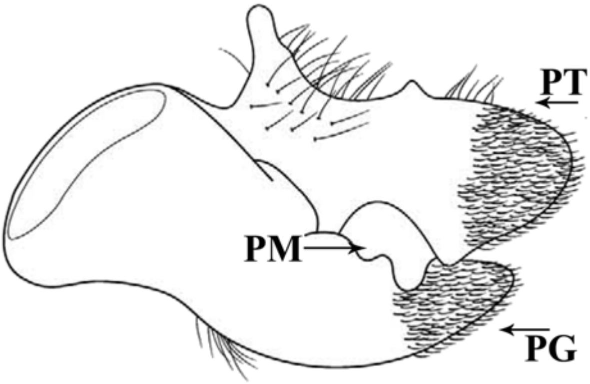


Fig. 6.8 General aspect of the abdomen of the gerromorphans. (**a**) *Merragata* (Hebridae), dorsal view of the micropterous form. (**b**) *Ocellovelia* (Veliidae), ventral view of the female (Modified from Andersen 1982)

Fig. 6.9 General aspect of the external male genitalia of *Paravelia* (Veliidae) in lateral view, with parameres omitted (*PG* pygophore, *PM* place of insertion of the paramere, *PT* proctiger; modified from Moreira and Barbosa 2012)



tal endosoma, which is usually subdivided into a membranous conjunctivum and a vesica normally armed with sclerotized pieces (Andersen 1982).

As for the female genitalia (Fig. 6.10), it is formed by the eighth and ninth abdominal segments. The eighth segment has a basal sclerite or first gonocoxa

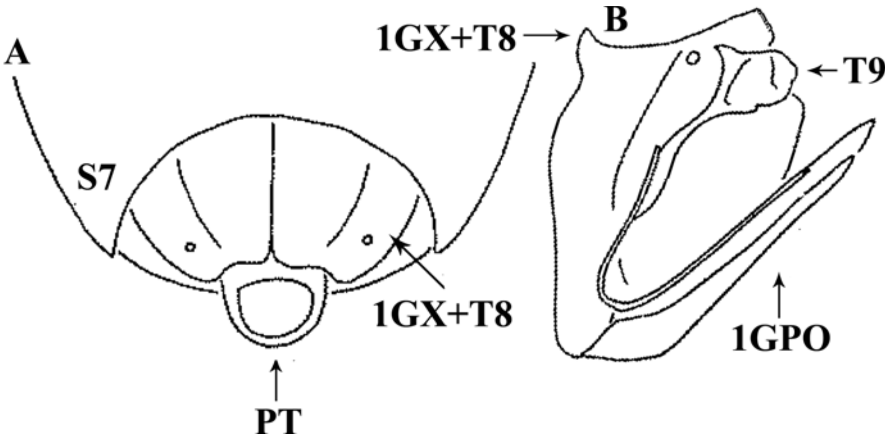


Fig. 6.10 General aspect of the external female genitalia in Gerromorpha. (**a**) *Rhagovelia* (Veliidae), apex of abdomen in ventral view. (**b**) *Hebrus* (Hebridae), dissected genitalia in lateral view (*1GPO* first gonapophysis, *1GX* first gonocoxa, *S7* seventh abdominal sternite, *PT* proctiger, *T8* paratergite 8, *T9* paratergite 9; modified from Scudder 1959)

ventrolaterally on either side, and this sclerite carries ventrally and caudally the first gonapophyses. The second pair of gonocoxae is found on segment nine, to which are attached the second pair of gonapophyses. Besides those, there is a cone-shaped structure named proctiger, which represents the tenth abdominal segment, and apically a plate that flanks the lower edge of the anal opening. The female ovipositor of most Gerromorpha is plate-shaped, with flap-like gonapophyses, adapted for depositing the egg on the surface of a substrate, embedded in a gelatinous mass. In Mesoveliidae, however, the ovipositor is laciniate and used to embed the eggs in the substrate (Andersen 1982).

6.3 General Biology and Ecology

The Gerromorpha occupy a wide variety of habitats from saltwater pools to mountain lakes, from hot springs to large rivers, and are the only group of insects found on open seas (Menke 1979; Cheng 1985). Andersen (1982) divided the kinds of habitats occupied by them in a few categories, as follows: (1) humid terrestrial habitats, not necessarily close to free water; (2) marginal aquatic habitats comprising wet soil, tufts of plants, or carpets of moss; (3) plant-covered water surface; (4) free surface of stagnant freshwater bodies; (5) free surface of flowing freshwater bodies; (6) surface of intertidal marine water; and (7) the surface of oceanic water. Representatives of most species of Gerromorpha will perish within a short time if kept dry (Andersen 1976), and although the vast majority of them is found above the water surface, the genus *Nieserius* Zettel from Asia includes subaquatic species of the family Hebridae (Zettel 1999).

In terms of habitat preferences, the better-known species are almost invariably European and North American, whereas tropical species are unfortunately very poorly studied. Among Neotropical Mesoveliidae, specimens of *Mesoveloidea williamsi* Hungerford can be found on wet moss close to streams or walking on top of fallen logs or boulders, similarly to *Mesovelia amoena* Uhler, which also dwells crevices at the edges of ponds and rivers. *Mesovelia mulsanti* White, by its turn, is a more active species commonly encountered running on floating leaves of aquatic plants on ponds (Andersen 1982; Damgaard et al. 2012). Other Neotropical mesoveliids inhabit environments very different from those commonly associated with the family (Damgaard et al. 2012). For example, *Speovelia mexicana* Polhemus was collected under rocks atop a reef-like coastal area, running about on the sea water trapped by the reef after the tide receded; species of *Darwinivelia* Andersen and Polhemus are associated with mangroves; and *Cryptovelia terrestris* Andersen and Polhemus is a semiterrestrial species, living on soil litter in primary or high secondary forests (Polhemus 1975; Andersen and Polhemus 1980; Andersen 1982).

As for the family Hebridae, the Neotropical species are very rarely collected or studied, and the habits of most of them are unknown. Representatives of the genus *Hebrus* Curtis commonly hide among the marginal vegetation alongside pools, lakes, and streams, occasionally being found on brackish water; *Merragata* White is typically associated with ponds completely covered by algal mats or heavy grown by plants with floating leaves; and specimens of *Lipogomphus* Berg have been collected on the water's edge of ponds, slow-moving parts of streams, and quiet secluded coves of lakes (Drake and Chapman 1958; Andersen 1982).

Among Neotropical Hydrometridae, the common and widespread genus *Hydrometra* is found on the reedy margins of rivers and streams where the current is subdued and at edges of lakes, ponds, and pools (Andersen 1982). However, species of the less diverse and rarer genera of the family are found in conditions very different from those. *Chepuvelia usingeri* China is endemic to forest leaf-litter in Chile; *Veliometra schuhi* Andersen was collected at marginal vegetation in the impounded area of a forest stream in the Amazon; and species of *Bacillometra* Esaki and *Bacillometroides* Polhemus and Polhemus are confined to swift rocky upland streams in the Guiana Plateau and the foothills of the Andes (China 1963; Andersen 1977; Polhemus and Polhemus 2010).

An even wider variety of habitats is found among the Veliidae and Gerridae. In the former family, most *Microvelia* Westwood are found near shore, on the plant-covered zone of stagnant waters. Some, however, can be found on open water surface of puddles and pools filled with rainwater or on the water pockets of terrestrial and arboreal bromeliads (an habitat shared only with *Paravelia* Breddin), inside crab holes or tree holes (Andersen 1982; Polhemus and Polhemus 1991). Species of *Husseyella* Herring are found on tidal streams of mangrove swamps; those of the poorly studied genus *Aegilipsovelia* Polhemus live hygropetrically on wet rock surfaces and in wet moss on rocks; *Platyvelia* Polhemus and Polhemus occupies ponds with overhanging vegetation and floating leaves or emergent plants along the margins; *Stridulivelia* Hungerford dwells among emergent vegetation or close to the shore under overhanging plants in both small and large rivers; and *Oiovelia* Drake and Maldonado-Capriles is common on foam masses in blackwater streams (Herring 1955; Wilson 1958; Drake and Menke 1962; Polhemus 1970; Andersen 1982; Spangler 1986). Finally, representatives of the highly diverse *Rhagovelia* are found almost exclusively on running freshwater, with the exception of those of the *salina* group *sensu* Polhemus (1997) from marine habitats, although they can be caught considerably distant from the sea (Drake and van Doesburg 1966; Andersen 1982).

Some genera of Neotropical Gerridae occupy a wide variety of habitats, like the *Rheumatobates* Bergroth, that can be caught in ponds, lakes, quiet pools of larger streams, artificial canals, estuaries, and mangrove swamps; *Eurygerris* Hungerford and Matsuda from margins of small streams, ponds of varied sizes, and lakes; and *Limnogonus* Stål and *Neogerris* Matsumura, which are a common sight in stagnant waters such as ponds, pools, and sometimes lakesides and backwaters of streams (Herring 1949; Polhemus 1969; Andersen 1982; Molano-Rendón et al. 2008). Others, however, are stricter in their environmental preferences. Species of *Metrobates* Uhler inhabit turbulent streams and rivers free of vegetation; specimens of *Brachymetra* Mayr and *Tachygerris* Drake are usually collected in running water, in or near the shaded areas of the habitat; those of *Cylindrostethus* Fieber can be found in streams, always avoiding both turbulent and still waters; *Potamobates* Champion and *Platygerris* White are exclusive of swift currents; and *Charmatometra* Kirkaldy is common in streams and rivers covered by dense vegetation (Hynes 1948; Andersen 1982; Molano-Rendón et al. 2008). The sea skaters of the genus *Halobates* Eschscholtz inhabit both coastal and oceanic marine waters, and *Hermatobates breddini* Herring, the only representative of the family Hermatobatidae from the Western Hemisphere, is associated with coral reefs and rubble (Andersen 1982; Schuh and Slater 1995).

In general, semiaquatic bugs are intermediate stage predators in the food chains of their communities, normally attacking small invertebrates that fall on the water surface and become trapped or those who swim up to it (Menke 1979). On the other hand, gerromorphans are prey to hunting spiders, damselflies, dragonflies, backswimmers, beetles, fishes, frogs, lizards, turtles, crocodiles, birds, and bats (Warren 1915; Riley 1925; Anderson 1932; Williams 1944; Corbet 1959; Haverschmidt 1962; Ashmole and Ashmole 1967; Hoyt 1970; Harrington and Harrington 1972; Callahan 1974; Andersen 1982; Cooper 1984; Cheng 1985; Teran et al. 1995; Svensson et al. 2002; Frick et al. 2009). Many species of Gerromorpha are also known to be cannibalistic, feeding upon weaker individuals of their own kind (Butler 1923; Sprague 1956; Andersen 1982).

Antipredator adaptations in gerromorphan bugs comprise structural features (camouflage) as well as behavioral means. Cryptic coloration and countershading, obscuring the contours of the bugs, are common phenomena. The slender body shape with stilt legs possibly also affords some camouflage protection against predators (Andersen 1982). *Hydrometra* is often seen to rise and lower its body rhythmically, which tends to obscure the outline of the insect (Rensing 1962). Another strategy observed in *Hydrometra* is death feigning. When specimens are roughly handled, they become immobile, the antennae are stretched forward, and the legs pressed against the body (catalepsy). The insect stays in this condition for several minutes and may be able to get a predator to lose interest (Steiniger 1933).

Although the function of the scent glands of gerromorphan bugs is rather obscure, they produce substances with a distinctly unpleasant smell and may function as a chemical defense against predators. However, fast escape movements are probably the most effective antipredator behavior in semiaquatic bugs and can be associated with gregarious behavior in many veliids and gerrids, reducing predation by larger animals (Andersen 1982). In addition, at least some species of *Rhagovelia* and *Halobates* can dive and swim underwater if disturbed, with movements similar to those used when skating on the surface (Wharton 1981).

Besides being attacked by numerous predators, semiaquatic bugs are also target to different groups of parasites. Ectoparasitic fungi of the order Laboulbeniales occur on mesoveliids, hebrids, macroveliids, and veliids (Poisson 1957; Benjamin 1967). Immature stages of water mites belonging to several families can attach to the exoskeleton of the gerromorphan host, being sometimes very numerous and interfering with its development (Menke 1979; Lanciani 1985; Smith 1989). A variety of endoparasites and commensals is also known to be associated with semiaquatic bugs, including cnidosporids, nematodes, trypanosomatids, and flagellates (Poisson 1957; Arnqvist and Mäki 1990). Hymenopterous parasitoids of the families Scelionidae, Mymaridae, and Trichogrammatidae attack the eggs of semiaquatic Hemiptera (Poisson 1957; Henriquez and Spence 1993), and Cobben (1965) described a microorganism found in eggs and nymphs of *Mesovelia* that he believed to be a symbiont, a condition unknown in other Gerromorpha.

Wing polymorphism is common in the water strider families, and apterous forms are often much more common than winged individuals. The evolutionary significance of flightless forms is complex, but the essential consequence of brachyptery is that it insures continued usage of the immediate resource. Generally, flightless morphs are found in permanent habitats, where brachyptery insures that at least a part of the population will survive and also allows more energy to be allocated on the process of reproduction instead of having to share it with flight muscle and wing developmental processes. On the other hand, the ability of at least a part of the population to migrate by flight is favored in temporary habitats (Menke 1979). Seasonal changes in wing morph proportions within a population are usually well defined in temperate species, but in one of the few studies of polymorphism regarding Neotropical species, Nummelin (1997) could not detect this effect on a population of *Limnogonus franciscanus* (Stål) from Barbados.

An interesting behavior involving the wings occurs in some macropterous rhagadotarsine and trepobatine Gerridae and some Mesoveliidae which break off a portion of their wings (de la Torre-Bueno 1908; Jordan 1951). The break occurs along a transverse cleavage line in gerrids. Two theories were proposed by Torre-Bueno to explain this autotomy. One is that after bugs have migrated to a new habitat, they no longer need their wings. It is well documented that macropters in *Gerris* F. resorb their flight muscle after spring populations are established (Brinkhurst 1959; Andersen 1973), and this fact adds credence to his theory. Torre-Bueno's second hypothesis is that wings hinder copulation, and a mechanism has developed enabling them to be broken off.

As for the locomotion of semiaquatic bugs, Andersen (1976) established that movement on surface film of the water by means of ordinary limb action is achieved in three different ways: walking on alternating tripods in a way comparable to ordinary locomotion in terrestrial insects (*Mesovelia*, *Hebrus*, *Hydrometra*, *Microvelia*), rowing by simultaneous strokes of the middle legs while at least the hind legs slide on the water (*Rhagovelia*), and jumping, where the simultaneous power stroke of the middle legs causes the insect to take off the water surface and glide through the air (Gerridae).

Besides these basic modes, Brinkhurst (1960) described an intriguing phenomenon in *Velia* Latreille: after struggling to make headway against a strong current without progress, bugs would stop all movement, but instead of being swept downstream, they suddenly shot forward. Linsenmair and Jander (1963) found that in *Velia* the saliva discharged from the rostrum acts as a detergent, lowering the surface tension. The insect is thus carried forward (or sideways or in an arc) by the contracting surface film, with direction of movement apparently being controlled by the highly mobile rostrum (Andersen 1976). This mode of locomotion was called "expansion skating" and is also found in adults and nymphs of *Microvelia* and *Rhagovelia*.

Living on the water surface, gerromorphans developed means of using superficial waves for prey location and for communicating with each other. This phenomenon is documented in the Gerridae and Veliidae and might also play a role in the life of other semiaquatic bugs (Polhemus 1990; Schuh and Slater 1995). Southwood and Leston (1959), for example, suggested that hydrometrids locate their prey by sensing vibrations caused by the struggling animal trapped on the superficial tension of the water. Veliids, by their turn, apparently perceive prey by a combination of visual and mechanical means. Meyer (1971a, b) performed experiments on *Velia caprai* Tamanini with various kinds of visual stimuli and concluded that this species locates prey by means of a visual "central flickering detector" in combination with a water surface vibration detector.

Besides ripple communication, stridulation might also occur in gerromorphans, particularly in those of the genus *Stridulivelia*, which have a row of pegs on the paratergites and a file or roughened patch on the hind femur. A similar apparatus occurs in *Paravelia stenoptera* Polhemus and Polhemus, with an arcuate row of pegs on the abdominal venter and a rasplike area on the hind trochanter (Andersen 1982; Polhemus and Polhemus 1984b). Polhemus (1994) also recorded a possible stridulatory apparatus in *Metrobates* (family Gerridae), in which males and females of some species have fine ridges on mesoacetabulum and a sharp ridge on hind trochanter.

6.3.1 Eggs and Oviposition

The eggs of gerromorphan bugs are laid in a wide variety of places, each usually characteristic for a particular species or genus (Menke 1979). In the most plesiomorphic state, the eggs are deposited freely or partly hidden, attached lengthwise by a gelatinous substance. Deposition of the egg in an upright position by means of a pedicel (*Hydrometra*) or without one (*Hermatobates* Carpenter), or embedding the egg in plant tissue (*Mesovelia*) are inferred to be derived conditions (Cobben 1968; Andersen 1982).

A thin, entirely solid egg shell, marked with a hexagonal pattern from the follicular cells, is considered plesiomorphic among the Gerromorpha. Porous, aerostatic layers have probably developed several times independently in the Heteroptera as well as in semiaquatic bugs. The evolution of the micropylar system has most likely started with a single micropyle in the center of the anterior pole of the egg. This primitive condition is shared by all families of Gerromorpha except the Macroveliidae, which may have up to five or seven micropyles, and the Veliidae, which usually have two to six micropyles. Primitively, the micropyle forms a single perpendicular canal through the chorion. Usually this canal has an internal projection pointing toward the fore side of the egg. Those species having many, displaced micropyles usually have the inner projections of these oriented in a clockwise direction (Cobben 1968; Andersen 1982).

Hebrus species lay their eggs on moss, usually secreting them in leaf axils or between closely spaced leaves. They are elongate, oval, about twice as long as wide, with rounded ends, and pearly white when laid, but yellowish white as the embryo develops. Incubation takes from 6 to 12 days, being shorter at higher temperatures. In the laboratory, *Merragata* species lay their eggs on moss leaves or under algae, with incubation taking about the same time as in *Hebrus* (Cobben 1968; Menke 1979). In nature, Porter (1950) found their eggs under filaments of algae on stones and in surface holes of the stones.

As for *Mesovelia*, eggs are inserted in plant tissue at the waters' edge by means of the well-developed, sawlike ovipositor which pierces stems by means of rocking motion of the body. The egg is elongate, oval, and the micropylar end curves up to a flat operculum or lid which is exposed when the egg is deposited. When laid, the egg is white, but it becomes transparent as the embryo develops (Menke 1979). *Mesovelia mulsanti* lays about 100 eggs, which have an incubation period of 7–9 days, while *M. amoena* lays from 100 to 200, which incubate for 12 days (Hoffmann 1932). Unlike most Gerromorpha which have a sharp egg burster, the mesoveliid embryo develops a bladderlike outgrowth in the frontal region which pushes off the egg cap. The nymph then struggles free and swims to the surface, breaking through the surface film easily (Ekblom 1930).

The eggs of *Hydrometra* are spindle-shaped, superficially sculptured, stalked, and pearly white when deposited, but turning brown upon exposure to moist air or wet surfaces. They are laid singly on almost any object, usually just above the surface of the water, although Takahashi (1921) often found *Hydrometra* eggs under water in Japan. The female exudes a glistening drop of a gummy substance from the genital opening, which she then presses against the oviposition site where it hardens rapidly. The base of the egg stalk follows this fluid, and as the egg emerges, the female lifts her body, drawing the egg out perpendicular to the support (Menke 1979). A single female can produced up to 11 eggs per day, with a total of 173 over 37 days, and the incubation time of studied species varies from 7 to 23 days, depending on temperature, with the average being 11 to 13 days. Hydrometrid embryos split the shell with a sclerotized egg burster and then thrust the head through the slit (Hungerford 1920; Menke 1979).

Among the Veliidae, eggs can be laid on floating objects, moss, duckweed, stones, and living or dead leaves either just above or below the water surface. Eggs are laid singly or in clusters and are attached with gelatinous glue that covers much of the egg (Cobben 1968). They are white when laid, but turn amber as development progresses, and are often covered with sparse lines, cubical projections, or a honeycomb mesh structure. The eggs are oval and usually slightly flattened lengthwise on one side. de la Torre-Bueno (1917) found only two eggs at a time being deposited in *Microvelia pulchella* Westwood, but Miyamoto (1953) found that *M. diluta* Distant laid an average of 7.4 eggs/day, and Frick (1949) noted that *M. pulchella* laid up to 505 eggs.

Finally, gerrids are known to normally lay their eggs singly or in rows, just under the surface on floating sticks, vegetation, or other material. The eggs can be white when first laid and then turning amber, and the incubation time usually ranges from 8 to 12 days. Both Hungerford (1920) and Hoffmann (1924) studied the life cycle of *Trepobates pictus* (Herrich-Schäffer) and found that it lays three to ten eggs at a time in solid masses of gelatinous material on the underside of leaves and sticks in the water, with an incubation time of 5–12 days. As for members of the subfamily Rhagadotarsinae, they are unique among gerrids by the presence of an ovipositor used to insert the eggs in plant tissue (Silvey 1931). Finally, in the marine *Halobates*, eggs of coastal species are laid in clusters on substrates near shore, being olive green when laid, but turning bright orange in 2–3 days. In the open ocean species, eggs are laid on floating substrates, including, among others, feathers, small pieces of wood, mollusk shells, seeds, tar lumps, and insect carcasses (Cheng 1985).

6.3.2 *Nymph Feeding and Development*

Nymphs of semiaquatic bugs differ from adults in their usually softer integument, which is more or less distinctly divided into darker sclerites and lighter membranes. The ecdysial line is usually visible as a pale, longitudinal, median line through the thoracic nota and first abdominal tergum; on the head, the line branches in front of the eyes, thus assuming the shape of a Y. The number of antennal segments is the same as in adults, but there is only one segment in each tarsus. The metathoracic scent apparatus is not formed until the adult stage, but differentiation of the genitalia begins to become apparent in the fourth instar, and fifth instar nymphs are easily separated by sex (Andersen 1982).

The postembryonic stages of semiaquatic bugs have several features which may be used in comparisons between higher taxa, but which are less useful than adult characters at species level since they are often reduced or otherwise modified during the ontogenetic development. Such features include the structure of the eyes and the chaetotaxy of the head and body, especially in the earlier nymphal stages (Cobben 1968, 1978).

It was suggested by Cobben (1978) that the most plesiomorphic number of ommatidia in the eye of the first instar nymph of Heteroptera is probably five. The gerromorphan bugs show a progressive increase in ommatidial number: *Hebrus* (10), *Microvelia* (28), *Hermatobates* (30), *Macrovelia* Uhler (35), *Hydrometra* (38), *Mesovelia* (55), *Hebrovelia* Lundblad (about 70), and *Gerris* (about 130) (Cobben 1978; Andersen 1982). The low number of ommatidia in *Hebrus* and the small increase from the first instar nymph (10) to adult (35) may be representative of the plesiomorphic condition among semiaquatic bugs (Andersen 1982).

The eye of the early instar nymphs has a pair of ocular setae inserted between the ommatidia of the posterior surface of the eye, except in *Hydrometra*. These setae are usually preserved through the postembryonic development, but are however absent from adults of Macroveliidae, Hydrometridae (except *Veliometra* Andersen), and some Veliinae (Andersen 1982; Polhemus and Polhemus 1993).

As for the chaetotaxy, the first instar nymph of *Hebrus* and *Mesovelia* has relatively few macrotrichia on the dorsal surface of the head, thorax, and abdomen. This primary hair pattern can be traced in first instar nymphs of *Hydrometra* and *Hermatobates*, but is lost or obscured by a dense macro-hair layer in first instar nymphs of Veliidae and Gerridae. The number of these macro-hairs increases gradually through the nymphal instars of all semiaquatic bugs, including *Mesovelia* and *Hebrus* (Andersen 1982).

Some works describing the nymphs of Neotropical Gerromorpha exist (Estévez and Schnack 1980; Mazzucconi and Bachmann 1997; Konopko and Mazzucconi 2005, 2011; Padilla-Gil and Arcos 2011), but life histories studies are available only for species with wide geographical distributions (*Mesovelia mulsanti*, *M. amoena*, *Microvelia pulchella*, *M. hinei* Drake), and the experiments were almost always conducted in temperate environments (Hungerford 1917; de la Torre-Bueno 1917; Lanciani 1987; McPherson 1988; Taylor and McPherson 1999, 2000, 2003; McPherson and Taylor 2006). The few exceptions are the works of Frick (1949), which took place in Panama, and Iglesias and Crespo (2003, 2008) about the growth pattern in exclusively Neotropical species of the genera *Brachymetra* and *Rheumatobates*.

The usual number of nymphal instars in the heteropterous bugs, including the Gerromorpha, is five. However, species with less than five instars are found throughout the suborder (Southwood and Leston 1959). In Gerromorpha, Hoffmann (1932) found only four instars in *Mesovelia cryptophila* Hungerford, and Cheng and Fernando (1971) recorded the same number in *Rhagovelia obesa* Uhler. However, it is in the genus *Microvelia* that this phenomenon has been studied most carefully (Andersen 1982).

When rearing *Microvelia borealis* Torre-Bueno (= *M. pulchella*), de la Torre-Bueno (1917) found only four nymphal stages. Hungerford (1920) reared the same species and found more than four stages in some individuals; he suggested that variation might exist or that apterous forms have fewer stages than macropterous. Contrary to the latter theory, Frick (1949), in rearings of what was probably *M. pulchella* (his *M. capitata* Guérin-Méneville), obtained nine apterous adults developing through four instars. The majority of apterous and macropterous adults, however, developed through five nymphal stages, and it is so far unsettled which factors determine the variation in number of instars in *Microvelia* and other Gerromorpha (Andersen 1982).

The process of molting in Gerromorpha may take place both on a firm substrate and on the surface of the water. Sprague (1956) described this process with details in *Hydrometra*, as follows: in the hour before molting, the nymph imbibes water more frequently than before, as the gut is distended. During the later part of the period, the nymph becomes less active. The actual molting process takes place rather rapidly. The fore and hind legs are extended forward and backward, respectively, and arranged so that they are parallel with the body axis; the middle legs are planted firmly on the substrate at right angles with the body. When the nymph has placed its legs securely, it starts to suck air rather than water. The cuticle of the thorax then begins to cleave longitudinally, in the median ecdysial line. Small bubbles of air pass through the digestive tube and distend and lengthen the abdomen; in this way, alternate waves of contraction and dilation move up and down the body. The head, which is strongly bent ventrad, splits along its Y-shaped ecdysial line. As the body stretches upward, the proximal parts of the legs emerge from the exuvium; first the prothoracic and then the meso- and metathoracic legs are pulled away; with the legs touching the substrate, the antennae and finally the rostrum pull free.

The growth of the two wing pairs starts relatively early during the postembryonic development. In the second and third instar nymphs, the posterolateral angles of the meso- and metatergum are produced, indicating the formation of the wing pads. The wing pads of those third instar nymphs that will become macropterous are normally much more conspicuous than those of nymphs that will give rise to apterous adults. After the final molt, the adult individual passes through the so-called teneral development. The teneral stage is largely taken up with hardening and pigmentation of the cuticle, resorbation of muscles which only function during nymphal life, and, in macropterous adults, with growth of endoskeleton and flight muscles (Andersen 1982).

Although temperature clearly is important to the rate of nymphal development (Spence et al. 1980), it is certainly not the only factor. Photoperiod, food, and crowding are known to affect the development of many insects, including Heteroptera. In species that occur in the Neotropics, total time of development is known for *Mesovelia mulsanti* (20.5 days at 21–27 °C, 12 days at 28–33 °C), *Microvelia pulchella* (14.2–20.7 days), *M. hinei* (25.0 days), and *Platyvelia brachialis* (Stål) (27 days) (Frick 1949; Wilson 1958; Galbreath 1973; Taylor and McPherson 2003).

Feeding, in particular in nature, has only been observed and described in relatively few species of semiaquatic bugs. All of them, including the nymphs, are polyphagous carnivores or scavengers, feeding upon dead or half-dead arthropods, mostly other insects. However, the food preferences and behavior during prey location seem to vary considerably among the Gerromorpha (Andersen 1982). Hungerford (1920) studied the food preferences of *Mesovelia mulsanti* and suggested that microcrustaceans may form the staple food for this species, especially the small nymphs. He reared *Mesovelia* in aquarium without other food resources than an abundant population of microcrustaceans and the weaker individuals of their own species.

Hungerford (1920) and Sprague (1956) recorded *Hydrometra* feeding upon adult midges, mosquito larvae and pupae, and various microcrustaceans. The former author observed a third instar nymph catching an ostracod resting on the surface film. The nymph stalked slowly up to the prey, its body aquiver and weaving from side to side. The tips of its antennae were turned down to the surface, and the rostrum directed down and slightly forward. When close enough, the prey was caught and carried upon the tip of the rostrum with a sudden move. Cannibalistic behavior, where adult hydrometrids feed upon their own nymphs and the older nymphs upon the younger ones, has frequently been observed in laboratory (Andersen 1982).

Among the Veliidae, Hungerford (1920) observed first instar nymphs of what was probably *Microvelia pulchella* eat ostracods larger than themselves. First they felt around twisting the distal article of their rostrum in order to find a vulnerable spot to insert their stylets. After succeeding in doing so, the prey was lifted from the surface upon the upturned rostrum. *Microvelia* also often attack individuals of their own kind, but usually without success (Andersen 1982). Cheng and Fernando (1971) managed to rear *Rhagovelia obesa* using commercial fish food containing pulverized insects.

In Gerridae, smaller species and nymphs of the larger species may feed on various microcrustaceans (Hungerford 1920; Ekblom 1926; Silvey 1931; Liche 1936; Wesenberg-Lund 1943; Wilson 1958; Southwood and Leston 1959). They are known to have strong cannibalistic tendencies, which add to the difficulties in rearing these insects in the laboratory, especially because nymphs are particularly vulnerable when molting (Andersen 1982). In marine species, attempts to feed newly hatched nymphs of *Halobates* in the laboratory have not been successful, and in one rearing study, they all died within 5 days. The young nymphs occasionally preyed on one another, but they did not feed on any marine organism or on freshly killed *Drosophila* Fallén offered to them, although older nymphs (from third instar onward) and adults readily take such food organisms. How first instar nymphs survive in the open ocean is still a mystery. They may be able to utilize nutrients from the organic-rich surface film, but this has not been substantiated (Cheng 1985).

6.3.3 Adult Feeding and Reproduction

As explained for the nymphs, most semiaquatic bugs are opportunistic predators and scavengers, although small- or medium-sized arthropods with a soft integument are preferred as food items in nature. Two basic types of predator strategies can be recognized among them: the searching strategy and the waiting strategy, with some overlapping occurring between them, as well as the same species changing its strategies from time to time (Andersen 1982).

Species of *Mesovelia*, *Hebrus*, *Hydrometra*, and probably also *Microvelia* seem to be largely searching predators which move around examining crevices and cavities in the vegetation or other floating objects on the water surface looking for something edible. The prey is probably recognized by the tactile or olfactorial sensory apparatus rather than by vision (Andersen 1982). *Mesovelia* have been observed feeding upon dead or half-dead midges of Culicidae and Chironomidae, ostracods, and cladocerans (Hungerford 1920; Ekblom 1930).

Individuals of the genus *Hydrometra* have been observed feeding upon ephemeropterans, adult chironomids which were floating on the surface of the water, larvae and pupae of ceratopogonids, microcrustaceans, and smaller individuals of their own kind (Hungerford 1920; Ekblom 1926; Sprague 1956; Maier 1977). *Microvelia* can feed upon ostracods, collembolans, mosquito eggs, Anophelinae larvae, and also their own nymphs (Hungerford 1920; Jordan 1932; Frick 1949; Laird 1956; Miyamoto 1953). Some individuals can even attack adults of their own kind, but usually without success (Andersen 1982).

In *Rhagovelia* and almost certainly most gerrids, the waiting strategy is the prevailing one. They can detect and locate live prey trapped in the surface film of water solely by the surface vibrations generated by the struggling animal. Visual stimuli are probably significant for close-range location of prey, whether moving or not, when the surface bug patrols the water (Jamieson and Scudder 1979; Andersen 1982). Representatives of the genus *Rhagovelia* usually aggregate in places where the water current may concentrate floating objects including potential food items, such as microcrustaceans and small insects (Bacon 1956; Andersen 1982). A similar feeding behavior is seen in *Oiovelia*, where individuals would gather around a dying adult ephemeropteran that was trapped on foam retained on the edge of a stream (personal observation).

The prey taken by freshwater gerrids consist of various soft-bodied arthropods, including microcrustaceans, terrestrial insects that fall on the water or emerging insects with aquatic larvae (Andersen 1982). Among the oceanic species of *Halobates*, food items include pelagic cnidarians, sea anemones, planktonic crustaceans, and fish larvae (Andersen and Polhemus 1976). Besides that, it was shown by Riley (2006) that *Limnogonus luctuosus* (Montrouzier), a freshwater gerrid, preferred mobile prey, whereas *Halobates hawaiiensis* Usinger preferred immobile prey.

The reproductive behavior of semiaquatic bugs has been extensively studied, but as mentioned for other aspects of their biology, the vast majority of the experiments are sadly restricted to temperate species. For example, the possible role of the stridulatory devices found in *Stridulivelia* in acoustic communication and reproduction has not yet been investigated.

Many temperate species of Gerromorpha, on the other hand, are models for the study of mating systems, sexual selection, and evolution, especially those of the genera *Aquarius* Schellenberg, *Gerris*, and *Limnoporus* Stål (e.g., Vepsäläinen et al. 1985; Kaitala 1991; Vermette and Fairbairn 2002; Rowe and Arnqvist 2011). One of the few studies of such type based on a species from the Neotropics is that of Villagra et al. (2001), who analyzed sexual dimorphism and behavior in the water strider *Aquarius chilensis* (Berg).

According to Spence and Andersen (1994), four basic mating systems have been described among gerromorphans: (1) a kind of monogamy resulting from extended postcopulatory guarding or monopolization of the female's sperm-storage apparatus; (2) resource defense polygyny through male territoriality and defense of oviposition sites, which has evolved independently in several gerrid genera; (3) pure dominance or lek polygyny, charactering the mating system of *Halobates robustus* Barber; and (4) the scramble competition polygyny associated with a prolonged search for receptive females and variable postcopulatory guarding, seen in *Microvelia* spp. and many gerrids.

The location of a mate itself apparently presents no problem for gerromorphans, at least in gregarious species like most Gerridae and Veliidae. Sexually active males seem to be attracted by any moving object, and attempts to copulate with females of a different species or even with other males have been observed (Andersen 1982). However, it has been shown that males of *Gerris* can accurately detect the sex of other adults by the type of surface wave they generate on the water, even without visual cues (Wilcox 1979).

The mating in semiaquatic bugs is usually initiated by the male, which can use a variety of strategies to conquer the female. The most simple copulation strategy observed in Gerromorpha is that of the *Mesovelia*, where the male jumps on and engages the female very quickly and leaves her almost immediately after the actual sperm transfer (Andersen 1982). Individuals of *Mesovelia mulsanti* often mate when resting on the water surface, with the male clasping its fore legs around the mesothorax of the female, resting the middle legs on the water or over the female, and holding the hind legs in the air (Hungerford 1920; Hoffmann 1932).

An interesting fact among the Mesoveliidae is the apparently parthenogenetic condition seen in *Mesovelia amoena*. Males of this species have only been collected in North America, Mexico, and Hispaniola and only females from other parts of the Neotropical Region and from Hawaii, where the species was introduced (Menke 1979).

Different copulating positions are seen in veliids, where the male jumps on the female and grasps her thorax with a firm grip, assisted by the grasping comb present on the fore tibia. Unlikely the *Mesovelia*, however, the hind legs are also used to secure his position on the female's back (Andersen 1982). In *Microvelia* several matings can take place, each lasting a couple of minutes, and between which the male follows the female closely (Frick 1949).

However, it is not only during reproduction that males ride on top of females; some males of *Microvelia* and *Rhagovelia* "piggyback" on the females' dorsum whether copulating or not, and female's thorax can show modifications that facilitate this habit (Polhemus 1974; Moreira et al. 2010). In *Platyvelia brachialis*, on the other hand, the two sexes have reversed their roles so that the female mounts the male and stimulates him to copulate by rubbing his abdomen with her hind legs (Wilson 1958).

Reproduction in gerrids usually occurs with the male passively riding on the back of the female during copulation, securing his position by clasping her thorax with his fore legs just in front of the mesoacetabula. During this period, which can last from days to weeks, they copulate several times; the male feeds on female preys and submerges when she is laying eggs beneath the surface.

From these observations on the sexual behavior of semiaquatic bugs, it appears that there is a distinct trend toward a prolongation of the time the male spends with the same female, whether actual copulation takes place or not. This way, the male protects his own gametes from competition with those of other males and also protects the female from possible risks involved in new mating attempts. Females, in their turn, have a longer period of time to feed and lay eggs without being pursued by other sexually active males (Andersen 1982).

In the Gerromorpha, primary sexual dimorphism involves the reproductive organs and terminal segments of abdomen. Male genital segments are often more conspicuous than those of females, which may be concealed. The secondary sexual dimorphism, however, involves many different body parts, varying from group to group (Andersen 1982).

Several modifications on the legs of Veliidae may enhance male's ability to copulate, like the grasping comb present on for tibiae and the many spines seen on the enlarged hind legs of some species of *Rhagovelia*. More striking forms of secondary dimorphism occur, for example, in *Microvelia longipes* Uhler, in which only the males have hind legs much longer than their own body, and in many species of *Rheumatobates* that have males with extremely modified antennae and legs, which probably evolved as a response to sexual conflict (Westlake 1998; Rowe et al. 2006).

6.4 Classification and Diversity

The more than 2,100 known species of Gerromorpha are currently divided into eight families and approximately 160 genera. Most of the known diversity of the infraorder was described from the Oriental Region, but more than 500 species and 45 genera have been recorded from the Neotropical Region, representing roughly 24 and 29 % of the global specific and generic diversities (Polhemus and Polhemus 2008).

The current classification of the semiaquatic bugs follows almost entirely that summarized by Andersen (1982), with the exception of the progressive abandonment of the superfamilies Mesovelioidea (Mesoveliidae), Hebroidea (Hebridae), Hydrometroidea [Paraphrynoveliidae + (Macroveliidae + Hydrometridae)], and Gerroidea [Hermatobatidae + (Veliidae + Gerridae)]. This rejection is especially true after the proposition of the phylogeny of the Gerromorpha by Damgaard (2008a) (Fig. 6.11), which showed that both Hydrometroidea and Gerroidea were paraphyletic entities.

Out of the eight currently recognized families of Gerromorpha, only Paraphrynoveliidae is not found on the Neotropical Region. This monotypic family holds only two species from South Africa, which have rarely been collected (Schuh and Slater 1995; Polhemus and Polhemus 2008). The also monotypic marine family Hermatobatidae has a single Neotropical representative, *Hermatobates breddini* Herring, which occurs along the West Indian islands. The eight remaining species

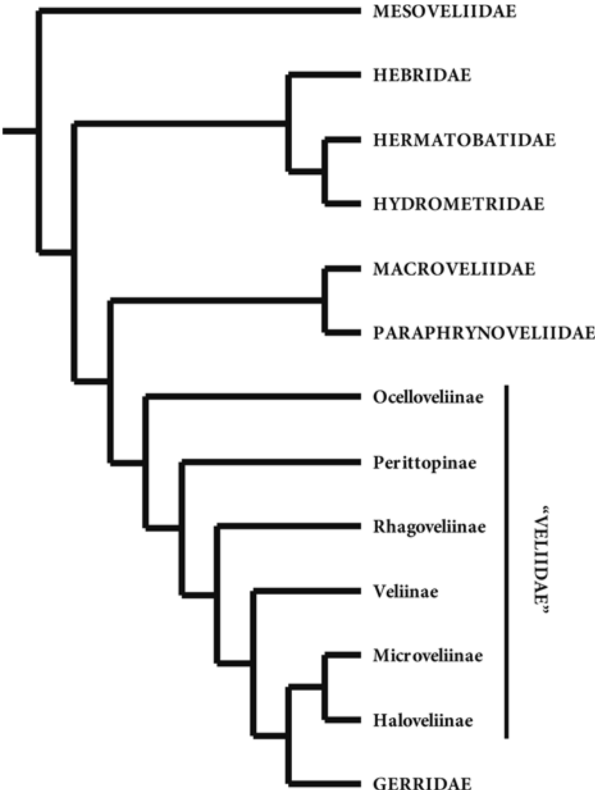


Fig. 6.11 Phylogeny of the Gerromorpha proposed by Damgaard (2008a)

of the family have been collected on the Indian and Pacific oceans (Polhemus and Polhemus 2008; Muñoz et al. 2010).

Macroveliidae is another family of semiaquatic bugs with very low diversity. Only three species, from three monotypic American genera, have been included in the family: *Macrovelia hornii* Uhler, *Oravelia pege* Drake and Chapman, and *Chepuvelia usingeri*. The last species was described from few specimens collected on southern Chile and is the only representative of the family to occur on the Neotropics.

A classification of the Mesoveliidae, which includes a few more than 45 extant species and subspecies, was presented by Andersen and Polhemus (1980) and later reanalyzed by Andersen (1999), with the acceptance of the subfamilies Madeoveliinae, including *Madeovelia* Poisson, and *Mesoveloidea*; and Mesoveliinae, with the remaining nine genera of the family. After that, the terrestrial genus *Seychellovelia* Andersen and Polhemus was described in the Mesoveliinae (Andersen and Polhemus 2003), and the status of the subfamilies and relationships among the genera were questioned by Damgaard et al. (2012). The phylogeny presented by the later authors showed both subfamilies of Mesoveliidae to be non-monophyletic, as well as some genera; however, no classificatory changes have been so far proposed.

On the Neotropical Region, Mesoveliidae is represented mainly by the common and widespread genus *Mesovelia*, with nine species ranging from Mexico to Argentina. Two of them, namely, *M. amoena* and *M. mulsanti*, also occur on the United States and Canada, besides being introduced in the Hawaiian Islands. The other genera of the family are less diverse and more rarely collected, like *Mesoveloidea* with just *M. williamsi* occurring from Mexico to southeastern Brazil and *M. peruviana* Drake, known only from the type series from Peru. *Darwinivelia* contains only three species from the coasts of Colombia, northern Brazil, and the Galápagos Islands; and both *Cryptovelia* and *Speovelia* have a single Neotropical representative each, respectively, from northern Brazil and Mexico (Damgaard et al. 2012).

According to the classification presented by Andersen (1981), Hebridae is subdivided into the Oriental Hyrcaninae and the cosmopolite Hebrinae. Probably because of the difficulties to collect and study the hebrids, they are very poorly represented in most collections and in taxonomic works, and no updated phylogenies or propositions of classification have been published after Andersen's study.

Out of the approximate 220 species described in the family (Polhemus and Polhemus 2008), 32 have been so far recorded from the Neotropical Region, included in three genera. *Lipogomphus* gathers four species, which are almost exclusively Neotropical except for *L. brevis* (Champion), which extends from southern United States to Panama (Polhemus and Polhemus 1988). The other species of the genus are known from Guatemala to Panama (*L. leucostictus* (Champion) and *L. acola* (Drake and Chapman)) and from central-southern South America (*L. lacuniferus* Berg) (Drake and Chapman 1958; Moreira et al. 2011b).

Merragata, on its turn, is represented on the tropical America by four of its five species, ranging from Mexico to Argentina. Out of the Neotropical species, *M. hebroides* White also occurs on Canada and United States and is the only species of the genus recorded from other zoogeographical regions, on the Hawaiian and Canary Islands, probably as a result of unintentional introduction. Finally *Hebrus*, which gathers the majority of the species of the family, is represented on the Neotropical Region by 23 species, several of which are unfortunately known only from the type series.

The current classification of the Hydrometridae and its approximately 125 species (Polhemus and Polhemus 2008) still follows almost entirely that proposed by Andersen (1977), with a subdivision in three subfamilies: Heterocleptinae, Limnobatodinae, and Hydrometrinae. Both Heterocleptinae and Limnobatodinae are represented on the Neotropical Region by a single species each, respectively, *Veliometra schuhi*, from northern Brazil, and *Limnobatodes paradoxus* Hussey, recorded from Honduras, Guyana, French Guiana, Brazil, and Peru (Schuh and Slater 1995; Moreira et al. 2011b; Cianferoni 2014).

As for the Hydrometrinae, it is the most diverse subfamily of Hydrometridae and holds *Hydrometra*, the only genus of the family known to occur outside the tropics.

This is represented on the Neotropical Region by 39 species ranging from Mexico to Argentina (Drake and Lauck 1959; Mychajliw 1961; Smith 1988a; Perez-Goodwyn 2001; Moreira and Barbosa 2013). Besides *Hydrometra*, other Neotropical Hydrometrinae are divided between the genera *Bacillometra*, with one species from French Guiana and Brazil, and *Bacillometroides* Polhemus and Polhemus, with three species from Peru and Bolivia that were previously held on the former genus (Schuh and Slater 1995; Polhemus and Polhemus 2010).

The greatest diversity of the family Veliidae is known from the Neotropical Region, especially because of the immense number of described species of *Rhagovelia* (Polhemus and Polhemus 2008; Padilla-Gil and Moreira 2013). About 300 out of the more than 900 species of the family have been described from the Neotropical Region, a number that will still increase much because many species of Microveliinae remain undescribed (Polhemus and Polhemus 2007, 2008).

Despite being shown by Damgaard (2008a) that Veliidae is paraphyletic because of the positioning of two of its subfamilies closer to Gerridae than to its other subfamilies, the group still has a generally accepted status of family. Some of its subfamilies and genera are probably also non-monophyletic, but an updated classification has not yet been proposed, and that summarized by Andersen (1982) and analyzed by Andersen and Weir (2004) is still followed. According to them, Veliidae is divided into the subfamilies Perittopinae, Rhagoveliinae, Veliinae, Microveliinae, Haloveliinae, and Ocelloveliinae.

Out of the six currently accepted subfamilies of Veliidae, Perittopinae, Haloveliinae, and Ocelloveliinae are not represented on the Neotropical Region. The first two are recorded only from the Oriental Region and gather one and five genera, respectively. The last one is monotypic and has a controversial positioning, with two species from South Africa that had been previously placed in the Mesoveliidae and Macroveliidae (Schuh and Slater 1995).

Two genera are currently accepted in Rhagoveliinae, and the cosmopolitan *Rhagovelia* is the only one with Neotropical representatives, because the species previously allocated on the genus *Trochopus* Carpenter were transferred by Polhemus (1997) to *Rhagovelia* under the *salina* group. Besides this synonymy, the same author reorganized the species of the genus in 17 groups, which formed five complexes (monophyletic) and a grade (non-monophyletic). After that, Moreira et al. (2012) proposed a new group for two species previously placed on the *robusta* group. A total of 184 species are distributed throughout the Americas, of which 97 % have a tropical distribution, and South America is the geographical area with the highest diversity (Padilla-Gil and Moreira 2013).

The subfamily Veliinae is currently divided into nine genera, out of which *Oiovelia*, *Paravelia*, *Platyvelia*, *Steinovelia* Polhemus and Polhemus, *Stridulivelia*, and *Veloidea* Gould occur on the Neotropical Region (Polhemus and Polhemus 1993; Schuh and Slater 1995). More genera of Neotropical Veliinae will surely be described in the future, because *Paravelia* is known to be a paraphyletic entity.

For a long period, *Oiovelia* was only represented by the type species from Venezuela, until Spangler (1986), Moreira et al. (2010), and Rodrigues et al. (2014) described seven additional species from South America. *Paravelia*, which is by far the most diverse of the subfamily, has 59 described species and used to gather even more before Polhemus and Polhemus (1993) transferred nine species to *Platyvelia* and five to *Steinovelia*. When described, these genera were fully composed by species previously allocated on *Paravelia*, and no new species have been described afterward.

Stridulivelia was divided by Polhemus (1979) into the subgenera *Aenictovelia* for the primarily Mesoamerican species that lack a stridulatory mechanism and *Stridulivelia* s.str. for the South American species with a stridulatory apparatus. Currently, five species are assigned to the subgenus *Aenictovelia* and ten to *Stridulivelia* s.str. (Polhemus and Spangler 1995). Finally, *Veloidea* is an exclusively Neotropical genus, now with five species distributed from Mexico to Honduras in Central America and on Colombia, Venezuela, and Ecuador in South America (Buzzetti and Zettel 2008).

Microveliinae is probably the most problematic subfamily of Veliidae on the Neotropics. Besides the small size of most species, the lack of diagnostic morphological characteristics makes the taxonomic study of the group very complicated, especially regarding the *Microvelia*. Many genera of Microveliinae are known only from Africa or from the Oriental region, and the lack of revisions focusing on the Neotropical fauna makes the number of genera recorded from tropical America be relatively small, despite of the large amount of described species.

Most of them (86 species from Mexico to Argentina) are held on the genus *Microvelia*, represented on the region by the subgenera *Kirkaldya* and *Microvelia* s.str. A few others are allocated on the genera *Euvelia* Drake (four species from Brazil, Peru, and Bolivia), *Husseyella* (one from Florida and the Caribbean, two from Brazil), *Xiphovelia* (one from central Brazil), and *Aegilipsovelia* (three from Mexico) (Polhemus 1970, 1977; Polhemus and Polhemus 1984a; Smith 1988b; Moreira et al. 2011b).

Lastly, following the classification summarized by Andersen (1982), Gerridae is divided into eight subfamilies: Charmatometrinae, Cylindrostethinae, Eotrechinae, Gerrinae, Halobatinae, Ptilomerinae, Rhagadotarsinae, and Trepobatinae. Out of these, Eotrechinae and Ptilomerinae are the only ones not occurring on the Neotropical Region, being known respectively from India and the Orient and from Madagascar to New Guinea (Schuh and Slater 1995).

Charmatometrinae is restricted to the Neotropics and comprised by three genera: *Brachymetra*, with nine species from Guatemala to Argentina (Harris and Drake 1945; Hungerford and Matsuda 1957; Drake 1957; Moreira et al 2011b); *Charmatometra*, with a single species from Venezuela, Colombia, and Ecuador (Mazzucconi et al. 2009); and *Eobates* Drake and Harris, with only one species from the island of Hispaniola and Peru (Aristizábal 2002).

Cylindrostethinae is also composed by three genera: the pantropical *Cylindrostethus*, represented on the Neotropics from Colombia and Trinidad and Tobago to Argentina by 10 of its 19 species (Floriano 2013; Floriano and Cavichioli 2013); *Platygerris*, with three species from Mexico to Colombia (Aristizábal 2002);

and *Potamobates*, with 19 described species that range from Mexico to Peru (Padilla-Gil and Damgaard 2011; Morales-Castaño et al. 2013).

Gerrinae is a cosmopolitan subfamily, currently divided into the tribes Gerrini and Tachygerrini. The former is cosmopolitan and represented on the Neotropical Region by the genera *Aquarius*, with two predominantly temperate species extending into Mexico and Guatemala and one species occurring on Chile and Peru, out of its 17 described species; *Gerris*, with a mainly Nearctic species reaching Mexico and one species endemic to the same country, from its 30 known species; *Limnogonus*, with seven species and subspecies ranging from Mexico to Argentina, out of a total of 28 species; and *Neogerris*, with eight species that range from the Caribbean to Argentina, out of a diversity of 13 species. The tribe Tachygerrini, restricted to Tropical America, is composed by *Eurygerris*, with nine species that range from Mexico to the Andean countries of South America; and *Tachygerris*, with 13 species distributed from Mexico to South America, except Chile, Argentina, and Uruguay (Damgaard et al. 2014).

Halobatinae is subdivided into the pantropical Halobatini and the Paleotropical Metrocorini. The former is composed by the genera *Asclepios* Distant and *Halobates*, out of which only marine species of the later are represented on the Neotropical Region. *Halobates robustus* Barber, from the Galápagos Islands, is the only coastal species occurring on the area; the remaining four are found on open ocean, and *H. micans* is the only species of the genus recorded from the Atlantic Ocean (Andersen and Cheng 2004).

Rhagadotarsinae is composed by only two genera, the Paleotropical *Rhagadotarsus* Breddin and the American *Rheumatobates*. According to Westlake et al. (2000), Polhemus and Westlake (still unpublished) recognized 37 taxa in *Rheumatobates*: 32 species, three undescribed species, and two subspecies, out of which 31 species and subspecies are Neotropical, being recorded from Mexico to Argentina. To that number, a species described from Colombia by Castro-Vargas and Morales-Castaño (2011) can be added.

Finally, the trepobatine water striders are currently organized on the tribes Naboandelini, Stenobatini, Metrobatini, and Trepobatini, of which only the last two are present on the Neotropical Region. Metrobatini is represented on the area only by 12 species of the genus *Metrobates*, which is exclusive of the New World. As for the Trepobatini, its Neotropical representatives include the single described species of *Lathriobatoides* Polhemus, from Northern Brazil; the four species of the exclusively South American *Halobatopsis* Bianchi; the eight species of *Ovatametra* Kenaga, ranging from Panama to Argentina; the six species of *Telmatometra* Bergroth, distributed from Mesoamerica to Brazil and Peru; the only known species of *Telmatometroides* Polhemus, recorded from Costa Rica, Panama, Colombia, and Ecuador; 7 out of the 12 described species of *Trepobates* Uhler, which is exclusive of the New World; and by the single species of *Trepobatoides* Hungerford and Matsuda, recorded from Bolivia and Peru (Polhemus and Polhemus 2002).

6.4.1 Identification Key to the Families and Genera of Gerromorpha from the Neotropical Region

1 Apterous, tarsal claws of forelegs preapical, tarsal claws of middle and hind legs apical, inhabitants of coral reefs.........................Hermatobatidae (*Hermatobates*)

1′ Apterous, brachypterous, or macropterous; positioning of tarsal claws equal on all legs; habitat variable...2

2 Tarsal claws apical (Fig. 6.7a, c, d, e) 3

2′ Tarsal claws preapical (Fig. 6.7b, f–k)..15

3 Body long and almost always slender (Fig. 6.1e); eyes located far from the the anterior margin of thorax; antennae and legs long and very slender (Fig. 6.1e) ....Hydrometridae (part) 4

3′ Body, legs, and antennae not as above; eyes located closer to anterior margin of thorax..7

4 Body length 3–5 mm; antennomere I much longer than II, distinctly passing apex of head...*Veliometra*

4′ Body length at least 6 mm; antennomere I subequal to or shorter than II, generally only slightly passing apex of head...5

5 Meso- and metasternum without longitudinal grooves.......................*Hydrometra*

5′ Meso- and metasternum with longitudinal grooves...6

6 Antennomere IV bulbous distally; coxae equally spaced..................*Bacillometra*

6′ Antennomere IV filamentous, not expanded distally; middle coxae farther from hind coxae than fore coxae...*Bacillometroides*

7 Body compact and robust (Fig. 6.1d); ventral surface of head with a deep rostral groove (Fig. 6.5b); tarsal formula 2-2-2...Hebridae 8

7′ Body delicate, elongated, and suboval (Fig. 6.1b, c); ventral surface of head without deep rostral groove; tarsal formula 3-3-3................................10

8 Antenna shorter than maximum pronotum width, antennomeres thick, antennomeres I and IV with similar lengths..*Merragata*

8′ Antenna as long as maximum pronotum width, antennomeres slender, antennomere IV longer than I...9

9 Antenna appearing 5 segmented because of a false membranous joint present on antennomere IV (Fig. 6.12)...*Hebrus*

9′ Antenna not appearing 5 segmented; false joint absent...................*Lipogomphus*

10 Eyes slightly removed from anterior margin of thorax; bucculae anteriorly produced, laterally covering base of rostrum; pronotum posteriorly produced, covering all mesonotum (Fig. 6.1b).........................Macroveliidae (*Chepuvelia*)

10′ Eyes located closer to anterior margin of thorax; bucculae not produced, not covering base of rostrum; pronotum at most partially covering mesonotum (Fig. 6.1c)..Mesoveliidae (part) 11

11 Macropterous...*Mesovelia* (part)

11′ Apterous..12

12 Body length 1.2–1.3 mm; eyes vestigial (Fig. 6.2a)............................*Cryptovelia*

12′ Body length at least 1.5 mm; eyes well-developed, globose...........................13

13 Mesonotum prolonged on middle, distinctly longer than pronotum ....*Mesovelia* (part)

13′ Mesonotum not prolonged, subequal in length or shorter than pronotum........14

14 Body shorter than 2 mm; ventral surface of head with a pair of prominent longitudinal carina behind base of pronotum.................................*Darwinivelia*

14′ Body length at least 2.5 mm, ventral surface of head without prominent longitudinal carina..*Speovelia*

15 Head elongated; eyes located far from the anterior margin of thorax ....Hydrometridae (*Limnobatodes*)

15′ Head not elongated; eyes located closer to anterior margin of thorax.............16

16 Middle coxae located much closer to hind coxae than to fore coxae (Fig. 6.13c); hind femur long, generally distinctly passing apex of abdomen..Gerridae (17)

16′ Middle coxae approximately equally distant from fore and hind coxae; hind femur shorter, usually at most slightly passing apex of abdomen (except for males of *Microvelia longipes*)..36

17 Eyes approximately reniform, emarginated on posterior portion of inner margin (Fig. 6.14a)..18

17′ Posterior portion of inner margin of eye not emarginated (Fig. 6.14b)...........24

18 Antenna as long as or longer than body; antennomere IV distinctly longer than others...*Tachygerris*

18′ Antenna shorter than body; antennomere IV not longer than others................19

19 Body length greater than four times its width.............................*Cylindrostethus*

19′ Body length smaller than four times its width..20

20 Tarsomere I of fore leg with about half the length of tarsomere II...................21

20′ Tarsomeres I and II of fore leg with subequal lengths.....................................23

21 Rostrum short, not reaching base of the prosternum........................*Potamobates*

21′ Rostrum longer, extending at least until the mesosternum..............................22

22 Pronotum with a large central light macula on anterior portion; middle tarsi without claws..*Neogerris*

22′ Pronotum with two relatively small elongated light maculae on anterior portion; middle tarsi with claws...*Limnogonus*

23 Pronotum not covering mesonotum; connexives without spines on posterior ends..*Eurygerris*

23′ Pronotum covering mesonotum; connexives with small spines on posterior ends..*Aquarius*

24 Tibia and tarsomere I of middle leg with a fringe of long erect setae; marine species..*Halobates*

24′ Tibia and tarsomere I of middle leg without fringe of long erect setae (except for some species of *Trepobates*); freshwater species..........................25

25 Antennomere II longer than III; antennomeres II–III of males distally widened..*Metrobates*

25′ Antennomere II subequal in length or shorter than III; antennomeres II–III of males not distally widened..26

26 Tarsomere I of fore leg longer than II...*Charmatometra*

26′ Tarsomere I of fore leg not longer than II..27

27 Tarsomere II of fore leg not longer than two times the length of I....................28

27′ Tarsomere II of fore leg longer than two times the length of I.........................29

28 Pronotum yellowish with several distinct black stripes............................*Eobates*

28′ Pronotum orange to reddish brown, usually only with lateral margins darkened, but sometimes with a median black stripe.......................*Brachymetra*

29 Middle femur longer than the middle tibia and than the hind femur, which can be modified in males...*Rheumatobates*

29′ Middle femur shorter than the middle tibia and than the hind femur...............30

30 Antennomere III 10–40 % longer than I..31

30′ Antennomere III with 40–80 % the length of I...33

31 Antennomere III longer than two times the length of II.................*Telmatometra*

31′ Antennomere III shorter than two times the length of II..................................32

32 Interocular space with a dark longitudinal stripe.......................*Telmatometroides*

32′ Interocular space without dark longitudinal stripe......................*Lathriobatoides*

33 Antennomere I much longer than II–III together...........................*Trepobatoides*

33′ Antennomere I not distinctly longer than II–III together.................................34

34 Middle tibia distinctly shorter than body length.................................*Ovatametra*

34′ Middle tibia at least as long as body..35

35 Eyes in lateral view not extending beyond half of propleura; hind tibia distinctly shorter than two times the length of hind tarsus..................*Trepobates*

35′ Eyes in lateral view extending beyond half of propleura; hind tibia longer than two times the length of hind tarsus...*Halobatopsis*

36 Head dorsum without impressed longitudinal line or pair of indentations near base; coxae of the same pair of legs inserted close to each other (Fig. 6.13a); male fore tibia without grasping comb..................Mesoveliidae [*Mesoveloidea*]

36′ Head dorsum with an impressed longitudinal line and a pair of indentations near base; coxae of the same pair of legs well separated between them (Fig. 6.13b); male fore tibia usually with an apical grasping comb (Fig. 6.15)..Veliidae 37

37 Tarsal formula 1-2-2...38

37′ Tarsal formula 2-2-2 or 3-3-3...43

38 Middle tarsus with four leaflike structures subapically (modified claws and bipartite ventral arolium) (similar to Fig. 6.7i)...39

38′ Middle tarsus with at most three leaflike structures...40

39 Tarsomere II of middle leg longer than I, widened and deeply cleft subapically ....*Euvelia*

39′ Tarsomere II of middle leg shorter than I, not widened and deeply cleft subapically..........*Husseyella*

40 Antennomere I long and slender, subequal to or longer than head width between eyes..........41

40′ Antennomere I much shorter and stouter..........42

41 Antennomere I at least twice as long as distance from base of antenna to apex of head; tarsal claws of middle and hind legs very long, subequal in length to tarsomere I..........*Aegilipsovelia*

41′ Antennomere I and tarsal claws shorter..........*Microvelia* (*Kirkaldya*)

42 Middle tarsus with three leaflike structures subapically (modified claws and ventral arolium)..........*Xiphovelia*

42′ Middle tarsus without leaflike structures..........*Microvelia* (*Microvelia*)

43 Tarsal formula 2-2-2 or 3-3-3; middle tarsus deeply cleft, with claws and arolia modified in a swimming fan (Fig. 6.7j)..........*Rhagovelia*

43′ Tarsal formula 3-3-3; middle tarsus unmodified..........44

44 Middle and hind tarsi each with four leaflike structures (modified claws and arolia) arising from a short cleft at middle of last article (Fig. 6.7i) ....*Veloidea*

44′ Middle and hind tarsi without leaflike structures..........45

45 Body surface with several glabrous depressed structures, rounded or elongated; abdominal sternites with lateral shining glabrous grooves (Fig. 6.16) ....*Stridulivelia*

45′ Body surface not as above; abdominal sternites without lateral grooves..........46

46 Last tarsomere laterally expanded, suboval (Fig. 6.7h); tarsomere II of middle leg with at most 1.5 times the length of I..........*Oiovelia*

46′ Last tarsomere not expanded, subcylindrical; tarsomere II of midleg with at least two times the length of I..........47

47 Tubercles of venter of thorax, if present, centrally located (in at least one species the mesoacetabula are slightly expanded centrally, but do not form distinct tubercles) (Fig. 6.17a)..........*Paravelia*

47′ Metasternum with pair of anterolateral tubercles, near mesoacetabula..........48

48 Mesoacetabula prolonged into tubercles, positioned in front of the tubercles of the metasternum (Fig. 6.17b)..........*Platyvelia*

48′ Mesoacetabula not prolonged into tubercles, only metasternal tubercles present (Fig. 6.17c)..........*Steinovelia*

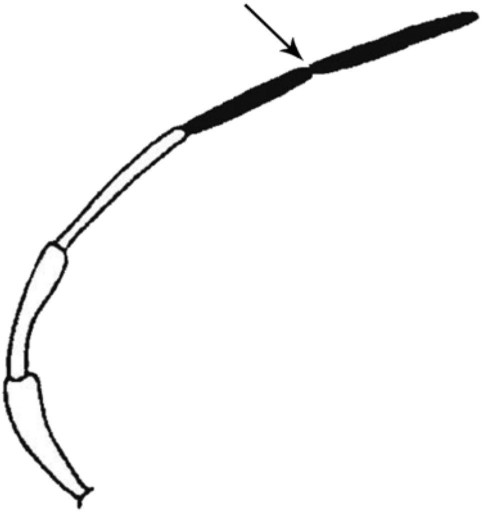


Fig. 6.12 Antenna of *Hebrus* (Hebridae) showing the superficial constriction present on the fourth article (Modified from Mazzucconi et al. 2009)

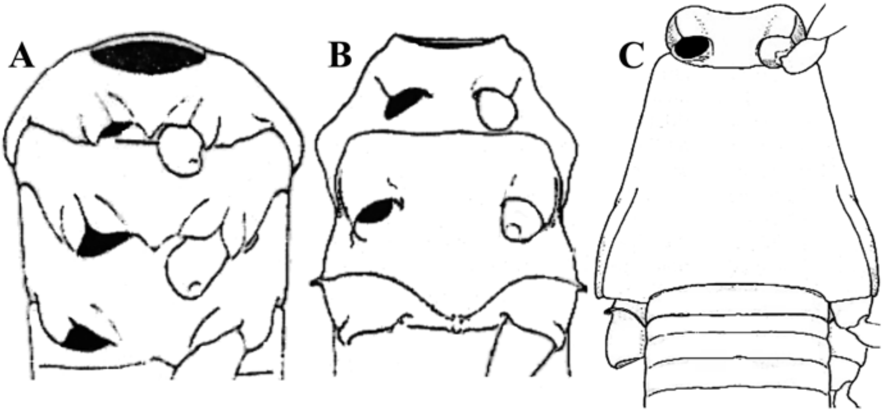


Fig. 6.13 Insertion of the coxae on different Gerromorpha. (**a**) *Mesovelia* (Mesoveliidae). (**b**) *Rhagovelia* (Veliidae). (**c**) *Charmatometra* (Gerridae) (Modified from Andersen 1982)

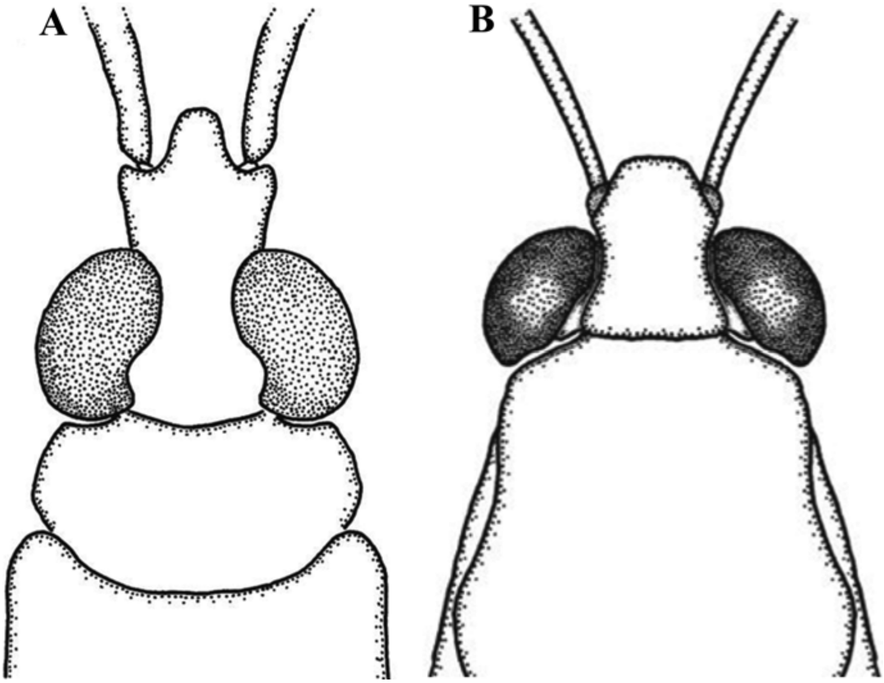
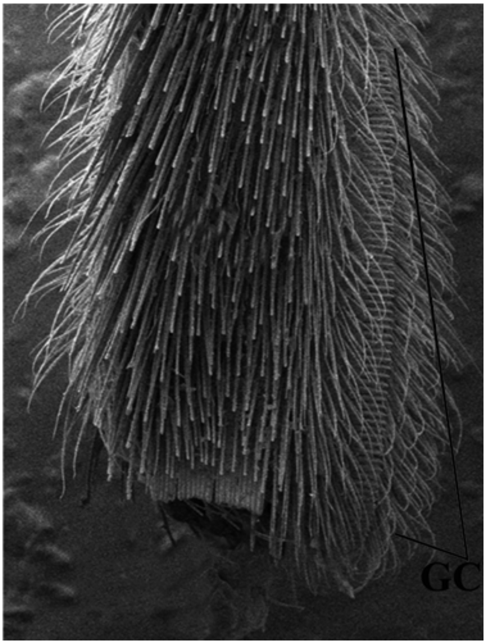


Fig. 6.14 Different eye shapes on Gerridae. (**a**) *Cylindrostethus*. (**b**) *Brachymetra* (Modified from Moreira et al. 2011a)

Fig. 6.15 Detail of the tibial grasping comb of *Velia*, a structure present on many males of the family Veliidae (*GC* grasping comb; modified from Cianferoni and Santini 2013)



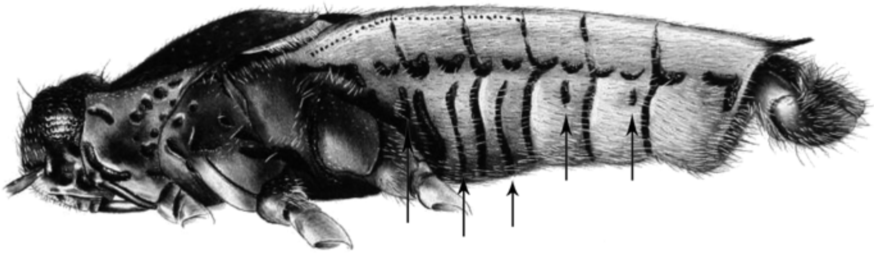


Fig. 6.16 *Stridulivelia* (Veliidae), lateral view of body showing grooves of abdominal sternites (Modified from Drake and Menke 1962). The number of grooved sternites varies from species to species

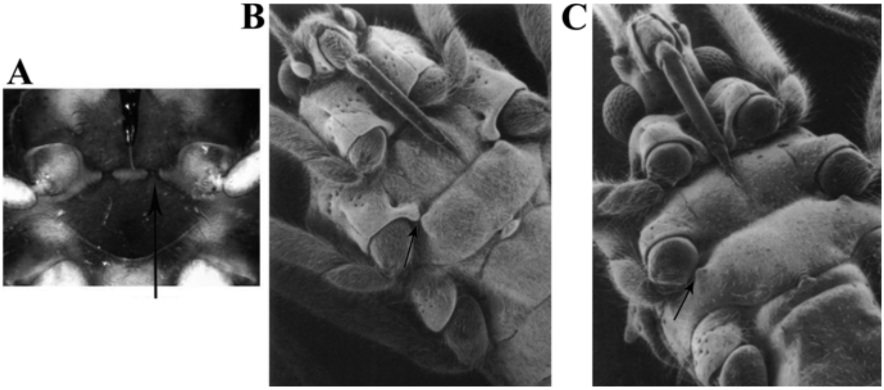


Fig. 6.17 Distribution of thoracic tubercles on different genera of Neotropical Veliinae (Veliidae). (**a**) *Paravelia*. (**b**) *Platyvelia*. (**c**) *Steinovelia* (Modified from: **a** – Moreira and Barbosa 2012; **b**, **c** – Polhemus and Polhemus 1993)

6.5 Concluding Remarks

On the last three decades, the Neotropical Gerromorpha have been target to many faunistical and taxonomic studies, and several species are being described as new or recorded from previously unknown localities. This effort serves as base for phylogenetic and biogeographical studies to be developed in the future, which will contribute to the understanding of the evolution and distributional patterns of the semiaquatic bugs.

Despite of that fact, there is still much to be researched concerning the Neotropical gerromorphans, and more than a hundred undescribed species from the region are known to exist (Polhemus and Polhemus 2008). The same authors pointed the Guiana Shield and the eastern slopes of the Andes as areas of high diversity and endemicity of gerromorphans and considered a very large area of the Atlantic coastal rainforests of Brazil extending from Rio de Janeiro north to the mouth of the

Amazon as "black holes" (under-collected areas) for the aquatic and semiaquatic bugs.

Finally, the formation on Neotropical countries of specialists in all fields of research with interest on the semiaquatic bugs is fundamental for the development of biological, ecological, and systematic studies regarding the group, which are currently extremely scarce when compared with those published concerning Nearctic and Palearctic species.

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Part IV
Infraorder Nepomorpha

Chapter 7
The True Water Bugs (Nepomorpha)

Julianna F. Barbosa and Higor D.D. Rodrigues

Abstract The infraorder Nepomorpha is one of the most specialized groups of heteropterans, with most of its species spending the entire life cycle within the water. True water bugs include ten families, 52 genera, and approximately 730 species in the Neotropical region, which shelters about 30 % of the global diversity of the group. Despite this fact, little is known about their biology, ecology, and geographical distribution in the Neotropics. Several genera need to be revised and many species remain with outdated descriptions. The systematics of the infraorder, although has received little attention in recent years, remains with various unresolved questions, and no phylogenetic study was conducted for any endemic group of this region.

7.1 Introduction

The most traditional classification of the Heteroptera was proposed by Latreille (1810), who used the Linnaean term Hemiptera to refer to the Rhyngota group of Fabricius (1803). In Latreille's classification, heteropterans were divided in two groups based on the lifestyle, namely, Hydrocorisae (currently Nepomorpha) for aquatic species and Geocorisae for terrestrial species. Subsequently, Dufour (1833) divided Geocorisae, recognizing a third group named Amphibicorisae, referring to the semiaquatic species living on the water surface (currently Gerromorpha). This classification, although based on behavioral characters, is highly typological and does not reflect their evolutionary history (Andersen 1979, 1982; Schuh and Slater 1995).

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Fieber (1861) introduces Gymnocerata (= Geocorisae) and Cryptocerata (= Hydrocorisae), names created in reference to the length of the antennae and used until recently in the literature (e.g., Mahner 1993). Leston et al. (1954) introduced the suffix "morpha" in their classification, proposing the infraorders Cimicomorpha and Pentatomomorpha. Popov (1968) suggested for the first time the name Nepomorpha for the aquatic bugs, and since then the suffix has been used for naming heteropteran infraorders (Štys and Kerzhner 1975). However, Mahner (1993) regarded Nepomorpha as an ambiguous name and advocated the usage of the old name Cryptocerata. In his review of Mahner's work, Andersen (1995) promoted the disuse of the old name to maintain the nomenclatural stability of infraordinal names.

Nepomorpha comprises more than 2,400 valid species distributed in all biogeographical regions, except Antarctica (Polhemus and Polhemus 2008a). This is a group of specialized true bugs, adapted to aquatic habitats, with species living in lentic environments, such as small pools and lakes, and lotic environments, ranging from small streams to large rivers. Species belonging to families Ochteridae and Gelastocoridae display riparian habits, occupying the margins of aquatic ecosystems, although they are commonly collected at considerable distances from water (Nieser and Melo 1997). Besides living in different aquatic habitats, many species are able to colonize degraded environments, which make this group of insects viable for biomonitoring programs of water quality. A few species are able to colonize saline (Naucoridae) or acidified waters (Corixidae) (e.g., La Rivers 1951; Henrikson and Oscarson 1981). Species of Corixidae and Notonectidae are the main colonizers of temporary waters, due to their good dispersion ability and adaptations to water level fluctuations (Williams 2006).

7.2 General Characteristics and Diagnosis

Aquatic heteropterans have a high morphological diversity, with body shape ranging from ovate and flattened dorsoventrally to globular and rounded, convex on the dorsal surface and straight ventrally, elongated, or elongate ovoid. Most species show a uniform brown color, varying from yellow to black. However, species with distinctly colored body, featuring different patterns of spots, are also common. Besides the variation of forms and colors, aquatic heteropterans are widely diverse in total body length, with some species measuring a little more than 1 mm (Pleoidea), whereas others are more than 100 mm long (Belostomatidae) (Schuh and Slater 1995).

In general, nepomorphans are mainly characterized by the reduced antennae, usually hidden under the compound eyes; the unique exception is the Oriental genus *Fischerotrephes* Zettel, 1994 (Helotrephidae), in which brachypterous specimens do not have antennae (Zettel et al. 2011). Antennae vary in number of segments (1–4) and are filiform, thickened, or flattened and may or may not have lateral projections. Compound eyes are well developed, occupying a large part of the dorsolateral margins of the head. In Ochteroidea, it has an internal emargination on the dorsal surface. Ocelli are absent in most groups, except in Ochteroidea and the subfamily Diaprepocorinae (Corixidae). Cephalic trichobothria are always absent (Popov 1971). The rostrum has three or four segments, generally being small and robust, except in Ochteridae, Aphelocheiridae, and some genera of Helotrephidae, where it can reach the middle coxae. Corixidae have unsegmented rostrum, usually triangular, tapering apically, with transverse sutures.

The pronotum is long, covering the meso- and metanotum. Scutellum is always exposed, but not reaching the middle length of the forewings. In some subfamilies of Corixidae, the pronotum almost entirely covers the scutellum. Forewings of various groups, traditionally named hemelytra, are divided into an anterior coriaceus part (clavus, corium, embolium) and a membranous posterior part. However, hemelytra are not shared by all families – species of Pleidae and Helotrephidae have forewings similar to elytra, entirely leathery in both brachypterous and macropterous forms (Bachmann and López-Ruf 1994).

Wing polymorphism occurs in several families of Heteroptera, usually being associated with dispersion, which can be a consequence of habitat instability, increasing population density (Muraji and Nakasuji 1988), hormonal changes (Southwood 1961), or photoperiod (Vepsäläinen 1971, 1974). According to Schuh and Slater (1995), nepomorphans generally have the following five types of wings: staphylinoid (covering less than half of the abdomen, usually ending at abdominal segment III; clavus and corium not delimited; with vestigial embolium or not; posterior margin of the wing truncated; hind wings may be absent or reduced), brachypterous (usually not covering abdominal tergites VI–VII; clavus and corium fused or not, generally with at most a fine suture present; embolium generally present and well defined; hind wings usually reduced), coleopteroid (usually covering the whole abdomen; clavus and corium elongated, generally fused; embolium developed or not; membrane reduced or inconspicuous, providing a uniform appearance to wing, similar to a coleopteran elytra), submacropterous (exposing only a small part of the posterior abdominal tergites, generally by reduction of part of the membrane; clavus, corium, embolium, and membrane present; hind wings reduced or developed), and macropterous (clavus, corium, embolium, and membrane developed; hind wings fully developed). Usually only the macropterous form has flight muscles developed (Schuh and Slater 1995). Despite the existence of these designations for wing types in Heteroptera, researchers working with aquatic heteropterans often use only the terms brachypterous and macropterous, with all other designations being included in brachyptery. However, staphylinoid and brachypterous individuals with at least three exposed abdominal tergites are rare, only occurring in Aphelocheiridae, and Naucoridae genera *Cryphocricos* Signoret and *Limnocoris* Stål. Intraspecific polymorphism is important in the taxonomy of these species, because some morphological characters are directly related to the polymorphic state (Polhemus and Polhemus 2008b). In some species of *Limnocoris*, the shape of the posterolateral angle of the pronotum and embolium varies considerably between brachypterous and macropterous individuals. Therefore, the correct identification of certain species can be hindered when this polymorphism is not well documented.

Forelegs of Nepomorpha are generally modified and may be raptorial (e.g., Belostomatidae, Gelastocoridae, Nepidae, Naucoridae) with forefemora enlarged and usually grooved at inner surface for reception of tibiae or scoop shaped with the foretarsi unsegmented and margined by a fringe of long setae (Corixidae). In some genera, foretarsi are fused with tibiae and claws may be reduced or absent. In others, such as Ochteridae and Pleidae, all legs are apparently cursorial. Hind legs are generally fringed with golden setae and in some groups can be slightly flattened, which helps in swimming. Tarsal formula varies among families and genera, being, for example, 1-1-1 (all Nepidae), 1-2-2 (all Potamocoridae), 2-2-3 (all Ochteridae), or 3-3-3 (some Pleidae). Dorsal and ventral arolia are usually present in adults and nymphs (Schuh and Slater 1995).

Some groups may have ventromedian carinae on thoracic sterna (e.g., *Belostoma* Latreille), on abdominal sternites (e.g., Notonectidae), or on the thorax and abdomen [e.g., Helotrephidae and *Limnocoris* (Naucoridae)]. Sexual dimorphism is observed in some families, especially regarding the relative length, presence of stridulatory structures, different tarsal formula, and symmetry of abdominal sternites. Abdominal tergite VIII is modified as a pair of siphons in Belostomatidae (retractable) and Nepidae (nonretractable). Male genital segments vary from symmetrical (e.g., Belostomatidae, Nepidae, Potamocoridae) to asymmetrical (e.g., Corixidae, Gelastocoridae, most Naucoridae and Notonectidae), including modifications such as 90° rotation of the genital capsule in Helotrephidae (Nieser and Chen 2002), Corixidae, Gelastocoridae and Ochteridae. Female ovipositor is generally not developed. However, it can be relatively well developed and possess robust spines in some groups, such as the Pleidae.

7.3 General Biology and Ecology

As stated above, wing polymorphism is very frequent in most families, with micropterous, brachypterous, staphylinoid, coleopteroid, submacropterous, and macropterous individuals. Wing reduction in the Nepomorpha was long thought not to exist except where there was an adaptation for underwater respiration (Schuh and Slater 1995). According to Popham (1960), once a plastron had been acquired, the need for gas store replenishment and for the hemelytra to collect air from the surface no longer exists. The loss of wings, flight muscles, and reduction of the median thoracic tracheal trunks can be explained as adaptations to permanent submergence in fast-flowing streams or rivers. Schuh and Slater (1995) argue that the reduction of the wings in the Nepomorpha is not necessarily related to adaptations to underwater respiration, because some species that use oxygen from the atmosphere (some Nepidae) also have reduced hind wings.

Little is known about the mechanisms responsible for generating forms that are unable to fly, and the only feature that seems to be common to most of these species is the stability of the habitat. Brown (1951) made this connection in Corixidae, observing that those species normally found on temporary habitats migrate a lot, while those found in permanent habitats do it less frequently. According to him, those species of Corixidae whose migration rate was restricted by brachypterism were also confined to permanent habitats.

For most individuals, wings perform an important role on respiration. Therefore, the full absence of wings is not observed on Nepomorpha, although their strong reduction is present. On first instars, respiration is cutaneous, and the wings and pterothorax having participation on respiration from the third instar on (Popham 1960). The main air supply of adult aquatic bugs is atmospheric, with replenishment of air stores. The secondary source is the oxygen dissolved in the water, which the insects obtain by means of the "physical gill" effect of their air stores (Parsons 1970). On fast-flowing streams or rivers, surface replenishment of these stores is not possible. Individuals living on this kind of habitats acquired a more specialized type of respiration through the plastron – a "gas store" communicating with the tracheal system and usually in the form of a thin film of constant volume and large surface area, retained by hydrofuge hairs, and therefore not liable to loss by diffusion (Thorpe 1950). On Neotropical bugs, this system can be observed in Neotrephinae (Helotrephidae), Cryphocricinae, and Laccocorinae (Naucoridae) (Parsons and Hewson 1974; Hinton 1976).

In Nepidae, the water scorpions, all air stores are normally concealed from the water (Parsons 1972), and there is a closure of the abdominal spiracles, associated with loss of the ventral gas stores and physical gill respiration (Popham 1960). In most representatives of Naucoridae and other families of aquatic bugs, air stores act as physical gills, with loss of air by diffusion and necessity of replenishment at the water surface. In Corixidae, Naucoridae, and Pleidae, secretion from scent glands is used on a grooming behavior related to prevention of contamination by microorganisms on ventral hydrofuge hairs (Kovac and Maschwitz 1989, 1991). Such contamination would lead to the wetting of the respiratory region, resulting in the loss of the ventral air bubble and drowning of the insects (Kovac and Maschwitz 1991). These glands are absent in Belostomatinae (Belostomatidae) (Staddon 1971), Anisopinae (Notonectidae) (Staddon and Thorne 1974), Nepidae and Nerthrinae (Gelastocoridae) (Staddon and Thorne 1979). Other common behavioral traits found among certain water bugs include grooming and cleaning of mouthparts and legs, especially after feeding, and production of unpleasant odors from the well-developed scent glands, the latter most probably as a defense mechanism (McCafferty 1981).

Aquatic bugs are observed in a great variety of habitats, including acidified lakes, saline ponds, and hot springs (Henrikson and Oscarson 1985; Papáček and Kovac 2001). Ochteridae and Gelastocoridae comprise riparian saltatorial bugs. Ochterids, the velvety shore bugs, are terricolous or littoral that live along the shores of ponds or streams, but they also run on aquatic plants (Papáček 2001). Two Neotropical species of *Ochterus* Latreille occur in salt marshes: *O. aeneifrons* (Champion) and *O. perbosci* (Guérin-Méneville) (Polhemus 1976). Commonly called toad bugs, individuals of Gelastocoridae can be observed jumping on margins of aquatic habitats, remaining motionless when disturbed. With pruinose surface, individuals of *Gelastocoris* Kirkaldy are perfectly camouflaged with sand grains, being also found on mud (Todd 1955). *Nerthra* Say, on the other hand, shows uniform color pattern and is more associated with leaf litter, sometimes being found far away from the margins of water bodies. They seem to spend much of their time burrowing in the soil, also being found on algae on rocky sea coasts, roots of orchids, leaf mold, and under debris of heaps of dry grass (Todd 1955, 1957, 1965). Estévez and López-Ruf (2006) and Estévez et al. (2010) observed adults and nymphs of *Nerthra ranina* (Herrich-Schäeffer) and *N. gaucha* Estévez & Schnack submersed and swimming underwater.

Corixids (water boatmen) are bottom dwellers. They are found in most stagnant or nearly stagnant aquatic habitats where there is a bottom of relatively fine soil particles (Macan 1938). Midlegs are used for clinging to the bottom or other substrate while feeding or resting (Lauck 1979). Belostomatidae (toe-biters or electric-light bugs) and Nepidae are constantly associated with vegetation, where they cling on with the tip of the abdomen in contact with the surface film (Hungerford 1919; Keffer 1996). In general, these bugs are observed in stagnant waters or small streams with slow current (Menke 1963; Keffer 1996). Until recently, no members of *Horvathinia* Montandon had been collected in the aquatic habitat. All of its species were described based on specimens attracted to the light. Schnack et al. (2006) examined two specimens collected in a shallow subtropical permanent pond. However, there is almost nothing published on their ecology or reproductive behavior (Estévez and Ribeiro 2011).

Limnocoris is a genus of benthic naucorids (creeping water bugs), while *Cryphocricos* has some species living under conditions of very strong current (Nieser and López-Ruf 2001). Specimens of *Ambrysus* Stål can be found on rocky streams with moderate to fast currents, clinging to the branches and stones on margins, and beneath leaves on bedrock streams (Usinger 1946; Nieser 1975; Rodrigues et al. 2012b). Very little is known about the life history and habitats of Potamocoridae. Most specimens have apparently been collected at lights (Schuh and Slater 1995), although on Macaé River (southeastern Brazil) individuals of this family were collected mainly on sandy and gravel bottom. In Costa Rica, *Potamocoris* Hungerford specimens were collected in environments with a certain level of contamination in a region of agricultural activity (Herrera and Springer 2012).

Notonectidae, Helotrephidae, and Pleidae are pleuston inhabitants, swimming on their backs and propelling the body with the hind legs. Helotrephids, or beetle backswimmers, have been found on holes in the rocky bottom, filled with soil and covered with a thin layer of mud (China 1936), and in large or small, stable or temporary, quiet, and running waters, rock pools, waterfalls, seeping rocks, hot springs, water tanks, and outdoor ceramic bowls (Papáček 2001). Pleids, or pygmy backswimmers, are found swimming actively both in normal and upside position, on clear or turbid waters (Bachmann 1968, 1998). These bugs live in tangles of dense aquatic vegetation which they use for grasping and maintaining their position on the water column of stagnant ponds, swamps, bogs, sluggish drainage ditches, secluded coves in lakes, and the more sluggish parts of slowly moving streams (Drake and Chapman 1953; Gittelman 1974). Notonectids, or backswimmers, live in both lotic and lentic waters, staying in the water column most of the time and being able to maintain their position without clinging on the vegetation. In *Buenoa* Kirkaldy this hability is related to the presence of hemoglobin (Miller 1964). Representatives of *Martarega* White have been observed jumping over the water surface when disturbed.

7.3.1 Eggs and Oviposition

The oviposition of this group of insects is very diverse, with females that deposit their eggs individually or grouped, submerged or slightly submerged above the water surface, or even distant from the water. Eggs may be deposited in different ways: in a horizontal position on the substrate, perpendicular to the substrate (exophytic oviposition), or inserted in the substrate, which are usually plant tissues (endophytic oviposition) or sediment present at the bottom of aquatic ecosystems (Mazzucconi et al. 2009).

Nepids can deposit their eggs glued to plants or algae masses, where part of the egg is submerged, and respiratory horns remain projected above the water surface. Some species of *Ranatra* F. can also deposit eggs far below the water surface (Hinton 1981). In some genera of Belostomatidae, more specifically the subfamily Belostomatinae, females lay eggs on the hemelytra of males, which carry them until the moment of eclosion (Hungerford 1925). On the other hand, females of Lethocerinae lay their eggs on substrates (rocks, logs, plants) that are slightly above the surface of water, leaving the tasks of moisturizing and protection from predators to the males (Ichikawa 1988).

In Corixidae, eggs are generally glued to substrates below the water surface and may or may not be attached by an elongated stalk. The females of Naucoridae also glue eggs on plants and rocky substrates, although endophytic oviposition is known for the Palearctic species *Ilyocoris cimicoides* (L.) (Cobben 1968). A series of articles describing American naucorid eggs has been published, and López-Ruf (1989) found that the disposition of aeropylar system is a taxonomic character at the genus level. In addition, eggs have specific taxonomic characters, with the chorionic sculpturing differing interspecifically (Sites and Nichols 1999). The number of micropyles ranges between 2 and 3 in *Ambrysus*, *Limnocoris*, and *Pelocoris* Stål (Sites and Nichols 1999, 2001) and 3 and 5 in *Cryphocricos hungerfordi* Usinger (Sites and Nichols 1993).

Females of Ochteroidea oviposit out of water. Those of Ochteridae usually deposit their eggs in sandy environments, remains of plant material, or wet soil. As for gelastocorids, oviposition occurs in sandy places (mainly *Gelastocoris*), and eggs may be partly or completely buried, or in small holes in the mud under stones, sometimes distant from the banks of water (mainly *Nerthra*) (Hinton 1981). Hungerford (1922) reared *Gelastocoris oculatus* (F.) in laboratory and observed that the number of eggs laid by a female may vary from 1 to 13. Brown and McPherson (1994) also reared the same species in laboratory and observed that females deposited their eggs singly or in groups of two or three, on the substrate or glued to gravel. Females of Notonectidae usually oviposit in plant tissues, individually or in rows; in *Notonecta* L. eggs can be deposited exposed on the surface of rocks or plants (Hinton 1981). In Pleoidea, oviposition is also endophytic, although Cobben (1968) suggested an entirely exposed deposition in some genera of Helotrephidae due to egg shape.

7.3.2 Nymph Feeding and Development

Nepomorphans are paurometabolous insects, in which nymphs develop gradually until they reach the adult stage, with the same lifestyle on both stages. There are generally five nymphal instars, although a few species have only four. Nymphs are predaceous and similar to adults in color and body shape, differing by the smaller size, absence of wings, and non-developed genitalia. Immatures seem to live in shallower sites and in general have more gregarious habits than adults. Usually in tropics and/or subtropics, species or populations can be multivoltine, with three or more generations annually (Saulich and Musolin 2007).

Little is known about the life history of Neotropical species of Nepomorpha. Most of the research and rearing was developed upon North American species, some of them occurring from Canada to Mexico. The development of these species is univoltine, typical of temperate regions. Hungerford (1922) wrote about the development of *Gelastocoris oculatus*, and as stated by Kevan (1942) for *Nerthra nepaeformis* (F.) from Trinidad, nymphs of both species rest upon the sand for molting. Under laboratory conditions, Brown and McPherson (1994) fed nymphs of *G. oculatus* with *Tenebrio molitor* L. and *Drosophila melanogaster* Meigen.

Nymphs of *Ochterus banksi* Barber (another North American species) construct small individual cells in the moist sand in which they molt. Nymphal stages move slower than adults and carry sand grains on their bodies, presumably for the purpose of concealment (Bobb 1951).

Konopko (2010, 2012, 2013), Konopko and Mazzucconi (2011), Konopko and Melo (2009), and Konopko et al. (2010, 2011) provided a series of descriptions of nymphs of the Corixidae from Argentina: *Ectemnostega montana* (Lundblad), *E. quechua* (Bachmann), *E. stridulata* (Hungerford), *Sigara schadei* (Hungerford), *S. denseconscripta* (Breddin), *Tenagobia incerta* Lundblad, *T. schadei* Lundblad, and *Trichocorixa mendozana* Jaczewski. Detritus, algae, cladocerans, and larvae of Chironomidae were supplied as food, the nymphs being fed solely with algae. López-Ruf and Bachmann (1994) and Estévez et al. (2010) described the nymphal instars of *Neoplea absona* Drake & Chapman, *N. maculosa* (Berg) (Pleidae), and *Nerthra gaucha* Estévez & Schnack (Gelastocoridae).

Descriptions of the immature stages were conducted for some Naucoridae species. Life cycle, including voltinism, eggs, and all immature stages of three species from the northernmost Neotropics were described: *Ambrysus l. lunatus* Usinger (Sites and Nichols 1990), *Cryphocricos hungerfordi* Usinger (Sites and Nichols 1993), and *Limnocoris lutzi* La Rivers (Sites and Nichols 2001). Regarding the fauna of Central and South America, Sites (1991) described eggs and nymphs of *Pelocoris poeyi* (Guérin-Méneville), nymphs of 3–5 instars of *Limnocoris ovatulus* Montandon (López-Ruf 1993), 3–5 instars of *Placomerus micans* La Rivers (López-Ruf 1996), 3–5 instars of *Ctenipocoris schadei* (De Carlo) (López-Ruf 2004), and 1, 3–5 instars of *Ambrysus attenuatus* Montandon (López-Ruf and Hernández 2007). For *Ambrysus lunatus* Usinger (Naucoridae), Sites and Nichols (1990) provided larvae of *Prosimulium* Roubaud. First instars of *Curicta scorpio*

Stål from Texas (a species that occurs up to Argentina) were fed in lab with *D. melanogaster* and the third instar with corixids or small notonectids (Keffer et al. 1994). Except for Sites and Nichols (1990, 1993, 2001), these works are usually taxonomic and lack data about life history.

The first nymphs of *Notonecta* and probably all of the Anisopinae feed to a large extent upon microcrustaceans in the water (Hungerford 1933). Pleidae feed as well on small crustaceans, probably *Cladocera* Latreille (Bachmann 1968).

Most of the features that allow distinguishing the genera of Nepomorpha are not complete developed on nymphs, with sexual and alar characteristics being absent. In Notonectidae, it is possible to identify the different genera based on the labrum, pronotum, and anteapical spur. In Belostomatidae, the number of tarsomeres and claws on the anterior leg and shape of the posterior femora and abdomen are reliable for genera identification. The shape of the pronotum and anterior legs are useful for distinguish genera of Gelastocoridae. This differentiation is not so simple for Corixidae. The pronotum of the nymphs are not developed, and the pala and tibia of the front legs still have a single segment (Hungerford 1948).

7.3.3 Adult Feeding and Reproduction

Except Corixidae, all aquatic Heteroptera are strictly predaceous. Anterior legs of Corixidae are used for collecting food, with the tarsi highly specialized for this purpose (Popham 1961). Its customary food consists of the matter found in deposits on the bottom of the pool and upon the dead leaves that have lodged in its shallow waters. It can include organic matter; diatoms; desmids; oscillatoria; sometimes threads of live (more often dead) filaments of *Zygnema* Agardh, Euglena, *Paramecium* Müller, and *Chlamydomonas* Ehrenberg; spores of various algae; unicellular plants; and animals (Hungerford 1917). There are, indeed, some species of Corixidae in which the palae are not flattened and spoon shaped and which may be predaceous (Hungerford 1948).

In general, nepomorphans feed on crustaceans, dipteran larvae, and other insects, sometimes even on small vertebrates, such as fishes and tadpoles. Belostomatidae, Gelastocoridae, Naucoridae, Nepidae, and Potamocoridae have raptorial forelegs, with enlarged femora and cylindrical tibiae. *Lethocerus* Mayr has frequently been observed feeding on animals many times larger than themselves: fishes, frogs, salamanders, and freshwater snakes (Menke 1963). In the laboratory, adults of *Lethocerus* killed and digested a large *Hydrophilus* Geoffrey and those of *Belostoma malkini* Lauck, the freshwater shrimp *Palaemonetes* Heller, the large tree frog *Hypsiboas crepitans* (Wied-Neuwied), and the fishes *Poecilia* Bloch & Schneider and *Rivulus* Poey (Cullen 1969). Individuals of *Ranatra* wait for their prey hiding between aquatic plants in a more vertical position, with the head directed downward (Nieser 1975). In Gelastocoridae, prey consist of small insects, especially the larvae of those with which they live in association (Todd 1955).

In Notonectidae, Pleidae, and Ochteridae, the forelegs are not modified, although important on predation. Specimens of *Buenoa* feed largely upon small crustaceans and mosquito larvae, which they hold in the crib formed by the bristles arming the forelegs (Truxal 1953). Pleids can feed on small crustaceans, small larvae of aquatic insects, annelids, and animals that fall onto the water surface, such as Collembola and small Diptera (Papáček 2001). The hind legs of *Neoplea striola* (Fieber) are sometimes used for crawling and prey handling, while other backswimmers use these legs strictly for swimming (Gittelman 1977).

Cannibalism is often observed in *Notonecta* and can occur regularly even under normal conditions, although it is more frequent among starved individuals (Zalom 1978) preying upon young nymphs (Fox 1975). There are also records of cannibalism in Pleidae (Papáček 2001), between nymphs of *Abedus* Stål (Belostomatidae), if their prey are not abundant (Hungerford 1919), and in *Ambrysus occidentalis* La Rivers, as a result of intraspecific aggression (Constantz 1974). Hungerford (1922, 1923) observed females of *Gelastocoris oculatus* feeding upon their own offspring and cannibalistic behavior in the first instar of *Cymatia* Flor (Holarctic/Oriental genera of Corixidae).

Nepomorphans generally mate in the water, whereas surface and shore bugs mate in their respective habitats (McCafferty 1981). Stridulation is quite common in these bugs, with an important role on mating. In *Buenoa*, the courting maneuver includes male stridulation, with a chirping sound by rubbing the front legs against the base of the rostrum as they approach the females (Hungerford 1933). Stridulation through anterior femoral ridges and anterior coxal pegs is also known in some species (Wilcox 1975). Male backswimmers stay below the female when mating, with the genital segments reaching around the right side of the female and the front and middle legs employed in the mating clasp (Hungerford 1924). A stridulatory mechanism was cited by Polhemus (1994) for males and females of an undescribed species of *Martarega* – denticles on costal margin of hemelytra/basal ridge on hind femur. Denticles on hemelytral costal margin are observed in females of *M. hungerfordi* Truxal; *M. nieseri* Barbosa, Ribeiro, & Nessimian; *M. oriximinaensis* Barbosa, Ribeiro, & Ferreira-Keppler; and *M. siolii* Barbosa, Nessimian, & Takiya, with no ridges on hind femora.

Males of Corixidae have distinctly asymmetrical abdomen. On mating, male and female are held together thanks to conical pegs of male anterior legs. The male darts onto the back of the female, which he holds by pressing his head against her pronotum and using the distal pegs of the pala to attach under the curved longitudinal ridge of the lateral flange on the female hemelytra (Popham 1961). There was a general conception that the strigil in this family has a stridulatory function; however, Popham et al. (1984) demystified and stated that this structure is in fact responsible for maintaining the subelytral gas stores, while surfacing during mating. In the subfamily Micronectinae, stridulation is better known in *Micronecta* Kirkaldy, an Old World genus, although the same mechanism is observed in *Tenagobia* Bergroth, and *Monogobia* Nieser & Chen with ridges present on abdominal segment 8 (genital capsule; right lobe in *Tenagobia*) or basally on the right paramere (Jansson 1989;

Jansson and Meyer-Rochow 1990; Nieser and Chen 2006). In Corixinae, anterior legs along with the head are involved in stridulation (Aiken 1985).

As in male corixids, the abdomen of male gelastocorids and ochterids is asymmetrical. The male mounts the female, grasping her with the middle pair of legs, the first pair flexed beneath him, and the abdomen somewhat to the left side, due to the asymmetrical structure of the male genitalia (Hungerford 1922; Polhemus 1976). Stridulation is known only in males of *Nerthra*, being generated by ridges on abdomen and proctiger (Polhemus and Lindskog 1994). Males of *Pelocoris femoratus* (Palisot) (Naucoridae) are said to also mounting females, with forelegs grasping the prothorax/mesothorax junction (Brewer and Sites 1994). In this family, stridulation is known in *Limnocoris*, produced by ridges on the abdominal sternites (at least on 2 and 3) and distal part of the hind femur (Aiken 1985; Polhemus 1994; Polhemus and Lindskog 1994).

Males of *Curicta* Stål (Nepidae), in their turn, approach a female, usually from her side, and grasp her with his three adjacent legs. The male twists the distal half of his abdomen ventrally under the female, which considerably deforms the male's abdomen and places his last abdominal tergum obliquely underneath the female's genital operculum (Keffer and McPherson 1993). In *Ranatra* (Nepidae), the male stridulation is produced by rubbing the coxae and femora of the forelegs (Torre Bueno 1905b).

Although sound production has been recorded in Belostomatidae, no stridulatory mechanism was described (Aiken 1985). This family is famous for its parental care. Belostomatinae are back-brooders: females lay eggs on the backs of the males, where they remain until the hatching of larvae. Male brood care is obligatory in the Neotropical belostomatine species of *Abedus* and *Belostoma* (Estévez and Ribeiro 2011). This behavior involves added risks, reduces predatory efficiency, and precludes additional mating for brooding males (Smith 1976, 1979).

Mating on Neotropical representatives of Helotrephidae and Pleidae is poorly known, and there are no records of stridulation in these families.

7.4 Classification and Diversity

Historically, the first studies made in an attempt to systematically classify the Nepomorpha began with Esaki and China (1927) and China (1933). In these classifications, they considered the Corixidae as the most basal group of the lineage. China (1955) proposed that the greater the specialization for aquatic environment, the greater the derivation on a scale of evolutionary time. This led him to consider Ochteroidea as the most basal family of water bugs, being a generalized group. Subsequently, Popov (1971), in his extensive study based on extant and fossil species, proposed that the Nepomorpha have arisen from a lineage of proto-heteropterans, whose nearest ancestor would be the proto-ochterids. In turn, this last lineage gave rise to three major groups in the mid-Triassic period: Nepoidea, Corixoidea, and Ochteroidea (which initially also included Naucoroidea, Notonectidae, and

Pleoidea). In his classification, for the first time, Nepoidea was considered as the basal group of Nepomorpha, followed by Corixidae, Ochteroidea, Naucoroidea, Notonectidae, and Pleoidea.

Rieger (1976) proposed his classification based on morphological characters, also recognizing Nepoidea as the basal group, followed by Ochteroidea, Corixidae, Naucoroidea, Aphelocheiridae, Notonectidae, and Pleoidea, the last six groups forming a monophyletic group based mainly on the clypeus and food pump structures. In addition, Naucoroidea was recovered as the sister group to Aphelocheiridae + Notonectoidea (Notonectidae and Pleidae + Helotrephidae). Later, Mahner (1993) presented one of the most comprehensive phylogenetic frameworks for the group so far, which was based on morphological characters (although not using a formal phylogenetic analysis). He also considered Nepoidea as the basal group, and unlike Rieger (1976), Corixidae was considered more closely related to Ochteroidea. However, the main critical to Mahner's work is the controversial use of the rules of classification and nomenclature. He created several suprageneric names, such as Tripartita and Cibariopectinata, characterized respectively by a tripartite food pump and possession of so-called cibariopectines in the food pump. In addition, he resurrected the old names Cryptocerata and Gymnocerata, justifying the hypothesis that aquatic true bugs are a sister group to the rest of the heteropterans.

Hebsgaard et al. (2004) proposed a classification using mostly the morphological characters of Rieger (1976) and Mahner (1993), in addition to molecular data (mitochondrial gene 16S and nuclear gene 28S), which were analyzed both separately and in a combined analysis. The final hypothesis was obtained by combined molecular and morphological data analysis, which supported the monophyly of all nepomorphan superfamilies and families, except Naucoroidea, that showed to be paraphyletic. The data strongly supported the relationship of Potamocoridae and Aphelocheiridae, and thus, the authors created the superfamily Aphelocheiroidea to allocate these two families; Naucoroidea was left with only the family Naucoridae.

Since then, Nepomorpha has always been considered a monophyletic group. The main synapomorphies of the infraorder, according to Mahner (1993), are (1) presence of three pairs of tympanal organs in the two pterothoracic and first abdominal segments, (2) particular structure of the midgut epithelium and ileum, (3) the spiral katatrepsis of the embryos, and (4) the presence of spiracular sieve plates and structure of the mesepimeron. However, more recently, Hua et al. (2009), based on an analysis of mitochondrial genomes from nine nepomorphan families, proposed a different hypothesis of relationship to this group of insects, with Nepomorpha being a paraphyletic group. The superfamily Pleoidea was elevated to the infraordinal level and considered the sister group of the Nepomorpha that consists Corixoidea + ((Naucoroidea + Notonectidae) + (Ochteroidea + Nepoidea)). They also recognized the old superfamily Naucoroidea (Aphelocheiridae + Naucoridae) as monophyletic, grouping Aphelocheiroidea *sensu* Hebsgaard et al. (2004) again within Naucoroidea. As Weirauch and Schuh (2011) mentioned, this great change in the systematics of the true water bugs still seems premature, because of the few taxa examined and the lack of a combined analysis using morphological characters.

Analyzing only morphological characters of the mouthparts, Brożek (2013) conclusions concur with Popov (1971), Mahner (1993), and Hebsgaard et al. (2004), in the placement of Nepoidea and Corixoidea as a sister group with respect to the remaining nepomorphan families, but differ in the placement of the Potamocoridae. This family is recognized as a sister group to Naucoridae, and they together form the superfamily Naucoroidea, with Aphelocheiroidea including only Aphelocheiridae. Li et al. (2014) reanalyzed the mitochondrial genomes of Hua et al. (2009) with new sampling strategies. Their analysis also recovered Corixoidea as a basal group, although it supports Nepomorpha as monophyletic and the close relationship between Notonectoidea and Pleoidea.

There are more than 2,400 species of Nepomorpha worldwide, divided into 11 families: Aphelocheiridae, Belostomatidae, Corixidae, Gelastocoridae, Helotrephidae, Naucoridae, Nepidae, Notonectidae, Ochteridae, Pleidae, and Potamocoridae (Štys and Jansson 1988). Polhemus and Polhemus (2008a) mentioned 732 species from the Neotropical region, divided into ten families and 52 genera. The only family that does not occur in the Neotropics is Aphelocheiridae, which is monotypic and recorded mainly from the Afrotropical, Oriental, and Australian regions, with a few species in the Palearctic. The genus *Aphelocheirus* Westwood has approximately 80 valid species (Zettel et al. 2008).

Currently, some authors consider Micronectinae and Diaprepocorinae as distinct families from Corixidae (Mahner 1993; Nieser 2002; Chen et al. 2005), with this family being restricted to Corixinae, Cymatiainae, Heterocorixinae, and Stenocorixinae. They are all treated as subfamilies of Corixidae here, since there are no robust studies to corroborate with the newly proposed classification. Corixinae is the most diverse subfamily, including ten of the 17 genera of Corixidae, about 60 % of them with less than ten species. The tribe Graptocorixini has two genera, both with Neotropical representatives: *Neocorixa* Hungerford, with two species, and *Graptocorixa* Hungerford with 12 species (Hungerford 1948; Jansson 1978). The other genera belong to the tribe Corixini, with *Centrocorisa* Lundblad (2), *Corisella* Lundblad (7), *Krizousacorixa* Hungerford (3), *Neosigara* Lundblad (7), *Orocorixa* (1),[1] *Ramphocorixa* Abbot (2), and *Trichocorixella* (1) being the least diverse (Hungerford 1948; Jansson 1979; Nieser and Padilla-Gil 1992; Nieser and Chen 2006; Tinerella and Polhemus 2006). The Neotropical genus *Ectemnostegella* Lundblad was downgraded by Bachmann (1979) to subgenus of *Ectemnostega* Enderlein and has currently 12 species; the New World *Trichocorixa* Kirkaldy and *Morphocorixa* Jaczewski have 13 species each (Hungerford 1948; Nieser 1969; Roback and Nieser 1980; Bachmann 1981; Jansson and Polhemus 1987). The cosmopolitan genus *Sigara* F. has some problems of delimitation, with great variation between species. At the moment, the genus includes 32 Neotropical species, held mainly in the subgenus *Tropocorixa* Hutchinson (Hungerford 1948; Bachmann 1961, 1979, 1981; Bernardo et al. 2012).

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[1] The recently described and still monotypic genus *Orocorixa* is very poorly known and feebly differentiated from *Neosigara*, being a little larger, with a smaller lower peg row on male pala.

Heterocorixinae includes solely the genus *Heterocorixa* White, which is exclusively Neotropical, and bears 20 species (Hungerford 1948; Jaczewski 1950; Nieser 1970). Micronectinae has three representatives in the Neotropical region: the monotypic *Monogobia* (Micronectini stat. nov.), with *M. elongata* Nieser & Chen, and *Synaptogobia* Nieser & Chen (Synaptogobiini stat. nov.), with two species, both known only from northern Brazil (Nieser & Chen 2006). The genus *Tenagobia* (Micronectini) has a widespread distribution on the Western Hemisphere, with 28 Neotropical species (Nieser 1977; Bachmann 1979; Polhemus and Nieser 1997; Nieser and Chen 2008).

Naucoridae is the second most diverse family of Nepomorpha in terms of Neotropical genera and the first in number of species (ca. 180) (Polhemus and Polhemus 2008a). The family is subdivided into five subfamilies, Cheirochelinae, Cryphocricinae, Laccocorinae, Limnocorinae, and Naucorinae (Štys and Jansson 1988), and only the first one does not occur in the Neotropics. Regarding the relationships among these subfamilies, only the study of Mahner (1993) was carried out so far. In this work, he proposed Laccocorinae as basal group and Limnocorinae as sister group of Cryphocricinae, considering both as monophyletic taxa. However, more studies are needed to corroborate or refute Mahner's hypothesis.

Cryphocricinae is endemic to the New World, with three tribes and five genera, all occurring in the Neotropical region. Cryphocricini has two genera: the widespread Neotropical *Cryphocricos*, with 13 species (De Carlo 1940; Usinger 1947; Bachmann 1998), and *Procryphocricos* Polhemus from Venezuela and Colombia, with four species (Polhemus 1991; Sites and Camacho 2014; Sites and Shepard 2015).

Ambrysini is currently composed of the genera *Ambrysus* and *Carvalhoiella* De Carlo. The former has 79 valid species, being most diverse of the family, distributed mainly in Mexico and southwestern USA; 29 species have been recorded from South America (La Rivers 1953a, b, 1958, 1962a, b; Polhemus and Polhemus 1983; Davis 1986; Bachmann 1998; Moreira et al. 2011; Rodrigues et al. 2012b; Sites and Shepard 2015). As for *Carvalhoiella*, it has only three species restricted to Brazil and Suriname (Nieser et al. 1999). Originally, this last genus was described in Ambrysinae but then moved to Naucorinae by Nieser (1975) due to the very close generic limits between it and *Pelocoris*. Later on, Nieser et al. (1999) moved it back to Ambrysinae (*sensu* Usinger 1941). Cataractocorini bears only the genus *Cataractocoris* Usinger, with three species ranging from south of Mexico to El Salvador (Sites 2004; Sites et al. 2013).

Although the subfamily Laccocorinae has been downgraded to tribe of Naucorinae by Popov (1970), the status of Montandon (1897) for this taxon was maintained in the literature, including a series of poorly diverse genera. *Decarloa* is monotypic, with *D. darlingtoni* La Rivers, known only from Haiti (Štys and Jansson 1988). *Interocoris* La Rivers, with only *I. mexicanus* (Usinger) endemic to Mexico, was originally described as a subgenus of *Heleocoris* Stål but then raised to genus by Polhemus and Polhemus (2008b). As for *Heleocoris*, all of its South American species were transferred to *Ctenipocoris* Montandon (Polhemus 1987; Polhemus and Polhemus 2008b), a genus that also occurs on Afrotropical and Oriental regions (Štys and Jansson 1988). The only exception is *Heleocoris plaumanni* De Carlo, which was not transferred to *Ctenipocoris* because Polhemus and Polhemus (2008b) could not examine material of this species. Moreover, they argued that according to De Carlo's (1968b) figure of the foreleg, this species is certainly very different from the other Neotropical *Ctenipocoris*. Despite that fact, some authors (e.g., López-Ruf 2004; Herrera 2013) consider this species as part of *Ctenipocoris*, which now has six species in the Neotropics, recorded from Central and South America.

Limnocorinae is currently monotypic, with only the valid genus *Limnocoris* being considered valid. The other three genera described within the subfamily (*Borborocoris* Stål, *Usingerina* La Rivers, and *Sattleriella* De Carlo) were regarded as groups of species with isolated modifications and synonymized (Nieser and López-Ruf 2001). *Limnocoris* is endemic to the New World and has a wide distribution throughout the Americas, occurring from the USA to Argentina. Most of its 73 valid species are South American, whereas only 16 have been recorded from Central America or southern USA (Nieser et al. 2013).

The subfamily Naucorinae is represented in the Neotropics by two genera. *Placomerus* was monotypic, with *P. micans* La Rivers, known from Argentina, Brazil, Bolivia, and Paraguay (Moreira et al. 2011). *Placomerus obscuratus* Sites & Camacho was recently described from Venezuela and Guyana. *Pelocoris*, on its turn, is a New World genus with 13 Neotropical species (Nieser 1969; Davis 1986; Manzano et al. 1995; Polhemus and Sites 1995).

Despite being treated as a subfamily of Naucoridae by Van Doesburg (1984), Potamocoridae was formally raised to family by Cobben (1978). It is monotypic and the sole family of Nepomorpha occurring exclusively on Neotropical region. The genus *Coleopterocoris* Hungerford was recently synonymized with *Potamocoris* by Polhemus and Carrie (2013). *Potamocoris* now includes 11 species from Belize, Costa Rica, Suriname, Brazil, Ecuador, Peru, Paraguay, and northwestern Argentina (Polhemus and Polhemus 1983; Longo et al. 2005; Mazzucconi et al. 2009; Moreira et al. 2011; Herrera and Springer 2012, 2014; Polhemus and Carrie 2013).

Belostomatidae currently comprises three subfamilies: Belostomatinae, Horvathiniinae, and Lethocerinae (Lauck and Menke 1961; Štys and Jansson 1988). Belostomatinae, the most diverse one, is represented in the Neotropics by three genera: *Abedus*, *Belostoma*, and *Weberiella* De Carlo. The first one is subject of continuous questionings, being cited by some authors as a subgenus of *Belostoma* (De Carlo 1968a; Schnack and Estévez 1990). If considered a genus, it includes 11 species from the Neotropical region, distributed along Central America and recently reported for Colombia (Menke 1960; Bogan et al. 2013; Romero and Noriega 2013). *Belostoma* is the most diverse genus, with 77 Neotropical species ranging from Mexico to Argentina (Lauck 1959; Lanzer de Souza 1980, 1992; Estévez and Polhemus 2001, 2007; Estévez and Armúa de Reyes 2003; Ribeiro and Alecrim 2008; Ribeiro and Estévez 2009). Finally, *Weberiella* is exclusively Neotropical, with *Weberiella rhomboides* (Menke), occurring in northern and central-western Brazil and French Guiana (Estévez and Ribeiro 2011).

Horvathiniinae, with only one genus, had all species synonymized with *Horvathinia pelocoroides* Montandon by Schnack and Estévez (2005), except for *H. lenti* De Carlo. The genus has records from Argentina, Bolivia, Brazil, and Paraguay (Estévez and Ribeiro 2011). Lethocerinae was recently reviewed by Perez-Goodwyn (2006). *Benacus* Stål, originally described as genus, was downgraded to a subgenus of *Lethocerus* by Lauck and Menke (1961). However, many authors continued treating it as a distinct genus (Brooks and Kelton 1967; Usinger 1968; Popov 1971), and it was formally reerected by Perez-Goodwyn (2006). It only includes one species, *B. griseus* (Say), that occurs on Mexico, Honduras, Cuba, Jamaica, and Colombia (Estévez and Ribeiro 2011). *Lethocerus* is a cosmopolitan genus, with 15 Neotropical species (Perez-Goodwyn 2006).

Nepidae is formed by two subfamilies: Nepinae and Ranatrinae. Nepinae is represented by two genera in the Neotropical region. *Curicta* is a New World genus with 22 species recorded from the Neotropical region (Keffer 1996). *Telmatotrephes* Stål occurs in the Neotropical and Oriental regions, with four species on the former (Lansbury 1972). Ranatrinae is represented by the cosmopolitan genus *Ranatra*, with 63 Neotropical species (Kuitert 1949; De Carlo 1972; Lansbury 1974; Roback and Nieser 1974; Nieser 1975; Menke 1979; Bachmann 1998; Nieser and Burmeister 1998; Naranjo et al. 2010; Moreira et al. 2011).

Notonectidae is represented in the Neotropics by its two subfamilies, with about a hundred species (Polhemus and Polhemus 2008a). Notonectinae includes the tribes Notonectini and Nychiini. *Enitharoides* Brooks (Notonectini), exclusively Neotropical, was created as a subgenus of *Enithares* Spinola to include its Neotropical species, being posteriorly raised to genus by Štys and Říha (1975). *Notonecta* (Notonectini) is the only cosmopolitan genus of Notonectidae, with about 40 Neotropical species (Hungerford 1933; Mazzucconi et al. 2009; Barbosa and Nessimian 2013). The genus was reviewed by Hungerford (1933), and few species were described since then. Truxal (1949) reviewed the New World genus *Martarega* (Nychiini), currently with 22 species. The subfamily Anisopinae is represented in the New World by the genus *Buenoa*, with 56 Neotropical species (Truxal 1949, 1953; Roback and Nieser 1974; Barbosa et al. 2010a, b, 2015; Padilla-Gil 2010, 2012; Moreira et al. 2011; Barbosa and Rodrigues 2013).

Gelastocoridae has two subfamilies. Gelastocorinae is monotypic, with *Montandonius* Melin synonymized with *Gelastocoris* by Todd (1955), although Nieser (1975) still considered them distinct genera. *Gelastocoris* occurs in New World, with 23 Neotropical species (Todd 1955; Estévez and Schnack 1980; Boulard and Jauffret 1984). Nerthrinae is also monotypic, with the cosmopolitan genus *Nerthra* and about 30 Neotropical species (Todd 1955; Schnack and Estévez 1979; Polhemus and Lindskog 1994).

Besides Potamocoridae, Ochteridae, Helotrephidae, and Pleidae are the families with the lowest number of Neotropical records, with less than 20 recorded species for each one. Ochteridae is represented by the genera *Ocyochterus* Drake & Gómez-Menor, with two species, *O. victor* (Bolívar) endemic to Ecuador (Cianferoni 2012) and *O. irmae* Polhemus & Polhemus described from Ecuador and Colombia (Polhemus and Polhemus 2014), and the cosmopolitan *Ochterus*, whose New World representatives were reviewed by Schell (1943a, b) and belong to the subgenus *Neochterus* Mahner (Cianferoni 2012), including 18 species (Drake 1952; Kormilev and De Carlo 1952; Nieser 1975; Polhemus and Polhemus 1976; Nieser and Chen 1992; Cordeiro et al. 2014).

The subfamily Neotrephinae (Helotrephidae) is endemic to the Neotropical region and includes two genera. *Paratrephes* is monotypic, with *P. hintoni* China occurring mainly in northern South America, with one record from southeastern Brazil (Rodrigues et al. 2012a). *Neotrephes* China has nine species (Papáček and Zettel 2004) recorded mainly from southeastern and southern Brazil and from northeastern Argentina (Bachmann 1998; Nieser and Chen 2002; Rodrigues et al. 2012a). Pleidae is a small family with most diversity occurring in the Neotropical region. *Neoplea* Esaki & China is a New World genus, with 12 Neotropical species, and *Paraplea* Esaki & China is cosmopolitan, with one species recorded from the Americas, *P. puella* (Barber). Finally, *Heteroplea* is monotypic, with *H. stictosoma* Cook being restricted to Venezuela (Cook 2011).

7.5 Economic Importance

Nepomorphans, although having no direct economic importance to humans, play a significant role on the environment. They are generally abundant in lentic or lotic, preserved or not, aquatic ecosystems developing a key part in the energy cycle of these environments. Individuals of all families are predators (not exclusively in the case of Corixidae) and certainly have great influence upon other organisms (Stout 1981, 1982; Sites and Willig 1991; Papáček 2000). Species of all families can be considered as potential biological control agents of invertebrates of medical importance, such as the larvae of mosquitoes and aquatic gastropods.

Immatures of some families of hematophagous dipterans that transmit diseases to humans have been reared in the laboratory to serve as food to species of aquatic heteropterans. For example, Sites and Nichols (1990) used larvae of Simuliidae to feed *Ambrysus lunatus*; Consoli et al. (1989) reared *Belostoma micantulum* (Stål) (Belostomatidae) using larvae and pupae of *Aedes fluviatilis* (Lutz) (Culicidae) as food; and Pereira et al. (1991) also reared *B. micantulum*, but using larvae of *Culex quinquefasciatus* Say (Culicidae). Many are the studies of predation on invertebrates of medical importance by nepomorphans under laboratory conditions, especially involving Belostomatidae, Naucoridae, and Nepidae, which can be seen in the list provided by Jenkins (1964).

In contrast, some species of Notonectidae can cause damage to cultures of several fish species (Torre Bueno 1905a). A single specimen of *Notonecta* can feed on more than 2,500 fish larvae/day. Corixidae also cause damage to various pisciculture tanks, by feeding on fish eggs and larvae (Papáček 2000). On the other hand, eggs, immatures, and adults of corixids and notonectids are used as human food in parts of Mexico (Hungerford 1948; Hutchinson 1993). Additionally, representatives of corixids can be dehydrated and used as food for ornamental fish and domestic birds (Hutchinson 1993).

The use of this group of insects as bioindicators of water quality is still incipient in the Neotropics. Additionally, considering that most of the published works have taken into account only generic identifications and that many nepomorphan genera occur in preserved, degraded, or modified environments, such studies might turn out uninformative. Despite the difficulty to identify specimens at specific level, this should be the path to be followed in order to reliably use aquatic Heteroptera in evaluations of water quality.

7.6 Key for Families and Genera of the Neotropical Nepomorpha

Modified from Hungerford (1948), De Carlo (1963), Nieser (1975), Nieser and Chen (2006), Cook (2011), Estévez and Ribeiro (2011), Cianferoni (2012), and Polhemus and Polhemus (2014).

1a. Ocelli present (if obsolete or absent, then head transverse and eyes pedunculate or subpedunculate) (Fig. 7.2A); species usually found on sandy shores of water bodies 2

1b. Ocelli absent; aquatic species 5

2a (1a). Antennae shorter than the head, not observed dorsally and hidden in a groove beneath head (Fig. 7.2C); rostrum short, reaching anterior coxae; scutellum tumid; fore femora enlarged with a groove for reception of the tibia (Fig. 7.2B) .... 3 (Gelastocoridae)

2b. Antennae a little longer than the head (Fig. 7.3A), observed dorsally; rostrum long, reaching at least posterior coxae (Fig. 7.3C); scutellum flat; all legs cursorial (anterior femora not enlarged) .... 4 (Ochteridae)

3a (2a). Pronotum rectangular, generally with anterior and posterior margin with the same width (Fig. 7.1A); fore femur subtriangular, very broad at base, about as wide as long; foretarsus fused with the tibia, bearing one claw (Fig. 7.1B); color commonly uniform .... *Nerthra* Say

3b. Pronotum with the anterior margin distinctly shorter than posterior margin (Fig. 7.2C); fore femur moderately incrassate, about twice as long as wide; foretarsus not fused with the tibia, bearing two claws (Fig. 7.2B); color heterogeneous, pruinose .... *Gelastocoris* Kirkaldy

4a (2b). Lateral expansions of pronotum as wide as an eye; vertex of head without channels parallel to inner margins of eyes; body length 6.75–8.20 mm .... *Ocyochterus* Drake & Gómez-Menor

4b. Lateral expansions of the pronotum distinctly narrower than an eye (Fig. 7.3B); vertex of head with channels parallel between the eyes; body length 3.30–6.30 mm.. .... *Ochterus* Latreille

5a (1b). Forelegs raptorial (femur enlarged, with a groove for reception of the tibia) (Figs. 7.4 and 7.7A) 6

5b. Forelegs not raptorial 26

6a (5a). Hemelytral membrane with venation; respiratory siphon present at the end of the body (Figs. 7.6B and 7.8D) 7

6b. Hemelytral membrane without venation; respiratory siphon absent from the end of the body (Figs. 7.11B and 7.12A) 15

7a (6a). All tarsi 1-segmented; hind legs without fringe of developed bristles; siphon long and not retractile (Fig. 7.6B) .... 8 (Nepidae)

7b. Tarsi 2- or 3-segmented, rarely foretarsus 1-segmented; hind legs with a fringe of developed bristles; siphon short and retractile (Fig. 7.8D).... 10 (Belostomatidae)

8a (7a). Body cylindrical; anterolateral corners of pronotum not wider than head (including eyes) (Fig. 7.4) .... *Ranatra* F.

8b. Body flattened; anterolateral corners of pronotum wider than head (including eyes) 9

9a (8b). Body and pronotum elongate; pronotum longer than wide, ratio length/larger width equal to 5–6 (Fig. 7.5) .... *Curicta* Stål

9b. Body oval; pronotum quadrate, ratio length/larger width equal to or smaller than 3 (Fig. 7.6A, B) .... *Telmatotrephes* Stål

10a (7b). Segment 1 of rostrum short, thicker than long and obviously shorter than segment 2; abdominal sternites 5 and 6 subdivided laterally by suture-like fold (Fig. 7.8A); spiracles located on or adjacent to mesal margins of connexivum 11

10b. Segment 1 of rostrum much longer than greatest thickness, subequal in length to segment 2; abdominal sternites not subdivided by a suture; spiracles located near center of connexivum 13

11a (10a). Body elongate (Fig. 7.8D); foretarsus 3-segmented (often appearing 2-segmented externally) and bearing one long claw (Fig. 7.8B); tibia and tarsus of hind leg thinly compressed, much more dilated than middle tibia and tarsus (Fig. 7.8C); genital operculum of females with spines and acutely rounded at apex 12

11b. Body oval (Fig. 7.7B); foretarsus 2-segmented (often appearing 1-segmented), bearing two very short, vestigial claws (Fig. 7.7A); tibia and tarsus of middle and hind legs similar, narrow, flattened, but not broadly dilated; genital operculum of females fringed with hairs, rounded at apex .... *Horvathinia* Montandon

12a (11a). Inner pad of setae of fore femur with two symmetrical furrows; pads of hind femur with just one; external borders of ventral laterotergites 2 and 3 narrowed, almost straight .... *Lethocerus* Mayr

12b. Inner pad of setae of fore femur without any trace of furrow; pads of hind femur with just a deep cleft, but not divided; external borders of ventral laterotergites 2 and 3 not narrowed, arcuate, following the border line of abdomen .... *Benacus* (Say)

13a (10b). Membrane of hemelytra well developed, with its greatest width larger than that of clavus; most of its cells equal in length, in the form of long, narrow rectangles (Fig. 7.9) .... *Belostoma* Latreille

13b. Membrane of hemelytron distinctly reduced, with its greatest width equal to or smaller than that of clavus; most of its cells usually small or feebly defined, or short and rectangular, of various lengths (Fig. 7.10) 14

14a (13b). Lateral margins of abdomen not smooth, interrupted at borders between segments (scalelike laterotergites) (Fig. 7.10) .... *Weberiella* De Carlo

14b. Lateral margins of abdomen smooth, not scalelike .... *Abedus* Stål

15a (6b). Antenna long, extending beyond the lateral margin of the head; fore femur can be expanded or not; male genitalia always symmetric; small bugs, body length less than 4 mm (Fig. 7.11A, B) .... *Potamocoris* Hungerford (Potamocoridae)

15b. Antenna short, not exceeding the lateral margin of the head in dorsal view; fore femur always expanded (Fig. 7.13B, 16A, 18C); male genitalia usually asymmetric; body length equal to or exceeding 4 mm .... 16 (Naucoridae)

16a (15b). Pro-pleurae covering the posterior part of the prosternum (Fig. 7.13B) 17

16b. Prosternum exposed posteriorly (Fig. 7.18B) 19

17a (16a). Ventral surface of abdomen pubescent almost or quite to lateral margins (Fig. 7.12B) .... *Ambrysus* Stål (Fig. 7.12A) (*Ambrysus montandoni* La Rivers has the lateral margins of the abdominal sternites naked, without pubescence. This species shares with those of *Carvalhoiella*, in addition to this feature, the anterior margin of pronotum slightly concave behind interocular space; absence of the male accessory genitalic process of tergite VI; and the shape of the divergent pseudoparameres of tergite VIII)

17b. Ventral surface margined by a glabrous area, especially on the abdomen (Fig. 7.13B, C)... 18

18a (17b). Anterior margin of pronotum deeply emarginate behind interocular space (as observed in *Ambrysus* sp. Fig. 7.12A).................... *Cataractocoris* Usinger

18b. Anterior margin of pronotum straight or somewhat concave behind interocular space (Fig. 7.13A) .... *Carvalhoiella* De Carlo

19a (16b). Foreleg pretarsus with 2 claws, often minute and closely appressed, sometimes resembling a single structure (Fig. 7.14C); middle and hind femora with two longitudinal rows of conspicuous bristles or spinelike setae on ventral face, in addition to 2 usual rows on posterior face (Fig. 7.14B) 20

19b. Foreleg pretarsus with or without 1 min claw (Fig. 7.18C); middle and hind femora without additional rows of bristles or spiniform setae on ventral surfaces, or with just an indication of the upper row, or with some scattered additional setae (Fig. 7.15B) 22

20a (19a). Posterior angles of pronotum pointing obtusely but distinctly backward; hemelytra separately pointed..*Decarloa* La Rivers

20b. Posterior angles of pronotum not pointing backward; hemelytra with fully developed membranes and covering the abdomen.. 21

21a (20b). Female with two tarsal segments on foreleg; male phallotheca symmetrical......................................*Ctenipocoris* Montandon (Fig. 7.14A, B)

21b. Female with one tarsal segment on foreleg; male phallotheca asymmetrical ....*Interocoris* La Rivers

22a (19b). Body broadly oval to subcircular, flattened (Fig. 7.15A, B); meso- and metasterna with prominent, broad, laterally expanded median longitudinal carinae bearing foveae or otherwise excavate (Fig. 7.15C, D); inner margins of eyes (dorsal view) distinctly diverging anteriorly (Fig. 7.15A)........... *Limnocoris* Stål

22b. Body more elongate, robust, dorsum moderately convex (Fig. 7.18A, B); meso- and metasternal longitudinal carinae inconspicuous, thin, platelike, or absent; inner margins of the eyes in dorsal view usually distinctly converging anteriorly, infrequently parallel sided to slightly diverging (Fig. 7.18A)... 23

23a (22b). Anterior margin of pronotum deeply emarginated behind interocular space (Fig. 7.16A) 24

23b. Anterior margin of pronotum straight behind interocular space (Fig. 7.17A)...25

24a (23a). Lateral margins of pronotum crenulate (Fig. 7.16A); abdominal tergites distinct (Fig. 7.16B); male abdominal tergite 7 asymmetrical .... *Cryphocricos* Signoret

24b. Lateral margins of pronotum smooth; abdominal tergites fused; male abdominal tergite 7 symmetrical .... *Procryphocricos* Polhemus

25a (23b). Mesofemur greatly flattened dorsoventrally, with its dorsoposterior margins extended into thickened, flap-like projections and equipped with fine brush (Fig. 7.17B); tarsi of meso- and metalegs longer than their corresponding tibiae .... *Placomerus* La Rivers (Fig. 7.17A)

25b. Mesofemur not flattened or margined as described above (Fig. 7.18B); tarsi of meso- and metalegs shorter than their corresponding tibiae .... *Pelocoris* Stål (Fig. 7.18A)

26a (5b). Body flattened (Fig. 7.19A); rostrum apparently not segmented, with transverse striations (Fig. 7.20B); foretarsi modified, spatulate, with a fringe of long bristles and without distinct claws (Fig. 7.22) .... 27 (Corixidae)

26b. Body convex (Fig. 7.36); rostrum distinctly segmented, without transverse striations (Fig. 7.33A); foretarsi not modified, with distinct claws (Fig. 7.34C) 42

27a (26a). Pronotum not covering the scutellum (Fig. 7.19A) 28

27b. Pronotum almost entirely covering the scutellum (Fig. 7.21B) 30

28a (27a). Mesosternum with a distinct carina (Fig. 7.19C) .... *Synaptogobia* Nieser & Chen (Fig. 7.19A, B)

28b. Mesosternum without carina (Fig. 7.20B) 29

29a (28b). Antennae three-segmented; metaxyphus short (Fig. 7.20B) .... *Tenagobia* Bergroth (Fig. 7.20A, B)

29b. Antennae one-segmented; metaxyphus long .... *Monogobia* Nieser & Chen

30 (27b). Infraocular portion of genae very broad, the lower margin of the eye concave, the hypo-ocular suture arising near the subacute production of the inferior angle of the eye (Fig. 7.21A) .... *Heterocorixa* White (Fig. 7.21B)

30b. Infraocular portion of gena not broad, or if broad, the hypo-ocular suture when present arising about midway along the ventral margin of the eye (Fig. 7.31) 31

31a (30b). With rather thick, well-developed apical claw on foretarsus of both sexes; pala of both sexes narrowly digitiform; males with row of stout short pegs along the upper edge of the palm (Fig. 7.22); usually with a mat of hairlike setae on frons in both sexes 32

31b. With apical claw on the foretarsus spinelike, usually resembling the spines along the lower margin of the palm; pala not narrowly digitiform, of various shapes, male with row of pegs usually well above the fringe of setae along the upper edge of the palm (Fig. 7.25); setae on frons not mat-like, often absent 33

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32b. Male abdomen dextral, strigil present; female face not concave and abdomen normal .... *Graptocorixa* Hungerford

33a (31b). Male foretibia not produced over pala (Fig. 7.23B 34

33b. Male foretibia distinctly produced over pala (Fig. 7.30........ 38

34a (33a). Vertex of males conically produced anterad (acuminate), frons deeply concave (Fig. 7.23A); pala of male forelegs nearly divided by deep transverse groove on dorsal surface (Fig. 7.23B); costal margin of elytra in females with an elongate-ellipsoid, polished thickening at basal third of length........ *Ramphocorixa* Abbott

34b. Vertex of males not produced, if produced, rounded with frons flat (Fig. 7.24A); pala of male forelegs without deep transverse groove on dorsal side; costal margin of females not thickened at basal third (Fig. 7.24B)........ 35

35a (34b). Inner posterior angle of eye acutely produced (Fig. 7.24A); pronotum and hemelytra smooth; anterior femur of male greatly inflated (Fig. 7.24B) .... *Krizousacorixa* Hungerford

35b. Inner posterior angle of eye not acutely produced; pronotum and hemelytra rastrated; anterior femur of male not inflated (Fig. 7.25)........ 36

36a (35b). Foretibiae with apical comb of spines (Fig. 7.25); males with dextral asymmetry, without strigil........ *Morphocorixa* Jaczewski

36b. Foretibiae without comb of spines (Fig. 7.26); males with sinistral asymmetry and without strigil, or with dextral asymmetry and with strigil........ 37

37a (36b). Male pala with one row of pegs (Fig. 7.26); metaxyphus short, triangular .... *Sigara* F.

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38a (33b).Inner posterior angle of eye sharply right angulate, occasionally slightly produced (Fig. 7.28)........ *Trichocorixella* Jaczewski

38b. Inner posterior angle of eye obtuse angulate........ 39

39a (38b). Ventral surface of hind femur pubescent only on basal third of the front margin........ 40

39b. Ventral surface of hind femur pubescent at least for one-half of the front margin........ 41

40a (39a).Apices of clavi not exceeding a line drawn through nodal furrows of the hemelytra in female and slightly exceeding in males; tibiae strongly produced apically over the pala (Fig. 7.29); males with sinistral asymmetry, strigil on left .... *Trichocorixa* Kirkaldy

40b. Clavi distinctly exceeding a line drawn through nodal furrows of the hemelytra in both sexes; tibiae slightly produced over the pala (Fig. 7.30); males with dextral asymmetry, strigil on right .... *Ectemnostega* Enderlein

41a (39b). Males with dextral asymmetry, without strigil .... *Centrocorisa* Lundblad

41b. Males with dextral asymmetry, with strigil........ *Corisella* Lundblad

42a (26b). Body elongate, without punctuations on the dorsal surface (Fig. 7.34A); hind legs longer than fore- and middle legs; hind tibiae and tarsi with distinct fringe of setae; hind tarsal claws apparently absent .... 43 (Notonectidae)

42b. Body globose, with dorsal surface punctuate (Fig. 7.36); legs almost symmetrical; setae of hind tibiae and tarsi do not form a fringe; hind tarsal claws normal 46

43a (42a). Labrum rounded (Fig. 7.32A); hemelytral commissure with definite hairlined pit at the anterior end (Fig. 7.32B); males with stridulatory comb at foretibia (Fig. 7.32C); spine at caudosinistral margin of seventh abdominal tergite (Fig. 7.32D).. *Buenoa* Kirkaldy

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45a (44b). Lateral margins of pronotum foveate (Fig. 7.34B); genital capsule asymmetrical .... *Enitharoides* Brooks

45b. Lateral margins of pronotum not foveate (Fig. 7.35); genital capsule symmetrical .... *Notonecta* L.

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47b. Rostrum short, not reaching the middle coxae, third and fourth segments with subequal length (Fig. 7.37); cephalonotal suture in brachypterous form distinctly curved backward behind the eyes; lateral margins of pronotum strongly sinuate, punctuation strong ....*Neotrephes* China

48a (46b). Head with distinct callus on vertex (Fig. 7.38); tarsal formula 3-3-3..*Heteroplea* Cook

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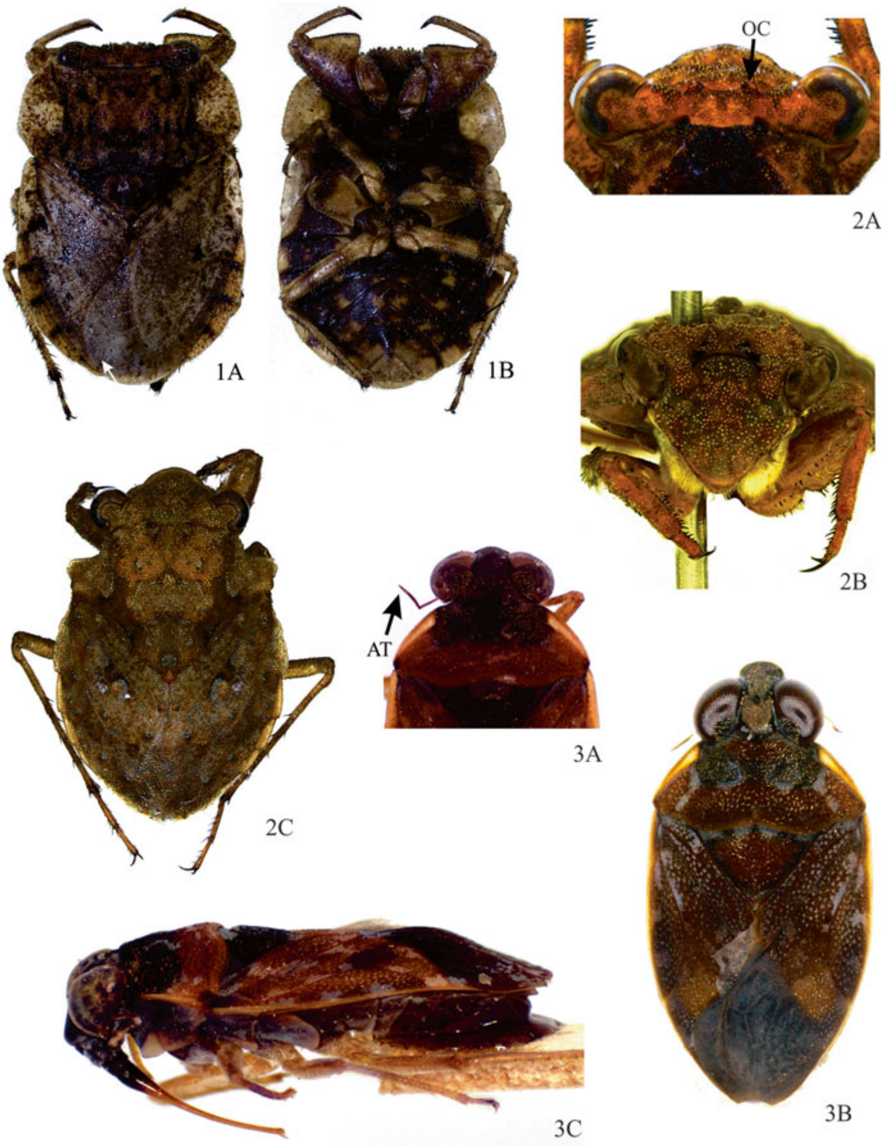
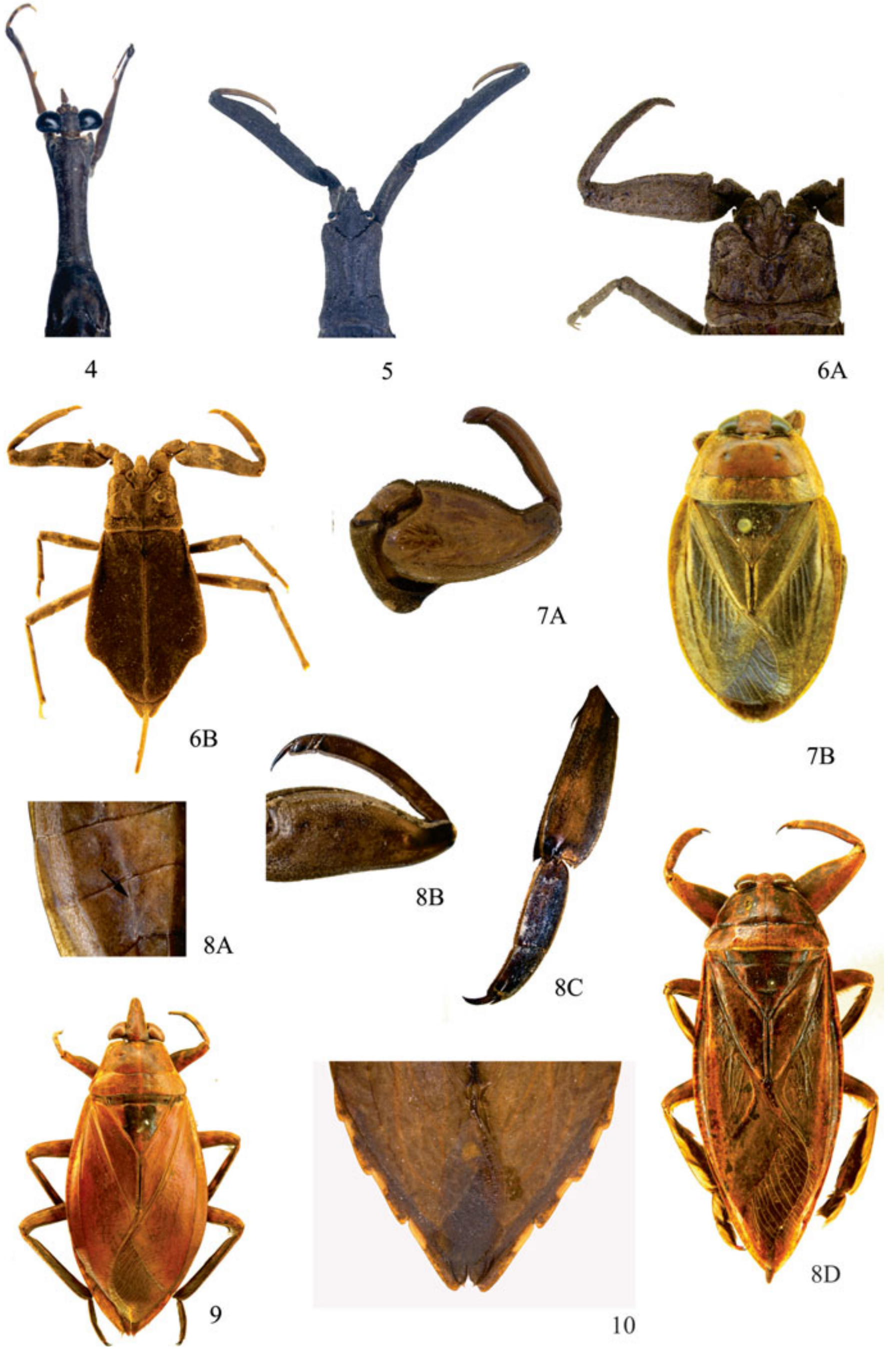
49a. Tarsal formula 3-2-3 (Fig. 7.39); median carinae on segments 2–5 of venter.. *Neoplea* Esaki & China

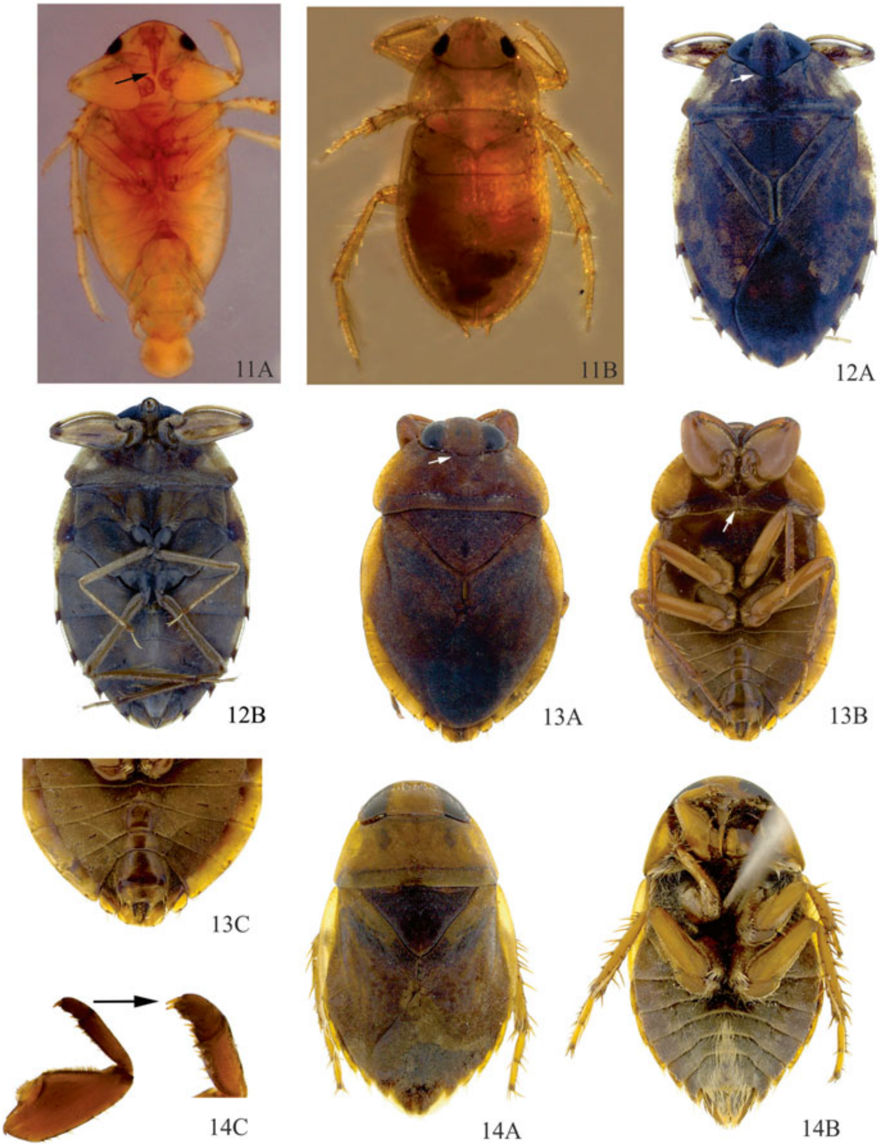
49b. Tarsal formula 2-2-3; median carinae on segments 2–6 of venter .... *Paraplea* Esaki & China



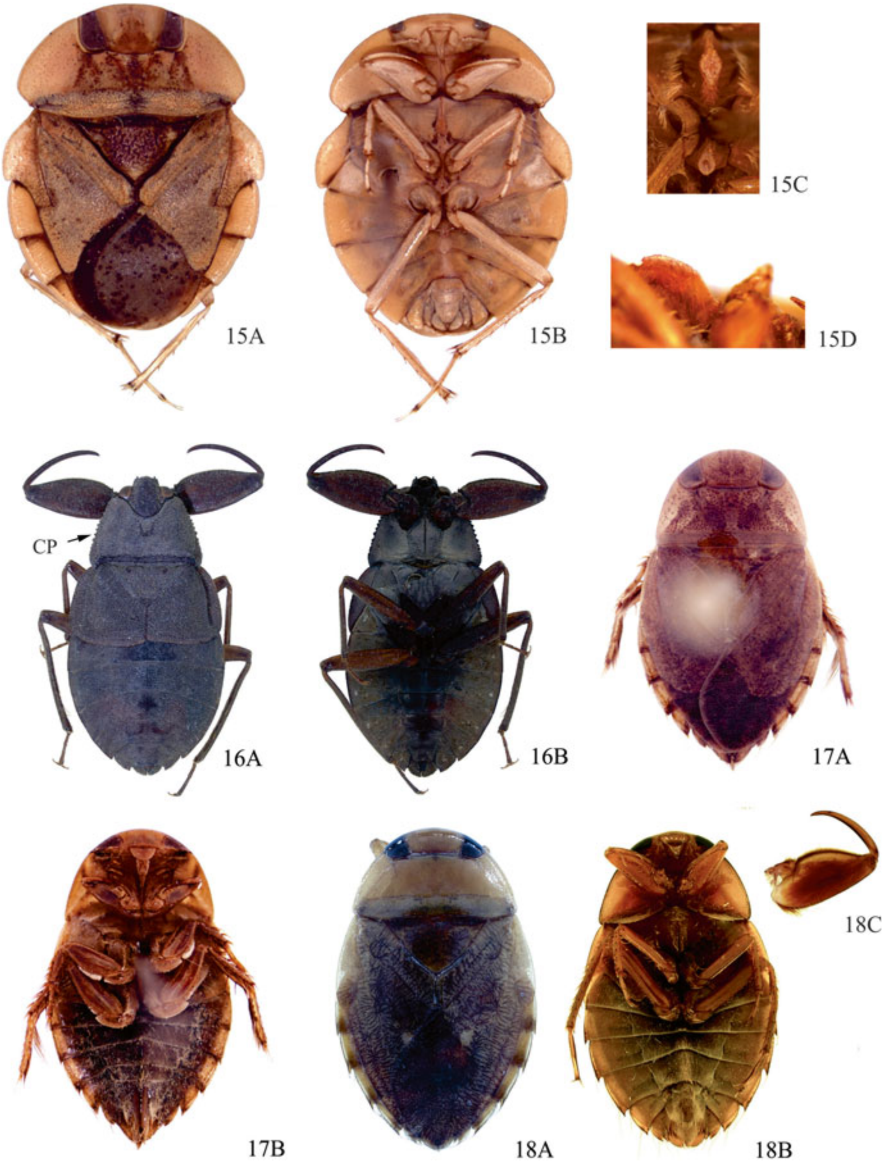
Figs. 7.1–7.3 1A–B: *Nerthra* sp. – A. *habitus* dorsal; B. *habitus* ventral. 2A–C: *Gelastocoris* sp. – A. head; B. frontal view of head and forelegs; C. *habitus* dorsal. 3A–C: *Ochterus* spp. A. head and pronotum; B. *habitus* dorsal of *O. aeneifrons surinamensis* Nieser; C. *habitus* lateral. *AT* antenna, *OC* ocelli (Photos by HDD Rodrigues, 2A by JFBarbosa)



Figs. 7.4–7.10 4–5: head and pronotum – 4. *Ranatra* sp.; 5. *Curicta* sp. 6A–B: *Telmatotrephes* spp. – A. head and pronotum of *Telmatotrephes carvalhoi* De Carlo; B. *habitus* dorsal of *Telmatotrephes grandicollis* Kuitert. 7A–B: *Horvathinia pelocoroides* Montandon – A. foreleg; B. *habitus* dorsal. 8A–D: *Lethocerus* sp. – A. suture-like fold on the abdomen; B. foreleg; C. hind tibia and tarsi; D. *habitus* dorsal. 9. *Habitus* dorsal of *Belostoma* sp. 10. Abdomen with scalelike laterotergites of *Weberiella rhomboides* (Menke) (Photos by HDD Rodrigues)



Figs. 7.11–7.14 11A–B: *Potamocoris nelsoni* (Longo, Ribeiro, & Nessimian) – A. *habitus* ventral; B. *habitus* dorsal. 12A–B: *Ambrysus usingeri* La Rivers – A. *habitus* dorsal; B. *habitus* ventral. 13A–C: *Carvalhoiella stysi* Nieser, Pelli & Melo – A. *habitus* dorsal; B. *habitus* ventral; C. ventral view of abdomen. 14A–C: *Ctenipocoris* sp. – A. *habitus* dorsal; B. *habitus* ventral; C. foreleg with detail of tarsi with two tarsomeres and two claws (Photos by HDD Rodrigues)



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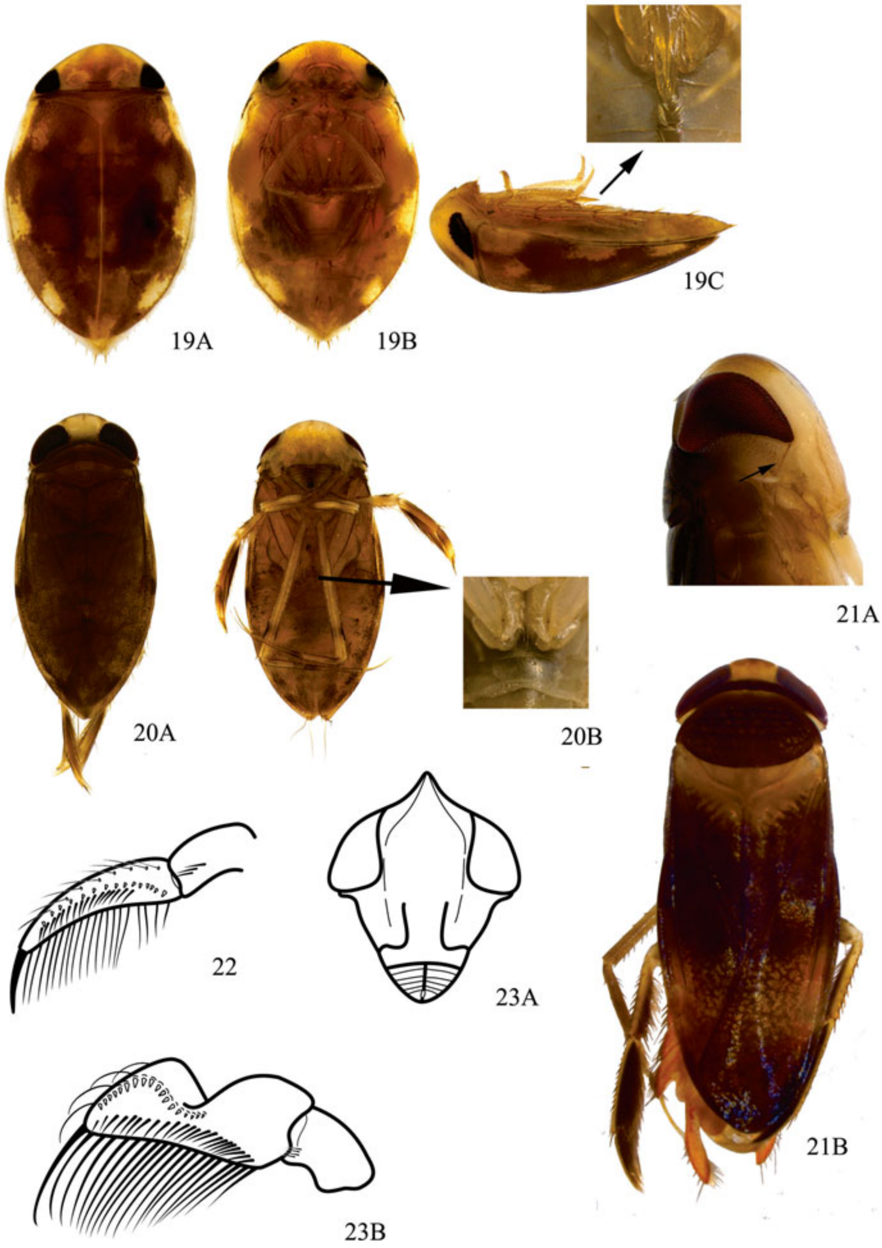

Figs. 7.19–7.23 19A–C: *Synaptogobia* sp. – A. *habitus* dorsal; B. *habitus* ventral; C. *habitus* lateral, with detail of carina on mesosternum. 20A–B: *Tenagobia* sp. – A. *habitus* dorsal; B. metaxyphus. 21A–B: *Heterocorixa* sp. – A. lateral view of the gena with hypo-ocular suture (*arrow*); B. *habitus* dorsal. 22. Pala of *Graptocorixa* sp. 23A–B: *Ramphocorixa* sp. – A. ventral view of the head; B. pala (Photos 19 to 21A by HDD Rodrigues, 21B–23B by JF Barbosa, illustrations modified from Hungerford 1948 and Bachmann 1981)

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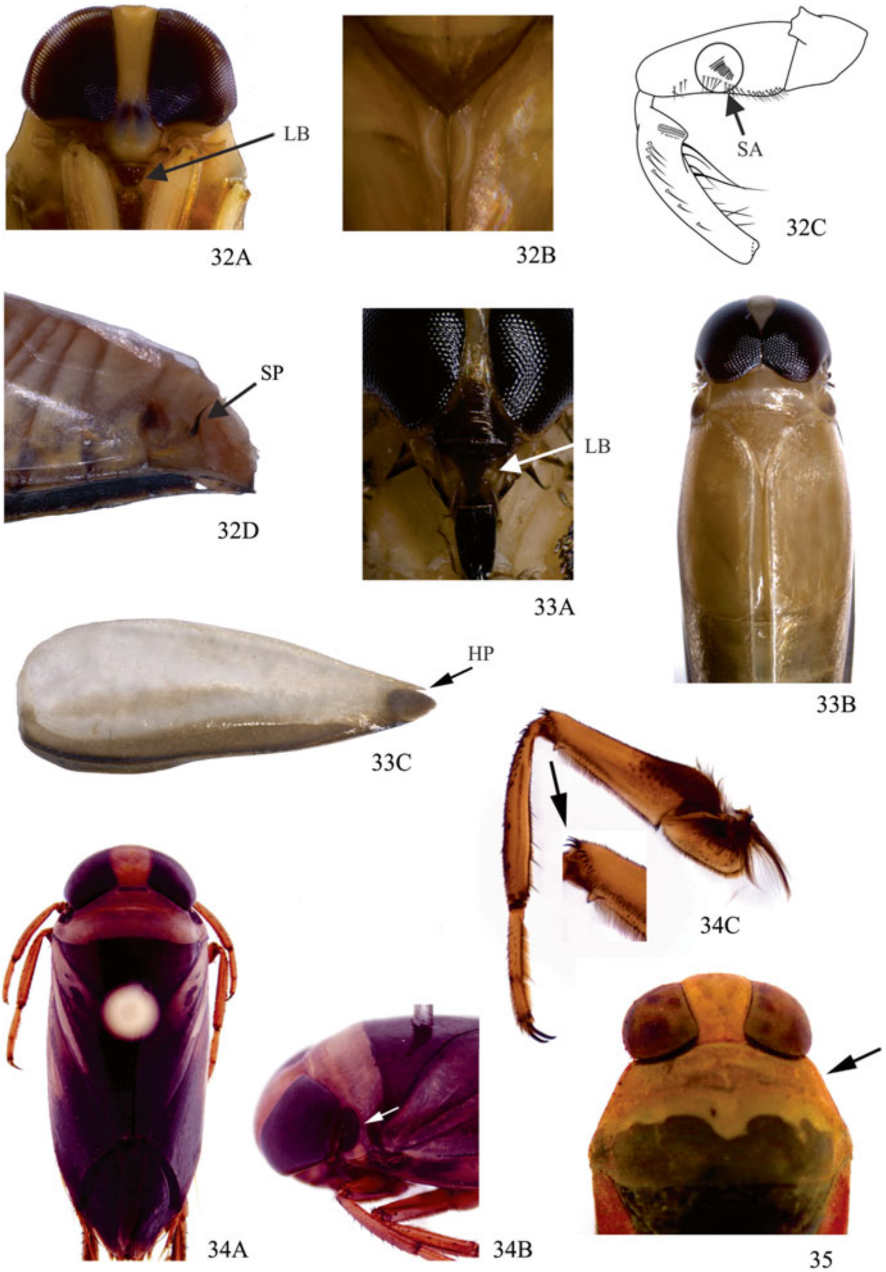
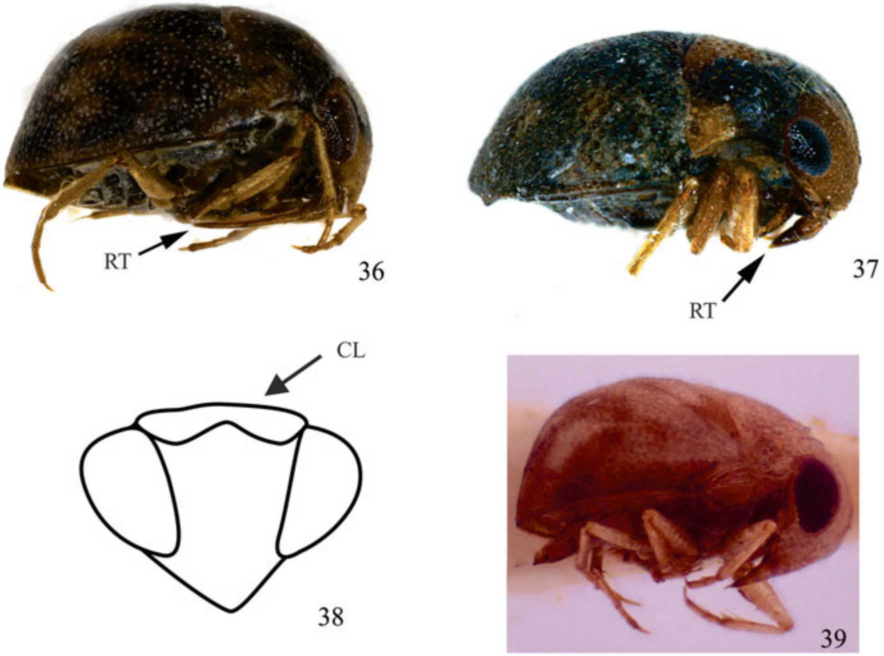


Figs. 7.32–7.35 32A–D: *Buenoa* sp. – A. ventral view of the head; B. hairlined pit at anterior end of hemelytra; C. foreleg; D. lateral view of abdomen. 33A–C: *Martarega* sp. – A. ventral view of the head; B. *habitus* dorsal; C. hemelytra. 34A–C: *Enitharoides* sp. – A. *habitus* dorsal; B. lateral view of head and pronotum (*arrow* indicates the pronotum foveate); C. middle leg with detail of anteapical spur. 35: Dorsal view of the pronotum of *Notonecta* sp. *LB* labrum, *SA* stridulatory area, *SP* spine, *HP* hemelytral process (Photos 32A–C by JF Barbosa, 32D–35 by HDD Rodrigues)



Figs. 7.36–7.39 36, 37, 39: *Habitus* lateral – 36. *Paratrephes hintoni* China (Modified from Rodrigues et al. 2012a); 37. *Neotrephes lanemeloi* Nieser & Chen; 39. *Neoplea* sp. 38: Frontal view of the head of *Heteroplea* sp. (Modified from Cook 2011). *CL* callus, *RT* rostrum (Illustration modified from Cook 2011 by JF Barbosa; Photos by HDD Rodrigues)

7.7 Concluding Remarks

Many Neotropical countries lack records or surveys concerning the infraorder Nepomorpha. Most taxonomic knowledge about the group is very restricted, mainly to Costa Rica, Cuba, Colombia, Venezuela, Suriname, Ecuador, Brazil, and Argentina. Polhemus and Polhemus (2008a) estimated as 107 the number of undescribed species of Nepomorpha in the Neotropical region. This number is probably higher when considering large holes on surveys. If the taxonomy is not well developed, knowledge about life histories and behavior, for example, become huge gaps for the most part of the region. Besides that, phylogenetic relationships of the subfamilies and genera of Nepomorpha are almost unknown. Despite all this lack of knowledge about Neotropical fauna, the number of researchers, or researchers in training process with this group, is increasing, which makes possible that part of this knowledge gap can be filled or enhanced in the coming years.

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Part V
Infraorder Leptopodomorpha

Chapter 8
Shore Bugs (Saldidae)

Alan L. de Melo

Abstract The Saldidae is one of the most ancient and extant families of insects belonging to the infraorder Leptopodomorpha that includes small (2–8 mm), oval-shaped insects known as shore bugs. They can be found in several habitats from marine intertidal places to edges of streams and lakes or far away from water in dry environments. Aspects of general characteristics, biology, and diagnosis are presented, and keys for the four extant families and for the subfamilies, genera, and known species of Saldidae occurring in the Neotropical region, mainly South America, are included.

8.1 Introduction

The infraorder Leptopodomorpha Popov includes about 400 species of small oval-shaped insects from four extant families: Aepophilidae with only known species from the marine intertidal zone in Palearctic region (Europe and maybe Mediterranean region of North Africa); Leptopodidae, with several species occurring worldwide, but only one species found in Ecuador and Colombia (Schuh and Slater 1995); Omaniidae with a few species of the marine intertidal zone in the Indo-Pacific region; and Saldidae with about 340 known species worldwide and from three extinct families (Archegocimicidae, Mesolygaeidae, Palaeoleptidae) (Popov 1989; Popov et al. 1994). Recently, some authors, after new fossil discoveries, accepted more families (Ryzhkova 2012, 2013). They are known as shore bugs and can be found in several habitats from marine intertidal places to edges of streams and lakes or be found far away from water in dry environments (Henry 2009).

Members of this group present some typical characteristics that can, with few exceptions, be easily recognized and can aid to separate individuals in different families; shore bugs are relatively uncommon in insect collections because they are easy to be overlooked by nonspecialists.

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Some fossils mainly from the Miocene period and belonging to this infraorder were found in amber from several localities in different countries. Fossils of the Cretaceous and Jurassic periods have been found, but some authors did not accept these species as members of the Leptopodomorpha (Cobben 1980, 1987; McKellar and Engel 2014; Ryzhkova 2013; Zhang et al. 2011, 2012).

There are a few records of parasites (protozoa, mites, and entomogenous worms) occurring in these intertidal insects (Poinar 1975, 2012; Polhemus and Chapman 1979; Stock and Lattin 1976).

8.2 General Characteristics and Diagnosis

Most shore bugs (Fig. 8.1) are typically small (2–8 mm) and ovate, and some tiny species morphologically resemble terrestrial species rather than members of Nepomorpha and Gerromorpha; however, they possess morphological and physiological attributes including parts of the body covered by fine setae that repel water and bind layers of air to the body indicating that they are able to survive and adapt to periods of submergence during high tides or other aquatic perturbation.

Fig. 8.1 A typical specimen of Saldidae (scale bar = 1 mm) (Photo A. L. de Melo)

All the apterous, brachypterous, and macropterous forms have visible antennae (filiform and longer than the head) with all segments of nearly equal diameter: segment 1 short and segments 2–4 longer. Compound eyes are always present and usually very large (sometimes reniform) and occupying the side of the head that is usually relatively short and broad and present at least three pairs of trichobothria dorsally. The labium is short or long, with three or four segments inserted ventrally and extending backwards between the legs; ocelli are usually present. Some species present the forewings undifferentiated or reduced being part of the body covered by a minute setae; others present the hemelytra covering the abdomen divided into a clavus, endocorium, exocorium, and membrane, and its veins form three, four, or five closed cells in macropterous forms. In Saldidae, wing polymorphism is common (Polhemus and Chapman 1979). Legs are usually relatively short, slender, or longer. The hind coxae are large, transverse with broad coxal cavity in thoracic pleurae, and adapted for hopping or jumping. Femora are sometimes armed with spines; all tarsi are usually three segmented with apical claws. Male genitalia are symmetrical; parameres are hook-shaped with a distinct processus; ovipositor valvulae are developed or reduced and platelike; spermatheca is present.

The Saldidae is one of the most ancient and the best-known families of insects belonging to Leptopodomorpha with about 340 species in two subfamilies: Chiloxanthinae and Saldinae (Popov 1971; Polhemus and Chapman 1979; Rasnitsyn and Quicke 2002). This cosmopolitan family is recorded in all continents (except Antarctic) being more speciose in Northern Hemisphere (Schuh et al. 1987; Schuh and Polhemus 2009).

8.3 General Biology and Ecology

The habits of various species are yet poorly known, and few of them that were studied do not allow generalizations concerning their life cycles. The lack of economic importance prevents more detailed studies in several countries.

Saldidae usually copulate side by side (Polhemus and Chapman 1979), and according to Cobben (1957), the female's forewing and male abdominal segments show some modifications to facilitate this copulatory position.

Eggs are laid in or on the vegetation or other substrates. They are pearly white oblong cylinders about 1 mm long. Maturation of most saldid eggs requires approximately a week.

Five nymphal instars are known. Egg to adult developmental time varies according to species and temperature and varies from 3 weeks to a month (Wiley 1922; Jordan and Wendt 1938). There are some cold-adapted species and others that can overwinter in the egg or adult stages, and depending on the temperature, they are uni- or multivoltine (Wroblewski 1966). Parental care is not well known in Saldidae.

Most members of Saldidae, which do not reach 2 mm, live along the edges of beaches, lake shores, and stream banks (including muddy or sandy shores), and all species of this group (adults and nymphs) are predaceous, feeding on small insects (Brooks and Kelton 1967), mainly Diptera larvae, each other (cannibalism) (Wroblewski 1966), and their own eggs (Rimes 1951). Some species can adapt to become scavenger or carnivore (Merritt et al. 2008). It is possible that some saldid species can find their prey submerged or on the surface by chemoreceptors located on the antenna and by visual means (Polhemus 1976). After catching the prey, the rostrum is inserted, and protease enzymes are injected to immobilize and liquefy the body contents before they can be as reported in several other predaceous Heteroptera sucked up (Picado 1937, 1939; Cheng 1967; Pereira and Melo 1998).

8.4 Classification and Diversity

The tentative classification of Saldidae was proposed by Cobben (1959), and since that time, works by Polhemus (1985a, b), Schuh and Polhemus (1980), and Schuh and Slater (1995) presented important contributions. The phylogenetic analyses for Saldidae were carried by Polhemus (1977) and Schuh and Polhemus (2009) with very interesting information.

The keys for Saldidae are adapted mainly from Heckman (2011) and several other sources cited in the references, and only the representatives for Neotropical region, mainly South America, are included.

8.4.1 Key to the Families

1. Labium short, not reaching beyond the apex of the fore coxa..........Leptopodidae
– Labium long, reaching at least beyond the hind coxa..2
2. Compound eyes small, not covering the head; ocelli absent. Wings reduced to small pads...Aepophilidae
– Compound eyes larger, covering most of the surface of the head. Wings cover most of the abdomen..3
3. Length 2 mm or shorter. Eyes covering about 1/3 of the lateral surface of the pronotum reaching beyond its collar..Omaniidae
– Length 2.2 mm or more. Eyes did not reach the pronotal collar; ocelli present. Wings cover the abdomen..Saldidae

8.4.2 Key to the Genera of Saldidae

1. Antennal segments 3 and 4 swollen, dorsum of pronotum with two distinct conical projections..*Saldoida* Osborn.
This genus is easily recognized by the two sharply conical projections of the pronotum, and antennal segments 3 and 4 are swollen. *Saldoida* is Nearctic and Oriental in distribution and contains few described species

– Antennal segments 3 and 4 not swollen, dorsum of pronotum without distinct conical projections..2

2. Embolar fracture longer, reaching at least as far as the hind end of the claval suture..3.

– Embolar fracture short, not reaching the hind end of the claval suture.................4.

3. Hemelytral membrane with four terminal closed cells..*Paralosalda* Polhemus & Evans.
One species, *Paralosalda innova* Polhemus & Evans, inhabits the rocky intertidal zone along the Pacific coasts of Costa Rica, Panama, and Colombia

– Hemelytral membrane with five terminal closed cells.................*Pentacora* Reuter
The five elongated cells of the membrane readily identify *Pentacora*. It is a relatively warm-adapted genus that is found in saline and rocky habitats. It is distributed mainly throughout North and Central America. There are records of *Pentacora sphacelata* (Uhler) in the Galapagos Islands and Spain

4. Head with a transverse swelling..5.

– Head without transverse swelling but covered with short setae................*Oiosalda* Drake & Hoberlandt.
One species, *Oiosalda caboti* Drake and Hoberlandt, is known only from Colombia

5. Hemelytral membrane with five cells..............................*Pseudosaldula* Cobben.
The presence of a transverse swelling on the head and the five closed cells of the hemelytral membrane identify this genus

– Hemelytral membrane with four cells..6.

6. Membrane with first (inner) cell protruding anteriorly half its length beyond second cell...*Salda* F.
The members of this genus are identified by the four elongated cells of the membrane and are large (up to 6 mm) dark coloration. Only few species are described and at least one was recorded from Florida. This genus is Holarctic and temperate to arctic adapted

– Membrane with all cells of subequal length or with first cell protruding anteriorly much less than half its length beyond the second cell...7.

7. Hypocostal ridge simple; without secondary hypocostal ridge...*Rupisalda* Polhemus.
The four closed cells of the membrane of approximately equal length and the simple structure of the hypocostal ridge identify species in this genus

– Hypocostal ridge complex, with secondary hypocostal ridge..............................8.

8. Corium with two distinct veins...*Saldula* Van Duzee. The four closed cells of the membrane readily identify *Saldula*, and it can be distinguished from *Micracanthia* by the distal veins of the corium (best viewed from the underside of the hemelytra). This genus is cosmopolitan

– Corium without veins...*Micracanthia* Reuter. Very similar to *Saldula* and is distinguished by the apparent lack of a forked vein in the corium, or the apex on the median vein is not forked. This is best viewed from the underside of the hemelytra. It is mainly Holarctic (at least one species reaching Alaska) in distribution. Several species are known from Asia, Europe, Mexico, the USA and from the Caribbean islands including Costa Rica and at least one from South America (Polhemus 1977)

8.4.3 Key to the Species of **Pseudosaldula**

1. First antennal segment with black marking or lateroventral stripe......................2.

– First antennal segment usually uniform, without black mark..............................4.

2. Fore and middle tibiae and sometimes the hind tibia with a defined dark stripe on the dorsal surface...3.

– All tibiae lacking distinct stripes on the dorsal surface..*Pseudosaldula penai* Schuh & Polhemus (Bolivia, Chile, Argentina)

3. Dorsum coated by golden setae; clavus and corium usually black, with pruinose areas. First antennal segment with black stripes on ventrolateral and dorsomedial surfaces..................................*Pseudosaldula chilensis* (Blanchard) (Argentina, Chile)

– Dorsum coated by black setae; corium with pale markings without pruinose areas. First antennal segment with a black longitudinal stripe on the ventrolateral surface...*Pseudosaldula salina* Schuh & Polhemus (Argentina)

4. Hemelytra with dull surfaces except along the overlapping borders of the claval commissure and sometimes on limited areas along the edge of the corium........5.

– Hemelytra with shiny surfaces on the corium, embolar area, veins, and sometimes along the claval commissure and some areas of the membrane..........8.

5. Dorsum with long, dark, and dull setae. Hemelytral setae twice as long as the diameter of hind tibia...........................*Pseudosaldula pilosa* Schuh & Polhemus (Argentina, Chile)

– Dorsum with short and recumbent setae. Hemelytral setae equal or shorter than the diameter of a hind tibia...6.

6. Pronotum campanulate, with slightly to strongly concave margins; irregular ivory-colored macula on the subapical surface of the exocorium..*Pseudosaldula saxicola* Schuh & Polhemus (Argentina, Peru)

– Pronotum flattened with slightly to strongly convex margins. Only a pale mark on the subapical surface of the exocorium..7.

7. Corium coated by shiny, golden, recumbent setae; corium, clavus, and membrane with several purplish, pruinose areas and numerous long setae on the membranes veins..............................*Pseudosaldula vulgaris* Schuh & Polhemus (Bolivia, Peru)

– Corium not coated by shiny, golden, recumbent setae; corium, clavus, and membrane with few purplish, pruinose areas and scattered setae on the membrane veins...*Pseudosaldula bergi* (Haglund) (Argentina, Chile)

8. Anterior part of exocorium and radial vein shiny; the rest of the corium is dull...*Pseudosaldula huamachuco* Schuh & Polhemus (Peru)

– Posterior part of exocorium shiny and variable...9.

9. Exocorium and part of the posterior half of the endocorium with polish and shiny areas...10.

– Exocorium at the embolar area with polish and shiny areas. If this area reaches the posterior half, then the radial vein is also polished......................................11.

10. Exocorium and some area of the posterior part of the endocorium and entire membrane of brachypterous specimens with shiny pattern (macropterous forms only basal third of the membrane polished).......................................*Pseudosaldula andensis* (Distant) (Ecuador, Peru)

– Exocorium and some area of the posterior part of the endocorium with shiny pattern interrupted by a dull area along the radial vein, basal area, and veins of membrane polished in brachypterous forms (macropterous forms have only basal third of the membrane polished).............................*Pseudosaldula bruesi* (Drake) (Peru)

11. Pronotum campanulate, with slightly to strongly concave margins; dorsum with black setae without pruinose areas..12.

– Pronotum not campanulate with slightly to strongly convex margins, dorsum with both black and shiny golden setae and pruinose areas...............................13.

12. Dorsum with erect and long setae.....*Pseudosaldula yungas* Schuh & Polhemus (Bolivia, Peru)

– Dorsum with erect and of moderate length setae..*Pseudosaldula antioquia* Schuh & Polhemus (Colombia)

13. Embolar area polished at posterior half; radial vein smooth and shiny..*Pseudosaldula aurea* Schuh and Polhemus (Argentina)

– Embolar area polished and extends for its entire length; radial vein is matt..*Pseudosaldula perula* (Drake) (Argentina, Peru)

8.4.4 Key to the Species of **Rupisalda**

1. Pubescence dense and yellowish brown; first antennal segment stout and yellowish...*Rupisalda verdica* (Drake & Hottes) (Brazil: Santa Catarina)
– Pubescence not dense and golden or grayish; first antennal segment slender or darker...2.
2. Legs testaceous, with whitish marks.............................*Rupisalda zelena* (Drake) (Peru)
– Legs light brown to pale, without markings..3.
3. First antennal segment brownish.................................*Rupisalda icolana* (Drake) (Brazil: Santa Catarina)
– First antennal segment lighter at apical part, with a broad whitish or yellowish ring..*Rupisalda ventralis* (Stål) (Brazil: Mato Grosso, Minas Gerais, Rio de Janeiro)

8.4.5 Key to the Species of **Saldula**

1. Lateral margins of pronotum, pale..2.
– Lateral margins of pronotum dark or fuscous brown..3.
2. Legs yellowish, with brown markings.................................*Saldula coxalis* (Stål) (North, South, and Central America including the Caribbean islands)
– Legs testaceous and sometimes marked with brown....................*Saldula doeringi* Drake & Carvalho (Argentina)
3. Head, pronotum, and scutellum black, not dull, rugulose...................................4.
– Head, pronotum, and scutellum polished, dull, or coated by pubescence, not rugulose..5.
4. Outer margin of male paramere with prominent swelling and a slight swelling along the inner surface..*Saldula humilis* (Say) (North America, Caribbean islands, Surinam, Brazil—Santa Catarina)
– Outer margin of male paramere without swelling, with prominent tubercle along the inner surface...*Saldula dentulata* (Hodgden) (Central America, Caribbean islands, Ecuador, Panama, Peru)
5. Lateral margins of pronotum concave or straight..6.
– Lateral margins of the pronotum convex..9.
6. Dorsal surfaces of head and thorax black, dull, and with a silvery or golden pubescence and a few longer black setae on thorax..*Saldula peruviana* (Cobben) (Peru)
– Dorsal surfaces of the head and thorax black, shiny, with a sparse, pale pubescence...7.

7. Pubescence on hemelytra is moderately long and dull velvet black with moderately long, golden; semi-recumbent pilosity..*Saldula scitula* Drake & Hottes (Brazil: Santa Catarina)

– Pubescence on hemelytra is long and dark brownish or short and silvery pilosity..8.

8. Head, pronotum, and scutellum with grayish brown pubescence and erect dark setae; dorsal surface of hemelytra with long, erect, dark brownish setae...*Saldula hodgdeni* (Drake) (Bolivia)

– Head, pronotum, and scutellum with pale and short pubescence and few longer black setae; dorsal surface of hemelytra with short silvery pubescence...*Saldula chartoscirtoides* Cobben (Brazil: Santa Catarina)

9. Shape of the female is broadly ovate; hemelytra fuscous brown...*Saldula lynchi* Drake & Carvalho (Argentina)

– Shape not broadly ovate; hemelytra with different pattern................................10.

10. Length about 4.35 mm................................*Saldula differata* Drake & Carvalho (Argentina)

– Length is usually up to 4 mm...11.

11. Hemelytra with pruinose or pubescent areas...12.

– Hemelytra without pruinose areas..*Saldula pallipes* (F.) (Holarctic Region, Mexico, Central America, Caribbean islands, South America, and Africa)

12. Corium with two or three dark spots..........*Saldula penningtoni* Drake and Carvalho [Argentina, Brazil (Minas Gerais, Santa Catarina), Chile, Paraguay, Peru, Uruguay]

– Corium with bluish white pruinose area on the inner part...*Saldula galapagosana* (Polhemus) (Galapagos Islands). Remark: The record of *Saldula saltatoria* (L.), a Holarctic species from Colombia (Polhemus and Chapman 1979) needs confirmation

8.5 Concluding Remarks

Many species of Leptopodomorpha have been misidentified mainly by nonspecialists, and apart from scarce references from the older literature that sometimes are difficult to obtain, there are today few specialists studying this group of insects, and for a better knowledge of this group, sampling must be improved. So, more people are needed to collect more intensively in faunal studies regarding shore bugs biology, including habitats, ecological traits, phylogenetics, historical biogeography, altitude, and temperature gradients of this interesting but little-known insects that can be found in almost all zoogeographic regions worldwide. Yet, fascinating questions concerning speciation and evolution, habitat disturbance, or fragmentation of natural habitats by rapid and continued anthropogenic changes arise. Shore bugs' relationship with the extinct Leptopodomorpha or with natural preys and predators needs be improved or in the future, with more collected specimens, studies could be extended further to include their parasites.

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Part VI
Infraorder Cimicomorpha

Chapter 9
Minute Pirate Bugs (Anthocoridae and Lyctocoridae)

Diego L. Carpintero

Abstract A brief historical overview of the study of Anthocoridae and Lyctocoridae (Hemiptera: Heteroptera) found in the Neotropical region is presented. Dichotomic keys are provided for the recognition of the subfamilies to the subtribal level and a taxonomic list of all species known to date as well as images for guidance. Comments on most important species and a summary of the main literature are included.

9.1 Introduction

The first and most extensive taxonomic revision of the Anthocoridae sensu lato was made by O. M. Reuter, in 1884, describing many new taxa and reviewing the known taxa until then. Knowledge of Neotropical fauna, little studied until then except for the work of Stål (1860, 1873), was widely enriched by Reuter's monograph. Subsequently, this author described some new taxa (1909).

Another essential work for understanding the Neotropical fauna of anthocorids was made by Champion (1900), describing new taxa and with the particularity of providing excellent drawings of many of the species described by him. Also Poppius (1909, 1913) provided a number of new taxa for the continental fauna.

Other important taxonomical and faunistic contributions were chronologically made by Herring (1966a, b, 1976), especially the latter, with an excellent key using metapleural scent gland as a discriminatory character for genera. Péricart (1972) made an excellent monograph, and the same author (1996) wrote the catalog of Palaearctic fauna, very useful to show us his very authoritative point of view regarding the taxonomy of this group. Kelton (1978) made an excellent work on the fauna of Canada, very useful for those who work with Neotropical fauna. Later, Froeschner (1981, 1985) and Carpintero et al. (1997) made regional catalogs. Schuh and Slater

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(1995) and Lattin (2000) presented an overview of the family worldwide; the latter concentrated his review in managed ecosystems; Carpintero (2002) wrote the first catalog devoted to Neotropical species. Carpintero and Dellapé (2006, 2012) revised and described new Neotropical taxa.

Monophyly of the family Anthocoridae, after the excellent work of Carayon (1972), was challenged by posterior analysis by Schuh and Štys (1991) and Schuh et al. (2009) who studied the phylogenetic relationships of this group among the Cimicomorpha. Ying et al. (2008) and Min et al. (2012) followed this criterion, but they did not use the "Lasiochilidae" for their molecular analysis. Carpintero and Dellapé (2008) described and analyzed a series of new characters of the tribe Cardiastethini, highlighting the need for more extensive studies of the morphology of this group, as a previous step toward a best comprehension of their taxonomy.

With respect to morphology, biology, ecology, and importance of these bugs, it should be mentioned the above works of Carayon (1972), Péricart (1972), and Schuh and Slater (1995) and also the work on the biology of the Heteroptera by Miller (1971). Slater (1982) made an excellent characterization of the family.

The taxonomic criteria used in this chapter, which will give validity to family status of the Lyctocoridae, considered their morphological characters, in addition to their ecology, warrant the use of such taxonomic status. As for lasiochilines, they continue to be considered among the Anthocoridae. A review of this subfamily is still in arbitration for publication, which restore its status as a subfamily of Anthocoridae.

9.2 General Characteristics and Diagnosis

Anthocoridae are small to minute (1.15–5 mm) insects, somewhat flattened, with porrect head and ocelli always present in macropterous forms. First instar nymphs have five ommatidia. The labium is four segmented (but appears to be three segmented). The labrum is wide and flap-like. The metathoracic scent gland is deeply bilobed behind, and a median accessory gland is present. The forewing has an elongated, median chorial groove, with a short ventral fold, which does not reach the cuneus along the costal margin. In macropterous forms, a cuneus is present (except in *Amphiareus*), and the membrane has 3–4 not very evident veins. The hind wing has or lacks a hamus. Abdominal terga II and III have the dorsal laterotergites separated from the mediotergites, but tergum IV to the posterior end is entire (II and III are entire in a few brachypterous species). Nymphs have dorsal abdominal scent gland openings present between terga III–IV, IV–V, and V–VI (a vestigial gland opening is sometimes present between VI and VII). The tibiae have spongy fossae either well developed or vestigial; foretibiae in males are, in most of genera, armed with a row of teeth or spines in the inner margin; the tarsi have three segments. Male genitalia are always asymmetrical. Hemocoelic insemination is present in Anthocorinae. It occurs by the aedeagus that becomes a membranous tube, sliding along a groove in the left paramere. The coupling mode of Lasiochilinae is controversial, regarding the “normal” coupling suggested by Carayon (1957, 1972). A parietovaginal gland is present (Lasiochilinae). The paragenital system has either advanced seminal conceptacles or copulatory tubes. Fertilization takes place in the vitellarium. There are two to seven testes follicles. The ovipositor is usually developed or sometimes reduced. The principal salivary gland is bilobed, and the accessory gland is elongated (modified from Slater 1982).

Lyctocoridae are characterized by having males with left paramere flat, with a single-sheet form, and without median sulcus. The *phallus* is tubular and well visible, with *ductus seminis* striated transversely and extended apically by a *processus gonopori* called acus and with the shape of an injection needle. The female has genital apophyses in the middle of the anterior region of sternite VII.

Most species of Anthocoridae have functional wings and are capable of flight. In a few taxa, it occurs in both long-winged (macropterous) and short-winged (brachypterous) forms, e.g., species of *Xylocoris* and *Lasiochilus*, and some other are known only for brachypterous species as *Astemmocoris* and some Lasiochilinae and Cardiastethini.

It is noteworthy that, for a correct taxonomic characterization of this family, at least until the generic level, the shape of metathoracic scent gland is a character constant enough to be used successfully.

9.3 General Biology and Ecology

Anthocoridae are chiefly predaceous bugs that occur on a variety of habitats where they feed on different arthropods, including mites and insects. A few are plant feeders, at least in part, chiefly on pollen [e.g., *Orius insidiosus* (Say), *O. tristicolor* (White), and *Paratriphleps laeviusculus* (Champion)]. A European species occurs in ant nests [(*Xylocoris formicetorum* (Boheman)]. Little is known about this myrmecophilus species, but what is known suggests that other anthocorids may be found in such sites, perhaps even in termite colonies. Other species occurs in the litter layer (*Lasiochilus* spp., *Xylocoris* spp.), on forbs (*Orius* spp.), on shrubs (*Anthocoris* spp., *Orius* spp.), and on different parts of trees (*Anthocoris* spp., *Brachysteles* sp., *Lyctocoris* spp., and most of Scolopini Scolopina).

Long-distance movement of species of Anthocoridae seems to involve trivial movement combined with movements by air currents. Individuals in the litter layer may be picked up by wind disturbances and moved considerable distances. Southwood (1960) provided an extensive review of the flight activity of the Heteroptera. He reviewed captures of Anthocoridae by means of light and suction traps and airplanes. Glick (1957) did early studies on the arthropod distribution in the air column. One anthocorid that is well represented in his samples was *Orius insidiosus* (Say), a common species in a variety of agroecosystems. Southwood felt that the small size and limited flight capabilities of these bugs made them more dependent on long-range movement via upper air layers. Herring (1958, 1966a) related evidence of Heteroptera that has been moved in this way, specifically via hurricanes.

In view of many continental species of Anthocoridae found on the Caribbean Islands (e.g., *Lasiochilus*, *Cardiastethus*, *Brachysteles*, *Buchananiella*, and *Orius*), long-range movements over water seem to be the most reasonable way for these small insects to have originally colonized these islands. A similar phenomenon was noted on the Seychelles Islands by Distant (1913).

9.3.1 Eggs and Oviposition

The egg is ovoid or elongated, with a pale sculptured chorion and a usually circular operculum. There are neither fertilization tubes nor micropyles, but numerous pseudomicropyles are present.

The characters most useful for egg systematics, apart from the general shape and size, include the appearance of the chorial surface (smooth or covered with bumps, cross-linked or not), the shape and the cross-linking of the operculum, and the flange.

Cobben (1968) studied the embryonic development of various Anthocoridae (*Anthocoris*, *Orius*, *Lyctocoris*). The duration of embryonic development after spawning depends greatly on the temperature. The total duration of the hatching takes few minutes.

Oviposition varies according to the different developmental levels of the ovipositor of the females.

9.3.2 Nymph Feeding and Development

The nymphs do not differ greatly from the adult, and growth is driven by shedding or ecdysis. The last one, called fledging, is accompanied by full development of wings (for winged forms) and sexual organs. The normal number of nymphal stages is five, but it is possible that some species have four stages.

All nymphs from 1st to 5th instars are equipped with three dorsal abdominal odoriferous glands, more or less circular; they appear reddish by transparency in the early stages and come out by two posterior holes on the intersegmental membranes III–IV, IV–V, and VI–V. Nymphs do not bear ocelli.

The wing development appears only gradually in nymphs. Completely absent in the 1st instar, they are sometimes detectable in the 2nd nymph as slight posterior edges of the mesonotum and metanotum. In the 3rd instar, these wing pads are always visible and present in the form of small-posterior lateral extensions of the meso- and metanotal plates. In the 4th instar they are more developed, but hemelytra do not completely cover the hind wings. At the last 5th instar, hemelytral and wing extensions usually hide the hind wings (except on the inner edge). Tarsi show two segments at all nymphal stages. The sexual organs are externally invisible except at the 5th instar, where ovipositor of the female is apparent.

Nymphal food does not differ substantially from that of adults. The young Anthocoridae, after hatching, are voracious predators of small arthropods, and they attack the same prey that of adults, preferring only individuals proportional to their size (eggs and young larvae). The number of prey consumed can reach or exceed, in *Anthocoris* and *Orius*, several hundred mites or a hundred aphids during nymphal development of a single individual, and predatory activity is most important during the 5th instar. It seems at least one meal is needed between two molts, and the main meal precedes the ecdysis. Growth is sometimes compatible with a not predatory feeding habit (Péricart 1972).

Key for determining the age of nymphs (modified from Péricart 1972):

1. Without or with barely distinguishable wing pads..2
– Wing pads distinguishable..4
2. Eyes with only five well-developed ommatidia..3
– Eyes clearly with more than five ommatidia...2nd instar
3. Body length substantially less than 1.7 times that of the egg..................1st instar
– Body length substantially greater than 1.7 times that of the egg............2nd instar
4. The hemelytral and hind wing pads are very small. The first did not arrive at the basis of the second...3rd instar
– The hemelytral and hind wing pads are larger. The first, covering at least part of the second...5
5. The hemelytral pads do not reach the apex of functional wings.............4th instar
– The hemelytral pads arrive beyond the apex of functional wings............5th instar

9.3.3 Adult Feeding and Reproduction

Much of the Anthocoridae live on plants, on leaves, on branches, on flowers, or under the bark, where they seek their prey: Sternorrhyncha (aphids, Coccoidea, and psyllids), other Heteroptera (eggs or small nymphs), Thysanoptera (preferred preys of many Oriini), Lepidoptera (eggs or small caterpillars), Psocoptera and Collembola (which are also attacked), and Coleoptera, small species living under bark. They also feed on mites (*Tetranychus*) and oribatida living on plants (Péricart 1972). *Xylocoris* was found in poultry farms feeding on Diptera larvae and eggs, which were developed in the deposits of their feces. Others are subcortical predators of bark beetles (e.g., *Lyctocoris*, *Scoloposcelis*, and *Xylocoris*).

The Lasiochilinae inhabit the soil, but they also live on plants. Many species were reported as introduced in the USA on flowers and fruits (Horton et al. 2013). It is also noted that *Lyctocoris campestris* has the blood-sucking habit, and its presence in bird nests is very common (Aramburú et al. 2009). A tendency toward hematophagy is also manifested occasionally in many species of Anthocoridae. Biting of *Orius* and *Anthocoris* in humans has been reported many times in the Old World (Péricart 1972).

Predatory habits of most Anthocoridae are well recognized; the plant-feeding habits of some are less well known and documented (Lattin 1999).

It is very important to note that many species of this family are polyphagous, feeding on prey and also on plant juices, which determines their success to develop in different environments, both natural and anthropized.

The Anthocoridae sensu lato have in common with other Cimicoidea families (Cimicidae, Polyctenidae, Plokiophilidae) and Nabidae a peculiar mode of insemination which distinguish them from other Hemiptera. In these groups, insemination is not done by pouring the sperm in the female genital tract but injecting it in the hemocoel or in organs secondarily developed for this purpose and not associated with the genital vias, which are subsequently reached. This phenomenon is called "traumatic insemination."

9.4 Classification and Diversity

The family Anthocoridae sensu lato contains between 400 and 600 species distributed worldwide (Lattin 1999) including two families: Anthocoridae and Lyctocoridae. In the Neotropical region, there are 39 genera and 128 known species of Anthocoridae and two genera and six species of Lyctocoridae.

- Anthocoridae Fieber *(sensu lato)*
  - Anthocorinae Fieber (*sensu* Schuh and Štys 1991)
    - Anthocorini Fieber
    - Oriini Carayon
    - Scolopini Carayon
    - Almeidini Carayon (not present in the Neotropics)
    - Blaptostethini Carayon
    - Cardiastethini Carayon
    - Xylocorini Carayon
  - Lasiochilinae Carayon
- Lyctocoridae Reuter

Key for suprageneric taxa of Anthocoridae (sensu lato) present in the Neotropics (modified from Carayon 1972; Péricart 1972; Herring 1976; Kelton 1978; Schuh and Slater 1995; and Carpintero 2014):

1. Male with left paramere flat, single-sheet form, without median sulcus. *Phallus* tubular, well visible, with *ductus seminis* striated transversely and extended apically by a processus gonopori called acus, with the shape of an injection needle. Female with genital apophyses in the middle of the anterior region of sternite VII...Lyctocoridae

– Male with left paramere with different shapes but always with a median sulcus throughout much of its length. *Phallus* in membranous tube shape, or with lateral membranous lobes, apically never as an acus. Females without a genital apophysis in sternite VII...Anthocoridae...2

2. Metapleural scent gland curved or straight and directed backward and never prolonged by a carina..Lasiochilinae
– Metapleural scent gland curved forward, sometimes prolonged by a carina. If curved backward, it is prolonged by a carina and directed forward.......................
.............................Anthocorinae...3
3. Antennal segments II–IV of equal thickness; segment III and IV fusiforms, with erected hairs never longer than twice the diameter of the segment.......................4
– Antennal segments III and IV always thinner than II, with erected hairs longer than twice the diameter of the segment..5
4. Claws with large pulvilli; anterior male tibiae with a row of teeth in their inner margin; left paramere spiraled..Oriini
– Claws without pulvilli; anterior male tibiae without a row of teeth in their inner margin; left paramere falciform...Anthocorini
5. Males with a brush of hair on the left side of the fourth abdominal sternum. Females with two short copulatory tubes opening medially in the intersegmental membranes VII–VIII, and each formed of an anterior segment and a posterior segment..Blaptostethini
– Males without the above brush of hairs. Females, if having copulatory tubes, are never with these features...6
6. Males with a unique glandular opening on sternum IV or V. Metapleural scent gland is short and gently curved forward and whose apex is located near the center of the metapleura.......................................Scolopini...............................7
– Males without glandular opening on sternum IV or V. Metapleural scent gland is long and strongly curved forward and whose apex reaches the anterior margin of the metapleura. If the apex of the scent gland does not reach the anterior margin of the metapleura that extends to the anterior margin by a thin carina.................8
7. The body is oval, with long and thin legs. Anterior femora are not thickened nor provided with teeth or spines. The corium is punctate. Metasternum with a median longitudinal carina...Calliodina
– Body depressed dorsoventrally, with subparallel sides. Legs robust. Femora, especially the anterior and posterior ones, are very thick and provided with spines or teeth on the ventral edge. The corium is smooth. Metasternum without a median carina...Scolopina
8. Ovipositor well developed; anterior tibiae widened at its apex, with a wide *fossula spongiosa*. Metapleural scent gland is never prolonged by a carina. Externally angular...Xylocorini
– Ovipositor vestigial; anterior tibiae thin, with *fossula spongiosa* vestigial or very small. Metapleural scent gland is prolonged by a carina and directed forward. If there is no carina, it is externally rounded..Cardiastethini

Plate 9.1

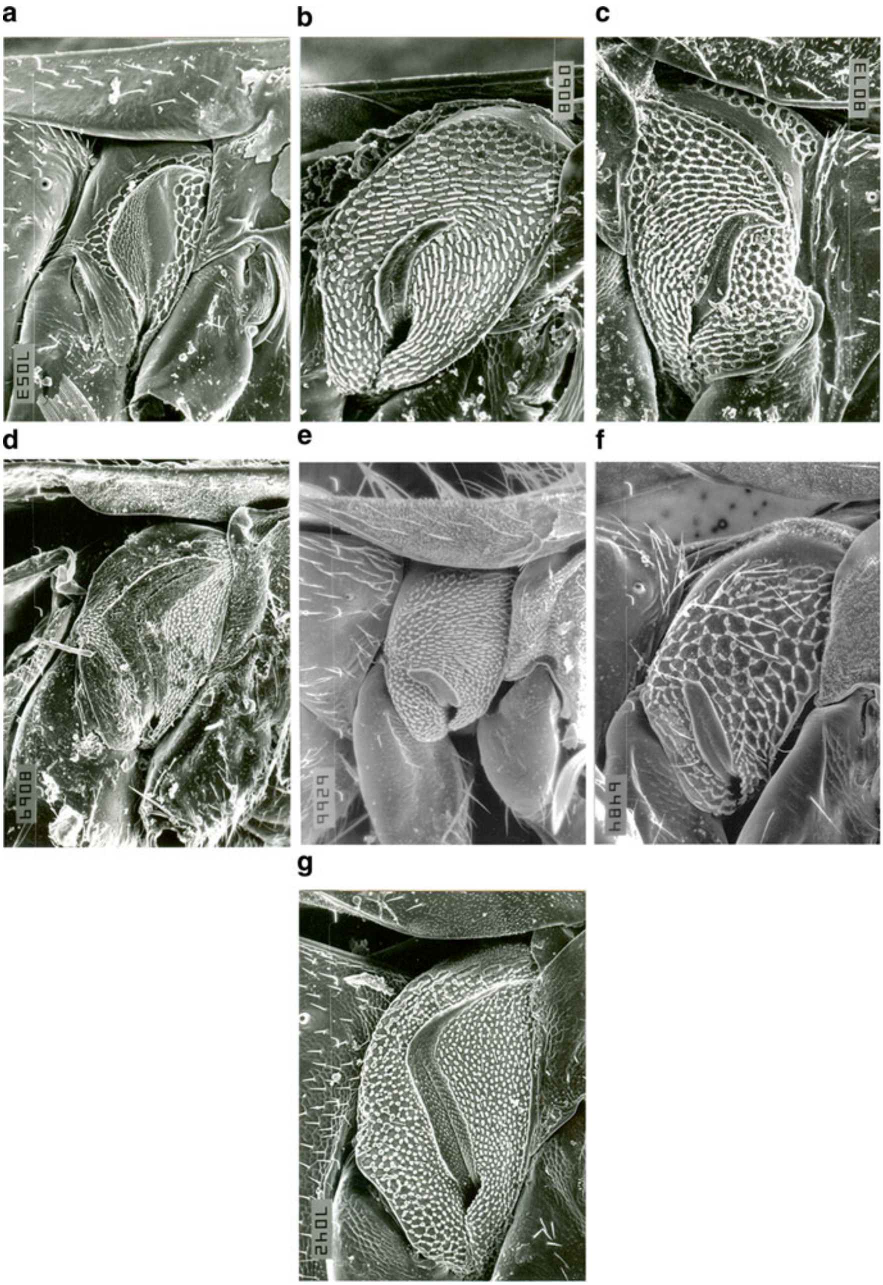

Plate 9.1 (**a**) Genus *Orius* (Oriini), metapleura. (**b**) Genus *Calliodis* (Scolopini), metapleura. (**c**) Genus *Buchananiella* (Cardiastethini), metapleura. (**d**) Genus *Xylocoris* (Xylocorini), metapleura. (**e**) Genus *Lasiochilus* (Lasiochilinae), metapleura. (**f**) Genus *Plochiocoris* (Lasiochilinae), metapleura. (**g**) Genus *Lyctocoris* (Lyctocorinae), metapleura (Photos by D Carpintero)

9.4.1 Main Species

Several species of Anthocoridae are used in biocontrol, some with great success in recent years, such as species of the genus *Orius*, *Anthocoris*, *Montandoniola*, and *Xylocoris*, to control important agricultural pests such as thrips, aphids, and lepidopteran larvae (Schuh and Slater 1995).

The Neotropical species of the tribes of Anthocoridae, most used as biocontrol agents, are listed below as well as their distribution:

Abbreviations: CA = Central America; CI = Caribbean Islands; PC = Pacific Islands; SA = South America

Family Anthocoridae Fieber
Subfamily Anthocorinae Fieber
Tribe Xylocorini Carayon
Xylocoris (*Arrostelus*) *flavipes* (Reuter)
  Dist. SA
X. (Proxylocoris) afer (Reuter)
  Dist. CA, CI, SA
X. (P.) albonotatus (Champion)
  Dist. CA
X. (P.) bimaculatus (Champion)
  Dist. CA
X. (P.) cacti Carayon
  Dist. CA
X. (P.) sordidus (Reuter)
  Dist. CA, CI, PC, SA
X. (X.) vicarius (Reuter)
  Dist. SA

Remarks: Yamada et al. (2006) Ballal et al. (2003), and Sing and Arbogast (2008) demonstrated the use of several species of this genus to control, especially of, stored grain pests.

Tribe Anthocorini Fieber
Anthocoris albiger Reuter
  Dist. CA
A. antevolens Buchanan-White
  Dist. CA, SA
A. dentipes Champion
  Dist. CA
A. fulvipennis Reuter
  Dist. CA
A. nigripes Reuter
  Dist. CA

A. obsoletus (Blanchard)
  Dist. SA
A. rufotinctus Champion
  Dist. CA
A. variicornis Champion
  Dist. CA
A. variipes Champion
  Dist. CA
Dufouriellus ater (Dufour)
  Dist. SA
Elatophilus (E.) antennatus Kelton
  Dist. CA
Macrotrachelia albovittata Champion
  Dist. CA
M. elongata Champion
  Dist. CA
M. nigronitens (Stål)
  Dist. CA, SA
M. nitida Champion
  Dist. CA
M. opacipennis Champion
  Dist. CA
M. thripiformis Champion
  Dist. CA
Melanocoris nigricornis Champion
  Dist. CA
M. obovatus Champion
  Dist. CA

Remarks: Species of this tribe are used in biocontrol of Homoptera (Mullois-Juan and Bravaccini 2009; Péricart 1972).

Tribe Oriini Carayon
Macrotracheliella conica (Blanchard)
  Dist. SA
M. laevis Champion
  Dist. CA, SA
Orius alcides Herring
  Dist. SA
O. brevicollis (Blanchard)
  Dist. SA

O. championi Herring
  Dist. CA, SA
O. euryale Herring
  Dist. CA
O. flaviceps (Poppius)
  Dist. CA, CI
O. florentiae Herring
  Dist. SA
O. fuscus (Reuter)
  Dist. CA, SA
O. insidiosus (Say)
  Dist. CA, CI, SA
O. ixionides Herring
  Dist. CA
O. jasiones Herring
  Dist. CA
O. lesliae Herring
  Dist. SA
O. pallidus (Poppius)
  Dist. SA
O. pele Herring
  Dist. SA
O. perpunctatus (Reuter)
  Dist. CA, CI, SA
O. pumilio (Champion)
  Dist. CA CI
O. thyestes Herring
  Dist. SA
O. tristicolor (Buchanan-White)
  Dist. CA, CI, PC, SA
Paratriphleps laeviusculus Champion
  Dist. CA, CI, SA
P. pallidus (Reuter)
  Dist. CI

Remarks: Probably this group includes the anthocorids which are more used as biocontrol. They are particularly used to control thrips populations in cultivated plants (Péricart 1972; Kelton 1978; Lattin 1999).

Plate 9.2

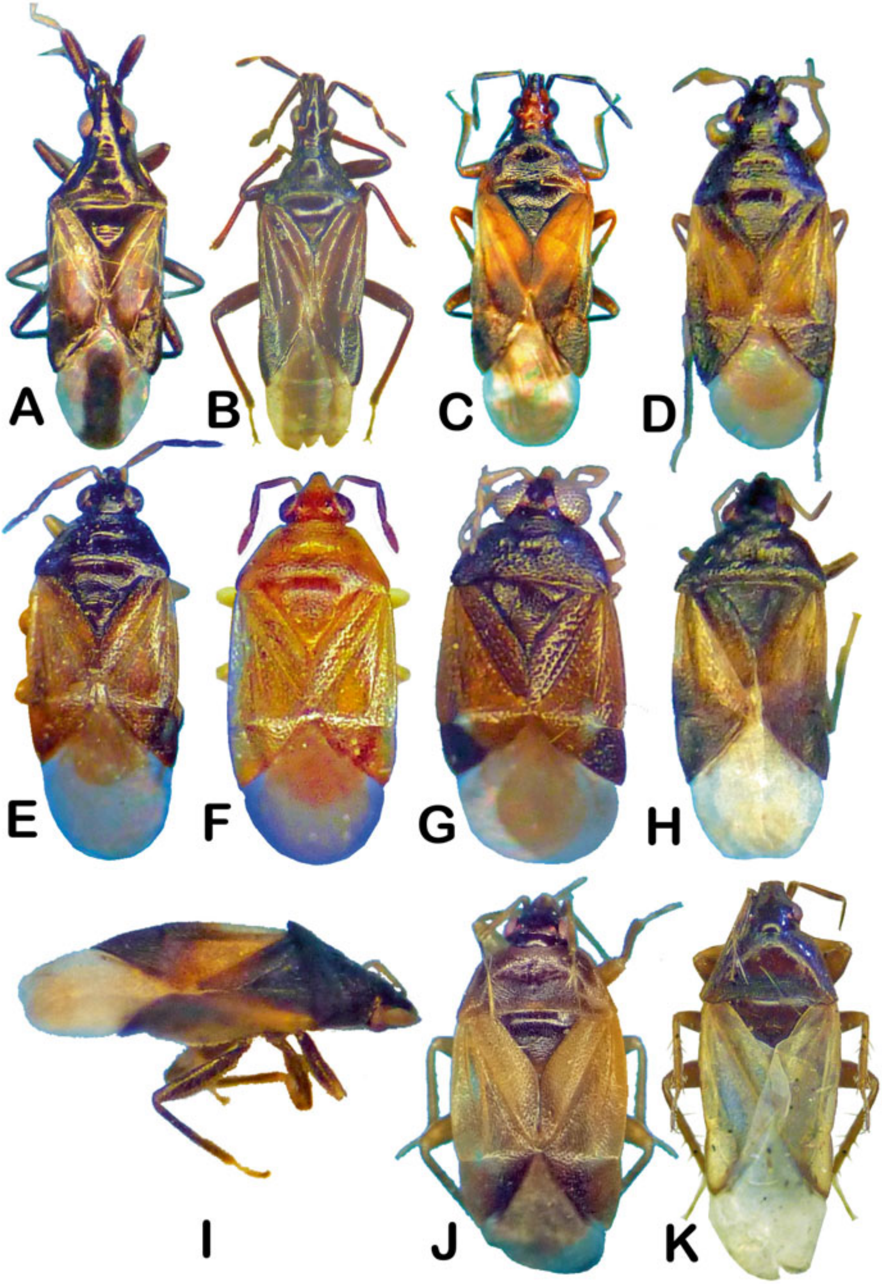

Plate 9.2 (**a**) *Montandoniola moraguesi* (Oriini), habitus. (**b**) *Macrotrachelia nigronitens* (Anthocorini), habitus. (**c**) *Anthocoris nemoralis* (Anthocorini), habitus. (**d**) *Orius insidiosus* (Oriini), habitus. (**e**) *Orius reedi* (Oriini), habitus. (**f**) *Orius pallidus* (Oriini), habitus. (**g**) *Orius perpunctatus* (Oriini), habitus. (**h**) *Orius tristicolor* (Oriini), habitus. Dorsal view. (**i**) *Orius tristicolor* (Oriini), habitus. Lateral view. (**j**) *Lyctocoris campestris* (Lyctocoridae), habitus. (**k**) *Xylocoris flavipes* (Xylocorini), habitus (Photos by D Carpintero)

There are also three known introduced species in the Neotropics: *Montandoniola moraguesi* (Puton) (Anthocorinae: Oriini).

Remarks: Palearctic distribution. Introduced in Bermuda and Hawaii for biocontrol of thrips (Dobbs and Boyd 2006). Expanded to Central and South America. First record for Brazil and Argentina.

Blaptostethus pallescens Poppius (Anthocorinae: Blaptostethini)
Remarks: This species is distributed in Asia and Africa, introduced in Brazil (first record), and studied as a biocontroller of the stored rice grain moth, *Corcyra cephalonica* Stainton (Ballal et al. 2003).

Anthocoris nemoralis (F.) (Anthocorinae: Anthocorini)
Remarks: Palearctic distribution. This species is introduced in Canada, first recorded in the Neotropics of Chile, and used in Europe for biocontrol of *Cacopsylla pyri*, a pest of pears (Carpintero 2014).

9.4.2 Secondary Species

Family Lyctocoridae Reuter
Astemmocoris cimicoides Carayon & Usinger
  Dist. SA
Lyctocoris (L.) *campestris* (F.)
  Dist. CA, PC, SA
L. (L.) latus Poppius
  Dist. SA
L. (L.) mexicanus Kelton
  Dist. CA
L. (Metriosteles) signoreti Reuter
  Dist. SA
L. (M.) spanbergii Reuter
  Dist. SA

Plate 9.3

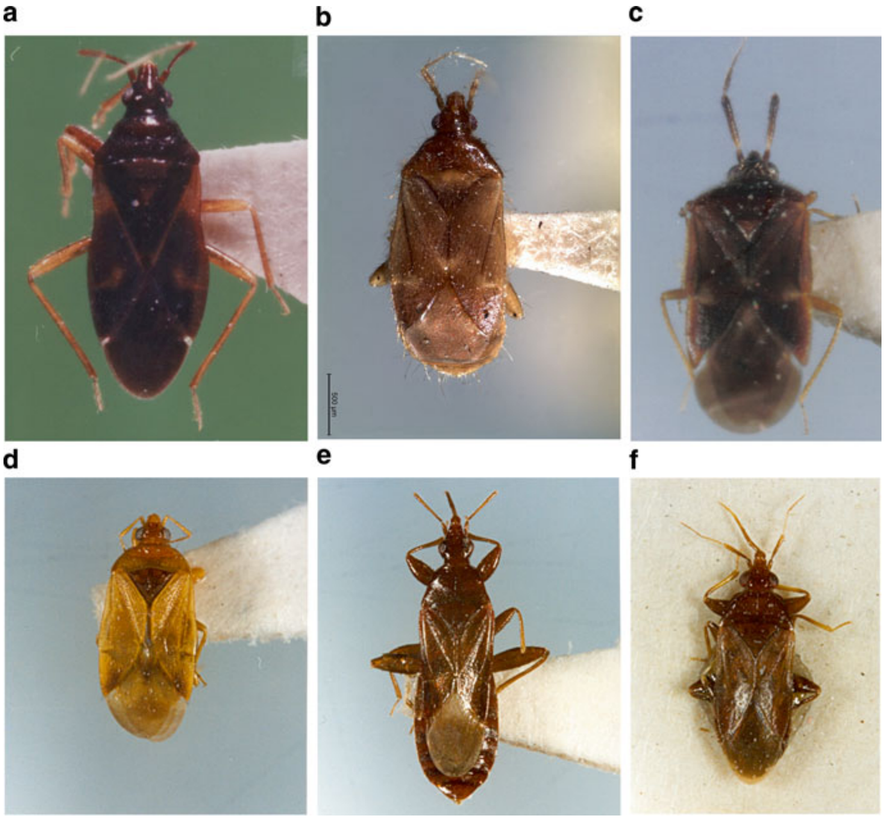

Plate 9.3 (**a**) *Lasiocolpus minor* (Lasiochilinae), habitus. (**b**) *Dilasia microps* (Lasiochilinae), habitus. (**c**) *Buchananiella continua* (Cardiastethini), habitus. (**d**) *Calliodis pallescens* (Scolopini Calliodina), habitus. (**e**) *Scolopocoris gracilicornis* (Scolopini Scolopina), habitus. (**f**) *Solenonotus* sp. (Scolopini), habitus (Photos by D Carpintero)

Family Anthocoridae Fieber
Subfamily Lasiochilinae Carayon
(Modified from Carpintero 2002)
Dilasia ashlocki (Herring)
  Dist. PC
D. basalis (Reuter)
  Dist. CA, CI, SA
D. colludens (Buchanan-White)
  Dist. SA
D. foveicollis (Champion)
  Dist. CA, CI
D. fuscula Reuter
  Dist. CA, CI

D. reuteri (Champion)
Dist. CA
D. unicolor (Reuter)
Dist. CA, CI, SA
Eusolenophora divisa (Champion)
Dist. CA, CI
E. testacea Poppius
Dist. SA
Lasiochilus galateae Reuter
Dist. SA
L. hirtellus Drake & Harris
Dist. CA, CI
L. microps Champion
Dist. CA, CI, SA
L. mirificus Drake & Harris
Dist. CA, CI
L. pallidulus Reuter
Dist. CA, CI, PC, SA
L. punctipennis Champion
Dist. CA, SA
L. sulcatus Champion
Dist. CA, SA
L. sulcicollis Reuter
Dist. SA
L. varicolor Uhler
Dist. CA, CI, SA
Lasiocolpus biguttatus Poppius
Dist. SA
L. elegans Reuter
Dist. SA
L. minor Champion
Dist. CA
L. rostralis (Poppius)
Dist. SA
L. sinuaticollis Reuter
Dist. CA
L. unicolor Poppius
Dist. SA
Plochiocoris longicornis Champion
Dist. CA, CI, SA
P. pilosus (Reuter)
Dist. SA

Tribe Cardiastethini Carayon
Alofa sodalis (Buchanan-White)
  Dist. CI, PC, SA
Amphiareus constrictus (Stål)
  Dist. CA, PC, SA
Buchananiella continua (Buchanan-White)
  Dist. SA
B. devia Bergroth
  Dist. PC
Cardiastethus aequinoctialis Poppius
  Dist. PC, SA
C. cubanus Poppius
  Dist. CI
C. elegans (Blanchard)
  Dist. SA
C. flavus Poppius
  Dist. CI
C. fraterculus Van Duzee
  Dist. CA, CI
C. rugicollis Champion
  Dist. CA, CI
C. testaceus (Blanchard)
  Dist. SA
C. tropicalis Champion
  Dist. CA, CI
C. uhleri China
  Dist. CA, CI
Dasypterus assimilis Reuter
  Dist. CA CI
D. discifer (Stål)
  Dist. SA
D. limbatellus (Stål)
  Dist. CA, PC, SA
D. ophthalmicus (Reuter)
  Dist. CA, SA
Dolostethus pubescens Henry & Herring
  Dist. SA
Pehuencoris gurguliophagus Carpintero & Dellapé
  Dist. SA
Physopleurella floridana Blatchley
  Dist. CI, SA

Tribe Scolopini Carayon
Subtribe Calliodina Carayon
Calliodis bifasciatus (Champion)
Dist. CA, CI
C. clarus (Buchanan-White)
Dist. SA
C. coloratus (Poppius)
Dist. SA
C. crawfordi (Poppius)
Dist. CA
C. maculipennis (Reuter)
Dist. CI
C. nebulosus (Uhler)
Dist. CA, CI, PC
C. pallescens (Reuter)
Dist. CA, CI, SA
C. picturatus Reuter
Dist. SA
C. pictus (Uhler)
Dist. CA, CI
C. punctatostriatus (Reuter)
Dist. CA, SA
C. signatus (Poppius)
Dist. CI
Eulasiocolpus megalops Champion
Dist. CA, SA
Guayascoris fereroi Carpintero & Dellapé
Dist. SA
Lasiocolpoides ciliatus Champion
Dist. CA
Lepidonannella opaca (Poppius)
Dist. SA
Nidicola aglaia Drake & Herring
Dist. CA
N. engys Drake & Herring
Dist. CA
N. etes Drake & Herring
Dist. CA
N. marginata Harris & Drake
Dist. CA

N. mazda Herring
Dist. PC
N. mitra Drake & Herring
Dist. CA
Opisthypselus punctaticollis Reuter
Dist. CA, SA
Zopherocoris armatus (Stål)
Dist. CA, SA

Subtribe Scolopina Carayon
Ameroscolopa flavicornis (Reuter)
Dist. CA, GT, MX
A. basilicus (Drake & Harris)
Dist. NA
Lasiochiloides denticulatus Champion
Dist. CA
L. socialis Drake & Harris
Dist. CA
Scolopa wygodzinskyi Carayon
Dist. SA
Scolopella brasiliensis Carayon
Dist. SA
Scolopocoris gracilicornis (Poppius)
Dist. SA

Remarks: Many of these species could potentially be used as biocontrol, using their versatility in the selection of their prey (Lyctocoridae), their wide diversity and large populations in the Neotropics (Calliodina), the diversity of environments that colonize (Cardiastethini), and their resistance (Lasiochilinae), allowing them to be transported over long distances and colonize new areas.

9.5 Concluding Remarks

Lattin (1999) mentioned that "colonization of non-native species is a worldwide problem that affects natural biological diversity and alters species richness whenever it occurs."

There are three species of Anthocoridae that have been introduced into Neotropical areas, accidentally or deliberately. Among them, only *Montandoniola moraguesi* (Puton) was intentionally introduced for biocontrol purposes and appears to have become established. Probably there are other nonindigenous species that await discovery and recognition.

Over recent years we have received inquiries about the identity of anthocorid species found in both wild and cultivated areas. The presence of alien species found in these samples, plus the purchase by producers of *Orius insidiosus* from abroad, should be of alert to those responsible for plant health and quarantine. We do not believe it is necessary to introduce new foreign species into our fauna for biocontrol, because the Neotropics has many species of anthocorids potentially suitable for such purpose.

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Chapter 10
Plant Bugs (Miridae)

Paulo S.F. Ferreira, Thomas J. Henry, and Lívia A. Coelho

Abstract The Miridae, or plant bugs, with more than 1,300 genera and 11,130 described species, represent the largest and most diverse family of Heteroptera. Although many plant bugs are phytophagous and may cause serious damage to crops, a great many are predatory and may be important in biological control programs. In the Neotropics, about 561 genera and more than 3,400 species are included in seven of the world's eight recognized subfamilies. In this chapter, we give an overview of the classification, general life history, and economic importance and provide identification keys to the Neotropical subfamilies and tribes. For each subfamily, we present a brief diagnosis, an overview of the respective tribes and subtribes, and key literature.

10.1 Introduction

The classification of the Miridae was first outlined by Reuter (1910), who recognized nine subfamilies and 18 divisions. Van Duzee (1917), in his catalog of the Hemiptera of North America north of Mexico, modified Reuter's names and arrangement and listed seven subfamilies. Knight (1923) recognized nine subfamilies based on studies of the arolia (parempodia), pretarsi, and genitalic structures, a grouping similar to that used by Van Duzee (1917). Carvalho (1952) published a synopsis of the higher classification of the family in which he listed six subfamilies, not including Isometopinae, and 24 tribes. Schuh (1976), in evaluating

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pretarsal structures and femoral trichobothria, presented a cladistic analysis that supported a novel six-subfamily arrangement, including the Psallopinae and Isometopinae, but with the Deraeocorinae merged with the Mirinae and the Orthotylinae merged with the Phylinae. Although generally accepted by European hemipterists, Schuh's inclusion of the Isometopidae as a subfamily of Miridae marked the first time that this arrangement had been accepted in the Western Hemisphere. Schuh et al. (2009) recognized seven subfamilies, omitting the Psallopinae, and Jung and Lee (2012), likewise, supported a seven-family classification (minus Psallopinae) based on molecular sequence data, although they considered the Bryocorinae polyphyletic with the bryocorines (Bryocorini) and dicyphines (Dicyphini) having widely separated positions on their cladogram. Carvalho's (1955a) keys to the genera of the world and first modern world catalog (Carvalho 1957, 1958a, b, 1959, 1960) stimulated major interest in the family, and Schuh's (1995) much-needed update was followed by an invaluable online version (Schuh 2013) that has given unprecedented access to information on the Miridae throughout the world. Currently, eight subfamilies (Bryocorinae, Cylapinae, Deraeocorinae, Isometopinae, Mirinae, Orthotylinae, Phylinae, and Psallopinae) are recognized (Henry 2009; Schuh 2013).

The Miridae, commonly called plant bugs (United States and Canada), capsids (Britain), *Blindwanzen* (Germany), and *blomstertaeger* (Denmark), represent the largest family of Heteroptera (Henry and Wheeler 1988; Schuh and Slater 1995; Wheeler 2000a; Henry 2009) and one of the 20 most diverse families of Insecta (Cassis and Schuh 2012), with more than 11,130 described species (Schuh 2013). Henry and Wheeler (1988) suggested that the world fauna will approach 20,000 once the Neotropical species are fully studied. Plant bugs are found in all major zoogeographic regions of the world, except the Antarctic, with centers of diversity in tropical and Mediterranean ecosystems (Wheeler 2001; Cassis and Schuh 2012; Schuh 2013).

The Miridae form a monophyletic group (Wheeler et al. 1993; Wheeler 2001; Schuh et al. 2009; Jung and Lee 2012) characterized by the presence of femoral trichobothria, the loss of nymphal dorsal abdominal scent glands between segments 4 and 5, asymmetrical parameres, two- or three-segmented tarsi, small pulvilli attached near the bases of the claws, a triangular cuneus at the apex of the corium, and a hemelytral membrane with one or two closed cells (Schuh et al. 2009).

The fossil Miridae are insufficiently studied, and although a large number of species have been named (Wheeler 2001), most of them need revision (Zherikhin 2002; Grimaldi and Engel 2005). The earliest fossil mirid is recorded from the Upper Jurassic (Kukalová-Peck 1991; Shcherbakov and Popov 2002; Yao et al. 2007; Jung and Lee 2012). Leston (1979) suggested that the primary speciation of the Miridae took place during the Upper Cretaceous or Lower Cenozoic, following the rise of the angiosperms to dominance (Crepet 1979; Wheeler 2001). Based on molecular data, using the oldest available fossils as calibration points, Jung and Lee (2012) hypothesized that the earliest mirids may have evolved as early as the Permian.

10.2 General Characteristics and Diagnosis (Fig. 10.1)

Many plant bugs are often brightly colored red, orange, and yellow, often with spots and stripes, but the majority are more cryptically colored, often mottled green, gray, brown, or black, blending in remarkably well with their surroundings (Henry and Wheeler 1988; Wheeler and Henry 2004; Henry 2009). Myrmecomorphy is common in the family (Henry 2009), especially in the subfamilies Mirinae (e.g., Herdoniini), Orthotylinae (e.g., Ceratocapsini), and Phylinae (e.g., Cremnorrhini and Pilophorini). The adults vary considerably in size and appearance. They range

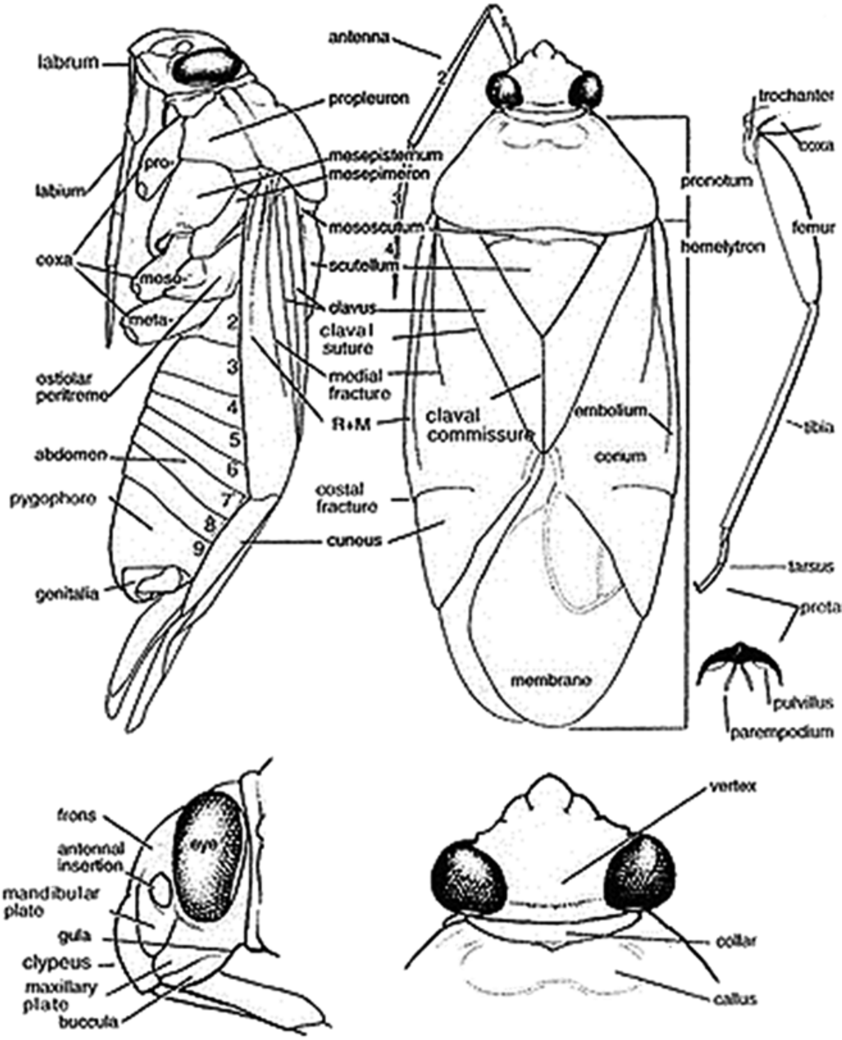


Fig. 10.1 Miridae general morphology (After Schwartz and Foottit 1992)

from little more than one mm, as in certain species of *Tytthus* Fieber, to 15 mm or more in some Neotropical Restheniini. They are elongate to ovoid. The head is triangular and usually prognathous. The eyes are usually large, and ocelli, considered plesiomorphic, are present only in the subfamily Isometopinae. The antennae and labium are four segmented. Most species are fully winged (macroptery), though submacroptery, brachyptery, microptery, and coleoptery are widespread, as are intraspecific wing polymorphism and sexual dimorphism. The hemelytra are distinctive, with the corium divided distally into a triangular cuneus and an apical membrane with one or two unequal cells divided by a short longitudinal vein, a character that is apomorphic for mirids. Trochanters of all legs are divided. The middle and hind femora possess two to 10 trichobothria on the ventral and lateral surfaces. The tarsi are most often three segmented. The pretarsus includes the claws, which can be simple or toothed, with setiform or fleshy parempodia and commonly with fleshy pulvilli and pseudopulvilli. The metathoracic scent glands are paired, and the external efferent or evaporative system is usually well developed. The evaporatorium occupies less than half of the metepisternum with a variably shaped and often diagnostic ostiolar peritreme. The metathoracic spiracle is either exposed and teardrop shaped or recessed. The male genitalia are asymmetrical, including the parameres and endosoma. The endosoma is partially membranous, often inflatable, and is confined by a sclerotized phallotheca. The female ovipositor is laciniate; the sperm storage organ is a large, saclike structure. Male and female genitalia have characters important in inferring higher-group relationships and identifying species (Davis 1955; Kelton 1959; Schuh 1975, 1976; Fontes 1981, 1989, 1996; Henry and Wheeler 1988; Schuh and Slater 1995; Wheeler 2001; Cassis and Schuh 2012).

10.3 General Biology and Ecology

Plant bugs are ecologically successful because of their high species diversity, large populations, and wide geographic ranges (Wheeler 2001). Various mirids have distributions that correspond with long-recognized biogeographic regions and intercontinental patterns (e.g., Gondwanan or Paleotropical) (Schuh and Slater 1995). Biogeographic studies have identified centers of endemism, interrelationships, and areas of species richness correlated with areas with high endemism (Wheeler 2001).

Mirids are abundant across a variety of habitats, ranging from mountain tops to salt marshes and coastal dunes (Southwood and Leston 1959; Marples 1966; Denno 1977; Wheeler 2001). Many species specialize in glandular-hairy and even carnivorous plants (Wheeler 2001), and species of *Ranzovius* Reuter are among the few heteropterans that live as commensals in spider webs (Wheeler and McCaffrey 1984; Henry 1999).

The habits and biology of the Miridae have been documented in numerous, widely scattered publications (Henry 2009). Wheeler (2000a, b, 2001) synthesized data on the biology, hosts, and habits, significantly increasing knowledge of the family. Much of what we know about courtship and oviposition behavior, fecundity, longevity, and voltinism is the result of studies involving species of agricultural importance. The life histories of most plant bugs, however, are unknown.

Miridae may have a significant economic impact on agricultural crops. Many species are major pests (Wheeler 2000a, 2001; Henry 2009; Cassis and Schuh 2012), whereas others are predatory and considered beneficial and have great potential as biological control agents (Wheeler 2000b; Sanchez et al. 2004; Cassis and Schuh 2012). Because even small mirid populations can cause severe injury, applied entomologists frequently underestimate the importance of plant bugs. Feeding symptoms in the Miridae probably are more diverse than in any other heteropteran family (Wheeler 2000a). Most crop plants have at least one mirid species among their complement of pests. Changes in agricultural practices have been responsible for increasing the host range of many plant bugs, and the introduction of numerous exotic plants has increased the supply of new hosts and has allowed the establishment of nonnative taxa around the world (Wheeler 2001).

Mirids often are not recognized as predators. Species with predatory habits do not exhibit the typical specialized morphological characteristics for capturing prey. Predation by mirids on arthropod eggs and early instars of other arthropods make them potentially important in biological control (Wheeler 2000b). Even plant bugs that are significant crop pests can, under certain conditions, be considered beneficial because they are able to switch from phytophagy to zoophagy (Wheeler 2000a, b, 2001). A mirid that is normally a key crop pest can become an important predator of other pests on the same crop. Some species have been described either as pests or as useful natural enemies, depending on where they occur, seasonality, hosts, control measures, and availability of alternative food sources (Wheeler 1976, 2000b, 2001).

Their piercing-sucking mouthparts and the presence of powerful salivary secretions allow mirids to explore nutrient resources, such as dried carrion and feces (Wheeler 2001). Most plant bugs are oligophagous, occurring on members of one plant family or on plants belonging to a few closely related families (Wheeler 2000a). Only a few species are considered monophagous (Wheeler 2001). For example, Pires et al. (2007, 2008) showed that *Platyscytus decempunctata* (Carvalho) feeds only on *Solanum cernuum* Vell. (Solanaceae). In contrast, some species are strongly polyphagous, such as *Lygus lineolaris* (Palisot de Beauvois), which may feed on more than 300 plants (Young 1986).

10.4 Life History

Mirids often have life cycles that last no more than six weeks. They usually have five nymphal instars, although the number may be as low as three or as high as six (Schuh and Slater 1995; Wheeler 2001). They reach the adult stage in 15–30 days. Eggs are usually inserted into plant tissue. In most temperate regions, mirids are univoltine and overwinter in the egg stage. Others, however, such as *Lygus* spp., have multiple generations per year and often overwinter as adults. Eclosion occurs in early to late spring in phytophagous species, which are associated with new growth and flower development of the host plant. Predatory species often have life cycles synchronized with those of their preferred prey and usually appear as adults later in the season than phytophagous species. The life histories of most tropical Miridae, however, are poorly studied or are unknown (Schuh and Slater 1995; Wheeler 2001).

Plant bugs are remarkable for their genitalic evolution (Kelton 1959; Cassis and Schuh 2012), including traumatic insemination and sexual antagonistic coevolution (Tatarnic et al. 2006; Tatarnic and Cassis 2010; Cassis and Schuh 2012). Parthenogenesis occurs in a few mirid species, such as the predatory *Campyloneura virgula* (Herrich-Schaeffer), where males are rare (Wheeler and Henry 1992; Henry 2012a).

The Miridae have significant potential as indicators of ecological changes, mainly because they are susceptible to many pesticides and are vulnerable to habitat disturbances (Fauvel 1999; Wheeler 2001). Brown (1991) presented a list of mirids as potential bioindicators in conservation biology studies. Taking into account their great species diversity, wide range of feeding habitats, and the damage they inflict on fruits, field crops, and ornamental plants, the Miridae are among the most important of all insect groups (Henry and Wheeler 1988; Wheeler 2001; Cassis and Schuh 2012).

10.5 Classification and Diversity

The Miridae, placed (with Thaumastocoridae and Tingidae) in the superfamily Miroidea, are currently separated into eight subfamilies: Bryocorinae, Cylapinae, Deraeocorinae, Isometopinae, Mirinae, Orthotylinae, Phylinae, and Psallopinae (Schuh 2013). More than 11,130 described species are included in 44 tribes worldwide (Schuh 2013; Schuh and Menard 2013).

All mirid subfamilies represented in the Neotropics (considering all of Mexico, Central and South America, and the West Indies), except the Psallopinae (Wolski and Henry 2015). About 3,429 species and 561 genera are included in 25 tribes, representing 27 % of the world mirid fauna. Mexico has about 621 species; Central America, 440; South America, 2,008; and the West Indies, 406. Tables 10.1 and 10.2 show countries of the Neotropical Region with their subfamilies, tribes, number of genera, and species represented. The countries with the largest number of genera and species are Brazil (280 genera, 1,081 species), Mexico (213, 621), Argentina (163, 524), Peru (124, 327), and Panama (112, 234). For the largest islands of the West Indies (Hernández and Henry 2010), Cuba has 57 genera and 105 species recorded; Puerto Rico, 40 and 63; Jamaica, 36 and 48; Hispaniola, 22 and 28; and Grenada, 15 and 23. Mexico has 20 tribes; Central America, 23; and South America, 22. The majority of the genera are represented by only a few species (Fig. 10.2); 49 % percent have only one species; 62 %, one or two species; and 75 %, one to four species.

The Neotropical genera with the greatest numbers of species in descending order are *Prepops* Reuter (Mirinae), *Phytocoris* Fallen (Mirinae), *Eccritotarsus* Stål (Bryocorinae), *Ceratocapsus* Reuter (Orthotylinae), *Taedia* Distant (Mirinae), *Orthotylus* Fieber (Orthotylinae), *Pycnoderes* Guérin-Menèville (Bryocorinae), *Lopidea* Uhler (Orthotylinae), *Fulvius* Stål (Cylapinae), and *Dagbertus* Distant (Mirinae).

The percentages of Neotropical species by subfamily (Fig. 10.3) in descending order are Orthotylinae (33 %), Mirinae (28 %), Deraeocorinae (14 %), Bryocorinae (10 %), Cylapinae (7.4 %), Phylinae (7 %), and Isometopinae (0.50 %). Ninety percent of the Miridae in the Neotropical Region are represented in the following tribes: Orthotylini (34 %) (Orthotylinae), Mirini (19 %) (Mirinae), Eccritotarsini (10 %) (Bryocorinae), Phylini (8 %) (Phylinae), Deraeocorini (8 %) (Deraeocorinae), Herdoniini (5 %) (Mirinae), Restheniini (3 %) (Mirinae), and Clivinematini (3 %) (Deraeocorinae).

Most of the literature supporting the study of Neotropical Miridae is found primarily in taxonomic papers, including keys; catalogs; reviews of subfamilies, tribes, and genera; and descriptions of genera and species (e.g., Carvalho 1955a, 1957–1960; Schuh 1995, 2013; Carvalho and Costa 1997; Ferreira 1980; Ferreira and Henry 2011).

Maldonado's (1969) Miridae of Puerto Rico and Hernández and Henry's (2010) Miridae of Cuba contain diagnoses and keys to the subfamilies, tribes, genera, and species that are useful in recognizing many of the more widely distributed taxa. Studies on insect-plant relationships, biogeography, and integrated pest management are few, but see literature cited in Ferreira et al. (2001), Ferreira and Henry (2011), Schuh (1991, 2014), and Wheeler (2000a, b, 2001). Carvalho and Carpintero (1993) and Carpintero et al. (2006) provided a checklist of the Miridae of Argentina. Although treating mostly North American taxa, H. H. Knight's (1923, 1941, 1968) comprehensive works on the Miridae of Connecticut, Illinois, and the Nevada Test Site are still useful for keying subfamilies, tribes, and genera.

There also are few Neotropical mirid studies hypothesizing phylogenetic relationships. Ferreira (1998) revised the tribe Clivinematini and gave a phylogenetic analysis of the tribe; Schuh (1991) treated the Pilophorini; Schwartz (1987, 2008), the Stenodemini; and Tatarnic and Cassis (2012), the Halticini. Forero (2008) revised and provided an analysis of the *Hadronema* Uhler group; Henry and Kim (1984), *Neurocolpus* Reuter; Henry (1991,1999, 2012b), *Keltonia* Knight, *Pseudatomoscelis* Reuter, *Ranzovius* Distant, and *Tytthus* Fieber; Sadowska-Woda et al. (2008), *Fulvius* Stål (based on molecular data); Schuh and Schwartz (1985), *Rhinacloa* Reuter; and Schwartz (1984, 2011), *Irbisia* Reuter and *Slaterocoris* Wagner.

One cannot consider the Miridae without mentioning José C. M. Carvalho. He published a majority of the taxonomic work on the Neotropical Miridae in an amazing, career-long series of nearly 500 papers in which he described almost 400 genera and more than 2,100 species (Schuh 2013). Carvalho and Froeschner (1987, 1990, 1994) listed the genera and species described by Carvalho from 1943 to January 1993, along with their type depositories.

Table 10.1 Number of genera and species by tribe in Central America and the West Indies

Mexico and Central America																									
		MEX		GUA		BEL		ELS		HON		NIC		CRI		PAN		CUB		JAM		DOR		WIN	
Subfamily	Tribe	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP
Bryocorinae	Bryocorini	1	1	0	0	0	0	1	1	0	0	1	2	1	1	0	0	1	1	1	1	0	0	2	3
Bryocorinae	Dicyphini	5	9	4	8	0	0	1	1	0	0	5	11	4	6	2	4	3	5	0	0	1	1	0	0
Bryocorinae	Eccritotarsini	24	74	18	39	0	0	10	15	5	6	12	28	17	29	23	56	9	13	3	5	1	1	6	9
Cylapinae	Cylapini	1	1	2	2	0	0	0	0	1	2	0	0	0	0	2	8	0	0	0	0	0	0	0	0
Cylapinae	Fulviini	3	21	2	6	0	0	2	3	1	1	2	15	2	7	6	18	1	3	2	2	0	0	2	5
Cylapinae	Vaniini	0	0	1	1	0	0	0	0	0	0	0	0	1	2	1	1	0	0	0	0	0	0	0	0
Deraeocorinae	Clivinematini	11	33	5	9	0	0	1	1	1	1	2	5	5	7	5	7	1	1	1	1	2	2	2	2
Deraeocorinae	Deraeocorini	6	6	4	4	0	0	0	0	0	0	2	2	2	2	6	9	1	1	0	0	1	1	0	0
Deraeocorinae	Hyaliodini	4	8	4	6	1	1	2	2	0	0	6	9	5	7	8	13	3	4	0	0	2	3	1	2
Deraeocorinae	Surinamellini	1	3	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	2	0	0	0	0	0	0
Deraeocorinae	Termatophylini	4	4	1	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2
Isometopinae	Diphlebini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Isometopinae	Myiommini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Mirinae	Herdoniini	10	16	3	3	0	0	0	0	0	0	0	0	1	1	5	6	0	0	0	0	0	0	0	0
Mirinae	Mirini	33	121	23	40	0	0	13	19	12	17	22	40	13	25	26	60	12	27	7	10	1	1	9	12
Mirinae	Restheniini	17	49	4	7	0	0	2	3	2	2	3	5	1	6	4	12	1	8	1	1	1	1	1	2
Mirinae	Stenodemini	7	15	4	6	1	1	3	3	3	3	3	4	2	2	4	4	4	4	0	0	0	0	0	0
Orthotylinae[a]	Ceratocapsini	1	1	2	3	0	0	0	0	0	0	2	4	0	0	1	2	2	6	1	2	0	0	1	3
Orthotylinae	Halticini	1	3	1	2	0	0	1	2	0	0	1	2	1	1	0	0	1	2	0	0	0	0	0	0
Orthotylinae	Orthotylini	53	179	6	15	0	0	6	6	0	0	13	14	9	14	7	10	7	9	9	11	1	2	10	12
Phylinae[b]	Hallodapini	2	5	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Phylinae	Phylini	27	65	7	7	1	1	5	5	6	9	10	25	4	6	9	21	6	13	7	7	5	7	8	11
Phylinae	Pilophorini	2	7	1	1	1	1	0	0	0	0	1	2	1	1	0	0	2	5	1	2	1	1	1	1
	Total	213	621	92	160	4	4	47	61	32	42	86	169	70	118	112	233	58	108	34	43	16	20	44	64

MEX Mexico, *GUA* Guatemala, *BEL* Belize, *ELS* El Salvador, *HON* Honduras; *NIC* Nicaragua, *CRI* Costa Rica, *PAN* Panama, *CUB* Cuba, *JAM* Jamaica, *DOR* Dominican Republic; Caribbean or West Indies (not included: Cuba, Dominican Republic, and Jamaica) Antigua and Barbuda, Bahamas, Barbados, Cayman Islands, Dominica, Grenada, Haiti, St. Kitts and Nevis, Montserrat, Saint Christopher-Nevis-Anguilla, Saint Lucia, Saint Vincent and the Grenadines, Trinidad and Tobago, and Turks and Caicos Islands; *GN* genus number, *SP* species number

[a] Excluding Coridromini

[b] Phylini (*sensu lato*), prior to Schuh and Menard (2013) and Menard et al. (2014)

Table 10.2 Number of genera and species by tribe in countries of South America

South America		COL		VEN		GUY		SUR		FGU		ECU		PER	
Subfamily	Tribe	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP
Bryocorinae	Bryocorini	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Bryocorinae	Dicyphini	3	9	2	3	1	2	3	5	1	2	4	12	6	13
Bryocorinae	Eccritotarsini	7	22	15	24	2	2	6	8	2	3	9	19	18	51
Cylapinae	Cylapini	0	0	2	2	0	0	0	0	0	0	2	2	1	6
Cylapinae	Fulviini	2	6	2	9	2	3	2	4	2	6	2	7	2	5
Cylapinae	Vaniini	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Deraeocorinae	Clivinematini	2	3	3	4	0	0	0	0	0	0	1	1	3	4
Deraeocorinae	Deraeocorini	4	6	2	3	0	0	0	0	1	1	1	1	3	7
Deraeocorinae	Hyaliodini	4	12	5	6	1	1	1	1	0	0	6	7	10	16
Deraeocorinae	Surinamellini	0	0	1	1	0	0	1	1	0	0	1	1	1	1
Deraeocorinae	Termatophylini	0	0	1	2	1	1	1	1	0	0	0	0	0	0
Isometopinae	Diphlebini	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isometopinae	Myiommini	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mirinae	Herdoniini	1	1	1	1	0	0	1	1	0	0	2	2	7	7
Mirinae	Mirini	20	46	19	39	3	3	9	10	12	28	25	68	38	96
Mirinae	Restheniini	7	17	4	9	0	0	1	3	1	2	5	14	7	51
Mirinae	Stenodemini	3	8	3	3	0	0	1	1	0	0	4	6	5	9
Orthotylinae	Ceratocapsini	0	0	1	3	1	1	1	2	0	0	1	1	1	3
Orthotylinae	Halticini	0	0	0	0	0	0	1	2	0	0	1	2	1	2
Orthotylinae	Orthotylini	7	13	7	14	1	1	1	1	3	3	8	11	10	20
Phylinae	Hallodapini	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Phylinae	Phylini	7	8	8	15	0	0	5	6	1	1	10	22	9	32
Phylinae	Pilophorini	0	0	0	0	1	1	0	0	1	1	0	0	1	3
	Total	69	153	76	138	13	15	34	46	24	47	83	177	124	327

Subfamily	Tribe	BOL		PAR		ARG		URU		CHI		BRA	
		GN	SP	GN	SP	GN	SP	GN	SP	GN	SP	GN	SP
Bryocorinae	Bryocorini	0	0	1	1	1	1	0	0	0	0	1	3
Bryocorinae	Dicyphini	1	4	4	4	4	10	1	2	2	3	5	27
Bryocorinae	Eccritotarsini	12	29	8	13	18	53	3	5	2	2	34	152
Cylapinae	Cylapini	2	2	0	0	1	1	0	0	0	0	12	23
Cylapinae	Fulviini	2	3	2	9	3	15	0	0	1	2	9	32
Cylapinae	Vaniini	1	1	0	0	0	0	0	0	0	0	1	1
Deraeocorinae	Clivinematini	0	0	0	0	6	9	0	0	0	0	4	10
Deraeocorinae	Deraeocorini	0	0	1	1	4	7	0	0	4	6	11	23
Deraeocorinae	Hyaliodini	6	6	3	4	7	13	0	0	2	2	11	38
Deraeocorinae	Surinamellini	0	0	0	0	1	2	0	0	0	0	4	9
Deraeocorinae	Termatophylini	0	0	0	0	0	0	0	0	0	0	1	1
Isometopinae	Diphlebini	0	0	0	0	0	0	0	0	0	0	0	0
Isometopinae	Myiommini	0	0	0	0	3	7	0	0	0	0	1	3
Mirinae	Herdoniini	2	2	7	11	10	27	1	1	0	0	20	54
Mirinae	Mirini	20	34	20	39	31	123	5	5	10	44	55	277
Mirinae	Restheniini	6	19	7	22	15	96	2	5	3	6	17	134
Mirinae	Stenodemini	2	2	3	3	10	26	3	4	1	2	10	20
Orthotylinae	Ceratocapsini	1	4	1	4	1	17	0	0	0	0	1	47
Orthotylinae[a]	Halticini	0	0	0	0	1	3	1	1	0	0	1	3
Orthotylinae	Orthotylini	8	13	8	13	30	79	1	1	10	33	55	145
Phylinae[b]	Hallodapini	0	0	0	0	1	1	0	0	0	0	1	1
Phylinae	Phylini	4	6	3	4	15	31	0	0	8	16	24	72
Phylinae	Pilophorini	0	0	1	1	1	3	0	0	0	0	1	7
	Total	67	125	69	129	163	524	17	24	43	116	279	1,082

COL Colombia, *VEM* Venezuela, *GUY* Guyana, *SUR* Suriname, *FGU* French Guiana, *ECU* Ecuador, PER Peru, *BOL* Bolivia, *PAR* Paraguay, *ARG* Argentina, *URU* Uruguay, *CHI* Chile, *BRA* Brazil

[a] Excluding Coridromini

[b] Phylini (*sensu lato*), prior to Schuh and Menard (2013) and Menard et al. (2014)

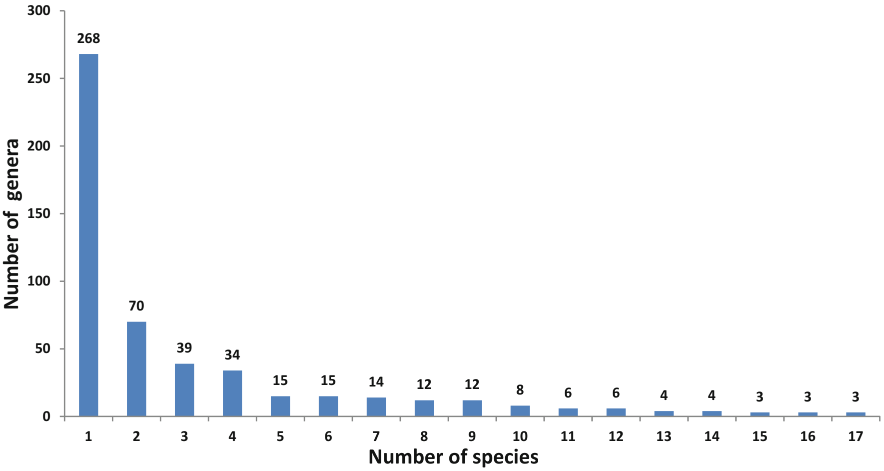


Fig. 10.2 Number of genera in relation to number of species of Neotropical Miridae

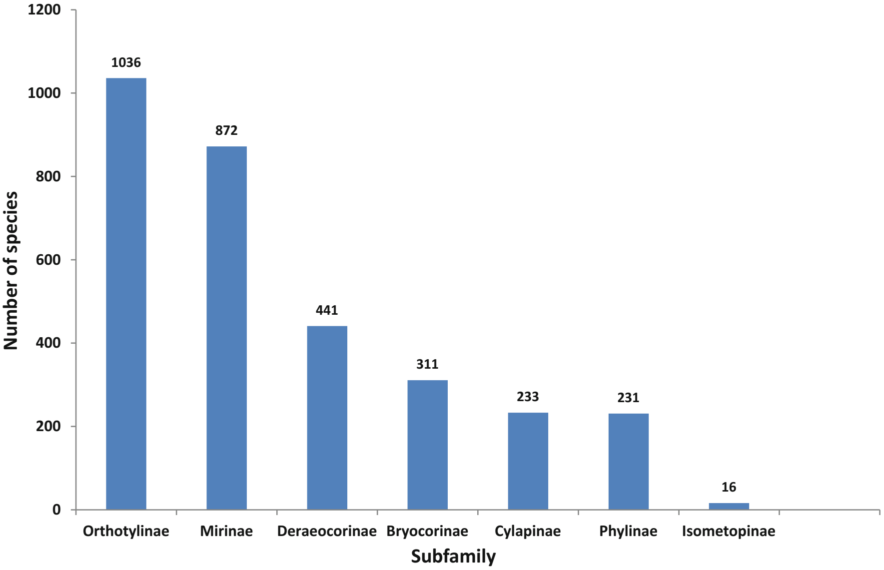


Fig. 10.3 Number of species by subfamily of Neotropical Miridae

In the following section, we provide keys to the subfamilies and tribes of Neotropical Miridae, modified from Schuh and Slater (1995), Carvalho and Costa (1997), and Hernández and Henry (2010), and other references as noted, followed by a diagnosis of the subfamily and a highlight of the most significant papers containing substantial numbers of new taxa and/or identification keys. Only seven of the eight recognized subfamilies are included. Previously, the Neotropical genus

Isometocoris Carvalho and Sailer had been considered the only New World representative of the subfamily Psallopinae (Henry and Maldonado 1982). In a forthcoming paper, however, Wolski and Henry (2015) document that *Isometocoris* is not a psallopine; thus, this subfamily is omitted from the key.

Key to the Neotropical subfamilies of Miridae

1. Tarsi two segmented, the first segment shorter than the second; ocelli............. present ....Isometopinae
– Tarsi two or three segmented; ocelli absent 2
2. Parempodia large, fleshy, apically convergent or divergent, arising between claws; phallotheca never cone shaped.. 3
– Parempodia setiform, if large, fleshy, and convergent, then with a cone-shaped phallotheca nested within the left paramere and protruding posteriorly from genital capsule.. 4
3. Parempodia divergent at apices, usually thickened; a prominent collar present, separated from anterior margin of pronotum by a deep furrow present .... Mirinae
– Parempodia convergent at apices, usually more slender; pronotal collar absent, if present, not separated from pronotum by a deep suture ....Orthotylinae
4. Pulvilli present, free, or connected along inner surface of claws, sometimes difficult to see, in which case a collar is always absent 5
– Pulvilli absent; collar present or absent 6
5. Pulvilli arising from base or inner margin of claw; hemelytral membrane with two cells; tarsi uniformly slender.. Phylinae
– Pulvilli arising from ventral surface of claw; hemelytral membrane with one or two cells; tarsi thickened distally or slender with tiny pretarsi.......... Bryocorinae
6. Claws distinctly toothed or thickened at bases; never toothed apically ....Deraeocorinae
– Claws not toothed or thickened basally; apex almost always with a fine subapical tooth .... Cylapinae

10.5.1 Subfamily Bryocorinae

This subfamily is recognized by the three-segmented tarsi, the often large and fleshy pulvilli (Eccritotarsini) attached to the bases of the claws and the often distally thickened (Eccritotarsini) or sometimes slender (Dicyphini) tarsal segments, with tiny indistinct claws. The Bryocorini and Eccritotarsini have only one closed cell on the hemelytral membrane, whereas the Dicyphini (Dicyphina and Monaloniina) have two.

Carvalho and Ferreira (1995) keyed 66 of the Neotropical genera of Bryocorinae (Eccritotarsini), and Ferreira and Henry (2011) provided a synopsis and keys to the four tribes, 24 genera, and 56 species of Minas Gerais, Brazil.

The following key is modified from Schuh and Slater (1995), Hernández and Henry (2010), and Ferreira and Henry (2011).

Key to the Neotropical tribes of Bryocorinae

1. Hemelytral membrane with two closed cells; tarsi uniformly slender; delicate slender species, sometimes spotted dorsally; genital capsule often bearing tubercules or processes on the right side; pretarsal structures very small, pulvilli small; parempodia present (includes Dicyphina and Monaloniina) .... Dicyphini
– Hemelytral membrane with only one closed cell; tarsi dilated distally; oval, robust species, without dorsal spots; genital capsule without tubercules on the right side; pulvilli large, distinct; parempodia present or absent 2
2. Claws without true pulvilli, but with pseudopulvilli arising from the unguitractor plate, recurved and convergent apically; parempodia absent; metathoracic scent efferent system with bulbous peritremal disc and distinct ostiolar canal .... Bryocorini
– Claws with large and flattened pulvilli, arising or continuing from the inner claw surface, without pseudopulvilli; parempodia asymmetrical; metathoracic scent efferent system usually with a narrow tongue-shaped peritremal disc and weakly developed ostiolar canal .... Eccritotarsini

Bryocorini (Fig. 10.4)

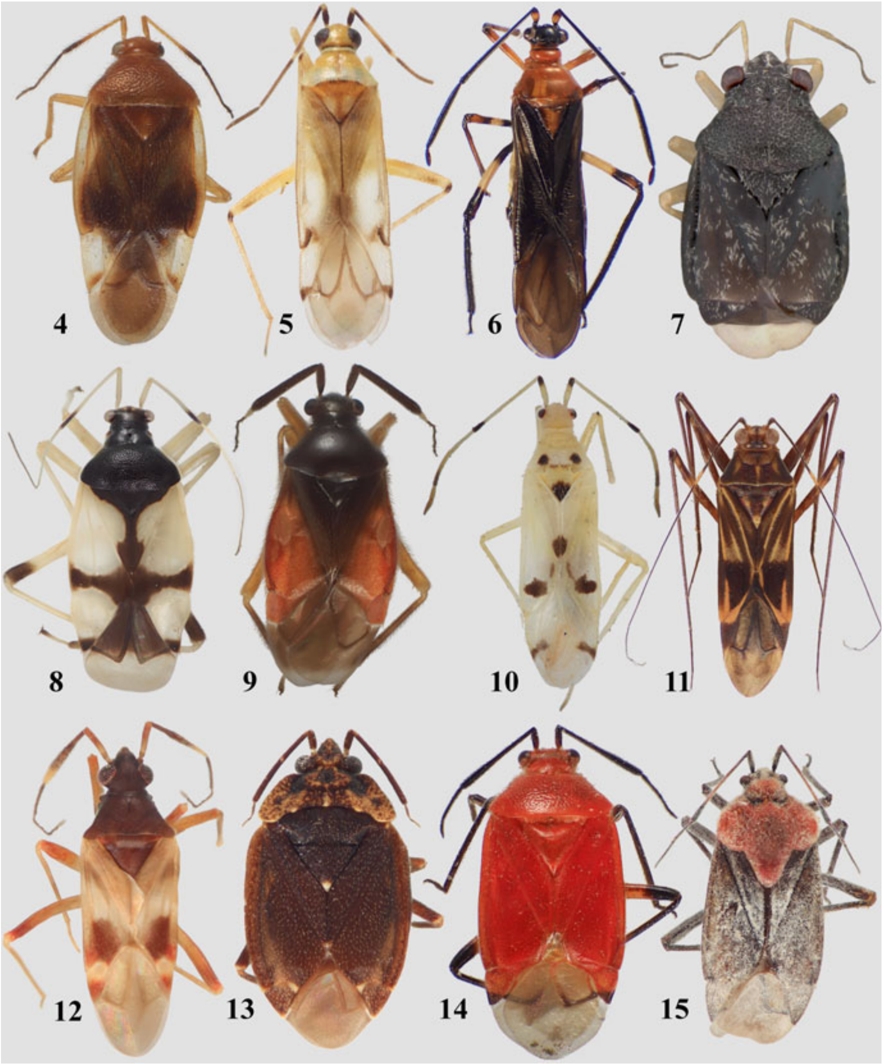
The Bryocorini are the smallest of the three tribes, containing four genera in the world, with only *Monalocoris* Dahlbom occurring in the Neotropics. These small, oval bugs are characterized by the rounded pronotal collar, reduced number of femoral trichobothria, and their specialized feeding on ferns (Pterophyta). Only seven Neotropical species are known (Schuh 2013).

Dicyphini (Figs. 10.5 and 10.6)

The Neotropical Dicyphini are recognized by their slender body form, elongate head, slender antennae, trapeziform pronotum with a distinct narrow collar, wide mesoscutum, translucent hemelytra, often reduced auricles and evaporative area, and respiratory horns on the egg.

The subfamily is separated into three subtribes, of which only the Dicyphina Monaloniina occur in the Neotropics. Cassis (1984) revised and keyed Dicyphina and gave generic status to many of the previous subgeneric names, such as *Engytatus* Reuter, *Nesidiocoris* Kirkaldy, and *Tupiocoris* China and Carvalho. Carvalho and Ferreira (1994b) keyed the Neotropical genera.

The widespread *Engytatus modestus* (Distant) and *Nesidiocoris tenuis* (Reuter) are well-known pests of various crop plants, including tobacco, tomato, and eggplant



Figs. 10.4–10.15 Neotropical Miridae. 4, *Monalocoris pallidiceps* (Reuter) (Bryocorinae: Bryocorini). 5, *Nesidiocoris tenuis* (Reuter) (Bryocorinae: Dichypini: Dicyphina). 6, *Monalonion annulipes* Signoret (Bryocorinae: Dicyphini: Monaloniina). 7, *Cyrtocapsus femoralis* Reuter (Bryocorinae: Eccritotarsini) 8, *Eccritotarsus brevicuneatus* Carvalho (Bryocorinae: Eccritotarsini). 9, *Pachymerocerus fairmairei* (Stål) (Bryocorinae: Eccritotarsini). 10, *Chius maculatus* Distant (Bryocorinae: Eccritotarsini). 11, *Cylapus striatus Reuter* (Cylapinae: Cylapini). 12, *Fulvius anthocoroides* Stål (Cylapinae: Fulviini). 13, *Peritropis izyai* Wolski and Henry (Cylapini: Fulviini). 14, *Ambracius dufouri* Stål (Deraeocorinae: Clivinematini). 15, *Clivinema regalisimilis* Carvalho (Deraeocorinae: Clivinematini) (Photos by G Ouellette)

(Tanada and Holdaway 1954; El-Dessouki et al. 1976; Wheeler 2000a, 2001), but both species also prey on aphids, mealybugs, lepidopteran eggs, and other small arthropods (Wheeler 2000b), becoming useful predators, especially in greenhouses.

The subtribe Monaloniina, containing 21 genera worldwide, is represented in the New World only by the genus *Monalonion* Herrich-Schaeffer. Carvalho (1972) reviewed the genus and provided a key to 11 of the 16 known species. Monaloniines are relatively large, shiny bugs, with laterally produced eyes and distinct pseudopulvilli. Several species of *Monalonion* have been reported damaging the developing fruits and pods of *Theobroma cacao* L. (Malvaceae) (de Abreu 1977; Wille 1944). Torres Jaimes et al. (2012) observed *M. velezangeli* Carvalho and Costa causing serious injury to the buds, flowers, and fruits of avocado, *Persea americana* Mill. (Lauraceae) in Colombia.

Eccritotarsini (Figs. 10.7, 10.8, 10.9, and 10.10)

Of the approximately 107 genera and 628 species of Eccritotarsini known in the world, 70 genera and about 452 species occur in the Neotropics (Schuh 2013). The tribe is recognized by the swollen femoral trichobothrial bases, the fleshy pulvilli attached to the inner surface of the claw, the asymmetrical parempodia, the dilated tarsi, the greatly reduced metathoracic scent gland opening, the single closed membranal cell, and the strongly developed male genitalia (Stonedahl 1988; Ferreira and Henry 2011).

Carvalho and Ferreira (1995) keyed 66 of the Neotropical genera, and Ferreira and Henry (2011) keyed the 18 genera and 42 species known from Minas Gerais, Brazil.

Other important contributions include Carvalho's (1953) revision and key to the species of *Eccritotarsus* Stål; Schaffner and Carvalho's (1981) review of *Hesperolabops* Kirkaldy; Carvalho and Schaffner's (1985) descriptions of numerous new species of *Adneella* Carvalho, *Neella* Reuter, *Sysinas* Distant, *Neofurius* Distant, *Neosilia* Distant, *Nototremates* Carvalho and China, and *Dichroocoris* Reuter; and Henry and Carvalho's (1987) key to the species of *Cyrtocapsus* Reuter. Uceli et al. (2009) reviewed *Pachymeroceroides* Carvalho and Gomes and described the peculiar male hemelytra.

This subfamily contains a number of economically important taxa. *Pycnoderes quadrimaculatus* Guérin-Meneville, often called the bean capsid, is a well-known pest of beans, squash, sweet potatoes, and garden crops, where it causes chlorosis, mottling, leaf drop, and premature aborting of fruits (Wheeler 2000a). Feeding by the Neotropical *Tenthecoris orchidearum* (Reuter) may produce chlorotic spots or even kill the foliage on orchids, and, in heavy infestations, the entire plants may die (Gimingham 1928; Wheeler 2001). In the early twentieth century, species of *Tenthecoris* were considered serious pests of orchids grown in greenhouses in the Britain (Carvalho and Leston 1952), France (Denis 1908), and the United States

(Weiss 1917), but with the advent of modern control practices, these eccritotarsines seldom become a problem (Wheeler 2001).

10.5.2 Subfamily Cylapinae

Of the cylapine tribes recognized by Cassis and Schuh (2012), only Cylapini (12 genera and 42 species), Fulviini (15 genera and 88 species), and Vaniini (one genus and four species) occur in the Neotropics (Gorczyca 2000, 2006; Schuh 2013). This subfamily is recognized by the long labium, often extending well beyond the hind coxae; the long, slender antennae; the membrane having two closed cells; and the long, slender legs, setiform parempodia, lack of pulvilli, and long, slender claws, usually with a distinct subapical tooth. Members of the Cylapini and Vaniini have relatively broad heads, often with stylate or protruding eyes (e.g., *Cylapus* Say), whereas the Fulviini (e.g., *Fulvius* Stål and *Peritropis* Uhler) have more elongate heads, with smaller, nonprotruding eyes.

Gorczyca (2006) cataloged the subfamily for the world, and Gorczyca (2000) and Cassis and Monteith (2006) studied the phylogeny of the group. Gorczyca (2006) recognized four tribes, whereas Cassis and Monteith (2006) and Cassis and Schuh (2012) listed five, with the addition of Vaniini. Carvalho and Ferreira (1994a) provided a key to the 20 Neotropical genera.

The following key is modified from Gorczyca (2000), with information from Cassis and Schuh (2012) incorporated.

Key to the tribes of Cylapinae

1. Body elongate oval; head horizontal, elongate, tapering anteriorly; eyes relatively small, not bulging or stylate; antenna usually shorter than body, second segment longest........ Fulviini
– Body elongate; head vertical, somewhat flattened in front; eyes bulging, often stylate; antenna usually longer than the body, third segment longest........ 2
2. Labium short, relatively stout, extending to or only slightly beyond hind coxae; parempodia flattened........ Vaniini
– Labium long, slender, extending well beyond hind coxae onto abdomen; parempodia rounded........ Cylapini

Cylapini (Fig. 10.11)

Members of the tribe are best recognized by their stalked eyes, long slender labium, often extending to the genital segments, auriculate evaporatorium, and toothed claws with setiform parempodia.

Twelve genera and 42 species of Cylapini are known in the Neotropics (Schuh 2013). Carvalho and Fontes (1968a) provided a key to six genera of the *Cylapus* complex (*Amapacylapus* Carvalho and Fontes, *Cylapocerus* Carvalho and Fontes, *Cylapus* Say, *Peltidocylapus* Poppius, *Trichocylapus* Poppius, and *Valdasus* Stål), Carvalho (1987a) added two new genera (*Cylapinus* Carvalho*, Tucuruisca* Carvalho) six new species, and Carvalho (1989a) described five genera (*Adcylapocoris* Carvalho, *Cylapocorella* Carvalho, *Cylapocorisca* Carvalho, *Microcylapus* Carvalho, *Valdasoides* Carvalho) and two species.

Fulviini (Figs. 10.12 and 10.13)

Fifteen genera and 88 species of Fulviini are known from the Neotropical Region (Schuh 2013). Carvalho and Costa (1994) revised and keyed the species *Fulvius*, one of the larger Neotropical mirid genera; Ferreira and Henry (2002) added two new species from Brazil, and Hernández and Henry (2010) described one from Cuba; Sadowska-Woda et al. (2008) presented a preliminary phylogenetic analysis, and Wolski and Henry (2012, 2013) revised *Peritropis* Uhler, describing 17 new species. Carvalho (1989a) described a number of new species (*Adcylapocoris* Carvalho, *Cylapocorella* Carvalho, *Cylapocorisca* Carvalho), and Henry and Silva de Paula (2004) described *Rhyparochromomiris femoratus*, a peculiar ant-mimetic species resembling a herdoniine mirine with greatly swollen front femora similar to those found in certain Rhyparochromidae (Lygaeoidea). Although Schuh (2013) included *R. femoratus* in the Cylapini, the long second antennal segment and male parameres suggest that this peculiar cylapine belongs in the Fulviini.

Vaniini

Vaniines are often brightly colored with orange and red markings. Their protruding eyes and flattened parempodia will distinguish them from most other Cylapinae. Gorczyca (1997) treated the *Vannius* complex (*Cylapus* Say, *Valdasus* Stål, *Vannius* Distant) and cataloged the world fauna. Cassis and Monteith (2006) presented a phylogenetic analysis of the *Vannius* complex, and Cassis and Schuh (2012) provided a summary of relationships.

Little is known of the habits of most cylapines. Species of *Fulvius* are often taken under the loose bark of dead trees, and most are thought to be predatory (Wheeler 2001; Henry et al. 2011), though a few observations suggest that some may feed on fungi (Schuh 1976). *Fulvius anthocoroides* (Reuter) has been observed feeding on mites and insects in stored nuts, and the North American *F. imbecilis* Say is documented feeding on Diptera and Coleoptera larvae and other arthropods (Henry et al. 2011). Herring (1976) considered his new genus and species, *Trynocoris lawrencei*, a predator of ciid beetle larvae associated with fungi growing on forest trees. Though long thought to be predaceous, Wheeler and Wheeler (1994) observed fungal spores and conidia in the gut contents of the North American *Cylapus tenuicornis* (Say) (and a Neotropical *Cylapus* sp.), providing evidence for mycophagous feeding habits in the genus. Cassis and Monteith (2006) noted that their new vaniine genus and species, *Kauakamiris krypton*, described from New Caledonia, was most easily collected in moldy cut-branch traps comprised of no particular plant species, suggesting it is mycetophagous.

10.5.3 Subfamily Deraeocorinae

Members of this subfamily can be distinguished by the distinctly punctate, often polished dorsum and the basally toothed claws, although certain other deraeocorines (e.g., Termatophylini) may lack distinct dorsal punctures and have a dull coloration (Schuh and Slater 1995; Cassis 1995; Hernández and Henry 2010).

The following key is adapted from Carvalho (1955a) and Hernández and Henry (2010).

Key to Tribes of Deraeocorinae

1. Head elongate, pointed apically, with anthocorid-like facies; eyes large, placed far from basal angle of the head .... Termatophylini
– Head not elongate, without anthocorid-like facies; eyes variable, placed near basal angle of the head 2
2. Pronotum with a distinct impressed line running from anterolateral corner to margin of calli, sometimes strongly punctate .... Clivinematini
– Pronotum without an impressed line 3
3. Hemelytra hyaline; emboliar margin of corium wide; males and females with an elongate anal tube .... Hyaliodini
– Hemelytra not hyaline; emboliar margin of corium narrow; males and females without an anal tube 4
4. Species ant mimetic; antennal segments linear; vertex depressed, sometimes punctate; male vesica with two membranous lobes apically .... Surinamellini
– Species not ant mimetic; antennal segment I thicker than remaining segments, segment II clavate at apex; vertex smooth, not depressed; male vesica without two membranous lobes apically .... Deraeocorini

Carvalho's (1955a) now outdated keys to the world genera include the most useful key to the Neotropical deraeocorine genera. Maldonado (1969) keyed the genera and species of Puerto Rico, and Hernández and Henry (2010) treated the Cuban genera.

Clivinematini (Figs. 10.14 and 10.15)

Seventeen genera and about 55 species of Neotropical clivinematines are known (Schuh 2013). Henry (1979a) reviewed *Bothynotus* Fieber, and Ferreira and Henry (2010) revised *Ambracius* Stål. Ferreira (1993, 1996a, b, 1998, 2001) provided a comprehensive treatment of the Clivinematini, describing four new genera and providing information on their biogeography and biology, a cladistic analysis, and a key to the 17 Neotropical genera. Ferreira and Schaffner (2004) reviewed *Admetus* Distant, and Kerzhner and Schuh (1998) provided the replacement name *Admetomiris* for the preoccupied *Admetus*. Carpintero et al. (2008) added the new genus *Valdesiana* Carpintero and Dellapé and provided a key to the six genera and nine species of Clivinematini from Argentina.

Based on a few observations, most clivinematines are thought to prey on species of Sternorrhyncha, especially those in the family Ortheziidae. Knight (1928) reported *Clivinema sericea* Knight feeding on a species of *Orthezia* (Hemiptera: Ortheziidae) in New Mexico, Miller and Schuh (1995) observed *C. coalina* Bliven preying on *O. annae* Cockerell on *Atriplex polycarpa* (Torr.) Wats. in California, Ferreira (1998) reported *Hemicerocoris bicolor* Carvalho feeding on soft scales on guava in Mexico, and Ferreira and Henry (2010) documented records of *Ambracius dufouri* Stål preying on *Orthezia* sp. in Brazil.

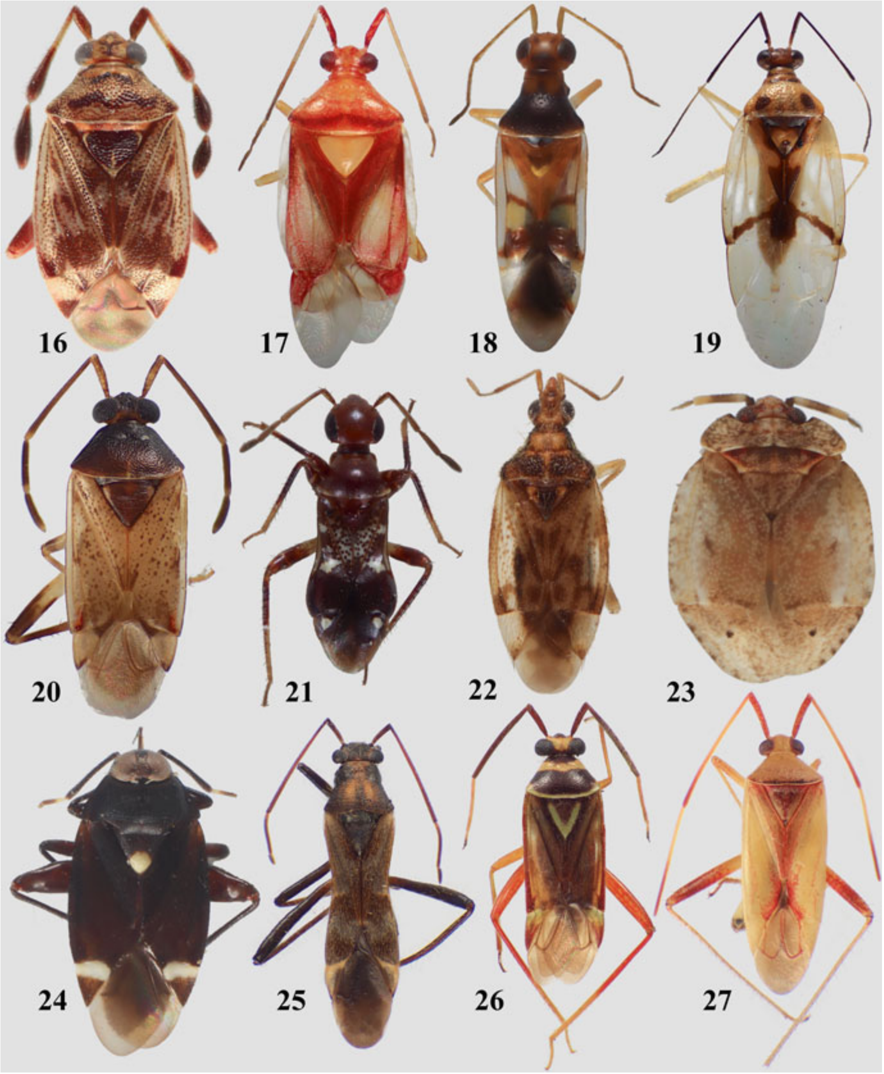
Deraeocorini (Fig. 10.16)

Twenty-seven genera and 62 species of the Deraeocorini are recorded from the Neotropical Region (Schuh 2013). Stonedahl et al. (1997) keyed the North American genera, which include a few of the Neotropical taxa. Most work on the nominotypical tribe has been descriptive. Papers containing keys to species include Carvalho and Maldonado's (1982) study of *Lundiella* and Carvalho and Costa's (1990c) review of *Diplozona* Van Duzee. Hernández and Stonedahl (1999) most recently added the three new genera *Acutifromiris*, *Cephalomiroides*, and *Scutellograndis* from Chile.

Nearly all members of this tribe are considered zoophagous. In North America, Wheeler et al. (1975) showed that *Deraeocoris nebulosus* (Uhler) was an effective predator of various ornamental pests, including mites, aphids, scales, whiteflies, psyllids, and lace bugs. Wheeler (2001) summarized the predatory habits of numerous species of *Deraeocoris* occurring mostly in the Nearctic and Palearctic regions.

Hyaliodini (Figs. 10.17, 10.18, and 10.19)

Twenty genera and about 111 species of Hyaliodini are known from the Neotropics (Schuh 2013). The most important works, including keys to species, are Carvalho and Schaffner (1977) for *Annona* Distant, Carvalho (1982) for *Antias* Distant, Carvalho (1974d) for *Auchus* Distant, and Henry and Ferreira (2003) for *Paracarniella* Henry and Ferreira. Several of the larger hyaliodine genera, particularly *Hyaliodes* Reuter, *Hyaliodocoris* Knight, *Knightonia* Carvalho and Drake, and *Paracarnus* Distant, are in need of revision.



Figs. 10.16–10.27 Neotropical Miridae. 16, *Diplozona collaris* Van Duzee (Deraeocorinae: Deraeocorini). 17, *Brasiliocarnus fraudans* (Carvalho) (Deraeocorinae: Hyaliodini). 18, *Bicuspidatiella conica* Maldonado (Deraeocorinae: Hyaliodini). 19, *Knightonia knighti* (Carvalho) (Deraeocorinae: Hyaliodini). 20, *Eustictus brunneus* Maldonado (Deraeocorinae: Surinamellini). 21, *Surinamella doesburgi* Carvalho and Rosas (Deraeocorinae: Surinamellini). 22, *Termatophylidea brunnea* Maldonado (Deraeocorinae: Termatophylini). 23, *Diphleps unica* Bergroth (Isometopinae: Diphlebini). 24, *Myiomma mexicanum* Henry (Isometopinae: Myiommini). 25, *Adxenetus petiolatus* (Stål) (Mirinae: Herdoniini). 26, *Calondas fasciatus* Distant (Mirinae: Mirini). 27, *Creontiades rubrinervis* (Stål) (Mirinae: Mirini) (Photos by G Ouellette)

Oliveira et al. (2002) studied *Hyaliodes beckeri* Carvalho (Hyaliodini) as a predator of the cassava pest *Vatiga illudens* (Heteroptera: Tingidae) in Brazil. Wheeler and Henry (2005) documented the association of *Bicuspidatiella conica* Maldonado with the formicine ant *Myrmelachista ramulorum* Wheeler (Formicidae) in Puerto Rico and speculated that this hyaliodine fed on the ant-attended mealybugs, soft scales, and whiteflies present on the host tree, laurel amarillo, *Nectandra turbacensis* (Kunth) Nees (Lauraceae).

Surinamellini (Figs. 10.20 and 10.21)

Five genera and 21 species of Surinamellini are known (Schuh 2013). The most important works for this group include descriptive papers by Carvalho (1988a) on *Craoiella* Carvalho, *Eustictus* Reuter, *Krainacoris* Carvalho and Wallerstein; Carvalho (1989b) on *Eustictus*, *Guapimirella* Carvalho; Carvalho and Rosas (1962) on *Surinamella* Carvalho and Rosas; and Carvalho and Costa (1990a, 1991) on *Eustictus*.

The habits of the surinamellines are poorly known. They are most often taken at lights or beaten from the branches of their hosts. Although there is little documentation, most or all members of this tribe probably are predatory, preying on small, coexisting arthropods. Most genera are in of need revision, and numerous undescribed taxa remain to be described.

Termatophylini (Fig. 10.22)

Only four genera and 10 species of this predatory tribe occur in the Neotropics (Schuh 2013). Maldonado (1970) reviewed the species of *Termatophylidea*, and Poppius and Carvalho (1955b) described new species of *Termatophylella* Carvalho, *Termatophylidea*, and *Termatophyloides* Carvalho. Cassis (1995) presented a phylogenetic analysis and provided a checklist and key to the genera of the world.

Most species of *Termatophylidea* are thought to be thrips (Thysanoptera) specialists. Wheeler (2001) documented that *Termatophylidea pilosa* Reuter and Poppius (Myer 1935) preys on redbanded thrips (*Selenothrips rubrocinctus*) in Jamaica, and *T. maculata* Usinger and *T. opaca* Carvalho (Callan 1943) feed on redbanded thrips and grass thrips (*Caliothrips insularis*), respectively.

10.5.4 Subfamily Isometopinae (Figs. 10.23 and 10.24)

The Isometopinae are recognized by the overall round to elongate-oval body form; the trapeziform pronotum with carinate lateral margins; the strongly modified head, often with holoptic eyes, and distinct ocelli between the eyes; the sexually dimorphic antennae with segment II longer and more thickened in males than females; and the small size, ranging from 2.00 to 3.00 mm.

Herczek (1993) discussed the systematic relationships and position of the subfamily and recognized the two tribes Diphlebini and Myiommini in the New World. For the latter, he further recognized three subtribes, two of which occur in the Neotropical Region: Myiommina and Plaumanocorina.

Nine genera and 31 species are known from the Neotropics (Schuh 2013). Ghauri and Ghauri (1983) keyed the genera of the world, but overlooked several Western Hemisphere genera. Henry (1980) provided a key to the New World genera, reviewed the genera *Lidopus* and *Wetmorea*, and described the new genera *Brailovskiocoris*, *Lidopiella*, and *Myiopus*. Henry and Herring (1979) revised *Corticoris* McAtee and Malloch, Henry (1979c) described new species and provided a key to the New World species of *Myiomma* Uhler, and Henry and Carpintero (2012) treated the Isometopinae from Argentina, parts of Brazil, and Paraguay and described nine new species.

The genus *Isometocoris* Carvalho and Sailer (1954), first placed in Isometopinae, was transferred to Psallopinae by Henry and Maldonado (1982). Wolski and Henry (2015) document the placement of this genus in the Cylapinae.

With the apparent exception of one Oriental species, evidence indicates that all Isometopinae are scale predators (Wheeler and Henry 1978a; Henry 1984b; Wheeler 2001).

10.5.5 Subfamily Mirinae

The Mirinae is recognized by the distinct pronotal collar, three-segmented tarsi, divergent fleshy parempodia, inflatable endosomal membrane, and the large, ringed secondary gonoporal opening.

The following key is modified from Hernández and Henry (2010).

Key to the Tribes of Mirinae

1. First segment of hind tarsus as long as second and third combined; antennae usually very long and slender; head porrect; frons usually with a distinct median sulcus; coloration brown or green .... Stenodemini
– First segment of hind tarsus shorter than second and third combined; antennae relatively short; frons without a median sulcus; coloration variable 2
2. Species mostly dull black, marked with red, orange, or yellow on head, pronotum, and/or scutellum, dorsal surface velvety; metathoracic evaporative area small; pronotal collar wide mesally .... Restheniini
– Species variably colored, usually green, brown, or black with variable markings, dorsal surface dull or shiny, but never velvety; metathoracic evaporative area prominent; pronotal collar more narrow 3
3. Strongly myrmecomorphic; abdomen constricted at base in most taxa, hemelytra usually constricted through middle, corium usually with pruinose patches and often with a white spot near middle margin... Herdoniini
– Not strongly myrmecomorphic; abdomen never constricted at base; hemelytra usually subparallel or convex, usually without pruinose patches and white spots .... Mirini

Herdoniini (Fig. 10.25)

Twenty-seven genera and 78 species of this group of strikingly ant-mimetic taxa are known from the Neotropics (Schuh 2013). Carvalho (1973a) provided a list of the genera, and Carvalho (1973b) keyed the genera of the world. In a series of well-illustrated papers, Carvalho and Ferreira (Carvalho and Ferreira 1973a, b, c, d, e, f, g, h, i, j, k, l) treated most of the herdoniine genera, usually accompanied by a key to species: *Adxenetus* Carvalho and Ferreira, *Allommatisca* Carvalho and Ferreira, *Allommatus* Reuter, *Barberiella* Poppius, *Camponotidea* Reuter, *Cearana* Carvalho and Ferreira, *Dacerla* Bergroth, *Guarania* Carvalho and China, *Haarupia* Poppius, *Herdonisca* Carvalho and Ferreira, *Herdonius* Stål, *Laurinia* Reuter, *Lepidoxenetus* Poppius, *Paradacerla* Carvalho and Usinger, *Paraxenetus* Reuter, *Proxenetus* Carvalho and Ferreira, *Sphinctothorax* Stål, *Xenetomorpha* Poppius, *Xenetopsis* Poppius, *Xenetus* Distant, *Zacynthus* Distant, and *Zosippus* Distant.

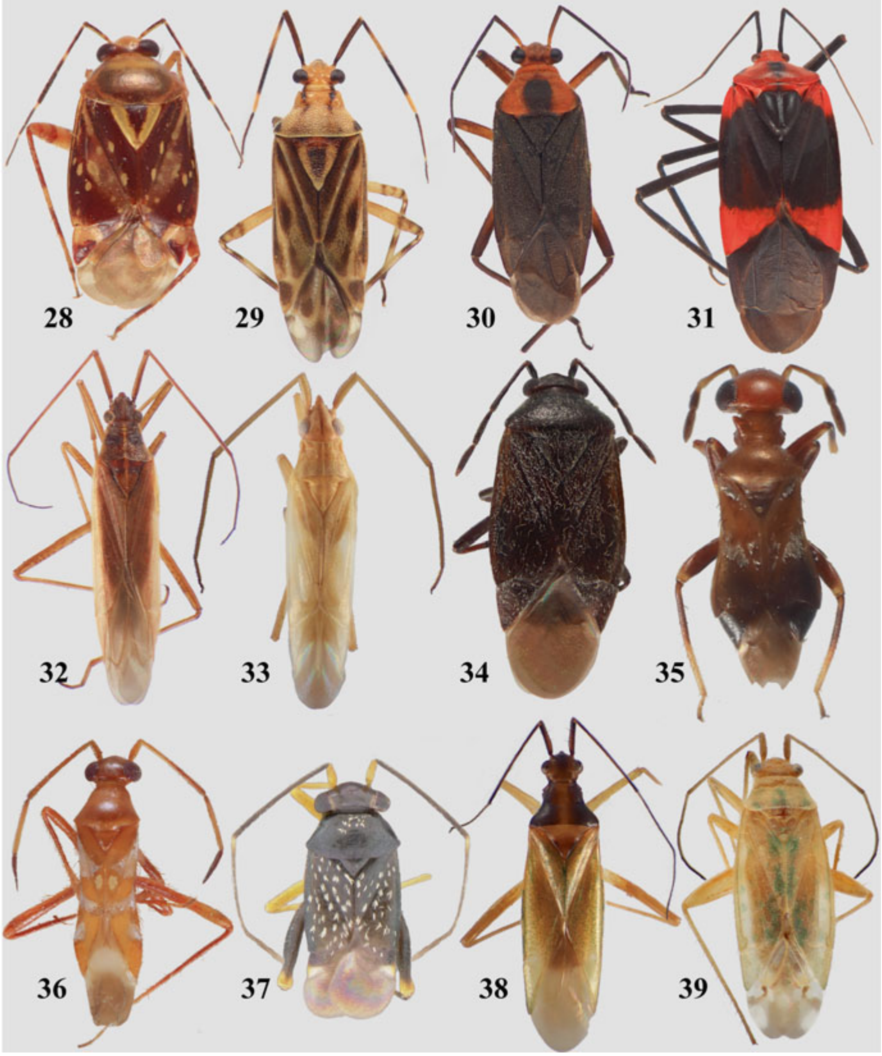
Herdoniines are remarkable in their resemblance to ants, with most having the abdomen constricted at the base and hemelytra narrowed through the middle. Wheeler and Henry (1980) studied *Barberiella formicoides* (Poppius) in the eastern United States and documented its habits and intimate association with three different species of ants. Little other information is available on the habits and life history of this fascinating group.

Mirini (Figs. 10.26, 10.27, 10.28, and 10.29)

Eighty-seven genera and more than 600 species of Mirini occur in the Neotropics. Carvalho's (1955a) key remains the only attempt to identify all genera of Mirini.

Phytocoris Fallén, the largest genus within the Miridae (Stonedahl 1988b), is represented in the Neotropics by 94 species (Schuh 2013), the second largest number after *Prepops* Reuter (Restheniini). Stonedahl (1988b) revised and keyed the western North American species, many of which range into Mexico, but few studies treat the Neotropical fauna much beyond describing new species. Other useful works on this genus include Maldonado (1969), Carvalho and Ferreira (1969), Carvalho and Gomes (1970), Carvalho (1990b), Carvalho and Costa (1990b, d, 1995), Carpintero and Chérot (2008, 2011), and Hernández and Henry (2010).

Important revisions of the largest genera, with keys to species, include Carvalho (1986a) for 12 species of *Calocorisca* Distant; Carvalho (1986b) for 12 species of *Chrysodasia* Carvalho; Carvalho and Fontes (1983) for 38 species of *Dagbertus* Distant; Carvalho and Gomes (1980), for 26 species of *Derophthalma* Berg; Carvalho (1986c) for 13 species of *Euchilocoris* Reuter; Carvalho (1976a) for 34 species of *Horcias* Distant; Carvalho and Jurberg (1976) for 12 species of *Horciasinus* Carvalho and Jurberg; Carvalho and Fontes (1972) and Carvalho (1985c) for 29 species of *Neostenotus* Reuter; Carvalho and Ferreira (1971) and Fontes (1981) for 19 of *Notholopus* Bergroth; Carvalho (1975c) for 18 species of *Poeas* Distant; Carvalho and Gomes (1969) and Ferreira (1980) for 22 species of *Polymerus* Hahn; Carvalho and Costa (1989) for 20 species (South American spp.



Figs. 10.28–10.39 Neotropical Miridae. 28, *Horcias nobilellus* (Berg) (Mirinae: Mirini). 29, *Piasus cribricollis* (Stål) (Mirinae: Mirini). 30, *Prepops latipennis* (Stål) (Mirinae: Restheniini). 31, *Resthenia scutata* Spinola (Mirinae: Restheniini). 32, *Stenodema dohrni* (Stål) (Mirinae: Stenodemini). 33, *Trigonotylus tenuis* (Reuter) (Mirinae: Stenodemini). 34, *Izyacapsus kerzhneri* Henry (Orthotylinae: Ceratocapsini). 35, *Zanchisme mexicanus* Carvalho and Schaffner (Orthotylinae: Ceratocapsini). 36, *Sericophanes ornatus* (Berg) (Orthotylinae: Ceratocapsini). 37, *Microtechnites bractatus* (Say) (Orthotylinae: Halticini). 38, *Carvalhomiris bifurcatus* Forero (Orthotylinae: Orthotylini). 39, *Chileria colla* Carvalho and Carpintero (Orthotylinae: Orthotylini) (Photos by G Ouellette)

only) of *Proba* Distant; Carvalho and Costa (1993) for 60 species of *Taedia* Distant; and Carvalho (1986d) for 20 species of *Tropidosteptes* Uhler.

Many Mirini, such as species of the genus *Phytocoris*, are predatory (Stonedahl 1988b). Others, however, may become serious pests of agricultural crops. Many species of *Lygus*, including the ubiquitous tarnished plant bug, *L. lineolaris* (Palisot de Beauvois), cause millions of dollars worth of damage each year in the United States (Schwartz and Foottit 1992, 1998). Other mirines, such as the black grass bugs, *Irbisia* spp., are major pests of forage grasses in western North America (Schwartz 1984). Species of genus *Tropidosteptes* cause severe injury to *Fraxinus* and other genera of the plant family Oleaceae (Henry et al. 2012). In Mexico and Colombia, *T. chapingoensis* Carvalho and Rosas is a serious pest of ornamental street plantings of *Fraxinus chinensis* Roxb., which sometimes causes heavy chlorosis and defoliation (Fonseca-González et al. 2007).

Restheniini (Figs. 10.30 and 10.31)

Restheniines are strictly a New World group. They are aposematically colored bugs, usually red or orange and black. This tribe contains the world's largest known mirids, with some species of *Resthenia* more than 15 mm long (Henry 2009). Twenty-seven genera and 320 species of Restheniini occur in the Neotropics (Schuh 2013). Carvalho and Fontes (1971a) provided a key to genera.

Prepops Reuter represents the largest genus in the Neotropics with 175 described species. Much of the work on this group has been descriptive. No one has attempted to key all of the species, although Carvalho and Fontes (1969a) gave a partial key to 18 species. The most important papers treating this genus include Carvalho (1974a, 1987b), Carvalho and Fontes (1968b, 1969a, b, 1970a, b, 1971b, c, d, e, f), Fontes (1989), Coelho (2012), and Coelho et al. (2012).

Some of the more comprehensive works include Carvalho and Fontes' (1971e) study of *Chiloxionotus* Reuter (28 species) and Carvalho and Fontes' (1970c) and Carvalho and Schaffner's (1975) work on *Platytylus* Fieber (30 species). Some of the most descriptive publications include Carvalho and Carpintero (1987) (*Nanniresthenia* Carvalho, *Platytylus* Fieber, *Prepops*), Carvalho and Carpintero (1989) (*Carpinteroa* Carvalho, *Chiloxionotus*, *Mimoncopeltus* Kirkaldy, *Nanniresthenia*, *Platytylus*, *Prepops*), Carvalho and Ferreira (1968) (*Lampsophorus* Reuter, *Mabelia* Kirkaldy), and Carvalho (1974b, c) [*Lampsophorus*, *Mabelia*, *Prepops*, *Prepopsella* Carvalho, *Resthenia* Spinola, *Restheniella* Carvalho]; Carvalho (1975a) [*Chiloxinotus*, *Opistheurista* Carvalho, *Prepops*]; Carvalho (1987b, c, d) [*Carpinteroa*, *Eurylomata* Reuter, *Fontesius* Carvalho, *Guaranimiris* Carvalho, *Oncerometopus* Reuter, *Platytylus*, *Prepops*, *Seabracoris* Carvalho]; Carvalho (1988b, c) [*Chiloxionotus*, *Prepops*, *Resthenia*]; Carvalho (1989c) [*Carpinteroa*, *Mimoncopeltus*, *Platytylus*, *Prepops*, *Resthenia*]).

Although the hosts and feeding habits of most restheniines are unknown, several species may cause economic damage to crops. *Opistheurista clandestina* (Van Duzee) causes extensive foliar spotting and blotching to beans, cowpeas, and sweet potatoes in the southern United States and Central America (Wheeler 2001), resulting in injury resembling that caused by mites and thrips (Jones 1921). *Prepops latipennis* (Stål), another Neotropical species, produces similar injury to beans and potatoes (King and Saunders 1984).

Stenodemini (Figs. 10.32 and 10.33)

Schwartz (2008) revised the Stenodemini, provided a key to the genera of the world, and presented a cladistic analysis supporting the monophyly of this tribe of grass-feeding bugs. Thirteen genera and about 46 species are known from the Neotropics (Schuh 2013).

Carvalho and Fontes (1981) reviewed the Neotropical species of *Collaria* Provancher, Carvalho (1975b) keyed the species of *Stenodema* Laporte, and Carvalho and Fontes (1969c) treated *Neotropicomiris* Carvalho and Fontes. Other mostly descriptive contributions include Carpintero and Estevez (2001) (*Cynodonmiris* Carpintero and Estevez, *Spartinomiris* Carpintero and Estevez), Carvalho and Fontes (1969c) (*Collaria*, *Dolichomiris* Reuter, *Kuscheliana* Carvalho, *Neotropicomiris*, *Ophthalmomiris* Berg, *Porpomiris* Berg, *Stenodema*, *Trigonotylus* Fieber), and Carvalho (1975b) [*Dolichomiris*, *Megaloceroea* Fieber, *Stenodema*, *Trigonotyliscus* Carvalho (a junior synonym of *Trigonotylus*), *Trigonotylus*].

Losses to prairie grasses, important graze for cattle and milk production in Colombia, have been attributed to stenodemines. *Collaria scenica* (Stål), the predominant pest species in that region, has caused losses up to 25 % of dry matter, the decrease of 10 % grass digestibility, and the reduction of milk production by up to 5 l/animal/day, resulting in an economic loss of 20 % to producers (Martinez and Barreto 1998; Duarte et al. 1998; Barreto 2011). Its biology has been studied on wheat, including adult morphometry (Carlessi et al. 1999).

Collaria oleosa (Distant) is a potential pest of wheat in Brazil (Da Silva et al. 1994) and is known to reduce sorghum yields in Cuba (Ryder et al. 1968). Ferreira et al. (2001) evaluated the economic importance of *Collaria oleosa* (Distant), *Dolichomiris linearis* Reuter, *Neotropicomiris costalis* Carvalho and Fontes, *N. longirostris* Carvalho and Fontes, *Opisthocoris carmelitanus* Carvalho and Costa, and *Trigonotylus tenuis* Reuter on grasses in Minas Gerais, Brazil.

10.5.6 Subfamily Orthotylinae

The Orthotylinae are distinguished by the usually complex male genitalia, especially the endosoma, often with multiple branching spicules, and parameres; the relatively large, open genital aperture; and the fleshy, convergent parempodia between the claws that are similar to those found in pilophorine Phylinae (distinguished, however, by the strap-like vesica similar to all other phylines).

The following key is modified from Hernández and Henry (2010).

Key to the Tribes of Orthotylinae

1. Small, oval, compact species with saltatorial hind femora 2
– Usually larger, more elongate, medium-sized species, hind femora not saltatorial 3
2. Black species; head strongly dorsoventrally elongate; dorsum usually with patches of white, scalelike setae; parameres small, simple .... Halticini
– Pale yellow to brown species; head not strongly dorsoventrally elongate; dorsum without scalelike setae; left paramere, long, sickle shaped .... Coridromini
3. Head truncate posteriorly, with a distinct basal carina; species often ant mimetic but, if not, antennal segments III and IV as thick or thicker than antennal segment II; male parameres sickle shaped to complex and branching; vesica without or, at most, with one simple spiculum; phallotheca readily visible within genital capsule when viewed caudally .... Ceratocapsini
– Head not truncate posteriorly, without a distinct basal carina; species not ant mimetic; antennal segments III and IV more slender than segment II; male parameres relatively simple; vesica with multiple, often branching or complex spiculi; phallotheca not visible within genital capsule .... Orthotylini

Ceratocapsini (Figs. 10.34, 10.35, and 10.36)

The Ceratocapsini are an exclusively New World group, comprising more than 10 genera (Henry 1979b, 1994, 2006, 2013) and about 200 species, about half of which occur in the Neotropics. Many ceratocapsines are remarkably myrmecomorphic and are frequently collected in association with ants (Wheeler 1991; Henry 1994). Carvalho (1958b), in his world catalog, synonymized the tribe with the nominate tribe Orthotylini. Since then, however, Carvalho et al. (1983) and Henry (e.g., 1994, 2006, 2013) have given evidence for its monophyly, and, more recently, Schuh (2013) recognized the tribe in his online catalog.

Carvalho et al. (1983) reviewed the species of *Ceratocapsus* Reuter for the Neotropical Region, described 45 new species, and provided a key to distinguish them. Carvalho and Costa (1988) reviewed the genus *Sericophanes* Reuter and provided a key to the Neotropical species, and Hernández and Henry (1999) treated the Cuban species of *Ceratocapsus*. Since then, most papers have been primarily descriptive. More recently, Henry (2006) added the new genus *Izyacapsus* to accommodate two new species from Mexico, Henry (2013) added the new genus *Joseocoris* to include two new species from Argentina and Brazil, and Henry (2015) revised the *Renodaeus* group of species, comprising eight genera and 48 species, including 26 new species, many of which are Neotropical.

Ceratocapsines are largely predatory. Wheeler and Henry (1978b) documented *Ceratocapsus modestus* (Uhler) preying on grape phylloxera, *Daktulosphaira viti-*

foliae (Fitch), in North America. Carvalho et al. (1983) provided an overview of the feeding habits of the group, including a report of *C. dispersus* Carvalho and Fontes feeding on the tobacco budworm *Heliothis virescens* (F.) in Peru. Gravena and Pazetto (1987) observed *C. dispersus* Carvalho and Fontes and *C. mariliensis* Carvalho and Fontes preying on the eggs and larvae of the cotton leafworm *Alabama argillacea* (Hübner) and tobacco budworm in Brazil. Wheeler (2000b, 2001) provided a summary of ceratocapsine feeding habits.

Coridromini

This newly recognized tribe was established for the Old World genus *Coridromius* Signoret (Tatarnic and Cassis 2012), based on hypodermic genitalia formed by the left paramere and aedeagus, the reduced female genitalia, the short round body, and strongly saltatorial hind femora (Tatarnic et al. 2006).

Only the adventive *Coridromius chenopoderis* Tatarnic and Cassis (2008) occurs in Neotropical Region. In addition to the Australian Region, it is now known from Hawaii, the southwestern United States (and Florida), and Mexico, where it feeds on plants in the family Chenopodiaceae (Tatarnic and Cassis 2008).

Halticini (Fig. 10.37)

The halticines are a group of mostly small, shiny, black mirids, with a dorsoventrally elongate head, often with silvery scalelike dorsal setae set in scattered patches, simple parameres, and a mostly membranous endosoma with two sclerotized spiculi (Tatarnic and Cassis 2012).

Only the genus *Microtechnites* Berg and five species are currently recognized from the Neotropics (Schuh 2013). Tatarnic and Cassis (2012) transferred most New World species of *Halticus* Hahn to *Microtechnites* and placed *Cafayatina* Carvalho and Carpintero as a junior synonym of it. Henry (1983) reviewed the New World *Halticus*, several of which are now in *Microtechnites*, and provided a key to distinguish species.

The ubiquitous garden fleahopper, *Microtechnites bractatus* (Say) (widely known in the literature under the combination *Halticus bractatus*), occurs throughout much of the Western Hemisphere from Canada to Argentina and Brazil (Henry and Wheeler 1988), where it may cause significant injury to agricultural crops. Beyer (1921) and Cagle and Jackson (1947) studied the life history. This species may cause severe foliar chlorosis or bleaching, often resulting in heavy crop losses. It has a wide host range, including small grains and many forage and garden crops; major losses to alfalfa, clover, and tomatoes have been recorded (Beyer 1921; Morrill 1925).

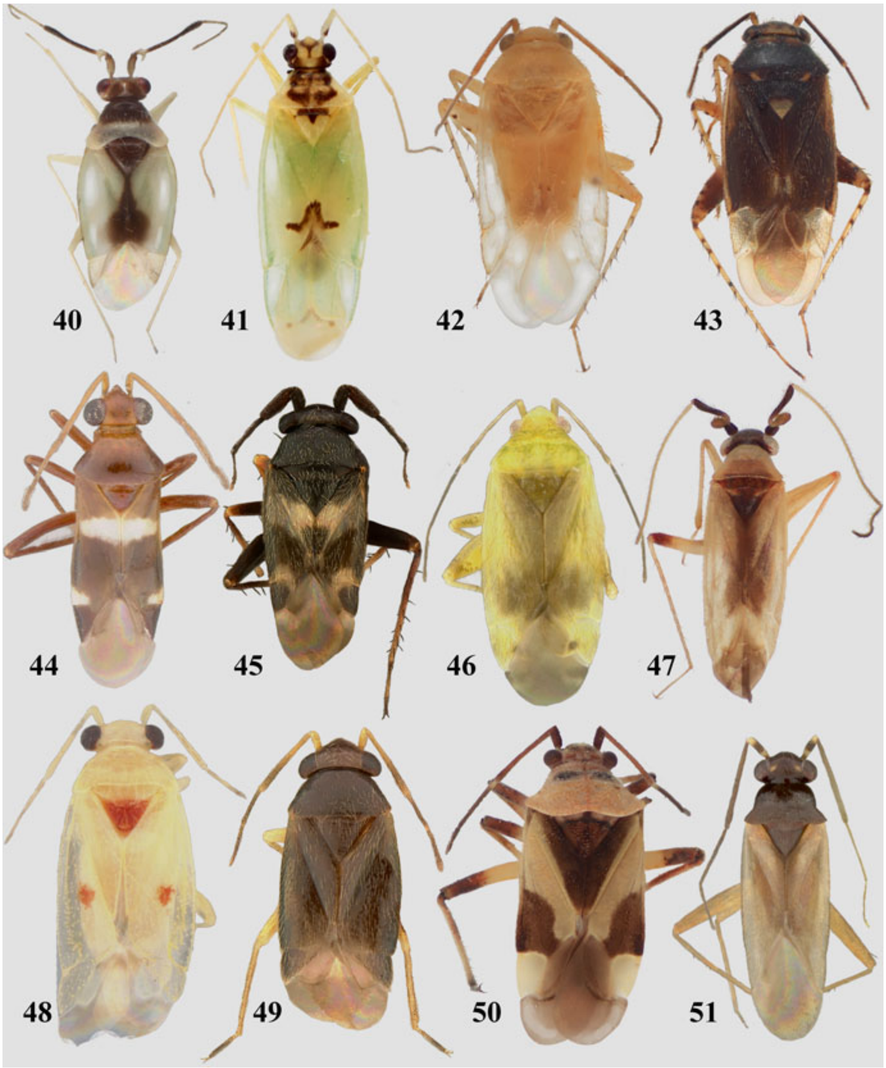
Orthotylini (Figs. 10.38, 10.39, 10.40, and 10.41)

Carvalho (1985b) provided a key to genera of Neotropical Orthotylinae.

Other important contributions to the study of this subfamily in the Neotropics are Forero (2008) (*Aoplonema* Knight, *Aoplonemella* Forero, *Daleapidea* Knight, *Hadronema* Uhler, *Hadronemidea* Reuter, *Lopidea* Uhler, *Origonema* Forero, *Scutomiris* Forero, *Tupimiris* Carvalho and Schaffner); Forero and Schwartz (2009) (*Aoplonema*); Forero (2009) (*Chileria* Carvalho, *Orthotylus* Fieber); Henry (1978, 2001) (*Hyalochloria* Reuter); Knight and Schaffner (1968) (*Lopidea*, *Mayamiris* Knight and Schaffner), 1975 (*Lopidea*), 1976 (*Ilnacora* Reuter); Maldonado and Ferreira (1971) (*Carvalhomiris* Maldonado and Ferreira); Maldonado (1980) (*Jobertus* Distant); Schaffner (1969) (*Lopidella* Knight); and Schaffner and Schwartz (2008) (*Ficinus* Distant, *Jornandes* Distant).

The habits of the Orthotylinae are widely varied. Numerous species may become pests of various crops and ornamentals. For example, Wheeler and Henry (1976) documented the life history and damage by the honey locust plant bug, *Blepharidopterus chlorionis* (Say), on ornamental honey locust, *Gleditsia triacanthos* L. (Fabaceae), in the United States. Species of the onion plant bug genus *Labopidea* Uhler may seriously injure commercial onions and garlic (Henry 1982), and *Falconia intermedia* (Distant) is known to discolor *Lantana camara* L. (Verbenaceae) in Mexico (Palmer and Pullen 1998), making it a potential biological control agent. Ferreira et al. (2001) and Pires et al. (2007, 2008) highlighted the feeding habits and life history of *Platyscytus decempunctatus* on its only known host plant, *Solanum cernuum* Vell. (Solanaceae).

A great number of other orthotylines are predatory and have potential as biocontrol agents. The Holarctic *Blepharidopterous angulatus* (Fallén), known as the black-kneed capsid, is a well-documented predator of aphid and mites in orchards and ornamental plantings (Wheeler and Henry 1992). Hsiao (1945) described *Hyalochloria denticornis* from specimens taken on cotton and beans heavily infested with a species of *Empoasca* (Cicadellidae), suggesting that it was attracted to the these leafhoppers as prey, and Beingolea (1959, 1960) observed this mirid feeding on *Anomis texana* Riley (Lepidoptera) and *Aphis gossypii* Glover (Aphididae) on cotton in Peru. Henry (2001) speculated that members of this genus are opportunistic predators, tracking their prey across multiple and often unrelated hosts. Numerous other members of this tribe, such as *Heterotoma planicornis* (Pallas), *Orthotylus ramus* Knight, and *O. marginalis* Reuter, have been observed preying on aphids, scales, and other small arthropods (Wheeler 2001), making it plausible that many of the poorly known Neotropical taxa should have similar predatory tendencies.



Figs. 10.40–10.51 Neotropical Miridae. 40, *Hyalochloria bispina* Henry (Orthotylinae: Orthotylini). 41, *Jobertus chryselectrus* Distant (Orthotylinae: Orthotylini). 42, *Hyalopsallus diaphanus* (Reuter) (Phylinae: Exaeretini). 43, *Moissonia cuneata* (Stål) (Phylinae: Exaeretini). 44, *Cyrtopeltocoris albofasciatus* Reuter (Phylinae: Hallodapini). 45, *Spanagonicus albofasciatus* (Reuter) (Phylinae: Nasocorini). 46, *Reuteroscopus hamatus* Kelton (Phylinae: Phylini: Keltoniina). 47, *Anomalocornis peyreti* Couturier and Costa (Phylinae: Phylini: Phylina). 48, *Platyscytus binotatus* Reuter (Phylinae: Phylini: Phylina). 49, *Sthenaridea vulgaris* (Distant) (Phylinae: Pilophorini). 50, *Semium subglaber* Knight (Phylinae: Semiini: Semiina). 51, *Tytthus neotropicalis* Carvalho (Phylinae: Semiini: Semiina) (Photos by G Ouellette)

10.5.7 Subfamily Phylinae

This subfamily is recognized by the hairlike parempodia in most taxa (except Pilophorini and some Hallodapini), the fleshy pulvilli often found along the ventral surface of each claw, the mittlike left paramere that usually cups the phallotheca, and the strap-like vesica of the male genitalia. Schuh (1974) noted that males are always macropterous, whereas females sometimes may be brachypterous.

Schuh (1995), in his catalog of the Miridae of the world, recognized five phyline tribes (Auricillocorini, Hallodapini, Leucophoropterini, Phylini, and Pilophorini) and, subsequently, listed six tribes in his online catalog (Schuh 2013), following Wyniger's (2010) resurrection of Knight's tribe Pronotocrepini. These studies were followed by Schuh and Menard (2013), who significantly revised the classification and proposed eight tribes, based on a combination of molecular and morphological evidence, and Menard et al. (2014), who further redefined the classification in a "total-evidence phylogenetic analysis," proposed the tribes Coatonocapsini, Cremnorrhini, Decomiini, Hallodapini, Leucophoropterini, Nasocorini, Phylini, Pilophorini, and Semiini.

Only six of these nine phyline tribes are known from the Neotropics. Unfortunately, several of the newly proposed taxa lack meaningful morphological support, so that they cannot be readily keyed or defined without supporting molecular data, and genera can be placed in their respective tribes and subtribes only by following Schuh and Menard's (2013) listing. As a consequence, we provide an overview of the tribes as defined by Schuh and Menard (2013) and Menard et al. (2014), but are unable to provide a key to distinguish them until these taxa are defined morphologically.

Cremnorrhini

Schuh and Menard (2013) and Menard et al. (2014) recognized this tribe based exclusively on molecular data, indicating that unifying morphological characters are yet to be defined. Two subtribes within this tribe were recognized (Schuh and Menard 2013), the Old World Coatonocapsina and the mostly north temperate Cremnorrhina, the latter of which includes all taxa occurring in the Western Hemisphere. Subsequently, Menard et al. (2014) elevated the Old World Coatonocapsini to tribal status.

Most members of this tribe occur in the western United States and Canada, with only six species of *Coquillettia* Uhler, one of *Teleorhinus* Uhler, and one species of the large Holarctic genus *Macrotylus* Fieber recorded from Mexico (Henry and Wheeler 1988; Wyniger 2010, 2012). Most are recognized by their elongate, often ant-like body, the frequently brachypterous females, the oblique head with the clypeus visible dorsally, the pronotum with an upturned collar-like area, the enlarged free pulvilli, and the distinctive male and female genitalia (Wyniger 2010; Schuh and Menard 2013). Wyniger (2010, 2012) revised and provided identification keys to the New World taxa under the tribal name Pronotocrepini, now treated as a synonym of Cremnorrhina by Schuh and Menard (2013).

Exaeretini (Figs. 10.42 and 10.43)

Only three Neotropical genera and about seven species are included in this tribe (Schuh and Menard 2013), including *Gonoporomiris* Henry and Schuh, *Hyalopsallus* Carvalho and Schaffner, and the circumtropical genus *Moissonia* Reuter. Schuh and Menard (2013) defined this tribe based on the relatively long labium extending beyond the hind coxae, the elongate claws without or with only very small pulvilli, a large twisted gonopore, a twisted S-shaped endosoma composed of two straps connected by a membrane, and an elevated posterior lobe on the left paramere.

Gonoporomiris contains two species (Henry and Schuh 2002; Schuh and Schwartz 2004), *Hyalopsallus* one (Henry and Wheeler 1982; Carvalho 1990a), and *Moissonia* four Neotropical species (Schuh 1995). Little is known of their habits, but they are probably phytophagous. Henry and Wheeler (1982) recorded adults and nymphs of *H. diaphanus* (Reuter) from *Crotalaria incana* L. (Fabaceae) in Florida, and Henry and Schuh (2002) reported adults of *Gonoporomiris mirificus* (Distant) from the flowers of cabbage palmetto, *Sabal* sp. (Arecaceae) on Grand Bahama Island.

Hallodapini (Fig. 10.44)

The Hallodapini are mostly Old World and include taxa previously placed in the Auricillocorini, a tribe recently synonymized with it by Schuh and Menard (2013). Hallodapines are recognized by the uniquely shaped flattened pronotal collar, projecting frons and clypeus, and the twisted endosoma. *Cyrtopeltocoris* Reuter, the only hallodapine genus represented in the Western Hemisphere, occurs primarily in the western United States, with one species known from Cuba and two ranging into Baja California, Mexico. Most species of *Cyrtopeltocoris* are shiny, dark brown, with distinct white maculae or spots on the hemelytra. Knight (1968) provided a key to distinguish eight of the eleven known species; Hernández and Henry (2010) redescribed *C. cubanus* Poppius.

Little is known of their habits. Females are brachypterous and extremely antlike. Males are most frequently taken at lights.

Nasocorini (Fig. 10.45)

Ten genera and about 63 species of this tribe occur in the Neotropics (Schuh and Menard 2013), including the widespread genera *Atractotomus* Fieber, *Rhinacloa* Reuter, *Chlamydatus* Curtis, and *Spanagonicus* Berg. Schuh and Menard (2013) defined the Nasocorini based on the flattened vertex of many species; the short, wide hind femora, often with a row of dorsal spicules on the hind femur; the sericeous or scalelike setae; and the cushion-like pulvilli covering the undersurface of the claws.

Recent revisions and keys to species of the Holarctic genera *Atractotomus* (Stonedahl 1990) and *Chlamydatus* (Schuh and Schwartz 2005), and the New World genera *Rhinacloa* (Schuh and Schwartz 1985) and *Spanagonicus* Menard (in press) will allow recognition of most species.

Members of this tribe are primarily phytophagous, but many have predatory tendencies. Stonedahl (1990) discussed the feeding habitus of the species of *Atractotomus*, noting that members of the *magnicornis* group probably were partially predacious. Wheeler (2001) summarized the predatory habits of *A. magnicornis* (Fallén) and *A. mali* (Meyer-Dür), both of which are well-known predators of aphids, scales, mites, and other small arthropods.

Phylini

As noted by Schuh and Menard (2013), this tribe "continues to be an amalgam of genera lacking easily characterized unifying characters," making it impossible to provide a diagnosis that will allow others to recognize the taxa included in this group. Schuh and Menard (2013) and Menard et al. (2014) recognized the subtribes Exocarpocorina (not in the Neotropics), Keltoniina, Oncotylina, and Phylina.

Keltoniina (Fig. 10.46)

Keltoniina contains one Afrotropical genus and three New World genera (Schuh and Menard 2013). This subtribe is recognized by the somewhat elongate head, small eyes; multiple types of vestiture, including long, erect, almost bristlelike setae, and clumps or patches of white sericeous setae; and the generally, stout, C-shaped endosoma.

The genus *Pseudatomoscelis* Reuter contains four species found from the southern United States to Panama and the West Indies, and *Keltonia* Knight includes 13 species, ranging from the southern United States and south to Colombia and Venezuela (Henry 1991). Henry (1991) revised and keyed the species *Keltonia* and *Pseudatomoscelis*, the latter of which includes the cotton fleahopper, *P. seriata* (Reuter), a well-known pest of cotton in the southern United States, and Henry (2002) added a new species of *Pseudatomoscelis* from the Dominican Republic.

The large genus *Reuteroscopus* Kirkaldy includes 54 species found from the United States to South America. The bright yellow body, marked with dark brown, is characteristic of most species, but the male endosoma with peculiar "feathered" appendages is unique in the Miridae. Kelton (1964) and Knight (1965) described and keyed most of the species, but the species limits, especially those described from females, are still unclear, reflecting the great need for revision.

Oncotylina

Although molecular data unites the taxa included in this subtribe, no morphological characters define them (Schuh and Menard 2013; Menard et al. 2014).

Schuh and Menard (2013) placed nine Neotropical genera in this subtribe, with most ranging only into Mexico: *Hamatophylus* Weirauch (one species), *Knightophylinia* Schaffner (1978) (one species), *Lineatopsallus* Henry (two species), *Maculimiris* Weirauch (two species), *Phymatopsallus* Knight (five species), *Schaffneropsallus* (one species), and *Viscacoris* Weirauch (four species).

Ranzovius Distant, with 10 described species occurring from the United States to southern Brazil (Henry 1999), is one of the more interesting phyline genera. All species are obligate spider commensals. Wheeler and McCaffrey (1984) studied the life history and association of the apparently kleptoparasitic *R. clavicornis* (Knight) (as *R. contubernalis* Henry) with the theridiid spider *Anelosimus studiosus* (Hentz); the bug appeared to feed mainly on small entrapped insects too small to attract the spider's attention and occasionally on dry cadavers. Henry (1984a, 1999) revised the genus and provided a key to species.

Phylina (Figs. 10.47 and 10.48)

The only morphological characters uniting this subtribe are the vaguely diagnostic long labium extending beyond the hind coxae and the absence of pronotal calli (Menard et al. 2014). Nevertheless, molecular evidence apparently always groups these taxa (Menard et al. 2014). Because of the lack of a morphological definition, all Neotropical genera placed in Phylina are treated as *incertae sedis* by Schuh and Menard (2013), indicating that much work remains to clarify the position of the taxa included in this group.

Thirteen genera and about 49 Neotropical species are placed in Phylina (Schuh and Menard 2013). Some of the included genera and the most important papers treating them are *Anomalocornis* Carvalho and Wygodzinsky (Couturier and Costa 2002), *Bicurvicoris* Carvalho and Schaffner (Carvalho and Schaffner 1973), *Crassicornus* Carvalho (Carvalho 1984), *Parafulvius* Carvalho (Costa and Couturier 2000), *Platyscytisca* Costa and Henry (Henry and Costa 2003), and *Platyscytus* Reuter (Maldonado and Carvalho 1981).

Pilophorini (Fig. 10.49)

This worldwide tribe, containing many myrmecomorphic taxa, is recognized by the fleshy convergent parempodia between the claws; the white sericeous or silky setae, often occurring in patches or distinct bands; and the carinate and upturned posterior margin of the vertex. Only three genera and about 11 species are known from the Neotropics.

Schuh and Schwartz (1988) treated the New World species of *Pilophorus* and the nine mostly Neotropical species of *Sthenaridea* Reuter, most of which are associated with grasses (Poaceae) and sedges (Cyperaceae). Schuh (1991) provided a phylogenetic, biogeographic, and host plant analysis of this tribe. Hernández and Henry (2010) described the new species *Pilophorus cubanus*, which is associated with *Pinus* (Pinaceae). Most species of *Pilophorus* are, at least partially predacious, feeding on aphids and other arthropods (Schuh and Schwartz 1988); Wheeler (2001) summarized the known hosts and feeding habits for some of the Nearctic and Palearctic species. More recently, Henry (2012c) described the peculiar new genus and species *Randallophorus schuhi* from Paraguay, which apparently is most closely related to *Sthenaridea* based on male genitalia.

Semiini (Figs. 10.50 and 10.51)

The tribe Semiini, as defined by Schuh and Menard (2013), contains two subtribes, the Exocarpocorina, with four Neotropical genera and six species restricted to Argentina and Chile, and the Semiina, with three genera and 16 species ranging from the United States to South America. The tribe is defined by the eyes being parallel to the anterior margin of the pronotum, the reduced scent gland opening, the sclerotized ventral sack in females, and the simple, elongate endosoma, with or without a well-developed secondary gonopore or a broad, flattened, T-shaped endosoma with a well-developed secondary gonopore.

Exocarpocorina

Only four genera [*Ampimpacoris* Weirauch (one species) and Schuh, *Araucanophylus* Carvalho (two species), *Chiloephylus* Carvalho (one species), and *Gonzalezinus* Carvalho (two species)] and six poorly known species of the subtribe are known in the Neotropics, all of which occur only in Argentina or Chile. All remaining genera are found in the Australian Region, making this the only transantarctic distribution in the Phylinae (Schuh and Menard 2013). These taxa are grouped based on unique asymmetrical sclerites of the female vestibulum, the elaborate posterior wall, the L-shaped phallotheca, and the expanded central portion of the left paramere (Schuh and Menard 2013; Menard et al. 2014).

Semiina

Some of the better-known genera of the subtribe Semiina include *Semium* Reuter, with five Neotropical species (Kelton 1974), and *Tytthus* Fieber, with 11 species (Henry 2012b). All species of *Semium* are associated with species of *Chamaesyce* (Euphorbiaceae; older records from *Euphorbia* sp. apply to this genus) (Kelton

1974). Species of the genus *Tytthus* prey exclusively on the eggs of grass-feeding plant hoppers (Delphacidae), making them important biological control agents on agricultural monocots, such as rice and sugarcane (Henry 2012b).

10.6 Concluding Remarks

The Miridae, with more than 11,000 species, represent one of the 20 most hyperdiverse insect groups (Cassis and Schuh 2012). As their common name implies, many plant bugs are phytophagous and often become pests of agricultural crops and ornamental plants. Lygus bugs (*Lygus* spp.), the cotton fleahopper (*Pseudatomoscelis seriatus*), the cocoa capsids (*Monalonion* spp.), the orchid bugs (*Tenthecoris* spp.), the garden fleahopper (*Microtechnites bractatus*), and the bean capsid (*Pycnoderes quadrimaculatus*) are just a few examples of mirid plant pests that bring notoriety to the family through their feeding (Wheeler 2000a), which may be expressed as chlorosis, cankers, shot holing, stunting, fruit drop, yellowing and wilting foliage, and defoliation (Wheeler 2001). Many others have the potential to cause enormous economic losses even when symptoms are not readily apparent (Wheeler 2001).

Though mirids have not evolved the obvious morphological adaptations for capturing prey, such as raptorial front legs found in phymatine reduviids or stout, piercing-sucking mouthparts found in asopine pentatomids and most Reduviidae, many mirids, nevertheless, are successful predators. Most mirids will feed on the eggs, early instar larvae, nymphs, and dead or dying invertebrates (Wheeler 2001). Some taxa possess powerful salivary enzymes that immobilize their prey (Cohen 1996). Most members of the subfamily Deraeocorinae and many species of Mirinae (e.g., *Phytocoris* spp.), Orthotylinae (e.g., *Blepharidopterus angulatus*), Phylinae (e.g., *Campylomma verbasci*), and Bryocorinae (e.g., *Campyloneura virgula*, *Engytatus modestus*) have strong predaceous tendencies.

Despite their great importance both as plant pests and as predators, many new taxa remain to be described, especially in the Neotropical Region, and the biology, host plants, and phylogenetic relationships of most are unknown, except for the most agriculturally important taxa. Henry and Wheeler's (1988) speculation that the world fauna will approach 20,000 species once the Neotropical species are more fully studied likely is an underestimation. We hope this brief overview will stimulate much-needed additional taxonomic and biological work on this highly diverse, speciose group of economically important bugs.

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Chapter 11
Damsel Bugs (Nabidae)

Maria del C. Coscarón, S. Kristine Braman, and Marcela Cornelis

Abstract Damsel bugs, Nabidae, are valued predators in agricultural and urban systems. Worldwide, there are considered to be 31 genera and 386 species known, with 11 genera and 83 species from the Neotropical region. While little bionomic information is available for Neotropical nabid species, highlighting the need for future research, the biology of *Nabis (Tropiconabis) capsiformis* Germar, is representative of the family. *N. (T.) capsiformis* demonstrated a type I functional response when feeding on bollworm eggs. Under laboratory conditions, total generation time was 51.6 days. Nabids insert their eggs into plant tissue with only the operculum remaining visible. *N. (T.) capsiformis* averaged 105.3 eggs/female. Much remains to be discovered concerning this fascinating and important group of predatory heteropterans. Knowledge about biology and taxonomy of this group is fundamental to developing future programs in integrated pest control.

11.1 Introduction

The Nabidae, or damsel bugs, are regarded as beneficial insects, appreciated for their predatory potential in suppressing insect pests in crops such as alfalfa, soybean, and cotton (Braman 2000). Nabids have been known to probe plants for moisture (Stoner 1972), occasionally carry plant pathogens (Burgess et al. 1983), and even

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occasionally bite humans (Faúndez and Carvajal 2011). They feed on small insects, many of which are considered pests, yet also feed on insects regarded as beneficial, e.g., anthocorids. Nabids also serve as prey for spiders, assassin bugs, birds, etc. Nabids possess raptorial front legs with thickened spines and have purportedly been given their common name from their habit of holding the front legs up like a damsel holding a skirt hem up while dancing. Nabids overwinter as adults or late-stage nymphs although some have been reported to overwinter as eggs (Harris 1928).

The majority of information published on biology and ecology and impact of nabids have focused on those inhabiting agroecosystems, with little known about the bionomics of the many species occurring outside managed ecosystems (Wheeler 2001). Characters used in identifying species include external morphological characters: size and shape of male claspers, interocular distances, trichobothria, length of antennal segments, degree of fuscous markings, spines on the legs, and size and shape of internal seminal depository of females. While there are considered to be 31 genera and 386 species known worldwide (Henry 2009), for the Neotropical region, 11 genera and 83 species are known (Volpi and Coscarón 2010; Coscarón and Volpi 2013). Neotropical Nabidae are not well known at present, but a key to the nabids of Argentina (Cornelis and Coscarón 2013) provides descriptions and identification characters for five genera and 14 species (Coscarón, in press). The biology, ecology, economic importance, and susceptibility to insecticides for the two best-studied species in the region, *Nabis (Tropiconabis) capsiformis* Germar and *Nabis punctipennis*, are provided herein. There continues to be a particular need for biological information on neotropical nabid species especially in defining potential and actual impact on known pest species.

11.2 General Characteristics and Diagnosis

11.2.1 General Characteristics

The Nabidae are a small group of insects ranging from 5 to 15 mm. Many are elongate and of drab coloration, whereas others are more stout bodied and occasionally possess distinctive red and black color patterns (Fig. 11.1a–d). The general aspect in different views can be seen in Fig. 11.2a, b.

11.2.2 Diagnosis

Labium flexible and usually curving, reaching onto pro- or mesothorax, with 4 distinct segments (Fig. 11.2a, b, e); antennal prepedicellite present, variable in length (Figs. 11.1b and 11.2e); fossula spongiosa present on fore and middle tibiae of most taxa (Fig. 11.2d, e); costal fracture present or absent; membrane with 2 or 3 elongate

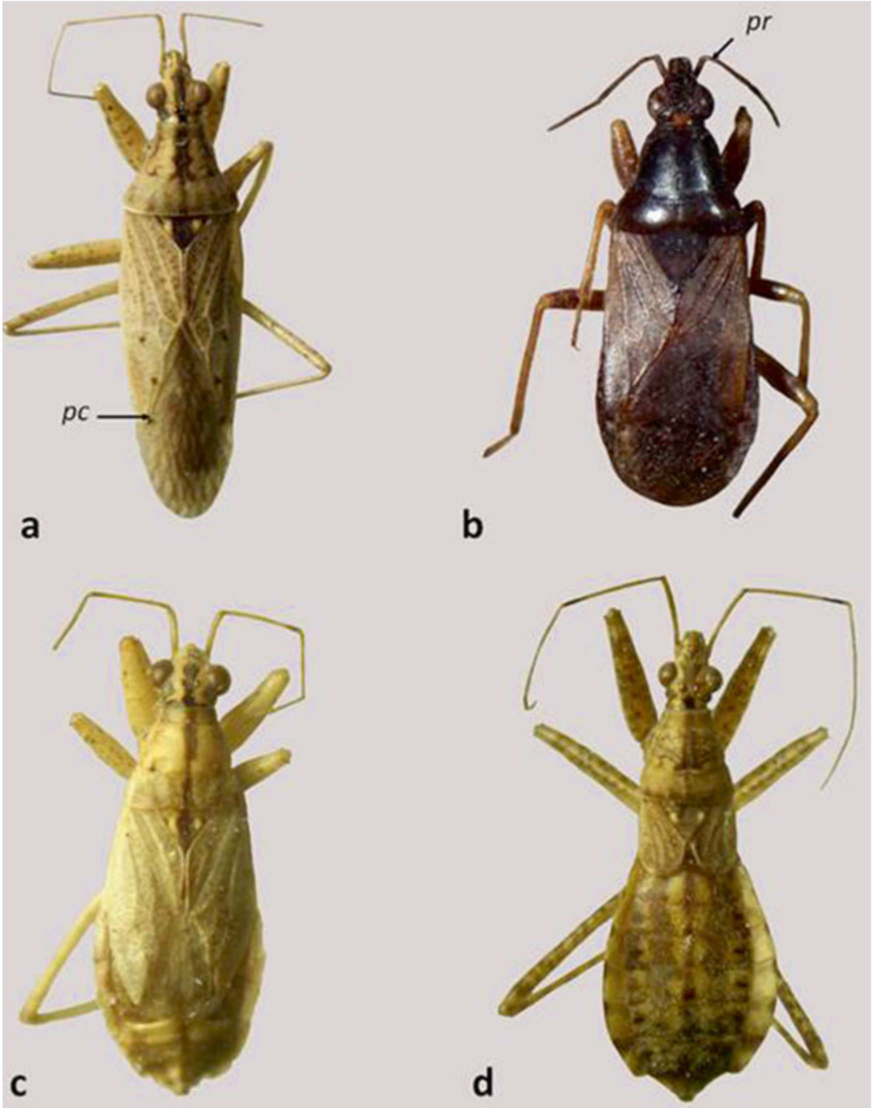

Fig. 11.1 Different color patterns of Nabidae, (**a**) *Nabis punctipennis* Blanchard (macropterous form), (**b**) *Pagasa fuscipennis* Reuter (macropterous form) (Cornelis and Coscarón 2013), (**c**) *Nabis faminei* Stål (brachypterous form), (**d**) *Hoplistoscelis* sp. Reuter (micropterous form) (*pc* processus corial, *pr* antennal prepedicellite) (Photos by M Cornelis)

cells, usually with emanating veins and a stub (processus corial) (Fig. 11.1a); abdominal spiracles 2–8 present, located either on laterosternites or medio-sternites; parastigmal pits present in most taxa; Ekblom's organ usually present in males (Fig. 11.3a, d, e).

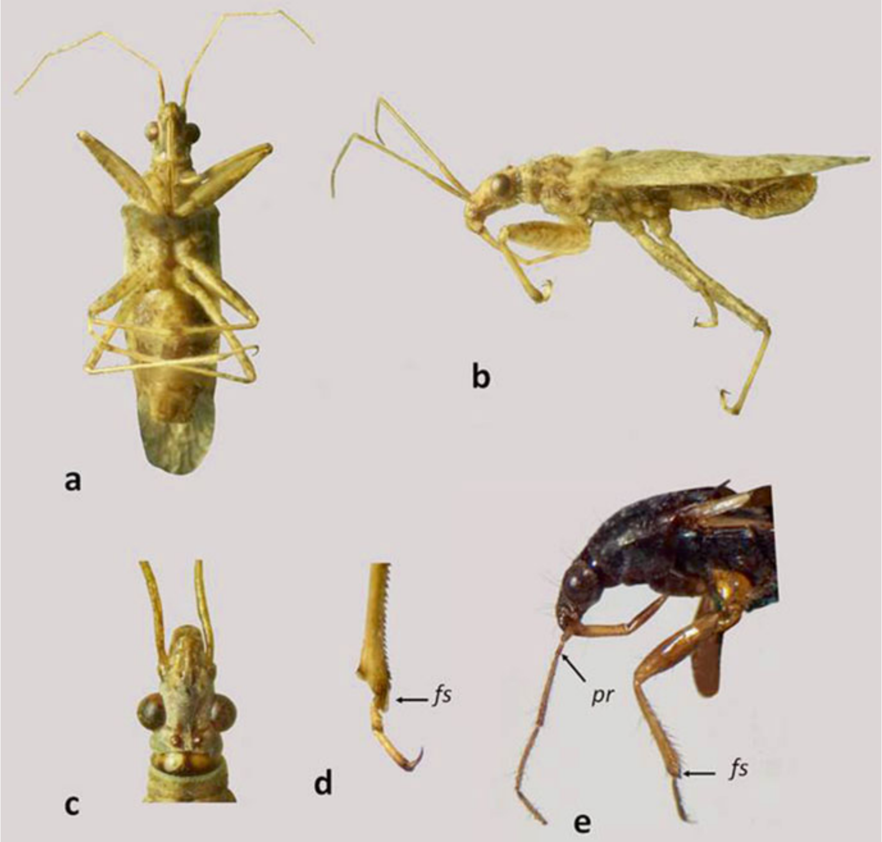

Fig. 11.2 (**a**, **b**) General aspect of *Nabis argentinus* Meyer-Dür, (**a**) dorsal view, (**b**) lateral view, (**c**) head of *Nabis capsiformis* Germar, (**d**) fossula spongiosa on middle tibiae of *Nabis mexicanus* Remane, (**e**) fossula spongiosa on fore tibiae and antennal prepedicellite of *Pagasa fuscipennis* Reuter (Cornelis and Coscarón 2013) (*fs* fossula spongiosa, *pr* antennal prepedicellite) (Photos by M Cornelis)

Head: the head of Nabidae is more or less elongated (Fig. 11.2c). Its posterior part, cylindrical, engaged in the collar of the prothorax with a neck.

Thorax: it is more or less bell shape (Fig. 11.1a–d).

Legs: according to the type of prey, foretibiae and forefemora are simple; others are enlarged and armed with heavy spines, forming a formidable apposable grasping apparatus.

Wings: polymorphism is common in many species (Fig. 11.1a–d) particularly in those living at higher latitudes (Asquith and Lattin 1990). According to Kerzhner (1983), *Nabis (T.) capsiformis*, "pale damsel bugs," are long-winged bugs that fly well and are the most widespread species in the Nabidae.

Abdomen: trichobothria are present on abdomen in some taxa.

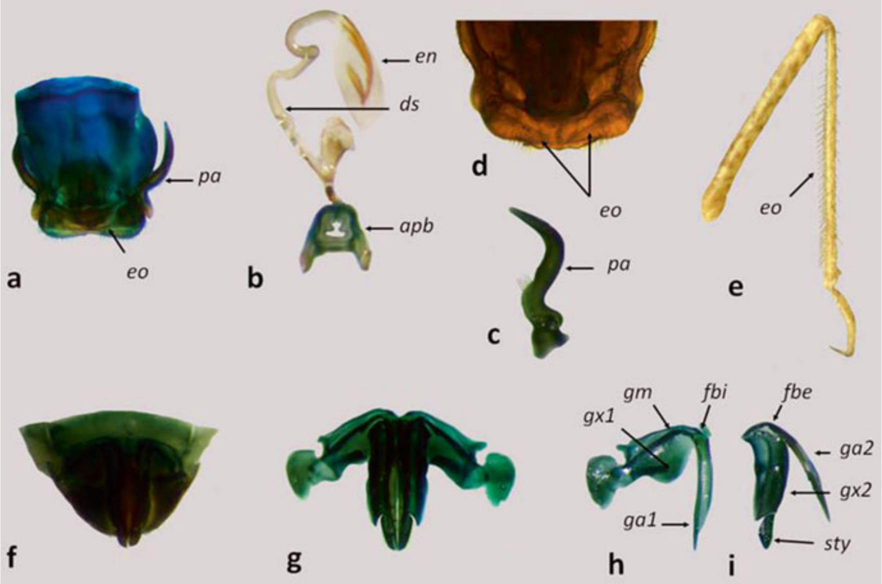

Fig. 11.3 (**a**–**c**) Male genitalia *Nabis faminei* Stål, (**a**) pygophore, (**b**) aedeagus, (**c**) paramere (Cornelis and Coscarón 2013), (**d**) detail of Ekblom's organ *Nabis argentinus* Meyer-Dür, (**e**) hind tibiae of male *Nabis argentinus* Meyer-Dür showing spines of Ekblom's organ, (**f**–**i**) female genitalia *Pagasa fuscipennis* Reuter, (**f**–**g**) genital segment, (**h**) first gonapophysis and gonocoxite 1, (**i**) second gonapophysis and gonocoxite 2 (Cornelis and Coscarón 2013) (*apb* articulatory apparatus, *ds* ductus seminis, *en* endosoma, *eo* Ekblom's organ, *fbe* external fibula, *fbi* internal fibula, *ga1* and *ga2* gonapophysis 1 and 2, *gm* gonangulum, *gx1* and *2* gonocoxites 1 and 2, *pa* paramere, *sty* styloid) (Photos by M Cornelis)

Male genitalia (Fig. 11.3a–c) are usually symmetrical, sometimes parameres (some Prostemmatinae) or phallus asymmetrical.

Female genitalia (Fig. 11.3f–i) are ovipositor laciniate reduced in some cases: spermatheca in the form of vermiform gland.

11.2.3 Specialized Morphology

Some Nabidae possess a structure known as Ekblom's organ Kerzhner (1981). It consists of two diagonal grooves surrounded by specialized setae, situated behind the posterior foramen of the pygophore (Fig. 11.3a, d), and a group of specialized setae at the posterodistal margin of the hind tibia (Fig. 11.3e) that are rubbed across the pygophoral portion of the organ to distribute attractant pheromones from rectal glands (Carayon 1970). The parastigmal pits are small depressions containing a concentration of apparently secretory setae, located adjacent to the spiracles on one or more of the ventral laterotergites of abdominal segments 3–7 or in the sternum 3 of others (Carayon 1948, 1950). Their function is unknown.

11.3 General Biology and Ecology

The biology of *Nabis (T.) capsiformis* is representative of the family (Hormchan et al. 1976). Adult nabids lived 14.9 and 21.6 days, respectively, for males and females under laboratory conditions (26–28 °C, 60–70 % RH, and 15:9 L:D photoperiod). Total generation time was 51.6 days. Longevity of adult *Nabis punctipennis* was 59.9 days (Rebolledo et al. 2005). The ability to predict population phenology as well as predator impact is necessary to incorporate mortality that is the result of predation by nabids into economic injury assessments. Very little such information is available for neotropical nabid species and highlights the need for future research. Even congeneric species partitioning the same environment can vary in intrinsic rates of increase and predatory potential. Among the three *Nabis* spp., inhabiting soybean, for example, *N. americoferus* (Carayon), showed the greatest potential for population increase with an r value of 0.72 compared with 0.50 and 0.44 for *N. roseipennis* Reuter and *N. rufusculus* Reuter (Braman and Yeargan 1988). This larger r value resulted from a larger net reproductive rate and shorter generation time compared with the other two species.

11.3.1 Eggs and Oviposition

Nabids insert their eggs into plant tissue with only the operculum remaining visible (Braman 2000). Embryonic development takes place after the eggs are laid. Eggs with 1 micropyle are shown in Fig. 11.4a. Eggs of *Nabis (T.) capsiformis* required 7.6 days to hatch under laboratory conditions described above (Hormchan et al. 1976).

11.3.2 Nymph Feeding and Development

Nymphal nabids are important predators in agroecosystems, yet few identification aids are available to assist the pest management practitioner. Elvin and Sloderbeck (1984) developed a key to the nymphs of four species of Nabidae from the southeastern USA: *Nabis roseipennis, N. americoferus, N. (T.) capsiformis,* and *Hoplistoceslis deceptivus* (Harris). Cornelis et al. (2012) provide a description of instars III–V of *N. (T.) capsiformis* collected in Argentina. Nymphal dorsal abdominal scent glands are present between terga 4/5, 5/6, and 6/7 (Fig. 11.4d). Trichobothria are present on the abdomen of nymphs of some taxa. The third, fourth, and fifth instars can be seen in Fig. 11.4b–d.

Péricart (1987) gave a general contribution to the knowledge of the immature stages of Nabidae. Currently, contributions on instars included three species of *Nabis*: *N. alternatus* Parshley (Taylor 1949), *N. roseipennis*, and *N. rufusculus* (Mundinger 1922); several species of *Nabicula*, *N. americolimbata* Carayon, *N. fla-*

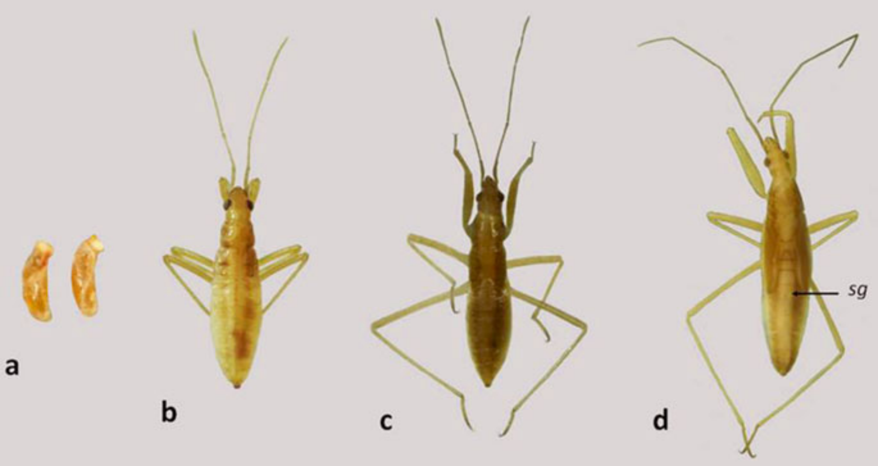

Fig. 11.4 (**a**) Eggs of *Pagasa fuscipennis* Reuter (Cornelis and Coscarón 2013), (**b–d**) nymphs of *Nabis capsiformis* Germar, (**b**) third instar, (**c**) fourth instar, (**d**) fifth instar (Cornelis et al. 2012) (*sg* scent glands) (Photos by M Cornelis)

vomarginata Scholtz, *N. limbata* Dahlbom, *N. nigrovittata nearctica* Kerzhner, *N. propinqua* Reuter, *N. subcoleoptrata* Kirby, and *N. vanduzeei* Kirkaldy (Larivière 1994); *Lasiomerus annulatus* Reuter (Larivière 1993); *Arachnocoris albomaculatus* Scott (Myers 1925) (Nabinae); and *Alloeorhynchus trimacula* Stein (Cervantes-Peredo 2004) (Prostemmatinae).

Ojeda-Peña (1971) described the nymphs, eggs, and biology of *Nabis (T.) capsiformis* Germar in Peru. *N. punctipennis* is an important predator of several insect pests of cotton in the central coastal region; *N. (T.) capsiformis* appears to play a similar role in the northern coastal region (Ojeda-Peña 1971). The egg and five nymphal instars averaged 9.3 and 17.8 days, respectively, at 27 °C and 75 % R.H. when fed with larvae of *Bucculatrix thurberiella* Busck. The adults lived for 3–8 days, females laying an average of 112.4 eggs each. A generation lasted 26–35 days in summer. Hormchan et al. (1976) determined that male *N. (T.) capsiformis* develop faster than females, 18 versus 22.4 days, respectively, at 26–28 °C on a diet of first instar tarnished plant bugs and bollworms.

11.3.3 Adult Feeding and Reproduction

All Nabidae practice vaginal copulation, with fertilization taking place in the mesodermal oviducts near the base of the ovarioles or near the pedicels. Insemination can be normal or hemocoelic. Others practice traumatic intravaginal insemination (Carayon 1977). *Nabis (T.) capsiformis* averaged 105.3 eggs per female (Hormchan et al. 1976) with 78 % viability under laboratory conditions. Adults survived less than a month at 26–28 °C when fed with tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) nymphs, supplemented occasionally with bollworm, *Helicoverpa zea* (Boddie) larvae. Greatest fecundity occurred on the 9th day after emergence as adults with a rapid decline after the 15th day.

11.4 Classification and Diversity

The Nabidae have been placed within the superfamily Cimicoidea in the infraorder Cimicomorpha (Leston et al. 1954; Schuh and Stys 1991). There is no clear consensus concerning the organization of the major subdivisions of the family. Stål (1873) provided the first useful classification, recognizing three subfamilies: Nabina, Coriscina, and Pachynomina. Carayon (1970), Kerzhner (1981), and Péricart (1987) recognized four subfamilies: Medocostinae, Velocipedinae, Nabinae, and Prostemmatinae. We follow the subfamily classification of Schuh and Stys (1991) in defining the Nabidae as including only the Nabinae and Prostemmatinae. They defined the nabids on the basis of 4-segmented labium, membrane venation, and the presence of Ekblom's organ; Kerzhner's (1981) classification is followed for the tribes.

The subfamily Nabinae is classified into four tribes, Arachnocorini, Carthasini, Gorpini, and Nabini, which are united by the presence of moderately long labial segments, the lack of scutellar trichobothria, and opening of pygophore oriented dorsad. The subfamily Prostemmatinae is divided into the Phorticini and Prostemmatini, each with only two genera, both of which possess scutellar trichobothria and have the posterior foramen of the pygophore in a caudal or ventral position. Prostemmatini is considered to be more primitive (Kerzhner 1981, 1996).

For the world, 31 genera and 386 species are known (Henry 2009); for the Australian region, 7 genera and 22 species; for the Palearctic region, 10 genera and 112 species (Kerzhner 1996); and for Canada and the continental USA, 10 genera and 41 species (Henry and Lattin 1988); Kerzhner and Henry 2008) and for the Neotropical region (Volpi and Coscarón 2010; Coscarón and Volpi 2013), 11 genera and 83 species. There are only partial catalogs for Argentina, two genera and seven species (Pennington 1920–1921); five genera and 14 species (Cornelis and Coscarón 2013); Ecuador, two genera and four species (Froeschner 1981); Galápagos, one genus and three species (Froeschner 1985); and Panama, 10 genera and 17 species (Froeschner 1999).

11.4.1 Main Species

Family Nabidae Costa
Subfamily Nabinae Costa
Tribe Arachnocorini Reuter

Genus *Arachnocoris* Scott
Arachnocoris alboannulatus Costa Lima
Distribution: Brazil

Arachnocoris albomaculatus Scott
Distribution: Brazil

Arachnocoris berytoides Uhler
Distribution: Guadeloupe. Grenada. Martinique. Puerto Rico

Arachnocoris dispar Scott
Distribution: Brazil

Arachnocoris eberhardi Kerzhner
Distribution: Costa Rica

Arachnocoris myersi China
Distribution: Brazil

Arachnocoris panamensis (Distant)
Distribution: Panama

Arachnocoris setosus Kerzhner
Distribution: Costa Rica

Arachnocoris simoni Bergroth
Distribution: Venezuela

Arachnocoris thesauri López
Distribution: French Guyana

Arachnocoris torquatus Bergroth
Distribution: Venezuela

Arachnocoris trinitatis Bergroth
Distribution: Trinidad

Arachnocoris varius López
Distribution: French Guyana

Tribe Carthasini Blatchley
Genus *Praecarthasis* Kerzhner
Praecarthasis froeschneri Kerzhner
Distribution: Brazil (Mato Grosso). Ecuador (Pastaza). Peru (Junin)

Praecarthasis gibbus Kerzhner
Distribution: Ecuador (Pastaza). Panama (Barro Colorado). Peru (Cuzco, Junin)

Praecarthasis nigrescens Kerzhner
Distribution: Brazil (Mato Grosso, Pará). Peru (Junin)

Praecarthasis panamensis (Harris)
Distribution: Panama (Porto Bello)

Praecarthasis paprzyckii Kerzhner
Distribution: Peru (Junin, Huánuco)

Praecarthasis pusillus Kerzhner
Distribution: Brazil (Rio de Janeiro)

Genus *Carthasis* Champion

Carthasis championi Harris
Distribution: Panama (Chiriqui)

Carthasis rufonotatus Champion
Distribution: Panama (Chiriqui)

Tribe Gorpini Reuter

Genus *Neogorpis* Barber

Neogorpis spinicollis Kerzhner
Distribution: Panama (Barro Colorado, Canal Zone, Colon)

Tribe Nabini Costa

Genus *Hoplistoscelis* Reuter

Hoplistoscelis confusa Kerzhner and Henry
Distribution: Colombia. Costa Rica. Dominican Republic. El Salvador. Grenada. Grenadines. Guatemala. Haiti. Honduras. Jamaica. México (Chiapas, Guerrero, Michoacan, Morelos, Oaxaca, San Luis Potosi, Sinaloa, Tabasco, Veracruz). Panama. Puerto Rico. Venezuela

Hoplistoscelis dentipes (Harris)
Distribution: México

Hoplistoscelis nigriventris (Stål)
Distribution: México

Hoplistoscelis pallescens (Reuter)
Distribution: Central America. Costa Rica. Venezuela. West Indies

Hoplistoscelis sericans (Reuter)
Distribution: Guatemala (Guatemala, Quetzaltenango, Sacatepequez). México (Guerrero, Jalisco, México City, Morelos, Veracruz)

Hoplistoscelis sordida (Reuter)
Distribution: Argentina (Entre Ríos). Brazil. Central and South America from central part of México to Argentina. Costa Rica (Cartago). Eastern North American. Guatemala (Sacatepequez, Vera Paz). México (Guerrero, Jalisco, Morelos, Tabasco, Vera Cruz). Panama (Chiriqui). West Indies

Genus *Lasiomerus* Reuter

Lasiomerus andabata Kerzhner
Distribution: Guatemala. México (Tabasco). Panama (Chiriqui)

Lasiomerus constrictus (Champion)
Distribution: Argentina (Buenos Aires). Guatemala. Honduras. México. Panama (Chiriqui). México to Panama

Lasiomerus signatus (Uhler)
Distribution: Grenada. México (Tabasco). Panama (Chiriqui)

Lasiomerus spinicrus (Reuter)
Distribution: Antilles. Argentina (Corrientes). Bolivia. Brazil. Cuba. Ecuador. Grenada. Guadeloupe. Guyana. Haití. México. Panama (Chiriqui). Peru. México to Brazil

Genus *Metatropiphorus* Reuter

Metatropiphorus alvarengai Kerzhner
Distribution: Argentina (Buenos Aires). Brazil (Bahia, Mato Grosso, Santa Catarina). Surinam (Marowijne)

Genus *Nabis* Latreille

Nabis argentinus Meyer-Dür
Distribution: Argentina (Buenos Aires, Catamarca, Córdoba, Chaco, La Pampa, Mendoza, Río Negro, Salta, San Luis). Uruguay (Artigas, Canelones, Colonia, Durazno, Maldonado, Montevideo, Paysandú)

Nabis crassipes Reuter
Distribution: Guatemala (Guerrero, Morelos). México (México City)

Nabis faminei Stål
Distribution: Argentina (Buenos Aires, Patagonia, Tierra del Fuego). Chile

Nabis ferus (L.)
Distribution: Guatemala (Quetzaltenango). México (Durango, Guerrero, Veracruz)

Nabis galapagoensis Kerzhner
Distribution: Ecuador (Galápagos Islands)

Nabis paranensis Harris
Distribution: Argentina (Buenos Aires, Jujuy, La Pampa, Misiones). Brazil (Parana)

Nabis punctipennis Blanchard
Distribution: Argentina (Chubut, Mendoza, Neuquén, Río Negro). Chile (Osorno). Continental Chile and Archipielago Juan Fernández

Nabis reductus Kerzhner
Distribution: Ecuador (Galápagos Islands)

Nabis roripes Stål
Distribution: Argentina (Misiones). Brazil (Mato Grosso). Colombia (Cundinamarca). Peru (Loreto, San Juan)

Nabis seticrus Harris
Distribution: Argentina (Salta). Brazil (Mato Grosso, Rio de Janeiro)

Nabis tandilensis Berg
Distribution: Argentina (Buenos Aires)

Subgenus *Nabis* Latreille

Nabis (Nabis) mexicanus Remane
Distribution: Guatemala. México

Subgenus *Tropiconabis* Kerzhner

Nabis (Tropiconabis) capsiformis Germar
Distribution: Argentina (Buenos Aires, Catamarca, Córdoba, Corrientes, Jujuy, La Pampa, Mendoza, Misiones, Salta, Santiago del Estero). Brazil (Mato Grosso do Sul, Rio de Janeiro, Pará). British Guyana. Chile (Arica). Continental Chile and Easter Island. México. Peru (Lima). Uruguay (Montevideo)

Nabis (Tropiconabis) consimilis Reuter
Distribution: Chile. Colombia. Ecuador (Galápagos Islands). Peru

Nabis (Tropiconabis) latior Kerzhner and Henry
Distribution: Bahamas

Subfamily Prostemmatinae Reuter

Tribe Prostemmatini Reuter

Genus *Alloeorhynchus* Fieber

Alloeorhynchus alayoi Kerzhner
Distribution: Cuba

Alloeorhynchus delicatus Harris
Distribution: Panama

Alloeorhynchus jamaicensis Kerzhner
Distribution: Jamaica

Alloeorhynchus maldonadoi Kerzhner
Distribution: Puerto Rico

Alloeorhynchus moritzii (Stein)
Distribution: Antigua and Barbuda (Saint John's). Argentina
(Formosa, Chaco, Corrientes, Misiones). Grenada

Alloeorhynchus slateri Kerzhner
Distribution: Jamaica

Alloeorhynchus trimacula (Stein)
Distribution: Guatemala. México (Oaxaca). Panama

Alloeorhynchus vittativentris Stål
Distribution: Argentina (Misiones). Colombia. Panama

Genus *Pagasa* Stål

Pagasa luctuosa Van Duzee
Distribution: Colombia

Subgenus *Lampropagasa* Reuter

Pagasa (Lampropagasa) cobbeni Kerzhner
Distribution: Curaçao Island (Lesser Antilles). Netherlands Antilles

Pagasa (Lampropagasa) confusa Kerzhner
Distribution: Costa Rica. Guatemala. México. Panama. Puerto Rico

Pagasa (Lampropagasa) flavipennis Kerzhner
Distribution: Bolivia

Pagasa (Lampropagasa) fusca (Stein)
Distribution: Guatemala. México. Panama

Pagasa (Lampropagasa) fuscipennis Reuter
Distribution: Argentina (Buenos Aires, Chaco, Chubut, Córdoba, La Pampa, Misiones, Río Negro, Salta, San Luis, Santa Fé). Brazil (Goiás, Minas Gerais, Santa Catarina, São Paulo). Paraguay. Uruguay (Montevideo, Colonia, Soriano)

Pagasa (Lampropagasa) similis Poppius
Distribution: Brazil (Amazonas, Mato Grosso). Surinam

Subgenus *Pagasa* Stål

Pagasa (Pagasa) aenescens Stål
Distribution: Brazil. Surinam

Pagasa (Pagasa) amazonica Poppius
Distribution: Brazil (Amazonas, Maranhão). Paraguay. Surinam

Pagasa (Pagasa) bimaculata Harris
Distribution: Brazil (Mato Grosso). Panama. Paraguay. Surinam

Pagasa (Pagasa) brailovskyi Kerzhner
Distribution: México. Panama

Pagasa (Pagasa) brunneipes Kerzhner
Distribution: Brazil

Pagasa (Pagasa) costalis Reuter
Distribution: Argentina (Buenos Aires, Salta). Ecuador. Paraguay. Surinam (Saramacca). Uruguay (Montevideo)

Pagasa (Pagasa) doesburgi Kerzhner
Distribution: Surinam

Pagasa (Pagasa) henryi Kerzhner
Distribution: Brazil. Panama. Peru

Pagasa (Pagasa) luteiceps (Walker)
Distribution: Argentina (Corrientes, Entre Ríos, Formosa, Santa Fe, Santiago del Estero) Brazil (Mato Grosso, Rio de Janeiro). Colombia (Magdalena). México (Vera Cruz). Panama (Barro Colorado Island). Peru. Surinam. Tobago Island. Uruguay. Venezuela

Pagasa (Pagasa) margaritae Kerzhner
Distribution: Surinam

Pagasa (Pagasa) pallidiceps (Stål)
Distribution: Brazil

Pagasa (Pagasa) pallipes Stål
Distribution: Colombia. Costa Rica. Cuba. Honduras. México. Panama (Chiriqui). Venezuela

Pagasa (Pagasa) planipes Harris
Distribution: Peru (Junin)

Pagasa (Pagasa) prostemmatoides Kerzhner
Distribution: México. Salvador

Pagasa (Pagasa) ruficeps (Walker)
Distribution: Brazil

Pagasa (Pagasa) signatipennis Reuter
Distribution: Argentina (Formosa). Bolivia. Brazil (Mato Grosso). Colombia. Paraguay. Surinam. Venezuela

Tribe Phorticini Kerzhner

Genus *Phorticus* Stål

Phorticus collaris Stål
Distribution: México

Phorticus speciosus Harris
Distribution: Panama

Phorticus viduus Stål
Distribution: Brazil (Rio de Janeiro)

Phorticus obscuripes Stål
Distribution: Brazil (Rio de Janeiro)

11.4.2 Fossils and Genomic Data

Asquith and Lattin (1990) suggested a Late Cretaceous age for the genus, predicting a much older age for the group as a whole. The extinct *Metatropiphorus succini* (Jordan) from the Late Eocene Baltic amber (40–35 Ma) belongs to the genus considered the most primitive in the subfamily Nabinae (Kerzhner 1981). Li et al. (2012a, b) presented the complete mt genome of *Alloeorhynchus bakeri*, a representative of Prostemmatinae, and provided analyses of the nucleotide composition, codon usage, compositional biases, and RNA secondary structure. They evaluated the phylogenetic position of Nabidae in Heteroptera based on the sequences of PCGs. This represented the first sequenced mitochondrial genome within the family Nabidae. Further, a study with additional species found that the relationship of three tribes from two subfamilies of Nabidae was well represented by the mitogenome data and was consistent with current phylogeny of the family Nabidae constructed mainly from morphological traits (Li et al. 2012a).

11.4.3 Economic Importance

Adult female *Nabis (Tropiconabis) capsiformis* were found to be potentially very effective predators of *Heliothis* spp. eggs and larvae (Samson and Blood 1980). *N. (T.) capsiformis* was the major consumer of small velvetbean caterpillar, *Anticarsia gemmatalis* Hübner larvae, in a Florida study (Godfrey et al. 1989). Ribeiro and Castiglioni (2008) reported *N. (T.) capsiformis* among the predators collected in soybean in Uruguay contributing to predation of red-shouldered stink bug, *Piezodorus guildinii* (Westwood) eggs. *Nabis (T.) capsiformis* demonstrated a type I functional response when feeding on bollworm eggs (Parajulee et al. 2006). *Nabis punctipennis* adults consumed a daily average of 12.4 aphids, *Acyrthosiphon pisum* (Harris) (Rebolledo et al. 2005). Nymphs consumed an average of 9.1 aphids daily. Adults and nymphs preferred adult aphids rather than nymphs.

Nabis spp. are among the main predators collected in soybean in Brazil (Correa et al. 1977; Campos et al. 1997; Thomazini 2001; Fernandes et al. 2010). Abundance of predators, including nabids, appeared not to be affected by cultivar when soybeans were sampled by sweeping or beat cloth (Belorte et al. 2004). Suction sampling and visual observation were equally effective sampling methods for nabids in tomatoes (Raga et al. 1990).

An assessment of selective insecticides targeting lepidopterous pests of soybean for potential nontarget effects on *Nabis (T.) capsiformis* indicated that both methoxyfenozide and indoxacarb had fewer nontarget effects than pyrethroid, organophosphate, or carbamate insecticides (Baur et al. 2003). *Nabis (T.) capsiformis* populations were reduced by lambda-cyhalothrin and monocrotophos applications targeting *A. gemmatalis* on soybean (White et al. 1992). Among four insecticides tested, spinosad had the least effect on *Nabis punctipennis* (Romero et al. 2009). Biopesticides did not affect nabid intrinsic rate of increase, net reproductive rate, or generation time for predators fed with healthy *Anticarsia gemmatalis* larvae and predators fed with larvae infected by a formulation of a nuclear polyhedrosis virus (NPV) of this host (Watanabe et al. 1999).

11.4.4 Tritrophic Interactions

Nabids are an important component of the natural enemy community impacting pest populations with plant feeding also important to development and persistence in the habitat (Braman 2000). Nymphal nabids screened from Bt corn in the field indicated that these natural enemies were among the three orders (Araneae, Coleoptera, and Heteroptera) found to contain Cry1Ab endotoxins above the threshold of 0.5 ng Cry1Ab per gram of fresh weight (Harwood et al. 2005). However, in field studies, the abundance of predators, including nabids, across 3 years in cotton fields with standard grower practices failed to exhibit any negative impact of Bt cotton on predator populations (Torres and Ruberson 2005). Nabids were among the arthropod faunae in orchard ground cover where plant species richness was a major driver for the fauna communities, both for the arthropod and pollinator assemblages (García and Miñarro 2013). Beneficial arthropods including nabids were higher in the presence of cover crops in an orchard under organic production (Fernandez et al. 2008). Nabid species were most abundant in hairy vetch in a study evaluating interplanting crops on cotton and effects on predatory hemipterans (Loya-Ramirez et al. 2003). Conservation biological control strategies that utilize non-crop plants to enhance populations of natural enemies and their persistence require careful selection of plant species to conserve nabids and other predatory heteropterans and serve as a source rather than a sink (Perdikis et al. 2011 and references therein).

11.5 Concluding Remarks

Much remains to be discovered concerning this fascinating and important group of predatory heteropterans. Taxonomic determination is still a difficult task, because characters of relevant importance, such as the external morphological and genital structures, have been inconsistently used. Therefore, the number of valid species may be different from the ones described so far. Knowledge about biology and taxonomy of this group is fundamental to developing future programs in integrated pest control.

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Chapter 12
Assassin Bugs (Reduviidae Excluding Triatominae)

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Abstract Reduviidae is the largest family of predaceous terrestrial Heteroptera, with about 7,000 described species in 25 subfamilies, and is one of the three most speciose families within Hemiptera. A general overview on Neotropical members of this family is furnished, with an updated account on the taxonomy for each subfamily. Keys to genera of almost all subfamilies are presented.

12.1 Introduction

Reduviidae is the largest family of predaceous terrestrial Heteroptera (Henry 2009). They are voracious predators and hence are also called "assassin bugs" (Ambrose 2000). About 25 subfamilies are recognized, although there is a lack of consensus on some of these concepts (Maldonado 1990; Schuh and Slater 1995; Weirauch et al. 2014). The family comprises nearly 7,000 described species and is therefore one of the three most speciose families within Hemiptera (Forero 2008; Henry 2009).

Reduviids show remarkable morphological diversity and range in size from relatively small and extremely delicate insects of few millimeters to very large insects (Schuh and Slater 1995; Weirauch 2008). With exception of Triatominae that feed on vertebrate blood, all reduviids are considered to be arthropod predators (e.g., Miller 1953; Readio 1927).

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12.2 General Characteristics and Diagnosis

The great majority of Reduviidae are medium to large true bugs and often show elongate or ovoid body shapes and long legs with stout fore femora. Overall, Reduviidae is one of the most morphologically diverse groups of Heteroptera ranging from delicate and elongate Emesinae (Wygodzinsky 1966) and Bactrodinae (Coscarón and Melo 2003) to large and robust Hammacerinae (Coscarón and Giacchi 1987b). Reduviidae can also mimic other groups of Heteroptera (Stride 1954), as well as other insects, such as Hymenoptera, with a number of species participating in Müllerian mimicry complexes (Haviland 1931; Hogue 1993).

The diagnostic characters include compound eyes usually large, ocelli often present (exceptions noted in the subfamily treatments); second antennal segment with trichobothria; labium with three visible segments (except in Centrocnemidinae and Hammacerinae that have four), usually stout and curved, but sometimes relatively thin and straight; the distal segment of labium with plectrum and prosternum with a stridulatory groove; membrane of hemelytra usually with two or three elongated cells; many taxa with a fossula spongiosa at the apex of the fore and mid-tibiae, present in one or more pairs of legs or absent; Brindley's glands between the metathorax and the first abdominal segment; female genitalia with lateral spermathecae; males with the eighth abdominal segment telescoped largely into the seventh segment and usually with symmetrical genitalia; and presence of three pairs of dorsal abdominal scent glands in nymphs (which can persist in adults) (Schuh and Slater 1995; Weirauch 2008).

12.3 General Biology and Ecology

Although many Reduviidae appear to feed on a wide variety of arthropods, assassin bugs in some groups show prey preferences or even prey specializations (see summary in Hwang and Weirauch 2012). For example, Ectrichodiinae seem to be specialized to prey on millipedes (Cachan 1952; Forthman and Weirauch 2012), several taxa are termite predators, e.g., Salyavatinae (McMahan 1983), and one species of Harpactorinae-Apiomerini, *Micrauchenus lineola* (F.) (Bérenger and Pluot-Sigwalt 2009); species of Holoptilinae prey on ants (Jacobson 1911) and certain Emesinae and Harpactorinae on spiders (Wignall and Taylor 2008; Jackson et al. 2010). Additional preferences, some of them tentative, are summarized by Ambrose (2000).

12.4 Phylogenetic Relationships

Recent phylogenetic work at the suprageneric level in Reduviidae has advanced our understanding of the relationships among the main lineages of reduviids. Weirauch (2008) was the first to present a morphology-based phylogenetic analysis of the

Reduviidae that incorporated species as terminal taxa, thus avoiding a ground plan approach and testing the monophyly of the included subfamilies. Representatives of 21 subfamilies were part of the analyses for which the main results can be summarized as follows: Hammacerinae is considered the sister group of all remaining Reduviidae; the Phymatine Complex (Phymatinae, Holoptilinae, and Centrocnemidinae) is monophyletic; Harpactorinae is the sister group of the remaining "higher Reduviidae"; Ectrichodiinae and Tribelocephalinae are sister groups; Emesinae, Saicinae, and Visayanocorinae are grouped in a clade; and Salyavatinae is paraphyletic with respect to Sphaeridopinae. The polyphyletic nature of Reduviinae was documented for the first time, although the extent of this problem remained largely unknown.

Weirauch and Munro (2009) reassessed the phylogeny of Reduviidae using molecular markers (~3.3 Kbp) of mitochondrial and nuclear ribosomal genes. Hammacerinae were not recovered as sister group to all remaining Reduviidae, but instead as sister to the Phymatine Complex. Reduviidae are therefore split into two main clades, the Hammacerinae + Phymatine Complex and the "higher Reduviidae." Peiratinae, not Harpactorinae, were found to be the sister group to the remaining higher Reduviidae, placing Harpactorinae in a more derived position. Other results corroborated relationships proposed in the morphological analysis (Weirauch 2008), most importantly the close relationship of Triatominae to some large Neotropical Reduviinae and to the Stenopodainae.

More recently, Hwang and Weirauch (2012) presented the most comprehensive molecular analysis of Reduviidae to date (178 terminals, 18 subfamilies) that emphasized additional investigation of the polyphyly of Reduviinae. The authors found 11 or 14 (depending on analyses) distinct clades of Reduviinae, the composition, relationships, and classification of which now warrant additional systematic study. Other noteworthy results were the paraphyly of Triatominae with respect to the reduviine genus *Opisthacidius* and the polyphyly of Cetherinae.

The classification of Reduviidae will be impacted by these and future phylogenetic results. In particular, investigating the phylogenetic positions of certain Neotropical taxa, most importantly the Bactrodinae, Elasmodeminae, and Phimophorinae, is the top priority.

12.5 Classification, Diversity, and Biology

Twenty-five subfamilies are currently considered as valid (Weirauch et al. 2014). Recent and future phylogenetic hypotheses will provide arguments for modifications of this classification that will recognize a monophyletic Reduviinae and accommodate other clades currently classified as Reduviinae in existing or new subfamilies. The following outline of subfamilies that occur in the Neotropics follows the subfamilies recognized by Schuh and Slater (1995), with addition of the Tribelocephalinae that were only recently documented to also occur in the New World (Weirauch 2010). Keys to assassin bug subfamilies that are distributed in the

Neotropics were presented by Forero (2004). The keys published by Schuh and Slater (1995) and Weirauch et al. (2014) are for all subfamilies of Reduviidae worldwide.

12.5.1 Bactrodinae

Bactrodinae are exclusively Neotropical and include only the genus *Bactrodes* Stål (McAtee and Malloch 1923; Maldonado 1990). *Bactrodes* was recently revised by Coscarón and Melo (2003), who recognized five species. Species in the genus are distributed from Mexico to Argentina (Maldonado 1990; Coscarón and Melo 2003).

Nothing much is known about the biology of *Bactrodes*. Forero (2006) reported *Chaetocnema* sp. (Coleoptera: Chrysomelidae) as field prey for *B. femoratus* (F.). This species has also been found on the plant species *Aciotis laxa* (Melastomataceae) in French Guiana (Bérenger and Pluot-Sigwalt 1997). Several species of *Bactrodes* appear to be associated with Melastomataceae species with sticky trichomes that the assassin bugs evade aided by their strongly modified, asymmetrical pretarsus (Weirauch and Zhang personal observation).

12.5.2 Cetherinae

Cetherinae (Fig. 12.1) are represented in the Neotropics only by the genus *Eupheno* Gistel, which includes three described species (Maldonado 1990). Champion (1898) presented a key to separate two of the three known species.

Species of *Eupheno* are found on tree trunks or under the bark of decaying trees (Champion 1898; Haviland 1931; Hwang and Weirauch 2012), where they prey upon different arthropods including beetles (Champion 1898) and termites (Haviland 1931).

12.5.3 Chryxinae

This small and rarely collected subfamily is composed of four genera and five species (Gil-Santana et al. 2007b; Weirauch 2012).

Very little is known about the biology of this secretive group of Reduviidae. *Lentia corcovadensis* has been collected in soft soil next to large trees and collected together with *Fulvius quadristillatus* Stål (Miridae) (Wygodzinsky 1946). Wygodzinsky (1946) remarked the similarity in coloration and movements of *Lentia* to some Anthocoridae and Miridae. *Petasolentia goellnerae* was collected at a mercury vapor light in Peru (Weirauch 2012).

Fig. 12.1 *Eupheno pallens* (Laporte) (Cetherinae), nymph, live specimen, covered with debris as camouflage

Key to genera and species of Chryxinae (based on Gil-Santana et al. 2007b; Weirauch 2012):

1. Total length 8.0–9.0 mm; veins on corium indistinct; connexivum with uniform clear coloration...*Wygodzinskyella travassosi* (Lent & Wygodzinsky)

1′. Total length 3.1–5.3 mm; veins on corium distinct, at least basally; connexivum with clear and dark alternate colors...2

2. Head with process on frons...............................*Petasolentia goellnerae* Weirauch

2′. Head without process on frons...3

3. with ocelli and an acute process on its ventral surface; corium of hemelytra with a small costal cell...*Lentia corcovadensis* Wygodzinsky

3′. Head without ocelli or an acute process on its ventral surface; corium of hemelytra without a small costal cell.................................*Chryxus* Champion......................4

4. Male of 5 mm in length; femora with uniform coloration; hemelytra with corium on basal half yellowish, apical half dark, membrane whitish with a large blackish spot inside discal cell and another blackish spot in the distal region; veins clear... ....*Chryxus tomentosus* Champion

4′. Male of 3.6 mm in length; femora with darkened rings; hemelytra with corium whitish, with a subbasal dark spot, apical half dark whitish area, giving the impression of a transverse pale band; membrane brownish with two whitish spots; veins darkened................*Chryxus bahianus* Gil-Santana, Costa & Marques

12.5.4 Ectrichodiinae

There are 22 genera and more than 100 described species of Ectrichodiinae (Figs. 12.2, 12.3, 12.4, and 12.5) in the New World (Maldonado 1990; Carpintero and Maldonado 1996; Bérenger and Gil-Santana 2005; Baena and Susín 2007; Gil-Santana and Baena 2009). Dougherty (1995) recognized 19 genera for the New World, including five described as new (*Cryptonannus*, *Doblepardocoris*, *Schuhella*, *Sinchocoris*, and *Wygodzinskyocoris*), whereas Carpintero and Maldonado (1996) listed only 17. She also proposed the following synonymies: *Anapothea* Miller, *Jorgcoris* Carpintero, and *Parapothea* Carpintero as junior synonyms of *Pothea* Amyot & Serville; *Pseudoracelda* Carpintero as a junior synonym of *Racelda* Signoret; and *Santainezia* Miller as a junior synonym of *Rhiginia* Stål. Carpintero and Maldonado (1996) either did not recognize or overlook these changes proposed by Dougherty (1995), with the exception of the synonymies regarding *Anapothea* and *Santainezia*, which had already been proposed by Wygodzinsky (1959) and Carpintero and Maldonado (1988), respectively (Gil-Santana et al. 2013a). Until a taxonomic revision and a phylogenetic analysis of all these genera are produced, we are accepting Carpintero and Maldonado (1996) arrangement with the addition of the new taxa proposed by Dougherty (1995) and Bérenger and Gil-Santana (2005) and the renewal of *Parapothea* as junior synonym of *Pothea* by Gil-Santana (2014).

Eleven of the Neotropical genera are currently monotypic, and we here list the included species: *Borgmeierina dentata* Wygodzinsky, *Cryptonannus punctella* Dougherty, *Jorgcoris aczeli* (Wygodzinsky), *Margacoris thaumastos* Carpintero, *Pseudopothea luacesi* (Bruner & Fracker), *Pseudoracelda macrocephala* Carpintero, *Schuhella hermosa* Dougherty, *Travassocoris pulchra* Wygodzinsky, *Wygodzinskyocoris nigripes* Dougherty, and *Xarada inca* Carpintero (Carpintero 1980; Maldonado 1990; Dougherty 1995; Carpintero and Maldonado 1996).

Brontostoma currently includes more than 20 species (Maldonado 1990; Dougherty 1995; Gil-Santana et al. 2004, 2005b, 2013a; Gil-Santana and Baena 2009), although Maldonado (1990) and Dougherty (1995) disagreed on the validity of some of them (see Gil-Santana et al. 2005b for a discussion). A taxonomic revision of *Brontostoma* is urgently needed. Keys to species by Wygodzinsky (1951) and Gil-Santana et al. (2004, 2005b, to Brazilian species) are of limited use due to intraspecific variation, misidentifications, and problematic species delimitations. For instance, Wygodzinsky (1951) misidentified *Brontostoma trux* Stål (Fig. 12.2) as *B. rubrovenosum* (Stål), an error that was carried over into later keys (Gil-Santana et al. 2004, 2005b; but see Gil-Santana et al. 2013a for correction).

Daraxa contains 15 species (Dougherty 1995; Carpintero and Maldonado 1996; Bérenger and Gil-Santana 2005), mostly described by Carpintero (1980). The monotypic genus *Cryptonannus* is extremely similar to *Daraxa* and may be congeneric (Forero 2004).

Pothea was subdivided into two subgenera by Carpintero (1980) and currently includes 33 species (Carpintero and Maldonado 1996; Gil-Santana and Costa 2005; Gil-Santana 2014). The Argentinean species were revised by Carpintero (1978).

Fig. 12.2 *Brontostoma trux* (Stål) (Ectrichodiinae), female, live specimen

Fig. 12.3 *Pothea jaguaris* (Carpintero) (Ectrichodiinae), female, dorsal view

Fig. 12.4 *Rhiginia lateralis* (Lepeletier & Serville) (Ectrichodiinae), male, live specimen

Fig. 12.5 *Racelda monstrosa* Carpintero (Ectrichodiinae), female, dorsal view. Scale 5.0 mm

Carpintero and Maldonado (1990) published a key to species in the subgenus *Pothea* (*Brachypothea*) Carpintero.

Baena and Susín (2007) provided an up-to-date checklist of the 19 species of *Rhiginia*, but outlined that the taxonomic status of some species is under discussion. There is no key to identify the species of *Rhiginia*.

The remaining genera of Ectrichodiinae currently comprise between two and six species. The four species of *Cricetopareis* can be identified with the key by Carpintero and Maldonado (1991). Dougherty (1995) provided a key for the two described species of *Doblepardocoris*. *Ectrichodiella* has two species, *E. minima* (Valdés) from Cuba and *E. rafaeli* (Gil-Santana and Coletto-Silva) from Brazil (Gil-Santana et al. 2013a). *Pseudodaraxa* also contains two described species, *P. albidops* Carpintero and *P. littoralis* Carpintero, both from Argentina (Carpintero 1980). Bérenger and Gil-Santana (2005) provided a key to the three species in the genus *Pseudozirta* that was described by them. *Racelda* has six species (Maldonado 1990; Carpintero and Maldonado 1996; Bérenger and Gil-Santana 2005). In this genus, the females are apterous (Dougherty 1995; Carpintero and Maldonado 1996) (Fig. 12.5). The two species of *Sinchocoris* were described and keyed by Dougherty (1995). The five species included in *Zirta* (Dougherty 1995, Carpintero & Maldonado 1996) were revised by Dougherty (1986).

Ectrichodiinae are frequently found in leaf litter (Miller 1953; Louis 1974; Hwang and Weirauch 2012). The scarce biological data suggest that Ectrichodiinae might be specialized millipede predators (reviewed in Forthman and Weirauch 2012), a behavior that was documented among Neotropical taxa for species of *Brontostoma* and *Rhiginia* (Carpintero and Maldonado 1996, Forthman and Weirauch 2012).

The Ectrichodiinae differ from most Reduviidae by the high frequency of wing length polymorphism, ranging from macropterous to apterous conditions, in which females commonly exhibit wing reduction (Dougherty 1995) (Figs. 12.2 and 12.5).

Key to the New World genera of Ectrichodiinae (modified from Gil-Santana et al. 2013a):

1. Antennal insertion shielded laterally by a small sclerite. Scutellum with two midlateral projections and an apical blunt tip. Tarsi two segmented. Fore and mid-tibia without spongy fossa................................*Ectrichodiella* Fracker & Bruner

1′. Antennal insertion with at most a small process on the antennifer. Scutellum with two distal prongs. Tarsi three segmented. Fore and mid-tibia with spongy fossa 2

2. Antennal insertion shielded laterally by a small process on the antennifer; vertex elevated, ocellar tubercle conical ....*Jorgcoris* Carpintero

2′. Antennal insertion not shielded by an antennifer process; vertex not elevated, ocellar tubercle conical or rounded.. 3

3. Four antennal segments.. 4

3′. Six or more [apparent] antennal segments... 5

4. Ocelli not raised on an ocellar tubercle; abdominal sternites with heavy punctuation.. *Schuella* Dougherty

4′. Ocelli raised on an ocellar tubercle; abdominal sternites without heavy punctuation..*Zirta* Stål

5. Fore femur with a ventral cleft...6

5′. Fore femur without ventral cleft, although it may be armed on ventral surface...9

6. Coloration uniformly black...........................*Wygodzinskyocoris* Dougherty 1995

6′. Coloration with a combination of dark and light brown....................................7

7. Abdominal sternites heavily punctuated.........................*Cryptonannus* Dougherty

7′. Abdominal sternites lacking heavy punctuation...8

8. Head elongated in lateral view, i.e., head length greater than the head height....... ....*Sinchocoris* Dougherty

8′. Head subtriangular in lateral view, i.e., head length and height subequal............ ....*Doblepardocoris* Dougherty

9. Fore femora with a row of large dentiform processes ventrally .... *Borgmeierina* Wygodzinsky

9′. Fore femora unarmed or at most with a series of minute denticles or stiffened hairs ventrally...10

10. Postocular region with a pair of blunt elevations; seven antennal segments; fore and mid-femora incrassate, with a ventral carina and a row of setigerous and dentiform tubercles; length 9–9.5 mm..................................*Xarada* Carpintero

10′. Postocular region without a pair of elevations; seven or eight antennal segments; fore and mid-femora incrassated or not incrassated, without a ventral carina and a row of setigerous and dentiform tubercles...11

11. Seven antennal segments; anterior pronotal lobe with a pair of paramedial carinated lobes, ocellar tubercle conical; prongs of scutellum close basally, divergent distally, spiniform...................................*Travassocoris* Wygodzinsky

11′. Seven or eight antennal segments; anterior pronotal lobe without a pair of paramedial carinated lobes; ocellar tubercle not conical: prongs of scutellum separated basally, subparallel...12

12. Robust species of 15 to more than 40 mm length; fore femora thickened, sometimes strongly so; mid-femora less frequently thickened, both with blunt tubercles or sharp and dentiform processes set on areas with short stiff hairs; fore and mid-trochanters with similar armature; fore and mid-tibiae slightly or strongly thickening toward the apex, with spongy fossa well developed......... ....*Brontostoma* Kirkaldy

12′. Smaller and/or less robust species; femora slender or slightly thickened; another set of characters...13

13. Head longer than wide...14

13′. Head length as long as or shorter than the width...19

14. First (visible) labial segment elongate, longer than second and third (visible) together; pronotum smooth and shiny.........................*Pothea* Amyot & Serville

14′. First (visible) labial segment shorter than or at most subequal to second and third (visible) together; pronotum opaque, typically rugose, seldom smooth and shiny...15

15. Second (visible) labial segment longer than first; anterior pronotal lobe with distinct sculpture, posterior pronotal lobe rugose; metasternum with two transverse carinae..*Margacoris* Carpintero
15′. Second (visible) labial segment subequal in length to first segment; different set of characters..16
16. First (visible) labial segment shorter than second and third together; second segment subequal to first, at most slightly longer or shorter; body red orange and black, rarely brownish species...17
16′. First (visible) labial almost as long as or longer than second and third together; second distinctly shorter than first; body dark brown, brownish, blackish, at most with yellowish markings on species..18
17. Longitudinal sulcus of the anterior pronotal lobe well developed anteriorly, but not reaching transverse sulcus; pronotum often rugose on anterior lobe, opaque, or moderately shiny; length 10–26 mm..*Rhiginia* Stål
17′. Longitudinal sulcus of the anterior pronotal lobe deep medially, but not reaching anterior or posterior margins of lobe; pronotum shiny, smooth; length 12–15 mm...*Pseudozirta* Bérenger & Gil-Santana
18. First antennal segment approximately half as long as the head; median longitudinal sulcus on anterior pronotal lobe obsolete; length 9–11.2 mm.......... ....*Pseudopothea* Wygodzinsky
18′. First antennal segment about as long as the head; median longitudinal sulcus well developed on anterior pronotal lobe and extending onto posterior lobe continuously; length 8–17 mm..*Racelda* Signoret
19. Body not flattened dorsoventrally..20
19′. Body flattened dorsoventrally...21
20. With ventrolateral elevations posterior to eyes; eyes, ocellar tubercles, and ocelli large to very large; legs slender, ventrally without spines or carinae; spongy fossa very small, less than 1/5 length of fore and 1/10 length of mid-tibiae; length 14–25 mm..*Cricetopareis* Breddin
20′. Without ventrolateral elevations posterior to eyes; eyes, ocellar callus conical or flattened; fore and mid-legs strongly carinated below, femora with setigerous tubercles and dentiform spines; spongy fossa on fore and mid-tibiae moderately developed, extending to between 1/5 and 1/3 length of segment; body length 6–13 mm...*Daraxa* Stål
21. Longitudinal sulcus of anterior pronotal lobe reduced to a fovea; anteocular region longer than postocular; head elongated; fore and mid-femora slightly enlarged, fusiform, ventrally carinated with setigerous tubercles ....*Pseudodaraxa* Carpintero
21′. Longitudinal sulcus of pronotum extending across both lobes; anteocular region much shorter than postocular; head hemispherical, vertical; fore femora enlarged basally, narrowing at the apex, curved, thinly carinated ventrally, on basal 2/3, with setigerous and teeth-like tubercles; mid- and hind femora similar, slender, straight, without carinae.................*Pseudoracelda* Carpintero

Fig. 12.6 *Ghinallelia brasiliensis* (Dohrn) (Emesinae), male and female in copula

12.5.5 Elasmodeminae

This subfamily includes only the genus *Elasmodema* Stål that contains three species known from Argentina, Brazil, and Paraguay (Wygodzinsky 1949a). Species can be identified using information in Wygodzinsky (1944) and Kormilev (1948). The biology of *Elasmodema* is essentially unknown. Wygodzinsky (1944) reported *E. setigerum* from a bird nest and mentioned that *E. erichsoni* was commonly collected under bark of wooden fence posts that were not occupied by ants.

12.5.6 Emesinae

Nearly 30 genera of Emesinae (Fig. 12.6) classified in five tribes occur in the Neotropics (Wygodzinsky 1966; Maldonado 1990). The monograph of Emesinae by Wygodzinsky (1966) remains the main source for study of this group, including keys to genera and species, although several new species and minor taxonomical changes have been proposed by diverse authors since then.

Wygodzinsky (1966) reviewed biological and ecological data for Emesinae. In addition to habitats shared with many other reduviids, some species have adapted to specific environments such as bird nests, caves, and spider and psocid webs

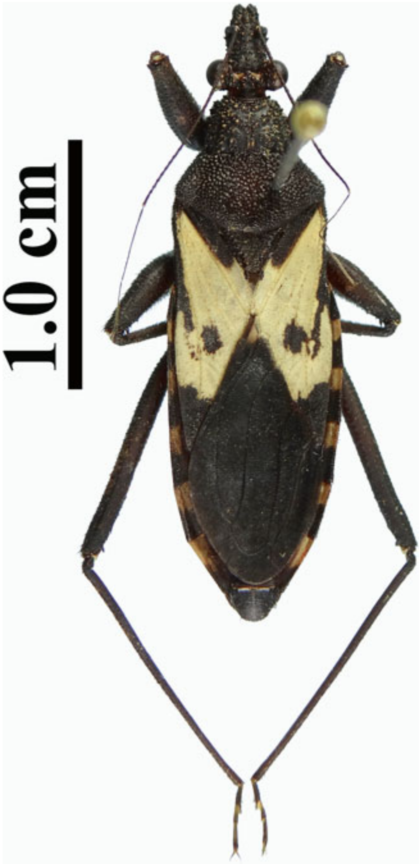

Fig. 12.7 *Microtomus conspicillaris* (Drury) (Hammacerinae), female, dorsal view

(Wygodzinsky 1966; Gil-Santana et al. 2007a). Especially, the association with spider webs has resulted in various anatomical modifications of body and legs (Wygodzinsky 1966; Soley et al. 2011). *Emesa mourei* Wygodzinsky has been found in both the webs of spiders and caterpillars (Gil-Santana and Jurberg 2003). Additional biological data on a few Neotropical species were published by Santiago-Blay and Maldonado (1988), Gil-Santana et al. (2005a), and Forero (2007).

12.5.7 Hammacerinae

This subfamily (Fig. 12.7) includes the genera *Homalocoris* Perty and *Microtomus* Illiger, which both are restricted to the New World (Maldonado 1990).

The eight species of *Homalocoris* can be identified using information in Maldonado (1987, 1996) and Maldonado and Santiago-Blay (1991). *Microtomus* includes 12 valid species (Maldonado 1990; Coscarón et al. 2003). *Microtomus* was first revised by Stichel (1926), and Costa Lima (1935) provided a now outdated key to species. About half of the currently recognized species have been treated in more recent taxonomic papers (Coscarón and Giacchi 1987a, b; Giacchi and Coscarón 1986, 1992; Melo and Coscarón 2004).

Little is known about the biology of Hammacerinae. They are usually found under bark of decaying trees (Champion 1898; Readio 1927), and *Homalocoris* has also been collected using light traps (Forero personal observation).

Key to the genera of Hammacerinae (adapted from Forero 2004):

1. Second antennal segment with 8–18 pseudosegments; total length less than 13 mm (except *H. nermini* Maldonado that measures ~20.5 mm); abdominal sternites of males without setose areas..*Homalocoris*

1′. Second antennal segment with 23–28 pseudosegments; total length more than 13 mm; abdominal sternites of males with setose areas....................*Microtomus*

12.5.8 Harpactorinae

This subfamily contains the greatest number of genera and species in the Neotropical region and worldwide (Schuh and Slater 1995; Forero 2011). Only two of the seven currently recognized tribes (Weirauch et al. 2014) occur in the New World, the Apiomerini and Harpactorini.

Key to New World tribes of Harpactorinae (based on Schuh and Slater 1995):

1. Ocelli lateral, more widely separated from one another than from eyes; labium straight; claws entire...Apiomerini

1′. Ocelli less widely separated from one another than from eyes; labium curved; claws with a basal tooth...Harpactorini

In addition, all Apiomerini except *Micrauchenus* Amyot & Serville have a sulcus on the apex of the fore tibia to receive the tarsus. The fore tibiae is densely pubescent, a feature shared with Harpactorinae tribes Diaspidiini and Ectinoderini from Old World (Forero 2004; Forero et al. 2011).

Apiomerini

There are 12 extant genera in Apiomerini (Gil-Santana et al. 2002, 2003; Bérenger 2006; Forero et al. 2011). With the exception of *Apiomerus* Hahn, which has several Nearctic species, Apiomerini (Fig. 12.8) are exclusively found in the Neotropical region (Maldonado 1990; Gil-Santana et al. 2003).

Seven genera of Apiomerini are monotypic, and their species are listed in the following: *Agriocoris flavipes* (F.), *Beharus cylindripes* (F.), *Calliclopius nigripes* (L.), *Fourcartus parecisi* Bérenger, *Micrauchenus lineola* (F.), *Ponerobia bipustu-*

Fig. 12.8 *Apiomerus nigricollis* Stål (Harpactorinae, Apiomerini), preying on a curculionid beetle

lata (F.), and *Sphodrolestes vittaticollis* Stål (Maldonado 1990; Gil-Santana et al. 2003; Bérenger 2006). The eight species of *Agriocleptes* Stål can be identified following Forero (2002).

Apiomerus comprises more than 100 described species (Maldonado 1990; Forero et al. 2010; Berniker et al. 2011). The first attempt to monograph the genus was that of Costa Lima et al. (1951). Later studies have improved our understanding of the taxonomy of the group (e.g., Gil-Santana and Milano 2007; Forero et al. 2010; Berniker et al. 2011), and additional revisionary work is underway (Forero and Weirauch personal communication).

Heniartes Spinola comprises 31 species (Maldonado 1990, Gil-Santana and Forero 2009), which can be identified using publications by Wygodzinsky (1947, 1953). *Manicocoris* includes two species that were keyed by Gil-Santana et al. (2002).

Apiomerini, particularly species of *Apiomerus*, have been observed to prey on bees, hence the common name "bee killer assassin bugs" (Marques et al. 2003; Silva and Gil-Santana 2004; Gil-Santana and Forero 2010), although their overall prey spectrum is not restricted to Hymenoptera. Some species of *Apiomerus* resemble meliponine bees (Hogue 1993) and are suspected to mimic them (Gil-Santana et al. 2003). *Apiomerus pictipes* Herrich-Schäffer has been speculated to attract *Trigona* bees using a chemical lure (Weaver et al. 1975). On more than one occasion, individuals of *Apiomerus nigricollis* Stål (Fig. 12.8) in the Southeast Atlantic Forest in Brazil have been noticed to exude a scent similar to flowers while being perched – with extended forelegs and waiting for prey – on top of leaves (Gil-Santana, personal observation). Almost all species of Apiomerini studied so far are polyphagous (Gil-Santana et al. 2003) except *Micrauchenus lineola* (F.) that feeds exclusively on termites (Bérenger and Pluot-Sigwalt 2009). Some species, mainly of *Apiomerus*, have been considered for use as biological control agents (Gil-Santana 2002).

Apiomerus species collect plant resins with their forelegs that may facilitate prey capture in immature and adults. In females, this resin is particularly important during oviposition (Eisner 1988; Choe and Rust 2007; Forero et al. 2011): stored on the ventral surface of the abdomen that in females of *Apiomerus* features distinct setose patches, the resin coating is transferred to the egg mass after oviposition using specialized leg structures, the metatibial combs; first instar immatures then use this resin from the egg mass to sticky-coat their own fore tibia, greatly facilitating prey capture (Eisner 1988; Forero et al. 2011). Other Apiomerini species are believed to gather resins as well, but direct observations for taxa other than *Manicocoris* (Melo et al. 2005) and *Beharus* Amyot & Serville (Uyttenboogaart 1901) are lacking.

Key to Apiomerini genera [based on Gil-Santana et al. (2003) and Bérenger (2006)]:

1. Head elongated, straight in lateral view; ocelli far to each other; antenna with all segments cylindrical..2
1′. Head short, bent posteriorly in lateral view, with a conspicuous spiniform tubercle in the gular region; ocelli close to each other; antennal segments third and fourth enlarged and laterally compressed.........................*Sphodrolestes* Stål
2. Head much longer than wide; postocular region longer than anteocular; anterolateral angles of pronotum acute; scutellum triangular, enlarged at the apex in some species; fore tibiae laterally compressed 3
2′. Head barely longer than wide; postocular region longer, as long or shorter than anteocular; anterolateral angles of pronotum blunt; scutellum of variable structure; fore tibiae cylindrical..4
3. Head about as long as the pronotum; first antennal segment somewhat thicker than the others; membrane of hemelytra darkened; apex of mid-tibiae curved...*Heniartes* Spinola
3′. Head longer than pronotum; first antennal segment about as thick as the other segments; hemelytra with hyaline patches on corium and membrane; apex of mid-tibiae not curved..*Agriocleptes* Stål
4. Anterior acetabula very prominent; scutellum generally triangular or rectangular; sulcus at the apex of mid-tibia absent 5
4′. Anterior acetabula not as prominent; scutellum with the apex somewhat rectangular; sulcus at the apex on mid-tibia present.......................................10
5. First antennal segment more than twice as long as the head; antennal insertion very close together..*Micrauchenus* Amyot & Serville
5′. First antennal segment shorter than the head; antennal insertion not very close together or distinctly separated..6
6. Postocular region twice as long as the anteocular or longer; hemelytra much longer than abdomen..7
6′. Postocular region about as long as the anteocular or slightly longer; hemelytra not surpassing or barely surpassing the abdomen..8
7. Head shorter than pronotum; interocular region with a concavity; fore and hind femora of approximately the same length; fore tibiae densely pilose, incrassate in the distal half.. *Calliclopius* Stål

7′. Head about as long as the pronotum; interocular region flat or slightly depressed; fore femora somewhat shorter than hind femora; fore tibiae not as densely pilose, slightly thickened in midportion, tapering distally .... *Manicocoris* Stål

8. Head oval, much shorter than pronotum; antenna short, with second segment twice as long as the first segment, which is expanded apically .... *Ponerobia* Amyot & Serville

8′. Head elongate, a little shorter than pronotum; antenna long, with second segment about as long as the first, which is cylindrical, although thicker than the others.. 9

9. Anterolateral angle of pronotum acute; fore femora longer than hind femora, the latter slightly thickened on basal half; median process of pygophore emarginate apically.. *Amauroclopius* Stål

9′. Anterolateral angle of pronotum blunt; fore femora approximately as long as the hind femora, of uniform thickness; median process of pygophore truncate apically.. *Beharus* Amyot & Serville

10. First (visible) labial segment shorter than anteocular region; scutellum posteriorly flat .... *Apiomerus* Hahn

10′. First (visible) labial segment approximately as long as the anteocular region; scutellum depressed posteriorly... 11

11. First antennal segment three times as long as the anteocular region; hind tarsi three segmented; female fully winged... *Agriocoris* Stål

11′. First antennal segment 1.3 times as long as the anteocular region; hind tarsi two segmented; female micropterous .... *Fourcartus* Bérenger

Harpactorini

Harpactorini (Figs. 12.9 and 12.10) is the most speciose tribe of Harpactorinae and Reduviidae as a whole (Schuh and Slater 1995; Zhang and Weirauch 2014) that comprises 51 genera in the Neotropical region alone (Forero 2011, 2012; Swanson 2012). The only published key to separate the genera is by Stål (1872) and now badly outdated (Forero 2011). A key that includes all Neotropical genera is being prepared (D. Swanson, personal communication). Many taxonomical changes including the description of new genera have occurred since the late nineteenth century, rendering identifications difficult without consultation of original descriptions and a well-identified reference collection (Forero 2011). Publications containing new descriptions and revisions within Harpactorini were referenced by Forero et al. (2008) and Forero (2011). The latter paper also supplied a checklist of Neotropical Harpactorinae genera.

Members of the Harpactorini are commonly associated with plant crops, and some have been studied as biological control agents of crop pests (Grundy 2007; Grundy and Maelzer 2003). Several observations show that certain Harpactorini may be associated with particular plants (summarized in Bérenger and Pluot-Sigwalt 1997). These polyphagous predators often live on a single plant species, not only as adults but sometimes also as immature instars and eggs. While seeking prey,

Fig. 12.9 *Arilus carinatus* (Forster) (Harpactorinae, Harpactorini), nymph, live specimen, preying on a termite

Fig. 12.10 *Zelus versicolor* (Herrich-Schäffer) (Harpactorinae, Harpactorini), female on flower of *Bidens rubifolia* Kunth (Asteraceae), preying on a meliponine bee

some Harpactorini apparently found certain plants to have other advantages and became adapted to visiting these plants species exclusively. In addition to hosting the arthropod prey species the assassin bugs feed on, these plants provide additional resources such as sugary or proteinaceous secretions produced in extrafloral nectaries or other structures (Bérenger and Pluot-Sigwalt 1997; Gil-Santana and Alves 2011). While Habib (1976) noted that several cultivated tree species in Brazil seem to be inhabited by *Zelus leucogrammus* (Perty), Gil-Santana and Alves (2011) observed an association between *Zelus versicolor* (Herrich-Schäffer) and *Bidens rubifolia* Kunth (Asteraceae) (Fig. 12.10), in the same country. Bérenger and Pluot-Sigwalt (1997) observed in French Guiana that *Zelus araneiformis* Haviland may complete its postembryonic development feeding exclusively on glandular formations of *Cecropia obtusa* Tréc. (Cecropiaceae). Harpactorini have also evolved a unique predation strategy using sticky traps that is restricted to species in the New World (Zhang and Weirauch 2013). Other than Apiomerini that rely on external supplies of resin that can be used as sticky traps, a large proportion of Neotropical species of Harpactorini produce sticky substances themselves (Zhang and Weirauch 2013, 2014). Derived from integumental glands mostly on the fore and mid-tibiae, these sticky secretions serve as sticky traps to facilitate prey capture.

Remarkable examples of mimicry occur between certain groups of Hymenoptera and several taxa of Harpactorini. Species of *Notocyrtus* are recognized as mimics of meliponine bees, which they resemble mostly because of the angular and inflated pronotum (Haviland 1931; Jackson 1973; Gil-Santana 2008). Two mimetic species pairs have so far been identified: *Trigona fulviventris* Guérin and *Ptilotrigona lurida* (Smith) are models of *Notocyrtus dorsalis* (Gray) and *N. colombianus* Carvalho & Costa, respectively (Jackson 1973; Gil-Santana 2008). Several species in different genera resembles wasps, especially ichneumonid wasps (Maldonado and Lozada 1992). Species of *Hiranetis* Spinola, *Graptocleptes* Stål, and several additional, closely related and hard to delineate genera mimetic Braconidae and/or Ichneumonidae. This group of genera is in need of a comprehensive revision in order to clarify their systematics (Gil-Santana et al. 2013b).

12.5.9 Holoptilinae

Neolocoptiris villiersi Wygodzinsky & Usinger, described from a female from Guyana is the only extant species of Holoptilinae known from the New World (Wygodzinsky and Usinger 1963; Maldonado 1990). Poinar (1991) described one additional species based on a Dominican amber fossil. Old World species are known to prey on ants (e.g., Jacobson 1911), but the biology of New World species is unknown, except one observation that found an early instar immature underneath tree bark (G. Zhang, personal communication).

12.5.10 Peiratinae

There are 11 genera of Peiratinae in the Neotropics (Maldonado 1990; Cai and Taylor 2006; Melo 2012). Among them, *Sirthenea* Spinola is exceptional in being circumtropical, thus comprising species from the Old and New Worlds (Maldonado 1990; Willemse 1985).

Four of the Neotropical genera are monotypic and comprise: *Froeschnerisca vittata* (Coscarón), *Lentireduvius brasiliensis* Cai & Taylor, *Synnamarinus rasahusoides* Maldonado & Bérenger, and *Zeraikia novafriburguensis* Gil-Santana & Costa (Coscarón 1995, 1997; Bérenger et al. 1996; Gil-Santana and Costa 2003; Cai and Taylor 2006; Melo 2012).

Eidmannia was revised by Coscarón (1986b), who recognized six South American species. According to Coscarón and Carpintero (1994), eight species of *Melanolestes* are found in the Neotropical region. *Phorastes* includes only two species, *P. femoratus* (Degeer) and *P. incognitus* van Doesburg (1981). *Rasahus* was revised by Coscarón (1983), followed by the description of additional species (Coscarón 1986a; Coscarón and Maldonado 1988), and more than 20 Neotropical species are currently recognized (Maldonado 1990). The 12 species of *Sirthenea* that occur in the Neotropics were revised by Willemse (1985). *Thymbreus* includes three species which were studied by Coscarón (1994). *Tydides* and its four included species were revised by Lent and Jurberg (1967).

Peiratinae are ground-dwelling reduviids (Miller 1953; Louis 1974) which feed on other arthropods (Ambrose 1987; Readio 1927). Little detail is known on the biology of the Neotropical species; specimens of various genera are typically collected at lights and are known to inflict very painful bites (Forero and Weirauch personal communication).

Key to Peiratinae genera [based on Lent and Jurberg (1967); Froeschner (1981); Coscarón (1986b, 1995); Bérenger et al. (1996); Gil-Santana and Costa (2003); Cai and Taylor (2006); Melo (2012)]:

1. Head with preocellar transverse groove deeply impressed; fore coxa elongated, apical third to half-extended caudad of the prosternal process............................2
1′. Head with obsolete or shallowly impressed transverse groove; fore coxa short, the apex not or only slightly extending caudad of prosternal process................9
2. Mid-tibia without spongy fossa...*Sirthenea* Spinola
2′. Mid-tibia with spongy fossa occupying a fifth or more of tibial length.............3
3. Metapleural sulcus straight...4
3′. Metapleural sulcus curved...5
4. Anteocular region distinctly longer than the postocular portion; connexivum uniformly colored...*Tydides* Stål
4′. Anteocular and postocular regions subequal in length; connexivum bicolored...*Sinnamarynus* Maldonado & Bérenger
5. Fore tibia with spongy fossa restricted to its apical third; hemelytra, when present, uniformly fuscous to black..*Melanolestes* Stål

5′. Fore tibia with spongy fossa occupying more than the apical third; hemelytra, when present, with at least two colors..6

6. Fore tibia with spongy fossa occupying the distal half; body robust, length about three times its width...*Lentireduvius* Cai & Taylor

6. Fore tibia with spongy fossa occupying the distal three fourths or more of its length, if shorter, then eyes small, about half as wide as the length of the interocular space in dorsal view (*Eidmannia*); body slender, three times longer than wide...7

7. Eyes small, about half as wide as the length of the interocular space in dorsal view, not reaching dorsal or ventral margins or the head in lateral view; scutellum with apical prolongation distinctly upcurved, apex erect...*Eidmannia* Taeuber

7′. Eyes large, about half as wide or wider than the length of the interocular space in dorsal view, reaching dorsal and ventral margins of the head in lateral view; scutellum with apical prolongation horizontal or oblique, apex not erect...8

8. Scutellum with posterior process acuminate; male pygophore subrectangular, basal plate of phallus complex; female with 10th tergite with a projection ....*Froeschnerisca* Coscarón

8′. Scutellum with posterior process short, rounded, not acuminate; male pygophore quadrangular or rounded, basal plate of phallus simple; female with 10th tergite without a projection .... *Rasahus* Amyot & Serville

9. Posterior lobe of the head abruptly converging from the eyes to neck; metapleural sulcus nearly straight, except near lateral margin of supporting sclerite...*Thymbreus* Stål

9′. Posterior lobe of the head abruptly converging to collar from a point considerably posterior to eyes; metapleural sulcus curved 10

10. Head distinctly shorter than the length of the anterior pronotal lobe; space between the hind coxae narrower than the hind coxal diameter ....*Phorastes* Kirkaldy

10′. Head somewhat longer than the anterior pronotal lobe; space between the hind coxae wider than the hind coxal diameter...........*Zeraikia* Gil-Santana & Costa

12.5.11 Phimophorinae

The monotypic genus *Phimophorus* Bergroth is the only representative of the subfamily Phimophorinae in the Neotropical region. *Phimophorus spissicornis* Bergroth was described based on a single specimen from Brazil (Bergroth 1886). Usinger and Wygodzinsky (1964) redescribed the species, and Maldonado (1990) also reported it from Ecuador.

Phimophorus spissicornis has frequently been found on palms in Colombia (Chaverra-Rodriguez et al. 2010), in microhabitats shared with various Triatominae species (Lent and Wygodzinsky 1979; Chaverra-Rodriguez et al. 2010). In addition, *P. spissicornis* has also been found in Bromeliaceae and bananas in Brazil (Lent and Jurberg 1977).

12.5.12 Phymatinae

Although treated as a separate family by some authors, Carayon et al. (1958) convincingly argued that the so-called ambush bugs should be regarded as part of the Reduviidae, a result that has been corroborated by all recent phylogenetic analyses (e.g., Hwang and Weirauch 2012). Two of the four recognized tribes occur in the Neotropical region, the Macrocephalini and Phymatini. Kormilev (1962) and Froeschner and Kormilev (1989) revised and cataloged, respectively, the group. Delimitation of species and even certain genera is difficult, due to widespread sexual dimorphism, color polymorphism, and the lack of comprehensive, well-illustrated taxonomic revisions. The group, and especially the speciose genus *Phymata* Latreille, is in severe need of a modern revision.

Phymatinae are sit-and-wait ambush predators that mostly hunt on flowers (Balduf 1941; Dodson and Marshall 1984). Little is known about the particular natural history of Neotropical species. Nearctic species have been shown to engage in mate guarding (Dodson and Marshall 1984) and have become models to investigate sexual selection (Punzalan et al. 2008).

Key to the tribes of Phymatinae [based on Froeschner and Kormilev (1989) and Forero (2004)]:

1. Head above the eye and propleura just ventral to the lateral margin each with a distinct longitudinal groove for reception of antennae at rest................Phymatini
1′. Head and propleura without such a longitudinal groove for reception of antennae...Macrocephalini

Macrocephalini

Two of the Neotropical genera of this tribe are monotypic and include *Extraneza nasuta* Barber from Puerto Rico and *Kormilevida iviei* (Kormilev & Doesburg) from Dominican Republic (Froeschner and Kormilev 1989; Kormilev and van Doesburg 1991). *Lophoscutus* Kormilev comprises approximately 65 Neotropical species (Froeschner and Kormilev 1989; Kormilev and van Doesburg 1991), although a clear distinction from *Macrocephalus* Swederus may not be possible in all cases. Keys are available for species occurring in North and Central America (Kormilev 1987) and the Caribbean (Kormilev and van Doesburg 1991), but not for South America. The 14 Neotropical species of *Macrocephalus* were keyed by Froeschner and Kormilev (1989).

Key to the American genera of Macrocephalini [modified from Kormilev and van Doesburg (1991) and Forero (2004)]:

1. Fore tibia without tarsi..2
1′. Fore tibia with tarsi...3
2. Pale spot on scutellum large, shaped as a spearhead or lancet, sometimes three-pronged posteriorly; parameres with a subapical branch...*Macrocephalus* Swederus
2′. Pale spot on scutellum small, restricted to the base of median carina; carina thin, reaching the tip of the scutellum, or lateral borders of abdominal segments III and IV produced into rounded lobes; parameres hook-shaped, lacking a subapical branch...*Lophoscutus* Kormilev
3. Second antennal segment 1.5 times as long as the first; buccula forming canals for reception of antennae at rest; abdominal segments II–IV with connexivum very large laterally...*Kormilevida* Doesburg
3′. Second antennal segment shorter than the first; buccula does not form such canals; abdominal segments II–IV with connexivum not very large laterally..*Extraneza* Barber

Phymatini

Three Neotropical genera of the tribe Phymatini are monotypic and include *Anthylla nervosopunctata* (Signoret) from Chile, *Kelainocoris farri* Kormilev from Jamaica, and *Paraphymata saileri* from Haiti (Froeschner and Kormilev 1989).

The three species belonging to *Neoanthylla* Kormilev, two from Brazil and one from Peru, were keyed by Froeschner and Kormilev (1989). *Phymata* Latreille has the highest number of species in the subfamily, 84 of which occur in the Neotropical region (Froeschner and Kormilev 1989). Kormilev (1962) monographed the genus and is the main source to identify species in this genus. Similar to the situation in Harpactorini, a well-identified reference collection is instrumental for identifying many taxa.

Key to the genera of Phymatini [modified from Froeschner and Kormilev (1989)].

1. Mid- and hind tibiae with upper side carinate laterally and sulcate medially..2
1′. Mid- and hind tibiae convex on the upper side, neither carinate nor sulcate...3
2. Fore femur subtriangular, more or less swollen........................*Phymata* Latreille
2′. Fore femur elongately ovate, gently constricted near midlength, subapically with a carina forming a ring on exterior surface.......................*Paraphymata* Kormilev
3. First (visible) labial segment twice as long as the second; sutures between sternites II–V indistinct..*Kelainocoris* Kormilev

3′. First (visible) labial segment at most as long as the second; sutures between sternites II–V generally distinct...4

4. Fore femur subtriangular, exterior surface convex, granulated, dull; sutures between abdominal sternites II and III clearly visible.......................*Anthylla* Stål

4′. Fore femur elongately ovate, external face flat, smooth, glossy, polished; sutures between abdominal sternites II and III indistinct...*Neoanthylla* Kormilev

12.5.13 Physoderinae

Two monotypic genera of Physoderinae are known from the New World that include *Cryptophysoderes fairchildi* Wygodzinsky & Maldonado, known from Panama and Venezuela (Wygodzinsky and Maldonado 1972; Carcavallo and Tonn 1976), and *Leptophysoderes orellana* Weirauch that was described from Ecuador (Weirauch 2006a). Forero and Weirauch (2005) synonymized the putative physoderine *Harpinoderes cicheroi* Martinez & Carcavallo under the reduviine *Aradomorpha crassipes* Champion. Additional, undescribed Physoderinae occur in the Neotropical region (W.S. Hwang personal communication).

Little is known on the biology of Neotropical Physoderinae, other than they are thought to be cryptic (Wygodzinsky and Maldonado 1972). *Cryptophysoderes* was observed preying on larvae of Calliphoridae (Diptera) in a dung trap (Martínez and Carcavallo 1989) and collected in a hollow tree (Wygodzinsky and Maldonado 1972). *Leptophysoderes* was collected by canopy fogging (Weirauch 2006a).

12.5.14 Reduviinae

In Reduviinae (Fig. 12.11), 14 Neotropical genera are currently included (Maldonado 1990; Melo 2012; Gil-Santana et al. 2013a). Four genera are monotypic and include the following species: *Corupaia brasiliensis* Lent & Wygodzinsky, *Namapa caroli* Wygodzinsky & Lent, *Patago patagonicus* Kirkaldy, and *Peregrinator biannulipes* (Montrouzier & Signoret) (Maldonado 1990). *Pseudozelurus* Lent & Wygodzinsky is not monotypic, but only *P. superbus* (Champion) occurs in the Neotropical region (Lent and Wygodzinsky 1959; Maldonado 1990).

Aradomorpha includes three species (Maldonado 1990), which can be recognized using the key by Wygodzinsky (1949b). *Leogorrus* was revised by Melo (2007), who recognized and keyed 14 species, although additional species await description (M.C. Melo personal communication). *Microlestria* has three described species (Maldonado 1990), two of which were keyed by Champion (1898). Seven of the ten species of *Nalata* were keyed by Champion (1898). *Neivacoris* has three species, which were discussed by Lent and Wygodzinsky (1947). The eight species

Fig. 12.11 *Zelurus lepeletierianus* (Kirkaldy) (Reduviinae), female, dorsal view

of *Opisthacidius* were studied and keyed by Lent and Wygodzinsky (1947, 1956). The two species of *Pantopsilus*, *P. bosqui* Lent & Wygodzinsky, and *P. longipes* (Berg) are known only from Argentina and were studied by Costa Lima (1940) and Lent and Wygodzinsky (1947). *Zeluroides* has two species, *Z. americanus* from the USA and Mexico and *Z. mexicanus* from Mexico (Maldonado 1990). Lent and Wygodzinsky (1959) recognized three subspecies for *Z. americanus* and two for *Z. mexicanus* and provided a key to distinguish them. With approximately 130 species and several subspecies, *Zelurus* is the largest genus of Neotropical Reduviinae (Maldonado 1990). The revision of Costa Lima (1940) included a key to the species. This key has been outdated for some time because of numerous taxonomical changes including the description of new species (e.g., Lent and Wygodzinsky 1945, 1951, 1955, 1966, 1968).

Most members of Reduviinae are thought to be general insect or arthropod predators and are nocturnal (Schuh and Slater 1995). Many species of *Zelurus* appear to be mimics of *Pepsis* F. wasps (Hymenoptera, Pompilidae) with respect to color and body shape as well as flight behavior (Costa Lima 1940). Some species of *Zelurus* have been observed preying on nymphs of Triatominae, both under natural and laboratory conditions (Carpintero 1981). In Brazil, predation on two species of *Leptinopterus* Hope (Coleoptera, Lucanidae) by *Zelurus angularis* (Stål) was recorded under natural conditions by Grossi et al. (2012). A species of *Zelurus* was reported to be a predator of harvestmen (*Goniosoma* sp., Arachnida, Opiliones, Gonyleptidae) in most caves studied by Machado et al. (2003). *Goniosoma spelaeum* (Mello-Leitão) was observed to be the prey of cave-dwelling *Zelurus travassosi* (Costa Lima) (Trajano and Bichuette 2010). *Zelurus travassosi* is also the most important predator of the trogloxene species *G. spelaeum* in the Brazilian state of São Paulo and the troglophile species *Daguerreia inermes* Soares & Soares (Opiliones, Gonyleptidae) in the state of Paraná (Machado et al. 2003). *Neivacoris steini* (Stål) (Reduviinae) was collected in termite nests on several occasions (Lent and Wygodzinsky 1947).

Key to the Neotropical genera of Reduviinae [based on Lent and Wygodzinsky (1948), Bérenger et al. (1996), Forero (2004), Gil-Santana and Coletto-Silva (2005), and Gil-Santana et al. (2013a)]:

1. Maxillary plates lamellate and elongated, including between them the base of the labium and surpassing the level of the first antennal segment; antenna inserted laterally in the head .... *Aradomorpha* Champion
1′. Maxillary plates different; antennae inserted dorsally in the head 2
2. Fore tibia without spongy fossa 3
2′. Fore tibia with spongy fossa 5
3. More than 20 mm long; legs long and slender, dorsal surface of femora smooth; lateral margins of scutellum with a pair of subbasal tubercles .... *Patago* Bergroth
3′. Less than 10 mm long; legs short, dorsal surface of femora strongly granulated; lateral margins of scutellum without tubercles 4
4. Fore trochanter ventrally with a stout spiniform process; corium and membrane of hemelytra sharply detached from each other, their relative dimensions as usual .... *Nalata* Stål
4′. Fore trochanter without a spiniform process; corium of hemelytra reduced to a narrow external band, not sharply detached from the membrane, the latter very large, elongated forward to reach the hind border of pronotum .... *Microlestria* Stål
5. Apex of all femora at ventral surface with a distinct pair of dentiform processes .... *Leogorrus* Stål
5′. Apex of all femora at ventral surface without such processes 6
6. Disc of anterior pronotal lobe without tubercles or spines 7
6′. Disc of anterior pronotal lobe with tubercles or spines 11
7. Fore and mid-femora with teeth along the ventral surface .... *Pantopsilus* Berg

7′. Fore and mid-femora without teeth processes on the ventral surface 8
8. Smaller species, 6–8 mm in length 9
8′. Larger species, over 10 mm in length 10
9. Body covered with long fine hairs; posterior angles of connexivum not salient .... *Peregrinator* Kirkaldy
9′. Body not covered with long fine hairs; posterior angles of connexivum with denticular lateral processes .... *Namapa* Wygodzinsky & Lent
10. Anterior femora slightly sulcate longitudinally on ventral surface, with two longitudinal rows of very numerous short bristles; the two membrane cells of equal width .... *Corupaia* Lent & Wygodzinsky
10′. Anterior femora not sulcate ventrally, with simple hairs only; the two membrane cells with different dimensions......... *Pseudozelurus* Lent & Wygodzinsky
11. Pronotum distinctly granulated 12
11′. Pronotum not granulated 13
12. Disc of anterior pronotal lobe with four tubercles; fore and mid-femora more incrassate than the hind femora.. *Opisthacidius* Berg
12′. Disc of anterior pronotal lobe with a pair of tubercles or short spines; fore and median femora slender, about the same diameter as the hind femora .... *Zeluroides* Lent & Wygodzinsky
13. Mandibular plates swollen, prominent, reaching or surpassing the apex of the head; clypeus vertical..................................... *Neivacoris* Lent & Wygodzinsky
13′. Mandibular plates less developed, not reaching the apex of the head; clypeus never vertical .... *Zelurus* Hahn

12.5.15 Saicinae

In this subfamily (Fig. 12.12), 10 genera are known from the Neotropical region (Gil-Santana and Costa 2009; Gil-Santana 2011). Five genera are currently monotypic, with the included species being *Bagriella ornata* McAtee & Malloch, *Buninotus niger* Maldonado, *Caprilesia almirantiana* Gil-Santana, Marques & Costa, *Kiskeyana palassaina* (Weirauch & Forero), and *Saicireta correntina* Melo & Coscarón (Maldonado 1990; Gil-Santana et al. 2006; Weirauch and Forero 2007a, b; Melo and Coscarón 2005).

Oncerotrachelus Stål has 14 New World species, with 13 of them occurring in the Neotropics (Gil-Santana 2013). McAtee and Malloch (1923) and Barber (1931) provided keys to four and five species of this genus, respectively. The two species of *Paratagalis* Monte, *P. spinosus* Monte, and *P. zikani* Gil-Santana & Costa (Fig. 12.12) can be identified by Gil-Santana and Costa (2009). Two species of *Pseudosaica* Blinn, *P. panamaensis* Blinn, and *P. florida* (Barber) occur in the Neotropical region (Blinn 1990; Gil-Santana and Marques 2005), and Blinn (1990) allows for their identification. *Saica* Amyot & Serville is the second largest genus of

Fig. 12.12 *Paratagalis zikani* Gil-Santana & Costa (Saicinae), male holotype, dorsal view

Saicinae in New World, with 13 recognized species (Maldonado 1990; Blinn 1994; Gil-Santana and Marques 2005). Champion (1898) keyed five species and McAtee and Malloch (1923) six. *Tagalis* Stål has seven described species (Gil-Santana 2011; Melo 2008), but a few more await description (Forero, personal observation). In the meantime, the known species can be identified by the key provided by Gil-Santana (2011).

Little is known of the biology and natural history of Saicinae. Specimens have been most commonly collected at lights (Schuh and Slater 1995) or swept and beaten from vegetation. Gil-Santana et al. (2010) included a synopsis of the biological and ecological information available for New World Saicinae, but also recorded *Tagalis evavilmae* Gil-Santana, Gouveia & Zeraik as an inhabitant of birds' nests, a first for Saicinae. *Kiskeyana palassaina* was found in leaf litter next to a stream and under rocks (Weirauch and Forero 2007a). Given that most Saicinae possess a scopula, a hairy attachment structure on the tarsi of all pairs of legs, it has been speculated that they can dwell on smooth plant surfaces (Weirauch and Forero 2007a).

Key to the New World genera of Saicinae (modified from Gil-Santana and Costa 2009):

1. Foreleg without spines, at most with erect setae 2
1′. Fore femur with two rows of spines, fore tibiae either with setae or with spines 5
2.Posterior pronotal lobe with upward projecting spines or tubercles; mesoscutum (scutellum) and metanotum apically with vertical spines or tubercles 3

2′. Pronotum generally unarmed, but sometimes with humeral spines; apex of mesoscutum produced into a long horizontal tapering spine, metanotum without spine or tubercle..*Oncerotrachelus* Stål

3. Opposed surfaces of labium and head with spinelike setae or bristles; forewing with two to three cells; metapleura without a tubercle near coxal cavity 4

3′. Opposed surfaces of labium and head without spinelike setae or bristles; forewing with four cells; metapleura with a tubercle near coxal cavity .... *Saicireta* Melo & Coscarón

4. Process on lower anterior angle of prothorax acute to subacute; second antennal segment about half as long as the first antennal segment; medial process of male pygophore bifurcate; posterior margin of seventh abdominal sternite in females vertical or subvertical...*Saica* Amyot & Serville

4′. Process on the lower anterior angle of the prothorax subconical; second antennal segment about ¾ as long as the first antennal segment; medial process of male pygophore a single, erect barbless spine; posterior margin of seventh abdominal sternite in females sloping ventrocephalad .... *Pseudosaica* Blinn

5. Fore tibia with a row of setae directed mediad.......*Kiskeyana* Weirauch & Forero

5′. Fore tibia with a ventral row of spines.. 6

6. Humeral angles of pronotum without processes, rounded..................*Tagalis* Stål

6′. Humeral angles of pronotum with spinelike processes 7

7. Fore coxae and anterior pronotal lobe unarmed......*Bagriella* McAtee & Malloch

7′. Fore coxae spined, anterior pronotal lobe with four spines or rounded humps 8

8. Anterior pronotal lobe with four spines; two labial segments spined .... *Paratagalis* Monte

8′. Anterior pronotal lobe with four humps; one or all three labial segments spined 9

9. Only the first (visible) labial segment spined; forewings with four closed cells..*Buninotus* Maldonado

9′. All three (visible) labial segments spined; forewings with two closed cells .... *Caprilesia* Gil-Santana, Marques & Costa

12.5.16 Salyavatinae

The only New World representative of the Salyavatinae is the genus *Salyavata* Amyot & Serville that was recently revised by van Doesburg and Forero (2012), who recognized and keyed 11 species.

Species of *Salyavata* feed on termites, particularly *Nasutitermes* species, using a bait and capture strategy (McMahan 1982, 1983). Different species of *Salyavata* might feed on different species of termites (van Doesburg and Forero 2012). Immatures of *Salyavata* are known to glue material of the termites' nests onto their integument, presumably to camouflage themselves (McMahan 1982, 1983). Integumental glands and trichomes involved in this camouflaging behavior were studied by Weirauch (2006b).

Fig. 12.13 *Sphaeridops aurantius* Gil-Santana, Costa & Zeraik (Sphaeridopinae), male paratype, dorsal view

12.5.17 Sphaeridopinae

The subfamily Sphaeridopinae (Fig. 12.13) currently includes three exclusively Neotropical genera and six species (Gil-Santana and Alencar 2001; Forero 2004). *Sphaeridops* comprises three species and *Veseris* two, which were keyed by Gil-Santana et al. (2000) and Gil-Santana and Alencar (2001), respectively. *Volesus* contains only a single species, *V. nigripennis* Champion (Maldonado 1990; Forero 2004).

Immatures of Sphaeridopinae share a unique type of integumental glands and trichomes with Salyavatinae, and it was therefore suspected that they might display camouflaging behavior similar to the one observed in Salyavatinae (Weirauch 2006b; McMahan 1982, 1983). In addition, Sphaeridopinae have been found in association with termites and fed on them in captivity (P. Wygodzinsky personal communication in: McMahan 1982) indicating that they might also share their prey specialization on termites with the closely related Salyavatinae.

Key to the genera of Sphaeridopinae [modified from Forero (2004)].

1. Interocular space larger than the width of an eye; antennifer apically straight .... *Volesus* Champion
1′. Interocular space shorter than the width of an eye; antennifer variable 2
2. Antennifer bifurcated; prosternum not excavated medially ....*Sphaeridops* Amyot & Serville
2′. Antennifer straight apically or only with lateral projection, never bifurcated; prosternum excavated medially.. *Veseris* Stål

12.5.18 Stenopodainae

In this subfamily Stenopodainae (Fig. 12.14), 18 genera are recognized in the Neotropical region (Wygodzinsky and Giacchi 1994). The key to New World genera of Stenopodainae by Wygodzinsky and Giacchi (1994) separates only Neotropical genera and excludes the recently described Nearctic genus *Arenaeocoris* Blinn (Blinn 2012).

The three species of *Achillas* Torre Bueno were keyed by Bérenger (2001). Five species of *Apronius* Stål were keyed by Maldonado (1986a) and two additional species described by Maldonado and Lozada (1991) and Bérenger (2001), amounting to seven valid species in this genus. *Ctenotrachelus* Stål has 21 species (Maldonado 1990, 1995a; Bérenger 2001), with partial keys presented by Barber (1930) (11 spp.) and Maldonado (1995a) (four spp.). The six species of *Diaditus* Stål were revised and keyed by Giacchi (1982). The three species of *Gnathobleda* (*Gnathobleda*) Stål were revised by Giacchi (1977), and three species have been included in *Gnathobleda* (*Pnohirmus*) Stål (Maldonado 1990). Wygodzinsky and Giacchi (1986) keyed five of the species included in both subgenera. *Kodormus* Barber has three species, which can be identified using Bérenger and Maldonado (1996). *Narvesus* Stål and its two species, *N. carolinensis* Stål and *N. minor* Barber, were revised and keyed by Giacchi (1974). *Ocrioessa* Bergroth has two species, *O. cornutulus* (Berg) and *O. lobuliventris* Bergroth. The genus and *O. cornutulus* were redescribed by Giacchi (1985). A revision of the American species of *Oncocephalus* Klug was presented by Giacchi (1984), who recognized ten American species in this genus. *Otiodactylus* Pinto is monotypic, including only *O. signatus* Pinto. *Pnirontis* Stål includes two subgenera: *Pnirontis* (*Pnirontis*) Stål and *Pnirontis* (*Centromelus*) Fieber (Wygodzinsky and Giacchi 1994). The species formerly included in *Rutuba* Torre Bueno were transferred to *Pnirontis* (*Pnirontis*) by Giacchi (1988a), who considered the genus *Rutuba* as a junior synonym of *Pnirontis*. Maldonado (1990) cataloged 31 Neotropical species in this genus (including three as *Rutuba* spp.). Maldonado (1994a) and Giacchi (1996) further described two more species. Barber (1930) keyed 18 species; Maldonado (1986b) keyed 12 species which he considered

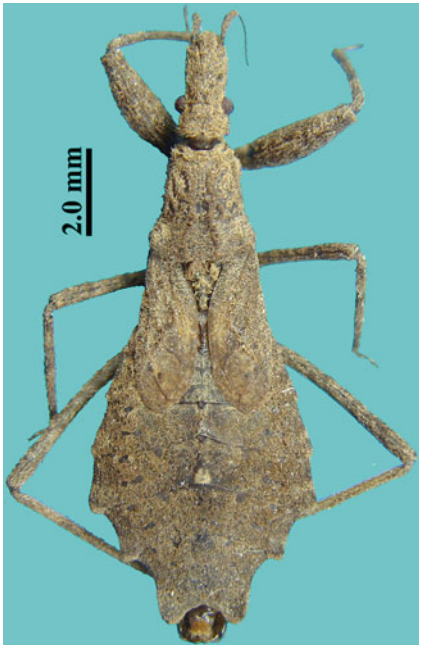

Fig. 12.14 *Rhyparoclopius aokiae* Gil-Santana (Stenopodainae), male holotype, dorsal view

as belonging to the "*subinermis*" group (species with first segment unarmed below), and Maldonado (1994a) presented a key to species of *Pnirontis* that measure 16 mm or more in length. *Podormus* Stål is monotypic, including only *P. granulatus* Stål, which was redescribed by Bérenger (2001). Maldonado (1990) cataloged six Neotropical species of *Pygolampis* Germar; Barber (1930) keyed four species, followed by the description of two other species by Costa Lima and Campos-Seabra (1945). The four species of *Rhyparoclopius* Stål were keyed by Gil-Santana (2012) (Fig. 12.14). Maldonado (1994b) provided a key to five species of *Seridentus* Osborn, followed by the description of the sixth species in this genus by Giacchi (1998). A revision and additional notes with a key to the 11 species of *Stenopoda* Laporte were published by Giacchi (1969, 1988b). *Stenopodessa* Barber has two species, *S. lanei* Costa Lima & Campos-Seabra and *S. piligera* Barber (Maldonado 1990).

Little is known about the biology of Stenopodainae. Species are collected under logs, on the ground in open grassy areas, in leaf litter, while sweeping and beating vegetation, and, most frequently, at lights (D. Forero and C. Weirauch personal observation).

Key to Neotropical genera of Stenopodainae [modified from Wygodzinsky and Giacchi (1994)]:

1. First antennal segment produced beyond insertion of the second segment; distinct hemelytral cell present proximad of the basal cell.. 2

1′. First antennal segment not produced beyond insertion of the second segment; distinct hemelytral cell proximad of basal cell absent....................................... 3

2. Antennifer armed with a distinct, nearly erect spine; first segment of mid- and hind tarsi as long as the second; posterior angles of connexival segments salient or strongly salient ....*Pnirontis* (*Pnirontis*) Stål

2′. Antennifer unarmed or provided with minute spines; first segment of mid- and hind tarsi shorter than the second; posterior angles of connexival segments varied .... *Pnirontis* (*Centromelus*) Fieber

3. First (visible) labial segment approximately twice as long as the second and third combined.. *Pygolampis* Germar

3′. First (visible) labial segment subequal to, or shorter than, the second and third combined.. 4

4. Prosternum distinctly elongate behind the fore coxae as long as, or longer than, coxae 5

4′. Prosternum shorter behind coxae than length of coxae, or coxae inserted at the hind margin of prosternum.. 8

5. First (visible) labial segment about as long as the second; anterolateral angles of collar and humeri acutely spinous; disc of anterior pronotal lobe with paired distinct spinelike tubercles; scutellum with long, erect spine; fore coxae elongate cylindrical, about twice as long as wide; hemelytral apical cu-pcu cross-vein obsolescent.. *Ocrioessa* Bergroth

5′. First (visible) labial segment much longer than second; anterolateral angles of collar and humeri bluntly rounded; disc of anterior pronotal lobe lacking spinelike tubercles; scutellum with short, blunt process; fore coxae shorter, less than twice as long as wide; apical cu-pcu cross-vein normally developed......... 6

6. Posterior angles of connexival segments 2–5 with spined foliaceous lobes; angles of seventh male abdominal segment long, acutely produced................................ ....*Achillas* Torre Bueno

6′. Posterior angles of connexival shortly produced; angles of seventh male abdominal segment not as above 7

7. Pronotum at least twice longer than wide; anterior prosternal processes short; sides of abdomen parallel or subparallel; last abdominal segment ending in two moderately developed, not acute apical lobes.........................*Ctenotrachelus* Stål

7′. Pronotum a little longer than wide; anterior prosternal processes strongly produced, curved apically; sides of abdomen subparallel anteriorly and diverging apically; last male abdominal segment ending in two flaring, widely developed, apically acute lobes...*Seridentus* Osborn

8. Body and appendages with dense, adpressed pubescence and numerous tiny, erect bristles; basal discal cell of the hemelytra fused to M, in many cases only for a comparatively short distance... 9

8′. Body glabrous or variously pubescent but not as above; basal cell fused to M for a considerable distance or not in direct contact with M at all.......................... 11

9. Fore tarsi two segmented; fore femora strongly incrassate, fusiform; humeri rounded; first antennal segment much shorter than head.......*Rhyparoclopius* Stål

9′. Fore tarsi three segmented; fore femora only feebly incrassate, subcylindrical; humeri pointed; first antennal segment about as long as the head or longer than the head.. 10

10. Anterior tibiae with elongate spongy fossa; postocular region of the head nearly parallel-sided in dorsal view, abruptly constricted at neck .... *Stenopoda* Laporte

10′. Anterior tibiae lacking spongy fossa; postocular region of the head gently converging behind eyes to neck..*Stenopodessa* Barber

11. Body elongate fusiform, often five times (or more) as long as the maximum width; head subcylindrical, anteocular and postocular regions of equal length; antennae long and slender, first segment always longer than anteocular region; pronotum narrow, its length along midline at least equal to width across humeri; male genitalia, when in situ, with cuplike posterior extension of pygophore completely covering parameres; female genital area narrowly pointed posteriorly 12

11′. Body not elongate fusiform, broader, always less than five times as long as the maximum width; head of varied shapes, anteocular region longer than postocular; antennae with first segment generally shorter than, only rarely as long as the anteocular region; pronotum wider across humeri than along midline; male genitalia, when in situ, with parameres not covered, clearly visible; female genital area not narrowly pointed posteriorly 13

12. Head with distinct, often branched, setigerous processes ventrolaterally behind eyes; maxillary plates shortly produced as rounded lobes, or strongly produced as acute lobes, on either side of base of labium .... *Gnathobleda* (*Gnathobleda*) Stål

12′. Head with or without distinct setigerous processes ventrolaterally behind eyes; maxillary plates not produced as described above.. *Gnathobleda* (*Pnohirmus*) Stål)

13. Fore femora strongly incrassate, at least twice as thick as the mid- and hind femora 17

13′. Fore femora slender, less than twice as thick as the mid- and hind femora.... 14

14. Mandibular plates produced anteriad between antennae, subcylindrical, parallel, rounded apically, projecting well beyond the apex of the head; apex of antennifer attaining the apex of the head; second (visible) labial segment only about half as long as the first one.. *Diaditus* Stål

14′. Mandibular plates not as above; apex of antennifer considerably short, not attaining the apex of the head; second (visible) labial segment not, or only very slightly shorter than the first segment....................................... 15

15. Head, thorax, abdomen ventrally, legs and base of hemelytra with numerous uniformly dense, small setigerous tubercles, metapleura with conspicuous sooty black evaporatory area .... *Podormus* Stål

15′. Setigerous tubercles when present not as above; metapleura with or without sooty black evaporatory area 16

16. Fore femora and to a lesser degree mid- and hind femora conspicuously tuberculate on ventral and dorsal surfaces; postocular region, in dorsal view, longer than eyes; vein emanating from basal discal cell conspicuously curved... *Nitornus* Stål

16′. Femora not tuberculate; postocular region shorter than eyes; vein emanating from inner basal cell almost straight .... *Narvesus* Stål

17. Fore tibiae with conspicuous spongy fossa, approximately twice as long as the diameter of the tibia .... *Apronius* Stål

17′. Fore tibiae without distinct spongy fossa, with spongy fossa as long or shorter than the diameter of the tibia 18

18. Head posterolaterally behind eyes with ramose setigerous processes; eyes distinctly though shortly pilose; fore and hind tibiae distinctly curved; connexival margins lobulate or denticulate 19

18′. Head posterolaterally behind eyes at most with simple setiferous spines; eyes not pilose; fore and hind tibiae almost straight; connexival margins entire .... *Oncocephalus* Klug

19. Disc of anterior pronotal lobe with paired conspicuous tubercles; evaporatory area of metapleura large, sooty black..................................... *Kodormus* Barber

19′. Disc of anterior pronotal lobe without conspicuous tubercles; evaporatory area of metapleura reduced in size, stramineous .... *Otiodactylus* Pinto

12.5.19 Tribelocephalinae

Until recently, no Tribelocephalinae were known to occur in the New World (Maldonado 1990; Weirauch 2010). A recently described new genus and species, *Tribelocodia ashei* Weirauch, from French Guyana, is currently classified to be part of the Tribelocephalinae. This species shares characters with both, Ectrichodiinae and the closely related Tribelocephalinae, but based on the results of a morphology-based cladistic analysis, it is currently placed in the Tribelocephalinae (Weirauch 2010). Nothing is known about the biology of *Tribelocodia*.

12.5.20 Vesciinae

The four Neotropical genera of the Vesciinae that accommodate 16 valid species can be distinguished based on the key provided below that is modified from Maldonado (1995b).

Microvescia Wygodzinsky comprises only *M. costalimai* Wygodzinsky (Wygodzinsky 1943; Maldonado 1990, 1995b). *Mirambulus* includes two species, *M. morio* Breddin and *M. niger* Breddin (Maldonado 1990, 1995b). The five species included in *Pessoaia* (Maldonado 1990, 1995b) can be identified using keys and descriptions by Wygodzinsky (1943) and Abalos (1945). *Vescia* includes eight species, five of which were keyed by Wygodzinsky (1943).

Mirambulus morio has been found in disturbed habitats in secondary forests, and *Pessoaia limai* was collected in Malaise traps and light traps in tropical dry forests in Colombia (Forero 2006).

Key to the genera of Vesciinae [modified from Maldonado (1995b)]:

1. Anteocular region shorter than the postocular; first antennal segment longer than the anteocular region 2
1′. Anteocular region longer than the postocular; first antennal segment shorter than the anteocular region 3
2. Spine between antennifers absent; ocelli present........ *Mirambulus* Breddin
2′. Spine between antennifers present; ocelli absent .... *Vescia* Stål
3. Pronotum glabrous and head nearly so, some species with scattered setae; the anterior pronotal lobe with short spinules and fine corrugations; the humeral angle spined or not; apex of prosternum reaching mesosternum........ *Pessoaia* Costa Lima
3′. Head and pronotum densely pilose; anterior lobe of pronotum without spinules and corrugations; the humeral angle always spined; apex of prosternum not reaching mesosternum .... *Microvescia* Wygodzinsky

12.6 Concluding Remarks

With this synopsis of the Neotropical Reduviidae, we make it clear that although a taxonomic framework exists, further work is needed to understand the full extent of the Neotropical biota. Future phylogenetic hypotheses, in particular at the species level, will help accommodate a wealth of natural history observations and let us ask deep evolutionary questions. It is also clear that many new taxa are waiting to be discovered and described in years to come, but this is only going to be accomplished with thorough fieldwork. We also have highlighted what we know with regard to basic biology and natural history of reduviids. Future reduviid researchers have an ample field to explore in both the taxonomic and biological aspects of the Reduviidae in the Neotropical region.

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Chapter 13
Hematophagous Bugs (Reduviidae, Triatominae)

José Jurberg, Cleber Galvão, Christiane Weirauch, and Felipe F.F. Moreira

Abstract The members of the subfamily Triatominae (Heteroptera, Reduviidae) are vectors of *Trypanosoma cruzi* (Chagas), the causative agent of Chagas disease or American trypanosomiasis. As important vectors, triatomine bugs have attracted ongoing attention, and thus, various aspects of their systematics, biology, ecology, biogeography, and evolution have been studied for decades. In the present chapter, the authors summarize the current knowledge on the systematics, phylogeny, evolution, and biology of these vectors and discuss the implications for human health.

13.1 Introduction

The Triatominae are bloodsucking bugs, which since the discovery of Carlos Chagas (1909) have been recognized as actual or potential vectors of Chagas disease. The first triatomine bug species was described in 1773, by C. De Geer (Fig. 13.1), but according to Lent and Wygodzinsky (1979), the first report on aspects and habits dated back to 1590 by Reginaldo de Lizárraga. While traveling to inspect convents in Peru and Chile, this priest noticed the presence of large hematophagous insects that attacked at night. In subsequent reports, various travelers and naturalists also mentioned the presence of these insects in South America. One of the most celebrated reports was by Charles Darwin, during his trip to South America in the H.M.S. Beagle in 1835, when he wrote: "One which I caught at Iquique, (for they

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Fig. 13.1 Male of *Triatoma rubrofasciata* (formerly *Cimex rubrofasciatus*), the first formally described species of Triatominae (From Jurberg and Galvão 2006)

are found in Chile and Peru,) was very empty. When placed on a table, and though surrounded by people, if a finger was presented, the bold insect would immediately protrude its sucker, make a charge, and if allowed, draw blood. No pain was caused by the wound. It was curious to watch its body during the act of sucking, as in less than ten minutes it changed from being as flat as a wafer to a globular form…" (Darwin 1845; Lent and Wygodzinsky 1979).

American trypanosomiasis or Chagas disease was discovered in 1909. Two years before, the Brazilian physician Carlos Chagas (1879–1934) was sent by Oswaldo Cruz to Lassance, a small village in the state of Minas Gerais, Brazil, to conduct an antimalaria campaign in the region where a railway was being built. Chagas stayed in the area for about 1 year, during which time a railroad engineer, Cantarino Mota, alerted him to the presence of hematophagous insects referred to locally as "barbeiros" (the local term for triatomines) (Fig. 13.2). Alerted to the presence of these insects inside the human dwellings, the doctor decided to investigate the possibility that they might transmit some parasite to humans, since besides malaria he had detected clinical signs that were difficult to interpret.

The local population complained about an uncomfortable feeling referred as palpitation, and Chagas observed arrhythmia and signs of heart failure among local

Fig. 13.2 *Panstrongylus megistus*, the species of Triatominae in which C. Chagas found *T. cruzi* (From Jurberg and Galvão 2006)

residents, along with reports of unexplained sudden death. Upon dissecting the triatomines he found flagellates in their intestinal tract. Believing that they belonged to *Trypanosoma minasense*, which infected black tufted-ear marmosets (*Callithrix penicillata*) in the same region, he sent several triatomine specimens to Oswaldo Cruz in Rio de Janeiro to feed on uninfected marmosets. Several weeks later he returned to Rio de Janeiro to discover a new trypanosome in the blood of one of the animals. As a tribute to his mentor, he named the species *Trypanosoma cruzi*. He then returned to Minas Gerais in an attempt to identify the parasite's vertebrate host. After numerous negative blood samples, he found an infected cat. Some 30 days later he returned to the house where he had discovered the infected animal and found a little girl named Berenice, just 2 years old, who was febrile and presented circulating forms of *T. cruzi* in her bloodstream.

From 1909 to 1912, Chagas described a new disease, its causative agent, natural reservoirs, and the vector, a set of discoveries unparalleled in international medicine to this day. As a result of his work, in 1912 Chagas received the Schaudinn Award from the Institute of Tropical Diseases in Hamburg, Germany (Chagas Fo 1968). Thus, one and the same researcher, in inverse order and in a short space of time, discovered a new disease that would later bear his last name, first recognizing the vector, next the parasite and reservoirs, and finally the clinical disease in humans (Chagas 1909). Chagas' discovery was overlooked by the Brazilian scientific community, as represented by the National Academy of Medicine, and was treated with disbelief for more than 20 years, because some scientists questioned the very existence of the disease. It was in Argentina in 1935 that Salvador Mazza submitted studies on the disease to the Annual Meeting of the Argentine Society of Tropical Medicine and together with Cecílio Romaña gave a new dimension and credibility to the problem (Chagas Fo 1968).

For more than one century, since the first description by De Geer, triatomines were studied merely from a descriptive point of view. However, beginning in 1909, when Chagas discovered the disease, and due to its newly acquired relevance to human health, studies began on the clinical form of the disease, the protozoan, and the vertebrate hosts, as well as the vector biology and transmission mechanisms. Advances in vector taxonomy began with Arthur Neiva, one of the most important scientists in this phase, who, in 1911, began describing various species, culminating with the publication of his dissertation "Revisão do gênero *Triatoma* Lap." in 1914. Important monographs were published subsequently by Pinto (1925) and Del Ponte (1930), in addition to other extensive studies published by Neiva and Lent (1936, 1941), Usinger (1944), Abalos and Wygodzinsky (1951), and Ryckman (1962), culminating in the grand works by Lent and Wygodzinsky (1979) and Carcavallo et al. (1998/1999). Relevant information concerning the triatomines was also compiled by Jurberg and Galvão (2006), which served as a basis for the preparation of the present chapter.

13.1.1 Chagas Disease

Currently there is no vaccine or effective cure for chronic Chagas disease, primarily a zoonosis, a parasitic disease of wild animals transmitted by sylvatic species of triatomine bugs. The adaptation of some triatomine species to human dwellings was secondary, as was the parasite's domiciliary cycle. American trypanosomiasis is now an endemic disease affecting mostly Latin America, primarily in rural populations of Central and South America, where it is an important public health problem. According to the World Health Organization, an estimated 28 million people are at risk of the disease, with 15 million currently infected (Guhl and Lazdins-Helds 2007).

Animals infected with *T. cruzi* are always mammals, as the parasite cannot develop in the blood of birds, reptiles, or amphibians. A triatomine bug that has sucked the blood of a mammal (including a human) infected with *T. cruzi* acquires the infection and the protozoan then reproduces, multiplying in the insect's digestive tract and producing the infective forms. Infection remains in the insect throughout its lifespan and can occur both in the nymphs and adults. Only the eggs are not affected, so the second generation remains uninfected until its first ingestion of infected blood (i.e., there is no transovarian transmission). Therefore, triatomine bugs reared in the laboratory with blood from uninfected animals can be used safely in experiments.

When the triatomine bug bites, it defecates during or right after bloodsucking, eliminating infective forms of the parasite in its feces. These forms can penetrate actively either through the bite's orifice, the mucosa, or small wounds and scratches on the skin. Upon entering the bloodstream the parasites are transported to the muscles or organs (mainly the heart and digestive tract), where they multiply and cause lesions. Penetration of *Trypanosoma cruzi* through the skin can cause a local reaction known as *chagoma*, and another important sign is unilateral bipalpebral swelling, leaving the patient's eye practically closed. This is the so-called Romaña's sign, named after its discoverer, an Argentine physician.

There are three distinct phases in the disease: acute, indeterminate, and chronic. In the acute phase (3–4 weeks), the infection varies from an asymptomatic to a severe and fatal form, the latter mainly in children or debilitated individuals, characterized by high fever, while other symptoms like diarrhea and vomiting can appear when the digestive tract is affected. The indeterminate phase is characterized by low parasitemia without clinical signs, which can persist or evolve into a chronic disease. The chronic form normally appears 10–15 years after the acute phase, and Chagasic cardiopathy is the most common manifestation, the digestive form producing visceromegalies, especially megaesophagus and megacolon.

13.1.2 Epidemiological Importance and Implications for the Human Health

All triatomine bugs must be regarded as potential vectors of *T. cruzi*, which infects a wide variety of sylvatic and domestic mammals, but so far only a few species have become well adapted to living in human dwellings, thereby acquiring epidemiological importance for humans (Jurberg and Galvão 2006). The most important vector species are *Triatoma infestans* (Klug), *T. brasiliensis* Neiva, *T. dimidiata* (Latreille), *Panstrongylus megistus* (Burmeister), and *Rhodnius prolixus* (Stål). Heavy domestic infestations of triatomines can be highly stressful, because these populations can reach several hundred individuals of different stages, representing a high daily blood loss.

According to the World Health Organization, Chagas disease is the third most important parasitic disease next to malaria and schistosomiasis, based on the resulting disability and work limitations. In Latin America, it is the fourth most important disease, following respiratory diseases, diarrhea, and AIDS (Schofield 1994). Each year about 500,000 people are infected with the disease, which is still incurable. The existing drugs are only partially effective in the acute phase, which mainly attacks the heart and digestive tract. Approximately 10 % of the infected individuals develop clinical signs and symptoms of chronic Chagas disease.

Occurrence of the classic form of the disease in a given area depends on three basic factors: presence of *T. cruzi* (the etiological agent), domiciliated triatomine bugs (vectors), and humans and other mammals (hosts) inhabiting the domiciliary environment. In addition to the classic infection model through contaminated triatomine feces, accounting for 80 % of the infections, other mechanisms contribute to cases of Chagas disease, such as transfusion of contaminated blood and blood products (16 %), congenital transmission from infected mothers (2 %), and the rest from organ transplants, infection by the oral route through ingestion of contaminated food, and laboratory accidents (Schofield 1994).

13.1.3 Control

After the successful campaign to control domestic triatomine populations in some South American countries, the new target of studies should be the species invading controlled areas. In recent years, there has been increased reporting of sylvatic species invading human dwellings and peridomiciliary environment in South America (Valente et al. 1998; Coura et al. 1999; Valente 1999; Almeida et al. 2000; Sandoval et al. 2000, 2004; Galvão et al. 2001b; Vivas et al. 2001; Wolff and Castillo 2002; Sousa et al. 2004; Sousa and Galvão 2004). The majority of these findings are adult insects and flight represents an important form of dispersion to previously controlled areas. Studies on triatomine flight capacity can facilitate identification of species with the tendency to invade dwellings and to allow the application of adequate vector surveillance. Effective surveillance is obviously important to avoid reinfestation after control, or resurgence of any vector population. Chagas disease control should be based on various independent but complementary work fronts and has become a public health priority in the affected countries due to epidemiological relevance and the high financial costs for the economy.

Use of Insecticides

Vector control uses residual-action insecticides, which must be applied both on the inside and outside parts of houses and outbuildings. One problem is that the insecticides do not affect eggs laid in inaccessible places like cracks and crevices in the buildings. The vector species that are subject to control should be considered, since the biological cycle should be the basis for systematizing the intervals and number of insecticide applications over the course of the year.

Housing Improvement

This should be a primary goal, because typical poor rural dwellings are made of mud and wattle, with thatched palm roofs and packed earthen floors, and have domestic and wild animals living in the same environment, thus facilitating massive infestations by triatomines. Anti-triatomine measures include construction of simple housing with measures like smooth walls without cracks, ceramic tile roofs protected below with ceilings, and well-organized furniture and utensils to avoid the formation of refuges for insects.

Health Education and Research

Despite extensive research on Chagas disease, little information has been generated to teach rural communities about it. The most effective control measure is a health education project targeting rural communities and health professionals. A population that is well informed about the disease is better prepared to prevent the entry and persistence of vectors and to notify the health authorities about existing problems. Information about the disease and vectors and the means to control them should be provided to the entire population, in the school system, on radio and television, and in community centers through leaflets, posters, and films. Unfortunately this is still a distant reality in Latin American countries.

When Carlos Chagas discovered the medical importance of triatomine bugs in 1909, only 33 species were known, and it was up to Arthur Neiva (through the Oswaldo Cruz Institute) to launch taxonomical studies on this group by creating the embryo for the Triatomines Laboratory that has been operating nonstop for more than a century. In 1989, the Triatomines Laboratory was transformed into the current *Laboratório Nacional e Internacional de Referência em Taxonomia de Triatomíneos* (LNIRTT; National and International Reference Laboratory for Triatomine Taxonomy) (Jurberg 1999), housing the world's largest collection of triatomines, with about 24,000 dry specimens, consisting of the Herman Lent Collection with 9,000 specimens and the Rodolfo Carcavallo Collection with 15,000 specimens. The laboratory has a large-scale insectary and is currently rearing 43 species in approximately 150 crystallizers, in addition to a collection kept in alcohol, with 45 species. The collections remain open and continue to receive material and make donations, and the laboratory is open to new scientific collaboration.

13.2 General Characteristics and Diagnosis

Most triatomine species can be identified on the basis of their external morphology. Their general appearance is similar to that of other reduviids, and the general external and internal morphologies are shown in Fig. 13.3. Detailed schemata of morphological traits were published by Lent and Wygodzinsky (1979) and several scanning electron microscopy illustrations were provided by Carcavallo et al. (1998/1999). The length of most species varies from 20 to 28 mm, but *Dipetalogaster maxima* (Uhler) can reach 44 mm in length, and the smallest species is *Alberprosenia goyovargasi* (Martínez & Carcavallo), with 5 mm. The color pattern (Figs. 13.4, 13.5, 13.6, 13.7, 13.8, and 13.9) varies, with an overall black or piceous color and spotted patterns of yellow, brown, orange, or red (Jurberg et al. 2004, 2012, 2014).

Adults differ from nymphs by the presence of ocelli and well-developed external genitalia and wings, with the exception of two species of *Mepraia* Mazza, Gajardo & Jörg 1940, which display wing polymorphism (Jurberg et al. 2002). Females are larger than males and have pointed or truncate abdominal apex, whereas in males

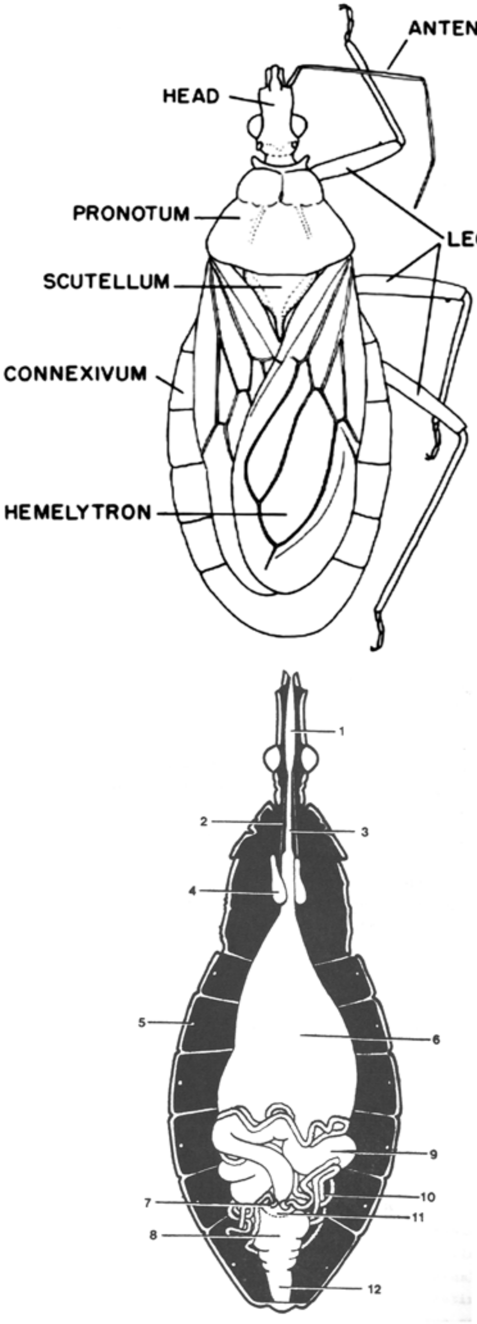


Fig. 13.3 General external and internal morphologies of the Triatominae (1, pharynx; 2, salivary duct; 3, esophagus; 4, salivary gland; 5, third respiratory spiracle; 6, promesenterium; 7, basal ampoule; 8, rectal ampoule; 9, postmesenterium; 10, Malpighian tubules; 11, light zone; 12, rectum) (From Lent and Wygodzinsky 1979 and Ramírez 1985)

Fig. 13.4 Color pattern of triatomine bugs: *Rhodnius brethesi* (From Jurberg and Galvão 2006)

Fig. 13.5 Color pattern of triatomine bugs: *Rhodnius nasutus* (From Jurberg and Galvão 2006)

Fig. 13.6 Color pattern of triatomine bugs: *Triatoma tibiamaculata* (From Jurberg and Galvão 2006)

Fig. 13.7 Color pattern of triatomine bugs: *Triatoma lecticularia* (From Jurberg and Galvão 2006)

Fig. 13.8 Color pattern of triatomine bugs: *Triatoma carcavalloi* (From Jurberg and Galvão 2006)

Fig. 13.9 Color pattern of triatomine bugs: *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

the apex is rounded. The morphology of triatomine eggs and nymphs (Fig. 13.10) has been the focus of several studies, and a summary of these works was provided by Galvão et al. (2005).

Besides the external structure, size, proportions, and coloration, genital features and the internal morphology also provide insights to the taxonomy and systematics of the Triatominae. The morphology of the salivary glands and proportions between the testicular tubes aid on the generic differentiation, and the structure of male genitalia can be used for the specific diagnosis, as demonstrated in Lent and Wygodzinsky (1979), Gonçalves et al. (1987), and Santos et al. (1997). These characters, in association with the study of live specimens when available, and the use of molecular, cytogenetic, morphometric, and histochemical tools provide support for the discovery of cryptic species and for the development of phylogenetic analysis (Jurberg 2003; Galvão 2003).

Fig. 13.10 Eggs, nymphs, and female of *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

13.2.1 Salivary Glands

The salivary complex is an important characteristic for the differentiation of the genera of Triatominae. The structures forming the complex are homogeneous among the genera, but display variable shapes (Figs. 13.11 and 13.12). Del Ponte (1921) was the first to demonstrate the importance of the salivary complex of the triatomines for the understanding of the taxonomy of the group, using *Triatoma infestans* as a model. Other comparative studies have been performed using different species of the genera *Triatoma* Laporte, *Mepraia*, *Panstrongylus* Berg, *Psammolestes* Bergroth, and *Rhodnius* Stål (Barreto 1922; Baptist 1941; Barth 1954).

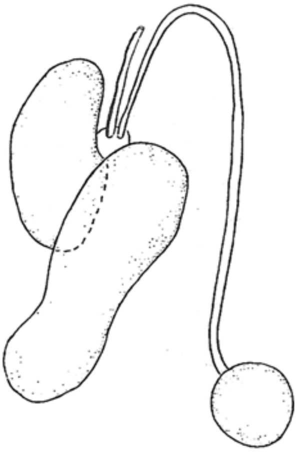


Fig. 13.11 Salivary complex of *Triatoma infestans* (From Santos et al. 1997)

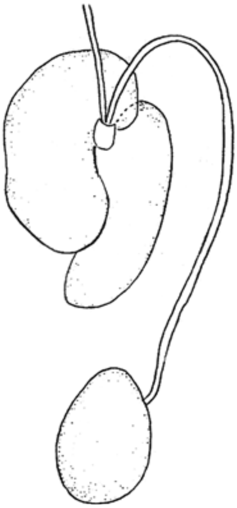


Fig. 13.12 Salivary complex of *Panstrongylus megistus* (From Santos et al. 1997)

13.2.2 Phallic Structure

Opposite to the females, in which the genital plates are simple and extremely homogeneous, the male genital complex of the Triatominae is composed of approximately 15 features, which are highly variable and can be used for generic and specific differentiation (Singh-Pruthi 1925; Dupuis 1955, 1963; Lent and Jurberg 1969, 1975) (Figs. 13.13 and 13.14). This variation was first studied by Lent and Jurberg (1965), who used the comparative analysis of the phallic structures as a tool for the identification of a new species in the genus *Psammolestes* (*P. tertius* Lent & Jurberg), at that time composed by only two species.

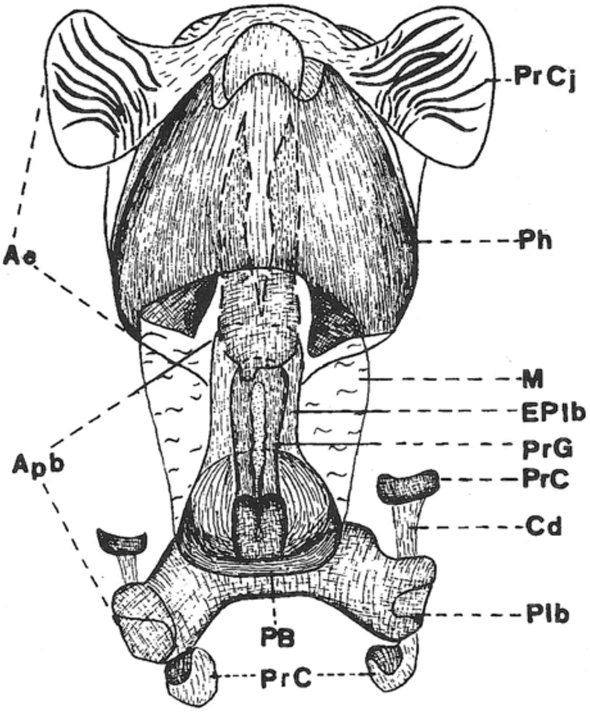


Fig. 13.13 Phallus of *Mepraia spinolai* in ventral view (*Ae* aedeagus, *Apb* articular apparatus, *Cd* dorsal connection, *EPlb* median extension of the basal plate, *M* membrane, *PB* basal bridge, *PrC* capitate process, *PrCj* conjunctive process, *Ph* phallosome, *PrG* process of the gonopore) (From Lent and Jurberg 1967)

Through the continuous use of this technique, phallic structures have been investigated in 16 genera and a great amount of species by the above cited authors, which culminated with the construction of a comparative table of presence/absence (+/−) and shape of the genital structure of the triatomines, which was presented in Carcavallo et al (1998/1999) and herein reproduced on Fig. 13.15. It is important to notice on the board that *Rhodnius stali* Lent, Jurberg & Galvão and *R. pictipes* Stål share some features with species of *Triatoma* that are not present on other species of the genus, which is an issue that needs to be further investigated (Figs. 13.16 and 13.17).

13.2.3 Testicular Tubes

Schreiber et al. (1968) noticed that the triatomines present a fixed number of seven testicular tubes (Fig. 13.18), but with different composition according to the genera, which proportioned taxonomists a new tool for characterizing and confirming

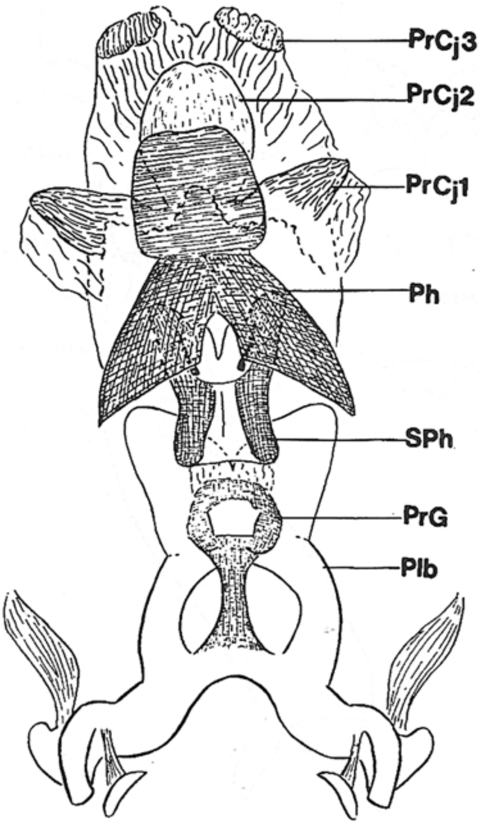
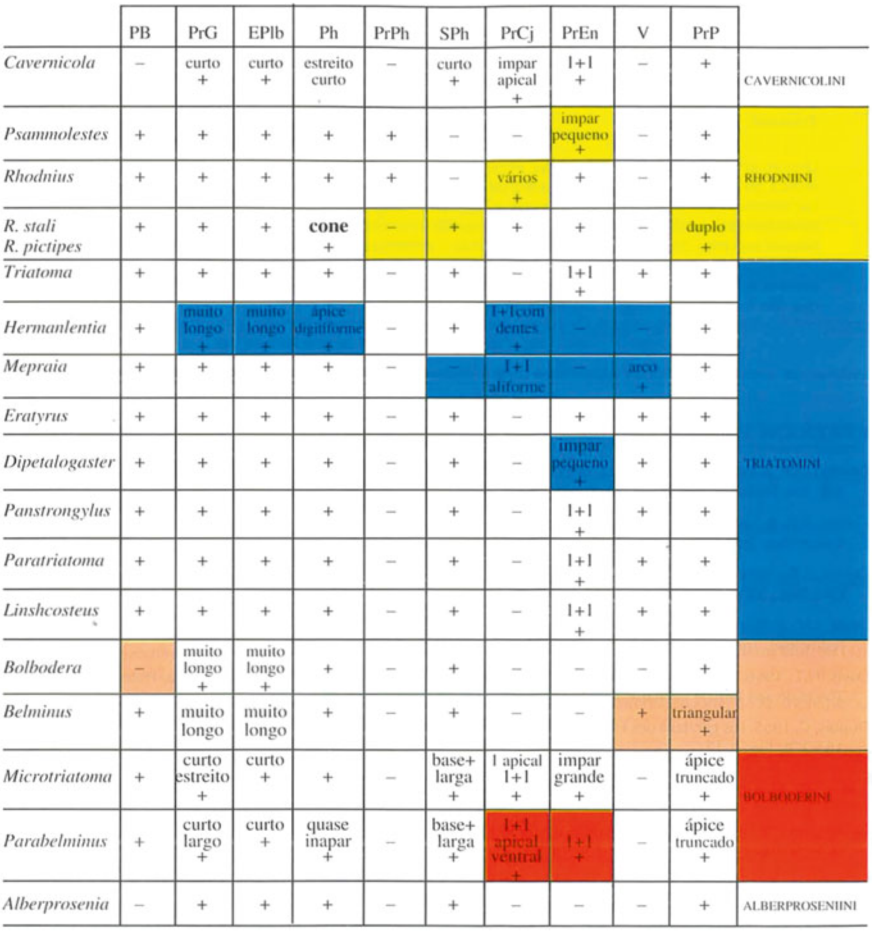


Fig. 13.14 Phallus of *Rhodnius stali* in ventral view (*Ph* phallosome, *PlB* basal plate, *PrCj 1, 2, 3* processes of the conjunctive 1, 2, 3, *SPh* support of the phallosome) (From Lent et al. 1993)

generic statuses. An example is the revalidation by Lent et al. (1994) of the genus *Mepraia*, in which there is a very short tube, two short tubes, two medium tubes, and one long tube. Males of *Rhodnius* present five short and two long; those of *Triatoma* have three short, two medium, and two long; and in *Panstrongylus* there are seven tubes of uniform size.

13.3 General Biology and Ecology

Knowledge of triatomine biology in the natural habitat is scarce, and for several species the natural ecotopes have not been described. Triatominae species are found in almost any habitat offering a degree of climatic stability and access to a blood source. Most of them tolerate a range of air humidity between 30 and 80 %, and temperatures of 24–28 °C are satisfactory. Their development is usually slow at temperatures below 16 °C, whereas temperatures above 40 °C are lethal. During the rigorous winters of Patagonia, they undergo lethargy, and on strong summers they increase the number of blood meals in order to compensate the higher loss of water.



	PB	PrG	EPlb	Ph	PrPh	SPh	PrCj	PrEn	V	PrP	
Cavernicola	–	curto +	curto +	estreito curto	–	curto +	impar apical +	1+1 +	–	+	CAVERNICOLINI
Psammolestes	+	+	+	+	+	–	–	impar pequeno +	–	+	RHODNIINI
Rhodnius	+	+	+	+	+	–	vários +	+	–	+	
R. stali *R. pictipes*	+	+	+	**cone** +	–	+	+	+	–	duplo +	
Triatoma	+	+	+	+	–	+	–	1+1 +	+	+	TRIATOMINI
Hermanlentia	+	muito longo +	muito longo +	ápice digitiforme +	–	+	1+1com dentes +	–	–	+	
Mepraia	+	+	+	+	–	–	1+1 aliforme	–	arco +	+	
Eratyrus	+	+	+	+	–	+	–	+	+	+	
Dipetalogaster	+	+	+	+	–	+	–	impar pequeno +	+	+	
Panstrongylus	+	+	+	+	–	+	–	1+1 +	+	+	
Paratriatoma	+	+	+	+	–	+	–	1+1 +	+	+	
Linshcosteus	+	+	+	+	–	+	–	1+1 +	+	+	
Bolbodera	–	muito longo +	muito longo +	+	–	+	–	–	–	+	[illegible]
Belminus	+	muito longo	muito longo	+	–	+	–	–	+	triangular +	
Microtriatoma	+	curto estreito +	curto +	+	–	base+ larga +	1 apical 1+1 +	impar grande +	–	ápice truncado +	BOLBODERINI
Parabelminus	+	curto largo +	curto +	quase inapar +	–	base+ larga +	1+1 apical ventral +	1+1 +	–	ápice truncado +	
Alberprosenia	–	+	+	+	–	+	–	–	–	+	ALBERPROSENIINI

Fig. 13.15 Comparative scheme of phallic structures on Triatominae genera (*PB* basal bridge, *PrG* process of the gonopore, *EPlb* median extension of the basal plate, *Ph* phallosome, *PrPh* process of the phallosome, *SPh* support of the phallosome, *PrCj* conjunctive process, *PrEn* process of the endosoma, *V* vesica, *PrP* process of the pygophore) (From Carcavallo et al. 1998/1999)

In general, most triatomines are nocturnal and during the day they remain in their resting places, although they may sometimes go out to suck blood during the day under adverse conditions. In colonies reared in the laboratory, the bugs seek food sources in broad daylight.

Most species of the subfamily are sylvatic, living in bird nests or animal dens, under tree bark, or in tree hollows, bromeliads, palm trees, and other ecotopes, feeding on various animals. Gaunt and Miles (2000) summarized the habitats of representatives of the triatomine genera *Rhodnius* and *Triatoma* showing that most species in the former genus live in or associated with palm trees, while most species in the latter genus live in or associated with rocky/terrestrial habitats. However, dur-

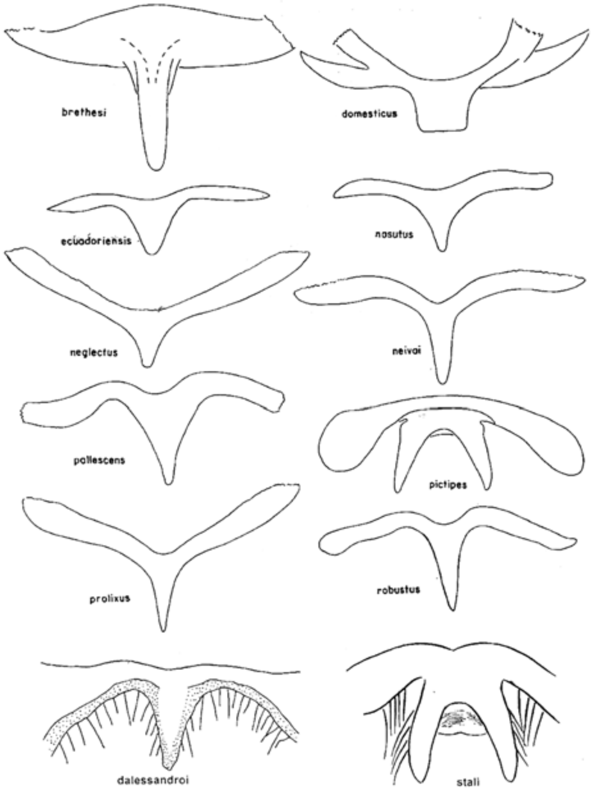


Fig. 13.16 Differences between the median processes of the pygophores of 11 species of the genus *Rhodnius* (From Carcavallo et al. 1998/1999)

ing their evolutionary process some species acquired the capacity to colonize man-made structures near human dwellings, like chicken coops and pigsties, and are thus referred to as peridomiciliated. Others can colonize the interior of human dwellings and are thus called domiciliated. The latter are epidemiologically more important, since they account for transmission of the disease to humans (Carcavallo et al. 1998/1999). Many rural inhabitants live in dwellings with straw roofs and mud walls, and these provide various forms of shelter for the triatomines (Fig. 13.19).

13.3.1 Locomotory Activity

According to Browne (1975), there are two forms of locomotory activity, one spontaneous (circadian), apparently without interference from external stimuli, and another oriented by external stimuli. Triatomines display various processes with temporal modulation, and spontaneous locomotor activity is one of these processes

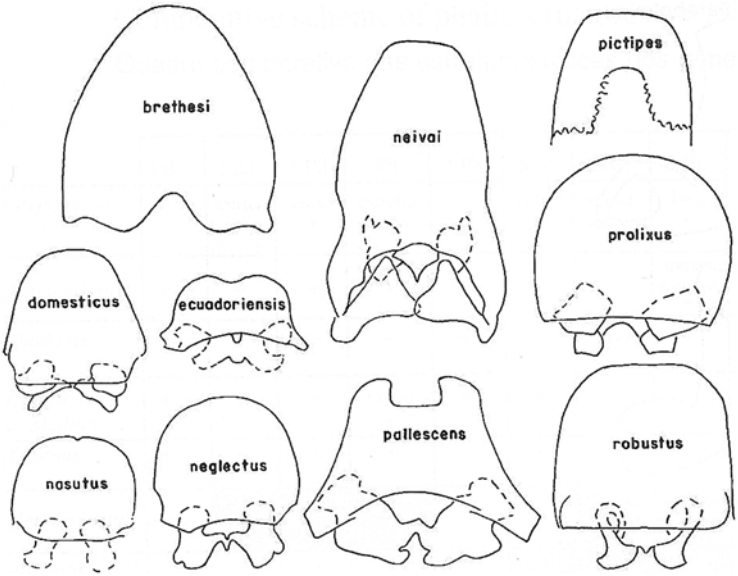


Fig. 13.17 Differences between the phallosomes of ten species of the genus *Rhodnius* (From Carcavallo et al. 1998/1999)

that can be observed individually and can be considered a true circadian rhythm. Various authors used actographic records to demonstrate that locomotor activity in both adults and nymphs is intensified during the early hours of the nocturnal period (Schofield 1976; Núñez 1982; Settembrini 1984; Lazzari 1992).

According to Lazzari (1992), the circadian rhythm of spontaneous locomotor activity is divided into two well-demarcated moments: the search for food occurs in late afternoon/dusk and the search for shelter occurs at dawn. This hypothesis was tested subsequently by Lorenzo and Lazzari (1998), who filmed the locomotor activity of insects in an arena containing refuges and concluded that *Triatoma infestans* demonstrated greater activity and motivation to feed in the early hours of the evening than at the end of this period.

13.3.2 Aggregation

Aggregative behavior in triatomines is mediated principally by the response to the presence of chemical signals (Velázquez-Antich 1968). Studies performed with *T. infestans* and *Rhodnius prolixus* demonstrated the existence of gregarious behavior as a response to volatile substances found in the feces (Schofield and Patterson 1977; Ondarza et al. 1986). Aggregation mediated by chemical substances contained in feces was recently demonstrated by Pires et al. (2002) in *Panstrongylus megistus* and by Vitta et al. (2002) in *Triatoma pseudomaculata* Corrêa & Espínola.

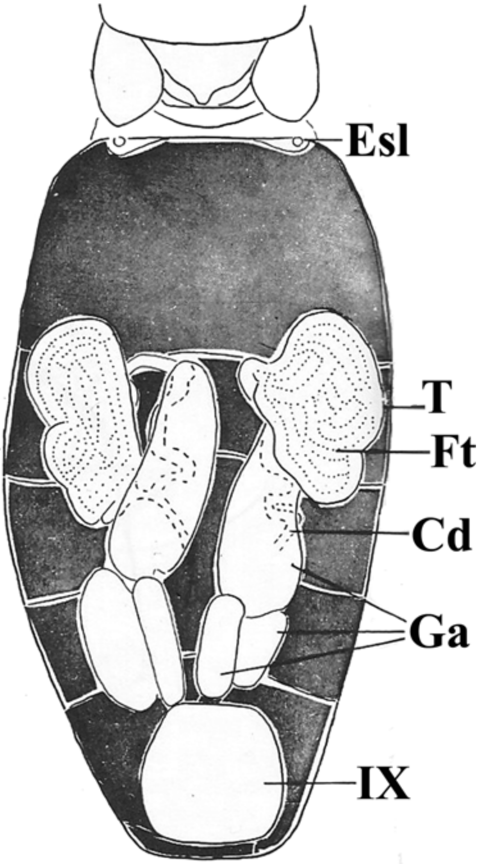


Fig. 13.18 Dissected abdomen of a male *Mepraia spinolai* showing structure of the sexual organs (*Cd* deferent canal, *Esl* spiracle, *Ft* testicular follicles, *Ga* accessory gland, *IX* pygophore or ninth abdominal segment, *T* testicle) (From Gonçalves et al. 1987)

Despite the various attempts of analysis, the nature of the chemical signal present in feces is still not well known, but it is known that feces act as signalers for the insects' refuges. These results show the need for future research aimed at the characterization of an interspecific gregarious chemical compound, in order to aid the control and monitoring of triatomine populations.

13.3.3 Camouflage

The ability of *Triatoma dimidiata* nymphs to camouflage themselves with particles of dust from the soil was described in detail by Hase (1940). Zeledón et al. (1969) observed the same species in both the field and the laboratory and called attention to this behavior's epidemiological importance. According to Zeledón et al. (1973), this behavior is present in various triatomine species, but to variable degrees, and it appears to be completely absent in others. One can clearly establish a correlation between the habitats where some species live (in contact with as opposed to distant

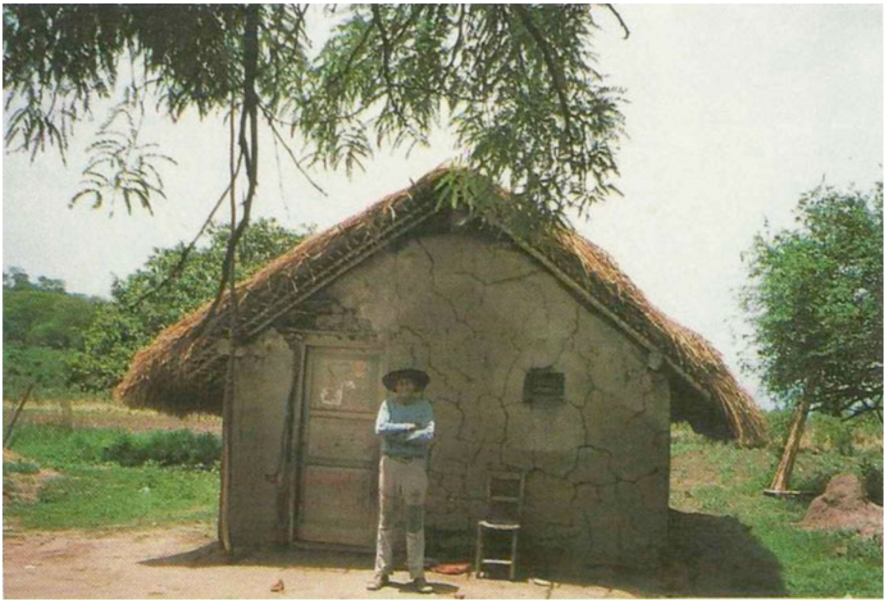


Fig. 13.19 Rural dwelling subject to infestation by triatomine bugs (From Carcavallo et al. 1998/1999)

from the ground) and the presence or absence of this behavior. This behavior's epidemiological implications deserve further investigation, since it interferes directly with the efficiency of control measures, and prior knowledge of the species presenting this behavior is necessary in order to develop entomological surveillance methodologies.

13.3.4 Dispersion

Dispersion in triatomines can occur passively, i.e., involuntarily by humans, or actively, through the adult insects' flight (Galvão et al. 2001b). Knowledge is still limited concerning the mechanisms involved in dispersion by flight. The insects apparently respond directly to external conditions, but not to an internal clock. This is an extremely relevant aspect because areas that have been chemically treated and are free of triatomine foci can be recolonized by flying specimens. In *Triatoma infestans*, the mean flight distance is about 200 m (Schofield and Matthews 1985), but flights of more than 1 km have been observed in the field (Schweigmann et al. 1988). Triatomine flight capacity has been studied both in the field and the laboratory primarily based on releasing and recapturing the insects and has furnished important information on the most flight-capable species. However, no experiments have been done so far focusing on observations of flight behavior itself (Lehane and Schofield 1981; Schofield et al. 1991, 1992; Galvão et al. 2001b).

Fig. 13.20 Triatomine eggs: agglutinated eggs of *Rhodnius domesticus* (From Jurberg and Galvão 2006)

Fig. 13.21 Triatomine eggs: free eggs of *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

13.3.5 Eggs and Oviposition

In general, the eggs of the majority of triatomine species are deposited free in the environment, although some species have an adhesive substance that makes the eggs stick to the substrate (Figs. 13.20 and 13.21). *Triatoma infestans*, a domiciliated species that originally inhabited rodent nests, is still found in the Bolivian altiplano and lays its eggs loose in the sites it inhabits. *Triatoma platensis* Neiva and *T. delpontei* Romaña & Abalos, ornithophilous species, stick their eggs to the substrate of the bird nests in which they live. Species of *Rhodnius* also stick their eggs to the substrate. *Rhodnius prolixus*, which inhabits the nest of *Mycteria americana* L., a migratory bird, can have its eggs spread when they are adhered to the bird's feathers. *Psammolestes arthuri* (Pinto), on its turn, oviposits in clusters, like members of the reduviid subfamilies Harpactorinae and Apiomerinae (Lent and Wygodzinsky 1979).

Oviposition normally occurs 10–30 days after copulation, which can be repeated several times during the adult's lifespan, although a female fecundated just once remains permanently fertilized. The number of eggs varies by species and principally as a function the female's degree of feeding. Recently laid eggs are whitish or pearly in color and change color over time until they become pinkish or brownish, near the day of hatching. During this phase, with the eggs transparent, one can see the black ocular spots, as the 1st stage nymphs emerge from the egg leaving the exuviae appearing (protonymph).

13.3.6 Feeding and Development

Triatomine bugs are obligatory hematophagous insects in all stages of their development and in both sexes, requiring numerous blood meals to complete their development. The amount of blood ingested varies according to the species as well as in relation to the life stage, and generally the 4th and 5th instar nymphs are the ones that feed the most. When they finish a meal, their body changes appearance, since the volume of blood ingested is so great that the abdomen dilates considerably, giving them a globose appearance by stretching the intersegmental and connexival membranes.

The vast majority of species feed on the blood of mammals or birds, but some can feed on reptile or amphibian blood (Carcavallo et al. 1998/1999). Coprophagy (ingestion of feces), kleptohematophagy (sucking blood already ingested by another triatomine), and hemolymphagy (sucking hemolymph from other arthropods) have also been reported by various authors (Lafont 1912; Brumpt 1914; Lent and Martins 1940; Wood 1941; Ryckman 1951; Sandoval et al. 2000). Lorosa et al. (2000) and Ruas-Neto et al. (2001) showed that hemolymphagy can be an important survival strategy in nature, observing *T. circummaculata* (Stål) and *T. rubrovaria* (Blanchard) sucking blattids (cockroaches) in natural rock piles. Laboratory experiments by these authors demonstrated that the biological cycle of both species can be completed exclusively with hemolymph from these insects; however, after the imaginal molt, the males and females of both species could not survive on hemolymph. According to some authors, this aspect could be correlated with studies on the evolution of these two species, which still show this ancestral predatory characteristic.

Some triatomines are considered stenophagic, that is, adapted to feeding only on given hosts, but the vast majority have eclectic feeding habits. Carcavallo et al. (1998/1999) published an extensive list correlating each species to its respective food source, which can be identified through techniques like the precipitin test (Siqueira 1960; Freitas et al. 1960). The results, however, may reflect much more the predominance of a given host or hosts in an area than a true food preference, and it is common to detect the presence of blood from various hosts in a single insect, which can lead to different interpretations. Could it mean great species mobility? Host mobility? Absence of preference? Opportunism? These questions can only be answered safely by associating these results with those obtained through ethological studies.

Feeding behavior depends on various types of stimuli in order to induce hematophagy. Various studies have demonstrated that heat and carbon dioxide are the principal stimuli involved in the search for and biting of the host (Botto-Mahan et al. 2002), but heat appears to act only on the search for food and does not interfere in the feeding itself. The thermoreceptors are concentrated mainly in the antennae, which perform characteristic movements in the presence of a heat source, and bilateral antennectomy results in the impossibility of locating a heat source. According to Lazzari and Núñez (1989), it is possible to make *Triatoma infestans* nymphs suck cold blood, as long as the bite is induced by thermal stimulation of the antennae. Other types of observations, aimed to characterize the species with greatest vector potentials, are to check the number of bites per meals, duration of the meal, and defecation site. These aspects are highly epidemiologically relevant, because with more contacts between vectors and hosts, greater is the probability of infection or transmission of *Trypanosoma cruzi* (Rocha et al. 1997).

Resistance to long periods of fasting and the fact that many species are generalists favor their survival in nature. This capacity of the triatomines has been known for decades. In 1926 Uribe reported the survival of a 3rd instar nymph of *Rhodnius prolixus* for 5 months. The literature shows discrepancies in the survival periods of various species studied according to the methodology employed, which can show variation in the feeding sources, relative humidity, and temperature, as well as the stress the insect suffers during handling (Wood 1951; Friend and Smith 1977; Mascarenhas 1990; Galvão et al. 2001a; Dias-Lima and Sherlock 2002, Martínez-Ibarra et al. 2003). Resistance to fasting can vary between and within species. Among the different stages, the 4th and 5th are normally most resistant, because of their higher capacity to ingest blood. Various authors have focused their laboratory studies on the resistance period to fasting among the various species, including Galvão et al. (1996, 1999a) and Jurberg and Costa (1989a, b).

In the domestic environment, these insects generally suck the blood of their victims at night while they are asleep, and the bites generally occur on the uncovered parts of the body. That is why the most popular name for the triatomine bugs in Brazil is *barbeiro* (meaning barber in Portuguese; for a list of vernacular names, see Table 13.1). The sleeping individuals are unaware of the bugs, because the bites are generally painless due to the anesthetic and anticlotting action of the saliva, although rare cases of hypersensitivity can occur. Some species may defecate while feeding, while others defecate soon afterwards or even abandon the food source and defecate far from the sucking site, a fact characterizes them as either good or bad transmitters of the Chagas disease.

The triatomines are parasites with slow development, whose life cycle from egg to adult includes five nymphal stages (Fig. 13.22), ranging from 3 to 4 months in *Rhodnius prolixus* up to 2 years in *Panstrongylus megistus.* This life span can vary considerably according to the temperature to which the bugs are submitted, a fact that was early studied by Neiva (1913), who observed that high temperatures accelerated the embryonic period of *Triatoma infestans*. Carcavallo and Martínez (1972) obtained shorter cycles in specimens of three species of *Triatoma* reared at high temperatures as compared to those reared at variable temperatures. Silva (1985,

Table 13.1 Examples of vernacular names for Triatominae

Region	Names
USA	Kissing bug, conenose bug, big bedbug (note that "assassin bug" refers to predatory Reduviidae)
	China bug (refers to *T. protracta* on the Pacific coast, once assumed to come from the orient)
	Red-banded conenose (refers to *T. rubrofasciata* and/or *T. sanguisuga*)
Mexico	Chinche besucona (Spanish—"kissing bug")
	Chinche hosicona [Spanish—"trunked bug" (trunked, as in elephant)]
	Chinche picuda (Spanish—"biting bug")
	Chinchona (Spanish—"big bug")
	Pik (Nahuatl, probably refers to the sound made when flying bug strikes wall)
Belize	Bush chinche (implies the absence of domestic Triatominae in Belize)
Central America	Chinche besucona (or just chinche; note that "telepate" more usually refers to cimicid bedbugs)
	Talaje (Spanish—"cutting bug," but mainly applied to cimicid bedbugs)
	Chuluyu (NE Honduras—usually applied specifically to *R. prolixus*, probably derives from *chuzu*, "needle" or "spear," + *uyu*, "alive")
	Polvoso (Spanish—"dusty"; in NE Honduras usually applied specifically to *T. dimidiata*, probably refers to the habit of nymphs to cover themselves with dust)
	Chinche bebe sangre (Costa Rica, Spanish—"blood-drinking bug")
Cuba	Sangrejuela (Spanish—"bloodstealer," also refers to leeches)
Colombia	Pito (Spanish—"whistle" or "horn," but may also refer to the bug's extended mouthparts)
	Chinche picuda
Venezuela	Chipo (colloquial Spanish—"little bug")
	Îipi (Macuxi Indians; refers specifically to *T. maculata*)
Ecuador	Chinchorro (Spanish + Quechua—"large bug")
Peru	Chirimacha (Quechua—"bug that dislikes the cold" or "drunk with the cold")
Paraguay	Chichá guazú (Guarani, probably derived from Spanish *chinche*, "bug," + Guarani *guazú*, "big")
	Itchajuponja (Ayoreo, probably derived from Spanish *chinche*, "bug," + *jupona*, "sucker")
	Sham bui tá (Aché—"insect that does harm by its dejections" mainly used for blister beetles)
	Timbucú (in the Guarani of the Chiriguano and Tapieté groups, signifies "long beak")
Bolivia	Vinchuca (Quechua—"bug that lets itself fall")
	Uluchi (Quechua—"bug without wings"; refers to nymphal stages)
	Timbucú
Chile	Vinchuca
Argentina	Vinchuca
Uruguay	Vinchuca

(continued)

Table 13.1 (continued)

Region	Names
Brazil	Barbeiro (Portuguese—“barber” or “shaver”)
	Furão (Portuguese—“big piercing bug”)
	Chupão (Portuguese—“big sucking bug”)
	Bicudo (Portuguese—“beaked bug”)
	Fincão [Portuguese (Brazil-RS)]—“big piercing bug”)
	Cascudo [Portuguese (Brazil-MG)—“thick-skinned bug,” used mainly for nymphs]
	Chupança [Portuguese (NE Brazil)—“sucking bug”]
	Procotó (or brocotó, borocotó) [Portuguese (NE Brazil)—“bug that hides in cracks”]
	Gigolô [Portuguese (NE Brazil)—“exploiter, esp. of women”]
	Percevejo (or bicho) de parede [Portuguese (NE Brazil)—“wall bedbug”]
	Gaudério (or bicho gaudério) [Portuguese (Brazil-PE)—“indigent thief”] rondão [Portuguese (NE Brazil)—“big bug that observes from hiding”]
	Percevejão (Portuguese—“big bedbug”)
	Percevejo do sertão (Portuguese—“bedbug from Sertão,” sertão = interior of Brazil)
	Percevejo das pedras (Brazil-RGS) (Portuguese—“bedbug among the stones”; *T. rubrovaria*)
	Piolho de piassava (Brazil-Amazon region) (Portuguese—“louse from the piassaba palm”; *R. brethesi*)
	Vunvum (Portuguese—probably onomatopoeic for the sound of bug flight)
	Josipak [Matacos Indians (Roraima)]
	Îipi [Macuxi Indians (Roraima and Venezuela); refers specifically to *T. maculata*]

From Schofield and Galvão (2009)

1988, 1989a, b, c, 1990a, b, 1992), Silva and Silva (1988a, b, c, d, e, 1989, 1990a, b, 1991, 1993), and Silva et al. (1995) compared the developmental times of several species reared at 25 and 30 °C, showing a reduction of approximately 30 days in three species of *Rhodnius* and from 40 to 60 days in *Triatoma* species. Various other authors have demonstrated acceleration in the developmental period of different species submitted to increased temperature (Galvão et al. 1995, 1999b; Rocha et al. 1994, 2001a, b).

According to most authors, when associated with low relative humidity, the cycle is shortened by metabolic alteration and dehydration, increasing the number of meals to balance the energy budget and water loss. These results support the hypothesis that higher temperatures and lower relative humidity, as possible consequences of global warming, could accelerate the life cycle of triatomines. The result is a change in the population dynamics of some Chagas disease vectors, extending their geographic distribution towards more temperate regions as well increasing the density of some populations.

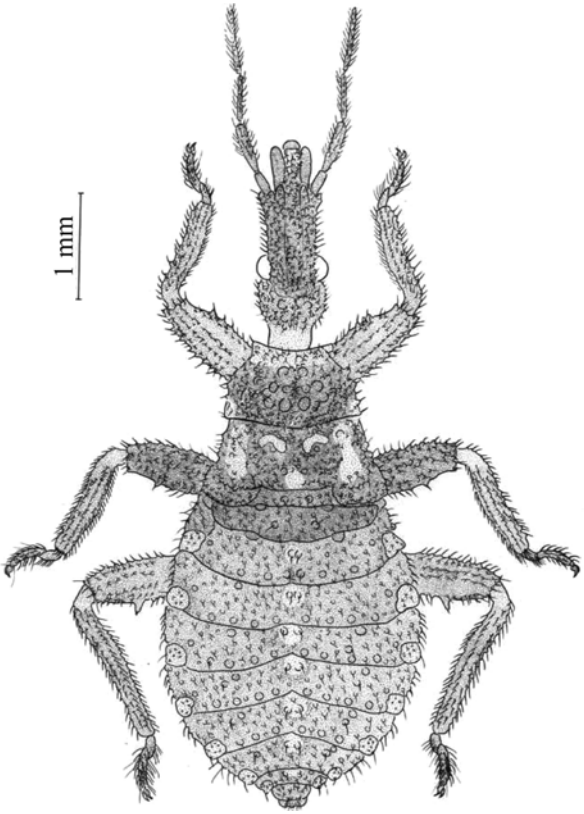


Fig. 13.22 Fourth instar nymph of *Belminus herreri* (From Rocha et al. 2002)

The longevity of nymphs and adults varies by species and ambient conditions. Laboratory experiments generally use what are considered ideal conditions for most species, with a mean temperature close to 28 °C and relative humidity around 70 %, blood feeding on adequate sources for each species, and a photoperiod of 12 h. Of course in nature the insect is influenced by various factors that are difficult to control in the laboratory. Results obtained in the laboratory are thus merely an approximation of what occurs in nature, but knowledge of the biological cycles and population dynamics allows an estimation of the species' growth and colonization capacity, principally for anthropophilic species, but also for so-called secondary species with a tendency towards domiciliation (Carcavallo et al. 1998/1999).

Laboratory Rearing

Important information on triatomine biology has been obtained through rearing and observation in the laboratory and it is not difficult to establish and maintain colonies of these insects. Some appropriate requirements include the control of air temperature and relative humidity. In the LNIRTT, Oswaldo Cruz Institute, Rio de Janeiro, colonies are maintained in glass crystallizers (20 cm high by 20 cm in diameter), covered with a reduced-mesh nylon screen to avoid the escape of 1st instar nymphs and the entry of predators (microhymenoptera, ants, and spiders). Strips of filter paper are placed inside the crystallizers to help absorb the humidity and increase the circulating area. A wooden stand placed inside each crystallizer serves as a support for the hosts (pigeons and mice), which are anesthetized and immobilized before being offered as the food source. Black paper strips are placed outside each crystallizer to limit the amount of light striking the recipient.

Success in maintaining the colonies depends on adherence to the abovementioned items, taking into consideration that offering the same food source repeatedly for long periods of time leads to deficiencies in the insect's development. When cleaning the recipients, the strips of filter paper, which become soiled with the insects' feces, are changed so the environment does not become overloaded, but some strips impregnated with feces are left in the crystallizers to allow recently hatched nymphs to have contact with their natural digestive tract symbionts, which aid in digesting blood.

13.3.7 Reproduction

The first information on copulation in triatomines was published by Neiva (1914), who noted that *Panstrongylus megistus* females appeared to copulate only once, maintaining the eggs fertile throughout their lifespan. Courting is not complex in this group of insects, and copulation in some species has been observed in the laboratory. Prior to copulation, the male approaches the female attempting to immobilize her with the three legs on one side of the body in a dorsolateral position (Fig. 13.23) (Abalos and Wygodzinsky 1951; Hack and Bar 1979; Lent and Wygodzinsky 1979; Lima et al. 1986; Rojas et al. 1990; Manrique and Lazzari 1994). Copulation itself can last 15–30 min, and the male fertilizes the female by depositing spermatophores in her vagina. The spermatophores then burst and release the spermatozoa that migrate to the spermathecae, where they remain protected while awaiting the passage of the successive ova to fertilize.

The presence of sexual pheromones in triatomines has been the target of research for many years, and evidence of chemical attraction between males and females was found in *Rhodnius prolixus* by Velazquez-Antich (1968) and in *Triatoma infestans* and *Panstrongylus megistus* by Neves and Paulini (1981). According to Baldwin et al. (1971), sexual pheromones are released during copulation, leading to an aggregation of males around the couple. Similar conclusions were obtained by Manrique and Lazzari (1994), studying *Triatoma infestans*. On the other hand, the complete absence of sexual attraction was demonstrated by Schofield and Moreman (1979), Hack and Bar (1979), and Lima and MacCord (1994), which can probably be explained by the differing methodologies applied.

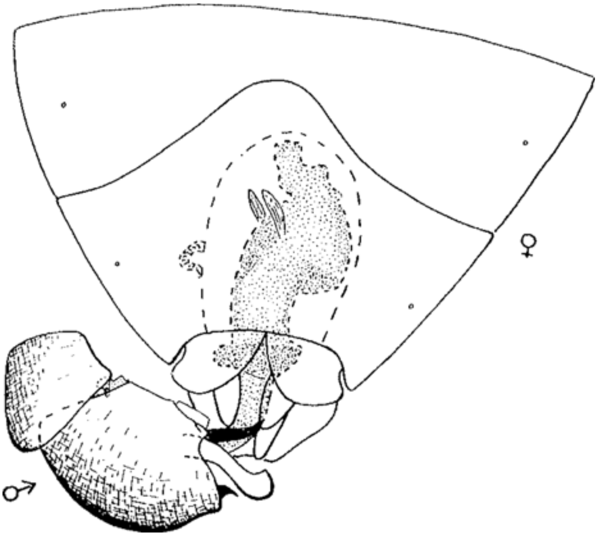


Fig. 13.23 Last abdominal segments of a male and a female of *Rhodnius prolixus* during copulation (From Carcavallo et al. 1998/1999)

13.4 Classification and Diversity

The subfamily Triatominae includes 146 extant species (Galvão et al. 2003; Schofield and Galvão 2009; Rosa et al. 2012; Gonçalves et al. 2013; Jurberg et al. 2013), and its current classification that recognizes five tribes is based mainly on the revision by Lent and Wygodzinsky (1979), the most important systematic study concerning the group. Since that revision, there has been considerable work, including the descriptions of several new taxa. Therefore, a summary of the recent classification and a list of Neotropical species updated from Galvão et al. (2003) and Schofield and Galvão (2009) are herein provided (Tables 13.2 and 13.3). Regarding the identification of the genera and species, extensive dichotomous keys were provided by Lent and Wygodzinsky (1979), Lent et al. (1994), and Carcavallo et al. (1998/1999).

13.4.1 Phylogeny and Evolution

Triatominae has long been classified as a subfamily of the predominantly predatory Reduviidae (Usinger 1943; Maldonado-Capriles 1990; Schuh and Slater 1995). The subfamily is diagnosed, among other features, by the slender and straight labium of its members and their blood-feeding habits (Lent and Wygodzinsky 1979; Clayton 1990; Weirauch 2008). However, phylogenetic relationships of Triatominae are not

Table 13.2 Current systematic classification of the subfamily Triatominae

Subfamily	Tribes	Genera	Number of valid names
Triatominae	Alberproseniini	*Alberprosenia*	2
	Bolboderini	*Belminus*	8
		Bolbodera	1
		Microtriatoma	2
		Parabelminus	2
	Cavernicolini	*Cavernicola*	2
	Rhodniini	*Psammolestes*	3
		Rhodnius	18
	Triatomini	*Dipetalogaster*	1
		Eratyrus	2
		Hermanlentia	1
		Linshcosteus	6
		Meccus	3
		Mepraia	3
		Nesotriatoma	3
		Panstrongylus	14
		Paratriatoma	1
		Triatoma[1]	71

Updated from Galvão et al. (2003) and Schofield and Galvão (2009)
[1] Excluding *T. dominicana*, a fossil species

Table 13.3 Checklist of the Neotropical species of Triatominae, with their geographical distribution

Species and author	Countries or territories
Alberprosenia goyovargasi Martínez & Carcavallo	Venezuela
A. malheiroi Serra, Atzingen & Serra	Brazil
Belminus costaricensis Herrer, Lent & Wygodzinsky	Costa Rica, Mexico
B. herreri Lent & Wygodzinsky	Colombia, Panama
B. laportei Lent, Jurberg & Carcavallo	Brazil
B. peruvianus Herrer, Lent & Wygodzinsky	Peru
B. pittieri Osuna & Ayala	Venezuela
B. rugulosus Stål	Colombia, Venezuela
Bolbodera scabrosa Valdés	Cuba
Microtriatoma borbai Lent & Wygodzinsky	Brazil
M. trinidadensis (Lent)	Brazil, Bolivia, Colombia, Peru, Trinidad and Tobago, Venezuela
Parabelminus carioca Lent	Brazil
P. yurupucu Lent & Wygodzinsky	Brazil
Cavernicola lenti Barrett & Arias	Brazil

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
C. pilosa Barber	Brazil, Colombia, Panama, Peru, Venezuela
Psammolestes arthuri (Pinto)	Colombia, Venezuela
P. coreodes Bergroth	Argentina, Bolivia, Brazil, Paraguay
P. tertius Lent & Jurberg	Brazil
Rhodnius amazonicus Almeida, Santos & Sposina	Brazil, French Guiana
Rhodnius brethesi Matta	Brazil, Colombia, Venezuela
R. colombiensis Mejia, Galvão & Jurberg	Colombia
R. dalessandroi Carcavallo & Barreto	Colombia
R. domesticus Neiva & Pinto	Brazil
R. ecuadoriensis Lent & León	Ecuador, Peru
R. milesi Carcavallo, Rocha, Galvão & Jurberg	Brazil
R. montenegrensis Rosa, Rocha, Gardim, Pinto, Mendonça, Ferreira-Filho, Carvalho, Camargo, Oliveira, Nascimento, Cilense & Almeida	Brazil
R. nasutus Stål	Brazil
R. neglectus Lent	Brazil
R. neivai Lent	Colombia, Venezuela
R. pallescens Barber	Belize, Colombia, Costa Rica, Panama
R. paraensis Sherlock, Guitton & Miles	Brazil
R. pictipes Stål	Belize, Brazil, Colombia, Ecuador, Guyana, French Guiana, Peru, Suriname, Trinidad and Tobago, Venezuela
R. prolixus Stål	Bolivia, Brazil, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Guyana, French Guiana, Honduras, Mexico, Nicaragua, Panama, Suriname, Trinidad and Tobago, Venezuela
R. robustus Larrousse	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru, Venezuela
R. stali Lent, Jurberg & Galvão	Bolivia, Brazil
R. zeledoni Jurberg, Rocha & Galvão	Brazil
Dipetalogaster maxima (Uhler)	Mexico
Eratyrus cuspidatus Stål	Colombia, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
E. mucronatus Stål	Bolivia, Brazil, Colombia, Ecuador, Guatemala, Guyana, French Guiana, Panama, Peru, Suriname, Trinidad and Tobago, Venezuela

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
Hermanlentia matsunoi (Fernández-Loayza)	Peru
Meccus bassolsae (Alejandre Aguilar, Nogueda Torres, Cortéz Jimenez, Jurberg, Galvão & Carcavallo)	Mexico
M. longipennis (Usinger)	Mexico
M. mazzottii (Usinger)	Mexico
M. pallidipennis (Stål)	Mexico
M. phyllosomus (Burmeister)	Mexico
M. picturatus (Usinger)	Mexico
Mepraia gajardoi Frias, Henry & Gonzalez	Chile
M. spinolai (Porter)	Chile
Nesotriatoma bruneri Usinger	Cuba
N. flavida (Neiva)	Cuba
N. obscura Maldonado & Farr	Jamaica
Paratriatoma hirsuta Barber	Mexico, USA
Panstrongylus chinai (Del Ponte)	Ecuador, Peru, Venezuela
P. diasi Pinto & Lent	Bolivia, Brazil
P. geniculatus (Latreille)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, French Guiana, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Uruguay, Trinidad and Tobago, Venezuela
P. guentheri Berg	Argentina, Bolivia, Paraguay, Uruguay
P. howardi (Neiva)	Ecuador
P. humeralis (Usinger)	Panama
P. lenti Galvão & Palma	Brazil
P. lignarius (Walker)	Brazil, Peru, Guyana, Suriname, Venezuela
P. lutzi (Neiva & Pinto)	Brazil
P. megistus (Burmeister)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
P. mitarakaensis Bérenger & Blanchet	French Guiana
P. rufotuberculatus (Champion)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, Venezuela
P. tupynambai Lent	Brazil, Uruguay
T. arthurneivai Lent & Martins	Brazil
T. baratai Carcavallo & Jurberg	Brazil
T. barberi Usinger	Mexico
T. bolivari Carcavallo, Martínez & Pelaez	Mexico
T. boliviana Martínez, Chávez, Sossa, Aranda, Vargas & Vidaurre	Bolivia
T. brailovskyi Martínez, Carcavallo & Pelaez	Mexico

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
T. brasiliensis Neiva	Brazil
T. breyeri Del Ponte	Argentina
T. carcavalloi Jurberg, Rocha & Lent	Brazil
T. carrioni Larrousse	Ecuador, Peru
T. circummaculata (Stål)	Brazil, Uruguay
T. costalimai Verano & Galvão	Brazil
T. deaneorum Galvão, Souza & Lima	Brazil
T. delpontei Romaña & Abalos	Argentina, Bolivia, Brazil, Uruguay, Paraguay
T. dimidiata (Latreille)	Belize, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela
T. dispar Lent	Colombia, Costa Rica, Ecuador, Panama
T. eratyrusiformis Del Ponte	Argentina
T. garciabesi Carcavallo, Cichero, Martínez, Prosen & Ronderos	Argentina, Bolivia
T. gerstaeckeri (Stål)	USA, Mexico
T. gomeznunezi Martínez, Carcavallo & Jurberg	Mexico
T. guasayana Wygodzinsky & Abalos	Argentina, Bolivia, Paraguay
T. guazu Lent & Wygodzinsky	Brazil
T. hegneri Mazzotti	Mexico
T. incrassata Usinger	USA, Mexico
T. indictiva Neiva	USA, Mexico
T. infestans (Klug)	Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru, Uruguay
T. jatai Gonçalves, Teves-Neves, Santos-Mallet, Carbajal-de-la-Fuente & Lopes	Brazil
T. jurbergi Carcavallo, Galvão & Lent	Brazil
T. klugi Carcavallo, Jurberg, Lent & Galvão	Brazil
T. lecticularia (Stål)	USA, Mexico
T. lenti Sherlock & Serafim	Brazil
T. limai Del Ponte	Argentina
T. maculata (Erichson)	Aruba, Brazil, Bonaire, Curaçao, Colombia, Guyana, French Guiana, Suriname, Venezuela
T. matogrossensis Leite & Barbosa	Brazil
T. melanocephala Neiva & Pinto	Brazil
T. mexicana (Herrich-Schaeffer)	Mexico
T. neotomae Neiva	USA, Mexico

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
T. nigromaculata (Stål)	Colombia, Peru, Venezuela
T. nitida Usinger	Costa Rica, Guatemala, Honduras, Mexico
T. oliveirai (Neiva, Pinto & Lent)	Brazil
T. patagonica Del Ponte	Argentina, Uruguay
T. peninsularis Usinger	Mexico
T. petrochiae Pinto & Barreto	Brazil
T. pintodiasi Jurberg, Cunha & Rocha	Brazil
T. platensis Neiva	Argentina, Paraguay, Uruguay
T. protracta (Uhler)	USA, Mexico
T. pseudomaculata Corrêa & Espínola	Brazil
T. recurva (Stål)	USA, Mexico
T. rubida (Uhler)	USA, Mexico
T. rubrofasciata (De Geer)	Andaman Islands, Angola, Argentina, Azores, Bahamas, Brazil, Burma, Cambodia, Caroline Islands, China, Comoros, Congo, Cuba, Dominican Republic, Formosa, French Guiana, Goa, Grenada, Guadeloupe, Haiti, Hawaii, Hong Kong, India, Indonesia (Borneo, Java, Sumatra), Jamaica, Madagascar, Malaysia, Martinica, Mauritius Islands, New Guinea, Okinawa, Philippines, Saint Croix, Saint Vincent, Saudi Arabia, Seychelles, Sierra Leone, Singapore, South Africa, Sri Lanka, Thailand, USA, Venezuela, Vietnam, Zanzibar
T. rubrovaria (Blanchard)	Argentina, Brazil, Uruguay
T. ryckmani Zeledón & Ponce	Costa Rica, Guatemala, Honduras
T. sanguisuga (Leconte)	USA, Mexico
T. sherlocki Papa, Jurberg, Carcavallo, Cerqueira & Barata	Brazil
T. sinaloensis Ryckman	Mexico
T. sordida (Stål)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
T. tibiamaculata (Pinto)	Brazil
T. vandae Carcavallo, Jurberg, Rocha, Galvão, Noireau & Lent	Brazil
T. venosa (Stål)	Bolivia, Colombia, Costa Rica, Ecuador, Peru
T. vitticeps (Stål)	Brazil
T. williami Galvão, Souza & Lima	Brazil
T. wygodzinskyi Lent	Brazil

Updated from Galvão et al. (2003)

resolved, with problems persisting in three areas. First, it is unclear if Triatominae are actually monophyletic, i.e., derived from a single ancestor that gave rise to the entire clade of blood-feeding assassin bugs (Hypsa et al. 2002; Schofield and Galvão 2009; Weirauch and Munro 2009; Patterson and Gaunt 2010; Hwang and Weirauch 2012). Second, different groups of predatory Reduviidae have been proposed to be the closest relatives of the Triatominae. Third, relationships and evolutionary history of clades within the Triatominae are not well understood.

Alternative phylogenetic hypotheses show Triatominae to be monophyletic (Hypsa et al. 2002; Weirauch and Munro 2009; Patterson and Gaunt 2010), paraphyletic (Hwang and Weirauch 2012), or polyphyletic (de Paula et al. 2005; Schofield and Galvão 2009). This directly impacts our understanding of the number of times blood feeding evolved within the Reduviidae, as well as the ecological circumstances under which this transition occurred. Triatominae were considered a natural group or clade until Schofield (1994) suggested that they may in fact represent a polyphyletic assemblage of multiple blood-feeding lineages derived independently from predatory ancestors. This hypothesis stimulated a number of phylogenetic studies that attempted to clarify origin and relationships of Triatominae. Several analyses were hampered by poor sampling of in-group (Triatominae) and/or out-group (remaining Reduviidae) taxa or were based on insufficient character data, e.g., Weirauch (2008; 162 morphological characters; only four spp. of Triatominae), Weirauch and Munro (2009; 3,300 bp of 16S, 28S, and 18S rDNA; only five spp. of Triatominae), Hypsa et al. (2002; 57 spp. of Triatominae, but mostly based on ~500 bp of 16S rDNA), or de Paula et al. (2005; 57 of Triatominae and 15 out-group spp.; 16S rDNA only).

Two recent analyses are derived from more substantial datasets: Patterson and Gaunt (2010) analyzed one ribosomal nuclear gene (D2 region of 28S rDNA) and four protein-coding mitochondrial loci (~2,700 bp), 45 out-group taxa, and 13 species of Triatominae representing the tribes Bolboderini, Triatomini, and Rhodniini. Despite a substantial amount of missing data, their analyses showed strong support for the monophyly of Triatominae. The dataset of Hwang and Weirauch (2012) comprised 178 spp. of Reduviidae and out-groups and included 13 spp. of Triatominae (Cavernicolini, Rhodniini, and Triatomini) and five molecular markers (rDNA: 16S, 18S, 28S D2, 28S D3–5; nuclear protein coding: wingless; ~3,700 bp). Triatominae were rendered paraphyletic by the reduviine genus *Opisthacidius* Berg that formed the sister group to the *Rhodnius* + *Cavernicola* clade. These current conflicting hypotheses ask for further testing using comprehensive molecular and morphological datasets and should aim on including representatives of all five triatomine tribes.

Even with the question of triatomine monophyly unresolved, recent analyses converge on placing kissing bugs in close relationship with a small number of predatory Reduviidae. Earlier authors proposed either an assemblage comprising Salyavatinae, Sphaeridopinae, and Reduviinae (Usinger 1943), Physoderinae (Lent and Wygodzinsky 1979), Stenopodainae (Clayton 1990; some trees only), Harpactorinae or Reduviinae (Hypsa et al. 2002), or Harpactorinae, Ectrichodiinae, Reduviinae, and Salyavatinae (de Paula et al. 2005) as closest relatives of the Triatominae. Subsequent analyses, based on molecular and morphological data sets,

Fig. 13.24 Lateral view of *Linshcosteus karupus*

found a sister group relationship of large-bodied Reduviinae (different combinations of the genera *Zelurus* Hahn, *Centrogonus* Bergroth, and *Opisthacidius*) with the Triatominae, with the Stenopodainae forming the sister group to that clade (Weirauch 2008; Weirauch and Munro 2009; Patterson and Gaunt 2010; Hwang and Weirauch 2012).

Given that the larger picture of triatomine relationships is only beginning to emerge, it is not surprising that lower-level relationships among kissing bugs are largely obscure. It is unclear if the five tribes are monophyletic and even the monophyly of the genera *Triatoma* and *Rhodnius* is not well established (e.g., Lent and Wygodzinsky 1979; Garcia and Powell 1998; Sainz et al. 2004; de Paula et al. 2005). The Oriental distribution of the *T. rubrofasciata* complex and the morphologically distinctive, genus *Linshcosteus* Distant that is classified within the Triatomini (Hypsa et al. 2002) has long puzzled researchers. Patterson and Gaunt (2010) found (based on a fixed molecular clock model) that Triatominae originated around 107 million years ago, before the Gondwanan breakup. Under this scenario, the disjunct distribution of Triatominae could be attributed to vicariance. Based on a (generally thought to be more reliable) relaxed clock model using fossil calibration points, Hwang and Weirauch (2012) showed Triatominae to be much younger (~32 million years), making dispersal from South America the currently better supported hypothesis.

13.4.2 Geographical Distribution

The vast majority of the triatomines is found only in the New World, although a few species occur in East Asia and the coast of Australia. In the Neotropical and Nearctic regions, species are found between 42°N and 46°S. One species, *Triatoma rubrofasciata*, is tropicopolitan, and additional seven species of *Triatoma* occur in Southern and Southeastern Asia and Northern Australia. *Linshcosteus* (Fig. 13.24) is the only genus restricted to the Old World, specifically to the Indian subcontinent (Galvão et al. 2003). Carcavallo et al. (1998/1999) provided several maps showing the geographical distribution and altitudinal/latitudinal dispersion of all American species of Triatominae.

13.5 Concluding Remarks

More than a century after the discovery of the medical importance of the triatomines, there are still millions of people infected or living at risk of contracting Chagas disease, of which they are vectors. In addition to the classical vectorial transmission of the disease by the direct contact with the contaminated feces of these insects due to their hematophagous habits, alternative ways of transmission emerge as serious public health issues. In some regions of northern Brazil, for example, the ingestion of food contaminated by infected triatomines, especially the locally appreciated *açaí* pulp, is responsible for outbreaks of acute Chagas disease (Nóbrega et al. 2009). Also, due to massive human migration, the disease has been more often reported from non-endemic areas, mainly due to blood transfusions or organ transplants from infected, but not symptomatic, immigrants from Latin America (Kirchhoff 1993). Considering these facts, it becomes clear that studies concerning the taxonomy, evolution, biology, and ecology of triatomine bugs are extremely urgent in order to support the control of a highly neglected disease.

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Chapter 14
Lace Bugs (Tingidae)

Marcus Guidoti, Sara I. Montemayor, and Éric Guilbert

Abstract The members of the Tingidae family are commonly known as "lace bugs" because of the lacelike appearance of their pronotum and hemelytra. The family is distributed worldwide and is constituted by three subfamilies, Tinginae, Cantacaderinae, and Vianaidinae; all of them represented in the Neotropical Region being the last one endemic of this region. There are around 300 genera and 2,500 species in this family, but for the Neotropical Region, there are known approximately 70 genera and 600 species; most of them belong to the subfamily Tinginae. All lace bugs are phytophagous and host specific, with a few exceptions. Among them, there are some that have economic importance as crop pests and others that are useful for controlling harmful weeds in field crops. Herein we characterize and diagnose the family, we mention some of the most relevant aspects of their biology and ecology, and we provide a summary of its taxonomy with some comments about its phylogeny. The economically most relevant species of the Neotropical Region are listed; for all of them, we provide information about their host plants, distributions, and related literature. We also developed a key to the most economically important Neotropical genera.

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14.1 Introduction

Tingidae is a family of small hemimetabolous, plant-feeding bugs usually called "lace bugs" due to the lacelike aspect of their hemelytra and pronotum of most of its species (Schuh and Slater 1995) (Fig. 14.1). They are unique among the Heteroptera because it is the single family with a high specific richness in which all its members are exclusively phytophagous. They are worldwide distributed and comprise about 2,500 species arranged in 300 genera. The family is composed of three subfamilies: Vianaidinae, Cantacaderinae, and Tinginae (Schuh et al. 2006); all of them are represented in the Neotropical Region, Vianaidinae being endemic of this region (though there are fossil records from the Nearctic Region). Approximately 600 species distributed in around 70 genera are currently known for this region.

The size ranges from 2 to 8 mm, and besides their highly complex morphology, they are poorly colored, generally varying in shades of brown. Tingids are characterized by a low flight activity presenting gregarious and sedentary habits and by being generally host specific (though they feed on a great number of botanical families). Adults and nymphs are usually found on the undersides of leaves (with some exceptions), where they feed on the sap of living plants by piercing the epidermis with their very slender stylets. These stylets are protrusive and retractile and can

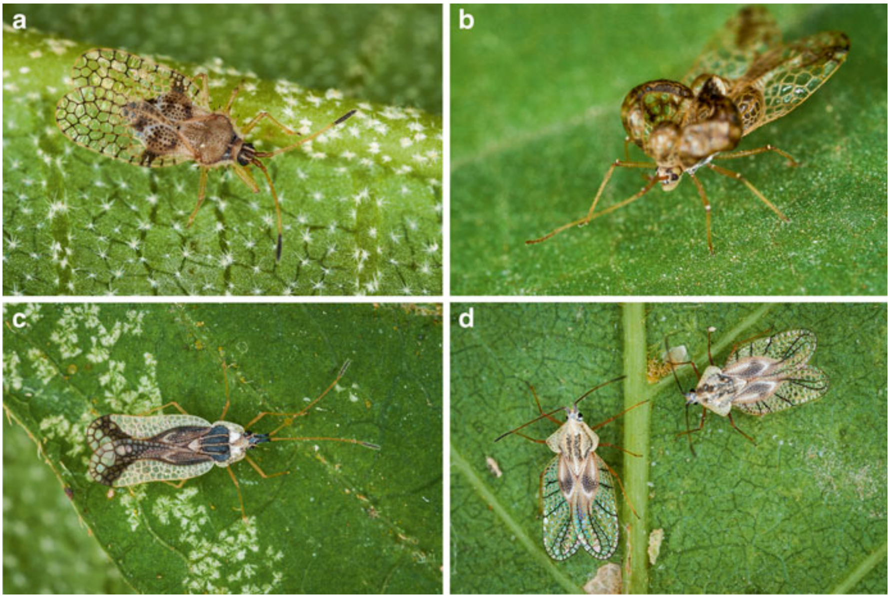

Fig. 14.1 Tingids on the leaves of their host plants: (**a**) *Acanthocheila* sp., (**b**) *Phymacysta* sp., (**c**) *Leptopharsa* sp., and (**d**) *Gargaphia* sp. (Photos by C. D'Haese)

easily penetrate the cellular tissue to extract the sap. Their feeding activities may cause great injury and plasmolysis of the foliage. Many cultivated and wild plants of prime importance in agriculture and horticulture are seriously affected by the feeding activities of these insects (Drake and Ruhoff 1965). The entire life cycle is completed on the same host plant species and on the very same part of the plant in most of the cases.

The members of this family are adapted to a wide range of habitats; some species occur on the ground, associated with the upper parts of the roots or lower parts of stems, some are subterranean, some live in middle height or on the plant canopy, and some non-Neotropical genera induce galls and feed on pollen and moss (Péricart 1983). Some are described as associated with ants, because they were found in ant nests or collected together (Van Doesburg 1977). They are small and difficult to see due to their hyaline structures and then remain poorly known, despite the number of species already described.

14.2 General Characteristics and Diagnosis

Most species are characterized by the lacelike network of areolae (Fig. 14.2a–c), but some species can present punctuations instead (Fig. 14.2d, e). The head is armed with a maximum of nine spines (Fig. 14.3). These spines are extremely relevant for tingid taxonomy, and they are named according to their position. The antennae have four segments as well as the labium which is inserted ventrally in the head. In Vianaidinae, compound eyes can be absent or extremely reduced (Fig. 14.4a), and the ocelli are absent in all but the macropterous forms of this subfamily. The bucculae are well developed (Fig. 14.4b), areolated, and sometimes joined anteriorly. The dorsum and the hemelytra are slightly or heavily punctuated and/or areolated. The pronotum is convex or flat and composed of a collar, a pronotal disk with or without carinae, and a pair of lateral expansions (paranota), with or without a posterior projection covering the scutellum (Fig. 14.2). The paranota and the carinae can be well developed or absent, with different degrees of reflection and numbers of rows of areolae. The collar can be developed forming a hood, which can fully or partially cover the head (Fig. 14.5). The rostral channel forms a groove which is framed with sternal laminae (Fig. 14.6). The dorsal laterotergites are present, but the ventral ones are absent. The abdominal spiracles 2–8 are located on abdominal sterna. The male genitalia are symmetrical; the phallus has some sclerotized eversible structures (Lee 1969). The parameres are usually directed backwards; the ovipositor is laciniate; the connection between the first valvula and first valvifer is lost, as in the Miridae (Schuh and Slater 1995). The spermatheca is absent and the pseudospermathecae present, but it seems to be unrelated with the sperm storage function (Marchini et al. 2010).

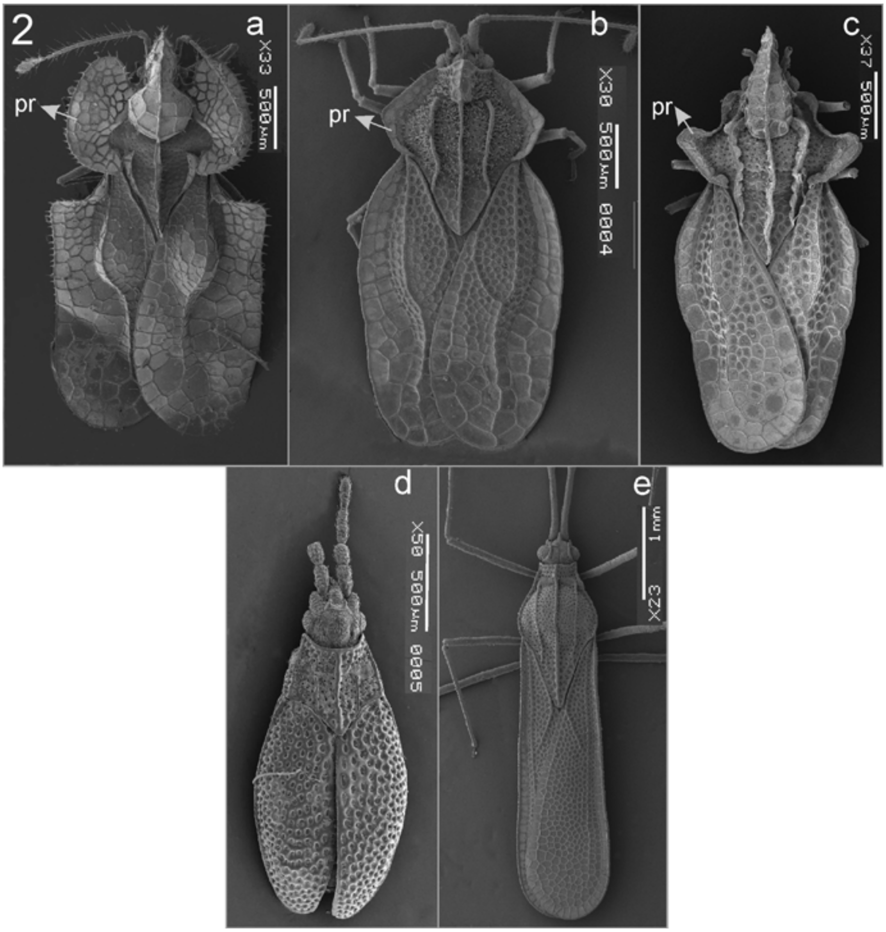

Fig. 14.2 Dorsal habitus, pr: paranota: (**a**) *Corythucha* sp., (**b**) *Gargaphia* sp., (**c**) *Corythaica* sp., (**d**) *Coleopterodes* sp., and (**e**) *Tigava* sp. (Photos by S. Montemayor)

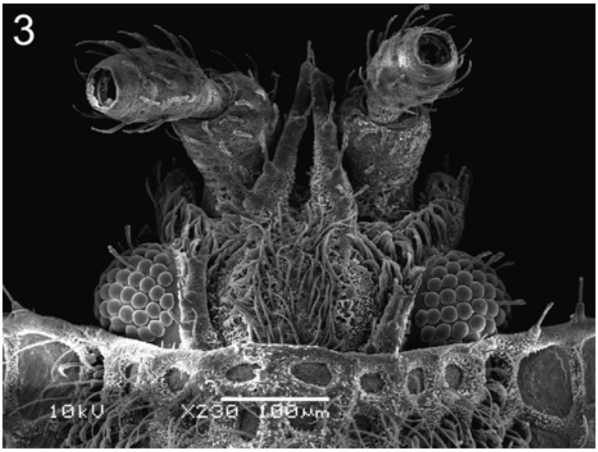

Fig. 14.3 Dorsal view of head of *Tingis americana*, presenting four spines (Photo by M. Guidoti)

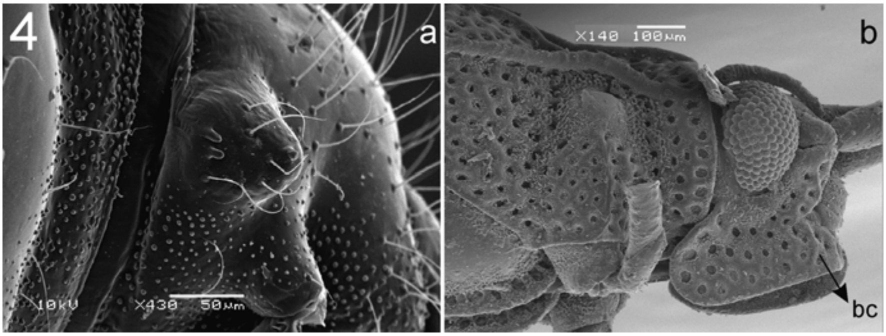

Fig. 14.4 Lateral view of the eye; bc, buccula: (**a**) *Thaumamannia vanderdrifti* Doesburg, 1977 (Vianaidinae), and (**b**) *Tigava* sp. (Photos by M. Guidoti and S. Montemayor)

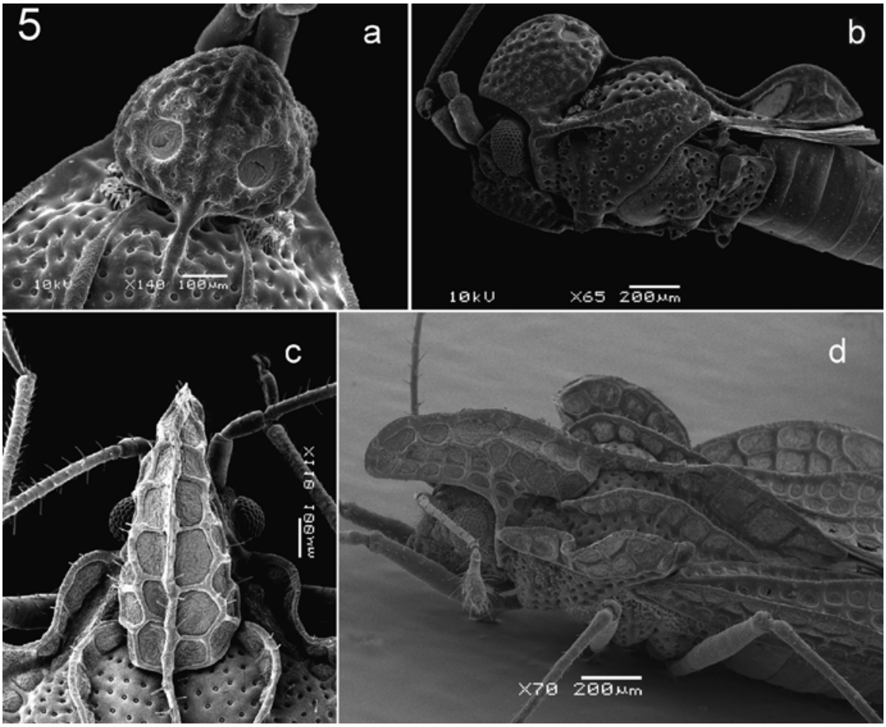

Fig. 14.5 Dorsal and lateral view of the hood: (**a**, **b**) *Sphaerocysta globifera* Stål, (**c**, **d**) *Corythaica* sp. (Photos by M. Guidoti and S. Montemayor)

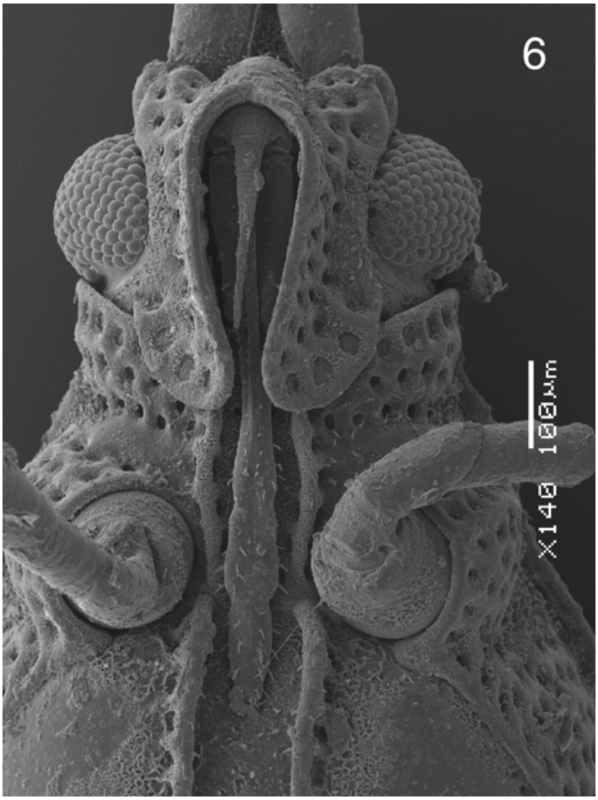

Fig. 14.6 Rostral channel of *Tigava* sp. (Photo by S. Montemayor)

14.3 General Biology and Ecology

14.3.1 Reproduction, Eggs, and Oviposition

The reproductive behavior has been described for very few species [e.g., Kogan 1960 – *Corythaica cyathicollis* (Costa)], and no courtship behavior has been reported. Reproductive parameters, such as fertility and fecundity, could vary in great scale between species, and most of the studies were carried with species from the Palearctic Region (e.g., Stusak 1968) and only a few with Neotropical species (e.g., Cividanes et al. 2004). The development of male and female reproductive organs was described in detail by Eguagie (1976), for *Tingis ampliata* (Herrich-Schaeffer), a non-Neotropical species of a cosmopolitan and probably paraphyletic genera. Generally, there are one or two generations per year (univoltine or bivoltine), although multivoltine species are known (e.g., some *Corythucha* Stål species – Neal and Douglas 1990). The mechanisms that regulate the number of generations in Tingidae are photoperiodic induction of diapause and noncleidoic eggs. The first one was reported in *Corythucha* (Neal et al. 1992) and perhaps is present in genera that overwinter as adults (Neal and Schaefer 2000). The last one was reported for *Stephanitis pyrioides* (Scott) and consists in a dependency on imbibing water from the host for the completion of the embryonic development (Neal and Schaefer 2000). Thus, during development, the absorption of moisture results in an increase in egg size and weight. As a possible consequence of the moisture requirement, seasonal fluctuations in the moisture availability could also affect voltinism (Neal and Schaefer 2000). And a third mechanism present in *Acalypha* Westwood species, a non-Neotropical genus, is to overwinter as nymphs (Pericart 1983).

Eggs have been poorly studied. Their size is around 0.4–0.85 mm (Péricart 1983), and their structure is similar to the one of the other Cimicomorphan families, particularly the Miridae. The posterior part is hemispherical; the sides are slightly compressed laterally and the axis slightly curved; the anterior part is concave and closed by an opercle. The chorion which constitutes the external envelop of the egg is often whitish or clear colored and sometimes brownish at the extremities. The egg shape and structure are quite homogeneous within tingid species.

The oviposition site is variable as there are species that drop their eggs on roots, stems, bud flowers, and/or leafs. The eggs can be inserted on the spongy mesophyll with only the operculum outside the vegetal tissue (endophytic oviposition), partially inserted in the vegetal tissue (pseudo-endophytic oviposition), or placed at the surface of the vegetal tissue (exophytic oviposition). They are usually oviposited in the abaxial surface of the leaf and can be arranged in small or big groups, or they can be isolated, in the midvein or lateral veins or on the leaf surface in several places. Generally, when oviposited on the leaf's veins, they are found on the veins' axillae. The same species can have more than one site for oviposition, so it is difficult to characterize an oviposition strategy at specific level. In some *Gargaphia* Stål species, more than one female oviposits on the same site, forming clusters of eggs from different females. Two Palearctic genera, *Copium* Thunberg and *Paracopium* Distant, are known as gall inducers, and the time and method of laying and fixation of the egg to the corolla are connected with floral cecidogenesis.

14.3.2 Nymph Development and Maternal Care

Most of the species have five instars although four-instar cycle was reported for *Stephanitis rhododendri* Horváth (Johnson 1936). The nymphal morphology varies from simple to highly complex, presenting impressive spinelike structures on the head and on the posterior margins of thoracic and abdominal segments (Fig. 14.7). Some of these cuticular structures present glandular activity, secreting chemical compounds that are related to osmoregulatory functions (Livingstone 1978) and sensorial functions (Aldrich et al. 1991) or have defensive properties (Mason et al. 1991; Scholze 1992). These structures have been described for species of several

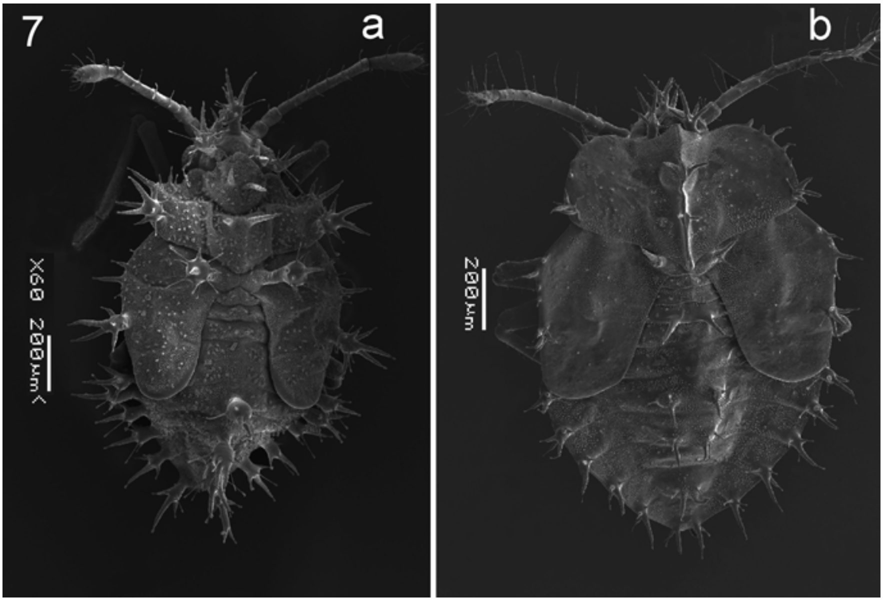

Fig. 14.7 Dorsal habitus of fifth instar nymphs: (**a**) *Corythaica* sp. and (**b**) *Corythucha* sp. (Photos by S Montemayor)

genera and are a reliable source of taxonomic characters (Guilbert 2004a, 2005; Lee 1969). Nymphs also have one pair of abdominal scent glands, which in the subfamilies Tinginae and Cantacaderinae are disposed on the center of the posterior margin of IV and V abdominal segments and in Vianaidinae they are laterally disposed in the posterior margin of the IV segment.

First and second instars are very similar among species; the interspecific differences are more evident from the third instar onwards. Wing pads become conspicuously developed at the fourth or fifth instar, but they are already visible as a small lateral development of the posterior margin of mesonotum in the second instar. Some species belonging to different genera present parental care of nymphs and eggs, sometimes with tricky and aggressive protective behaviors (Tallamy and Denno 1981; Tallamy and Iglay 2004). Very often, nymphs exhibit a gregarious habit; when disturbed and scattered, they quickly group together again. They usually feed and develop to adults on the same plant and even on the same leaf. Some species have all their nymphs fully studied and described, and most of them are from the Palearctic Region (e.g., Livingstone 1976). But only recently (e.g., Guilbert and Montemayor 2010; Guidoti and Barcellos 2013; Montemayor 2009; Montemayor and Dellapé 2010; Montemayor et al. 2011), Neotropical nymphs started to figure in the specialized literature. It has been reported, for example, that an oligophagous Neotropical species, *Tingis americana* Drake, could present different fitness and nymphal development rates in different host plants, due to unequal biological parameters (Moreira et al. 2013). The nymphal morphology is well known for some genera, but little is known about its functionality and evolution (Scholze 1992; Guilbert 2004b). Scholze (1992) studied its functionality, whereas Guilbert (2004b) its evolution and hypothesized nymphal outgrowths as adaptations rather than merely hyperthelic structures. The evolutionary pattern of the development of these structures was studied, and the heterochronic events involved were classified as generally peramorphic, where the next stage (instar) has overdeveloped structures and, in some cases, paedomorphic, where the next stage has underdeveloped structures (Guilbert et al. 2008).

Maternal care of offspring, a rare behavior within Cimicomorpha's families, has been described for three tropical genera, two of them distributed in the Neotropics (*Gargaphia* and *Leptobyrsa* Stål). Chemical compounds were isolated from nymphs and adults, and they seem to play an important role in communication and also as predatory protection strategy (e.g., Aldrich et al. 1991; Mason et al. 1991; Scholze 1992). In *Gargaphia solani* Heidemann, one female takes care of groups of eggs oviposited by several other females until this brood becomes adult (Tallamy and Denno 1981). This probably occurs because the maternal care induces a great survivor rate for the species, but also exposes the female involved in danger. Thus, the smaller is the number of females exposed to predatory activity, the higher is the number of females that could survive (Tallamy 1985). *Leptobyrsa decora* Drake, presents some communal effort to protect the brood (Loeb and Bell 2006), and there are a couple of biological studies where the effect of such maternal care on the brood success through the nymphal development is clear (Melksham 1984). In the Afrotropical species *Compseuta picta* Schouteden, adult females push away the aggressor from the brood and move the wings against the aggressor (Tallamy and Iglay 2004). Besides the mentioned examples, it is expected that more tingids, including Neotropical genera, present these ethological traits.

14.4 Classification and Diversity

The classification of tribes, genera, and species is mostly based on external morphological characters, especially the lacy outgrowths of the pronotum and of the hemelytra. Systematics and taxonomy of the Tingidae are a hard and paradoxal task, due to such particular outgrowths. In contrast to what happens in other families, characters of the genitalia are not frequently used since Drake and Davis (1960) noted that the male genitalia were not of taxonomic value, in spite of Lee's (1969) observation of useful variations of the phallys for the oriental species of the genus *Stephanitis* Stål. Tegumentary structures used to identify the species are not always constant. Today, some genera remain unclearly defined, especially in tropical groups. Drake (with his many coauthors) is the single most prolific author of the group. Drake's latest works were illustrated with habitus views of various tingids, although only few of his works contain aids to identification.

For almost a century, the placement of Piesmatidae within Tingidae has been a case of argument. Tullgren (1918) recognized that Tingidae lacked abdominal trichobothria, whereas Piesmatidae possessed them, and Reuter (1910) classified Piesmatidae and Tingidae together in the superfamily Tingitoidea. Finally, Leston et al. (1954) and Drake and Davis (1960) have clearly shown that these two families are not closely related. Piesmatidae were consistently divorced from the Tingidae and placed in the infraorder Pentatomomorpha. Drake and Davis (1960) proposed the superfamily Miroidea Hahn, based on morphological structures from a global concept, to hold the families Tingidae Laporte and Miridae Hahn, and then systematized the Tingidae into the subfamilies Cantacaderinae Stål, Tinginae Laporte, and Vianaidinae Kormilev. This concept was followed in the catalog of Drake and Ruhoff (1965). Stys and Kerzhner (1975), following Scudder's (1959) conclusion, which was based on a study of the female genitalia of the Heteroptera, treated it as a superfamily including two families: Tingidae (with two subfamilies, Cantacaderinae and Tinginae) and Vianaididae. Owing to its distinct general facies and unique characters, the Vianaidinae were treated as a family by Kormilev (1955) in its original description and later by Scudder (1959), Carayon (1962), and Stys and Kerzhner (1975). Schuh and Stys (1991) and Schuh and Slater (1995) followed Drake and Davis (1960) and Drake and Ruhoff (1965) and treated this taxon as a subfamily of the Tingidae.

On the basis of the first phylogenetic analysis of the Tingidae, Lis (1999) raised the subfamilies Cantacaderinae sensu Drake & Davis and Tinginae sensu Drake & Davis into families: the Cantacaderinae and the Tingidae grouped into the superfamily Tingoidea together with the Vianaididae. Cantacaderinae was divided into two subfamilies, Cantacaderinae and Carldrakeaninae, whereas Phatnomatini sensu Drake & Davis was raised as a subfamily and transferred into the newly raised Tingidae, together with the Tinginae (Tingidae sensu Drake & Davis). In a different phylogenetic analysis, Guilbert (2001) found the Cantacaderinae monophyletic but included into the Tinginae. In a third phylogenetic analysis, including larval characters, Guilbert (2004b) retrieved Cantacaderinae sensu Drake & Davis and Tinginae sensu Drake & Davis. Schuh et al. (2006), on the basis of Lis' study, presented evidences to justify the placement of Vianaidinae as a sister group of Tinginae + Cantacaderinae. Guilbert (2012) validated the groups within Cantacaderinae proposed by Lis (1999), but showed a different relationship within these groups. Guilbert et al. (2014) presented a phylogenetic hypothesis based upon molecular and morphological characters in which Vianaidinae is included in Tingidae, as a sister group of Cantacaderinae + Tinginae, with the Phatnomatini included in Tinginae. In the same contribution, the phylogenetic status of the Tinginae tribes is discussed (Guilbert et al. 2014), as they were in previous contributions (Guilbert 2001, 2004b).

14.5 Economic Importance

14.5.1 Main Genera/Species

Amblystira Stål

This American genus is constituted by 20 species, most of them distributed in the Neotropics. The only member of the genus that has been recorded as a pest is *A. machalana* Van Duzee. It is commonly known as “black lace bug” and feeds on cassava, *Manihot esculenta* Crantz, an important crop of South America. Arias and Belloti (2003) studied the life cycle, behavior, and damage caused by *A. machalana* on cassava. This species is distributed in Venezuela, Colombia, Ecuador, and Peru (Arias and Belloti 2003; Drake and Ruhoff 1965). The only key to species available for the genus is restricted to the South American *Amblystira* (Montemayor 2010a).

Acanthocheila Stål

This is a genus originally constituted by 16 species. Froeschner (1995) reviewed the genus and synonymized some of its species and presented a key to identify them. Currently, it is constituted by seven species distributed in the entire continent, though most of them are known from South and Central America. *Acanthocheila armigera* (Stål) is frequently mentioned because it causes damages in plants of the genera *Nicotiana*, *Ouratea*, and *Pisonia* (Stonedahl et al. 1992; Neal and Schaeffer 2000). It is known from the USA, Mexico, Guatemala, Cuba, El Salvador, Honduras, Haiti, Costa Rica, Panama, Puerto Rico, Trinidad, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and Argentina (Froeschner 1995).

Carvalhotingis Froeschner

Froeschner (1995) described this Neotropical genus to accommodate five species originally described as *Acanthocheila*, and, in this same contribution, he provides a key to species. The two species with economic importance are *C. visenda* (Drake & Hambleton) and *C. hollandi* (Drake). *Carvalhotingis visenda* was the first biological control agent approved for release against cat’s claw creeper *Macfadyena unguis-cati* (L.) (Bignoniaceae) in Australia (Dhileepan et al. 2010), and it has also been released in South Africa (King et al. 2011). Cat’s claw creeper, a climbing woody vine, is native from Mexico through Central America to tropical South America including Trinidad and Tobago. In Australia, cat’s claw creeper is a major environmental weed in coastal Queensland and New South Wales, where it is a major threat to biodiversity in riparian and rain forest communities (Dhileepan et al. 2007). *Carvalhotingis visenda* was originally distributed in Brazil, Peru, and

Argentina. *Carvalhotingis hollandi* (Drake), which is also being used as a biological control agent of *Macfadyena unguis-cati* in South Africa (King et al. 2011), was originally distributed in Brazil, Paraguay, and Argentina.

Corythaica Stål

This is an American genus comprised of 21 species, 14 of which are distributed in the Neotropical Region. Hurd (1945) made a comprehensive review of the genus that includes a key to species, redescriptions of all the species known at that moment, and drawings of them. Montemayor and Melo (2012) made a review of the Argentinean *Corythaica* where they describe new species, provide a key to the Argentinean *Corythaica*, and raised from synonymy *C. passiflorae* (Berg). *Corythaica cyathicollis* Costa is frequently mentioned in the literature as a major pest for several solanaceous crops (Kogan 1960; Neal and Schaefer 2000; Stonedahl et al. 1992). Montemayor and Melo (2012) discussed the identity of *C. cyathicollis* Costa and mentioned that probably almost all the citations of *C. cyathicollis* in the literature do not refer to Costa's species and most likely pertain to *C. monacha* (Stål) or *C. passiflorae* (Montemayor & Melo 2012). Because of this identity confusion, the distribution and host plants of these three species must be reevaluated (Montemayor and Melo 2012).

Corythucha Stål

This is a large genus with more than 75 species. It is widely distributed in the Americas, and it has also been accidentally introduced into Europe and Asia. The great majority of its species are from North America (Montemayor 2009). Despite the number of species in this genus, there is a remarkable uniformity among them. One striking feature of the host plants of this genus is that a large number of trees are included, in contrast to the herbaceous plants which predominate as hosts for the majority of tingids (Hurd 1946). Gibson (1918) made a review of the genus in which he described several species and provided a key to 56 species (among them *C. gossypii* F. and *C. ciliata* Say known from the Neotropical Region and with economic importance); this is the last comprehensive study of the genus. *Corythucha gossypii* is a serious pest of beans and cotton, hence the common name "cotton or bean lace bug." However, it has been reported in another 24 host plants including castor bean (*Ricinus communis* L.) (Herney-Varón et al. 2010) and sunflower (*Helianthus annuus* L.). Cotton lace bug damage can be observed on the plant's foliage, ranging from some leaf stippling from considerable yellowing to bleaching. This can reduce plant vigor, and as a consequence, fruit production can be affected or even prevent fruit from forming when infestations are heavy (Miller and Nagamine 2005). All immature stages of this species are described and illustrated by Lopez-Montes et al. (1982). It is known from almost all the New World. *Corythucha ciliata*, commonly known as the sycamore bug, is a pest of the popular ornamental tree *Platanus* *occidentalis* L., sycamore, and of its hybrids. These trees are frequently used as street-side trees in urban areas. In cases of severe infestations, host trees have been observed defoliated in late summer. Several consecutive years of severe *C. ciliata* damage, combined with other stress factors, may kill the trees. It is suspected that *C. ciliata* may serve as vector of two fungi, *Ceratocystis fimbriata* Hell. et Halsted forma *specialis platani* Walter and *Apiognomonia* (= *Gnomonia*) *veneta* (Sacc. and Speg) (Ruiting et al. 2009). It is believed that the pest came from North America, from where it has spread throughout Europe and parts of Asia (Õszi et al. 2005). In the Neotropical Region, it has been only reported for Chile (Prado 1990).

Dictyla Stål

This genus is constituted by over 60 species distributed worldwide. There are 17 known species from America and 13 from the Neotropical Region. Brailovsky and Torres (1986) provided a redescription of the genus and mentioned its possible Neotropical origin. The most mentioned species in the literature is *D. monotropidia* (Stål), a Neotropical species that has been frequently reported on *Cordia* spp. (Drake and Ruhoff 1965) as well as on cotton in Argentina (Fenton 1934) and on orchids from Mexico to the boarder of Texas (Swezey 1945; Drake and Ruhoff 1965; Neal and Schaefer 2000). The feeding activities of this insect damage the leaves that fall prematurely causing low flowering and fruiting and a developmental delay of the plants (Arguedas and Fallas 1993). There are some studies about the biology of the species (e.g., Fallas et al. 1993; Martínez et al. 2012). *Dictyla monotropidia* is known from Mexico, Cuba, Costa Rica, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Panama, Puerto Rico, Trinidad, Venezuela, Colombia, Peru, Brazil, Bolivia, Paraguay, and Argentina. Up to now, the known host plants are *Cordia alliodora* (Ruiz & Pav.) Cham., *C. curassavica* (Jacq.) Roem. & Schult., *C. gerascanthus* L., *C. tomentosa* Cham. & Schltdl., *C. trichotoma* (Vell.) Arráb. ex Steud, and *Gossypium* sp. Guilbert and Montemayor (2010) provided a description and illustrations of the fifth instar as well as some comments on the fourth and third instars. There is no key to recognize the species of *Dictyla*, and because of the great number of species that constitute it and its morphological diversity, it is not easy to properly identify them.

Gargaphia Stål

This is a large American genus constituted by over 50 species, most of them distributed in the Neotropical Region. The interrupted rostral channel at meso-metasternal suture with transverse laminae converging medially is a diagnostic character of the genus. It includes several species which are economically important as plant feeders. Drake (1917) developed a key for the Nearctic species of *Gargaphia*. Some years later, Gibson (1919a) made a review of the genus when it was constituted by 25 species and provided a key to 16 of them (none of the Neotropical species with economic importance were included), and this was the last comprehensive study of the genus. The Neotropical species most mentioned as pests are *G. lunulata* (Mayr), *G. sanchezi* Froeschner, and *G. torresi* Costa Lima. *Gargaphia lunulata* feeds on many important South American plants from several families: Euphorbiaceae (*Euphorbia* sp., *Manihot* sp., *Ricinus* sp.), Leguminosae [*Cassia* sp., *Glycine max* (L.), *Phaseolus* spp.], and Malvaceae (*Gossypium* sp., *Hibiscus* sp., and *Urena* sp.) (Stonedahl et al. 1992; Neal and Schaefer 2000). It is also a pest of *Passiflora caerulea* L., a climbing plant with ornamental, medic, and alimentary interest (Ajmat et al. 2003). It is distributed in Colombia, Brazil, Paraguay, Argentina, and Uruguay. *Gargaphia sanchezi* is known from Colombia and attacks beans, *Phaseolus vulgaris* L. The biology of this species was studied by Schoonhoven et al. (1975), and usually the populations of *G. sanchezi* are very high, causing great damage on the plants. Finally, *G. torresi* feeds on several economically important plants such as cotton, sweet potato, bean, corn, and sunflower as well as other plants (*Canavalia* sp., *Gossypium* sp., *Ipomoea* sp., *Helianthus* sp., *Hibiscus* sp., *Parthenium* sp., *Phaseolus*, *Sida* sp., *Triumfetta* sp., *Xanthium* sp., and *Zea* sp.). It has some natural enemies such as *Xylocoris* sp. (Hemiptera: Anthocoridae), *Franklinothrips* sp. (Thysanoptera: Aeolothripidae), and *Bochartia* sp. (Acari: Erythraeidae) (Silva and Barbosa 1986). *Gargaphia torresi* is known from Brazil, Bolivia, Paraguay, and Argentina. The two most important studies that have been performed on the biology of *G. torresi* are related to the effects of temperature on their development, fecundity, and longevity (Domingues-da-Silva 2004) and to different aspects of its life cycle (Arce-de-Hamity et al. 2006).

Leptobyrsa Stål

This genus was described by Stål for *Tingis steini* Stål, and later Champion (1897) redefined the genus to include five more Central American species. Since Champion's modification, 11 more species were added. Drake and Poor (1937) reviewed the genus, and from the 17 species that constituted the genus, only eight were left, all of them Neotropical. Unfortunately, there is no key for the genus. Among the *Leptobyrsa* spp., *L. decora* Drake has importance as a control agent of the weed *Lantana camara* L. to which it causes severe defoliation (Day and Zalucki 2009). Harley and Kassulke (1971) studied the life history of this species as a potential biological control agent of *L. camara*. Melksham (1984) compared the oviposition and maternal care of two populations from Colombia and Peru, and Thomas and Ellison (2000) listed the countries where *L. decora* has been released as a biocontrol agent. This species was described by Drake from Colombia and Ecuador, and later it was reported from Peru (Harley and Kassulke 1971) and the Galapagos Islands (Henry and Wilson 2004). *Leptobyrsa decora* has been introduced widely around the world, including Australia, the Cook Islands, Fiji, Guam, Ghana, Hawaii, Palau, South Africa, and Zambia, to help control *Lantana camara* L. (Thomas and Ellison 2000; Henry and Wilson 2004). A photograph of this species is also available in Henry and Wilson (2004).

Leptocysta Stål

This genus was erected to accommodate *L. sexnebulosa* (Stål), first described in the genus *Tingis*. Currently, the genus includes six species, all distributed in South America. Monte (1946) provided the first key for the genus, when it was constituted by three species, and excellent drawings of these species. Several years later, Montemayor (2010b) provided another revision of the genus with the description of new species and a key to all the currently known species. The only species mentioned feeding on economically important plants is *L. sexnebulosa* (Stonedahl et al. 1992), and the host plants are *Antennaria* sp., *Ipomoea batatas*, *Mikania* sp., and *Parthenium*, and *Vernonia* sp. *Leptocysta sexnebulosa* is distributed in Venezuela, Colombia, Peru, Brazil, Paraguay, and Argentina (Montemayor 2010b). For the remaining species of the genus, there are no records of host plants.

Leptodictya Stål

This genus is confined to the Americas; it is constituted by more than 50 species, most of them distributed in the Neotropical Region. The *Leptodictya* mentioned as pest is *L. tabida* (Herrich-Schaeffer), commonly known as the sugarcane lace bug because it feeds on sugarcane (*Saccharum* spp. hybrids) as well as other species of Poaceae (Setamou et al. 2005). High populations of *L. tabida* reduce plant vigor, cause leaves to senesce prematurely, and reduce the total area of photosynthesis (Neal and Schaefer 2000). It is known from the USA (Florida, Hawaii, and Texas), Mexico, Cuba, Costa Rica, El Salvador, Guatemala, Nicaragua, Panama, and Venezuela (Chang 1986). This author provided a good review with respect to the life cycle, bionomics, damage, and control along with a morphological description of adults and nymphs of *L. tabida*.

Leptopharsa Stål

This is a very large and diverse genus highly variable in its morphology. Through the years, several genera have been described on the base of species originally described as *Leptopharsa*. It is constituted by over 100 species, most of them from America, except for four African ones and two Australian ones. Most of its members are distributed in the Neotropical Region. There are two Neotropical species well known for their economic importance: *L. gibbicarina* Froeschner and *L. heveae* Drake & Poor. Adults and nymphs of *L. gibbicarina* cause important yield losses in the crops of the African oil palm (*Elaeis guineensis* Jacquin). The lesions caused by the feeding activities of this tingid allow the infestation of the plant by a fungi complex that causes a severe disease called *Pestalotiopsis* or gray leaf blight (Escalante et al. 2010). *Leptopharsa gibbicarina* is distributed in Colombia. The original description (Froeschner 1976) provides very good drawings of the species. The rubber tree lace bug, *L. heveae*, is known from Brazil, and it was described as a pest of *Hevea brasiliensis* Muell. Arg. known as the Pará rubber tree, sharinga tree, or, most commonly, the rubber tree. This tree is of major economic importance because the milky latex extracted from it is the primary source of natural rubber. *Leptopharsa heveae* occurs in high populations in rubber tree plantations, and it is a limiting factor in rubber production due to the loss of photosynthetic tissue (Santos and De-Freitas 2008). The control of the pest has been made mainly with chemical products, which cause environmental contamination. The alternative would be the use of biological control agents; however, information about *L. heveae* natural enemies is scarce. The entomopathogenic fungus Sporothrix insectorum (Hoog & Evans) (Neal and Schaeffer 2000) and the parasitoid *Erythmelus tingitiphagus* (Soares) have been found naturally on eggs of the rubber tree lace bug (Santos and De-Freitas 2008).

Pleseobyrsa Drake & Poor

This is a genus that belongs to the tribe Tingini and was erected to place four species, three previously assigned to the genus *Leptobyrsa* Stål and a new species. After the description of *Pleseobyrsa*, five other species were described for the genus. Until 1969, *Pleseobyrsa* was constituted by nine species, but Froeschner (1969) described a new genus belonging to the tribe Litadeini Drake and Ruhoff, *Stragulotingis*, to place two *Pleseobyrsa* species. In a later publication, Froeschner transferred two other species from *Pleseobyrsa* to *Stragulotingis*, described a new *Pleseobyrsa*, and provided a key to the species of both genera (Froeschner 1991). Some years later, another *Pleseobyrsa* was described, and in this contribution, an updated key to the species of *Pleseobyrsa* was provided as well as illustrations and photographs of adult and fifth nymph of *P. persea* (Montemayor et al. 2011). The genus includes currently seven species, and three feed on avocado tree, causing damage: *P. boliviana* (Drake & Poor), *P. chiriquensis* (Champion), and *P. persea. Pleseobyrsa boliviana* is known from Bolivia; *P. chiriquensis* from Costa Rica, Panama, Venezuela, and Colombia; and *P. persea* from Costa Rica.

Pseudacysta Blatchley

This genus only includes *P. perseae* (Heidemann), first described as *Acysta* Champion, and is commonly known as the avocado bug. As its vernacular name indicates, it is harmful for *Persea americana* P. Miller (avocado). *Pseudacysta persea* destroys leaf cells (Moznette 1922) and causes chlorosis and browning (Medina-Gaud et al. 1991). Other host plants mentioned in the literature are *Comphora officinalis*, *Persea carolinensis*, and *Persea gratissima* (Heidemann 1908). In the original description of the species, egg and nymphs were also described, and drawings of the adult, fifth nymphal instar, and eggs were provided. Hurd (1946) redescribed the genus and discussed some other aspects such as resemblance with *Acysta* and distribution. The known distribution of *P. perseae* includes the USA, Mexico, Cuba, Dominican Republic, Guatemala, Jamaica, Puerto Rico, St. Lucia, St. Thomas, St. John, St. Croix, French Guiana, and Venezuela (Humeres et al. 2009).

Stephanitis Stål

This is a large genus constituted by around 60 species. Hórvath (1912) divided it into four subgenera: *Stephanitis* Stål, *Menodora* Hórvath, *Norba* Hórvath, and *Omoplax* Hórvath; only the first one is present in America (Hurd 1946). One of the species with economic importance is *S. pyrioides* (Scott), an important pest of azaleas (*Rhododendron* spp.). The azalea lace bug has become of increasing importance as azaleas have been more and more popular as ornamentals. Its origin is thought to be Japan, from where it was first described, and it has been accidentally introduced in several countries. The azalea lace bug is considered one of the most important problems affecting azaleas since its introduction (Shakunthala and Braman 2012). Illustrations of *S. pyrioides* are available at Dickerson and Weiss (1917), Weiss and Headlee (1918), Shen et al. (1985), and Gomez-Menor (1954). Shakunthala and Braman (2012) provided an excellent review of all the information available related to the azalea lace bug.

Teleonemia Costa

Teleonemia Costa is a taxonomically complex genus with a high interspecific variation. It is constituted by over 80 species distributed worldwide. *Teleonemia elata* Drake, *T. harleyi* Froeschner, *T. prolixa* (Stål), and *T. scrupulosa* Stål are Neotropical important species because they feed on *Lantana camara* (Winder & Harley 1983) and therefore have been used for the biocontrol of this weed which is considered to be among the world's ten worst invasive weeds. *Teleonemia elata* has been released in Australia, Cook Islands, South Africa, Uganda, and Zambia; *T. harleyi* and *T. prolixa* in Australia; and *T. scrupulosa* in Ascension Island, Australia, Fiji, Ghana, Guam, Hawaii, India, Indonesia, Kenya, Madagascar, Micronesia, New Caledonia, Niue, Northern Mariana Islands, Palau, Papua New Guinea, Samoa, Solomon Islands, South Africa, St. Helena, Tanzania, Tonga, Uganda, Vanuatu, Zambia, Zanzibar, and Zimbabwe (Thomas and Ellison 2000). Photographs of adults and nymphs of *T. elata* as well as comments on the species are provided by Harley and Kassulke (1971). The original distribution of this species is Brazil, Chile, Paraguay, and Peru (Drake and Ruhoff 1965). Harley and Kassulke (1973) provided SEM photographs of adults, fifth instar, and egg of *T. harleyi*. This species is distributed in Trinidad. *Teleonemia prolixa* has not only been considered for the biological control of *L. lantana* but also for *Mikania micrantha* Kunth, a Neotropical vine that is causing great damage to crops of tea, teak, rubber, oil palm, and coconut in Southeast Asia (Cock 1982). It is distributed in the Neotropical Region in Guatemala, Jamaica, Panama, Surinam, Trinidad and Tobago, British Guiana, Venezuela, Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, and Argentina. *Teleonemia scrupulosa* eggs, nymphs, and adults are described and illustrated by Roonwal (1952), and more recently, SEM photographs and redescriptions of the nymphs were provided (Guidoti and Barcellos 2013). It is distributed in the Neotropical Region in the following countries: Cuba, Costa Rica, Guatemala, Haiti, Jamaica, Netherlands Antilles (Aruba, Curacao, Klein Bonaire, Bonaire), Panama, Trinidad, Windward Islands (Grenada, St. Vincent), French Guiana, British Guiana, Venezuela, Peru, Brazil, Colombia, and Paraguay.

Vatiga Drake & Hambleton

The species of the genus *Vatiga* are native to the Neotropics and exhibit a decided preference for plants of the genus *Manihot* Miller, mainly *Manihot esculenta* Crantz, commonly known as cassava and one of the most important crops in Africa, Central and South America, and Asia. Froeschner (1993) reviewed the genus, provided a key to species, synonymized some species, and elevated to species status a subspecies, so as a result of Froeschner's study, the genus is currently constituted by five species. *Vatiga illudens* (Drake) is one of the species most frequently mentioned in the literature and also most frequently misidentified. It is mentioned from Brazil, Colombia, Cuba, Dominican Republic, Ecuador, Guyana, Haiti, Jamaica, Lesser Antilles, Puerto Rico, Reunion Island, Trinidad and Tobago, USA, and Venezuela. Oliveira et al. (2001) studied the biology of this species in experimental conditions, and Fialho et al. (2009) evaluated the economic damage caused in cassava root and foliage yield. *Vatiga manihotae* (Drake) is the second most mentioned species, and it is also the most widely distributed. According to Froeschner (1993), it is known from Cuba, Trinidad, Venezuela, Colombia, Peru, Brazil, Paraguay, and Argentina. The other species of the genus have more restricted distributions, such as *V. cassiae* (Drake & Hambleton), only known from Brazil; *V. pauxilla* (Drake & Poor), from Argentina; and *V. varianta* (Drake), restricted to Brazil and Colombia.

Phatnoma Fieber

This genus occurs in several geographic regions of the world. Most of the 27 species of the genus are similar in structure and intraspecific variability and therefore are difficult to separate (Froeschner 1996). For this genus, only a very outdated partial key exists (Gibson 1919b). *Phatnoma* is distributed in South and Central America, Africa, Asia, and Oceania. For the Neotropics, the species that has been reported feeding on plants with economic importance is *P. marmorata* Champion. It feeds on cacao and pineapple, and it is distributed in Costa Rica, Honduras, Panama, Trinidad, Brazil, and Ecuador. Its fifth nymph has been described by Guilbert (2005); however, very little is known about its biology.

14.5.2 Key to the Most Economically Important Neotropical Genera

The key below is valid for the genera of economic importance, and it may lead to erroneous results if used for other genera.

1. Seven cephalic spines, anterolateral paranotal angle projecting as a distinct angle or spiniform process .... *Phatnoma* Fieber
– Less than seven cephalic spines, paranota otherwise 2
2. Hood absent or scarcely developed 3
– Hood well developed 10
3. Radio-cubitus vein "C" shaped, paranota folded over pronotum .... *Dictyla* Stål
– Radio-cubitus vein not "C" shaped, paranota not folded over pronotum 4
4. Paranota lacking or poorly developed 5
– Paranota well developed 6
5. None or two rudimentary cephalic spines present (occipital pair), paranota represented by a small pale earlike appendage at each lateral angle, discoidal area not closed behind .... *Pseudacysta* Blatchley
– Two cephalic spines present (occipital pair), paranota absent or very slender carina like, discoidal area closed behind .... *Amblystira* Stål
6. Paranota projected forward, much broader anteriorly .... *Pleseobyrsa* Drake & Poor
– Paranota not projected forward, same width in all its length or posteriorly broader 7
7. Paranota armed with spines, lateral carinae absent or only posteriorly developed 8
– Paranota without spines, lateral carinae fully developed 9
8. Without occipital spines, paranota armed with 7–10 long, stout spines .... *Carvalhotingis* Froeschner
– With occipital spines, paranota armed with 5–10 long, stout spines .... *Acanthocheila* Stål
9. Generally five cephalic spines (sometimes less), elytra broadening from base, discoidal area not surpassing middle of hemelytra .... *Leptopharsa* Stål
– Between two and five cephalic spines; elytra elongated, parallel margined; discoidal area generally surpassing middle of hemelytra .... *Teleonemia* Costa
10. Hood not surpassing length of head 11
– Hood surpassing length of head 14
11. Mesosternal rostral laminae deeply constricted at mesosternum .... *Vatiga* Drake & Hambleton
– Mesosternal rostral laminae subparallel 12
12. Rostral channel interrupted at meso-metasternal suture by the metasternal laminae that converge and contact to each other .... *Gargaphia* Stål
– Rostral channel not interrupted at meso-metasternal suture 13
13. Hood tectiform shaped, paranota folded over pronotum, posterior process fully developed, elytra and paranota .... *Leptodictya* Stål
– Hood globose or subglobose, paranota not folded, projected forward in front, posterior process abbreviated, elytra and paranota armed with hairs and/or spines .... *Leptobyrsa* Stål
14. Paranota not projected forward 15
– Paranota projected forward 16

15. Hood gradually narrowing toward apex, tip surpassing antennal segment I; paranota with basal folds wider at the callus .... *Corythaica* Stål
– Hood tectiform, not surpassing antennal segment I; paranota without basal fold, produced evenly .... *Leptopharsa* Stål
16. Hood compress, slightly wider backwards, narrow through all its length; discoidal area not raised, surpassing middle of hemelytra .... *Leptocysta* Stål
– Hood globose or subglobose, much wider backwards, narrower anteriorly; discoidal area raised, not surpassing middle of hemelytra 17
17. Hemelytra rectangular shaped abruptly widened at base, broadest anteriorly, margins parallel or slightly concave .... *Corythucha* Stål
– Hemelytra gradually widening toward apex, broadest apically, margins rounded .... *Stephanitis* Stål

14.6 Concluding Remarks

Tingidae are exclusive plant feeders and usually monophagous, features that make them particularly interesting from an economical point of view. However, there is a noticeable lack of information about this group of insects. The economic importance of lace bugs will continue increasing as species emigrate (e.g., as concealed eggs) and as minor crops gain importance and expand to serve a burgeoning world population (Neal and Schaefer 2000).

Among the Neotropical lace bugs are some potential pests for different economically important crops, though usually only large populations cause serious damage. It is not easy to control and manage lace bug populations because of their different reproductive strategies (e.g., oviposition strategies), the annual number of generations, and the habit of living in the underside of the leaf. The ecology and behavior of most of the species remain unknown, and the knowledge of these different aspects of their biology is fundamental for the establishment of management strategies of their populations. Another little known aspect of these complex insects is their chemical communication, which seems to play an important role in intraspecific interactions, particularly between females and offspring. Predator and parasitoid information are scarce, and it could be useful when establishing control strategies for Tingidae populations.

The taxonomy of Tingidae is mostly based on external morphological characters which exhibit a high diversity of shapes. As such, relationships within Tingidae subfamilies and tribes are far from known. Suprageneric taxa have been currently discussed without highly supported hypothesis proposed so far. Immature forms seem to present very important characters that should be more explored in a taxonomic and phylogenetic framework. Morphological studies on unexplored structures could reveal important source of information. The tingid taxonomy and systematics are still in need of further studies to improve our knowledge on biological, ecological, ethological, and evolutionary questions.

Behavior and ecological parameters are the keys to understand economic problems raised by tingid species. As such, they will help provide the adequate solution. Considering that this chapter focused on Neotropical tingids, a more comprehensive work should be done since the last worldwide contribution was published 13 years ago (Neal and Schaeffer 2000).

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Part VII
Infraorder Pentatomomorpha

Chapter 15
Flat Bugs (Aradidae)

Maria del C. Coscarón and Eugenia F. Contreras

Abstract Aradidae or “flat bugs” have a flattened shape and somber colors well adapted for a lifestyle on or under the bark of dead trees. The pronounced elongation of the stylets is a remarkable adaptation to exploit juices of fungi during feeding. For the Neotropical Region, 80 genera and 509 species are recognized. General characteristics, diagnosis, biology, and ecology of Neotropical aradids are presented.

15.1 Introduction

Aradids are commonly known as “flat bugs.” Their flattened form and somber colors are adaptations for a life on or under the bark of dead trees. They have succeeded in utilizing the mycelia of various fungi. This ability has been accomplished by a remarkable elongation of the stylets, which lie in a vast coil within the head of the bug when it is not feeding and extend for a long distance into the slender threads of the fungus when it is feeding. Many flat bugs are mycophagous, as suggested by the fact that the majority of the species live either under the bark of decaying trees or under bark chips, twigs, or debris on the floor of moist forests; probably others feed on the sap of dying or living trees. Macropterous species tend to live on a restricted number of host trees; some species feed on the phloem, cambium, and xylem of living trees and may affect the growth of these trees. Some aradids may be associated with termites and occasionally they are observed infected by mites.

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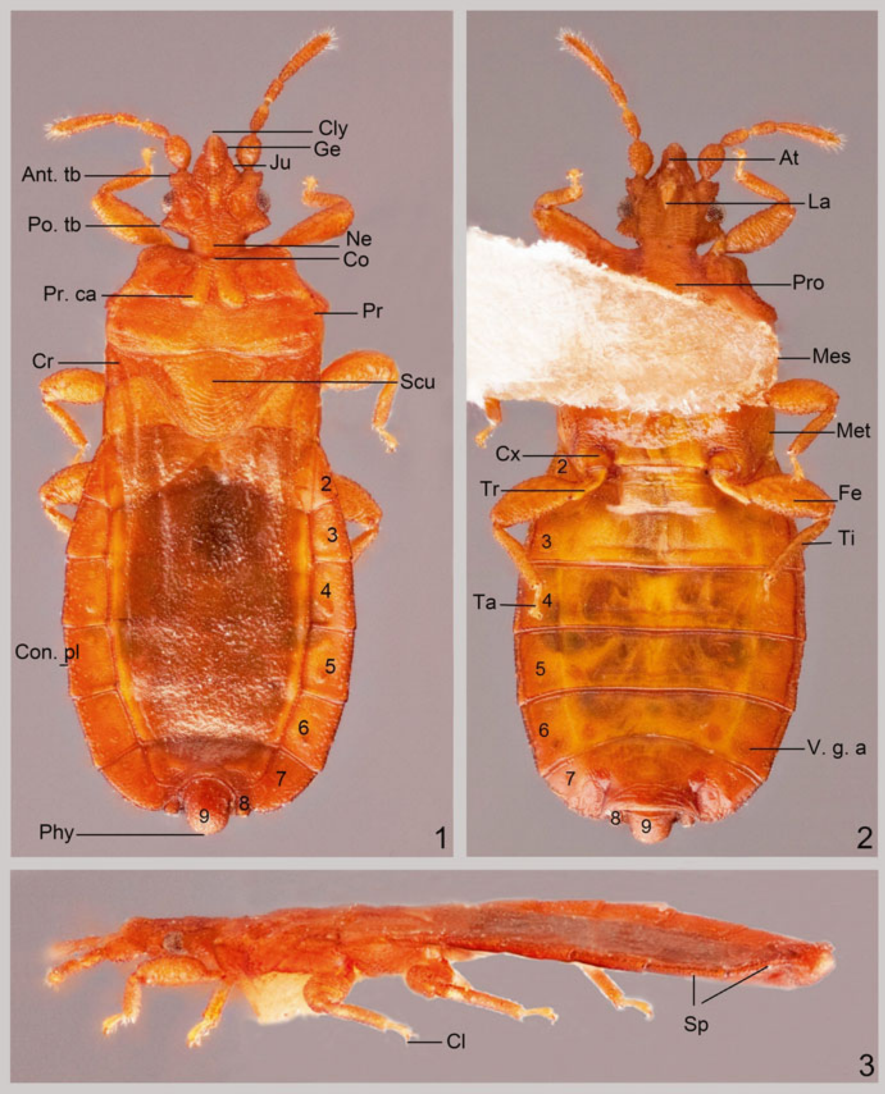

Plate 15.1 *Aneurus patriciae* Picchi. Fig. 1, dorsal view: Ant. tb: antenniferous tubercles; Cly, clypeus; Co, collar; Con. pl, connexival plate; Cr, corium; Ge, gena; Ju, jugum; Ne, neck; Phy, pygophore; Po. tb, postocular tubercles; Pr, pronotum; Pr. ca, pronotal callosities; Scu, scutellum. Fig. 2, ventral view: At, atrium; Cx, coxa; Fe, femur; La, labium; Mes, mesosternum; Met, metasternum; Pro, prosternum; Ta, tarsus; Ti, tibia; Tr, trochanter; V.g.a, ventral glabrous areas. Fig. 3, lateral view: Cl, claws; Sp, spiracles

Aradids are generally somber in color, black or brown, and elliptical, oval, or rectangular in shape. They range from 3 to 11 mm in length. Many tropical species are wingless and the dorsal surface is frequently appearing granular or rugose.

The family Aradidae exhibits a variety of wing development, macroptery, brachyptery, and aptery. There is camouflage, plus a rough surface that holds layers of dirt and debris which are important antipredator survival adaptations in these litter dwelling species.

Many species never go out of the bark, spending their whole life under it, whereas some tropical species have flights of dispersion during the spring.

15.2 General Characteristics and Diagnosis

Flat bugs are easily identified by bearing mandibular and maxillary stylets extremely elongated and coiled. Ocelli are absent, labia usually short and stout with four distinct segments, trochanters sometimes fused with femora, and tarsi bisegmented. Figures 1, 2, and 3 (dorsal, lateral, and ventral views, respectively) show the main characters used for the description of species.

The head (Figs. 4, 5, and 6) is of the prognathous type, and it is highly specialized to accommodate the mycetophagous sucking mouth parts; mouth parts have a general similar pattern among species, but they differ strikingly in degree of development of the various parts. The insertion of the rostrum is distinctive for each subfamily. They have elongated maxillary and mandibular stylets that are coiled within the head. In the anterior part of the head (clypeus), the bugs have coiled setae composed of mandibular and maxillary stylets. In the resting position, both the stylets are coiled up to form a compact double spiral (Weber 1930), and when the bug is feeding, the length of the uncoiled stylets may be as much as five to six times that of the insect body length.

The thorax (Fig. 1) bears the wings which are well developed and are diverse in development and venation. The wings may fall off, and this character is usually dimorphic, females usually being brachypterous and males macropterous; occasionally, females might be in both forms, and rarely males are dimorphic (Schuh and Slater 1995). Wing reduction is known to occur on half of the known species, and it can be extreme, leaving no trace of wings. Miller (1938) recognized that the apterous tropical flat bug that was considered a nymph was, in fact, an adult. Micropterous forms are not easily distinguishable from truly apterous forms; the latter shows more or less extreme reduction and fusions of the thoracic sclerites, especially the scutellum, and may also be covered with coarse incrustations that almost obscure the body texture and shape. Monteith (1969) demonstrated that forms that were considered new genera were in fact macropterous and apterous morphs of the same species.

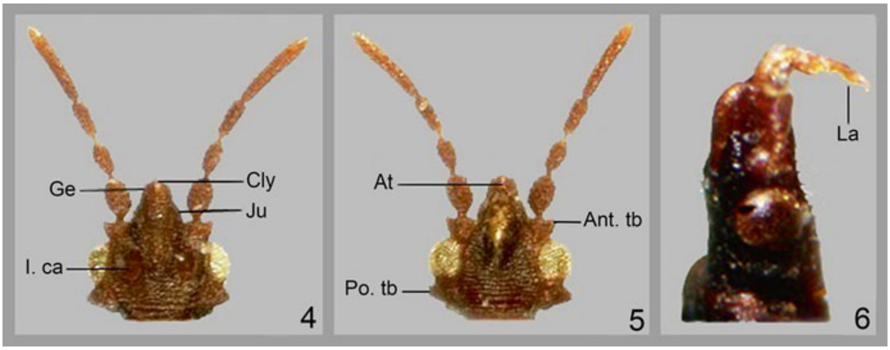

Plate 15.2 *Aneurus mexicanus* Kormilev. Fig. 4, head dorsal view: Cly, clypeus; Ge, gena; Ju, jugum; I. ca, interocular callosities. Fig. 5, head ventral view: Ant. tb, antenniferous tubercle; At, atrium; Po. tb, postocular tubercles. *Isodermus gayi* Erichson. Fig. 6, head lateral view: La, labium

The metathoracic scent glands are well developed (Carayon 1955), and the canals and evaporating areas are variously and often strikingly developed. The dorsal scent glands may persist in adults.

The legs in Aradidae vary considerably. The trochanters are commonly distinct from the femora; in some subfamilies those of the front and middle legs are fused with scarcely a trace of the dividing suture; in other cases, trochanters are completely fused. The front tibiae have an apical comb on the inner side; in a few groups this structure is preapical, spine-like, and directed inward at right angles to the main axis of the tibia. Tarsi are typically two segmented. Arolia occur in most subfamilies and in a majority of the genera of the world. The legs are variously modified for stridulation, the femora with scrapers, and the tibiae with files.

The abdomen (Figs. 1 and 2) shows the connexivum as a part of the tergum, since the spiracles are considered to mark the lower limit of the tergum. The connexiva of the first segment or the lateral parts of the first tergite are absent. The spiracles are clearly recognizable from the 2nd to the 8th segments in both sexes in all subfamilies.

The female genital segments (Fig. 7) begin with the 7th segment. The median longitudinal split of the 7th sternum is common to all subfamilies, except Aneurinae. Male genital segments (Fig. 8) begin with the 8th segment.

Stridulatory structures are present in the ventral surface of the abdomen. These take the form of a comb on the hind margin of the 4th segment on either side, a file-like curved elevation on the 3rd segment, and long longitudinal knife-like carinae on the 4th segment. The file or comb-like structures are opposed by carinae on the femora and knife-like surfaces of the hind tibiae.

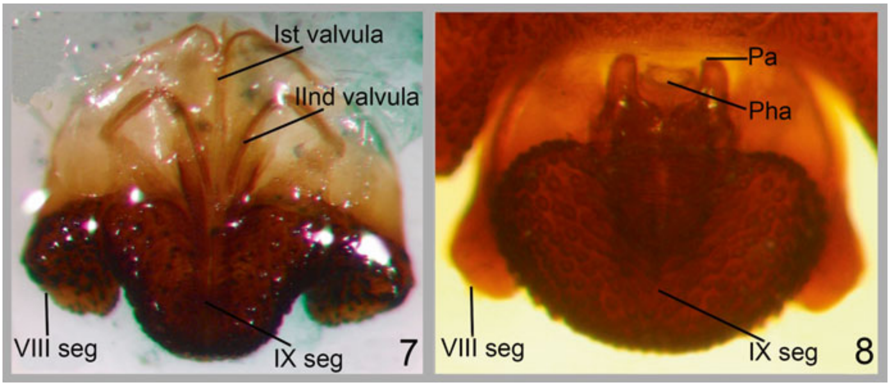

Plate 15.3 *Neuroctenus subandinus* Kormilev. Fig. 7, female genitalia: Ist valvula, first valvula; IInd valvula, second valvula; VIII seg, eighth segment; IX seg, ninth segment. Fig. 8, male genitalia: Pa, paramere; Pha, phallus; VIII seg, eighth segment; IX seg, ninth segment

15.3 General Biology and Ecology

Flat bugs are inhabitants of the wet rainforest floor, where they find the food sources (fungi) to feed on; the loss of wings is due to the no need for dispersal flights. However, the macropterous species, which live subcortically feeding on ephemerous food sources, are believed to use wings for a dispersal flight to colonize new wood sources. Several bark flat bugs species are known to live on small-diameter branches (Heiss and Péricart 2007) where fungi are generally more diversified (Heilmann-Clausen and Christensen 2004; Nordén et al. 2004).

Most of the available information on their biology and ecology is based on occasional observations (Heiss and Péricart 2007). Gossner et al. (2007) studied habitat requirements (e.g., habitat continuity, host and resource availability, and shade tolerance). According to Marchal et al. (2012), aradids vary in their habitat preferences and can be sensitive to different types of exploitations. Some species need large senescent trees, while others depend on small fresh deadwood and, therefore, are more sensitive to fuelwood harvesting.

Flat bugs sometimes live with termites in nests (Hendee 1933; Kormilev and Froeschner 1987; Usinger 1936). Aradids have been reported living in nest of birds (Vásárhelyi 1979) and rodents (Blatchley 1934) and in galleries of wood-boring beetles. According to Usinger and Matsuda (1959), they hibernate under any bark that is loose, and many records are not necessarily related to their feeding habits.

McClure (1932) reported prenatal care and stated that females leave the egg mass, and presumably males move on top of the eggs and remain there for 2 weeks or until the eggs hatch and even remain with young nymphs for 1 or 2 days. Taylor

Plate 15.4 Cryptic: *Mezira paragranuliger* Kormilev Figs. 9 and 10

(1988) suggests the occurrence of paternal care rather than maternal care. Although paternal care is known in a few Heteroptera (e.g., Ralston (1977), Ridley (1978), Smith (1980)) most notably in the Belostomatidae, maternal care is by far more typical.

Aradids are cryptical (Figs. 9 and 10) and move quickly when disturbed. They are difficult to see when resting on the surface of the bark but more often, and especially in the nymphal stage, are conspicuous against the white surface of the fungus when feeding.

15.3.1 Eggs and Oviposition

Copulation in aradids takes place in their natural habitats on fungi, beneath the bark. During copulation, the male positions below the female. Eggs are deposited in frass beneath the bark or in rotten logs or stumps or glued to the surface of the bark or fungi. Some species lay their eggs on the substrate free, while others lay their eggs with a sticky substance to adhere to the substrate. Some eggs are found partially embedded in the softwood in the galleries of termites and also laid in a regular manner attached to pieces of bark. Eggs are elongate-oval in shape, without a cap but with several micropylar processes at the anterior end. Hexagonal reticulations are a characteristic feature of these eggshells after hatching. A single female may lay from 14 to 45 eggs. In general, aradids have one or two annual generations and are represented in all the biogeographical regions of the world (Usinger and Matsuda 1959).

15.3.2 Nymph Feeding and Development

Nymphs (Figs. 11, 12, 13, and 14) are commonly found with the adults under a loose bark, and in these circumstances, it is not known whether this represents a concentration on or about a limited source of food or whether a genuine gregarious instinct is involved (Usinger and Matsuda 1959). Nymphal abdominal scent glands are present between terga 4/5 and 5/6 or between 4/5 and 5/6 or, less common, between terga 3/4. They are prominent and functional (Schuh and Slater 1995).

In general, aradids are uni- or bivoltine (i.e., one or two generations per year). However, the species *Aradus cinnamomeus* Panzer has a 2-year life span in most parts of Europe; in northern Europe, the life span is 3 years (Brammanis 1975; Heliövaara and Väisänen 1987). Eggs are laid in May; nymphs hatch in June and reach the 4th instar during the first summer. After hibernation, at the base of the tree or in the surrounding litter (Brammanis 1975; Heliövaara 1982), the bugs become adult in July–August of the following year, after which they hibernate. It is not until the following spring that the bugs mate and begin laying eggs (Tropin 1949; Brammanis 1975; Heliövaara 1984; Vásárhelyi and Böröcz 1987).

15.3.3 Adult Feeding and Reproduction

Most of the species are subcortical and mycetophagous. They live on or under the bark of dead trees and the coiled setae are remarkable adaptations for feeding on juices of fungi. They are mostly found on branches that have died recently and are not totally desiccated. When the tree becomes too dry, they apparently abandon it for another branch. They are, however, weak fliers and have a low vagility (Jacobs 1986).

The association of aradids with a particular species of trees has been summarized by Kiritshenko (1913), Stichel (1957), and Usinger and Matsuda (1959) for Europe and by Parshley (1921) for the Nearctic Region. Aradids are generally found in quiescent state, feeding, resting, or in hibernation. According to Yonke (1991), a particular aradid may be suitable for specific fungal growth.

Several species of aradids have been collected using the Berlese funnel on ground forest litter or by sweep netting the dry foliage or by means of using malaise or light traps (Table 15.1).

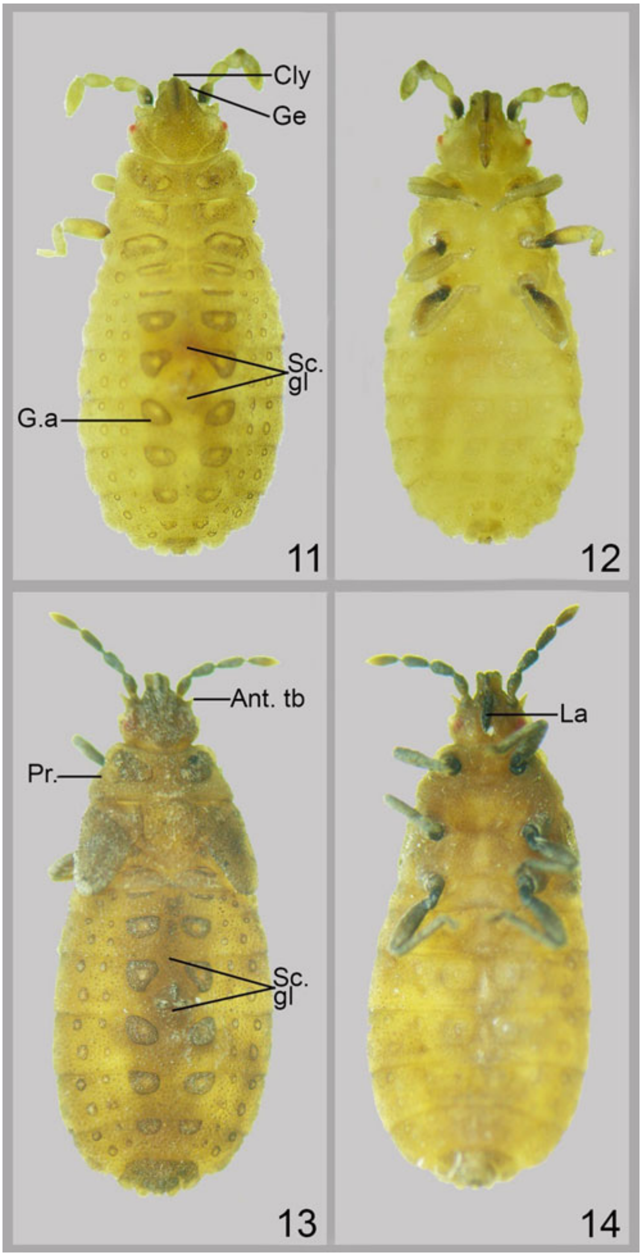

Plate 15.5 *Neuroctenus subandinus* Kormilev. Fig. 11, first immature stage, dorsal view: Cly, clypeus; G. a, glabrous area; Ge, gena; Sc gl, scent glands. Fig. 12, first immature stage, ventral view. Fig.13, fourth immature stage, dorsal view: Ant. tb, antenniferous tubercles; Pr, pronotum; Sc gl, scent glands. Fig. 14, fourth immature stage, ventral view: La, labium

Table 15.1 Collecting methods used to sample aradids

Species	Collecting methods
Eretmocoris disparis Drake & Maldonado	Berlese funnel from ground forest litter (Drake and Maldonado 1955)
Peggicoris zeteki Drake	Berlese funnel from forest litter (Drake 1956)
Acaricoris barroanus Drake & Kormilev; *Acaricoris clausus* Drake & Kormilev	Berlese funnel from forest litter (Drake and Kormilev 1958)
Proxius (Neoproxius) nicaraguensis Kormilev	Swept from dry foliage (Kormilev 1982)
Aradus pericarti Heiss; *Aphleboderris comata* Champion; *Aphleboderris pubescens* (Walker); *Dysodius magnus* Heiss; *Helenus hesiformis* White; *Hesus acuminatus* (F.); *Hesus cordatus* (F.); *Hesus flaviventris* (Burmeister); *Hesus humeralis* Heiss; *Mezira cf. boliviana* Kormilev; *Mezira barberi* Kormilev; *Mezira handlirschi* (Bergroth); *Mezira laeviventris* (Champion); *Neuroctenus longulus* Bergroth; *Neoproxius gypsatus* (Bergroth); *Phyllotingis eximia* (Haglund); *Phyllotingis cf. triangula* Heiss; *Placogenys cockerelli* Usinger & Matsuda; *Santaremia robusta* Kormilev	Interception trap, malaise trap, light trap (Heiss and Moragues 2009)

15.4 Classification and Diversity

The family Aradidae has been placed within the infraorder Pentatomomorpha (Leston 1954). Today, flat bugs are grouped into 8 subfamilies: Aneurinae, Aradinae, Calisiinae, Carventinae, Chinamyersiinae, Isoderminae, Mezirinae, and Prosympiestinae (Schuh and Slater 1995). The subfamily Chinamyersiinae is classified in two tribes, Tretocorini and Chinamyersiini, and the subfamily Prosympiestinae is divided in two tribes, Llaimacorini and Prosympiestini. Usinger and Matsuda (1959) provided a systematic account of the family and Kormilev and Froeschner (1987) a world catalog. Vásárhelyi (1987) and Grozeva and Kerzhner (1992) provided a hypothesis on the relationship among the Aradidae.

The family consists of about 1,931 species distributed in approximately 233 genera in the world. For the Nearctic Region, 10 genera and 123 species are known (Henry 2009); for the Neotropical Region, 80 genera and 509 species are referred (Table 15.2) (Coscarón and Contreras 2012); the Palearctic Region is represented by 28 genera and 204 species, and for the Australian Region, there are 38 genera and 143 species cited (Henry 2009).

Table 15.2 List of species of aradids from the Neotropical Region and their geographical distribution

Subfamily	Genera	Species	Distribution
Aneurinae	*Aneurillus*	*A. doesburgui* (Kormilev)	Suriname: Albina
	Aneurosoma	*A. dissimile* (Bergroth)	Argentina: Misiones; Chaco. Brazil: Amazonas; Rio Grande do Sul Colombia and Guadeloupe
			Panama: Chiriqui. Paraguay: Villa Rica
	Aneurus	*A. aterrimus* Kormilev	Costa Rica: Puntarenas
		A. barberi Kormilev	Saint Lucia, British West Indies
		A. bosqui Kormilev	Argentina: Misiones. Brazil: Rio Grande do Sul. Paraguay: Villarica
		A. brailovskyi Kormilev	Mexico: Veracruz
		A. bucki Kormilev	Brazil: Rio Grande do Sul
		A. burmeisteri Bergroth	Colombia
		A. championi Kormilev	Guatemala: Sacatepequez. Mexico: Veracruz
		A. equatoriensis Kormilev	Ecuador
		A. fiskei Heidemann Kormilev	Cuba: Cienfuegos. Mexico: Nueva León
		A. froeschneri Kormilev	Mexico: Veracruz. Panama: El valle
		A. guanacastensis Kormilev	Costa Rica: Guanacaste
		A. haitiensis Kormilev	Haiti
		A. herediensis Kormilev	Costa Rica: Guanacaste; Heredia
		A. hispaniolensis Picchi	Haiti
		A. hrdyi Ŝtys	Cuba
		A. maryae Picchi	Mexico: Michoacan
		A. mexicanus Kormilev	Mexico: Veracruz
		A. minutus Bergroth	Guatemala. Panama: Chiriqui
		A. montanus Champion	Guatemala: Totonicapan
		A. nasutus Kormilev	Guadeloupe
		A. neojamaicensis Picchi	Jamaica

		A. patriciae Picchi	Jamaica. Cuba: Villa Clara.
		A. pisoniae Kormilev	Puerto Rico: Maricao
		A. pusillus Kormilev	Guatemala: Alta Verapaz. Panama
		A. schuhi Kormilev	Brazil: Amazonas
		A. slateri Picchi	The Bahamas
		A. usingeri Picchi	Costa Rica: Guanacaste. Guatemala: Escuintla
			Mexico: Veracruz. Panama: Chiriqui
		A. vauriei Kormilev	Guadeloupe. Jamaica
		A. veracruzensis Picchi	Mexico: Veracruz
		I. aibonitensis (Kormilev)	Puerto Rico: Aibonito
		I. bergi (Kormilev)	Argentina: Corrientes
		I. bispinosus (Kormilev)	Brazil: Santa Catarina; Rio Grande do Sul
		I. bolivianus (Kormilev)	Bolivia
		I. carioca (Kormilev)	Brazil: Rio de Janeiro
		I. costaricensis (Kormilev)	Costa Rica: Guanacaste
		I. flavomaculatus (Distant)	Ecuador: Pichincha
		I. fritzi (Kormilev)	Bolivia. Peru
		I. leptocerus (Hussey)	Guatemala: Baja Verapaz. Mexico: Chiapas
			Panama. Chiriqui
		I. longicornis (Kormilev)	Costa Rica
		I. marginalis (Walker)	Bolivia. Colombia
		I. monrosi (Kormilev)	Argentina: Salta
		I. plaumanni (Kormilev)	Brazil: Santa Catarina
		I. politus (Say)	Cuba. Guatemala. French Guiana: St Laurent du Maroni
		I. sahlbergi (Bergroth)	Brazil: Minas Gerais; São Paulo

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		I. simulans (Walker)	Brazil: Rio de Janeiro
		I. subdipterus (Burmeister)	Argentina: Misiones; Buenos Aires; Chaco; Córdoba; Formosa; Jujuy; Formosa; Salta; Santiago del Estero; Tucumán. Brazil
		I. tenuis (Champion)	Panama: Chiriqui. Mexico: Guerrero. Nicaragua: Rivas
		I. wygodzinskyi (Picchi)	Jamaica
Aradinae	*Aradiolus*	*A. chemsaki* Kormilev	Mexico
		A. paradoxus Kormilev	Mexico: Oaxaca
		A. angustellus (Blanchard)	Argentina: Buenos Aires; Córdoba; Chaco; Santa Cruz; Rio Negro. Chile. Peru: Cuzco
		A. brasiliensis Usinger	Argentina: Misiones. Brazil: Mato Grosso; Santa Catarina; São Paulo. Paraguay: San Bernardino
		A. compressicornis Stål	Colombia. Venezuela: Trujillo
		A. falleni Stål	Brazil: Chapada; Rio de Janeiro. Guatemala: Alta Verapaz
			Panama. Mexico: Guerrero; Chiapas. Belize: Cayo
		A. fronterana Drake	Costa Rica: Guanacaste. Mexico: Tabasco
		A. gracilicornis Stål	Cuba. Mexico: Morelos; Chiapas
		A. granuliger Kormilev	Mexico
		A. mexicanus Usinger	Argentina: Misiones; Tucumán. Brazil: Espirito Santo
			Mexico: Temascaltepec
		A. pallidicornis Stål	
		A. penningtoni Drake	Argentina: Buenos Aires; Corrientes; Chaco; Formosa; Jujuy; Misiones; Mendoza; Santa Fé
			Bolivia: Santa Cruz. Brazil: Chapada
			Paraguay: Horqueta

		A. pericarti Heiss	Suriname: Marowijne. French Guiana
		A. testaceus Kormilev	Mexico
Calisiinae	*Calisiopsis*	*C. ampliceps* Champion	Brazil: Porto Alegre; Santa Catarina. Panama
		C. brasiliensis Kormilev	Brazil: Rio Grande do Sul; Santa Catarina
		C. brodzinskyorum Froeschner	Dominican Republic
		C. kormilevi Froeschner	Peru: Madre de Dios
		C. minuta Kormilev	Mexico: Tampico
		C. nigrotuberculata (Froeschner)	Mexico: Texas
		C. planiceps Kormilev	Brazil: Santa Catarina
	Calisius	*C. affinis* Barber	The Bahamas
		C. bilobatus Kormilev	Bolivia
		C. brasiliensis Kormilev	Brazil: Santa Catarina
		C. confusus Kormilev	Brazil: Santa Catarina
		C. contubernalis Bergroth	Guadeloupe
		C. elegantulus Bergroth	Guadeloupe
		C. farri Kormilev	Jamaica: Saint Thomas
		C. ferox Champion	Panama
		C. gracilis Kormilev	Guatemala
		C. insignis Kormilev	Guatemala
		C. longiventris Kormilev	Panama
		C. major Bergroth	Venezuela: La Guaira
		C. pallipes Stål	Brazil
		C. pangoaesnsis Kormilev	Peru
		C. placidus Horváth	Brazil: Goiáz; São Paulo
		C. pulcher Kormilev	Brazil: Minas Gerais

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
Carventinae	*Acaricoris*	*A. austeris* Drake & Kormilev	Guadeloupe
		A. barroanus Drake & Kormilev	Panama
		A. clausus Drake & Kormilev	Puerto Rico: Mayagüez
		A. haitiensis Kormilev	Haiti
		A. lattini Heiss	Dominican Republic
	Aglaocoris	*A. clarkei* Drake	Dominica in Leeward West Indies Islands
		A. comes Drake	Guadeloupe
		A. cubanus Drake	Cuba
		A. drakei Kormilev	Haiti: Port-au-Prince
		A. invisus Drake	Guadeloupe Island.
		A. natalii Drake & Maldonado	Puerto Rico: Yauco; Mayaguez
		A. orientalis Grillo Ravello	Cuba
		A. rectangularis Usinger & Matsuda	Santo Domingo
		A. vicinus Drake	Guadeloupe
	Alayocoris	*A. hirsutus* Grillo Ravelo	Cuba: La Habana
	Aparilocoris	*A. mexicanus* (Kormilev)	Mexico: Oaxaca
		A. venezuelanus Kormilev	Venezuela: Aragua
	Apterocoris	*A. surinamensis* Kormilev & Doesburg	Suriname: Brokopondo
	Atactocoris	*A. farri* Kormilev	Jamaica
		A. perneri Heiss	Jamaica
	Baracoris	*B. alayoi Grillo Ravelo*	Cuba
	Carpocoris	*C. cubanus* Grillo Ravelo	Cuba
	Carventus	*C. chilensis* Kormilev	Chile: Concepción
		C. mexicanus Bergroth	Colombia: Cundinamarca. Panama: Chiriqui
	Cubanocoris	*C. alayoi* Grillo Ravelo	Cuba

	Dihybogaster	*D. incrustatus* Kormilev	Brazil: Santa Catarina
		D. plana Kormilev	Brazil: Santa Catarina
		D. plaumanni Kormilev	Brazil: Santa Catarina
		D. wygodzinskyi Usinger & Matsuda	Brazil: Rio de Janeiro
	Eretmocoris	*E. cubensis* Usinger & Matsuda	Cuba
		E. dominicus Kormilev	Dominica in Leeward West Indies Islands
		E. gigas Usinger & Matsuda	Puerto Rico
		E. longicornis Usinger & Matsuda	Haiti
		E. minimus Usinger & Matsuda	Cuba: Cienfuegos
		E. productus Usinger & Matsuda	Guadeloupe
		E. prominens Usinger & Matsuda	Puerto Rico
		E. tatei Harris & Drake	Puerto Rico
	Glyptocoris	*G. annulatus* Kormilev	Brazil: Santa Catarina
		G. confusus Kormilev	Brazil: Santa Catarina
		G. espiritosantensis Wygodzinsky	Brazil: Espirito Santo
		G. fluminensis Wygodzinsky	Brazil: Rio de Janeiro
		G. insularis Drake	Guadeloupe
		G. milleri Wygodzinsky	Brazil: Rio de Janeiro
		G. minutus Kormilev	Brazil: Santa Catarina
		G. plaumanni Kormilev	Brazil: Mato Grosso
		G. sejunctus Harris & Drake	Brazil
		G. spinosus Usinger & Matsuda	Brazil: Parana; Rio de Janeiro
		G. verus Drake	Guadeloupe in Leeward West Indies Islands
	Kolpodaptera	*K. minuta* Kormilev	Guatemala
		K. panamensis Usinger & Matsuda	Panama

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		K. prominens Usinger & Matsuda	Guadeloupe
		K. rugosa Kormilev	Cuba
	Laevsoicoris	*L. lissonotus* Grillo Ravelo	Cuba
	Lepidocoris	*L. garcesi* Grillo Ravelo	Cuba: Camagüey
	Neoproxius	*N. amazonicus* (Kormilev)	Brazil: Amazonas
		N. carioca (Kormilev)	Brazil: Rio de Janeiro
		N. costariquensis (Kormilev)	Costa Rica: Turrialba
		N. gypsatus (Bergroth)	Bolivia: Santa Cruz. Brazil: Pará; São Paulo
			French Guiana. Guatemala: Alta Verapaz. Panama. Peru. Venezuela
		N. incaicus (Kormilev)	Peru
		N. lindemannae (Kormilev)	Brazil: Amazonas
		N. magdalenae (Kormilev)	French Guiana. Nicaragua
		N. nicaraguensis (Kormilev)	Nicaragua
		N. palliatus (Champion)	Guatemala. Panama. Peru
		N. panamensis (Kormilev)	Panama
		N. personatus (Champion)	Guatemala: Alta Verapaz. Panama: Chiriqui
		N. peruvianus (Kormilev)	Peru
	Peggicoris	*P. zeteki* (Drake)	Panama
	Planocoris	*P. orientalis* Grillo Ravelo	Cuba
	Pokoldaptera	*P. humicola* Grillo Ravelo	Cuba
	Protokolpodaptera	*P. habanense* Grillo Ravelo	Cuba: La Habana
	Proxius	*P. incrustatus* Stål	Brazil: Rio de Janeiro
		P. schwarzii Heidemann	Cuba: Camagüey; La Habana
	Psorosoma	*P. forficulinum* Champion	Panama
	Reeceicus	*R. saileri* Drake	Peru

	Rhysocoris	*R. cubanus* Kormilev	Cuba: Cienfuegos
		R. disparis (Drake & Maldonado)	Puerto Rico: Mayagüez
		R. jamaicensis Kormilev	Jamaica
		R. rugosus Usinger & Matsuda	Haiti
	Tainocoris	*T. alayoi* Grillo Ravelo	Cuba
	Yvacoris	*Y. litoralis* Grillo Ravelo	Cuba
	Zayasocoris	*Z. trinitarius* Grillo Ravelo	Cuba
Isoderminae	*Isodermus*	*I. gayi* (Spinola)	Chile. Argentina: Neuquén; Río Negro; Santa Cruz; Tierra del Fuego
Mezirinae	*Allelocoris*	*A. dryadis* Drake & Harris	Brazil: Rio de Janeiro
	Aphleboderrhis	*A. alata* Kormilev	Brazil
		A. comata Champion	Brazil: Pará; Rio Grande do Sul. French Guiana
			Panama: Chiriqui. Peru
		A. hirticornis (Bergroth)	Brazil
		A. pilosa Stål	Argentina: Misiones; Jujuy; Tucumán. Paraguay. Peru
		A. procerula (Bergroth)	Brazil
		A. pubescens (Walker)	Brazil: Pará. French Guiana. Guatemala: Alta Verapaz
			Mexico. Panama: Chiriqui. Peru. Suriname: Paramaribo
		A. tomentosa (Bergroth)	Brazil
	Artagerus	*A. crispatus* Stål	Bolivia. Brazil: Pará; Rio de Janeiro. Panama: Chiriqui. Peru
		A. hispidus Champion	Brazil: Amazonas; Para. Panama: Chiriqui. Peru: Huánuco
		A. histricus Stål	Brazil. Mexico: Veracruz
		A. martinezi Kormilev	Bolivia: Cochabamba. Brazil: Amapá; Amazonas. Peru

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		A. montandoni Bergroth	Brazil: Amazonas
		A. plaumanni Kormilev	Brazil: São Paulo; Santa Catarina
		A. setosus Stål	Colombia: Bogotá. Panama
	Asterocoris	*A. australis* Drake & Harris	Brazil: Rio de Janeiro
		A. schubarti Wygodzinsky	Brazil: Espirito Santo; São Paulo
	Banksiessa	*B. pubescens* Usinger & Matsuda	Panama
	Bergrothiessa	*B. confusa* Kormilev	Brazil: Parana
		B. grossa Kormilev	Brazil: Parana
		B. intermediaria (Kormilev)	Brazil: Santa Catarina
		B. paranensis Kormilev	Brazil: Parana
		B. plaumanni Kormilev	Brazil: Santa Catarina; Minas Gerais
		B. rufa Kormilev	Brazil: Parana
		B. usingeri (Wygodzinsky)	Brazil: Rio de Janeiro
	Chapadia	*C. alata* Kormilev	Brazil
	Cinyphus	*C. alatus* Kormilev	Mexico: Xalapa
		C. amazonicus Kormilev	Bolivia: Santa Cruz
		C. andinus Kormilev	Peru
		C. armillatus Bergroth	Bolivia. Colombia
		C. emarginatus (Stål)	Guatemala: Alta Verapaz. Mexico: Chiapas
		C. lutosus Champion	Panama. Peru
		C. meziroides Kormilev	Peru
		C. minutus Blöte	Bolivia: Coroico
		C. ovatus Kormilev	Brazil. Peru
		C. peruvianus Kormilev	Peru
		C. saileri Kormilev	Mexico: Veracruz

		C. squalidus Champion	Nicaragua: Chontales. Panama: Chiriqui. Venezuela
		C. subtruncatus Bergroth	Nicaragua: Chontales. Panama: Chiriqui. Venezuela
		C. terminalis Kormilev	Venezuela: Aragua
		C. venezuelanus Kormilev	Venezuela: Aragua
	Coloborrhinus	*C. ovatus* (Kormilev)	Brazil: Minas Gerais. Peru. Suriname
		C. peruvianus Kormilev	Peru
		C. pumilio Champion	Brazil: Minas Gerais. Panama
	Ctenoneurus	*C. necopinatus* Bergroth	Saint Thomas in Leeward West Indies Islands
	Delnocoris	*D. micropterus* Kormilev	Costa Rica: Heredia
	Dysodius	*D. ampliventris* Bergroth	Brazil: Amazonas. Colombia. Panama. Suriname
		D. brailovskyi Heiss	Mexico
		D. brevipes Bergroth	Costa Rica: Guanacaste. Mexico: Chiapas; Guerrero; Oaxaca
		D. crenulatus (Stål)	Colombia. Costa Rica: Guanacaste; Puntarenas
			Guatemala: Alta Verapaz; Baja Verapaz. Panama: Chiriqui
			Mexico
		D. equatorianus Kormilev	Ecuador: Napo-Pastaza. French Guiana: Saint-Laurent
			du Maroni. Suriname: Brokopondo
		D. lunatus F.	Argentina: Chaco. Bolivia: Cochabamba; Coroico; Chapare; Santa Cruz. Brazil: Amazonas; Mato Grosso; Pará; São Paulo; Santa Catarina. Colombia
			Costa Rica. Ecuador: Napo; Pichincha. French Guiana:
			Saint-Laurent du Maroni. Guatemala: Alta Verapaz. Honduras: Cortés. Mexico: Campeche; Quintana Roo; Oaxaca; Veracruz; Yucatan. Nicaragua: Chontales. Panama: Chiriqui. Paraguay. Peru: Cuzco; Madre de Dios. Suriname: Brokopondo. Venezuela: Caracas. Trinidad and Tobago

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		D. magnus (Heiss)	Bolivia: Coroico. Brazil: Santa Catarina; Mato Grosso.
			Ecuador: Napo. British Guiana. French Guiana: Saint-Laurent du Maroni. Peru: Amazonas; Madre de Dios. Suriname: Paramaribo
	Emydocoris	*E. montanus* Drake	Brazil
		E. stali Kormilev	Brazil: Rio de Janeiro
		E. testudinatus Usinger	Brazil: Rio de Janeiro.
	Eunotoplocoris	*E. ruckesi* Kormilev	Peru
	Forficulassa	*F. lobulata* Kormilev	Brazil: Pará
	Helenus	*H. hesiformis* White	Brazil: Amazonas. French Guiana: Saint-Laurent du Maroni. Peru: Amazonas. Suriname
		H. hirsutus Champion	Panama
	Hesus	*H. acuminatus* (F.)	Bolivia: Chapare; Cochabamba. Brazil: Chapada; Amazonas; Pará. Colombia. Ecuador: Napo; Sucumbios. French Guiana: Saint-Laurent du Maroni. Peru
		H. cordatus (F.)	Brazil: Pará; Chapada; Amazonas. French Guiana: Saint-Laurent du Maroni. Nicaragua: Chontales. Panama: Chiriqui. Peru: Amazonas. Surinam: Paramaribo
		H. humeralis Heiss	Brazil: Amazonas; Rondônia. Colombia. Ecuador: Napo; Sucumbios. French Guiana. Peru: Amazonas; Huánuco; Madre de Dios
		H. flaviventris (Burmeister)	Bolivia: Santa Cruz. Brazil: Amazonas; Chapada; Pará. Colombia. French Guiana: Saint-Laurent du Maroni. Nicaragua. Panama: Chiriqui. Peru: Madre de Dios. Venezuela
		H. mexicanus Kormilev	Guatemala. Honduras. Mexico: Chiapas; Yucatan
			Panama. Trinidad and Tobago. Venezuela

		H. subarmatus Stål	Bolivia: Cochabamba. Ecuador: Napo; Sucumbios.
			Colombia. Suriname: Paramaribo. Brazil: Rio de Janeiro; Rondônia. Peru: Amazonas
	Illibius	*I. laticeps* Stål	Colombia. Costa Rica: Heredia. Panama
	Kelaino	*K. kjellanderi* Kormilev	Colombia
	Kormilevia	*K. aberrans* Kormilev	Colombia
		K. dureti (Kormilev)	Argentina: Misiones
		K. gerali Kormilev	Brazil: Santa Catarina
		K. montrouzieri (Kormilev)	Brazil: Santa Catarina
		K. plaumanni (Kormilev)	Brazil: Santa Catarina
		K. setifera Usinger & Matsuda	Brazil
		K. teresopolitana (Wygodzinsky)	Brazil: Rio de Janeiro
	Limonocoris	*L. jolyi* Kormilev	Venezuela
	Lobocara	*L. oblonga* Bergroth	Argentina: Misiones. Bolivia: Coroico. Brazil: Amazonas. French Guiana
		L. ovata Bergroth	Brazil: Amazonas. British Honduras. French Guiana.
			Guatemala. Nicaragua: Chontales
	Mapiri	*M. paradoxa* Kormilev	Bolivia
	Melanosterphus	*M. spinosus* (F.)	Brazil: Amazonas; Pará; Chapada. French Guiana
	Mezira	*M. abdominalis* (Stål)	Cuba. Puerto Rico
		M. amazonica Kormilev	Peru: Amazonas
		M. americana (Spinola)	Argentina: La Rioja; Neuquén; Río Negro. Chile: Los Ríos
		M. andina Kormilev	Bolivia: Cochabamba. Brazil: Amazonas. Peru
		M. angustata (Champion)	Panama: Chiriqui

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		M. argentinensis Kormilev	Argentina: Córdoba; Corrientes; Entre Ríos; Santa Fé. Paraguay: Caaguazu. Brazil: Santa Catarina. Peru
		M. armata Kormilev	Peru
		M. arnaudi Kormilev	Peru
		M. auripilosa Kormilev	Mexico
		M. barberi Kormilev	Brazil: Amazonas. Venezuela. Peru: Huánuco. French Guiana
		M. birabeni Kormilev	Argentina: Cordoba
		M. boliviana Kormilev	Bolivia: Cochabamba, Chapare
		M. bonaerensis Kormilev	Argentina: Buenos Aires
		M. bouvieri (Bergroth)	Colombia
		M. brachyptera Kormilev	Jamaica
		M. brasiliensis Kormilev	Brazil: Santa Catarina
		M. bridarollii Kormilev	Bolivia: Chapare
		M. bruchi Kormilev	Argentina: Cordoba
		M. carinata Usinger	Mexico
		M. carioca Kormilev	Brazil: Rio de Janeiro
		M. championi Kormilev	Mexico: Veracruz
		M. chemsaki Kormilev	Costa Rica: Cartago
		M. cimicoides Walker	Brazil
		M. constricta (Champion)	Guatemala
		M. costalimai Kormilev	Brazil. Paraguay
		M. crenulata Kormilev	Venezuela
		M. cubana Kormilev	Cuba
		M. divisa (Champion)	Guatemala

		M. doesburgi (Kormilev & Froeschner)	Suriname
		M. dybasi Kormilev	Colombia: Villavicencio
		M. emarginata (Say)	Mexico
		M. equatoriana Kormilev	Ecuador: Esmeralda
		M. eurycephala Kormilev	Brazil: Rio Grande do Sul
		M. flavicans (Stål)	Brazil: Rio de Janeiro. Suriname
		M. formosa Kormilev	Argentina: Corrientes; Formosa
		M. fritzi Kormilev	Brazil: Santa Catarina
		M. gracilis Kormilev	Brazil: Amazonas
		M. gradata (Bergroth)	Brazil: Rio Grande do Sul
		M. granulata (Say)	Cuba: Guantanamo
		M. granuliger (Stål)	Argentina: Buenos Aires; Entre Ríos; Misiones; Salta; Santa Fé; Tucumán
			Brazil: Rio Grande do Sul; Chapada; Rio de Janeiro; Espirito Santo. Paraguay: Caaguazú
		M. guanacastensis Kormilev	Costa Rica: Guanacaste
		M. guianensis Kormilev	British Guiana
		M. halaszfyae Kormilev	Peru
		M. handlirschi (Bergroth)	Brazil: Amazonas; Pará. French Guiana: Saint-Laurent du Maroni. Panama: Chiriqui. Suriname
		M. hondurensis Kormilev	Honduras
		M. horvathi (Bergroth)	Brazil
		M. hyperlobata Kormilev	Brazil: Amazonas
		M. inca Kormilev	Peru
		M. incrustata Kormilev	Brazil
		M. jamaicensis Bergroth	Jamaica

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		M. kjellanderi Kormilev	Brazil: Amazonas. Colombia. Panama. Suriname
		M. laeviventris (Champion)	Brazil: São Paulo. Ecuador: Napo-Pastaza
			French Guiana. Panama: Chiriqui
		M. lata (Champion)	Guatemala: Alta Verapaz
		M. ligneola (Bergroth)	Brazil. Peru
		M. lobata (Say)	Mexico: Chiapas; Oaxaca
		M. longipilis (Champion)	Mexico: Guerrero
		M. luteonotata Kormilev	Brazil: Chapada
		M. maculata Kormilev	Mexico: Zacatecas
		M. maculiventris (Champion)	Guatemala: Alta Verapaz
		M. mexicana Kormilev	Mexico: Veracruz; Nuevo Leon
		M. minor Kormilev	Brazil
		M. moesta Stål	Mexico
		M. nana (Champion)	Guatemala
		M. nasalis Kormilev	Colombia: Tolima. Mexico: Veracruz
		M. neonigripennis Kormilev	Venezuela
		M. neonigripennis neonigripennis Kormilev	Argentina: Salta
		M. neonigripennis misionensis Kormilev	Argentina: Misiones
		M. neotropicalis (Champion)	Mexico: Chiapas; Michoacan. Guatemala: Alta Verapaz
		M. nigripennis Usinger	Argentina: Chaco; Jujuy; Misiones; Salta; Tucumán. Brazil: Santa Catarina; Río Grande do Sul. Paraguay: Horqueta
		M. oblonga Kormilev & Heiss	Brazil: Rio de Janeiro
		M. obscura (Distant)	Ecuador: Chimborazo
		M. occidentalis Kormilev	Mexico: Veracruz
		M. paraangustata Kormilev	Mexico

		M. paraensis Kormilev & Heiss	Brazil: Pará
		M. paragranuliger Kormilev	Argentina: Chaco; Jujuy; Salta; Misiones; Tucumán. Brazil: Santa Catarina; Espirito Santo; Rio de Janeiro
		M. paraguayensis Kormilev	Paraguay: Horqueta
		M. paralata Kormilev	Costa Rica: Limon
		M. paratropicalis Kormilev	Mexico: Chiapas
		M. parvicornis Kormilev	Bolivia
		M. pauperula Kormilev	Brazil: Rio de Janeiro. French Guiana
		M. peruviana Kormilev	Peru
		M. pilosa Kormilev	Mexico
		M. placida placida Kormilev	Puerto Rico
		M. placida haitiensis Kormilev	Haiti: Port-au-Prince
		M. plaumanni Kormilev	Brazil: Rio Grande do Sul
		M. proseni Kormilev	Argentina: Salta. Peru
		M. proxima Kormilev	Peru.
		M. punctiventris (Stål)	Colombia
		M. pusilla Kormilev	Guatemala: Alta Verapaz
		M. regularis (Champion)	Argentina: Tucumán. Costa Rica
			Guatemala. Mexico: Veracruz
		M. reuteri (Bergroth)	Argentina: Buenos Aires; Santa Fé; Misiones. Brazil
		M. romani Kormilev	Brazil: Amazonas
		M. rugicornis (Champion)	British Honduras: Belize. Mexico: Oaxaca
		M. rugiventris (Champion)	Guatemala. Peru
		M. saltensis Kormilev	Argentina: Salta; Tucumán. Brazil
		M. sangabrielensis Kormilev	Brazil
		M. sanmartini Kormilev	El Salvador. Peru. Venezuela: Bolivar

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		M. scheveni Heiss	Dominican Amber
		M. sinuata (Champion)	Mexico: Guerrero
		M. spissigrada Kormilev	Argentina: Misiones
		M. surinamensis Blöte	Suriname
		M. tartagalensis Kormilev	Argentina: Salta
		M. timida Kormilev	Brazil: Mato Grosso
		M. trinidadensis Kormilev	Trinidad and Tobago
		M. tropicalis Kormilev	Mexico: Jalisco
		M. variegata Kormilev	Mexico: Veracruz
		M. venezuelana Kormilev	Venezuela
		M. veracruzensis Kormilev	Mexico: Veracruz
		M. vianai Kormilev	Argentina: Cordoba
		M. vicina Kormilev & Froeschner	Peru
		M. vulcanica Kormilev	Ecuador: Chimborazo
		M. yucatana (Champion)	Mexico: Yucatan
	Miorrhynchus	*M. angulatus* Kormilev	Peru
		M. bolivianus Kormilev	Bolivia: Cochabamba. Peru
		M. brasiliensis Kormilev	Brazil: Mato Grosso; Santa Catarina
		M. championi Kormilev	Bolivia: Santa Cruz. Peru
		M. jatahyensis Kormilev	Brazil: Goiás
		M. longicornis Kormilev	Peru: Madre de Dios
		M. longipes Champion	Panama: Chiriqui
		M. paraguayensis Kormilev	Brazil: Santa Catarina. Paraguay: Guairá
		M. peruvianus Kormilev	Ecuador: Napo. Peru: Pachitea
		M. plaumanni Kormilev	Brazil: Mato Grosso

		M. proseni Kormilev	Bolivia: Cochabamba. Brazil: Amazonas. Colombia
		M. schuhi Kormilev	Peru: Junin
		M. undulatus Kormilev	Peru
		M. usingeri Kormilev	Panama
	Mystilocoris	*M. pubescens* Usinger & Matsuda	Colombia
	Nannium	*N. bituberculatum* Champion	Guatemala
		N. brasiliense Kormilev	Brazil: Santa Catarina
		N. elongatum Bergroth	Peru. Venezuela
		N. kormilevi Doesburg	French Guiana. Suriname
		N. parvum Bergroth	Costa Rica: Guanacaste. Guatemala. Panama: Chiriqui. Peru
		N. subovatulum Bergroth	Brazil
	Neormenocoris	*N. costaricensis* (Kormilev)	Costa Rica: Heredia
	Neuroctenus	*N. amazonicus* Kormilev	Brazil: Amazonas; Mato Grosso. Colombia. Peru
			Venezuela: Portuguesa
		N. amplus Champion	Mexico: Guerrero
		N. andrei (Kormilev)	Colombia
		N. aztequi Kormilev	Mexico
		N. bergrothi Champion	Guatemala: Alta Verapaz. Mexico: Chiapas; Oaxaca. Peru
		N. centralis (Berg)	Argentina: Buenos Aires; Corrientes; Catamarca; Córdoba; Jujuy; La Rioja; Salta; Santa Fé; Tucumán
			Brazil: Santa Catarina
		N. chilensis Kormilev	Chile
		N. colombianus Kormilev	Colombia: Villavicencio
		N. dilatatus Bergroth	Costa Rica. Guatemala. Mexico: Veracruz

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		N. discrepans Kormilev	Mexico
		N. distanti Bergroth	Mexico
		N. insignis Kormilev	Brazil: Santa Catarina
		N. litigiosus (Stål)	Bolivia: Santa Cruz. Guatemala: Alta Verapaz. Costa Rica
			Panama: Chiriqui. Mexico
		N. longissimus Kormilev	Brazil: Pará
		N. longiusculus Kormilev	Brazil: Santa Catarina
		N. longiventris Kormilev	Bolivia: Coroico. Colombia: Cauca. Panama. Peru
		N. longulus Bergroth	Brazil: Amazonas; Mato Grosso. Peru
		N. mexicanus (Champion)	Colombia. Mexico: Oaxaca
		N. niger Bergroth	Guatemala. Mexico: Morelos
		N. ovatus Stål	Mexico
		N. papyrinus Bergroth	Mexico: Morelos
		N. proseni Kormilev	Bolivia: Santa Cruz
		N. punctulatus (Burmeister)	Argentina: Corrientes; Misiones. Brazil: Rio Grande do Sul
			Colombia. Guatemala. Nicaragua: Chontales. Panama: Chiriqui. Paraguay: Caaguazú
		N. robustus Kormilev	Colombia. Peru
		N. rossi Kormilev	Ecuador: Napo-Pastaza
		N. rubiginosus Bergroth	Bolivia: Coroico. Colombia. Cuba. Mexico. Peru
		N. schlingeri Kormilev	Ecuador: Napo-Pastaza. Peru
		N. simplex (Uhler)	Cuba

		N. subandinus Kormilev	Argentina: Catamarca; Jujuy; Mendoza; Tucumán; Salta. Bolivia
		N. subparallelus Champion	Guatemala: Alta Verapaz. Mexico: Veracruz
		N. substitutus Kormilev	Mexico: Chihuahua
		N. surinamensis Kormilev	Suriname
		N. terginus (Stål)	Brazil: Rio Grande do Sul; Rio de Janeiro
			Colombia. Guatemala. Venezuela.
		N. trigonus Bergroth	Guatemala
		N. uhleri Bergroth	Mexico: Michoacan
		N. uruguayensis Kormilev	Uruguay
		N. vanduzeei Kormilev	Panama
	Notapictinus	*N. amazonicus* Kormilev	Brazil: Amazonas
		N. angulatus Kormilev	Peru
		N. araguaensis Kormilev	Venezuela: Aragua
		N. beckeri (Kormilev)	Brazil: Rio Grande do Sul; Santa Catarina
		N. bimaculatus Kormilev	Brazil: Santa Catarina
		N. brachypterus (Drake & Kormilev)	Brazil: Santa Catarina
		N. breviceps (Champion)	Panama: Chiriqui
		N. christae Kormilev	Brazil: Amazonas
		N. denticollis (Champion)	Panama: Chiriqui
		N. derivatus (Kormilev)	Brazil: Mato Grosso
		N. diharpagus Kormilev	Peru
		N. dissimilis Kormilev & Heiss	Brazil
		N. dollingi Kormilev	Costa Rica
		N. dominicus (Usinger)	Dominican Republic
		N. dyscritus Kormilev	Peru

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		N. equatoriensis Kormilev	Ecuador
		N. hoguei Kormilev	Brazil: Rio de Janeiro
		N. incaicus Kormilev	Peru
		N. kjellanderi Kormilev	Peru
		N. luteoincrustatus (Kormilev)	Bolivia
		N. maculatus (Kormilev)	Peru
		N. martinezi (Kormilev)	Argentina: Salta
		N. micropterus Kormilev	Brazil: Parana
		N. nanus (Kormilev)	Paraguay
		N. notatus Kormilev	Suriname
		N. ornatus Kormilev	Brazil: Rio de Janeiro
		N. paramaculatus Kormilev	Brazil: Chapada
		N. parviceps (Champion)	Panama: Chiriqui
		N. parvulus Kormilev	Panama
		N. piliger Kormilev	Colombia: Cauca
		N. platyceps Kormilev	Brazil: Chapada
		N. plaumanni Kormilev	Brazil: Santa Catarina
		N. quadraticeps (Champion)	Ecuador: Napo-Pastaza. Panama: Chiriqui
		N. rutilus (Kormilev)	Brazil: Santa Catarina
		N. sanmigueli (Kormilev)	Argentina: Tucumán; San Luis
		N. similis Kormilev & Heiss	Brazil: Rio de Janeiro
		N. subparallelus Kormilev	Brazil: Amazonas
		N. surinamensis Kormilev	Suriname
		N. terminalis Kormilev	Brazil: Santa Catarina
		N. testaceus Kormilev & Heiss	Brazil: Rio de Janeiro
		N. uruguayensis Kormilev	Uruguay

		N. varelai Kormilev	Venezuela: Bolívar
		N. venezuelanus Kormilev	Venezuela
	Notoplocoris	*N. guanabarensis* Kormilev	Brazil
		N. leptocerus Kormilev	Brazil
		N. mendesi Wygodzinsky	Brazil: Rio de Janeiro
		N. montei Usinger	Brazil: Rio de Janeiro
		N. ovatus Kormilev	Brazil: Parana
		N. potensis Drake & Harris	Brazil: Rio de Janeiro
		N. robustus Kormilev	Brazil: Espirito Santo
		N. sobrali Wygodzinsky	Brazil: Rio de Janeiro
		N. triangulatus Kormilev	Brazil: Santa Catarina
		N. usingeri Kormilev & Heiss	Brazil: São Paulo
	Ormenocoris	*O. stylatus* Usinger & Matsuda	Ecuador: Napo
	Parahesus	*P. truncatus* Kormilev	Bolivia
	Paramezira	*P. meziroides* (Kormilev)	Brazil
	Phyllotingis	*P. eximia* (Haglund)	Brazil: Amazonas; Rondônia. Colombia: Caquetá. French Guiana
		P. interjecta (Bergroth)	Bolivia. Brazil. Colombia. Panama
		P. lanceolata (F.)	Brazil: Amazonas. Peru: Amazonas; Iquitos
			Cayenne, French Guiana. Suriname: Brokopondo
		P. reducta Heiss	Trinidad
		P. triangula Heiss	Brazil: Mato Grosso. French Guiana
	Pictinus	*P. armatus* Champion	Panama
		P. bechynei Kormilev	Brazil: Amazonas
		P. brasiliensis (Wygodzinsky)	Brazil: Rio de Janeiro

(continued)

Table 15.2 (continued)

Subfamily	Genera	Species	Distribution
		P. carioca Kormilev	Brazil: Rio de Janeiro
		P. cinctipes Stål	Bogotá
		P. fictus Kormilev	Brazil: Santa Catarina
		P. fronto Bergroth	Brazil: Santa Catarina
		P. granuliferus Kormilev	Brazil: Parana
		P. pilosulus Kormilev	Brazil: Parana
		P. rhombocarinatus Kormilev	Brazil: Santa Catarina
		P. simulans (Walker)	Brazil: Rio de Janeiro
		P. spiniger Champion	Panama: Chiriqui
		P. stali Kormilev	Peru
		P. stolidus Kormilev	Brazil: Santa Catarina
		P. venezuelanus Kormilev	Venezuela: Bolivar
		P. wittmeri Kormilev	Brazil: São Paulo
	Placogenys	*P. brachyptera* (Kormilev)	Brazil: Santa Catarina; Minas Gerais
		P. clarkei Kormilev	Argentina: Tucumán.
		P. cockerelli Usinger & Matsuda	Brazil: Rondônia; Pará. British Guiana
			French Guiana: Saint-Laurent du Maroni
		P. constricta Kormilev	Ecuador
		P. explanata (Kormilev)	Brazil: Amapá; Pará. Peru
		P. parva Kormilev	Brazil: Espirito Santo
	Pseudopictinus	*P. dispar* Kormilev	Brazil: Parana
	Rhynchomirus	*R. brachypterus* Kormilev	Peru: Junin
	Saileriessa	*S. stigmata* Usinger & Matsuda	Panama
	Santaremia	*S. robusta* Kormilev	Brazil: Pará. French Guiana
Prosympiestinae	*Llaimocoris*	*L. penai* Kormilev	Chile: Cautin

In the Neotropical Region, for Argentina four genera and five species were reported (Pennington 1921); Coscarón (in press) increased these numbers to 14 genera and 41 species; records from Ecuador comprise nine genera and 15 species (Froeschner 1981); from Panama 30 genera and 60 species were reported (Froeschner 1999), and from Chile six genera and six species were referred (Prado 2008).

Regional keys for the Neotropical Region were only made for Argentina by Contreras and Coscarón (2012) including diagnosis of genera, geographic distribution, and additional distributional records (Contreras et al. 2011).

Aradids were found in the following substrates: under the bark of a rotten log (Wygodzinsky 1948); on the bark during night (Heiss and Moragues 2009), under the bark (Kormilev 1982); under the bark of dead trees (Wygodzinsky 1948); beneath the bark of decaying branches of sourwood (*Oxydendrum*) and beneath the loose bark scales on dry and decaying branches of trees (Heidemann 1904); *Zanthoxylum americanum*, *Oxydendrum*, *Platanus*, *Quercus*, *Carya*, *Rhus*, beneath the bark of *Pinus montezumae*, elms, and oaks (Usinger and Matsuda 1959); on orchid plants, under *Schinopsis lorentzii* and on *Pisonia subcordata* (Kormilev 1953, 1958, 1964); in larval galleries of Cerambycidae abandoned of *Celtis tala* (Kormilev 1956); and in deserted galleries of a small cerambycid in dead branches of sumac (Heidemann 1904).

In this family an important forest pest is the species *Aradus cinnamomeus* Panzer (usually called bark bugs); it feeds on the phloem, cambium, and xylem of living *Pinus* sp. and *Larix* sp. (Pinaceae) (Kiritshenko 1913) and causes stunting of the growth of these trees (Strawinski 1925). It has a Palearctic distribution (Helioövaara 2000). This bug forms groups in large colonies preferably on young pine trees, 7–12 cm in diameter, sucking the leaves and twigs.

Records of aradids from ambar include registers from Birmanian ambar (100 million years ago) (Heiss and Grimaldi 2001, 2002), registers from the Baltic dated 40–50 million years ago (Heiss 1997, 1998, 2002, 2012) also Dominican amber (Heiss 2000).

15.5 Concluding Remarks

The understanding of Aradidae diversity from a systematic, phylogenetic, biological, ecological, and economic viewpoint, including their role in conservation biology and global warming, is fundamental. An enormous amount of important and biological, biogeographical, and host information useful to other disciplines remains to be discovered in the world and especially in the Neotropical Region.

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Chapter 16
The Big-Eyed Bugs, Chinch Bugs, and Seed Bugs (Lygaeoidea)

Thomas J. Henry, Pablo M. Dellapé, and Alexandre S. de Paula

Abstract The Lygaeoidea, representing the second largest superfamily in the infraorder Pentatomomorpha, are one of the most diverse groups of Heteroptera with about 700 genera and more than 4,200 species in the world. In the Neotropics, about 184 genera and 836 species are included in 12 of the world's 16 families. For each family, we provide a diagnosis; an overview of the classification; information on the general life history, ecology, and economic importance; and comprehensive keys to subfamilies, tribes, and genera for the Neotropical Region, including Mexico, Central and South America, and the West Indies.

16.1 Introduction

The Lygaeoidea represent the second largest superfamily within the Pentatomomorpha with more than 4,200 species worldwide (Henry 2009). Though the superfamily currently is recognized by most contemporary workers, its status has fluctuated. For example, Štys (1961, 1967) grouped the Lygaeoidea and Pyrrhocoroidea with the Coreoidea but kept the superfamily Piesmatoidea; Henry and Froeschner (1988) accepted the Lygaeoidea but retained Piesmatoidea as a separate superfamily;

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Schaefer (1993) also recognized Lygaeoidea but included the Piesmatidae and Idiostolidae; and Henry (1997a) recognized six superfamilies within the infraorder based on a cladistic analysis, merging the Piesmatoidea with the Lygaeoidea and giving nearly all subfamilies within the Lygaeidae (sensu lato) family status. More recently, Li et al. (2005), in using molecular sequence data, concluded that the Berytidae and Piesmatidae nested within the Pyrrhocoroidea, making the Lygaeoidea paraphyletic. Given the strong morphological support for a monophyletic Lygaeoidea Henry (1997a), including the Berytidae and Piesmatidae, the acceptance of such a novel hypothesis needs further investigation (Forero 2008).

We recognize 12 of the 16 families within the Lygaeoidea as occurring in the Neotropical Region, following Henry (1997a). For each family, we give a diagnosis, an overview of the classification, and keys to all of the subfamilies, tribes, and genera. In addition, we provide a brief overview of the general life history, habits, ecology, and economic importance of the major lygaeoid species.

The Artheneidae are all Old World, except for two Palearctic species, *Chilacis typhae* (Perrin) (Wheeler and Fetter 1987) and *Holcocranum saturejae* (Kolenati) (Hoffman and Slater 1995), recently established in the United States. *Polychisme poecilus* (Spinola), a South American species previously placed in Artheneidae (Slater and Brailovsky 1986), has been shown to belong in the lygaeid subfamily Ischnorhynchinae (Kerzhner 1997). The Cryptorhamphidae, containing only two genera and four species, are restricted to the Australian Region (Hamid 1971; Cassis and Gross 2002), and the Malcidae, with three genera and about 29 species, are restricted to the Oriental and Palearctic regions (Štys 1967; Kerzhner 2001). The Meschiidae, the most recently recognized family of Heteroptera, was described from Australia and India to accommodate the genus *Meschia* Distant, containing four species, the new genus *Neomeschia* Malipatil, and the new species *N. queenslandicus* Malipatil (Malipatil 2014).

Our classification closely aligns with Sweet's (2000a) interpretation of the Lygaeoidea, with the exception of his proposal to elevate the lygaeid (sensu stricto) subfamilies Ischnorhynchinae and Orsillinae to family status, but without giving specific character information to support his hypothesis. As a consequence, we feel that the strong character support for a monophyletic Lygaeidae (Henry 1997a), which includes these two subfamilies and the Lygaeinae, precludes any argument to separate them until new evidence is offered.

Slater (1964a) and Slater and O'Donnell (1995) cataloged the Lygaeidae (sensu lato) of the world; Ashlock and Slater (1988) cataloged the Nearctic species, which includes numerous taxa also occurring in the Neotropics; Schuh and Slater (1995) provided a good overview of the subfamilies and tribes; and Henry (1997a) provided a key to help distinguish 15 of the 16 recognized families of Lygaeoidea. There have been a number of outstanding treatments of the Lygaeoidea with keys, including Froeschner's (1981) list and keys to the Ecuadorian Heteroptera and (Froeschner 1985) synopsis of the Galapagos fauna; Slater and Baranowski's (1990) Lygaeidae of Florida; Slater and Brailovsky's (2000) Lygaeidae of Mexico, with keys to tribes and a checklist of species; Peck's (2001) list and keys to the Heteroptera of the Galapagos Islands; Baranowski and Slater's (2005) Lygaeidae of the West Indies; and Dellapé's (2014) Lygaeoidea of Argentina, with keys to genera and a checklist of species. More regional checklists include Paula and Ferreira's (1998, 2000) list for Minas Gerais, Brazil; Cervantes and Brailovsky's (2011) list for Veracruz, Mexico; and the lists for Argentina by Melo et al. (2004) (Corrientes), Melo et al. (2011) (Chaco National Park), and Dellapé and Carpintero (2012) (Buenos Aires Hills). Also, although aimed primarily at the North American fauna, this author went by Torre-Bueno's (1946) synopsis and keys and Slater and Baranowski's (1978) *How to Know the True Bugs* are useful for many taxa ranging into Mexico, Central America, and the West Indies.

Sweet (1964a, b) detailed the ecology and feeding habits of many widespread New World Lygaeoidea. Sweet (2000a, b) provided an especially thorough overview of the economic importance of many of the most important taxa in the superfamily.

16.2 Life History, Ecology, and Economic Importance

The Lygaeoidea are a diverse, highly successful group of true bugs found in all zoogeographic regions. Important reviews of the habits, life history, and economic importance include Sweet (1960, 1964a, b, 2000a) and Schuh and Slater (1995) and the many papers cited in these works. Many lygaeoids have attracted considerable attention as model species for the study of insect physiology (Slater and O'Donnell 1995) and agriculture (Sweet 2000a). More recently, Burdfield-Steel and Shuker (2014) provided an overview emphasizing their behavior, evolution, and ecology.

Lygaeoid nymphs typically are associated with the adults (Schuh and Slater 1995) and are often gregarious (Aller and Caldwell 1979). Although parental care is widespread in the Heteroptera, no evidence has been found for this behavior within the Lygaeoidea. A number of species in temperate areas, including *Lygaeus equestris* (L.) and *L. simulans* Deckert, show reproductive diapause and migratory capabilities affected by temperature and photoperiod (Solbreck 1979; Dingle et al. 1980). These adaptations allow them to avoid or survive low temperatures during the winter months, as well as to migrate by following seasonal patterns and host plant abundance (Dingle et al. 1980; Attisano et al. 2013).

Wing modifications within the Lygaeoidea fall into four categories (Slater 1977): (1) aptery, or the complete absence of wings; (2) sub-brachyptery, where the forewings extend only to the end of the fifth abdominal tergite; (3) brachyptery, where the forewings are reduced and do not cover the sixth and seventh abdominal terga and the hind wings are reduced but usually not flaplike; and (4) macroptery, where the clavus and corium are distinct, the membrane is well developed, and the hind wings are elongate. Flightless morphs are favored by habitat permanency (Slater 1977).

Slater (1977) and Slater and Baranowski (1990) recognized three major lygaeoid habitats: arboreal, geophilic, and laminophilic. Many arboreal species live on plants above ground level. These species are fully winged and usually readily fly when disturbed. Geophiles live on the ground in the litter layer, where they feed on fallen seeds. A number of the geophilous species may climb plants to feed on mature seeds, but most spend most of their lives on the ground. Laminaphiles live between the sheaths of leaves and stems of grasses, sedges, and rushes. Unlike arboreal species, they often are brachypterous (Slater and Baranowski 1990).

The feeding habits of seed bugs were extensively discussed by Sweet (1960, 1964a, b, 2000a). Most lygaeids feed on seeds or plant sap, whereas only a few are predatory. They have piercing-sucking mouthparts, which are made up of the mandibles and maxillae modified to form needlelike stylets lying within a grooved labium (Schuh and Slater 1995). Feeding methods can be divided into two "types": "stylet-sheath" feeders and "lacerate-flush" feeders (Schuh and Slater 1995; Sweet 2000a). The majority of Lygaeoidea are lacerate-flush feeders, a method commonly used by Miridae and other heteropterans that feed on portions of the plant rich in nutrients, such as seeds (Schuh and Slater 1995; Wheeler 2001), whereas the families Blissidae, Malcidae, and Colobathristidae are predominantly sap feeders.

16.3 General Characteristics and Diagnoses of the Lygaeoidea

Henry (1997a) documented the paraphyly of Lygaeidae as treated by previous authors (e.g., Slater 1964a; Slater and O'Donnell 1995; Schuh and Slater 1995). That the Berytidae, Colobathristidae, Malcidae, and Piesmatidae nested within the Lygaeidae in his analysis provided sufficient evidence to either reduce these well-defined families to subfamily status within the Lygaeidae (sensu lato) or to elevate many of the subfamilies within the paraphyletic Lygaeidae to family level. Henry (1997a) chose the latter as the more informative strategy to reflect his hypothesized phylogeny, based on three synapomorphies, the reduced venation nearly always lacking closed cells on the hemelytral membrane, and the incrassate fore femora found in all basal taxa but lost in a number of distal groups. Thus, 16 families are now recognized in the superfamily Lygaeoidea.

The following key modified from Henry (1997a) and Dellapé (2014) will distinguish the Neotropical lygaeoid families.

Key to the Neotropical families of Lygaeoidea

1. Abdominal spiracles on segment II ventral 2
– Abdominal spiracles on segment II dorsal 4
2. Trichobothria present on head; ovipositor, at most, dividing abdominal sternite VII; suture between abdominal sterna IV and V usually curving anteriorly and usually ending before attaining lateral abdominal margin, except in Plinthisinae .... Rhyparochromidae
– Trichobothria never present on head; ovipositor dividing at least sternites VI and VII; suture between abdominal sterna IV and V straight, always attaining lateral abdominal margin 3

3. Profemora weakly incrassate, little thicker than metafemora; base of hemelytral membrane with a distinct closed cell .... Heterogastridae
– Profemora strongly incrassate, much thicker than metafemora; base of hemelytral membrane without a closed cell .... Pachygronthidae
4. Tarsi two segmented; ocelli present or absent; trichobothria lacking on abdominal segments IV and V, often lacking on other segments as well .... Piesmatidae
– Tarsi three segmented; ocelli present; trichobothria present on abdominal segments IV and V 5
5. Each ocellus nearly encircled by a distinct groove 6
– Each ocellus not encircled by a groove 11
6. Abdominal spiracles on segments V and VI ventral .... Colobathristidae
– Abdominal spiracles on segments V and VI dorsal 7
7. Connexiva on abdominal segments V to VI produced into conspicuous dentate lobes .... Malcidae (Old World only)
– Connexiva on abdominal segments V to VII simple, never produced into conspicuous lobes 8
8. First antennal segment long, slender, often apically clavate, subequal in thickness to and nearly always longer than segments II and III .... Berytidae
– First antennal segment short, stout, barrel shaped, much shorter and thicker than segments II and III 9
9. Hemelytra impunctate or with only a few indistinct punctures, corium hyaline to translucent beyond constricted base; apex of scutellum bifid; head broad, eyes substylate, vertex wider than anterior width of pronotum .... Ninidae
– Hemelytra distinctly punctate on clavus and corium, corium opaque throughout, never constricted; apex of scutellum rounded or acute; head not broadened, eyes never substylate, vertex always narrower than anterior width of pronotum 10
10. Buccula short, not extending posteriorly beyond bases of antennae; abdominal trichobothria present on sternites II to VII .... Cymidae
– Buccula long, extending posteriorly to base of head; abdominal trichobothria present only on sternites V and VI .... Cryptorhamphidae (Old World only)
11. Abdominal spiracles on segments III and IV ventral 12
– Abdominal spiracles on segments III and IV dorsal 13
12. Lateral pronotal margin explanate or with a wide flattened carina; female abdomen rounded caudally; male abdominal sternite VII without clusters or combs of setae ventrally ....
.... Artheneidae (Old World, except for two introduced Nearctic species)
– Lateral pronotal margin rounded or, at most, weakly carinate; female abdomen often rounded caudally; male abdominal segment VII with transverse combs or clusters of setae ventrally .... Oxycarenidae
13. Abdominal spiracles on segments V to VI ventral; sutures between tergites 4/5 and 5/6 curving forward through middle .... Geocoridae
– Abdominal spiracles on segments V to VI dorsal; all abdominal tergites transverse, sutures never curving forward 14

14. Abdominal spiracles on segment VII dorsal; each pronotal callus with an impressed, transverse, usually shiny groove; scutellum usually with a cross-shaped carina...Lygaeidae
– Abdominal spiracles on segment VII ventral; pronotal calli without impressed grooves; scutellum without a cross-shaped carina................................Blissidae

16.4 Family Berytidae

16.4.1 General Characteristics and Diagnosis

Berytidae, commonly referred to as stilt bugs, comprise a small group of morphologically diverse lygaeoids. Typical stilt bugs, such as the metacanthine genera *Jalysus* Stål and *Metacanthus* Costa, are elongate, slender insects, with long slender legs and antennae, often as long as or longer than the body. Other taxa, however, deviate from this general appearance. Members of the genus *Hoplinus* Stål have spindle-shaped bodies and shorter and stouter legs and antennae and often are armed with spines on the head, pronotum, and hemelytra, species of *Parajalysus* Distant are more robust and armed with three long, erect spines on the pronotum, and the recently described *Cuscohoplininus pagoreni* Dellapé and Carpintero has only a single spine on the middle of the anterior pronotal lobe (Dellapé and Carpintero 2007). Other taxa, such as *Pronotacantha* Uhler, have spines on the pronotum and scutellum and distinctly banded appendages, those of *Phaconotus* Harris are adorned with pearl-like tubercles on the anterior lobe of the pronotum, and the genus *Diabolonotus* Henry has two anteriorly directed “devil-like,” pronotal horns.

Synapomorphies defining the family are the elongate bilobed head; basally tapered buccula; long, slender, apically clavate first antennal segment; basally narrowed scutellum; subparallel to basally constricted hemelytra; grooved metasternum; dentate claws; grooved, quadrate abdominal segment II; undivided abdominal segment VII in females; hidden dorsal spiracles; and midlateral position of the trichobothria on abdominal segment III (Henry 1997b, c).

16.4.2 Classification and Diversity

Thirty-seven genera and about 174 species of Berytidae are known in the world (Henry and Froeschner 1998; Henry 2002, 2007; Dellapé and Carpintero 2007; Cai et al. 2011, 2013). The family is separated into three subfamilies and six tribes: the Berytinae (and Berytini and Berytinini), Gampsocorinae (and Gampsocorini and Hoplinini), and Metacanthinae (and Metacanthini and Metatropini) (Henry 1997b).

All three subfamilies but only four of six tribes are known from the Neotropical Region. The Neotropical Berytinae are represented only by the widespread North American *Neoneides muticus* (Say), which also occurs in Baja California, Mexico. The Neotropical Gampsocorinae are represented only by the genus *Gampsocoris* Fuss and four species in the nominate tribe Gampsocorini and nine genera and 36 species in the Hoplinini (Henry and Froeschner 1998; Henry 2002; Dellapé and Carpintero 2007). Two genera and 12 species of Neotropical Metacanthinae are known, all of which are placed in the nominate tribe Metacanthini (Henry and Froeschner 1998; Henry 2007).

Most early work on Neotropical berytids was limited to descriptions of a few new genera and species. Stål (1874) provided the first synopsis of the family with the first keys to genera and the species of *Jalysus*. Most subsequent papers were mostly descriptive (e.g., Distant 1880–1893; Horváth 1905), until McAtee's (1919) review of the Nearctic fauna, which included several Neotropical genera. Harris (1943) added additional South American genera and species but little was provided to aid identification until berytid specialist J. M Štusák (e.g., 1967, 1968, 1971, 1973, 1977) provided a series of well-illustrated descriptions of new genera and species and clarification of previously confused taxa. Other important works include Štusák and Cobben's (1975) keys to the Antillean species and Froeschner's (1981) checklist and keys to the Ecuadorian genera and species. More recently, Henry (1997c) monographed the family for the Western Hemisphere, treating 13 genera and 52 species, including 12 genera and 49 species from the Neotropics. Subsequently, Henry (2002) reviewed the genus *Hoplinus*, clarified the identity of the type species, *H. spinosissimus* Signoret and described the new species *H. paulai* from Brazil; Henry (2007) described the new species of *Jalysus ossesae* from Brazil; and Dellapé and Carpintero (2007) described the new hoplinine genus and species *Cuscohoplininus pagoreni* from Peru.

The following keys to the Neotropical subfamilies, tribes, and genera of Berytidae are modified from Henry (1997c).

Key to the Neotropical subfamilies of Berytidae

1. Head, pronotum, and undersurface of thorax bordering rostral sulcus always clothed with appressed sericeous or woolly pubescence; ventral surface of abdomen deeply punctate (except Old World genus *Yemmatropis*) .... Berytinae
– Head, pronotum, and undersurface of thorax along the rostral sulcus without appressed sericeous or woolly pubescence; ventral surface of abdomen never punctate 2
2. Metathoracic scent channel smooth, extended onto an elongate spout or digitiform spine (except Old World genus *Metatropis*)........................ Metacanthinae
– Metathoracic scent channel lined with overlapping scalelike plates, extended onto a pouchlike structure, or scent channel and spout completely absent, at most, with a blunt to elongate tubercle comprised of honeycombed chambers .... Gampsocorinae

Subfamily Berytinae Puton

Only one genus and species of this subfamily, belonging to the tribe Berytini Puton, occurs in the Neotropical Region. The widespread *Neoneides muticus* (Say) occurs throughout much of the United States and Canada and into northern Mexico (Henry 1997c).

Subfamily Metacanthinae

Only the nominate tribe Metacanthini occurs in the Neotropical Region.

Key to the genera of Neotropical Metacanthini

1. Ostiolar spout ending in an acutely produced apical spine (Fig. 2).... *Jalysus* Stål
– Ostiolar spout without an apical spine, instead apically rounded and weakly recurved near the level of the hemelytra .... *Metacanthus* Costa

Subfamily Gampsocorinae Southwood and Leston

Key to the Neotropical Tribes of Gampsocorinae

1. Ostiolar scent channel distinct, set within a pouchlike spout lined with overlapping scalelike plates; each side of pronotal collar with an erect spine or tubercle ....Gampsocorini
– Ostiolar scent channel absent, never with a pouchlike spout; pronotum often variously armed with spines or tubercles, but never with a distinct collar having a spine or tubercle on either side ....Hoplinini

Tribe Gampsocorini

Gampsocoris Fuss (Fig. 1) is the only Neotropical genus belonging to this tribe. Henry (1997c) provided a key to the four known species.

Tribe Hoplinini

The nine genera included in this tribe are restricted to the Western Hemisphere. Henry (1997c) revised the group and included keys to species.

Key to the Neotropical genera of Hoplinini

1. Posterior lobe of pronotum armed with erect spines 2
– Posterior lobe of pronotum without spines 4
2. Head with five or more median spines... *Hoplinus* Stål

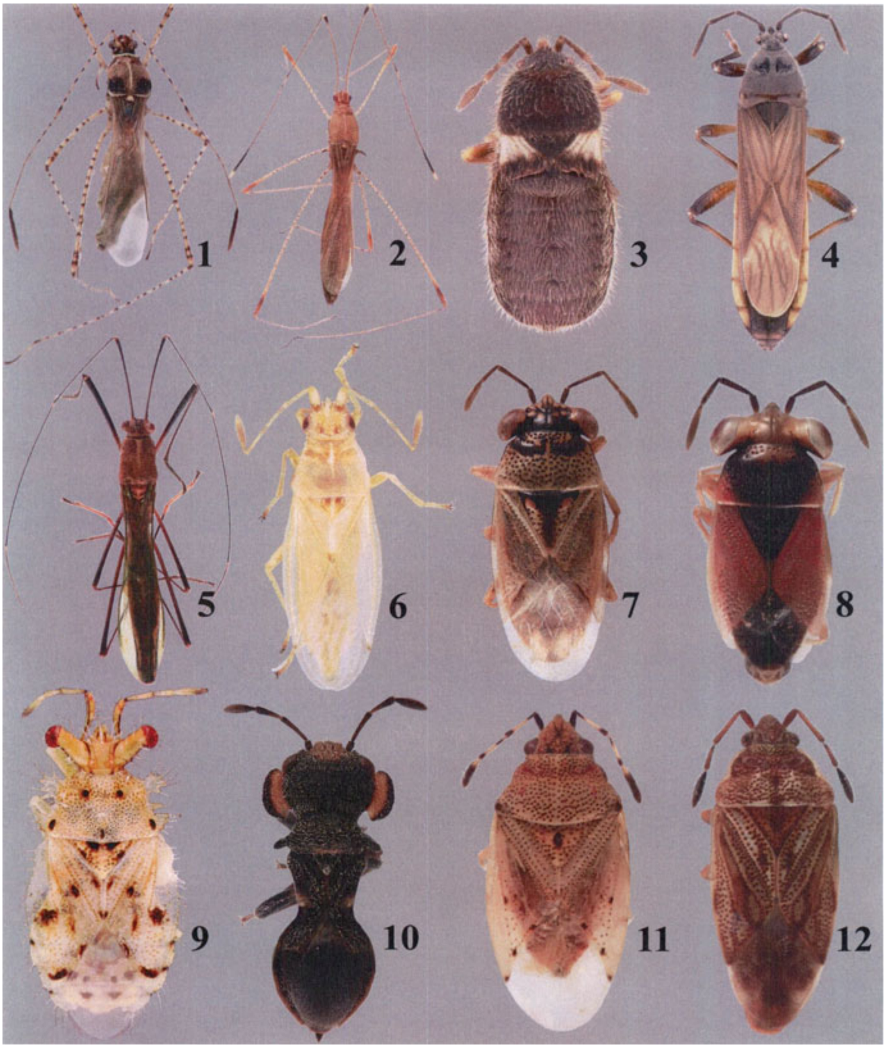

Plate 16.1 Figs. 1–12. 1, *Gampsocoris tuberculatus* Štusák (Berytidae: Gampsocorinae). 2, *Jalysus sobrinus* Stål (Berytidae: Metacanthinae). 3, *Blissus parasigaster* Drake (Blissidae). 4, *Patritius grossus* Haglund (Blissidae). 5, *Colobasiastes similis* Horváth (Colobathristidae). 6, *Cymodema breviceps* Stål (Cymidae: Cyminae). 7, *Geocoris callosulus* Berg (Geocoridae: Geocorinae). 8 *Isthmocoris imperialis* Distant (Geocoridae: Geocorinae). 9, *Epipolops frondosus* Herrich-Schaeffer (Geocoridae: Pamphantinae). 10, *Cephalocattarus waorani* Slater and Henry (Geocoridae: Pamphantinae). 11, *Kleidocerys virescens* (F.) (Lygaeidae: Ischnorhynchinae). 12, *Polychisme ferruginosus* (Stål) (Lygaeidae: Ischnorhynchinae) (Photos by G Ouellette)

– Head without median spines, at most, with a small rounded tubercle on vertex or a slender spine on middle of posterior lobe 3

3. Pronotum with three rows of long, slender spines, one row along each lateral margin and one along meson; posterior lobe of head with six white tubercles, the middle one often spinelike .... *Pronotacantha* Uhler

– Pronotum with four stout spines, one on anterior lobe and three along basal margin of posterior lobe; posterior lobe of head without tubercles .... *Parajalysus* Distant

4. Base of pronotal disc with three high, acute ridges; head and pronotum with a well-developed median carina; legs and antennae with pilose setae three or more times the diameter of the segments .... *Metajalysus* Štusák

– Base of pronotal disc often convex, but never with three high ridges; appendages with or without pilose setae three or more times diameter of segment.................. 5

5. Scutellum hidden by a strongly explanate basal edge of pronotum; body and appendages with erect, bristlelike or long, simple setae; metafemora distinctly bowed 6

– Scutellum clearly visible and armed with a distinct spine or tubercle; body and appendages without bristlelike or pilose setae; metafemora not bowed 7

6. Anterior lobe of pronotum with two long, stout, anteriorly directed, blunt spines or tubercles; side of pronotum without a swollen protuberance visible from dorsal aspect; appendages with long, pilose setae, setae on tibiae three or four times longer than the diameter of the respective segments .... *Diabolonotus* Henry

– Anterior lobe of pronotum unarmed, without stout spines; side of pronotum with a swollen protuberance visible from dorsal aspect; appendages sometimes with erect, bristlelike setae, but those on tibiae at most subequal to diameter of respective segments.. *Xenoloma* Harris

7. Anterior lobe of pronotum with an erect spine at middle between calli .... *Cuscohoplininus* Dellapé and Carpintero

– Anterior lobe of pronotum lacking an erect spine... 8

8. Anterior lobe of pronotum with 6–11 white, rounded tubercles; posterior edge of pronotum unarmed; posterior lobe of head with a short white tubercle between ocelli and often with a white tubercle on either side of each ocellus .... *Phaconotus* Harris

– Anterior lobe of pronotum with only five white, rounded tubercles restricted to narrow collar region (two rounded ones on either side and one in between two erect, white spines); posterior edge of pronotum with four upturned tubercles; posterior lobe of head without tubercles .... *Oedalocanthus* Henry

16.5 Family Blissidae

16.5.1 General Characteristics and Diagnosis

The Blissidae, or chinch bugs, are elongate to broadly oval, often flattened to access leaf sheaths of their hosts, and range in size from less than 3 mm to more than 15 mm. They are recognized by the often entirely or partially pruinose surfaces of head and pronotum, a tubercle on the genital capsule, the peculiarly winged sperm reservoirs in many taxa, and the dorsal position of the abdominal spiracles and by being the only lygaeoid group to feed entirely on plant sap, rather than seeds. Blissids range from fully winged to frequently short winged or brachypterous, having only remnant wing pads as in the genera *Blissus* Burmeister and *Ischnodemus* Fieber or even the complete loss of wing pads as in the genera *Aulacoblissus* Slater and *Howdenoblissus* Štys.

16.5.2 Classification and Diversity

The Blissidae comprise about 51 genera and 436 species worldwide (Cassis and Gross 2002; Henry 2009). Only 16 genera and about 109 species are known from the Neotropical Region (Slater 1979; Slater and O'Donnell 1995; Dellapé and Montemayor 2009). Of these, about 72 % are in the genera *Blissus* (12 spp.), *Ischnodemus* (34 spp.), *Patricius* Distant (12 spp.), and *Toonglasa* Distant (21 spp.; see discussion below). Slater (1979) monographed the world fauna and provided keys to all genera and most species except for the genus *Blissus*. Although Leonard (1968a) studied the species of *Blissus* for eastern North America and described a few new species (Leonard 1968b, 1970), members of the genus remain difficult to identify and are in great need of revision. Slater and Brailovsky (1983, 1990), in revising the primarily Neotropical genus *Toonglasa* Distant, synonymized *Extarademus* Slater and Wilcox (1966) and provided keys to the 21 known species. Slater (1986b) established the genus *Aulacoblissus* to accommodate a new micropterous species from Venezuela, Štys (1991) described *Howdenoblissus slateri*, a similar-appearing apterous species from Colombia, and Brailovsky and Barrera (2012) added *Napoblissus foreroi*, also with greatly abbreviated hemelytra from Ecuador. Dellapé and Montemayor (2009) described the most recently recognized species of *Ischnodemus* and provided descriptions of the male and immature stages of *I. subflavus* Slater and Wilcox. Henry (1997a) elevated Blissinae to family status.

The following key to genera was created in part from Slater (1979) and in part based on our original research. In our opinion, the genus *Toonglasa* is not monophyletic as now interpreted. As a consequence, until additional revisionary studies can be conducted, we are reestablishing *Toonglasa* as a monotypic genus, containing only the type species *T. forficuloides* Distant and resurrecting *Extarademus* to accommodate the remaining 20 species, including its type species, *Macropes collaris* Signoret, as designated by Slater and Wilcox (1966).

Key to the Neotropical genera of Blissidae

1. Fore coxal cavities open behind 2
– Fore coxal cavities closed behind 9
2. Pronotum at least partially pruinose 3
– Pronotum shiny, without pruinose areas 5
3. Pronotum entirely pruinose (Fig. 3) .... *Blissus* Burmeister
– Anterior half of pronotum shiny; posterior half pruinose 4
4. Membrane entirely white; posterior margin of pronotum tan, contrasting with a darker anterior area .... *Caveloblissus* Slater and Wilcox
– Membrane dark brown, with a subbasal pale band; posterior pronotal lobe entirely dark .... *Praeblissus* Barber
5. Macropterous to micropterous (with at least short wing pads) 6
– Apterous (without wing pads) 7
6. Abdominal venter with a prominent stridulitrum on segments 3 to 6; metathoracic scent-gland auricle simple and rounded; only fore femur with one large and several small spines .... *Heteroblissus* Barber
– Abdominal venter lacking a stridulitrum; metathoracic scent-gland auricle strongly produced anteriorly; all femora with spines .... *Praetorblissus* Slater
7. Fore femur lacking spines .... *Howdenoblissus* Štys
– Fore femur with one or two spines 8
8. Fore femur with only one small spine; scutellum lacking a median elevation .... *Aulacoblissus* Slater
– Fore femur with two spines, one large and one small; scutellum with a median elevation 9
9. Labium short, not reaching fore coxae; pronotum pruinose .... *Patritiodemus* Slater and Ahmad
– Labium longer, always reaching fore coxae or beyond; pronotum shiny or in part pruinose 10
10. Fore femur lacking spines .... *Ischnodemus* Fieber
– Fore femur with one or more spines 11
11. Fore femur with only one spine 12
– Fore femur with two or more spines 14
12. Membrane composed of numerous small reticulate cells .... *Reticulatodemus* Slater and Wilcox
– Membrane without small reticulate cells 13
13. Broad flattened species; fore femur strongly incrassate; pro- and mesosternum grooved to receive labium; each side of seventh abdominal segment in males with a prominent posteriorly directed projection; scent-gland auricle relatively broad, slightly curving forward distally, and distinctly raised above the evaporative surface .... *Toonglasa* Distant, revised status
– Slender, elongate species; fore femur not strongly incrassate; pro- and mesosternum not grooved to receive labium; seventh abdominal segment in males without projections; scent-gland auricle slender, curving forward, and flat against evaporative surface .... *Extarademus* Slater and Wilcox

14. Fore femur with two spines; head and pronotum with scalelike setae .... *Xenoblissus* Barber
– Fore femur with three or more spines 15
15. Relatively slender species; only fore femur multispinose, middle and hind femora without spines .... *Procellademus* Slater and Wilcox
– All femora with multiple spines 16
16. Body broad and strongly flattened; head shiny; pruinose areas of pronotum confined to the area around collar and sometimes a narrow line across the transverse impression .... *Riggiella* Kormilev
– Body elongate and not flattened; head pruinose; pronotum usually at least in part pruinose (Fig. 4) .... *Patritius* Distant

16.6 Family Colobathristidae

16.6.1 General Characteristics and Diagnosis

The Colobathristidae (Fig. 5) comprise a small group of tropical bugs with about half the known genera found in the Neotropical Region. They range from about 6.0 mm to over 20 mm. They are characterized by their slender elongate bodies, long slender legs and antennae, bulging eyes, quadrate bilobed thorax, slender often spined scutellum, hyaline hemelytra with few hardly visible membranal veins, and slender elongate abdomen constricted at the base. Colobathristids also possess characters appearing in part coreoid and lygaeoid (Henry 1997a). Štys (1966) indicated they have a platelike ovipositor similar to those in the Coreoidea or Pyrrhocoroidea but internal genital structures similar to those in the malcid line. Cobben (1968) indicated that the eggs were most similar to the Coreoidea. Kumar (1968), however, considered the three-lobed salivary glands and the fingerlike gastric ceca on the midgut "decidedly lygaeid features" (sensu lato), as well as the aedeagus, the arrangement of the trichobothria, and the position of the spiracles. In Henry's (1997a) phylogenetic analysis, the colobathristids nest within the Lygaeoidea, forming a sister-group relationship with the Berytidae.

16.6.2 Classification and Diversity

Twenty-five genera and more than 80 species of Colobathristidae (Kerzhner 2001; Štys and Exnerová 2012) are placed in two subfamilies, the nominate Colobathristinae and the monogeneric Dayakiellinae, containing only two Indonesian species of *Dayakiella* Horváth (Štys 1966). Štys and Exnerová (2012) provided a key to the 13 Old World genera. Thirteen genera and about 40 species are recorded from the Neotropics. *Phaenacantha saileri* Kormilev, described from Guatemala, is the only representative of an otherwise exclusively Old World genus. Horváth (1904) monographed the family and Kormilev (1949a, 1949b, 1951) described additional new Neotropical taxa. Carvalho and Henry (1986) described the new genus *Parathristes* to accommodate *P. carajaensis* from Pará, Brazil, the largest species of the family yet discovered. Štys and Henry (2015) added the new genus *Neolabradoria* and new species *N. inexpectata* from Peru, provided the replacement name *Bradaloria* for the preoccupied *Labradoria* Kormilev, and gave a revised key to the Neotropical genera.

Kormilev (1951) provided a key to the Neotropical genera, modified from Horváth (1904), and Carvalho and Costa (1989) provided a well-illustrated update, with the addition of *Parathristes*. The following key is modified from Štys and Henry (2015). The genus *Curupira* Distant (1888), tentatively placed as a synonym of *Colobathristes* Burmeister by Carvalho and Costa (1989), is not included until type material is studied and its identity clarified.

Key to the genera of Neotropical Colobathristidae

1. Side of head with a distinct nearly straight to lunate stridulitrum 2
– Side of head without a stridulitrum.. 7
2. Scutellum with a long, erect, spine, usually longer than the scutellum 3
– Scutellum without an erect spine, apex spiniform, horizontal or subhorizontal, usually shorter than the scutellum.. 6
3. Distance between ocelli greater than space from an ocellus to an eye; sternite IV as long as III...*Diascopoea* Horváth
– Distance between ocelli much less than distance between an ocellus and an eye 4
4. Antennal segment IV with a distinct white ring at base....................................... ....*Neocolobrathristes* Kormilev
– Antennal segment IV without a white ring at base 5
5. Scutellar spine nearly glabrous; length of antennal segments III and IV subequal; vertex with one groove...*Calliseidus* Horváth
– Scutellar spine with numerous long setae; antennal segment IV distinctly longer than III; vertex with two grooves ....*Trichocentrus* Horváth
6. Anterior lobe of pronotum bulbous or horn shaped, higher than head; scutellar spine horizontal or subhorizontal; undersurface of fore tibia with distinct denticles ....*Peruda* Distant
– Anterior lobe of pronotum not bulbous, lower than the head and posterior lobe; scutellum without horizontal spine, upper surface with a small dent or impression; fore tibia without distinct denticles.......................................*Perudella* Kormilev
7. Scutellum with a long, erect, spine, usually longer than scutellum..................... 8
– Scutellum without an erect spine, apex spiniform, horizontal or subhorizontal, usually shorter than scutellum 11
8. Head and anterior lobe of pronotum almost glabrous, with only thin, simple setae 9
– Head and anterior lobe of pronotum densely coated with adpressed, woolly, silvery pubescence 10

9. Rostrum extending only to bases of fore coxae; anterior lobe of pronotum much longer than posterior lobe .... *Parathristes* Carvalho and Henry
– Rostrum extending nearly to middle coxae; anterior lobe of pronotum shorter than posterior lobe...*Phaenacantha* Horváth
10. Distance from an ocellus to an eye about twice the distance between ocelli; rostral segment IV longer than III; ventral edge of genital capsule with a sharp, protruding process..*Carvalhoia* Kormilev
– Distance from an ocellus to an eye subequal or slightly greater than the distance between ocelli; rostral segments III and IV equal in length; ventral edge of genital capsule lacking a sharp process ....*Colobathristes* Burmeister
11. Distance from an ocellus to an eye less than distance between ocelli; vertex with a median groove in front of ocelli.. 12
– Distance from an ocellus to an eye three times greater than distance between ocelli; vertex in front of ocelli with two shallow grooves............................... 13
12. Distance between ocelli slightly greater than distance from an ocellus to an eye; scutellum subtriangular, with a slender, pointed, horizontal spine (meso- and metanotum covered); hemelytra narrower than abdomen.................................... ....*Bradaloria* Štys and Henry
– Distance between ocelli subequal to distance from an ocellus to an eye; scutellum transverse, oval, with only a low dentiform tubercle (medial parts of meso- and metanotum exposed); hemelytra as wide as abdomen.. ....*Neolabradoria* Štys and Henry
13. Scutellum with subhorizontal spine visible in lateral aspect; fore femora lacking or with only a few tiny denticles on distal third; antennal segment III short, only about one-third of body length..*Piptocentrus* Horvath
– Scutellum with horizontal spine, not visible in lateral aspect; fore femur with numerous small denticles over entire length; antennal segment III long, longer than half the body length...*Colobasiastes* Breddin

16.7 Family Cymidae

16.7.1 General Characteristics and Diagnosis

New World cymids are small, punctate, usually yellowish-brown bugs, measuring from 3.0 to nearly 5.0 mm. Members of this family have the ocelli nearly encircled by a groove, a short barrel-shaped antennal segment I, a short buccula not extending posteriorly beyond the level with the bases of the antennae, spiracles II to VI dorsal, and the dorsal abdominal scent-gland scars appearing singly between terga 4/5 (*Cymodema* and a few *Cymus*), in twos between terga 3/4 and 4/5 (*Cymus*), and threes between terga 3/4, 4/5, and 5/6 (Ontiscinae).

16.7.2 Classification and Diversity

Nine genera and about 54 species known worldwide (Hamid 1975; Henry 2009) are placed in two subfamilies, the Cyminae and Ontiscinae, of which only the former occurs in the New World. In the Neotropical Region, only two genera and eight species are known. *Cymodema* Spinola contains only two species, with *C. breviceps* (Stål) (Fig. 6) the most widespread, occurring from the United States to Argentina and Brazil, and *C. barberi* Hamid, known only from Mexico. *Cymus* Hahn contains six species, with one known only from Brazil, four recorded from Mexico, and one from Guatemala and Mexico. Hamid (1975) monographed the group as a subfamily and provided keys to the genera and species of the world. Henry (1997a) gave Cyminae family status (minus the Ninini) and hypothesized it as the sister group to the remainder of the "malcid line," including in sequence the Ninidae, Malcidae, Colobathristidae, and Berytidae.

The following key will separate the only two Neotropical cymid genera.

Key to the Neotropical genera of Cymidae

1. First antennal segment not exceeding apex of clypeus; with two dorsal abdominal scent-gland scars between terga 3/4 and 4/5; seventh abdominal spiracle ventral .... *Cymus* Hahn

– First antennal segment exceeding the apex of clypeus; with only one dorsal abdominal scent-gland scar between terga 4/5; seventh abdominal spiracle dorsal (Fig. 6).. *Cymodema* Signoret

16.8 Family Geocoridae

16.8.1 General Characteristics and Diagnosis

Members of this subfamily are readily recognized by their kidney-shaped to stylate eyes, extending laterally beyond the anterior margins of the pronotum; the broad heads; the relatively stout ovoid bodies; and the posteriorly curved abdominal sutures between terga 4/5 and 5/6. In addition, the abdominal spiracles on segments II, III, and IV are dorsal and those on V, VI, and VII usually are ventral (Henry 2009), except for members of the Australian tribe Australocorinae, in which all abdominal spiracles (II–VII) are dorsal (Malipatil 2012).

16.8.2 Classification and Diversity

The Geocoridae, or big-eyed bugs, are a worldwide group comprising 27 genera and about 280 species (Henry 2009, 2013; Malipatil 2012; Rengifo-Correa et al. 2013). The family is separated into five subfamilies: the Australocorinae Malipatil, Bledionotinae Reuter, Geocorinae Stål, Henestarinae Douglas and Scott, and Pamphantinae Barber and Bruner (Slater 1999; Henry 1997a, 2009, 2013; Malipatil 2012). The Australocorinae, including one genus and four species restricted to Australia (Malipatil 2012); the Bledionotinae, containing one genus and species restricted to the Palearctic (Slater 1964a; Péricart 2001); and the Henestarinae, with three genera, are restricted to the Old World, with the exception of the problematic *Coriantipus inopinatus* Bergroth described from Argentina. The Geocorinae occur in all zoogeographic regions and the Pamphantinae are found only in the New World tropics (Henry 2013; Rengifo-Correa et al. 2013), with the exception of one genus and species described from Queensland, Australia (Slater 1981).

The Neotropical Geocorinae are represented by only four genera and about 25 species (Slater 1964a; Slater and O'Donnell 1995), which represents only about 10 % of the world fauna (Readio and Sweet 1982). The eastern US species of *Geocoris* Fallén and *Isthmocoris* McAtee were revised by Readio and Sweet (1982). Brailovsky (2013) provided a key to the fourteen Neotropical species of *Ninyas* Distant. The monobasic geocorine genus *Stenogeocoris* and the species *S. horvathi* were described by Montandon (1913) based on one specimen from Córdoba Province, Argentina; the type specimen is lost and there have been no additional records since Montandon's description.

The Pamphantinae, comprising ten genera and 48 species (Henry 2013; Rengifo-Correa et al. 2013), are separated into three tribes, the Cattarini Slater, the Epipolopini Slater, and the nominate Pamphantini (Slater 1999). Brailovsky (1989b) described one new genus and two new species of Pamphantini and provided a key to the genera. Slater and Henry (1999) reviewed the cattarine genus *Cattarus*, with four new species, and described the remarkable ant-mimetic *Cephalocattarus waorani* from Ecuador. Baranowski and Slater (2005) gave a key to the three genera and 13 species known from the West Indies. Henry (2006) revised the stalk-eyed genus *Epipolops*, described five new species, and provided a key to distinguish the 14 known species, and Henry (2013) described the new genus and species *Cymapamphantus valentineorum* from the British Virgin Islands and provided a checklist and keys to the tribes and genera of the Pamphantinae. Rengifo-Correa et al. (2013) described two additional species of *Epipolops* and provided a revised key to species and a phylogenetic analysis of the genus.

The following key to the genera of Geocorinae is modified from Readio and Sweet (1982) and Baranowski and Slater (2005). The keys to tribes and genera of the Pamphantinae are from Henry (2013).

Key to the Neotropical subfamilies of Geocoridae

1. Sutures on abdominal sterna II, III, and IV fused and without lateral trichobothria; body elongate, antlike .... Pamphantinae
– Sutures on abdominal sterna II, III, and IV entire and with distinct, lateral trichobothria; body more stout, not antlike .... Gecorinae

Key to the Neotropical genera of Geocorinae

1. Claval commissure well developed; clypeus with a slight sulcus; basal three abdominal sterna often fused .... *Ninyas* Distant
– Claval commissure not present; clypeus with a complete median sulcus; basal three abdominal sterna not fused 2
2. Rostral segment II longer than III; eyes stylate, remote from anterior angles of pronotum; ocular suture incomplete, extending laterally from the ocellus around base of eye stalk to apical margin of head, ending at anterior margin of eye (Fig. 8)... *Isthmocoris* McAtee
– Rostral segment II shorter than III; eyes semistylate, sometimes near or in contact with anterior angles of pronotum; ocular suture absent or suture complete, extending laterally from the ocellus, around base of eye stalk to apical margin of head and posteriorly back to ocellus (Fig. 7).. 3
3. Body elongate, about three times longer than wide; pronotum subquadrangular, wider at the level of and slightly constricted behind the calli............................... .... *Stenogeocoris* Montandon
– Body short and stout, never more than twice as long as wide. Pronotum subquadrangular... *Geocoris* Fallén

Key to the Neotropical tribes of Pamphantinae

1. Males and females with a distinct lunate stridulitrum on side of head below eyes and a plectron on inner face of fore femur; male abdomen with a distinct tubercle on each side of segment III; anterior and posterior pronotal lobes separated by a deep transverse impression .... Cattarini
– Males and females without a stridulitrum on head or a plectron on fore femur; male abdominal segment III without a tubercle, though sometimes slightly swollen; pronotal lobes usually not separated by a deep transverse impression . 2
2. Eyes strongly stylate, extending laterally well beyond outer margin of head; pronotum usually with lobes and/or spines along lateral margins; includes only *Epipolops* (Fig. 9) .... Epipolopini
– Eyes not stylate, never extending beyond outer margin of head; pronotum entire, without lateral lobes or spines.. Pamphantini

Key to the Neotropical genera of Cattarini

1. Lateral margins of pronotal lobes unarmed .... *Cattarus* Stål
– Lateral margin of anterior pronotal lobe with a broad winglike process and each humeral angle of posterior lobe with a spinelike projection (Fig. 10) .... *Cephalocattarus* Slater and Henry

Key to the Neotropical genera of Pamphantini

– Anterior femur without a distinct subapical spine 2
– Anterior femur with one or two distinct subapical spines.................................. 3

2. Anterior and posterior lobes of pronotum little separated, without a deep transverse impression; posterior lobe of pronotum almost flat, without swellings .... *Parapamphantus* Barber
– Anterior and posterior lobe of pronotum separated by a deep transverse impression; posterior lobe with a distinct swelling or blunt tubercle on each side .... *Tropicoparapamphantus* Brailovsky
3. Head lacking ocelli 4
– Head with distinct ocelli between eyes 5
4. Anterior pronotal lobe greatly swollen or globose; narrow posterior lobe with a long, slender, curving spine arising at each humeral angle.................................... .... *Abpamphantus* Barber
– Anterior pronotal lobe not greatly swollen, two and half times as long and only slightly wider than posterior lobe; humeral angles unarmed .... *Cymapamphantus* Henry
5. Eyes large and substylate, inner margin of eye extending past anterior angle of pronotum; distance between ocelli less than to subequal to the distance from an ocellus to an eye; posterior half of hemelytra convex or rounded; profemur with two spines (apical spine broken on three specimens examined) .... *Neopamphantus* Barber and Bruner
– Eyes prominent, but not substylate, inner margin of eye not extending past anterior angle of pronotum; each ocellus closer to eye than to each other; hemelytra subparallel throughout; profemur with only one spine .... *Pamphantus* Stål

16.9 Family Heterogastridae

16.9.1 General Characteristics and Diagnosis

This family is recognized by the ventral abdominal spiracles, the lack of trichobothria on the head, the weakly incrassate fore femora, the distinct closed cell at the base of the hemelytral membrane, and the deeply inserted ovipositor often extending to abdominal segment V (Scudder 1962a; Henry 1997a, 2009).

16.9.2 Classification and Diversity

The Heterogastridae are primarily an Old World group comprising about 24 genera and 100 species (Cassis and Gross 2002; Henry 2009), with only two native (Ashlock and Slater 1988) and one introduced (Wheeler and Hoebeke 2013) species of *Heterogaster* Schilling occurring in North America. Only *H. behrensii* (Uhler) gets into northern Mexico as the sole Neotropical member of the family. Scudder

(1962a) provided a key to the genera of the world and Henry (1997a) elevated Heterogastrinae to family status.

16.10 Family Lygaeidae

16.10.1 General Characteristics and Diagnosis

The Lygaeidae are recognized by the impressed, often shiny, transverse line across the calli; the Y-shaped pattern on the scutellum; and the dorsal position of abdominal spiracles II through VII. Members of the subfamily Ischnorhynchinae are dull brown to reddish brown, elongate-oval, nearly glabrous bugs having the clavus punctate and the base of the pronotum entire and not depressed on either side of the scutellum. The Lygaeinae are usually moderate to large, often aposematically colored, orange and red bugs having an impunctate clavus, the base of the pronotum depressed on either side of the scutellum, and a distinct subcosta on the hemelytra. The Orsillinae are relatively small, dull, yellowish brown, often pubescent bugs having a depressed area at the base of the pronotum and lacking punctures on the clavus and a subcosta.

16.10.2 Classification and Diversity

The Lygaeidae (sensu stricto) comprise about 102 genera and 970 species worldwide (Slater and O'Donnell 1995; Henry 2009). The family is separated into three subfamilies, the Ischnorhynchinae, Lygaeinae, and Orsillinae (Henry 1997a). Sweet (2000a) suggested that the Ischnorhynchinae and Orsillinae should be given family status. He did not, however, provide information to support his hypothesis; thus, we maintain the family as documented by Henry (1997a). Brailovsky (1982a) and A. ("A" used to distinguish Alex Slater from James A. Slater – i.e., Slater without initials throughout text) Slater (1992) provided keys to the Neotropical genera; Baranowski and Slater (2005) monographed the Lygaeoidea of the West Indies and gave keys to all of the genera and species. Henry (1997a) accorded the Lygaeidae (sensu stricto), including the Ischnorhynchinae, Lygaeinae, and Orsillinae, family status.

The Ischnorhynchinae comprise about 15 genera and 77 species worldwide, with only four genera and nine species known from the Neotropics (Slater 1964a; Slater and O'Donnell 1995; Baranowski and Slater 2005). The primarily Holarctic genus *Kleidocerys* Stephens contains four Neotropical species. *Neokleidocerys* Scudder, with three Neotropical species and previously treated as a subgenus of *Kleidocerys*, was elevated to generic rank by Slater and Brailovsky (1989). *Polychisme* Kirkaldy, with only one species, previously was placed in the family Artheneidae (Slater and Brailovsky 1986) but was returned to Ischnorhynchinae by Kerzhner (1997).

Syzygitis Bergroth, previously considered a synonym of *Polychisme* (Slater 1967), was reinstated by Slater and Brailovsky (1986). Scudder (1962a) revised the subfamily and provided a key to the world genera.

Lygaeinae is largest of the three subfamilies, with about 57 genera and 500 species worldwide. Twenty-two genera and about 175 species are known in the Neotropics (A. Slater 1992; A. Slater and Baranowski 2001). Brailovsky (1982a) and Baranowski and Slater (2005) provided keys to all or a substantial number of the Neotropical genera, and A. Slater (1992) revised the subfamily and provided keys to all New World genera and a checklist of species. Slater and O'Donnell (1995) summarized the many new combinations resulting from A. Slater's (1992) work. A. Slater and Baranowski (2001) described the most recent Neotropical genus, *Melanopleuroides*, from the Dominican Republic. Other important works include Brailovsky's revisions of *Lygaeus* F. (1978), *Craspeduchus* Stål (1979), *Acroleucus* Stål (1980), *Ochrimnus* Stål (1982b), and *Torvochrimnus* Stål (1983), among other important papers. Many lygaeines, such as the genera *Lygaeus* F. and *Oncopeltus* Stål, are aposematically colored red and orange. The vast literature base involving mostly laboratory studies of *Oncopeltus fasciatus* (Dallas), commonly called the large milkweed bug, was compiled by Slater and O'Donnell (1995).

The Orsillinae comprise about 30 genera and 250 species, separated into four tribes (Ashlock 1967a; Henry 2009). In the Neotropics, three tribes, nine genera, and about 46 species are known. Ashlock and Lattin (1963) established *Xyonysius* for ten species previously placed mostly in *Nysius* Dallas, Ashlock (1967a) revised and provided a key to the orsilline genera of the world, and Hamilton (1983) established *Neortholomus* for the New World species of *Ortholomus* Stål. Barber (1947) revised the North America species of *Nysius*, but this work is badly outdated and the Neotropical species remain confused and difficult to identify.

We provide keys to the subfamilies and keys to the genera of Ischnorhynchinae modified from Scudder (1962b), Lygaeinae modified from A. Slater (1992) and Baranowski and Slater (2005), and the Orsillinae modified from Ashlock (1967a).

Key to the Neotropical subfamilies of Lygaeidae

1. Clavus punctate; base of pronotum entire, not depressed .... Ischnorhynchinae
– Clavus impunctate; base of pronotum bordering either side of scutellum depressed or flattened 2
2. Hemelytra with a distinct subcosta and membrane lacking intervannal veins; coloration often in large part red or orange; most species nearly glabrous .... Lygaeinae
– Hemelytra lacking a subcosta and membrane with intervannal veins; coloration dull gray to yellowish brown; species often pubescent .... Orsillinae

Key to the Neotropical genera of Ischnorhynchinae

1. Lateral margin of pronotum lacking a distinct carina; corium with a short row of punctures along claval suture near inner angle and a complete row extending the entire length; middle of hemelytra largely hyaline 2

– Lateral margin of pronotum distinctly carinate; corium with only a single row or two or more entire rows of punctures; middle of corium more opaque.............. 3
2. Anterior half of pronotum narrowed and elongate; corium with apical margin and apex with a rectangular or L-shaped macula.................................... ....*Neokleidocerys* Slater and Brailovsky
– Anterior half of pronotum not narrowed and elongate; corium at most with two small maculae apically (Fig. 11).......................................*Kleidocerys* Stephens
3. All abdominal spiracles dorsal; basal two-thirds of lateral margin of hemelytra broadly explanate, broader at middle than diameter of antennal segment I.......... ....*Syzygitis* Bergroth (Chile)
– Spiracles on abdominal segments III to VII ventral; basal two-thirds of lateral margin of hemelytra only narrowly explanate, subequal at middle to diameter of antennal segment II (Fig. 12)..*Polychisme* Kirkaldy

Key to the Neotropical genera of Lygaeinae

1. Eyes on stalks...*Nicuesa* Distant
– Eyes not on stalks... 2
2. Callus depressed on either side of median carina; hemelytral membrane dark with apical margin or rounded macula clear or hyaline.......................*Acroleucus* Stål
– Callus not depressed or interrupted medially; hemelytral membrane not dark with a hyaline apical area.. 3
3. Pronotum with four transverse depressions behind the calli......... *Ochrimnus* Stål
– Pronotum without four transverse depressions behind the calli 4
4. Scutellum swollen, raised above hemelytra; basal margin of pronotum on either side of scutellum flattened and produced posteriorly (Fig. 14) ....*Oncopeltus* Stål
– Scutellum not swollen; basal margin of pronotum not produced posteriorly...... 5
5. Posterior pronotal lobe, at most, as high mesally as lateral margins; disc flat or nearly flat; median carina on basal third distinct 6
– Posterior pronotal lobe higher mesally than at lateral margins; disc distinctly convex; median carina absent 9
6. Clavus pale, with a dark vein on inner and outer margin..................................... ....*Neacoryphus* Scudder
– Clavus unicolorous... 7
7. Dorsal pubescence short, usually semierect, and dense; membrane uniformly dark ....*Dalmochrimnus* Brailovsky
– Dorsal pubescence short, recumbent, and sparse; membrane usually marked with white.. 8
8. Larger species, length 6 mm or more; membrane dark with narrow lateral margin white or entirely white, with dark veins; brachypters uncommon........................ ....*Melacoryphus* A. Slater

– Smaller species, length usually less than 6 mm; membrane usually with a large, central white spot, if largely white with dark veins, then basal third dark; brachypters common .... *Lygaeospilus* Barber

9. Pronotum coarsely punctate, punctures extending onto disc .... *Oxygranulobaphus* Brailovsky

– Pronotum finely punctate, punctures restricted to depressed areas just before and after calli 10

10. Pronotum dark, at most with anterior angles paler 11

– Pronotum extensively pale, at least with more than anterior angles pale 12

11. Head with pale spots; posterior metapleural margin nearly straight (Fig. 13) ....*Melanopleurus* Stål

– Head without pale spots; posterior metapleural margin distinctly concave (Dominican Republic).........................*Melanopleuroides* Slater and Brailovsky

12. Claval veins either paler or darker than surrounding area 13

– Claval veins concolorous with surrounding area 14

13. Lateral margin of the pronotum dark brown; veins on corium and membrane darker than surrounding areas (Fig. 15)....................*Torvochrimnus* Brailovsky

– Lateral margin of pronotum pale; veins on corium paler than surrounding area; veins on membrane concolorous with surrounding area.................................... ....*Hadrosomus* A. Slater

14. Claval margin bordering scutellum pale, contrasting with dark margin bordering corium or a semicircular, submedian spot 15

– Clavus unicolorous or pale basally and dark apically or with only the commissural margin pale... 16

15. Apical margin of corium red or orange with a narrow outer black border .... *Anochrostomus* A. Slater

– Apical margin of the corium yellow 17

16. Postcallar impression interrupted on either side of median line forming a short accessory branch .... *Craspeduchus* Stål

– Postcallar impression entire, not interrupted on either side of median line ....*Ochrostomus* Stål

17. Pronotum longer medially than wide at anterior margin; hemelytral membrane brown with a pale median line .... *Ektyphonotus* A. Slater

– Pronotum distinctly shorter medially than wide anteriorly; hemelytral membrane not brown with a pale median line.. 18

18. Costal margin of corium pale apically and basally, dark brown to black between; dark markings on corium either restricted to the costal margin and a small discal spot or a triangular spot with the longest side at costal margin; thoracic pleura almost entirely gray or black..*Lygaeus* Fabricius

– Costal margin of corium usually entirely pale, if interrupted, then dark markings of corium forming a subrectangular spot with anterior and posterior edges straight; thoracic pleura with wide pale margins 19

19. Length more than 10 mm; pronotum pale orange with a small, transverse, brown spot on either side of basal margin and a dark quadrate spot on each callus .... *Biblochrimnus* Brailovsky

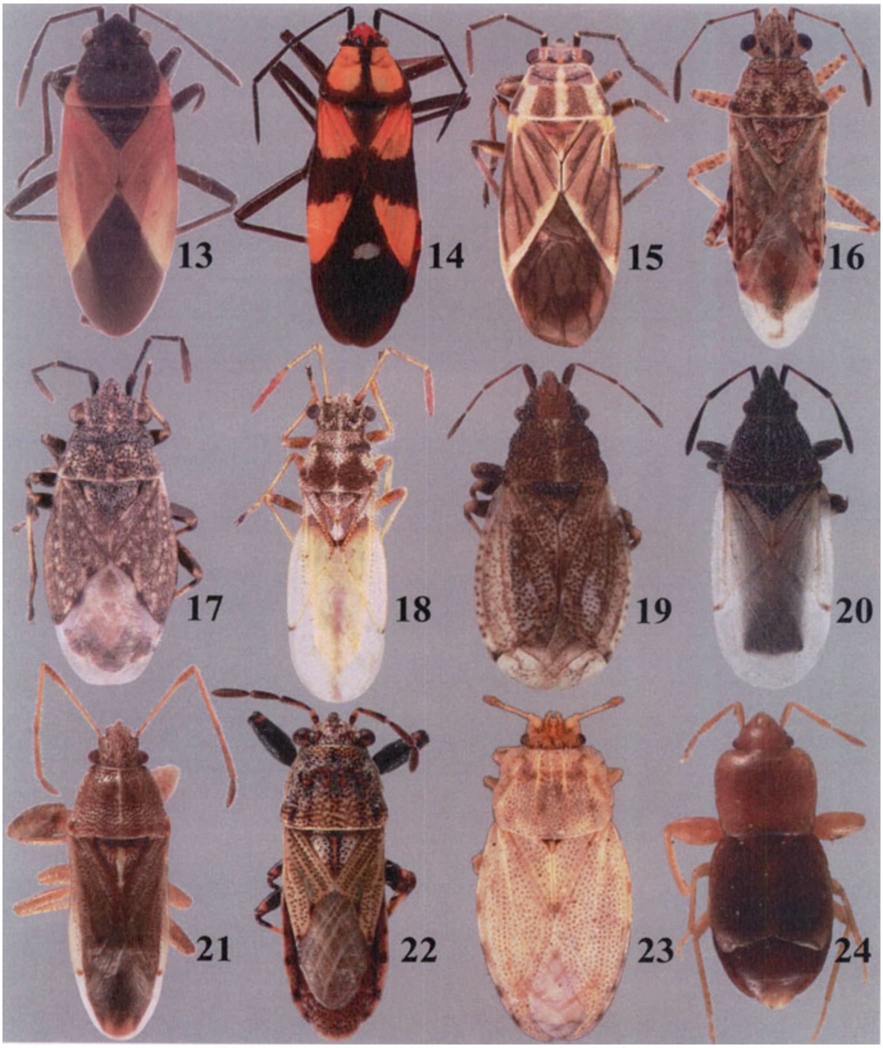

Plate 16.2 Figs. 13–24. 13, *Melanopleurus bistriangularis* (Say) (Lygaeidae: Lygaeinae). 14, *Oncopeltus sexmaculatus* Stål (Lygaeidae: Lygaeinae). 15, *Torvochrimnus poeyi* Guérin-Méneville (Lygaeidae: Lygaeinae). 16, *Neortholomus jamaicensis* (Dallas) (Lygaeidae: Orsillinae). 17, *Nysius irroratus* (Spinola) (Lygaeidae: Orsillinae). 18, *Cymoninus notabilis* (Distant) (Ninidae). 19, *Crophius convexus* Barber (Oxycarenidae). 20, *Oxycarenus hyalinipennis* (Costa) (Oxycarenidae). 21, *Pachygrontha compacta* Distant (Pachygronthidae: Pachygronthinae). 22, *Phlegyas annulicrus* Stål (Pachygronthidae: Teracriinae). 23, *Parapiesma cinereum* (Say) (Piesmatidae). 24, *Plinthisus parvioculatus* Slater (Rhyparochromidae: Plinthisinae) (Photos by G Ouellette)

– Length 7 mm or less; pronotum with pale orange to red, but with at least a large dark quadrate spot on the posterior lobe 20

20. Pronotum uniformly dark brown, with only median line pale .... *Achlyosomus* A. Slater

– Anterior pronotal lobe orange to red; posterior lobe dark, with median line pale 21

21. Head slightly swollen; ocelli lower than vertex when viewed laterally .... *Pseudacroleucoides* Brailovsky

– Head slightly less swollen; ocelli about level with vertex when viewed laterally .... *Latochrimnus* Brailovsky

Key to the Neotropical genera of Orsillinae

1. Costal margin of hemelytron straight to at least level with apex of clavus; fore femur sometimes spined; connexivum often exposed (Orsillini) 2

– Costal margin of hemelytron straight only to level with apex of scutellum; fore femur never spined; connexivum not exposed 4

2. Mesopleuron and propleuron evenly meeting, not overlapping (widespread) (Fig. 16)... *Neortholomus* Hamilton

– Mesopleuron appearing to overlap the propleuron 3

3. Vertex with a carina extending from each ocellus to antenniferous tubercle; head short, anteocular length less than two times length of an eye; labium extending to hind coxae (Brazil)... *Aborsillus* Barber

– Vertex lacking carinae; head elongate, anteocular length more than two times length of an eye; labium long, extending to apex of abdomen (North America and Mexico) .... *Belonochilus* Uhler

4. Hemelytron without a complete row of punctures on either side of claval suture; buccula impunctate (Nysiini) (widespread) (Fig. 17) .... *Nysius* Dallas

– Hemelytron with a distinct row of punctures on either side of claval suture; buccula usually punctate (Metrargini) 5

5. Buccula not extending beyond level with middle of eye (widespread) .... *Xyonysius* Ashlock and Lattin

– Buccula nearly reaching base of head.. 6

6. Antenniferous tubercle acute or quadrate; explanate costal margin of hemelytra with alternating light and dark spots 7

– Antenniferous tubercle not produced; costal margin of hemelytra without alternating light and dark spots 8

7. Scutellum longer than prothorax; veins of corium raised; hemelytral membrane reduced (Juan Fernandez Islands)............................... *Robinsonocoris* Kormilev

– Scutellum shorter than prothorax; veins of corium not raised; hemelytral membrane fully developed (Galapagos Islands)................. *Darwinysius* Ashlock

8. Apex of scutellum rounded; macropterous (brachypters unknown) (Argentina) .... *Balionysius* Ashlock

– Apex of scutellum acute; hemelytra coleopteriform; hemelytral membrane greatly abbreviated (Colombia).. *Coleonysius* Ashlock

16.11 Family Ninidae

16.11.1 General Characteristics and Diagnosis

Most Ninidae range from about 3.0 to 4.0 mm long and are recognized by the broad head, the stylate eyes, the broad vertex, the transverse sulcus before the ocelli, the mostly hyaline and often basally constricted hemelytra, the bifid apex of the scutellum, and the dorsal position of abdominal spiracles II–IV (Scudder 1957; Henry 1997a). The head and pronotum of several taxa are coated with a powdery white residue.

16.11.2 Classification and Diversity

Ninids are a small family comprising five genera and 16 species worldwide (Slater 1964a; Slater and O'Donnell 1995). Scudder (1957) revised the Ninini as a tribe of the Cyminae and provided a key to genera and species. Only three genera and six species of Ninidae occur in the Neotropics. *Cymoninus notabilis* (Distant) is the most widespread New World species, ranging from the southern United States, throughout the West Indies, and into much of South America (Scudder 1957), and *C. wilcoxae* Brailovsky is known only from Mexico (Brailovsky 1975). *Neoninus illustris* Distant occurs from Mexico to Brazil, *N. argentinus* Kormilev is known only from Argentina, and *N. montanellus* Brailovsky occurs in Brazil and Venezuela (Brailovsky 1989a). The monotypic genus *Paraninus* Scudder is represented by *P. gracilis* Scudder, described from Brazil and British Guiana. This small family previously was included as a tribe of the Cyminae prior to its elevation to family status (Henry 1997a). The following key is modified from Scudder (1957).

Key to the Neotropical genera of Ninidae

1. Apical half of first labial segment slender................................*Paraninus* Scudder
– Apical half of first labial segment swollen.. 2
2. Antennal segments II and III more slender than segment IV; distal half of clavus clear or transparent (Fig. 18).. *Cymoninus* Breddin
– Antennal segments II and III as thick as segment IV; distal half of clavus pruinose and opaque ....*Neoninus* Distant

16.12 Family Oxycarenidae

16.12.1 General Characteristics and Diagnosis

Oxycarenids are characterized by the punctate porrect head; hyaline often explanate hemelytra; abdominal spiracles III to VII ventral and II dorsal; lack of lateral trichobothria on sterna III, IV, and V; a median trichobothrium on sternum V; abdominal sutures complete to lateral margins (segments III, IV, and V often fused); a truncate female abdomen; and a transverse comb of glandular setae on the male abdomen (Henry 1997a, 2009; Henry and Dellapé 2009). Previously treated as a subfamily of the Lygaeidae (sensu lato), the group was accorded the group family status by Henry (1997a).

16.12.2 Classification and Diversity

The Oxycarenidae include about 24 genera and 150 species, most of which occur in the Old World (Péricart 2001; Henry 2009; Henry and Dellapé 2009; Brailovsky and Cervantes 2011). Five genera and 22 species are found in the Neotropics (Slater 1964a; Dellapé and Cheli 2007; Henry and Dellapé 2009; Brailovsky and Cervantes 2011). The largest genus *Crophius* Stål, comprising 19 species, including eight from the Neotropics (Slater 1964a; Dellapé and Cheli 2007), was synonymized by Hoberlandt (1987) under the Palearctic *Anomaloptera* Amyot and Serville, an action followed by a number of subsequent authors (e.g., Slater and O'Donnell 1995; Péricart 1998, 2001; Dellapé and Cheli 2007). Henry et al. (2015), however, have shown that *Crophius* is distinct from *Anomaloptera*, as is *Mayana* Distant (containing the two species *M. costatus* Distant and *M. diruptus* Distant), also previously placed in synonymy with *Crophius* (Van Duzee 1910). The genus *Dycoderus* Uhler (1901) is represented by the species *D. picturatus* (Uhler), known only from the western United States; *Neaplax* Slater (1974) contains two species, *N. mexicanus* Slater and *N. baja* Brailovsky and Cervantes (2011), both known only from Mexico; and *Notocoderus* Henry and Dellapé (2009) was described to accommodate *N. argentinus* Henry and Dellapé from Argentina. The large Palearctic genus *Oxycarenus* Costa is represented in the New World by the introduced *O. hyalinipennis* (Costa) (Fig. 20), a pest of cotton first detected in Brazil as early as 1917, now known to occur throughout much of South America and the West Indies (Slater and Baranowski 1994). More recently, it was detected in the Florida Keys on naturalized wild cotton, *Gossypium* sp. (Nagoshi et al. 2012), but apparently it has been eradicated (NAPPO 2014).

The following key is modified from Henry et al. (2015).

Key to the Neotropical Genera of Oxycarenidae

1. Ocelli absent.. 2
– Ocelli present 3
2. Head strongly globose in front of eyes; pronotum trapeziform, not separated into two lobes, but with a wide collar-like area; costal margin of hemelytra explanate ....*Neaplax* Slater
– Head not strongly globose; pronotum lacking a collar and separated into two distinct lobes, with anterior lobe two or more times longer than posterior lobe; costal margin of hemelytra not explanate............*Notocoderus* Henry and Dellapé
3. Fore femora with only one spine; labium usually extending only to middle coxae, if longer, never onto abdomen.. *Crophius* Stål
– Fore femora with two or more spines; labium extending to or beyond middle coxae 4
4. Fore femora with two spines; labium extending only to middle coxae or slightly beyond; hemelytral membrane with numerous closed cells .... *Mayana* Distant
– Fore femora with four spines; labium extending beyond hind coxae, well onto abdomen; hemelytral membrane without closed cells (Fig. 19) .... *Oxycarenus* Costa

16.13 Family Pachygronthidae

16.13.1 General Characteristics and Diagnosis

Members of this family are separated into two subfamilies, the Pachygronthinae and the Teracriinae (Slater 1955). Pachygronthines are distinguished by the elongate bodies, strongly incrassate spined fore femora, and the frequently unusually long first antennal segment. Teracriines are more stout bodied, have shorter antennae, and are held together as a subfamily by the ventral position of the abdominal spiracles (Henry 1997a).

16.13.2 Classification and Diversity

The Pachygronthidae comprise about 13 genera and 78 species worldwide (Cassis and Gross 2002; Henry 2009). Only the two pachygronthine genera *Oedancala* Amyot and Serville, with 14 species, and *Pachygrontha* Germar, with six species, are known from the Neotropics (Slater 1955, 1964a; Slater and O'Donnell 1995). The teracriine genus *Phlegyas* Stål contains only three species, two of which occur in the Neotropical Region. *Phlegyas annulicrus* Stål is known from the western

United States and Mexico and *P. patruelis* Berg has been reported from Argentina, Paraguay, and Uruguay. All members of the family feed on monocots of the families Cyperaceae (sedges), Juncaceae (rushes), and Poaceae (grasses) (Slater 1955). Slater (1955) revised the family for the world and gave keys to genera and species, and Henry (1997a) gave the group family status. The following key is modified from Slater (1955) and Dellapé (2014).

Key to the Neotropical subfamilies and genera of Pachygronthinae

1. Antennal segment I not or barely attaining apex of clypeus, always much shorter than antennal segments II–IV (Teracriinae) (Fig. 22)...................... *Phlegyas* Stål
– Antennal segment I greatly exceeding apex of clypeus, usually as long or longer than antennal segments II–IV (Pachygronthinae)... 2
2. Eye as wide as or wider than long; distance between base of the antenna and anterior margin of eye as long as or longer than length of eye; antennal segment I clavate; antennal segment IV shorter than either segment II or III (Fig. 21) .... *Pachygrontha* Germar
– Eye longer than wide; distance between base of antenna and anterior margin of eye less than length of eye; antennal segment I gradually swollen to apex; antennal segment IV longer than either segment II or III..................................... .... *Oedancala* Amyot and Serville

16.14 Family Piesmatidae

16.14.1 General Characteristics and Diagnosis

The Piesmatidae, often called ash-gray plant bugs, are recognized by the small size (5 mm or less); the dull yellowish-gray coloration; the broad head; the produced juga often surpassing the apex of the clypeus; the widely placed ocelli (often reduced or absent in brachypters); the uni-, bi-, or tricarinate pronotum; the reticulate or areolate hemelytra; the dorsal spiracle on abdominal segment II; the absence of trichobothria on abdominal segments IV and V; and the two-segmented tarsi.

16.14.2 Classification

The Piesmatidae superficially resemble certain Tingidae because of the reticulate hemelytra and the two-segmented tarsi. Drake and Davis (1958), however, showed that they belonged in the infraorder Pentatomomorpha based on the presence of abdominal trichobothria, a true spermatheca, and a differentiated endophallus. Their superfamily placement has fluctuated from being included in their own superfamily, the Piesmatoidea, to their current position in the Lygaeoidea (Henry 1997a). Worldwide nine genera and about 45 species are separated into two subfamilies, the widespread Piesmatinae and the Afrotropical Psamminae (Henry 1997a, 2009; Dellapé 2014).

Drake and Davis (1958) treated the world genera and Heiss and Péricart (1983) revised the Palearctic fauna. Péricart (1974) established two new subgenera, *Afropiesma* and *Parapiesma*, for the widely distributed genus *Piesma* Le Peletier and Serville, and Heiss and Péricart (1997) later gave these subgenera generic status. As a consequence, most of the New World species previously placed in *Piesma* now belong in *Parapiesma* Péricart, including the widespread *P. cinereum* (Say). Two genera and two species occur in the Neotropics. *Miespa reedi* (Drake) is known only from Chile, and *Parapiesma cinereum* (Say) occurs throughout much of the New World.

Key to the genera and species of Neotropical Piesmatidae

1. Spiracles VI and VII subventral laterally; pronotum tricarinate (Fig. 23) .... *Parapiesma* Péricart
– Spiracle VI dorsal, only VII subventral laterally; pronotum with only a single median carina .... *Miespa* Drake

16.15 Family Rhyparochromidae

16.15.1 General Characteristics and Diagnosis

The Rhyparochromidae are commonly called seed bugs because most feed on mature seeds (Sweet 1964a, b). They are recognized by the presence of head trichobothria; a fused suture between sterna IV and V, usually curving forward anterolaterally from the midline of the sternum and not reaching the dorsal margin of the abdomen (except in Plinthisinae); and the fore femora usually incrassate and armed below with spines (Schuh and Slater 1995; Henry 1997a; Dellapé 2014). Most are dull brown to black, often with contrasting pale or white marks or mottled patterns on the hemelytra. They range from very small (e.g., Antillocorini, Lilliputocorini) to large (e.g., some Lethaeini and Myodochini).

Rhyparochromids have a broad range of feeding habits. Many species live on the ground, feeding on fallen seeds. Other species climb vegetation when mature seeds are available, some live on weedy vegetation (Slater 1977; Slater and Baranowski 1990), and others are arboreal and live in forests canopies (Slater et al. 2009; Dellapé and Henry 2010). The Cleradini, which feed on vertebrate blood, are the exception to the seed-feeding habit within the family.

Numerous species are myrmecomorphic, and although many are not extremely similar to ants in their morphology, adults and especially nymphs of some genera (such as the myodochines *Neopamera* Harrington, *Pseudopachybrachius* Malipatil, and *Heraeus* Stål) mimic ants in their movements (Slater and Baranowski 1990).

16.15.2 Classification and Diversity

The Rhyparochromidae are the most diverse group of the Lygaeoidea, comprising more than 2,000 species in 14 tribes or about a half the world's fauna. According to Henry's (1997a) phylogenetic classification, the family, defined by the presence of head trichobothria, contains the subfamilies Plinthisinae and Rhyparochrominae. The Plinthisinae, with only the nominate tribe, have complete abdominal sutures reaching the dorsal margins of the abdomen, whereas most other rhyparochromines have abdominal sutures IV–V abbreviated and not reaching the dorsal margin of abdomen. The apparent presence of a complete abdominal sternal suture on segments IV–V in at least 11 tribes of Rhyparochrominae suggests multiple independent origins of this character as discussed by Slater et al. (2009). We note (personal observation), however, that in most of these exceptions segments IV–V are modified in some way, indicating that the previous oversimplified presence or absence interpretation of the abbreviated abdominal sutures needs to be redefined and expanded.

Key to the subfamilies of Rhyparochromidae

1. Males with a stridulatory mechanism on abdominal segment I and hind wing; females with a conjunctival membrane between abdominal sterna 4/5; pronotum wider across anterior one-third than across humeral angles .... Plinthisinae
– Males without abdominal and hind-wing stridulatory mechanisms; both sexes usually with abdominal sterna 4/5 fused; pronotum variable, usually wider across humeral angles than across anterior lobe ....Rhyparochrominae

16.15.3 Subfamily Plinthisinae

The Plinthisinae possess head trichobothria, similar feeding habits, and an overall general appearance but lack the fused suture between the abdominal terga 4/5 found in most rhyparochromids.

Plinthisines usually have the pronotum expanded across the anterior lobe; the fore femora are heavily incrassate and spined; the wings are often greatly reduced or staphylinoid; males have a stridulatory mechanism on abdominal segment I and the hind wing; and females have a conjunctival membrane between sterna 4/5 (Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000). Putshkov (1958) argued that plinthisines merit subfamily status. According to Slater and Woodward (1982), the Plinthisini represent the basal group of the family, and Henry (1997a) corroborated the monophyly of the group based on the head trichobothria and maintained its subfamily status.

The subfamily includes only two genera, the monotypic *Bosbequius* Distant from Myanmar and the large genus *Plinthisus* Stephens (Fig. 24), with most of the species distributed in the Palearctic, a few species in North America, and only three Neotropical species described by Slater (1971).

16.15.4 Subfamily Rhyparochrominae[1]

Key to the tribes of Rhyparochrominae

1. Abdominal spiracles II, III, and IV dorsal 2
– All abdominal spiracles ventral 3
2. Inner laterotergites absent; lateral pronotal margins almost always rounded .... Myodochini
– Inner laterotergites present; lateral pronotal margins variable from rounded to carinate .... Udeocorini
3. Posterior pair of trichobothria on abdominal sternum V positioned one above the other 4
– Posterior pair of trichobothria on abdominal sternum V positioned one in front of the other in a linear series on segments IV and V 7
4. Ocelli lateral and behind eyes; suture between abdominal sterna IV and V attaining a lateral connexival margin; abdominal tergum III usually not sclerotized; labial segment II usually not attaining the base of the head .... Cleradini
– Ocelli between and slightly posterior to eyes; suture between abdominal sterna IV and V usually not attaining lateral connexival margin and usually markedly curving anteriorly from venter dorsally; labium variable, but usually with segment II reaching or exceeding base of head 5
5. Medium sized, length usually more than 5 mm; apical corial margin straight .... Ozophorini
– Very small to minute, length usually less than 3.5 mm; apical corial margin usually concave 6
6. Inner laterotergites absent; metathoracic scent-gland auricle strongly curved anteriorly; tarsi two segmented .... Lilliputocorini
– Inner laterotergites present; metathoracic scent-gland auricle straight or curved posteriorly; tarsi three segmented 7
7. Apical corial margin deeply concave; inner laterotergites present; head lacking iridescent areas; abdominal scent-gland scars between terga III/IV, IV/V, and V/VI .... Antillocorini
– Apical corial margin straight; inner laterotergites absent; head with iridescent areas basally; abdominal scent-gland scars between terga V/VI minute or absent .... Lethaeini

Tribe Antillocorini

The Antillocorini are a cosmopolitan group, with about 100 species occurring in tropical and subtropical regions of the world. Seventeen of the 34 currently recognized genera and 34 species occur in the Neotropics (Slater 1964a; Slater and O'Donnell 1995; Brambila 2000).

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[1] In the proof stage of this chapter, we discovered that we omitted the tribe Rhyparochromini and the adventive genera *Dieuches* Dohrn (see Henry and Froeschner 1993) and *Elasmolomus* Stål (see Slater 1972) from the keys.

The Antillocorini are characterized by the bucculae joined by a carina well behind the labium; a deeply concave apical corial margin; the ventral abdominal spiracles; the linear trichobothria on abdominal sternum V; the presence of inner laterotergites; and immatures with a double or "troughed" suture between terga 3/4 and 4/5 and with a field of spines or tubercles laterally, with three pairs of scent glands between abdominal terga 3/4, 4/5, and 5/6 (Ashlock 1964; Sweet 1977; Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000).

Slater (1980) described several new taxa, discussed the phylogenetic relationships, and provided a key to the genera of the Western Hemisphere. Some Neotropical species lack a deeply concave apical corial margin and the linear arrangement of abdominal trichobothria. Schuh and Slater (1995) stated that the group may not be monophyletic.

The following key is modified from Slater's (1980) key.

Key to the Neotropical genera of Antillocorini

1. Apical corial margin straight or, at most, very slightly sinuate near inner angle 2
– Apical corial margin with inner third deeply and conspicuously concave 5
2. Suture between abdominal sterna 4/5 straight, reaching dorsal margin .... *Caeneusia* Strand
– Suture between abdominal sterna 4/5 curving anteriorly, not reaching dorsal margin 3
3. Lateral pronotal margins rounded; metathoracic scent-gland auricle weakly curved posteriorly .... *Parademа* Slater
– Lateral pronotal margins bluntly calloused or subcarinate; metathoracic scent-gland auricle curved posteriorly 4
4. Body elongate and slender, more than 3 mm long, macropterous .... *Schuhocoris* Slater
– Body small to minute, less than 2 mm long, robust, coleopteroid .... *Branstettocoris* Brailovsky
5. Lateral pronotal margins rounded or faintly calloused 6
– Lateral pronotal margins calloused or carinate 7
6. Body above and below polished and shining .... *Acolhua* Distant
– Head and abdominal sternum shining, constrasting with dull pruinose or subpruinose surface on remainder of body .... *Bathydema* Uhler
7. Trichobothria on abdominal sternum V linear, the posterior trichobothrium directly below or well behind the spiracle 8
– Trichobothria on abdominal sternum V not linear; if linear then the posterior trichobothrium anterior to the spiracle 9
8. Fore femur mutic; posterior trichobothrium on abdominal sternum V well behind spiracle .... *Arimacoris* Baranowsky and Slater
– Fore femur with two rows of spines, larger in males; posterior trichobothrium on abdominal sternum V directly below or slightly caudad of spiracle (Fig. 26) .... *Valeris* Brambila
9. Trichobothria on abdominal sternum V linear, anterior to spiracle 10

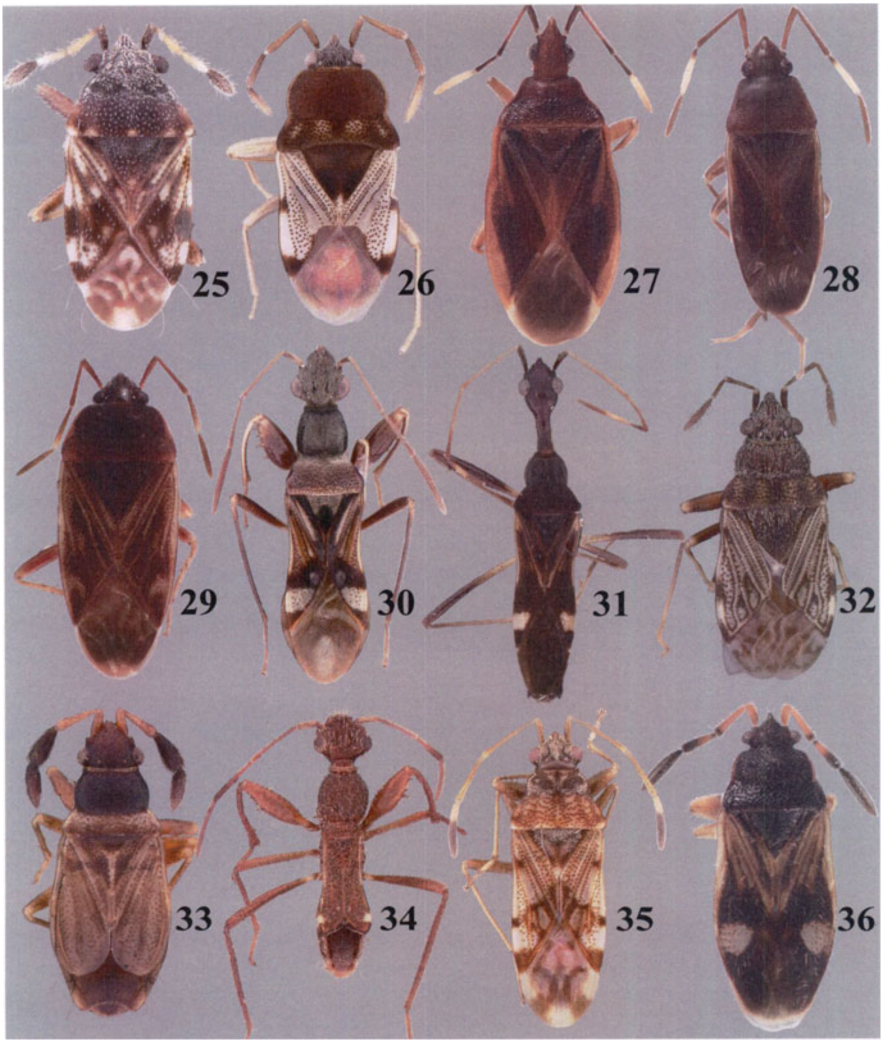

Plate 16.3 Figs. 25–36. 25, *Bathydema jamaicensis* Slater and Baranowski (Rhyparochromidae: Rhyparochriminae: Antillocorini). 26, *Valeris subcavicola* (Scudder) (Rhyparochromidae: Rhyparochriminae: Antillocorini). 27, *Clerada apicicornis* Signoret (Rhyparochromidae: Rhyparochriminae: Cleradini). 28, *Cistalia signoretii* (Guérin-Méneville) (Rhyparochromidae: Rhyparochriminae: Lethaeini). 29, *Paragonatas divergens* (Distant) (Rhyparochromidae: Rhyparochriminae: Lethaeini). 30, *Distingphyses insignis* Distant (Rhyparochromidae: Rhyparochriminae: Myodochini). 31, *Myodocha froeschneri* A. Slater (Rhyparochromidae: Rhyparochriminae: Myodochini). 32, *Prytanes confusus* (Barber) (Rhyparochromidae: Rhyparochriminae: Myodochini). 33, *Ptochiomera nodosa* Say (Rhyparochromidae: Rhyparochriminae: Myodochini). 34, *Xenydrium formiciforme* Bergroth (Rhyparochromidae: Rhyparochriminae: Myodochini). 35, *Ozophora costaricensis* Slater and O'Donnell (Rhyparochromidae: Rhyparochriminae: Ozophorini). 36, *Tempyra biguttula* Stål (Rhyparochromidae: Rhyparochriminae: Udeocorini) (Photos by G Ouellette)

– Trichobothria on abdominal sternum V not linear, somewhat dorsoventral relative to one another, usually below or behind spiracle 11
10. Prosternum with a deep median groove ....*Cligenes* Distant
– Prosternum lacking a deep median groove ....*Botocudo* Kirkaldy
11. Dorsal surface almost or entirely shiny and polished 12
– Dorsal surface either completely pruinose or with head shiny, contrasting with the pruinose pronotum 14
12. Dorsal surface completely shiny, not pruinose 13
– Dorsal surface almost entirely shiny and polished, pruinose only narrowly across the base of head between ocelli .... *Germacoris* Baranowsky and Slater
13. Fore femora with 8–9 sharp spines; head and anterior pronotal lobe smooth and impunctate.. *Terenocoris* Slater
– Fore femora with only 2–3 spines; head and pronotum with numerous, irregular, coarse punctures...*Trachinocoris* Slater
14. Lateral pronotal margins sharply and acutely carinate .... *Paurocoris* Slater
– Lateral pronotal margins with a blunt calloused ridge, but lacking a sharp, acute edge 15
15. Dorsal surface with strongly variegated coloration; metathoracic scent-gland auricle broad, lobate, not strongly curved caudad; evaporative area with grooves .... *Antillodema* Slater
– Dorsal surface dull yellow, brown or chestnut, without bright variegated contrasting coloration; metathoracic scent-gland auricle slender and strongly curved posteriorly; evaporative area lacking conspicuous grooves 16
16. Outer margin of metathoracic scent-gland evaporative area elevated into a raised subcarinate ridge, only slightly removed from outer lobe of scent-gland auricle; head pruinose, similar in texture to that of pronotum; spiracle of abdominal segment IV below lateral shelf; paramere with an elongate, acutely pointed inner projection .... *Scythinus* Distant
– Outer margin of metathoracic scent-gland evaporative area not strongly elevated into a ridge, well removed from outer lobe of scent-gland auricle; head shiny, strongly contrasting with texture of pronotum; spiracle on abdominal segment IV on lateral shelf; paramere lacking a well-developed inner projection .... *Antillocoris* Kirkaldy

Tribe Cleradini

The Cleradini, with 20 genera and 54 species, are confined to the Old World tropics, except for *Clerada apicicornis* Signoret (Fig. 27) introduced into the Western Hemisphere (Schuh and Slater 1995). This species has been recorded from Cuba, the Dominican Republic, Grenada, Haiti, Jamaica, Puerto Rico, St. Vincent, St. Thomas, and the Virgin Islands in the West Indies and Brazil, Colombia, and

Venezuela from South America (Slater 1964a; Morales et al. 1969; Torres et al. 2000; Baranowski and Slater 2005).

Members of the Cleradini have laterally placed ocelli; a short antennal segment III and a short labium not exceeding the base of the head; an unarmed, slender fore femur; the abdomen with all spiracles ventral and without inner laterotergites; an expanded connexival membrane; a secondary longitudinal abdominal suture; complete abdominal sutures between sternal suture IV–V; bifurcate parameres; and eggs with a pseudoperculum (Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000; Slater et al. 2009).

Tribe Lethaeini

The tribe Lethaeini, with 38 genera and more than 160 species worldwide (Li et al. 2011), has its greatest diversity in the tropical and subtropical parts of the Afrotropical, Oriental, and Australian regions (Slater 1986a). It is one of the most diverse tribes in the Neotropics, with 13 genera and 36 species known.

Lethaeines are recognized by the linear placement of the trichobothria on abdominal sternum V; a rounded buccular groove joined immediately behind the labium; a carinate juga; a trichobothrium at each anterior corner of the pronotum; the abdomen with all spiracles ventral and with or without inner laterotergites; the absence of a Y chromosome; the extreme modification of the sperm reservoir; the immatures with a double or "troughed" suture between terga 3/4, 4/5, and 5/6 and with a field of spines or tubercles laterally; the reduced scent gland between abdominal terga 5/6; and the presence of an iridescent area or areas on the head (Ashlock 1964; Slater and Woodward 1982; O'Donnell 1991).

The following key is modified from Baranowski and Slater's key (2005) to the West Indian lethaeines.

Key to the Neotropical genera of Lethaeini

1. Pronotal trichobothria absent; eyes large, occupying more than half the length of the head; juga reduced; densely setose species .... *Lipostemmata* Berg
– Pronotum with a pair of trichobothria on anterolateral region; eyes small; juga well developed; less setose species 2
2. Dorsal surface of body strongly shiny 3
– Dorsal surface of body only partly shiny 5
3. Pronotum trapeziform, narrowing anteriorly; head with two iridescent patches; fore femur slightly incrassate 4
– Pronotum subquadrangular; head with one iridescent patch; fore femur strongly incrassate and compressed .... *Rhaptus* Stål
4. Body with long setae dorsally; eyes with two long, forward-curving setae .... *Xestocoris* Van Duzee
– Body almost glabrous or with only a few long, scattered setae dorsally; eyes without two long, forward-curving setae .... *Bubaces* Distant

5. Head with two iridescent patches 6
– Head with one iridescent patch 8
6. Inner laterotergites absent; body with short setae dorsally ....*Stictolethaeus* O'Donnell
– Inner laterotergites present; body with long setae dorsally................................ 7
7. Dorsal surface weakly punctate; evaporative area extensive; macropterous or brachypterous species .... *Valtissius* Barber
– Dorsal surface strongly punctate; evaporative area reduced, restricted to areas surrounding auricle; coleopteroid species..*Esuris* Stål
8. Transverse pronotal impression distinct, dividing pronotum into anterior and posterior lobes; lateral pronotal margins broadly explanate and sinuate; collar triangular, well separated from the pronotum by a row a punctures ....*Neopetissius* O'Donnell
– Transverse pronotal impression indistinct; lateral pronotal margins carinate and narrowly explanate; collar not differentiated 9
9. Evaporatory area extended anteriorly over the mesopleura, reaching or nearly reaching dorsal margin.. 10
– Evaporatory area not extended anteriorly, distant from dorsal margin of the mesopleura ....*Cryphula* Stål
10. Antennal segment I with a pale annulus (Fig. 28) .... *Cistalia* Stål
– Antennal segment I without a pale annulus 11
11. Larger, length over 6 mm...*Petissius* Distant
– Smaller, length less than 5 mm 12
12. Lateral margin of pronotum explanate................................... *Gonatoides* Slater
– Lateral margin of pronotum rounded (Fig. 29).................. *Paragonatas* Distant

Tribe Lilliputocorini

The Lilliputocorini are circumtropical and comprise the nominotypical genus *Lilliputocoris* Slater and Woodward and ten species (Slater and O'Donnell 1995). The only record from the Neotropics is *L. neotropicalis* Slater and Woodward, described from a female from Pará, Brazil.

The Lilliputocorini are minute bugs, less than 2 mm long, recognized by the clavate antennal segments II and III; the reduced and modified ovipositor; the two-segmented tarsi; the uniquely formed metathoracic scent-gland auricle and adjacent evaporative area; the abdomen with all spiracles ventral and without inner laterotergites; the immatures with a double or "troughed" suture between terga 3/4, 4/5, and a field of spines or tubercles laterally; and the reduction or loss of the scent gland between abdominal terga 5/6 (Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000).

Tribe Myodochini

The tribe Myodochini is among the most diverse groups of Rhyparochromidae (Dellapé and Henry 2010), comprising 75 genera and 307 species worldwide, with 36 genera and 117 species occurring in the Neotropics.

The Myodochini usually possess a deeply incised transverse impression across the pronotum and a rounded anterior pronotal lobe; the abdomen has the spiracles on segments II, III, and IV dorsal and lacks inner laterotergites; and immatures have a Y-suture between abdominal terga 3/4 and three pairs of scent glands between abdominal terga 3/4, 4/5, and 5/6 (Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000).

Three Neotropical species now assigned to the genera *Pseudocnemodus* Barber, *Ptochiomera* Say, and *Sisamnes* Distant are misplaced. *Pseudocnemodus martinezi* Brailovsky from Paraguay probably should be included in *Bergicoris* Dellapé and probably is a synonym of *B. multifarious* Berg; the identity and position of the Chilean species in *Ptochiomera* are doubtful; and *Sisamnes annulicollis* (Berg) from Argentina probably belongs in *Neopamera* Harrington. Clarification of these taxa will be presented in a forthcoming paper by PMD.

Some myodochines, such as species in the genera *Neopamera*, *Pseudopachybrachius*, and *Prytanes*, are abundant and commonly collected in disturbed habitats and generally climb vegetation, whereas other taxa are strict geophiles, presumably in specialized habitats, and are poorly represented in collections. Most genera have fewer than ten species, and in the case of genera with more species (e.g., *Paromius*), only a few are Neotropical. The actual diversity of this group is much higher than present numbers indicate, and many new taxa remain to be described.

Harrington (1980) revised Myodochini and provided a generic key and a cladistic and biogeographic analysis. Nine Neotropical genera have been described since her work. *Ashlockobius* Slater and A. Slater (1999) was synonymized with *Villalobosothignus* Brailovsky 1984 by Dellapé and Montemayor (2011). The following key is modified from the Harrington's (1980) key to the myodochine genera of the world.

Key to the Neotropical genera of Myodochini

1. Interocular distance less than postocular distance 2
– Interocular distance equal to or exceeding postocular distance 4
2. Posterior margins of ocelli posterior to posterior margins of eyes; eyes round (Fig. 31).. *Myodocha* Latreille
– Posterior margins of ocelli anterior to posterior margins of eyes; eyes elongate-oval 3
3. Fore femur incrassate, with strong spines; ocelli sessile; antennal segment I not extending beyond clypeus (tylus) .... *Pephysena* Distant
– Fore femur weakly incrassate, slender, with only a few medium-sized and minute spines; ocelli protuberant; antennal segment I extending beyond clypeus .... *Dushinckanus* Brailovsky

4. Ocelli absent....................................... *Andercnemodus* Brailovsky and Cervantes
– Ocelli present 5
5. Crescent-shaped, striated stridulitrum present ventrolaterally on anterior portion of abdomen.. 6
– Striated stridulitrum lacking on anterior portion of abdomen 10
6. Head prolonged into a distinct neck; stridulitrum confined to abdominal sterna II and III; plectrum on hind femur consisting of two chisel-like projections ....*Erlacda* Signoret
– Head not prolonged into a neck; stridulitrum extending onto sternum IV; plectrum on hind femur consisting of a line or scattered field of minute tubercles 7
7. Pronotum shiny; length of antennal segment I greater than interocular distance; pronotum shiny, not pruinose, and never deeply punctate; male fore tibia typically armed with a spine or spines ....*Pseudomera* Distant
– Pronotum pruinose; length of antennal segment I less than interocular distance; pronotum pruinose, in some cases very deeply punctate; male fore tibia unarmed 8
8. Stridulitrum diffuse, not readily apparent; pronotum and head deeply punctate; abdomen with a band of long silvery setae covering much of sternum IV in lateral view ....*Stridulocoris* Harrington
– Stridulitrum readily apparent; pronotum and head not deeply punctate; abdomen of uniform vestiture, without a band of long silvery setae.................................. 9
9. Lateral margin of posterior pronotal lobe angled posterolaterad at approximately a 45 degree angle; pronotum markedly bilobed, with a deeply incised, transverse impression; always macropterous; antennal segment IV with a pale proximal band; fore femoral spines clearly in two rows (present on both the inner and outer edge of ventral surface)...*Froeschneria* Harrington
– Lateral margin of the posterior pronotal lobe angled posterolaterad at less than a 45 degree angle; transverse impression not deeply incised; often submacropterous; antennal segment IV usually uniformly dark; if with a pale band, then fore femoral spines in a single row (present only along inner edge of ventral surface) .... *Ligyrocoris* Stål
10. Evaporative area reduced, occupying much less than half of metapleural area; claval punctation usually in three rows; pronotum shiny, never pruinose...........11
– Evaporative area not reduced, occupying much more than half of metapleural area; claval punctation in more than three rows; pronotum dull, shagreened, or pruinose.. 14
11. Antennae with enlarged segments; segment III strongly swollen, distally of much greater diameter than segment I (Fig. 33).......................*Ptochiomera* Say
– Antennae filiform; segment III generally filiform, if somewhat clavate, diameter no greater distally and often more slender than segment I 12
12. Collar not apparent on the anterior pronotal lobe; ventral surface of head not grooved; buccular juncture not near labial insertion, occurring at level of eyes; pronotum dorsoventrally compressed, lateral margins subcarinate 13

– Collar apparent on anterior pronotal lobe but not demarked posteriorly; ventral surface of head grooved; buccular juncture U shaped near labial insertion; lateral margins of both pronotal lobes rounded (Fig. 32) .... *Prytanes* Distant

13. Buccular juncture broadly U shaped; fore femur with spines only along the inner edge of the ventral surface; anterior margin of abdominal sternum II scalloped .... *Kolenetrus* Barber

– Buccular juncture elongate, terminating in a V-shaped end; fore femur with spines not confined to a single row; anterior margin of abdominal sternum II not scalloped ....*Scintillororis* Slater and Brailovsky

14. Pronotum dorsoventrally compressed with a distinct lateral carina on both lobes .... *Megacholula* Harrington

– Pronotum not compressed; lateral pronotal margins ecarinate 15

15. Both lobes of pronotum and head uniformly and coarsely punctate; head broad, posterior margin of eyes touching anterior pronotal angles; sternal scalloping prolonged and clearly visible on sternum II; a very narrow anterior pronotal collar vaguely indicated but never demarked posteriorly by a groove............. 16

– Head and anterior pronotal lobe impunctate or only vaguely punctate; head generally with eyes removed from anterior pronotal angles; sterna scalloping usually lacking, if present, largely hidden under metapleuron and not prolonged; in most cases, with a distinct anterior pronotal collar demarked posteriorly by a distinct groove.. 18

16. Clavus with three regular rows of punctures; apex of scutellum rounded, elevated, and distinctly pale; buccula with a posterior projection .... *Paracholula* Harrington

– Clavus often with more than three rows of punctures; scutellum unicolorous; buccula without a posterior projection.. 17

17. Abdomen with a large glabrous area or diffuse stridulitrum on lateral portions of sterna II and III; hind femur with a plectrum of scattered spines on basal half; abdomen often with a band of long silvery setae covering much of sternum IV in lateral view; lateral pronotal margins ecarinate .... *Stridulocoris* Harrington

– Abdomen without a stridulitrum or band of long setae as above; hind femur devoid of spines; lateral margin of posterior pronotal lobe with a blunt carina, sometimes forked over humeral angles...................................... *Cholula* Distant

18. Mesacetabulum with mesepimeron emergent (or barely) from between the meso- and metepisternum 19

– Mesepimeron enclosed by metepisternum; touching mesepisternum 28

19. Head elongate, often with a distinct neck; postocular distance equal to or greater than distance between ocelli 20

– Head less elongate, never with a distinct neck; postocular distance less than distance between ocelli 24

20. Eyes elongate-oval; posterior margin of ocelli anterior to posterior margin of the eyes 21
– Eyes rounded; posterior margin of ocelli posterior to posterior margin of eyes 22
21. Head with a clearly defined cylindrical neck; vertex of head convex; anterior pronotal lobe pruinose........ *Pephysena* Distant
– Head with a much less well-defined neck; vertex of head flat, depressed between the eyes; anterior pronotal lobe shiny .... *Tenuicoris* Slater and Harrington
22. Head essentially flat when viewed laterally, not showing a gradual rounded constriction from eyes to insertion of head; fore coxa without a spine .... *Catenes* Distant
– Head when viewed laterally showing gradual rounded constriction from eyes to insertion of head; fore coxa armed with a spine 23
23. Ventral portion of collar produced anteriorly........ *Heraeus* Stål
– Ventral portion of collar not produced anteriorly........ *Paisana* Dellapé
24. Juga rounded; pygophore with anterior margin of dorsal aperture with small denticles; aedeagus with large, stout spines on conjunctiva and vesica .... *Myodacanthus* Dellapé
– Juga forming a ridge; pygophore with anterior margin of dorsal aperture smooth; aedeagus spined or unspined........ 25
25. Eyes not protruding or surpassing dorsal margin of head in lateral view 26
– Eyes protruding, inserted high, and surpassing dorsal margin of head in lateral view 27
26. Head and anterior pronotal lobe lower than posterior pronotal lobe in lateral aspect; fore coxal spine poorly developed or absent; color predominantly blackish brown, posterior pronotal lobe with characteristic orange areas along lateral margins and paired orange maculae medially adjacent to transverse impression .... *Orthaea* Dallas
– Dorsal surface of head and both lobes of pronotum essentially in the same plane; fore coxal spine(s) well developed; posterior pronotal lobe lacking orange markings along lateral margins .... *Neopamera* Harrington
27. Profemur elongate and slender, with a few spines restricted to distal end; mesepimeron clearly emergent; aedeagus spined........ *Neomyocoris* Dellapé and Montemayor
– Profemur incrassate with two rows of spines ventrally; mesepimeron barely emergent; aedeagus without spines........ *Thoraea* Dellapé and Montemayor
28. Head broad, interocular distance equal to or greater than width of pronotal collar 29
– Head not broad, interocular distance less than width of pronotal collar 31
29. Strikingly ant mimetic, with lateral margin of head between eye and insertion of antenna expanded into a platelike curving ridge; lateral margin of pronotal collar with a rounded but distinct spine (Fig. 34) .... *Xenydrium* Poppius and Bergroth

– Not ant mimetic, lateral margin of head between eye and base of antenna not expanded into a ridge; lateral margin of pronotal collar without a spine 30

30. Head elongate behind eyes, forming a short cylindrical neck; V-shaped buccular juncture with a strong midventral carina; antennal segment I short, remote from apex of head; scutellum pruinose on basal half, shiny on black tumid central area and apex .... *Acrolophyses* Dellapé and Henry

– Head with a shorter neck; midventral carina of buccular junction less developed; antennal segment I longer, almost attaining apex of head; scutellum completely pruinose (Fig. 30) .... *Distingphyses* Scudder

31. Head and anterior pronotal lobe, including collar, impunctate, or collar with only a few faint punctures; pronotal collar narrow and ringlike .... *Perigenes* Distant

– Pronotal collar usually broad and distinctly punctate; rest of anterior pronotal lobe and head also often punctate, though sometimes with indistinct, minute punctures 32

32. Pronotum tapering cephalad with anterior lobe flattened and weakly convex; anterior lobe distinctly lower than posterior lobe in lateral view; collar with a characteristic median depression to posterior margin; abdomen equal to or longer than combined length of head and pronotum .... *Paromius* Fieber

– Anterior pronotal lobe usually strongly convex, not lower than posterior lobe in lateral view; collar without median depression; abdomen shorter than combined length of head and pronotum 33

33. Small, length 4.0 mm or less; ant mimetic, head strongly swollen in lateral view; eyes small, rounded, protruding, and beadlike .... *Bacacephalus* Harrington

– Larger than above; if small, then not ant mimetic with a swollen head and beadlike eyes 34

34. Large, usually greater than 6 mm long; head broad and jugal ridge above antennal segment I distinct 35

– Small, generally less than 5 mm long; jugal ridge above antennal segment I usually narrow and poorly developed .... *Pseudopachybrachius* Malipatil

35. Hemelytra with a broad, dark, transverse band at level of corial apex; male fore tibia unarmed; aedeagus with serrated projections on vesica and two strong spines on conjunctiva .... *Pseudoparomius* Harrington

– Hemelytra without a broad, dark, transverse band at level of corial apex; male fore tibia with or without spines; aedeagus spined or unspined but without serrate projections 36

36. Antennal segment IV with apex paler; anterior pronotal lobe elongate, at least 1.5 times as long as posterior pronotal lobe, but never globose; male fore tibia not strongly curved, with only a few short, sharp spines; aedeagus unspined .... *Villalobosothignus* Brailovsky

– Antennal segment IV with or without a broad yellowish band subbasally, but never with apex paler; anterior pronotal lobe elongate and globose; male fore tibia curved on anterior half and straight distally, with a large spine medially; aedeagus spined .... *Bergicoris* Dellapé

Tribe Ozophorini

The Ozophorini have a worldwide distribution, with most taxa occurring in the Neotropical and Oriental regions (Slater 1986a; Schuh and Slater 1995; Cassis and Gross 2002). Twenty-eight genera and 194 species are currently included in the tribe, with 13 genera and about 87 species known from Neotropics, mostly in the large genus *Ozophora* Uhler.

Ozophorines usually have a porrect, grooved head; the hind wing lacks a hamus and secondary veins; the abdomen lacks inner laterotergites and all spiracles are ventral; and the immatures possess a Y-suture between abdominal terga 3/4 and three pairs of scent glands between abdominal terga 3/4, 4/5, and 5/6 (Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000). The genus *Ozophora* is one of the most speciose taxa of Rhyparochromidae in the Western Hemisphere. Slater (1995) provided a key to the 51 mainland Neotropical species.

The following key is based on Ashlock and Slater's (1982) key to the New World Ozophorini and Ashlock's (1985) key to the *Bergidea* group.

Key to the Neotropical genera of Ozophorini

1. Fore femur unarmed beneath, at most with a patch of 20 or more minute spicules 2
– Fore femur beneath with one or more stout, compound spines set on the tubercles in both sexes 5
2. Ocelli present 3
– Ocelli absent 4
3. Fore femur with a patch of 20 or more minute spicules, more evident in males; hemelytra with clavus and corium differentiated, macropterous .... *Pamozophora* Ashlock and Slater
– Fore femur unarmed; hemelytra with clavus and corium indistinguishably fused and nearly uniformly, coarsely punctate .... *Allotrophora* Slater and Brailovsky
4. Body short, stout, elliptical; vertex of head strongly convex; eyes large; pronotum extremely short and broad, width more than two times median length, disc strongly convex, lateral margin broadly explanate .... *Icaracoris* Slater
– Body elongate-oval; vertex of head flattened, eyes smaller, dorsoventrally elongate; pronotum nearly quadrate, width two times median length, disc less convex, lateral margins not explanate .... *Longinischus* Brailovsky
5. Basal segments of abdomen laterally with a cross-striated, crescent-shaped stridulitrum; plectrum consisting of scattered small tubercles on base of hind femur .... *Lygofuscanellus* Scudder
– Basal segments of abdomen laterally without stridulatory structures................. 6
6. Lateral edge of corium (viewed laterally) with a finely striated stridulitrum; hind femora with plectrum (with a regular and dense field of tubercles on apical half); lateral margins of pronotum sharply and broadly explanate, gently narrowing to humeral angles, without a posterior notch .... *Balboa* Distant
– Lateral edge of corium without a stridulitrum, at most with minute crenulations on narrow lateral edge; hind femora without a plectrum; lateral margins of pronotum bluntly carinate or, if explanate (some species of *Ozophora*), then ending abruptly to form a notch at humeral angles.. 7

7. Pronotal collar and pronotal lobes usually distinct 8
– Pronotal collar and pronotal lobes always indistinct 10
8. Coleopteroid; ocelli absent 9
– Usually macropterous, if hemelytra modified, then not extremely so, or if coleopteroid (*Ozophora ovalis*, Colombia), ocelli present (Fig. 35) .... *Ozophora* Uhler
9. Eyes protruding laterally on short stalks; costal margin of corium clearly emarginate; claval commissure shorter than length of head and pronotum combined... *Pseudomenotelus* Brailovsky and Cervantes
– Eyes large, sessile, not protruding laterally; costal margin of corium weakly emarginate; claval commissure longer than length of head and pronotum combined.. *Pseudomenus* Ashlock and Slater
10. Coleopteroid, claval commissure longer than pronotum; ocelli absent; metapleural evaporative area covering less than one-third of metapleuron..... 11
– Often submacropterous or brachypterous, but never coleopteroid, claval commissure shorter than pronotum; ocelli present; metapleural evaporative area occupying at least one-half of metapleuron (Chile and Argentinean Patagonia) .... *Bergidia* Breddin
11. Body short, elliptical, strongly convex; hemelytra without any trace of membrane, claval commissure longer than head and pronotum taken together .... *Brailovskyocoris* Slater
– Body elongate oval; hemelytra with membrane reduced, claval commissure shorter than head and pronotum taken together... 12
12. Antennal segment III longer than segment I and more than half as long as segment II; pronotum and hemelytra with surface, including punctures, dull, not sculptured or rugose; texture of anterior lobe of pronotum and base of scutellum not distinct from remainder of dorsum; evaporative area covering mesepimeron (Juan Fernandez Islands).. *Micrymenus* Bergroth
– Antennal segment III shorter than segment I and less than half as long as segment II; pronotum and hemelytra with surface, especially punctures, shiny, obviously rugose and sculptured; anterior lobe of pronotum and basal area of scutellum with a finely pebbled texture, strongly contrasting with surrounding areas; evaporative area covering only posterior part of mesepimeron (Juan Fernandez Islands) .... *Rugomenus* Ashlock

Tribe Udeocorini

The Udeocorini, comprising 17 genera and 38 species, are most abundant in the Australian Region (Slater 1964a; Slater and O'Donnell 1995). Only three genera and five species have been recorded from the Neotropics. The presence of the Nearctic *Tempyra biguttula* Stål in Argentina probably represents an introduction. Slater (1986a) argued for a Gondwanan origin of the group.

Members of the tribe have rounded, carinate, or explanate pronotal margins; the abdomen has dorsal spiracles on segments II, III, and IV and inner laterotergites; and the immatures possess a Y-suture between abdominal terga 3/4 and have three pairs of scent glands between abdominal terga 3/4, 4/5, and 5/6 (Sweet 1967; Slater and Woodward 1982; Schuh and Slater 1995; Slater and Brailovsky 2000).

Key to the Neotropical genera of Udeocorini

1. Body surface shiny and uniformly dark .... *Astemmoplitus* Spinola
– Body surface dull and not uniformly dark 2
2. Hemelytra covering abdomen in dorsal view; corium with a pale, round macula distally (Fig. 36) .... *Tempyra* Stål
– Hemelytra narrower than abdomen, connexiva visible in dorsal view; corium with a pale, elongate macula distally .... *Bathycles* Distant

16.16 Main Species

The Lygaeoidea include many species of economic importance. Sweet (2000a) gave a detailed account of the most important ones, which are concentrated in the families Blissidae, Geocoridae, Lygaeidae, and Oxycarenidae, though the diverse family Rhyparochromidae has a large number of economically important seed-feeding species (e.g., Henry and Froeschner 1993) and numerous nuisance pests that often cluster in and around homes and commercial buildings (Henry and Adamski 1998; Henry 2004).

The Blissidae, also known as chinch bugs, are probably the most economically important group of Lygaeoidea (Sweet 2000a; Samuels et al. 2002). The chinch bugs are sap suckers specialized for feeding on monocotyledonous plants (Slater 1976). Many blissids are among the most important pests of grasses (Poaceae), including barley, corn (maize), millets, oats, rice, rye, sorghum, and wheat (Sweet 2000a). *Blissus leucopterus* (Say) is considered the most important New World species (Slater 1976; Sweet 2000a). Pereira and da Silva (1988) reported *B. leucopterus* (Say) attacking *Brachiaria radicans* Napper in Minas Gerais, Brazil. Valério et al. (1999) documented *Blissus antillus* Leonard damaging more than 800 acres of Tangola grass pastures in southern Mato Grosso.

Members of the family Geocoridae are in large part predaceous, although they also feed on seeds and foliage of plants, especially as early instars (Sweet 1960; Tamaki and Weeks 1972). As noted by Sweet (2000b), geocorids have complex nutritional requirements and evidently require plant food for optimal development. Species such as *Geocoris uliginosus* (Say) may be considered omnivorous (Carstens et al. 2008). Nevertheless, their importance as biological control agents is well documented (Naranjo and Gibson 1996; Coll and Ruberson 1998; Hagen et al. 1999). A list of the prey for species of *Geocoris* in the United States was compiled by Readio and Sweet (1982).

The family Lygaeidae is separated into three subfamilies, the Ischnorhynchinae, Lygaeinae, and Orsillinae. The life cycles and habitats of most of the species of Ischnorhynchinae are not known. Scudder (1962b) gave available host records, Wheeler (1976) studied the seasonal history and summarized hosts of the Holarctic birch catkin bug, *Kleidocerys resedae* (Panzer) and Cervantes and Baez (2010) presented the life histories of *K. punctatus* Distant and *K. virescens Fabricius*. Only a few species of Lygaeinae are recorded as pests on agricultural crops (Slater 1964b). Aposematically colored members of the genus *Oncopeltus* are restricted to milkweeds and other plants of the family Asclepiadaceae (Wheeler 1983), from which they sequester toxic cardenolides, making them unpalatable to potential predators (Scudder and Duffy 1972).

Other species, such as *Lygaeus kalmii* Stål (Wheeler 1983) and *Neacoryphus bicrucis* (Say) (Solbreck and Pehrson 1979), have been found feeding on numerous plant families, even though asclepiads remain their preferred hosts (Wheeler 1983). The Orsillinae include species that feed on seeds, as well as on vascular tissues. Much of the recorded damage occurs when large populations migrate from wild hosts to crop plants, especially during times of water stress (Ashlock 1967b). Economically important population of *Nysius* develop when the seed supply of the preferred host becomes insufficient for a large population, and the bugs move to a new host, often one of agricultural importance. *Nysius simulans* Stål has been reported from São Paulo state, attacking corn, cotton, and rice, and *Neopamera bilobata* (Say), from Minas Gerais, attacking tobacco (Costa Lima 1940).

The Oxycarenidae feed on both seeds and sap, chiefly of the plant family Malvaceae. The introduced *Oxycarenus hyalinipennis* (Costa) often is of major economic importance on cotton and other Malvaceae, sometimes developing large numbers and feeding between the fibers of the cottonseeds, causing staining of the cotton bolls (Annecke and Moran 1982). Almost nothing is known of the feeding habits of the largest New World genus, *Crophius*, though (Blatchley 1926) reported *C. disconotus* (Say) in numbers on goldenrod, *Solidago* sp. (Asteraceae).

Only a scattering of records are available for the economic species of Rhyparochromidae (Sweet 2000a). Species such as *Neopamera bilobata* (Say), *Pseudopachybrachius vincta* (Say), and their relatives sporadically damage crops, especially strawberries (Slater and Baranowski 1990). Sweet (1964b) found *Cryphula trimaculata* (Distant) inhabiting old fields, feeding on seeds of perennial bunch grasses, such as *Schizachyrium scoparium* J. Presl, *Festuca rubra* L., and *Panicum* sp. *Elasmolomus sordidus* (F.) and *Dieuches armatipes* (Walker) are potential pest of peanuts (Slater 1972; Henry and Froeschner 1993). Though documented as feeding on the blood of small rodents (Harrington 1983, 1990), *Clerada apicicornis* Signoret apparently prefers feeding on other insects, including the blood-feeding reduviid *Rhodnius prolixus* Stål (Torres et al. 2000).

Although the Berytidae were long thought to be primarily phytophagous (Wheeler and Schaefer 1982; Péricart 1984), many have strong predatory tendencies (Henry 1997a, 2000). *Parajalysus spinosus* Distant is said to cause serious damage on cacao, though a later study considered it an important predator of *Heliothis virescens* (F.) eggs (Wille 1951). Other species, such as *Parajalysus andinus* (Horváth), may play an important role in pollinating cacao (Henry 1997b).

Henry and Froeschner (1998) documented the known hosts, and Henry (2000) provided an overview of the feeding habits in the family.

The Colobathristidae and Piesmatidae are also sap feeders (Sweet and Schaefer 1985; Heiss and Péricart 1983; Sweet 2000a). Colobathristids, found in the Neotropical and the Oriental-Australian regions, all feed on grasses, including bamboos. No economically important colobathristids have been reported in the Neotropics, although *Phaenacantha* (*Anorygma*) *saccharicida* (Karsch) is a pest of sugar cane in Australia (Cassis and Gross 2002). Many piesmatids specialize on plants of the family Chenopodiaceae, including the widespread *Parapiesma cinereum* (Say) (Schaefer 1981; Heiss and Péricart 1983).

16.17 Concluding Remarks

The Lygaeoidea, though predominantly seed feeders, include some of the most economically important species of Heteroptera, such as the sap-feeding chinch bugs. A lesser number of others, such as the geocorids, are in large part predatory. The group represents the second largest superfamily of the infraorder Pentatomomorpha, with 16 families, more than 700 genera, and 4,200 species worldwide (Henry 2009). The Neotropical fauna treated in this chapter comprises about 184 genera and 836 species, representing 26 % of the world's genera and only 20 % of the species, suggesting that the number of new taxa awaiting description is immense. That nearly 30 new species of *Heraeus* Stål are being described in a forthcoming revision (Dellapé et al. in review) further illustrates the amount of work that remains to be done in the Neotropics. We hope this review of the superfamily, which includes information on hosts, habits, economic importance, classification, and keys to all Neotropical genera in 12 families, will stimulate interest in this large, diverse group of taxonomically and ecologically important insects.

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Chapter 17
Cotton Stainers (Pyrrhocoridae) and Bordered Plant Bugs (Largidae)

Carl W. Schaefer

Abstract The Pyrrhocoridae and the Largidae, making up the superfamily Pyrrhocoroidea, are moderately sized insects, often with bright and contrasting colors. Several genera of Largidae resemble ants, either in color or in form. These insects range from 7 to 18 mm (Pyrrhocoridae) and from 5 to 16 mm (Largidae). They feed on seeds, on the ground, or in the fruits. However, for most largids, we do not know much at all about their host plants or biology. *Dysdercus* (the only Neotropical genus in Pyrrhocoridae) can be harmful, feeding on cotton seeds; however, this damage occurs rarely in the Neotropics and more often in the Paleotropics.

17.1 Introduction

The superfamily Pyrrhocoroidea contains two families, the Largidae and the Pyrrhocoridae. Pyrrhocoroidea is grouped with the trichophora (which is not a formal name), together with the Lygaeoidea, Coreoidea, and Pentatomoidea; each of these superfamilies has regularly placed trichobothria (sensory hairs) on their abdominal sternites (the third through the seventh). These families constitute the infraorder Pentatomomorpha, to which some have included the superfamily Aradoidea [but see Sweet (2006), who treats it as a separate infraorder].

17.2 Classification

The Pyrrhocoridae are of course most closely related to the Largidae, sharing several characters such as the lack of ocelli, the (usually) distinct division of the pronotum into anterior and posterior regions, a characteristic pattern of trichobothria (long sensory hairs arranged symmetrically on abdominal sterna three through

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seven), and more arcane characteristics of the male and female genitalia (Schaefer 1964, 1966). Indeed, the two families were in the past considered subfamilies of a larger Pyrrhocoridae until Hussey (1929) suggested that each be raised to family level; China (1954) raised Largidae to family level, and Southwood (1956) created the formal term "Pyrrhocoroidea." Two families, Pyrrhocoridae and Largidae, in a superfamily Pyrrhocoroidea, are now the accepted classification.

Of the two families, the Largidae may be the more primitive, a view put forth by Schaefer (1964, 1966), partly because the largid ovipositor is laciniate (designed for cutting into plant tissue for the inserting of eggs) like that of the presumably ancestral Lygaeoidea and unlike the flattened broadened ovipositor of the Pyrrhocoridae (designed for the laying of eggs onto surfaces); for an opposing view, see Kumar (1968). In addition, as mentioned above, the forefemora of the Pyrrhocoridae are often (not always) swollen, and the family's metathoracic scent gland apparatus lacks a raised "auricle"; both may be advanced features, and the unswollen (or slightly swollen) condition of the forefemora in Largidae and the presence in this family of an auricle are possibly primitive features.

The superfamily Pyrrhocoroidea is distinguished by the absence of ocelli, thus making it easy to identify. So also is the Miridae, but mirids are smaller and easily distinguished in many other features. See also Schaefer and Stehlík (2013) for an account of the Pyrrhocoroidea of the Caribbean Sea Region.

A key to families of the Pyrrhocoroidea (this key will work for New and Old World Pyrrhocoroidea) is given below.

Forefemora not or slightly swollen, terete, sometimes distinctly sulcate; metathoracic scent gland complex, usually auriculate; terminus of 7th venter in female medially cleft; ovipositor laciniate; male's aedeagus without thecal appendage and vesica with distinct coils.............................Largidae

Forefemora usually distinctly swollen, neither terete nor sulcate; metathoracic scent gland complex but not auriculate; terminus of 7th venter in female entire (not cleft); ovipositor platelike; aedeagus with or without thecal appendage and vesica straight or slightly coiled .... Pyrrhocoridae

Because only the single genus of Pyrrhocoridae occurs in the New World, the key separating Largidae and Pyrrhocoridae will perforce identify *Dysdercus*.

17.3 Pyrrhocoridae

There are at least 30 genera in the family Pyrrhocoridae (Hussey 1929), but only *Dysdercus* occurs both in the New World and the Old. The other genera, some with many species, occur in the Paleotropics [e.g., *Dindymus*, with 78 species (Stehlík 2013b)], but only *Dysdercus* has reached the Neotropics. About 65–70 species occur worldwide in this genus (van Doesburg 1968; Beccari and Gerini 1970), and nearly 40 species and about 25 subspecies of New World *Dysdercus* occur in the Neotropics and the sub-Neotropics, extending up to the southern United States (van Doesburg 1968; Henry 1988a). These Neotropical species and subspecies of *Dysdercus* have been ably revised and keyed by van Doesburg (1968). Costa Lima et al. (1962) also has a key, but it is less conclusive.

The Pyrrhocoridae have been tentatively divided into two subfamilies, a division which I believe has not been published. However, because only one genus occurs in the New World, this controversy is here moot. This single genus, *Dysdercus*, occurs also throughout the Old World tropics [including Australia, but no Pyrrhocoroidea occur in New Zealand (Lariviére and Larochelle 2004, p. 191, 2014)].

At least 25 species are Paleotropical (Hussey 1929, Freeman 1947), and in the Paleotropics, they are far more diverse. Nevertheless, the actual numbers of species are more in the Neotropics (about 40 species) than in the Paleotropics (about 25–30 species). It seems likely that the New World species are all descended from a single species (or closely related members) of one of two subgenera of subgenera found only in Africa (the only other subgenus is mostly Oriental and Australasian) (see Freeman 1947; Stehlík 1965a, b; van Doesburg 1968; Schaefer 2013). The greater diversity of *Dysdercus* species in the Old World, as well as the far greater diversity of pyrrhocorid genera, supports the idea that the New World *Dysdercus* are derived from an Old World group and not the reverse. More recently, Zrzavý and Nedvěd (1997) show cladistically that the New World *Dysdercus* are all closely related, that they came from an Afrotropical group, and that the Afrotropical group did not come from the Neotropical group (see also van Doesbug 1968). The phylogenetic relationships of the New World species of *Dysdercus* have also been ably if tentatively discussed by van Doesburg (1968).

In the Galapagos Islands, there are two species of *Dysdercus* (*D. concinnus* Stål and *D. lunulatus* Uhler). These are not closely related, so Froeschner (1985) believes these two originated from two separate invasions of these islands. The first is on Santa Cruz and the second is on San Cristóbal Island.

17.3.1 Diagnosis

Species of *Dysdercus* are neither particularly large nor particularly small, ranging from 8 to 18 mm long; they are elongate oval, and their bodies are somewhat flattened (Figs. 17.1 and 17.2). Nearly all species are aposematic (warningly colored), red, yellow, or orange, and these colors may be contrastingly patterned with black; ventrally, each thoracic and abdominal segment is often vividly striped with white or yellow and a darker color—red, orange, deep yellow, or black; many species have a contrastingly black or white spot dorsally. The result is a striking and quite lovely

Fig. 17.1 Pyrrhocoridae: *Dysdercus andreae* (L.) (Dominican Republic) (length: = 9 mm) (Photo by J O'Donnell)

Fig. 17.2 Pyrrhocoridae: *Dysdercus ruficeps* (Perty) (Panama) (length = 15 mm) (Photo by J O'Donnell)

insect, whether viewed from above or below. They often feed on common plants (mostly members of the order Malvales) and often occur in aggregations, so they are frequently seen.

17.3.2 Characterization

Like all hemipterans, *Dysdercus* species have slender elongated sucking mouthparts that reach from the front of the head well onto the middle of the thorax and occasionally onto the abdomen, and, like most heteropterans, their hind wings are membranous, but their forewings are partly membranous and partly sclerotized. Characteristic of Pyrrhocoroidea, the superfamily to which they (and Largidae) belong, is the presence of two closed cells in the forewing's membrane and a lack of ocelli; in addition, the pronotum is clearly divided into an anterior third and a posterior two thirds, these sometimes of different colors.

Pyrrhocoridae can be distinguished from Largidae most readily by the presence in the females of the latter of a median split in sternum seven, indicative of an elongate or laciniate ovipositor; the ovipositor of Pyrrhocoridae is platelike, and the female's seventh sternum is entire. Other differences between members of the two families are as follows: in Pyrrhocoridae, the forefemora are at the most slightly swollen (usually slender), and the metathoracic scent gland lacks an auricle (a raised ridge surrounding the opening); the forefemora of Largidae are often swollen, and the metathoracic scent gland has an auricle. In *Dysdercus* itself, the metathoracic scent gland apparatus is somewhat reduced, and the associated evaporative area is much reduced [as seems to be true generally of aposematic bugs related to Pyrrhocoroidea (Schaefer 1972)]. No region of the body is densely covered with setae or hairs, nor does any part bear a thick coating of tiny hairs (as does occur in some New World Largidae). Also, most species of *Dysdercus* are larger than the New World species of Largidae; those *Dysdercus* species that are smaller are far more brightly and contrastingly colored.

17.3.3 Natural History

Members of *Dysdercus* live for the most part on or near the ground, often on fairly low plants upon which they feed. Preferring members of the dicotyledon order Malvales, *Dysdercus* can become serious pests of cotton, a member of that order (see below). Like other pyrrhocorids—and indeed like the bugs in related families—*Dysdercus* feeds upon the ripening seeds, or secretions on the seeds, but not other parts of the plant. Because such food is seasonal, some species of *Dysdercus* migrate during periods when food is scarce (Schaefer and Ahmad 2000). These movements are in some cases correlated with the bugs' reproductive cycle. In at least one Neotropical species, *Dysdercus fulvoniger* (De Geer), the flight muscles of females become greatly reduced, presumably to provide additional nutrients to developing eggs (Davis 1975).

That the adults and nymphs are warningly colored strongly suggests that the bugs are bad tasting and may warn away prospective predators (Svádová et al. 2010 and references therein), who studied a common European species, *Pyrrhocoris apterus* (L.). These bugs also often live in groups and perhaps thus collectively warn off vertebrate predators, which can see the brightly colored assemblages from a distance. There are some isolated records of vertebrates feeding on *Dysdercus* and some records of other arthropods doing so. The scattered nature of these records and particularly their paucity suggest predators are not important in population control. Also, of little importance are parasites (on predators and parasites, see Schaefer and Ahmad 2000). It appears thus that populations of *Dysdercus* are held in check by availability of food.

Despite their occasional economic importance, their wide distribution, and their high visibility to humans, these bugs' biologies and ecology remain poorly known. An excellent account of the Neotropical *Dysdercus* species may be found in van Doesburg (1968) and a more general summary of pyrrhocorid biology and ecology in Schaefer and Ahmad (2000).

17.3.4 Economic Importance

Dysdercus species feed mostly on malvalean plants, a group which includes cotton. In some parts of the tropics, *Dysdercus* can do serious harm to cotton crops, but they do much less harm in the New World than in the Old. However, at least one New World *Dysdercus*, *D. peruvianus* (Guérin), feeds in Peru on wild malvalean plants in the spring and then moves to cotton in the summer and can cause damage (Anonymous 1961).

In the West Indies, *Dysdercus* species feed on four families of the Malvales (Malvaceae, Sterculiaceae, Bombaceae, and Tiliaceae), but prefer Malvaceae. These species prefer wetter islands (Grenada, St. Vincent) rather than drier ones (Montserrat). On these islands, wild malvaceous hosts have nearly been eradicated and, in general, *Dysdercus* is no longer a threat to cotton production (Squire 1939); however, this was written many years ago.

Like many other heteropterans, *Dysdercus* sucks juices from the reproductive parts of plants and, in so doing, may weaken or, when abundant, even kill young cotton bolls. However, unique to *Dysdercus* is another form of damage: the microorganisms that cause internal boll disease can be transmitted mechanically from infected cotton boll to uninfected boll. Luckily, this infection seems to occur less often and less seriously in the New World than in the Old. The excreta of the bugs, and the symptoms of boll disease, discolor the cotton fibers, rendering them unfit for cloth production. For more details and a review of published work, see Schaefer and Ahmad (2000).

17.3.5 Movements and Changes in Food Plants

Dysdercus species feed mostly on seeds, a food rich in nutrients, but one less readily available than other plant tissues. The seeds of a given plant species ripen, fall, and remain available and edible over a relatively brief period. An insect subsisting on seeds must either tie its life cycle closely to that of its host or feed on the seeds of several plants whose phenologies do not greatly overlap. Usually, of course, these plants will be fairly closely related (being fed on by the same insects) and share similar defenses against predators. Such an insect breaching the defenses of one plant species will more easily breach those of that species' relatives. As different populations of the insect species, in different parts of its range, become adapted to different species of plants, speciation of the insects may occur endemically if the original host should be lost. Speciation may be hastened if newly attached species of plants develop new defenses in response to this attack, defenses which the new attacker breaches but which its conspecifics cannot.

Something of the opposite may also occur if a population of a species which feeds generally on members of a plant group be carried somehow beyond its range. Encountering there other species of its plant group, the insect may flourish and, now allopatric, speciate. Both phenomena probably explain both the Pyrrhocoroidea itself and the genus *Dysdercus*.

Some *Dysdercus* feed fairly generally on plants of the Malvales, but prefer certain species: for example, *D. mimus* (Say) on *Sida* spp. and *D. fernaldi fuscofasciatus* Blőte on *Hibiscus bifurcatus* (van Doesburg 1968). Other species, such as those with narrow isolated ranges (van Doesburg 1968), may have arrived as a small population (perhaps a gravid female) and, adapted to living on some malvalean plants at home, continued to live on others abroad. Indeed, the original colonizing stock of *Dysdercus* in the New World (from Africa: see van Doesburg 1968; Stehlík 1965a, b) survived on one side of the Atlantic on plants it had grown accustomed to on the other.

The ability to feed on several members of a related group of plants has economic consequences, if of course the plant group contains species of economic importance. It appears that the most economically important species of *Dysdercus* are those whose fairly broad food-plant range allows them to feed on non-crop reservoir plants until crop monocultures (usually cotton) become available. These reservoirs are the more important the more evanescent the food source is: and seeds are relatively short lived. *Dysdercus* species thus resemble *Leptocorisa* (Alydidae: Micrelytrinae: Leptocorisini) and *Clavigralla* (Coreidae: Pseudophloeinae) species, which damage river and pulse crops, respectively [references and brief discussion in Schaefer and Mitchell (1983)].

Of the twenty New World species listed by van Doesburg (1968) as feeding on cotton, twelve are also recorded from at least three other plants (excluding species of doubtful identification); it is likely, moreover, that several of those apparently restricted to cotton actually feed on other malvalean plants as well, the biology of most of those species not having been studied.

Dysdercus cingulatus (F.) can withstand several days' starvations, and indeed, there is some evidence this period can be extended through selection (Ahmad and Khan 1980). This being so, and other species doing the same thing, it increases the likelihood that species which feed on one plant species may, in time, feed on another.

Dysdercus migrate as adults and, during this time, may gather water and energy from nectar of various flowers and from probing fruits, both sometimes of plant species not usually used as hosts (Myers 1927; van Doesburg 1968); even other insects may be so used (Schouteden 1912; Kamble 1978). Citrus seems to be such a favored plant (Moizant and Téran 1970, Riley and Howard *in* Myers 1927) and indeed Myers quote a West Indian source that fresh orange juice is a good bait for *Dysdercus*. The fondness for citrus may however only reflect the likelihood that citrus groves often lay near cotton fields.

Because seasonal oviposition follows migration, the amino acids gathered from nectar may be used for egg production as well as for quick energy; a larger source of nitrogen is of course the histolyzed flight muscles in *Dysdercus* (Davis 1975).

This habit of *Dysdercus* (and other pyrrhocorids) may have led to the adoption of new hosts. Srivastava and Gupta (1971) suggest a population of *D. cingulatus* may move from cotton to wheat in this way; nymphs damaged the ears of the latter in a field where the former had grown shortly before. This switch seems unlikely to be permanent, for feeding on wheat can probably not yield reproducing adults. Nevertheless, if migrating females deposit more eggs upon nonhost plants visited for a brief sustenance, and if these plants are not too dissimilar chemically from the usual host (as cotton and wheat are), populations of pyrrhocorids may develop upon new hosts. If the process is repeated, each new host visited by a migrating female, being different from its predecessor, a "chain" of populations may develop the host of whose last link is a plant species markedly different from that of the first.

This explanation may account for the choices by *Dysdercus* species which, although each preferring a difference malvaceous host, will when that host senesces move to another less preferred (Dingle and Arora 1973; Robertson 1977; Kamble 1978). As a result, several species of bug may occur on one host, although for only one species is that host both the primary preferred one; for other bugs, that host is a temporary necessity. Thus, *Dysdercus koenigii* (F.) much prefers *Althea rosea* to *Hibiscus* or cotton and *Hibiscus* slightly over cotton (Shukla and Upadhaya 1972) [but see Chatterjee and Raychaudhuri (1976)], who found cotton preferred in the field by this species).

It appears then that *Dysdercus* leaves the preferred malvaceous host when it becomes unsuitable and flies to a less preferred plant, malvaceous or not. It is not clear from the literature if [as Janzen (1972) believes] a non-malvaceous secondary host merely provides water to a bug on the way to a malvaceous plant, or if the now-unsuitable primary host is always forsaken for a non-malvaceous plant by some species of *Dysdercus* (e.g., those studied by Myers in Cuba). More usually—perhaps always—a malvaceous secondary host is sought (as by the bugs Robertson studied in Tanzania), and this explains why *Dysdercus* species are so widespread as pest of cotton, even though several species do not prefer it (Shukla and Padhyaya 1972). Indeed, *Hibiscus esculentus* has been suggested as a trap plant in India.

As populations of *Dysdercus* move from host to host, different preferences will build up, depending upon how long different hosts—or the same hosts in different regions—are available. It is quite likely that *D. koenigii* in Uttar Pradesh does prefer *Althea* to cotton (Shukla and Padhyaya 1972), whereas in West Bengal the reverse is true (Chatterjee and Raychaudhuri 1960); the differences may lie in the different relative abundances and availabilities of these two plants in these two Indian states.

It is unfortunate that these ideas have not really been applied to the Neotropics, especially as the New World *Dysdercus* are all more closely related to each other than are the Old World *Dysdercus*. Perhaps because the pest status of New World *Dysdercus* is far less than that in the Old World, these speculations on the movement of these insects are merely speculative and, for now, of small importance. Note that the Indian subcontinent species *Dysdercus koenigii* has been confused with other species, for many years (see also Hussey 1929). Qadri and Ahmed (sic: Ahmad) (2001) have cleared much of this confusion. However, with global warming, *Dysdercus* may move to the north into cotton fields (and other malvaceous crops) and even to the south in southern South America.

17.4 Largidae

We recognize two subfamilies in Largidae: Physopeltinae, which is exclusively Old World, and Larginae, whose 14 genera occur only in the New World. Within Larginae, we recognize the tribes Largini (six genera) and Arhaphini (four genera and Largulini (four genera)). Here, we key the subfamilies and tribes of the World Largidae and the genera of Neotropical Largidae.

We have been unable to discover how it was and why Largidae have been called "the bordered plant bugs." They do feed, in general, on plants. But why *bordered*? Some *Largus* and many *Arhaphe* species do have horizontal stripes across their pronotum or wings. However, in some species of *Largus*, there may be a horizontal stripe on the pronotum, but the stripe may be absent. Perhaps these stripes are the reason for "bordered plant bugs." But so of course do many *Dysdercus*, as well as other Pyrrhocoridae of the Old World.

A key to the subfamilies and tribes of Largidae (this key will work for New and Old World Largidae) is presented below.

1. Eyes pedunculate or sessile; head never with depression behind bucculae; labium not reaching hind coxae; forefemur not sulcate. Metathoracic scent gland apparatus with small, rounded, or elongated, sessile auricle (New World) Larginae 2

   Eyes sessile; head with shallow depression behind bucculae; labium reaching at least to hind coxae; forefemur distinctly sulcate. Metathoracic scent gland apparatus with large, semicircular, partly free-standing auricle (Old World) Physopeltinae 3
2. (a) Eyes pedunculate or sessile. Never ant mimetic. Occipital suture present. Hemelytra usually fully developed. Auricle of metathoracic scent gland apparatus rounded. Without conspicuously slender antennae. Callar and pronotal lobes separated from one another. Genital capsule without parandria nor with a high lamellar, broken ventral rim (New World) .... Larginae: Largini

   (b) Eyes sessile. Never ant mimetic. Occipital suture present. Hemelytra fully developed. Auricle of metathoracic scent gland apparatus rounded. "With conspicuously slender antennae, callar and pronotal lobes almost unseparated." Genital capsule "with massive parandria or with a high lamellar, broken ventral rim" [from Stehlík and Jindra's (2007) description of Largulini] (Jamaica, Dominican Republic) .... Larginae: Largulini Stehlík and Jindra (2007)

   (c) Eyes sessile (but bulging in *Thaumastaneis* and *Vasarhelyecoris*). Always ant mimetic. Occipital suture absent. Hemelytra usually reduced. Auricle of metathoracic scent gland apparatus rounded (*Vasarhelyecoris*) or elongate (New World) .... Larginae: Arhaphini
3. Antenna very long, first segment longer than head plus prothorax. Sexually dimorphic (male's abdomen longer). One species: *Macrocheraia grandis* (Gray) (Asia) .... Physopeltinae: Lohitini

   Antenna not very long, first segment never as long as head plus prothorax. Not sexually dimorphic (Old World) .... Physopeltinae: Physopeltini

17.4.1 Subfamily Larginae (Figs. 17.3, 17.4, 17.5, 17.6, 17.7, and 17.8)

This exclusively New World subfamily is in general smaller than *Dysdercus* and not so warningly colored. Except for *Largus*, the species are considerably longer than wide; in *Largus*, the species are wider. Several species, especially in the genus *Largus*, are pale reddish, but no Larginae appear to warn away predators by tasting bad. In Arhaphini, protection is accomplished by appearing antlike, either in color (*Arhaphe* and *Pararhaphe*) or in structure (*Thaumastaneis* and *Vasarhelyecoris*). In Largini, a few species may mimic velvet ants.

The distribution of Larginae is in the New World, including southern (and occasionally northern) United States through South America.

Tribe Largini Amyot and Serville

This tribe consists of six species, of which *Largus* is the larger and stouter. The key to genera of Largini [modified from van Doesburg's (1966)] is presented below. The distributions are taken from Stehlík (2013a).

Fig. 17.3 Largidae: Larginae: Largini: *Largus convivus* (Stål) (Mexico) (length = 15 mm) (Photo by J O'Donnell)

Fig. 17.4 Largidae: Larginae: Largini: *Rosaphe stylophthalmum* (Stål) (French Guiana) (length = 12 mm) (Photo by J O’Donnell)

Fig. 17.5 Largidae: Larginae: Largini: *Acinocoris lunaris* (Gmelin) (Bolivia) (length = 10 mm) (Photo by J O’Donnell)

Fig. 17.6 Largidae: Larginae: Largulini: *Largulus parallelus* Hussey (Jamaica) (length = 6 mm) (Photo by J O'Donnell)

Fig. 17.7 Largidae: Larginae: Arhaphini: *Arhaphe argula* (Bliven) (Mexico) (length = 10 mm) (Photo by J O'Donnell)

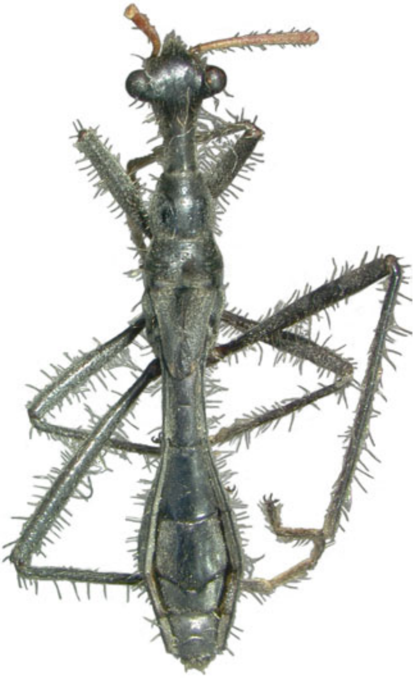

Fig. 17.8 Largidae: Larginae: Arhaphini: *Vasarhelyecoris ophthalmicus* Brailovsky & Barrera (Peru) (length = 18 mm) (Photo by J O'Donnell)

1. Eyes pedunculate (on stalks), eyestalks at least as long as the eyes are seen from above 2
   Eyes barely or not at all pedunculate 4
2. Anterior lobe of pronotum longer than pronotal posterior disk (Mexico to Brazil and Paraguay) .... *Fibrenus*
   Anterior lobe shorter than disk 3
3. Posterior corners of pronotum rounded; head and pronotum without many long black setae (Costa Rica to Argentina) .... *Acinocoris* (Fig. 17.5)
   Posterior borders of pronotum acute; head and pronotum with many long black seta (Venezuela and Guyana to Argentina)........... *Rosaphe* (Fig. 17.4)
4. Body broad, its length less than 2.5 times its length (northern United States to Argentina) .... *Largus* (Fig. 17.3)
4. Body slender, its length at least three times its width 6
5. Length of pronotum about 1.1 times its width; eyes large [Honduras to Argentina (Dellape and Melo 2012)] .... *Theraneis*
6. Length of pronotum about 1.3 times its width; eyes small (southern United States to Brazil) .... *Stenomacra*

Distribution is New World, southern (and occasionally northern) United States through South America.

These six genera are not antlike and in general are narrow. *Largus* is the largest genus (about 60 species); the others range from a few species up to 16 (*Acinocoris*) and 21 (*Theraneis*) (Stehlík 2013a). The five genera are generally brown, light brown, or yellow brown; *Largus* is an exception. One species, *Rosaphe stylophthalmum* Stål (Fig. 17.4) has a red corium, and others, *Fibrenus gibbicollis* Stål and some *Acinocoris* (Fig. 17.5), have a pattern reminiscent of *Dysdercus*—a yellow or black corium with two broad black or yellow stripes or dots across it. Some species of *Theraneis* and of *Rosaphe* (= *Astemma*) (Stehlík 2007) are thought to mimic velvet ants (Hymenoptera: Mutillidae) (Costa Lima 1940).

Largus species (Fig. 17.3) are also brown or dark brown, but there are some species with black and/or black and red. They are larger than most other genera of Largini and are wider.

Of these genera, a few species of *Largus* extend further north, into the United States: *L. cinctus* Herrich-Schaeffer and *L. succinctus* (L.) occur in some northern states, but these species also are far more abundant in the southern United States and Mexico (Henry 1988a, b).

The genus *Wupatkius*, described by Bliven (1956), is quite clearly a synonym of *Largus*, and Stehlík (2013a) mentions this as well. Halstead (1972a) synonymized this genus. Nevertheless, Bliven (1973) continued to recognize the genus *Wupatkius*. Since then, no formal description of the synonymy has occurred or any discussion of it. Therefore, the name still stands.

Tribe Largulini Stehlík and Jindra

The key is simplified from Stehlík and Brailovsky (2011), and the distributions are from Stehlík (2013a).

1. Anterior lobe of pronotum swollen (Dominican Republic) .... *Neolargulus*
   Anterior lobe of pronotum not swollen 2
2. Body larger (♂♂ 8.75–9 mm; ♀♀ 10–11 mm) (Jamaica) .... *Armilargulus*
   Body smaller (♂♂ 7–8 mm; ♀♀ 8–10 mm) 3
3. Pronotum pale, with two black spots anteriorly (Jamaica) .... *Largulus*
   Pronotum pale, no dark spots (Jamaica) .... *Paralargulus*

Three of the genera (and species) are found only in Jamaica; the fourth is found in the Dominican Republic. It is uncertain if these species will be found elsewhere. The biogeography will be interesting.

The tribe Largulini was raised from the tribe Largini by Stehlík and Jindra (2007), largely because of the peculiar shape of the male genitalia, "with massive parandria or with a lamellar broken ventral surface" (p. 14). The tribe consists of four genera (above), each with only one species.

Tribe Arhaphini Bliven

The distribution of the Arhaphini goes from southern (occasionally northern) United States into Brazil.

A note on Bliven's odd movement of this group into the family Alydidae: Bliven (1973) erected the subfamily Arhaphinae and moved it from Pyrrhocoroidea into Alydidae; at the same time, he moved the alydid subfamily Micrelytrinae (=Leptocorisini and Micrelytrini) from Alydidae to Coreidae, without discussion [for a current view of the higher classification of Alydidae, see Schaefer (1999)]. Bliven was impressed by several morphological features shared by Arhaphinae and Alydinae, particularly "general body form," type of pubescence, partial pronotal carina, the resemblance of nymphal alydines and adult arhaphines to ants, and the stridulitrum-plectrum complex. The last of these similarities (which Bliven considered the most important) does not prove phylogenetic affinity (Schaefer and Pupedis 1981), particularly as most alydines (contrary to Bliven's belief) lack it (Schaefer et al. 1989). The other similarities occur too generally within Heteroptera to warrant including Arhaphinae within Alydidae. Indeed, some alydid micrelytrines (e.g., *Dulichius*, *Trachelium*, some *Cydamus*), which Bliven moved into Coreidae, are ant mimetic and look rather like arhaphines. So also do two Old World genera of Pyrrhocoridae, *Myrmoplasta* Gerstaecker, and *Courtesius* Distant.

As mentioned, Bliven (1973) believed that similarities between the two pulled Arhaphinae into Alydidae (in his restricted sense, *sans* Micrelytrinae). To quote him: "there was a successful mingling of genes between a *Tollius*-like (a genus in Alydinae) form and a largid." He also believed differences between Arhaphinae and other largids pushed this subfamily out from Largidae; but his only evidence is the undocumented statement that "these insects (i.e., arhaphines) have long been recognized as aberrant within the family Largidae" (Bliven 1973, p. 125).

This removal of Arhaphinae to Alydidae was at best curiosity; Henry (1988a, b) was quite correct to mention it and then to restore Arhaphinae to Largidae. See another account of these movements of Bliven in Stehlík (2011).

In creating the higher-group category Arhaphinae, Bliven (1973) did not consider the Old World forms in Largidae. Having done so, we believe (as did Bliven) that *Arhaphe* and its relatives form a group equivalent to *Largus* and its relatives, but, *contra* Bliven, we believe that each group should be of tribal rank (see the key above).

A key to the genera of Arhaphini is given below, with the distributions from Stehlík (2013a).

1. Body not elongated; body black or reddish brown, with some white, yellow, or orange markings; pronotal humeri without sublateral spines; metathoracic scent glands elongated...2
   Body elongated, all black or dark brown; pronotal humeri with sublateral spines; metathoracic scent glands elongated or not 3

2. Head shorter than pronotum (United States north to Illinois and Virginia and into Central America .... *Arhaphe* Herrich-Schaeffer (Fig. 17.7).
   Head longer than pronotum (Guatemala) .... *Pararhaphe* Henry
3. Scutellum with blunt spine; eyes in lateral view not higher than vertex of head; metathoracic scent glands elongated (South America, including Bolivia (Schaefer 2000) and Paraguay (Arnold 2013)...........*Thaumastaneis* Kirkaldy and Edwards
   Scutellum without blunt spine; eyes in lateral view higher than vertex of head; metathoracic scent glands rounded (Peru) .... *Vasarhelyecoris* Brailovsky & Barrera (Fig. 17.8).

The bodies of the Arhaphini are brachypterous, elongate, black or reddish brown, or black with white-to-orange markings. In *Arhaph*e and *Pararhaphe*, the hemelytra are pale orange to white, with a black medial portion and a subterminal band of black to brown. The other two genera are black and white. The head is very prominent, sometimes with a distinct neck, and their eyes are also prominent, but never stylate. The species range in size from 5–10 mm (*Arhaphe* and *Pararhaphe*) to 8–13 mm (*Thaumastaneis*, females larger) and 16–17 mm (*Vasarhelyecoris*).

Members of all four genera more or less resemble ants. Members of *Arhaphe* and *Pararhaphe* are less antlike than are those of *Thaumastaneis* and *Vasarhelyecoris*. The last two are shaped like ants, whereas *Arhaphe* and *Pararhaphe* achieve their antlike appearances through color pattern: contrastingly pale spots or bands so placed as to resemble the head-thorax constriction and thus the petiole of ants.

Thaumastaneis and *Vasarhelyecoris* also have pronotal spines, which the other two genera lack. The former bears a spine also on the scutellum; similar spines are found elsewhere, in ant-mimicking micrelytrines (Alydidae) and colobathristids. A similar structure occurs in the immature (and myrmecomorphic) forms of the larguline (Largulini) *Largulus parallelus* Hussey, but not in the (nonmyrmecomorphic) adults (Schaefer 2000).

17.4.2 Diagnosis

Arhaphe and *Pararhaphe* may most easily be distinguished from *Thaumastaneis* and *Vasarhelyecoris* by having some white or yellow structural (not setal) coloration, and by lacking the “neck” of the last two genera, *Vasarhelyecoris* most closely resembles *Thaumastaneis*, but is larger and lacks the scutellar spine.

*Pararhaph*e: Henry (1988b) changed the more commonly used name *Japetus*, because of the homonymy of Stål’s name (1863, of a Hemiptera: Fulgoridae) with the more recent *Japetus* of Distant (1883).

17.5 Habitats and Food Plants of Larginae

Nearly nothing is known about habitats, and even less about food plants, particularly for the tribe Arhaphini. But some isolated, and often unsubstantiated, comments have been published on Arhaphini. There are more, and somewhat better substantiated, comments on *Largus* (Largini), a genus of more species.

Arhaphe species are not uncommon, scurrying like ants in and under dried leaves (Barber 1910, 1911; de la Torre-Bueno 1942; Halstead 1972b; Brailovsky 1981), occasionally with water nearby; not much else is known about them. In particular, nearly nothing is known about food plants. de la Torre-Bueno (1942) wrote that he brought four adults of *Arhaphe arguta* (Bliven 1956) onto Bermuda grass (*Cynodon dactylon,* Gramineae), "on which they proceeded to feed, as I carefully noted." However, they may have been only getting water because, usually on the ground, it is quite possible arhaphines actually feed on fallen seeds.

It is probably significant that, although abundant locally, there is no mention of the Arhaphini in Ahmad and Schaefer (1987), which is a list of food plants of Pyrrhocoroidea. There are some references to the other tribe, Largini. In general, several *Largus* appear to feed on seeds, in fruits, or on the ground. *Largus* may also feed on dead insects (Myers 1927, P. L. Mitchell personal communication) and even dog food (P. L. Mitchell personal communication). *Largus* eggs are laid on the ground. *Acinocoris* and *Fibrenus* appear to feed on seeds on plants (van Doesburg 1966).

Although eggs of *Largus* are laid on the ground, the nymphs seem usually to be upon plants and usually on flowering or fruiting plants. This may also be the case with other Largini.

Like other phytophagous heteropterans, many of these largines probably get water and, especially, proteins and salts from bird droppings and dead bodies (and dog food) (Schaefer 1980; Schaefer and Mitchell 1983).

17.6 Concluding Remarks

Overall, these bugs are of a size and conspicuousness that many are easily collected. As a result, the taxonomy of Pyrrhocoroidea has been well worked out, thanks to van Doesburg (1968) (*Dysdercus*) and several papers by Brailovsky and Stehlík (Largidae). However, we need to know the biologies, especially for the Largidae. For *Dysdercus*, it would be very useful to know more about how many species, and where and when, they feed on cotton, which was a worse problem years ago than now (Schaefer and Ahmad 2000). With global warming, this problem may occur again.

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Chapter 18
Broad-Headed Bugs (Alydidae)

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Abstract The broad-headed bugs (Alydidae) are divided into two subfamilies, Alydinae and Micrelytrinae, each divided into two tribes, Daclerini and Alydini, and Micrelytrini and Leptocorisini, respectively. The family has 53 genera and about 250 species; in the Neotropics, there are 21 genera. Alydids are small (8–20 mm), slender, with a triangular head; nymphs of alydines mimic ants, the adults of some Micrelytrini also mimic ants. The most studied species in the Neotropics is the alydine *Neomegalotomus parvus* (Westwood), usually associated with legumes, and may be a pest on soybean. Other common genera include *Hyalymenus* Amyot & Serville, *Stenocoris* Burmeister, *Cydamus* Stål, and *Trachelium* Herrich-Schäffer. Studies on taxonomy and bioecology on alydids of the Neotropics are needed.

18.1 Introduction

Alydidae Amyot and Serville, 1843, were treated as a subfamily of the family Coreidae and even as a tribe (Schaffner 1964); now it has been treated as a family, together with Coreidae, Rhopalidae, Hyocephalidae, and Stenocephalidae, in the superfamily Coreoidea (Schaefer 1964).

This family contains 53 genera and approximately 250 species, mostly tropical or subtropical, in all regions of the world. There are only two genera that span both the Old and the New World, *Alydus* and *Megalotomus*. These genera are Holarctic, but *Alydus* extends from Alaska through Canada into Mexico (Brailovsky and Flores 1979; Froeschner 1988; Maw et al. 2000).

The genera of Alydinae have been revised by Schaffner (1964; 22 species worldwide); the world genera of the subfamily Micrelytrinae, tribe Leptocorisini, were

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revised by Ahmad (1965; seven species worldwide). There has been no list of the subfamily Micrelytrinae, tribe Micrelytrini; our data came from Dolling's "Catalogue of the Palaearctic Region" (2006) (eight genera, Palearctic), which may be undercounted, especially for tropical Asian and African genera. The Alydinae contains two tribes, the Alydini and the Daclerini, the latter with only one genus, *Daclera*; this latter tribe has not been accepted by some workers and is included in Schaffner (1964) as a genus. *Acestra* has also been considered a Micrelytrinae tribe (Li and Zheng 1993); both suggested tribes (Daclerini and Acestrini) are from the Old World.

Schaefer (1999) worked out the higher classification of the family Alydidae. It now has two subfamilies (Alydinae and Micrelytrinae). The Alydinae contains two tribes (Daclerini and Alydini); Micrelytrinae also has two tribes, the Micrelytrini and the Leptocorisini, both distributed worldwide.

Within the Neotropics, there are eight genera of Alydinae and 13 genera of Micrelytrinae in the tribes Micrelytrini (11 species) and Leptocorisini (2 species). These genera have been keyed in Schaefer (2004), as well as the subfamilies, tribes, and subtribes (of Leptocorisini).

18.2 General Characteristics and Diagnosis

Species of Alydidae are fairly small, ranging from 8 to 20 mm. Alydids are narrow, i.e., they are much longer than wide, especially in many of the Leptocorisini and some of the Micrelytrini. The dorsa of the head and thorax lack ridges or bumps (except for spines on some Micrelytrini) and are flattened. The head is triangular and resembles the heads of ants. Some of the adults of Micrelytrini (genera *Cydamus* and *Trachelium*), as well as the nymphs of Alydinae, are antlike, presumably to ward off predators. This ant mimicry (myrmecomorphy) has been reported for several species of Alydidae by several authors for the past 80+ years (Nicholson 1927; Mathew 1935; Costa Lima 1940; Kormilev 1953; Kumar 1966; Schaefer 1972; Elzinga 1978; Sisson 1980; Oliveira 1985). The family's common name, broad-headed bugs, actually refers only to the Alydinae: their "heads are indeed broader between the eyes than are those of other coreoids" (Schaefer 2004).

Additional diagnostic characters include bucculae very short, antennae dorsally inserted with segment 1 not constricted at base, ocelli not placed on elevations, corium elongated on costal margin, metathoracic scent glands auricles well developed, and tibia nonsulcate (Schuh and Slater 1995).

18.3 Classification and Diversity

The family Alydidae was divided into three subfamilies [Leptocorisinae, Alydinae, and Micrelytrinae (Ahmad 1965)]. More recently, the family was divided into two subfamilies (Alydinae and Micrelytrinae), this last containing two tribes, Leptocorisini (a former subfamily of Ahmad's classification) and Micrelytrini

(Schaefer 1999). A key for the two subfamilies, including the tribes for the last, is presented below according to Schaefer (2004), with slight modifications.

1. Hind femur bearing spines; trichobothria of abdominal sternum five arranged in a row lateral or anterior to spiracle .... Alydinae

– Hind femur without spines; trichobothria of abdominal sternum five arranged in a triangle posterior to spiracle... Micrelytrinae (2)

2. Second rostral segment shorter than 3rd and 4th together; 3rd rostral segment more than half long as 4th; evaporative area of metathoracic scent gland smooth.. Leptocorisini

– Second rostral segment longer than 3rd and 4th together; 3rd rostral segment less than half long as 4th; evaporative area of metathoracic scent gland ridged .... Micrelytrini

The complete higher classification of Alydidae based on Schaefer (1999) is shown below:

Family Alydidae Amyot and Serville

- Subfamily Alydinae Amyot and Serville
  - Tribe Alydini (New and Old World)
  - Tribe Daclerini (Old World)
- Subfamily Micrelytrinae Stål
  - Tribe Micrelytrini Stål (New and Old World)
  - Tribe Leptocorisini Stål
    - Subtribe Leptocorisidi Stål (New and Old World)
    - Subtribe Noliphidi Ahmad (Old World)

The most comprehensive taxonomic study of the Alydidae family is by Schaffner (1964), Ahmad's revision of the Leptocorisini (1965), and Kormilev's (1953) revision of part of the Micrelytrini: these are the only family-group taxonomic revisions. Much work needs to be done on revisions of other family groups and genera and also on alydids' biology. For the Neotropics (South America), Froeschner (1981) keyed the subfamilies and genera.

18.3.1 Alydinae

This subfamily contains individuals in all major zoogeographic zones. The best-known genera include *Alydus* F., *Hyalymenus* Amyot and Serville, *Megalotomus* Fieber, *Neomegalotomus* Schaffner and Schaefer, and *Riptortus* Stål. In the Neotropics, *Hyalymenus* and *Neomegalotomus* include the most common and known species (Grazia et al. 2012).

The Alydinae prefer legumes (Schaefer 1972, 1980; Schaefer and Mitchell 1983; Panizzi 1988; Santos and Panizzi 1998a, b), and some species are considered pests on leguminous crops (see section 4 on main species). There are also several references to different species of alydines being attracted to and feeding on carrion, vertebrate fecal matter, and cow urine and ammonia (Schaefer 1980; Adler and Wheeler 1984; Ventura and Panizzi 2000; Silva et al. 2010). These nitrogen-rich materials attract alydines, and it has been speculated that these bugs might require higher concentration of nitrogen than do other bugs, based on this behavior and their association with nitrogen-rich plants (i.e., legumes) (Panizzi et al. 2000).

18.3.2 Micrelytrinae

In this subfamily, several genera (*Cydamus*, *Darmistus*, *Esperanza*) reach the southwestern states of the USA. *Protenor* occurs throughout the USA and into Canada (Froeschner 1988). *Esperanza texana* Barber occurs farther north and its range may be expanding (Johnston 1927; Hussey 1948; Froeschner 1980). With global warming, *Esperanza*'s distribution is expanding, not only to the north but to the south. It now occurs as far south as Costa Rica (Schaefer 2003).

In the Neotropics, the main genera in Micrelytrinae (Micrelytrini) are *Stenocoris* Burmeister, *Cydamus* Stål, and *Trachelium* Herrich-Schäffer (Grazia et al. 2012). We do not know what Micrelytrini feed on. Leptocorisini feed on grasses; in the Orient, some species may become pests on rice.

18.4 General Biology

Data on the biology of alydids are available for those species with major or minor economic importance, such as species of *Leptocorisa* [*L. acuta* (Thunberg) and *L. oratorius* (F.)], associated with rice throughout Asia; species of *Riptortus* [*R. dentipes* (F.), *R. linearis* (F.), *R. pedestris* (F.), and *R. serripes* (F.)] associated with legume crops in Asia, Africa, and Australia; and *Alydus pilosulus* Herrich-Schäffer and *Megalotomus quinquespinosus* Say, associated with legumes in the Nearctic region (Canada and USA) (references in Panizzi et al. 2000).

For the Neotropical alydids, not much data is available on their biology. Most information has been published on the species which have some economic importance, such as *Neomegalotomus parvus* (Westwood), pest of legume crops, particularly in Brazil (section 5.1); other species studied in greater detail are those on the genus *Hyalymenus* which show mimetic association with ants (Oliveira 1985).

18.5 Main Species

Most members of Alydidae in the world are not pests, and in general their biology, ecology, and host plants are largely unknown. There is only one species which is considered common and is of somewhat economic importance in the Neotropics. The second species in this genus is less common, and they are presented below.

18.5.1 Neomegalotomus parvus (Westwood)

The new genus *Neomegalotomus* Schaffner & Schaefer was erected to accommodate the Neotropical species formerly included in the genus *Megalotomus* (Schaffner & Schaefer 1998; Schaefer & Panizzi 1998). *N. simplex* (Westwood), *N. latifascia* (Berg), and *N. pallescens* Stål were all synonymized with *N. parvus* (Schaefer & Ahmad 2008).

N. parvus (Westwood) occurs in the Neotropics between 24° N and 30° S longitude; the northernmost are from central Mexico on the west and St. Vincent and Barbados on the east; the southernmost distribution is northern Argentina, southern Brazilian states, and Uruguay (Schaefer and Ahmad 2008); these authors do not include Rio Grande do Sul, the southernmost state of Brazil, where specimens of *N. parvus* have been collected recently (in Passo Fundo, 28 ° S, AR Panizzi, unpublished).

N. parvus is, by far, the most studied species of alydid in the Neotropics, particularly in Brazil. It was first reported on *Crotalaria* sp. in Rio de Janeiro state (Costa Lima 1919), and other hosts include common bean, soybean, cotton, tomato, lupin, pigeon pea, and lablab (Panizzi 1988; Chandler 1989; Santos and Panizzi 1998a).

Eggs (Fig. 18.1) are laid singly or in groups. On soybean, eggs are laid on the upper third of the plant, preferably on the lower side of leaves, close to the midrib (Panizzi et al. 1996). On pigeon pea, *Cajanus cajan* (L.), eggs are laid preferably in-between seeds (crevices) of mature pods (Ventura and Panizzi 2000, 2003). Interesting to mention that during maintenance of *N. parvus* colony in the laboratory, in seven occasions, females laid eggs on the body of conspecifics, and on three events, eggs remained on the insect body until they hatched (Panizzi and Santos 2001).

Nymphs mimic ants (Fig. 18.2) and are darkish. Adult males are pale brown, with a whitish band along both sides of the thorax; females are entirely darkish brown (Fig. 18.3). Body length is ca. 10 mm (Costa Lima 1919, Paradela Fo et al. 1972).

Several studies on the nymphal and adult biology, population dynamics, oviposition, and feeding preferences of *N. parvus* on selected cultivated and noncultivated legumes (e.g., soybean, pigeon pea, lablab, green bean, indigo, lupin, and cowpea) have been published (Panizzi 1988; Ventura and Panizzi 1997; Santos and Panizzi 1998a; Ventura et al. 2000a, b; Ventura and Panizzi 2003, 2004, 2005). In general,

Fig. 18.1 Eggs of *Neomegalotomus parvus* on a soybean stem (**a**) and on crevices of a pigeon pea pod mature (**b**) (Courtesy of JJ Silva)

Fig. 18.2 Ant-mimic nymph of *Neomegalotomus parvus* on a soybean pod (Courtesy of JJ Silva)

Fig. 18.3 Adult (female) of *Neomegalotomus parvus* on green bean pods (Courtesy of JJ Silva)

this alydid is most associated with mature soybean and pigeon pea plants. In the laboratory, colonies of *N. parvus* are easily kept using mature seeds of pigeon pea, to allow the use of this bug for research and teaching purposes (Ventura and Panizzi 1997).

Although considered a minor pest, this alydid damages common beans by transmitting the yeast spot disease caused by *Nematospora coryli* Peglion and by causing seedling mortality (Paradela Fo et al. 1972; Chandler 1984, 1989). It also can cause reduction in seed vigor and viability in soybean (Santos and Panizzi 1998b). In Brazil, *N. parvus* adults are parasitized by at least three species of tachinids (Santos and Panizzi 1997).

18.5.2 Neomegalotomus rufipes (Westwood)

This second species in the genus *Neomegalotomus*, *N. rufipes*, occurs from southeastern Florida south to Central America and the West Indies islands in the Caribbean, including Antigua, Bahamas, Cuba, Dominican Republic, Grand Cayman, Grenada, Guadeloupe, Jamaica, Martinique, Puerto Rico, St. Lucia, and St. Martin; despite its affinity to legumes, apparently it is not a pest in these islands (Schaefer and Ahmad 2008). These authors provide a key to species of *Neomegalotomus*, shown below:

1a. Metathoracic scent gland auricle usually somewhat flattened and separation between anterior and posterior parts of auricle shallow; median protuberance of ventral rim of male's genital capsule pointing medially .... *Neomegalotomus parvus* (Westwood)
1b. Metathoracic scent gland auricle rounded, convex, separation between anterior and posterior parts deep; median protuberance of male's genital capsule pointing .... *Neomegalotomus rufipes* (Westwood)

The reference to the occurrence of *Neomegalotomus rufipes* in São Paulo state in Brazil on cotton, on sunn hemp, *Crotalaria juncea* L., on the legume *Macroptilium heterophyllum* (Humb. and Bonpl. ex Willd.), and on the ornamental plant *Asclepias curassavica* L. mentioned by Silva et al. (1968) is probably a mistake, because this species is not known to occur in this area.

18.6 Secondary Species

There are several genera/species of alydids in the Neotropics. Froeschner (1981) keyed the genera of South American alydids, and he included the following: in Alydinae, *Apidaurus* Stål, *Alydus* F., *Hyalymenus* Amyot and Serville, *Burtinus* Stål, and *Megalotomus* Fieber (now *Neomegalotomus* Schaffner and Schaefer); in Micrelytrinae (Leptocorisini), *Stenocoris* Burmeister and *Lyrnessus* Stål; and in Micrelytrinae (Micrelytrini), *Calamocoris* Breddin, *Cydamus* Stål, *Trachelium* Herrich-Schäffer, *Bactrophya* Breddin, and *Bactrocoris* Kormilev.

Among these genera, species worth of mention are *Hyalymenus pulcher* (Stål), *Stenocoris americanus* Ahmad, *S. fabricii* Ahmad, *S. tipuloides* (De Geer), *Bactrophya aequatoriana* Breddin, *Calamocoris erubescens* Breddin, *C. nigrolimbatus* Breddin, and *Cydamus inauratus* Distant. *Cydamus pictipes* (Stål) is reported on grasses and on castor bean, *Ricinus communis* L. in São Paulo state, Brazil (Silva et al. 1968).

In Brazil, two species of *Hyalymenus* have been studied in detail regarding myrmecomorphy (ant mimicry): *Hyalymenus limbativentris* Stål, which is usually associated with solanaceous plants, feeding on fruits, and *Hyalymenus tarsatus* (F.), which is found on plants of several (five) families, feeding on flower and/or fruits (Oliveira 1985). This last species is reported on the legume *Cassia occidentalis* in Brazil (Silva et al. 1968).

18.7 Concluding Remarks

Alydids in the Neotropical region are largely unknown, and their biology, except for *Neomegalotomus parvus* (Westwood), which has occasional a pest status, is little studied. Data in the literature are scant, and most information in the literature is restrained to lists of species (catalog type of publication) and taxonomic keys for subfamilies and genera (e.g., Schaffner 1964; Froeschner 1981; Schaefer 2004; Schaefer and Ahmad 2008). Moreover, information (published and not) seems to be confused, such as the reference to *Leptocorisa filiformis* (F.) occurring in coffee plantations in São Paulo state, Brazil (Silva et al. 1968), and *Leptocorisa* sp. occasionally infesting soybean and rubber plant, *Hevea brasiliensis* (Willd. ex Adr. de Juss.) also in São Paulo, Brazil (AM Faria, pers comm to ARP). The genus *Leptocorisa* is distributed in the Orient and Australia (Ahmad 1965, Livermore et al. http://Coreoidea.SpeciesFile.org) and is not supposed to occur in the Neotropics. This example, clearly illustrates the strong need to revise the taxonomic status of the species of alydids in the Neotropics. In addition, research work on their biology, particularly on their life history in nature, to reveal their association with host plants either cultivated or not is needed.

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Chapter 19
Leaf-Footed Bugs (Coreidae)

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Abstract The family Coreidae is distributed worldwide, but these phytophagous bugs are most abundant in the tropics and subtropics. In the Neotropical region, all of the subfamilies and 16 tribes are represented. In tropical ecosystems, these bugs feed on herbs and shrubs in open areas of forests as well as at the forest edge. Some species are spectacularly colored, and unusual expansions of antennae, humeral angles, femora, or tibiae occur in many groups. Some of them move lazily even when disturbed and hardly fly to escape; others are extremely nimble, fast flying away when disturbed. They are frequently encountered in crops, representing important pests in several commodities. No one common name is universally accepted for the family, and none of the frequently used names (e.g., squash bug, leatherbug, leaf-footed bug, Randwanzen) are collectively appropriate for all members of the family.

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19.1 Introduction

The family was established by Leach (1815), but Stål (1867, 1870) was the first author to propose a suprageneric structure to Coreidae. Surprisingly not much has been done at this level since then, and much of the suprageneric organization is still the same. The most comprehensive work at this level since Stål was presented by Schaefer (1964, 1965). For many years, the literature on Coreidae was fragmentary; keys are still lacking for several important groups. During the last few decades, Brailovsky and coworkers have revised or contributed to the knowledge of several Neotropical genera of Coreidae (see throughout the chapter). Only recently, a print catalog for the Neotropical Coreidae (Packauskas 2010) and an online catalog for Coreoidea of the world (CoreoideaSF Team 2015) were compiled. These recent revisions and catalogs will allow future works on Coreidae, especially on relationships among taxa.

19.2 General Characteristics and Diagnosis

Coreids are usually heavy-bodied insects, elongate or elliptical in shape. Species of the genus *Thasus* are bulky insects reaching 30–40 mm, and species of *Vilga* are delicate 6–10 mm bugs. Many have the hind femora enlarged, with spines and tubercles; hind tibiae curved, with spines or leaflike expansions; and third and fourth antennal segments dilated or tumid (Plate 19.1). Most of the species have dull colors like brown, gray, and yellow, but some have bright colors like red, green, orange, or sometimes a metallic coloring. Head smaller than pronotum; antennae with four segments and inserted above a line drawn through the eye; membrane of forewing with several veins; femora of hind legs frequently incrassate; hind tibiae terete or slightly to strongly dilated; abdominal spiracles ventral; 3 trichobothria on abdominal segments III–VI, 2 on segment VII; nymphal dorsal abdominal scent gland openings between terga 4/5 and 5/6; genital plates flattened; spermatheca only with proximal pump flange; eggs with pseudoperculum except in Pseudophloeinae.

19.3 General Biology and Ecology

Coreids are plant feeders; hosts include gymnosperms and angiosperms and monocots and dicots. However, dicots are far more common as hosts than monocots, and few coreid species are exclusive feeders on gymnosperms (Schaefer and Mitchell 1983). Opportunistic feeding on fecal matter, carrion, and insect eggs has been reported (Adler and Wheeler 1984; Menezes-Netto et al. 2012) but is never the primary source of nutrients. Plant preference spans a wide spectrum from specialization on a single genus to extreme polyphagy; reported host plants of one African

Leptoglossus zonatus
PHOTO: *W.O. Ree, Jr.*

Pachylis sp.
PHOTO: *José A.M. Fernandes*

Pachylis sp.
PHOTO: *José A.M. Fernandes*

Holhymenia sp.
PHOTO: *José A.M. Fernandes*

Eubule farinosa.
PHOTO: *José A.M. Fernandes*

Crinocerus sanctus
PHOTO: *Arthur Anker*

Spartocera sp.
PHOTO: *Andreas Kay*

Spartocera sp.
PHOTO: *Andreas Kay*

Plate 19.1 Field images of Coreidae

mictine species, *Anoplocnemis curvipes* (F.), represent >30 plant families. Legumes are the primary host plants of Pseudophloeinae and several tribes of Coreinae (Acanthocerini, Mictini, Nematopodini); this may be a primitive trait of Coreoidea (Schaefer and Mitchell 1983). Some genera or tribes may be characterized by their host plant preferences (e.g., *Chelinidea* spp. on Cactaceae), but most cannot; a single genus (e.g., *Leptoglossus* Guerin) may include polyphagous species and those with highly restricted feeding habits (Mitchell 2006).

Most coreids are winged, but members of the Australian tribe Agriopocorini are usually wingless (Schuh and Slater 1995), and the single described species of Barreratalpini is brachypterous (Packauskas 1994). Both macropterous and brachypterous forms are known in the Neotropical pseudophloeine *Vilga mexicana* Distant (Dolling 1977). At least one coreid has been described as migratory (Aldrich et al. 1982), but most movement involves shorter distances. Coreids move seasonally among host plants and between hosts and overwintering areas in temperate regions, occasionally becoming a problem in houses. Dispersal may occur in the nymphal stage, but in polyphagous species such as *L. phyllopus*, most movement occurs when recently molted winged adults disperse from deteriorating nymphal hosts (Mitchell 2006). Vast geographic range expansion has occurred through commercial movement of plants. For example, the conifer-feeding *Leptoglossus occidentalis* Heidemann, formerly restricted to western North America, spread eastward as far as Ontario and Connecticut and then, following accidental introductions, has spread through most of Europe, most recently being reported from Turkey (Hizal 2012) and parts of Asia, most recently Korea (Ahn et al. 2013). The Neotropical *Leptoglossus zonatus* (Dallas), long known as a highly polyphagous crop pest in Central and South America and Mexico, has also expanded its range recently, moving across the southern United States from Texas to Florida, becoming a problem in satsuma oranges and other citrus (Xiao and Fadamiro 2010).

A number of coreids are economic pests; grain legumes, tree nuts, rice, fruits, and garden vegetables are among the crops attacked. Several species pose problems in forest management (conifers and eucalypts). Only a small proportion of coreid species damage crops, but those few can cause serious losses (Mitchell 2000). Worldwide, legume feeders are likely the most important economically, especially in combination with alydids and pentatomids. Pests in the Neotropics include *Anasa* spp. on cucurbits, *Spartocera* spp. on Solanaceae and tobacco, *Phthiacnemia picta* (Drury) on tomatoes and *Leptoglossus* spp. on a variety of crops. Direct damage to grains and developing seeds within pods and seed heads is most common; pod abortion or reduced seed production may result from feeding damage. Fruits may become malformed, pithy, or corky, or develop blotches, spots, depressed areas or lesions. Wilting due to vascular damage can also result in losses, and the role of coreids and other Heteroptera in transmission of diseases is only recently becoming appreciated (Mitchell 2004). No coreids are known to transmit viruses or phytoplasmas, but 13 species are associated with fungal pathogens (Mitchell 2004) and 30 species representing 17 primarily Neotropical genera harbor trypanosomatids (adapted from Camargo and Wallace 1994 and Godoi et al. 2002). A survey of Amazonian Heteroptera showed coreids to far outnumber other families in frequency of trypanosomatid infection; >80 % of Coreidae were infected, many with the plant parasite *Phytomonas*, compared with <10 % of other phytophagous families examined (Godoi et al. 2002). *Phthiacnemia picta* not only harbor phytomonads but have been shown to acquire and infect tomatoes with these flagellates (Jankevicius et al. 1989; Fiorini et al. 1993). *Leptoglossus zonatus* (Dallas) can transmit a trypanosomatid to corn kernels (Jankevicius et al. 1993). In the United States, transmission by *Anasa tristis* De Geer of the fastidious phloem-colonizing bacterium causing cucurbit yellow vine disease has recently been documented and extensively studied (Bruton et al. 2003). Although a few coreid species have been investigated as potential biocontrol agents (Mitchell 2000), none have been successfully adopted, either due to failure to disperse or insufficient host specificity.

Natural enemies of coreids include parasitic tachinid flies; several species of egg parasitoids in the families Encyrtidae, Eurytomidae, and Platygastridae; and both vertebrate and invertebrate predators, particularly reduviids, spiders, and ants. Guarding of eggs by females has been reported for one species (Hemmingsen 1947). Scent glands, present in both adults and nymphs, provide effective protection from some predators. Blackbirds feeding on *Coreus marginatus* (L.) and various pentatomid species will wipe bugs along on the ground, or hit them repeatedly against the ground, to avoid consuming the defensive secretions (Schlee 1992). Adult scent glands are located ventrally on the metathorax, whereas nymphal scent glands are on the dorsum of the abdomen. Compounds produced by these glands differ between juveniles and adults. Chemical composition of the scent fluid was reviewed by Aldrich (1988).

19.3.1 Eggs and Oviposition

Egg shapes vary among coreid species. Ovoid or elliptical eggs are most common, but hemicylindrical, cuboidal, globular, and oblong eggs are known (Cobben 1968; Moulet 1995). The portion attached to the substrate may be flattened, producing an egg that is triangular in cross-section (e.g., *Acanthocephala terminalis* (Dallas), Yonke and Medler 1969b). However, in pseudophloeines, the side of the egg facing the substrate is convex (Cobben 1968). The hemicylindrical eggs of *Leptoglossus*, *Phthia s.l.*, and *Narnia* (as well as several Old World genera) are laid in long chains, end to end (Amaral 1981a; Mitchell and Mitchell 1986; Mitchell 2000), but other types may be oviposited singly, in small groups, adjacent rows, large clusters, or even atop one another as in the Old World pseudophloeine, *Ceraleptus gracilicornis* H.-S. (Cobben 1968). Most eggs are laid on host plants, generally on the undersides of leaves, but the egg chains of *Leptoglossus phyllopus* (L.) may be placed along virtually any linear surface—host or non-host, living or nonliving (Mitchell and Mitchell 1986). Females of *Phyllomorpha laciniata* (Villers) may choose to place eggs on leaves of the host plant or on the backs of males. Such oviposition blocks wing movement so that individuals carrying eggs cannot fly and are subject to higher predation (Reguera and Gomendio 1999). Paternal care was found to be higher in a population subjected to heavy egg parasitism; eggs laid on males suffered less parasitism than those laid on plants (Gomendio et al. 2008).

Cobben (1968) provides detailed descriptions of the eggs of several species. A pseudoperculum is present in most Coreinae in the shape of a round cap, but not in Pseudophloeinae. In the latter subfamily, the extensive eclosion fracture may entirely separate the two halves of the eggshell. The number and placement of aero-micropyles also varies, from just a few to 60 in the species studied. They are most commonly arranged in a ring which crosses or more rarely coincides with the circular pseudoperculum. The chorion may be up to 100 μm thick, and the egg burster is triangular with a sclerotized ridge (Cobben 1968).

Eggs are cemented to the substrate by the female, and it has been suggested that trypanosomatid cysts may survive in this material, thereby providing a source of infection (Camargo and Wallace 1994). However, *Burkholderia* bacterial symbionts are not acquired from the eggs in *Thasus neocalifornicus* Brailovsky & Barrera and must be acquired de novo, presumably from the soil, by the early instars (Olivier-Espejel et al. 2011).

19.3.2 Nymph Feeding and Development

Five stadia occur between hatching and adult emergence. First instars often remain in the vicinity of the egg mass and appear to need only a source of water for successful molt to the second stadium (Cook and Neal 1999). Probing into plant tissue may occur, but the tissue selected is always vegetative (tendrils, leaves, terminal buds) (Rodrigues et al. 2007a; Wheeler and Miller 1990). Under laboratory conditions, survivorship of first instars provided with only a water wick was equivalent to that of first instars provided green bean and sunflower seed, and only the bean was used by the nymphs when food was provided (Mitchell 1980a).

Second through fifth instars require a nutrient source and feed similarly to the adults in most cases, although the shorter stylets may prevent access to deeper plant tissues. Younger instars are generally gregarious; research with *Phthia picta* (Amaral 1981a) has shown that grouped nymphs develop faster than isolated nymphs. Experimental studies of nymphal social groupings in the cactus bug *Chelinidea vittiger aequoris* McAtee (Miller et al. 2012) indicate that females reared alone are less likely to forage socially as adults than nymphs reared in a group; no similar effect of nymphal environment on adult behavior was found for males. Aggregation of juvenile bugs has been attributed to a number of factors, including both abiotic (humidity) and biotic (protection from predation) (Panizzi 2004a). Coreid nymphs are often highly visible—brightly colored with flattened hind tibiae and/or antennal segments—and all have dorsal abdominal scent glands. Aposematic feeding aggregations of nymphs of a Costa Rican coreid species responded to disturbance by pulsating, spraying anal fluid, and releasing scent fluid (Aldrich and Blum 1978). The various secretions of the dorsal abdominal glands function in defense against natural enemies as repellents, deterrents, and/or toxins (Noge et al. 2012) and as an alarm pheromone. Nymphs will also respond to the alarm pheromones of adults in *L. zonatus* (Leal et al. 1994), but not in *T. neocalifornicus* (Prudic et al. 2008). Interestingly, the chemistry of coreid nymphal secretions differs from that of pentatomids, in that aldehyde chains are shorter and little or no *n*-tridecane is present. The short chain keto-aldehyde of coreids (4-oxo-(E)-2-hexenal) is potent against ants, whereas the longer chain compounds of pentatomid nymphs are less potent but are synergized by *n*-tridecane (Eliyahu et al. 2012).

19.3.3 Adult Feeding and Reproduction

Coreids feed on a range of plant parts, including vegetative tissue, phloem, buds, fruits, developing seeds, and mature seeds (Mitchell 2000). Such preferences are often specific at the tribal level; bugs are either associated with vegetative and vascular tissue or with reproductive plant parts. Kumar (1966) separated Australian coreids into those that fed exclusively on sap or those that fed on sap and fruit, and this early observation has held for other groups studied subsequently (Schaefer and Mitchell 1983). Like all Pentatomomorpha, coreids produce two types of saliva, gelling saliva to line the path of the stylets, producing a salivary sheath, and watery saliva containing enzymes (Miles 1972; Cobben 1978). The mode of feeding in several species of Australian coreids has been described as an "osmotic pump." In this process, a short salivary sheath extends into parenchyma associated with vascular tissue. Sucrase in the watery saliva induces phloem unloading and discharge of parenchyma cell contents into the spaces between cells, and nutrients are thereby obtained from the extracellular spaces without direct penetration of the membranes of individual cells. The resulting effect on the plant may be a necrotic lesion or wilting of shoots beyond the feeding site (Miles and Taylor 1994). This feeding mode has been associated with species from Amorbini, Mictini, and Dasynini but may be more widespread within the family. True phloem feeding—similar to that of aphids, in which stylets penetrate phloem sieve elements—is assumed for the very few coreid species (*Hygia cliens* Dolling, *Notobitus affinis* (Dallas), and *Cloresmus* sp.) in which ant-tending for honeydew has been observed (Maschwitz et al. 1987). No coreids feed exclusively from xylem, but hydration from xylem certainly occurs. Stylet sheaths terminating in xylem are reported for *Leptoglossus phyllopus* (L.), which feeds primarily on developing seeds (Mitchell 2006), and wilting of squash leaves has been attributed to xylem blockage by the gelling saliva of *A. tristis* (Neal 1993).

The number of generations per year varies with latitude and as a function of crop cycles, host plant phenology, and host plant specificity. In temperate zones, the overwintering stage is usually the adult. Adults are long-lived; mark-release-recapture studies indicate maximal lifespan of over 50 days (Mitchell 2006). Courtship and mating have been described for several species and involve antennation, touching with the legs, or other body contact prior to copulation (Eberhard 1998; Miller 2011; Tatarnic and Spence 2013). Both males and females may mate multiple times. Duration of mating varies within and between species but may be as long as 6–7 h (McLain et al. 1993; Tatarnic and Spence 2013). Mating often occurs on fruits, and feeding by one or both partners during copulation is common. The most frequent mating position is end to end, with the male facing the opposite direction from the female. Copulatory success appears to correlate with size of male (McLain et al. 1993; Tatarnic and Spence 2013).

In several coreid tribes, a pronounced sexual dimorphism occurs in the size and armament of the hind femur, although the expression of this trait may vary within and across populations (Miller and Emlen 2010). This trait has been linked to male-male combat and territoriality or female defense polygyny in at least 8 species (Fujisaki 1980, 1981; Mitchell 1980b; Aldrich et al. 1982; Miyatake 1995, 1997; Eberhard 1998; Miller and Emlen 2010; Miller 2013). However, large mixed gender aggregations occur in other species (Mitchell 1980b; Solomon and Froeschner 1981), and male-specific attractant compounds have been identified for several species (Millar 2005). These species-specific volatile compounds are released from epidermal cells, ventral abdominal glands, or the lateral lobe of the metathoracic scent gland, depending on species (Aldrich et al. 1982, 1993; Soldi et al. 2012), and may serve in short-range communication, as attractants for females only or as aggregation pheromones.

19.4 Classification and Diversity

Although distributed worldwide, coreids are most abundant in the tropics. A recent catalog of New World Coreidae (Packauskas 2010) lists 158 genera that contain species with distribution records from the Neotropical region. All three subfamilies—Coreinae, Meropachyinae, and Pseudophloeinae—are represented in this region. A detailed study of the species richness of the coreoid fauna of relict pluvial subtropical forest in southern Brazil revealed 20 species of Coreidae present, with one species, *Cebrenis supina* Brailovsky, dominating beat-sheet collections (Barcellos et al. 2008). A number of economically important species have been extensively studied, but for the majority of Neotropical species, unfortunately little or nothing is known about their biology. Here we present keys to the subfamilies and the tribes of Coreinae of the Neotropical region; in addition, we present information on the biology of these groups, insofar as it is known. Species of major economic importance, and others that have been studied in depth, are treated separately in Sect. 19.5.

Key to subfamilies of the Neotropical Region Coreidae (adapted from Packauskas 1994).

1. Tibiae not sulcate on outer surface; metathoracic scent gland orifices with a single large or two nearly fused auricles; meso- and metasterna sulcate; posterior coxae contiguous or nearly so; all species less than 12 mm long............................Pseudophloeinae

– Tibiae clearly or slightly sulcate on outer surface; other characteristics different from above; length variable...................................2

2. Metathoracic scent gland orifices deep between coxae; hind coxae far separate; hind femora strongly clavate and curved; hind tibiae with an apical tooth or spine...................Meropachyinae

– Scent gland lateral to coxae; hind coxae not so separate; hind femora not or rarely strongly clavate and usually straight; hind tibiae unarmed at apex..Coreinae

19.4.1 Pseudophloeinae Stål (Plate 19.2)

Pseudophloeinae species are known to feed on legumes (Fabaceae) that grow in open woodlands or grasslands with scattered trees; apparently dense forests are not occupied by most of the species (Dolling 1986).

Pseudophloeinae is composed of two tribes: Clavigrallini and Pseudophloeini. The former apparently is monophyletic and the latter paraphyletic according to Dolling (1986). Pseudophloeinae is represented in the New World by three genera: *Coriomeris* Westwood, *Ceraleptus* Costa, and *Vilga* Stål, all belonging to Pseudophloeini. The first two genera are Holarctic in distribution, but one species of *Coriomeris* is found in the mountainous areas of Oaxaca, Mexico. Only *Vilga* Stål is registered to the Neotropical region.

Packauskas (1994) in the key to subfamilies of the New World Coreidae characterized Pseudophloeinae by the tibiae not sulcate; metathoracic scent gland orifices with a single large or two nearly fused auricles; meso- and metasternum sulcate; males with a bilobed genital capsule opening filled by the clearly visible parameres. Dolling (1986, 1987) and Schuh and Slater (1995) presented a more complete diagnosis for Pseudophloeinae including: antennae inserted at sides of head; antennifers with porrect or deflexed process at outer apical angles; rostrum at rest reaching metasternum; posterior coxae separated by about the width of a coxa or less; femora moderately to strongly clavate; posterior femora typically with two or more large subapical spines beneath on anterior side with some smaller spines, tubercles, or granules between them and a terminal series of about four spines diminishing in length toward apex of femur; tibiae without apical spines; membrane of hemelytron with a compound vein near base almost parallel with apical margin of corium; posterolateral angle of sternite VII almost always and of sternites III–VI commonly produced into teeth or spines; female paratergite VIII without functional spiracle; first valvula of ovipositor without peg-like setae; spermatheca with bulb lunate and duct devoid of prominent flange; egg not operculate or pseudoperculate, opening by a transverse eclosion rent. Pseudophloeines are easy to recognize because they do not

1. *Ceraleptus denticulatus* 2. *Ceraleptus pacificus* 3. *Ceraleptus probolus* 4. *Coriomeris humilis*

5. *Coriomeris insularis* 6. *Coriomeris occidentalis* 7. *Vilga (Echinovilga) dallasi* 8. *Vilga (Laevivilga) divaricata*

9. *Vilga (Platyvilga) peruviana* 10. *Vilga (Trichovilga) mexicana* 11. *Vilga (Vilga) westwoodi* 12. *Vilga (Vilgula) dissimilis*

Plate 2 - Pseudophloeinae Stål, 1868 (Scalebars = 5mm): 1. *Ceraleptus denticulatus* Froeschner, 1963 [USNM]; 2. *Ceraleptus pacificus* Barber, 1914 [USNM]. 3. *Ceraleptus probolus* Froeschner, 1963 [USNM]; 4. *Coriomeris humilis* (Uhler, 1872) [BMNH]; 5. *Coriomeris insularis* Dolling & Yonke, 1976 [BMNH]; 6. *Coriomeris occidentalis* Dolling & Yonke, 1976 [CAS]; 7. *Vilga (Echinovilga) dallasi* Distant, 1881 [BMNH]; 8. *Vilga (Laevivilga) divaricata* Distant, 1893 [BMNH]; 9. *Vilga (Platyvilga) peruviana* Dolling, 1977 [BMNH]; 10. *Vilga (Trichovilga) mexicana* Distant, 1892 [BMNH]; 11. *Vilga (Vilga) westwoodi* (Kolenati, 1845) [BMNH]; 12. *Vilga (Vilgula) dissimilis* Distant, 1893 [BMNH].

Plate 19.2 Coreinae plate—Pseudophloeinae have the dorsal surface of the tibiae sulcate; a tribe of Coreinae—Hydarini—also lack these sulci, but do not occur in the Neotropical region. All remaining Coreinae taxa present tibiae sulcate.

The genus *Vilga* is composed of 14 species divided into 6 subgenera (Dolling 1977). This genus has a striking feature, probably apomorphic, grouping all species and not presented in any other genera of the subfamily—the freely projecting lobe on the seventh tergum of the male. This taxon is also characterized by the absence of an antevannal vein ("glochis") in the hind wing, a feature used by Stål (1870) to characterize Pseudophloeinae. Dolling (1977) noted that this absence can be a plesiomorphic state shared with the Old World *Hoplolomia* Stål and *Risbecocoris* Izzard. This genus was revised and keyed by Dolling (1977); he also included in his key a pair of couplets to separate *Vilga* from *Ceraleptus* and *Coriomerus*. No host plants are known for this genus, but legumes are likely based on the feeding habits of other Pseudophloeini. One species, *Vilga mexicana* Distant, is unusual in having both macropterous and brachypterous forms (Dolling 1977).

19.4.2 Meropachyinae Stål (Plate 19.3)

Meropachyinae has a striking characteristic that is the hind tibiae with an apical spine or tooth used in keys to separate Meropachyinae from other subfamilies. Other characteristics used are the small head and narrow thorax; metathoracic scent gland opening deep between coxae, opening anteriorly; projections of peritreme fused; evaporatorium moderate and without ridges; veins of the forewing arising from a vein close to corial border; widely separated hind coxae; hind femur curved and strongly incrassate; second through fifth abdominal sterna fused in both sexes; plus several characteristics from male and female genitalia.

This subfamily has a history of name changes that started with Stål (1867) erecting it under Meropachydida afterwards changed to Merocorina (Stål 1870). Further authors used both names to designate the same group of genera; thus, Meropachydinae was indicated as the correct name for the subfamily by Schaefer (1964) followed by Froeschner (1981), Henry and Froeschner (1988), Schuh and Slater (1995), and Brailovsky (1998a, 1999a) among others. Merocorinae was used by Van Duzzee (1916), Torre-Bueno (1941) and Kormilev (1954). Packauskas (1994) explained that Meropachyinae should be used rather than Meropachydinae, and more recently Brailovsky (2009a) and CoreoideaSF Team (2015) also use this name.

Kormilev (1954) revised Meropachyinae and proposed three tribes: Merocorini Stål, Meropachyini Stål, and Spathophorini Kormilev. After that, only keys and lists of regional fauna were presented till Brailovsky (1998a) started a series of works dealing with the entire subfamily. Additional keys to the tribes may be found in Packauskas (1994). The subfamily currently includes 27 genera, most of them monotypic, comprising about 60 species (CoreoideaSF Team 2015).

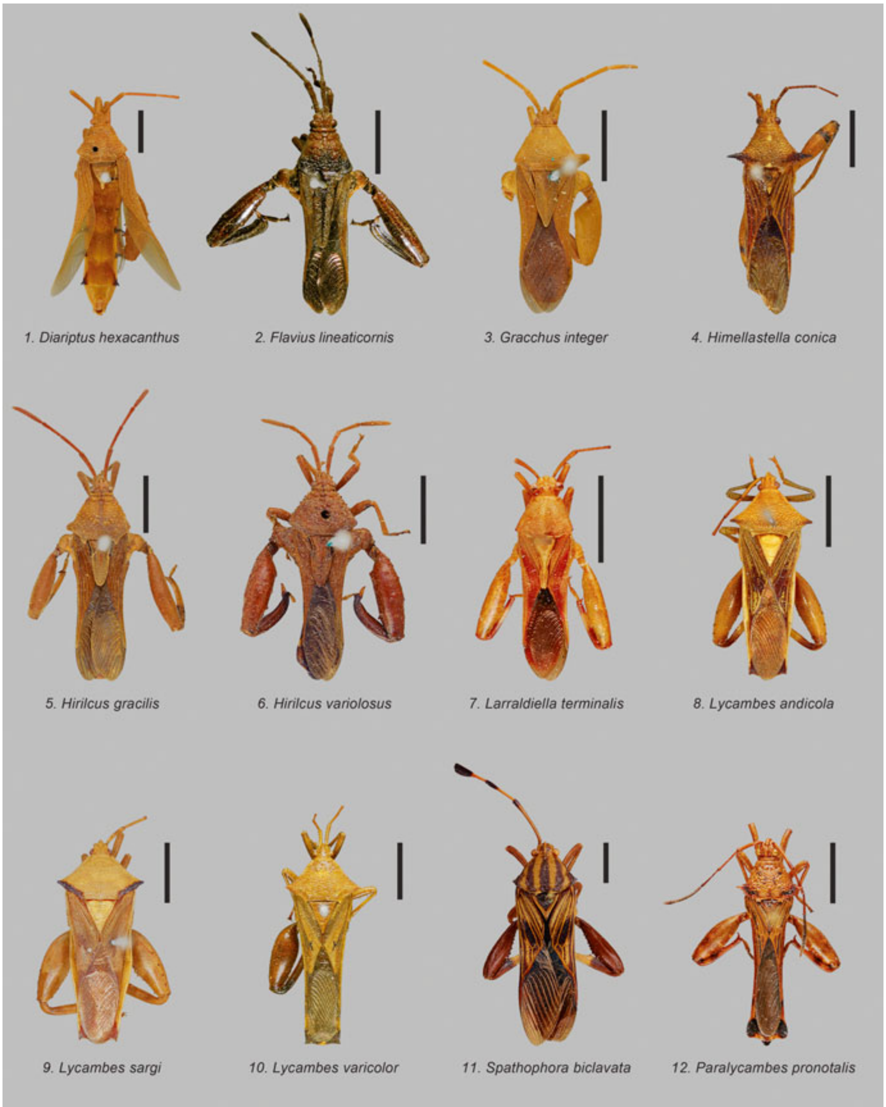


Plate 3 - Meropachyinae Stål, 1867 (Scalebars = 5mm): 1. *Diariptus hexacanthus* Stål, 1860 [ZMHB]; 2. *Flavius lineaticornis* Stål, 1862 [NHMW]; 3. *Gracchus integer* (Burmeister, 1835) [ZMHB]; 4. *Himellastella conica* Brailovsky & Barrera, 1998 [ZMHB]; 5. *Hirilcus gracilis* (Burmeister, 1835) [ZMHB]; 6. *Hirilcus variolosus* (Burmeister, 1835)[ZMHB]; 7. *Larraldiella terminalis* Brailovsky, 1999 [UNAM]; 8. *Lycambes andicola* Breddin, 1903 [DEI]; 9. *Lycambes sargi* Breddin, 1904 [DEI]; 10. Lycambes varicolor Stål, 1862 [NHMW]; 11. *Spathophora biclavata* (Fabricius, 1803) [ZMUC]; 12. *Paralycambes pronotalis* Brailovsky, 1998 [UNAM].

Plate 19.3 Meropachyinae plate

Merocorini Stål

This tribe can be identified by the small size of the species; scutellum triangular, short, not surpassing base of claval commissure, the apex of scutellum elevated as a small knob and not hiding claval commissure; abdominal spiracles circular and located almost on the anterior third of each sternite (Kormilev 1954). Only one genus is currently included—*Merocoris* Perty—divided in two subgenera. The nominal subgenus has five species spread from Argentina to Central Part of Brazil; this group can be recognized by the scutellar disk with a high conical tubercle. The subgenus *Corynocoris* Mayr has three species, but one is registered only to North America, the other two distributed in Central America and Great Antilles; this group can be recognized by the scutellar disk almost flat. Brailovsky and Barrera (2009a) described a new species from Brazilian Cerrado areas collected on grassland, and presented a key to subgenera and species of *Merocoris*. Other *Merocoris* spp. are reported to feed on milkworts (*Polygala* sp.) (Schaefer and Mitchell 1983).

Meropachyini Stål

This tribe is easily recognized by the elongate scutellum extending beyond the distal end of the clavus; hind acetabulae laterally projected, visible in dorsal view; posterior tibiae broadly curved distally. The hind coxae widely separated looking like thoracic appendages, and the hind coxae strongly incrassate and long produce a unique facies remarkable among coreids.

This tribe contains 18 genera so far with 30 species chiefly South American and only a few species registered to Central America. Brailovsky (1999a) started the study with Meropachyini describing several genera and presenting a key to the known genera. Further contributions (Brailovsky and Barrera 2001; Brailovsky and Luna 2000; Brailovsky 2009a) included several new genera and species plus an updated key. The large old genera—*Hirilcus* Stål, *Marichisme* Kirkaldy, *Meropachys* Burmeister, and *Peranthus* Stål—are still to be revised. Little is known of the biology of this group. A key to genera can be found in Brailovsky (1999a, 2009a) and Brailovsky and Barrera (2001).

Spathophorini Kormilev

Spathophorini is a tribe recognizable by the triangular scutellum, flat, shorter than clavus; hind femora not attaining the apex of the abdomen; antennal segment IV usually slender; and abdominal spiracles elliptical and positioned between the anterior and middle third of the segment. This tribe is quite neglected because after Kormilev (1954), not much was added to it, except works by Brailovsky (1998a, 2000, 2008) and Brailovsky and Barrera (1998a). *Lycambes varicolor* Stål is reported to feed on *Lonchocarpus guatemalensis* and *L. cruentus* (Peredo 1999). A key to genera can be found in Brailovsky (1998a, 2000, 2008).

19.4.3 Coreinae Leach

Most of the coreids are included here. Extremely diverse in shape, color, and size; distance from eye to ocellus smaller than that between ocelli; anterolateral opening of the metathoracic scent gland well developed, peritreme with developed projections, auricle usually occupying half of the size of evaporatorium; corial margins straight or slightly sinuate; membranal veins of forewing arising from a transverse vein very close, or touching, corial margin; abdominal terga 1–2 and 3–7 fused; genital capsule of male without lateral prolongations; articulation of female genital plates usually membranous; gonangulum usually flat and folded.

These are the most common and striking coreids both in the field and in collections. This is by far the largest subfamily, with a mostly tropical worldwide distribution. This is also the subfamily in which discussions about taxonomical levels of certain groups are concentrated. Neotropical tribes are not much affected by such discussions; thus, they will not be treated here (see Schuh and Slater 1995 for more on suprageneric changes). Hydarini was raised by Ahmad (1970) to subfamily level, but recent works (i.e., Schuh and Slater 1995; Brailovsky 2010a) have considered this taxon as a tribe, which is the position followed here. Coreinae comprises 32 tribes, but Neotropical fauna comprises only 11 tribes, presented below. Several authors worked with Coreinae, but the subfamily still needs a phylogenetic analysis to raise hypotheses about relationships among genera. Packauskas (1994) presented a key to the Neotropical tribes, which is a keystone to understanding Coreinae.

Key of Coreinae (adapted from Packauskas 1994). Packauskas used Coreini to refer to the set of genera we are considering under Hypselonotini according to the Coreoidea catalog (CoreoideaSF Team 2015).

1. Tylus projecting conspicuously beyond juga as a distinct knob or strongly compressed plate; juga strongly deflex...2
– Tylus not or only vaguely projecting beyond juga; juga variable.........................3
2. Tylus projected as a distinct knob; ventral surface of the body with several small black spots; hind femur of the males not or slightly incrassate...Placoscelini
– Tylus well projected as a strongly compressed plate; ventral surface of the body with ventral color greatly variable but not as above; hind femur of the males greatly incrassate.................................Acanthocephalini

3. With the combination of hind femora spinose or tuberculate; strongly incrassate in males; head not over half as long as pronotum and not extending past antenniferous tubercles or very slightly so; antenniferous tubercles occupying most of anterior head width, space between them rarely wider than one tubercle..........4

– Not with this combination of characters..........5

4. Metathoracic scent gland with a single fused auricle (sometimes bilobed); ocellar tubercles large; usually with a spine present on antenniferous tubercles; parameres membranous..........Acanthocerini

– Metathoracic scent gland with two completely separated auricles (area between them depressed); ocellar tubercles small; antenniferous tubercles never armed; parameres sclerotized..........Nematopodini

5. Head porrect; juga and tylus extended forward beyond antenniferous tubercles; bucculae never reaching midlength of head; all femora spinose below, rostrum almost reaching or extending onto abdomen..........Anisoscelini

– Not with this combination of characters..........6

6. Juga extended and exceeding or equal to tylus in length..........7

– Juga deflexed or at least not exceeding nor equal to tylus in length..........8

7. Head shorter than pronotum; antennae terete; brachypterous..........Barreratalpini

– Head equal in length to pronotum; antennae triangular in cross-section; macropterous..........Chelinideini

8. Distance between hind coxae equal to distance from coxa to lateral margin; antenniferous tubercles prominent, subcontiguous above deflexed tylus and juga..........Spartocerini

– Distance between hind coxae much narrower than distance from coxa to lateral margin, if distances nearly equal then head elevated between antenniferous tubercles; tylus and juga variable..........9

9. Third antennal segment expanded, other segments terete; tylus and juga deflexed; not filling space between antenniferous tubercles; all femora armed distally..........Chariesterini

– Third antennal segment never expanded, if appearing expanded, then other segments also appearing expanded; tylus and juga usually extended anteriorly between antenniferous tubercles; femora rarely armed..........10

10. Spiracles situated twice as far from posterior border of middle abdominal segments (III–VI) as from anterior border..........Discogastrini

– Spiracles equidistant from anterior and posterior borders of middle abdominal segments (III–VI)..........11

11. Fourth antennal segment flattened; third antennal segment over twice as long as second..........Hydarini

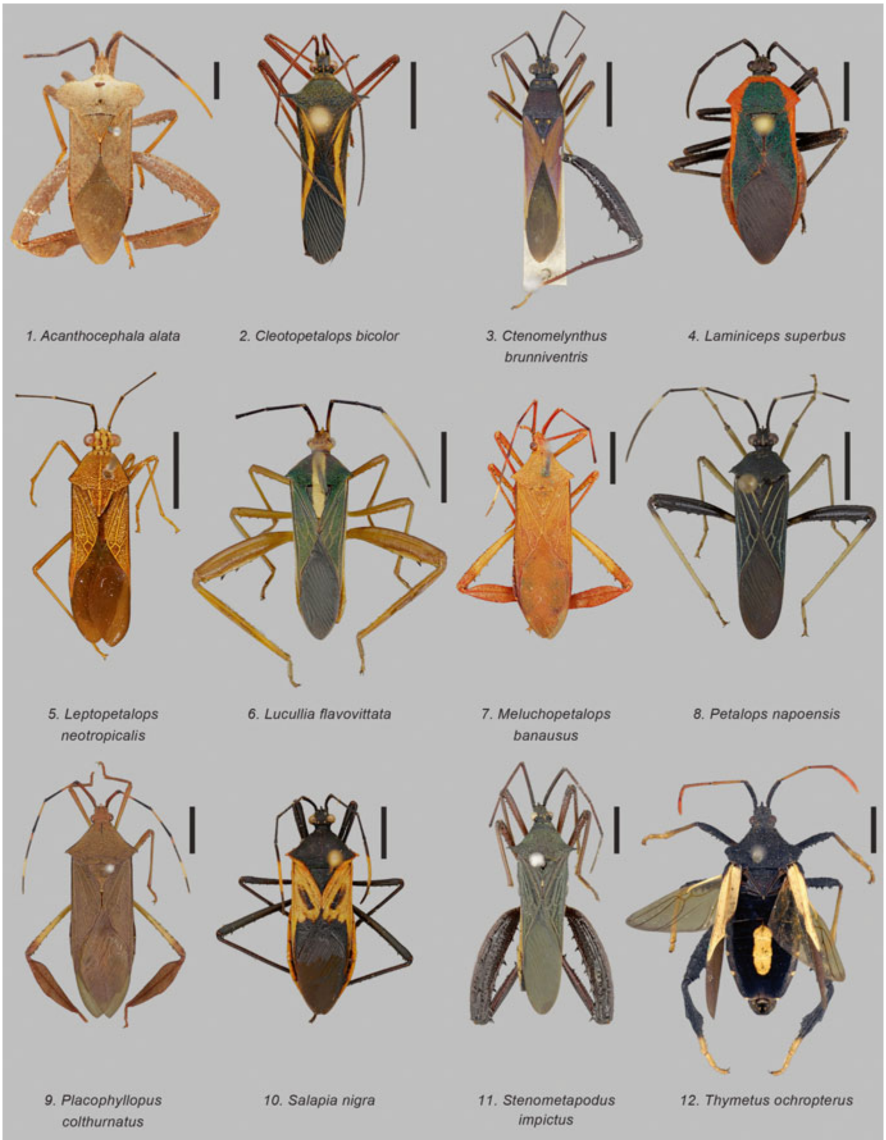
– Fourth antennal segment not flattened; third antennal segment usually shorter than second, never twice as long as second..........Hypselonotini

Acanthocephalini Stål (Plate 19.4)

This tribe groups species with medium to large size and interesting color patterns that are found in well-preserved forest. The tribe was established by Stål (1870) as Acanthocephalina, but no description was given. Schaefer (1964) also did not present a description of the tribe but mentioned the striking spinelike tylus. The most significant features of this tribe are the tylus, which projects conspicuously beyond the juga as a distinct acute plate, juga deflexed, abdominal spiracles close to anterior margin of the sternum, hind femur of males greatly incrassate, all femora of both sexes spinose ventrally, and hind tibia slightly or strongly expanded in both sexes (Packauskas 1994; Brailovsky 1997a). Several genera were described and revised or new species added in the last decades mainly by Brailovsky and coauthors (Brailovsky 1991, 1999b; Brailovsky and Barrera 1999, 2005). The largest genus *Acanthocephala*—one of the most common and conspicuous—still needs revision; Brailovsky (2006b) reviews the Mexican species, and McPherson et al. (2011) treats the species of America north of Mexico. No key to the entire tribe has been published so far.

This tribe is distributed across the Americas, but the largest number of species is found in the North and Central parts of South America, especially Peru and Ecuador; only a few are distributed across Central America and Nearctic region. Acanthocephalini includes 15 genera: *Acanthocephala* Laporte (27 species, three of them invading Nearctic region and three exclusively Nearctic), *Cervantistellus* Brailovsky & Barrera (two), *Cleotopetalops* Brailovsky (three), *Ctenomelynthus* Breddin (five), *Empedocles* Stål (two), *Ichilocoris* Brailovsky & Barrera (two), *Laminiceps* Costa (18), *Leptopetalops* Breddin (two), *Lucullia* Stål (one), *Meluchopetalops* Breddin (two), *Petalops* Amyot & Serville (12), *Placophyllopus* Blöte (one), *Salapia* Stål (17), *Stenometapodus* Breddin (five), and *Thymetus* Stål (two) (CoreoideaSF Team 2015).

The natural history and behavior of *Acanthocephala* spp. have been studied in depth by several authors. The incrassate hind femora of males are used as a weapon in aggressive encounters in two species. Eberhard (1998) provides a detailed description of feeding, aggression, and mating behavior in *Acanthocephala declivis guatemalensis* [which may be *Acanthocephala alata* Burmeister; see McPherson et al. (2011) and Brailovsky (2006a, b) and similar aggressive behavior occurs in *A. femorata* (Mitchell 1980b)]. The trunks and branches of *Cordia* sp. (Boraginaceae) trees were the feeding site for *A. declivis*, whereas *A. femorata* males defended territories on the stalks of cultivated sunflower. McPherson et al. (2011) provide host plant records for two species whose distribution extends into the Neotropics: *Acanthocephala femorata* (F.) and *Acanthocephala declivis* (Say). Vegetative plant parts (stems, shoots, and branches) appear to be the preferred sites for species in this genus, but more information is needed regarding other genera before a generalization may be made regarding the tribe.



1. Acanthocephala alata

2. Cleotopetalops bicolor

3. Ctenomelynthus brunniventris

4. Laminiceps superbus

5. Leptopetalops neotropicalis

6. Lucullia flavovittata

7. Meluchopetalops banausus

8. Petalops napoensis

9. Placophyllopus colthurnatus

10. Salapia nigra

11. Stenometapodus impictus

12. Thymetus ochropterus

Plate 4 - Acanthocephalini Stål, 1870 (Scalebars = 5mm): 1. *Acanthocephala alata* (Burmeister, 1835) [ZMHB]; 2. *Cleotopetalops bicolor* Brailovsky, 1999 [CAS]; 3. *Ctenomelynthus brunneiventris* Breddin, 1903 [ISNB]; 4. *Laminiceps superbus* Breddin, 1903 [USNM]; 5. *Leptopetalops neotropicalis* Brailovsky, 1991 [RNHL]; 6. *Lucullia flavovittata* Stål, 1865 [BMNH]; 7. *Meluchopetalops banausus* Breddin, 1903 [DEI]; 8. *Petalops napoensis* Brailovsky, 1991 [BMNH]; 9. *Placophyllopus colthurnatus* Blöte, 1938 [BMNH]; 10. *Salapia nigra* Brailovsky, 1992 [CAS]; 11. *Stenometapodus impictus* Breddin, 1903 [ISNB]; 12. *Thymetus ochropterus* (Stål, 1860) [BMNH].

Plate 19.4 Coreinae plate—Acanthocephalini

Acanthocerini Bergroth (Plate 19.5)

Species belonging to this tribe can be found in open areas on herbs, shrubs, and small trees but also in crops. Bugs belonging to Acanthocerini have the head subquadrate; ocelli placed on prominent tubercles; blunt tylus slightly exceeding the jugae; antenniferous tubercles often armed laterally with a spine; antennal segment four robust; metathoracic scent gland opening placed almost ventrally, with a single, sometimes double, fused auricle; femora incrassate especially in males, sometimes armed subapically on ventral surface; hind tibiae lacking foliaceous expansions; spermatheca with the bulb elongate; parameres membranous (O'Shea 1980a; Packauskas 1994). This tribe has received little attention since O'Shea (1980a) for a group with species easy to find and catch, very common in collections, and with a certain economic importance. Brailovsky (1987a, 1988a) and Brailovsky and Barrera (2003a) described new genera and added important information to identify some genera.

Acanthocerini includes 17 genera (most of them with very few species) and 50 species: *Acanthocerus* Palisot de Beauvois (three species), *Athaumastus* Mayr (8), *Beutelspacoris* Brailovsky (two), *Camptischium* Amyot & Serville (three), *Crinocerus* Burmeister (one), *Dersagrena*, Kirkaldy (three); *Elachisme* Kirkaldy (one), *Euthochtha* Mayr (one), *Golema* Amyot & Serville (two), *Lybindus* Stål (four), *Machtima* Amyot & Serville (three), *Moronopelios* Brailovsky (two), *Rondoneva* Brailovsky & Barrera (one), *Sagotylus* Mayr (one), *Schaeferocoris* O'Shea (one), *Thlastocoris* Mayr (two), and *Zoreva* Amyot & Serville (12) (CoreoideaSF Team 2015). This group is basically South American, but genera like *Acanthocerus* and *Euthochtha* have a North American and Antillean distribution, and *Sagotylus* can be found in the northern part of the Neotropical region and United States.

The natural history of *Athaumastus haematicus* (Stål) has been described in Brazil (Merti 1940, cited in O'Shea 1980a); Schaefer and Mitchell (1983), Schaefer and O'Shea (1979), and Bosq (1937) also give host plant records for this minor crop pest. On pineapple, *Lybindus dichrous* Stål adults and nymphs cluster on the peduncle of the fruit and suck plant juices; plants without fruits are not attacked (Mariconi 1953). Other minor economic pests include *Thlastocoris laetus* Mayr on pineapple; *Machtima crucigera* (F.) and *Euthochtha galeator* (F.) on flowers; *Dersagrena flaviventris* (Berg) on cotton; *Camptischium clavipes* (F.) on castor bean, ice cream bean, and the medicinal plant, guaco; and *Sagotylus confluens* (Say) on cowpea (Mead 2014; Mitchell 2000; Schaefer and O'Shea 1979, and references therein). The immature stages of *E. galeator* in North America were described by Yonke and Medler (1969a), and combat between males of this species was noted by Mitchell (1980b). *Crinocerus sanctus* (F.), a major pest of cowpea in Brazil, is treated below (section "*Crinocerus* Burmeister"). A key to the genera of Acanthocerini can be found in O'Shea (1980a).

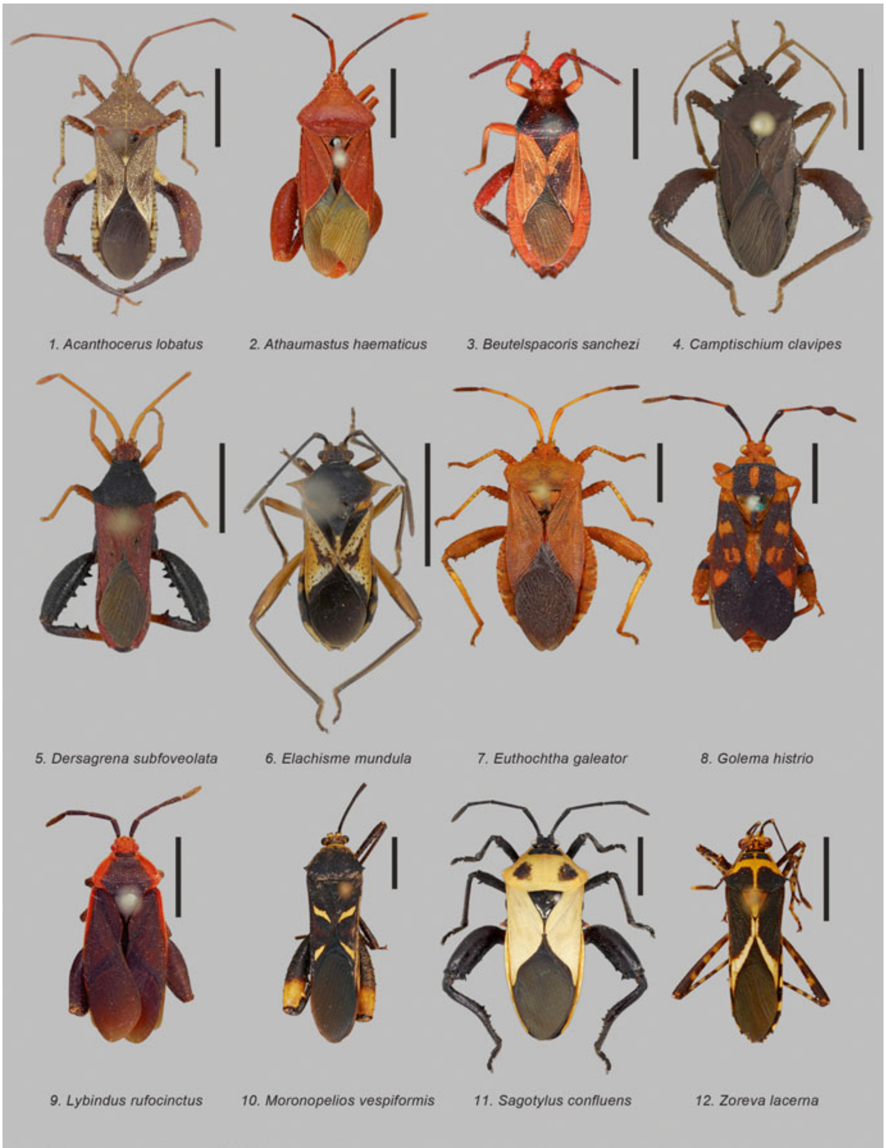


Plate 5 - Acanthocerini Bergroth, 1913 (Scalebars = 5mm): 1. *Acanthocerus lobatus* (Burmeister, 1835) [BMNH]; 2. *Athaumastus haematicus* (Stål, 1860) [ZMHB]; 3. *Beutelspacoris sanchezi* Brailovsky, 1987 [UNAM}; 4. *Camptischium clavipes* (Fabricius, 1803) [BMNH]; 5. *Dersagrena subfoveolata* (Berg, 1892) [BMNH]; 6. *Elachisme mundula* (Stål, 1859) [BMNH]; 7. *Euthochtha galeator* (Fabricius, 1803) [USNM]; 8. *Golema histrio* (Burmeister, 1835) [ZMHB]; 9. *Lybindus rufocinctus* Stål, 1860 [ZMHB]; 10. *Moronopelios vespiformis* Brailovsky, 1988 [CAS]; 11. *Sagotylus confluens* (Say, 1832) [BMNH]; 12. *Zoreva lacerna* Brailovsky & Barrera, 1982 [CAS];

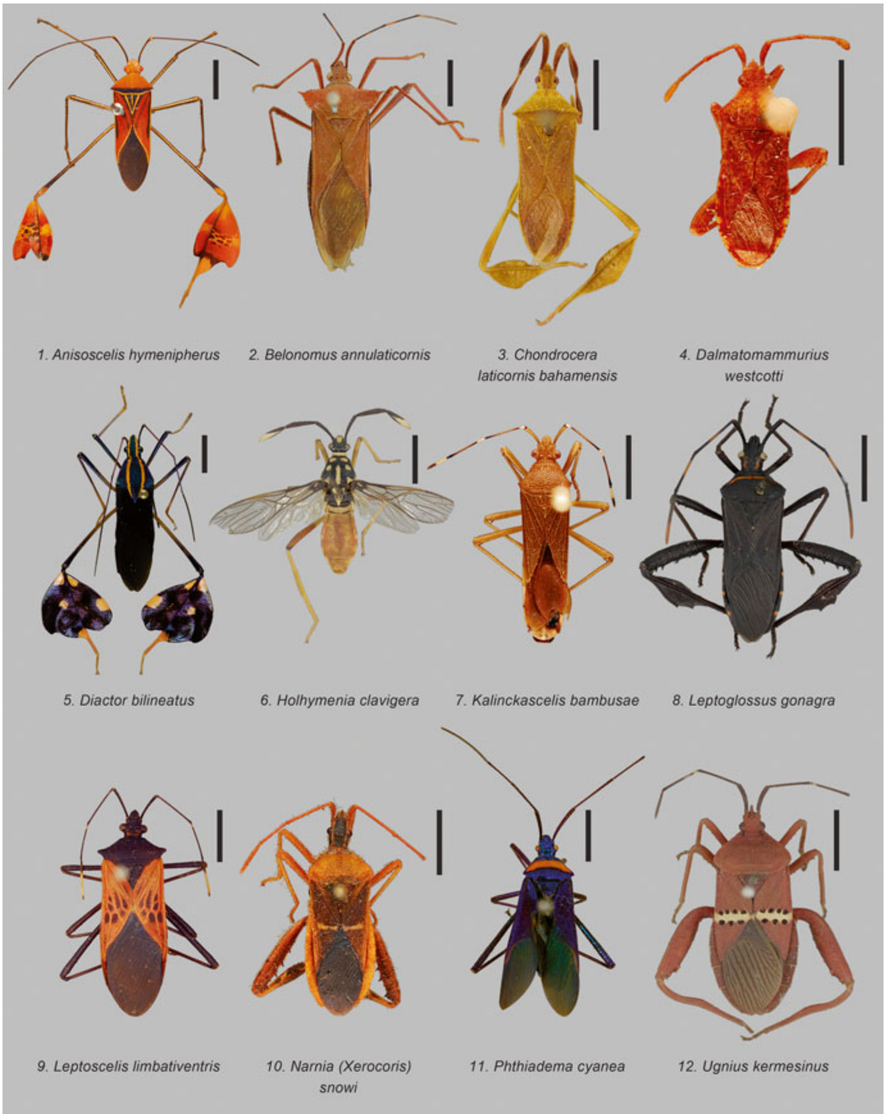
Plate 19.5 Coreinae plate—Acanthocerini

Anisoscelini Laporte (Plate 19.6)

Since Stål (1868), several authors have used erroneously the name Anisocelidini to designate this tribe. Species belonging to Anisoscelini are very characteristic because of the foliaceous expansion of the hind tibiae, bright colors, and abundance in agricultural and urban environments. Body elongate and narrow, ratio of body length to width greater or equal to three, less than four. Head usually longer than scutellum. Head usually porrect; tylus and mandibular plates never deflexed; both usually extend beyond antenniferous tubercles. Distance between antenniferous tubercles greater than width of one tubercle. Antennal segment IV never the shortest and longer than segment III. Antennal segment I usually longer than head. Bucculae short extending or not to the level of anterior margin of the eye. Rostrum extending to at least metacoxae, usually onto abdomen. Pronotum steeply declivent; with distinct collar, punctate, occasionally rugose, never tuberculate; humeral angles acute to obtusely angled; posterior angles obtuse to rounded; callar region raised. Usually lacking metapleural supracoxal spine. Metapleural scent gland opening separated, with two auricles; anterior auricle larger. Abdomen rarely wider than thorax. Spiracle of abdominal segment IV closer to lateral edge of segment than to anterior or posterior edge. Abdominal segments never spined posterolaterally. Connexivum VI separated from dorsum or slightly fused at apex; connexivum VII fused to dorsal plate. Scutellum longer than wide or subequal, rarely wider than long. All femora spined below, at least distally. Hind femora rarely incrassate or spined above.

This tribe is one of the largest in the Neotropics and the subject of recent revisions: taxonomic and nomenclatural changes led Leptoscelini to be considered part of Anisoscelini; important revisions affected *Leptoglossus* and *Phthia*, genera that contain several species quite common in human-altered environments and causing damage to a number of crops; other studies revealed several new genera and species (Packauskas 1994, 2008; Packauskas and Schaefer 2001; Allen 1969; Osuna 1984; Gibson and Holdridge 1918; Brailovsky 1989, 1990a, 1990b, 1996, 1997b, 2001a; Brailovsky and Barrera 1994, 1998b; Brailovsky and Sánchez 1983a).

Anisocelini comprises 27 genera: *Anisoscelis* Latreille (11 species); *Baldus* Stål (one); *Bellamynacoris* Brailovsky (two); *Belonomus* Uhler (one); *Chondrocera* Laporte (two); *Coribergia* Casini (one); *Dalmatomammurius* Brailovsky (six); *Diactor* Perty (two); *Holhymenia* Lepeletier & Serville (eight); *Kalinckascelis* Brailovsky (one); *Leptoglossus* Guérin-Méneville (57); *Leptopelios* Brailovsky (one); *Leptoscelis* Laporte (25); *Leptostellana* Brailovsky (one); *Malvana* Stål (three); *Malvanaioides* Brailovsky (five); *Narnia* Stål (seven, mostly Nearctic with four species invading northern boundaries of Neotropical region); *Onoremia* Brailovsky (one); *Phthia* Stål (four); *Phthiacnemia* Brailovsky (one); *Phthiadema* Brailovsky (three); *Phthiarella* Brailovsky, 2009 (4); *Plunentis* Stål, 1860 (2); *Rhytidophthia* Brailovsky, 2009 (1); *Sephinioides* Brailovsky (two); *Tarpeius* Stål (two); and *Ugnius* Stål (two) (CoreoideaSF Team 2015). Most of the species belonging to this tribe are found in tropical areas, but a few are found in North America (e.g., species of *Leptoglossus*). Osuna (1984) made several changes,



1. Anisoscelis hymenipherus

2. Belonomus annulaticornis

3. Chondrocera laticornis bahamensis

4. Dalmatomammurius westcotti

5. Diactor bilineatus

6. Holhymenia clavigera

7. Kalinckascelis bambusae

8. Leptoglossus gonagra

9. Leptoscelis limbativentris

10. Narnia (Xerocoris) snowi

11. Phthiadema cyanea

12. Ugnius kermesinus

Plate 6 - Anisoscelini Laporte, 1832 (Scalebars = 5mm): 1. *Anisoscelis hymenipherus* Westwood, 1840 [OXUM]; 2. *Belonomus annulaticornis* Uhler, 1869 [USNM]; 3. *Chondrocera laticornis bahamensis* Brailovsky & Barrera, 1994 [USNM]; 4. *Dalmatomammurius westcotti* Brailovsky, 1982 [UNAM]; 5. *Diactor bilineatus* (Fabricius, 1803) [MNHN]; 6. *Holhymenia clavigera* (Herbst, 1784) [BMNH]; 7. *Kalinckascelis bambusae* Brailovsky, 1990 [UNAM]; 8. *Leptoglossus gonagra* (Fabricius, 1775) [BMNH]; 9. *Leptoscelis limbativentris* Breddin, 1901 [DEI]; 10. *Narnia (Xerocoris) snowi* Van Duzee, 1906 [CAS]; 11. *Phthiadema cyanea* (Signoret, 1862) [NHMW]; 12. *Ugnius kermesinus* (Linnaeus, 1758) [BMNH].

Plate 19.6 Coreinae plate—Anisoscelini especially splitting *Leptoglossus* into several genera, but this arrangement was not recognized by other authors, and these genera were given only species-group status by Packauskas and Schaefer (2001). Brailovsky and coauthors contributed new species and genera, mainly in the former tribe Leptoscelini (i.e., Brailovsky 1990b, 1993, 1997b, 2001a, b, 2009b; Brailovsky and Barrera 1994, 1998b, 2004, 2011, 2013; Brailovsky and Sánchez 1983a). Despite the visibility of the tribe, no comprehensive key to the genera is presented in the literature.

Anisosceline biology has been studied more extensively than that of most other tribes, partly due to the economic importance of a few species but also because of their very noticeable physical and behavioral traits, including the large and often colorful tibial foliations, flattened antennal segments, and territorial defense involving the spined incrassate femora. Perhaps the most striking of all anisoscelids are the two species of *Diactor*, with their broad, spotted tibial foliations and bright orange or yellow stripes on the metallic green body. Antennal expansions are found in nymphs of many species, but appear in the adult stage as well in *Holhymenia*, *Tarpeius*, and *Chondrocera laticornis* Laporte (Brailovsky and Barrera 1994). Not all species have incrassate femora, nor is the enlargement as impressive as in, for example, Nematopodini, but male combat has been noted in species of *Leptoglossus*, *Narnia*, and *Leptoscelis* (Miyatake 1997; Miller 2011, 2013; Miller and Emlen 2010) The natural history, ecology, and behavior of *Leptoscelis tricolor* Westwood on inflorescences of *Heliconia* spp. have been particularly well-studied. Both female choice and male combat operate in this species. Males defend territories on flower spikes, and femur width varies among locations and between *Heliconia* species within a location. Furthermore, the scaling relationship between body size and femur width varies; for a given body size, femur width differs across populations (Miller and Emlen 2010). Females may accept or reject courting males and usually feed during the mating, while males stroke the female's abdomen and perform other courtship behaviors. Natal host plant species and seasonal quality of the host affect female fecundity and male courtship behavior (Miller 2008).

No strong association with a particular host plant family is evident for the tribe as a whole. Feeding preference ranges from highly polyphagous [e.g., *Leptoglossus zonatus* (Dallas)] to specialization on a single genus or family. As mentioned above, *L. tricolor* specializes on *Heliconia* species. All *Narnia* spp. plus two species of *Leptoglossus* are specialists on cactus. Species in several genera (*Holhymenia*, *Anisoscelis*, *Diactor*) feed exclusively on Passifloraceae; anisoscelines constitute the second most important group of pests on cultivated passion fruit in the Lake Maracaibo region of Venezuela (Aguiar-Menezes et al. 2002). The latter authors provide information on the life history of *Diactor bilineatus* (F.).

Most if not all anisoscelines seem to be associated with reproductive plant parts. Feeding on vascular tissue (primarily xylem) and nectar is reported, but xylem represents a source of hydration (Rodrigues et al. 2007a; Mitchell 2006). Nymphs are usually observed on buds or fruits. When two species of oligophagous anisoscelines were offered a mixed diet of *Passiflora* spp., food preference (species and tissue) changed with instar (Rodrigues et al. 2007b). Polyphagous species [e.g., *Leptoglossus phyllopus* (L.)] may move generationally among host plants, tracking plant reproductive structures (Mitchell 2006).

Host plant records for various species are given by Brailovsky and Sánchez (1983a) and Schaefer and Mitchell (1983). Species and genera of major importance, including targets of ecological and behavioral research as well as serious economic pests, are treated separately in Sect. 19.5.2 (*Anisoscelis*, *Holhymenia*, *Leptoglossus Narnia*, and *Phthia s.l.*).

Barreratalpini Brailovsky (Plate 19.7)

This tribe can be recognized by body brown, medium size, dorsoventrally flattened; head longer than wide, shorter than pronotum; mandibular plates longer than tylus but not contiguous in front of it; antennae terete, first antennal segment strong, fourth the shortest; brachypterous; ventral surface of the femora with two short distal spines; tibiae terete; abdomen enlarged; connexival angles not developed.

This tribe was proposed by Brailovsky (1988b) for the new genus and species—*Barreratalpa bambusii*—collected on bamboo in Mexico. After the initial description, only Packauskas (1994) mentioned this tribe. Brailovsky (1988b) provides a short but useful discussion justifying the separation of the new tribe from others.

Chariesterini Stål (Plate 19.7)

This small tribe is formed by four genera and 24 species, most living in Central America and the northern part of South America. No formal description has been made, but species can be identified by the small size; body narrow with lateral margins almost parallel; third antennal segment expanded, other segments terete; tylus and juga deflexed not filling space between antenniferous tubercles; all femora armed distally; distance between hind coxae much narrower than distance from coxa to lateral margin, hind tibiae never expanded. The single species of *Chariesterus* registered to Brazil—*C. armatus*—can be collected on Euphorbiaceae (*Euphorbia* spp.). The Caribbean species *Chariesterus gracilicornis* (Stål) is reported from amaranth and cucurbits in addition to euphorbs (Schaefer and Mitchell 1983). The two most comprehensive works are the revision of *Chariesterus* by Ruckes (1955) and the description of *Ruckesius* by Yonke (1972) that also presented a key to the genera.

Chelinideini Blatchley (Plate 19.7)

Species of Chelinideini belong to a single genus—*Chelinidea* Uhler. They are known as cactus bugs because they live on these plants causing damage to certain species. Hamlin (1924) revised *Chelinidea* Uhler and gave a more comprehensive description of the genus. Herring (1980) revised *Chelinidea* again adding new species, a key to the species, and new information about distribution, biology, and host plants. They can be recognized by the body short somewhat broader, oval. Head as

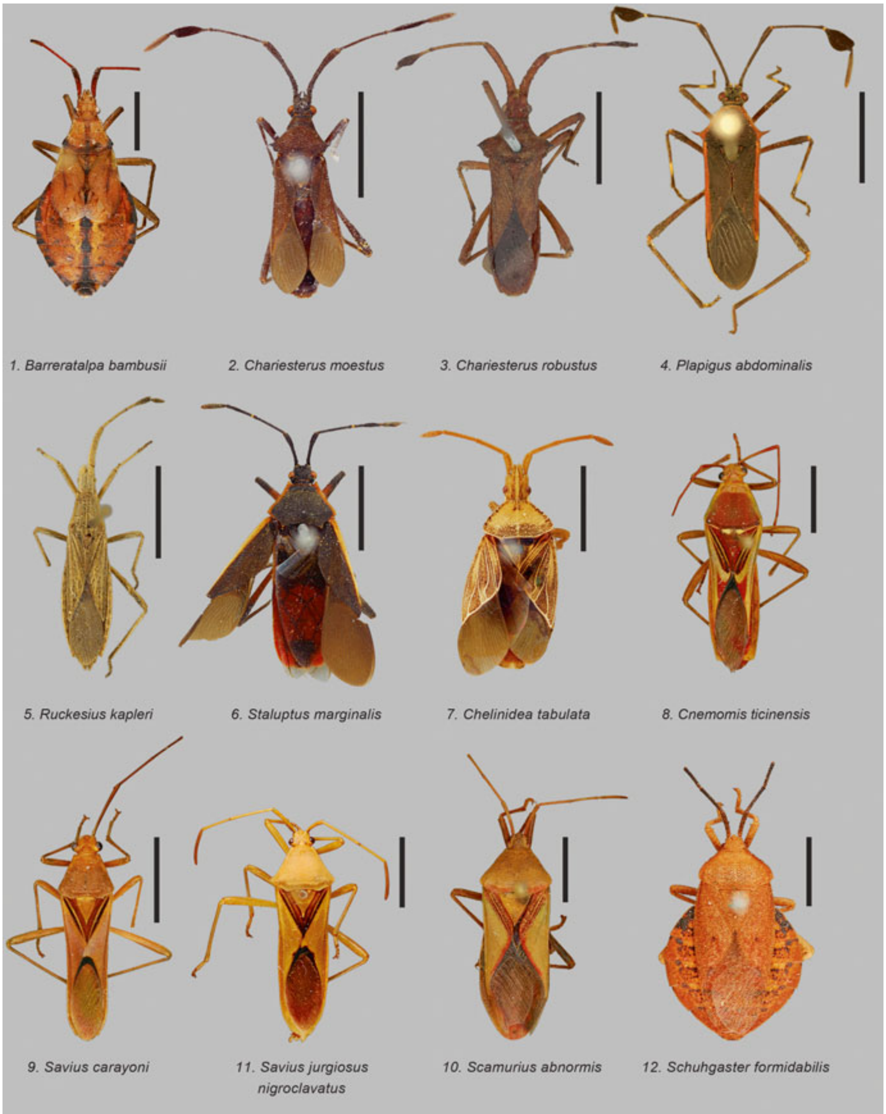


Plate 7 - Barreratalpini Brailovsky, 1988 (Scalebars = 5mm): 1. *Barreratalpa bambusii* Brailovsky, 1988 [UNAM]; **Chariesterini Stål, 1868:** 2. *Chariesterus moestus* Burmeister, 1835 [ZMHB]; 3. *Chariesterus robustus* Distant, 1892 [BMNH]; 4. *Plapigus abdominalis* (Dallas, 1852) [BMNH]; 5. *Ruckesius kapleri* Yonke, 1972 [USNM]; 6. *Staluptus marginalis* (Burmeister, 1835) [ZMHB]; **Chelinideini Blatchley, 1926:** 7. *Chelinidea tabulata* (Burmeister, 1835) [ZMHB]; **Discogastrini Stål, 1868:** 8. *Cnemomis ticinensis* Brailovsky & Barrera, 1986 [RNHL]; 9. *Savius carayoni* Brailovsky, 1986 [RNHL]; 10. *Savius jurgiosus nigroclavatus* Brailovsky, 1986 [UNAM] 11. *Scamurius abnormis* Brailovsky, 1986 [RNHL]; 12. *Schuhgaster formidabilis* Brailovsky, 1993 [UNAM].

Plate 19.7 Coreinae plate—Barreratalpini-Chariesterini-Chelinideini-Discogastrini long as pronotum. Tylus appearing conical from above. Juga acutely pointed and level with or surpassing tylus. Eyes small, subcircular, and closer to base of the head than to antennal tubercle. First three antennal segments prismatic; basal segment flattened and crested on inner edge; second and third subequal; distal rounded and tapered toward either extremity. Bucculae about one-third length of the basal segment of rostrum. Rostrum just attaining the abdomen; first segment slightly longer than the head; second subequal to first; third the shortest and fourth two-thirds the length of the second. Pronotum nearly twice as long as wide; anterior margin forming a narrow collar; anterolateral margin entire straight to slightly rounded; humeral angles rounded to obtuse and not developed. Sterna sulcated to receive the rostrum. Connexivum bent upward and distinctly dilated. Posterior femora enlarged and armed with two rows of teeth on under surface; anterior and middle femora armed with smaller and fewer teeth on under surface (adapted from Hamlin 1924).

The genus *Chelinidea* Uhler is formed by five species found in Nearctic region but also reaching or crossing Neotropical northern boundaries. Only *C. tabulata* (Burmeister) has a larger distribution in the Neotropical region, reaching Venezuela. *Chelinidea staffilesi* and *C. tabulata* nymphs were studied and described by Brailovsky et al. (1994). Several species, including *C. tabulata*, have been considered as biological control agents for cacti (*Opuntia* spp.) but have either failed to disperse or were never released due to the potential to damage other plants (Mitchell 2000 and references therein).

Discogastrini Stål (Plate 19.7)

Species belonging to this tribe are usually medium in size; elongate; light green to green. Head is square and shorter than pronotum. Tylus longer than mandibular plates but not projected in a spine, both usually anteriorly extended between antenniferous tubercles. Rostrum short not reaching mesosternum. Pronotal disk rough and transversely sulcate. Pronotal angles rounded or subacute but never developed. Evaporatorium slightly developed and sulcate. Femora and tibiae terete. Spiracles on anterior third of each abdominal segment. Spine of the sternite VII bifid.

This tribe is formed by eight genera [*Cnemomis* Stål (eight species), *Coryzoplatus* Spinola (two), *Discogaster* Burmeister (five), *Karnaviexallis* Brailovsky (one), *Lupanthus* Stål (two), *Savius* Stål (nine), *Scamurius* Stål (11), and *Schuhgaster* Brailovsky (one)]. Most of the species are found in South America with only a few specimens living in the northern part of the Neotropical region. Only *Cnemomis* and *Scamurius* were revised (Brailovsky and Barrera 1986a; Brailovsky 1987b), but Brailovsky added valuable information to four other genera (Brailovsky 1986a, b, c; Brailovsky and Barrera 2003b) and described two others (Brailovsky 1984, 1993). Information on biology is limited; *Savius jurgiosus jurgiosus* Stål was reported from leaves and pods of *Prosopis laevigata* and leaves of *Ziziphus pedunculata* (Brailovsky et al. 1995) and from *Buddleja sessiliflora* (Brailovsky 1986b) in Mexico; immatures of this subspecies are described by Brailovsky et al. (1995). *Savius* sp. was also reported from the petioles and shoots of Texas ebony, *Ebenopsis*

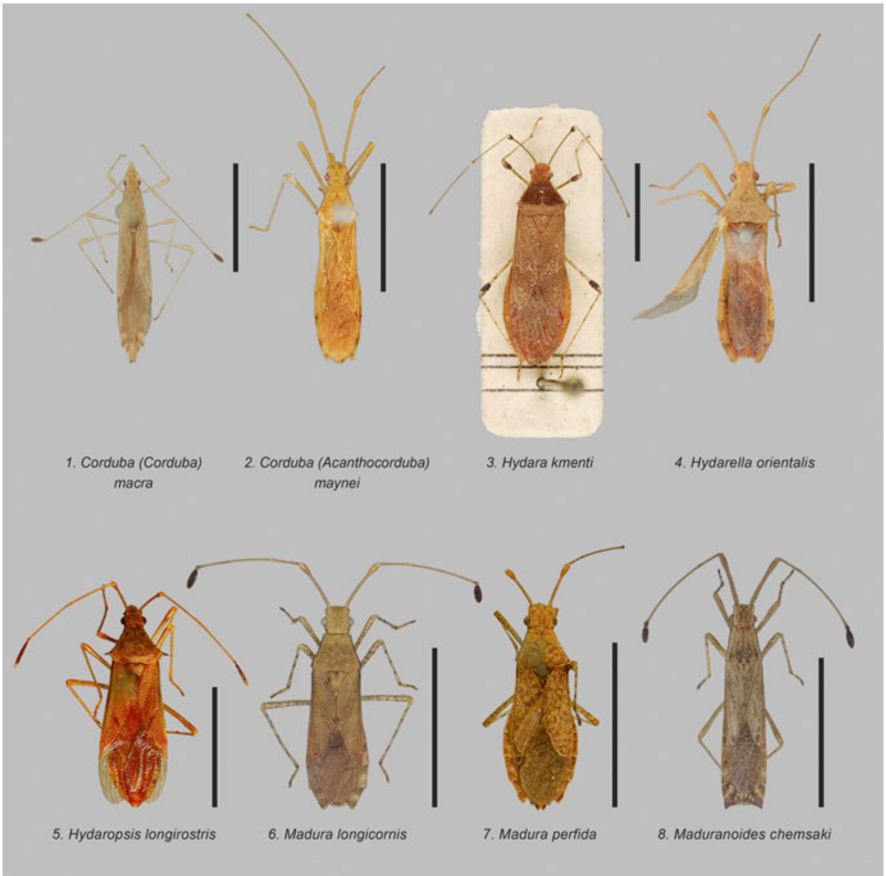


Plate 8 - Hydarini Stål, 1873 (Scalebars = 5mm): 1. *_Corduba (Corduba) macra_ Stål, 1862 [MRAC]; 2. *_Corduba (Acanthocorduba) maynei_ Schouteden, 1938 [MRAC]; 3. *_Hydara kmenti_ Brailovsky, 2006 [MNHN]; 4. *_Hydarella orientalis_ (Distant, 1902) [BMNH]; 5. *_Hydaropsis longirostris_ (Hsiao, 1963) [IOZ]; 6. _Madura longicornis_ Stål, 1862 [BMNH]; 7. _Madura perfida_ Stål, 1862 [BMNH]; 8. _Maduranoides chemsaki_ Brailovsky, 1988 [NHMW].
Note: Species marked with an asterix (*) are only found in the Old World.

Plate 19.8 Coreinae plate—Hydarini

ebano (Berl.) Barneby & Grimes (as *Pithecellobium*) in southern Texas (Schaefer and Mitchell 1983). A key to the genera included in Discogastrini can be found in Brailovsky (1984, 1993).

Hydarini Stål (Plate 19.8)

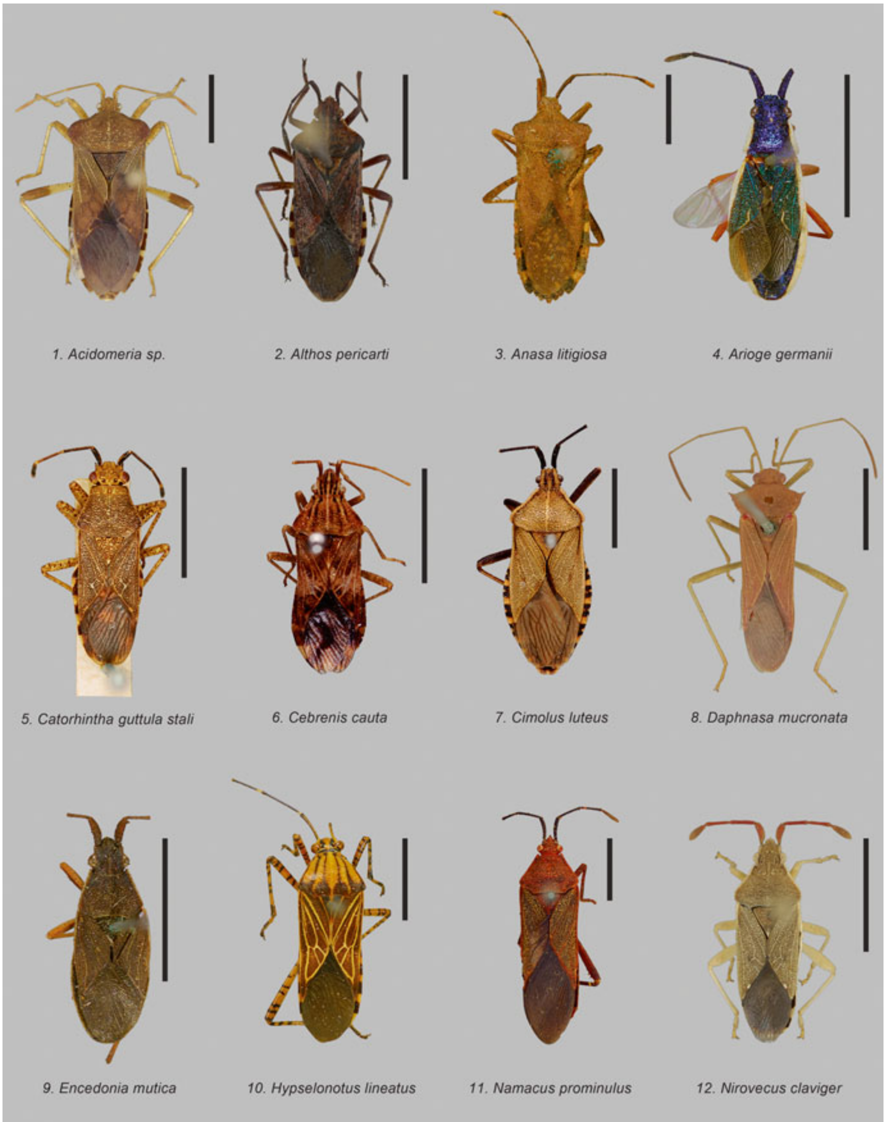
This tribe was always considered quite apart from other taxa (Stål 1873; Schaefer 1964) and Ahmad (1970) raised this taxon to subfamily level, but later authors (with the exception of (CoreoideaSF Team 2015) are still considering Hydarini as a tribe. The tribe is characterized by the lack of a dorsal tibial sulcus; paramere with a subdistal projection; broad direct articulation of the first valvifer and valvula; and lack of a spermathecal bulb. Head squared to rectangular and rough; first antennal segment slightly swollen distally; antennal segment III more than twice as long as segment II, and antennal segment IV short and flattened; spur of the third metathoracic axillary sclerite well developed; the anterior and posterior lobes of metathoracic peritreme completely separated; evaporatorium without ridges; connexivum ending at sixth tergite; trichobothria of third sternum level with spiracles; anterior spur of the seventh sternum double; trichobothria of fourth sternum anterior to spiracle; all femora slightly swollen anteriorly; and the hind tibiae not expanded.

This small tribe is formed by nine genera and 23 species; most of the genera and species are found in Africa and Asia. The Neotropical fauna is composed of *Hydarellamixia* (one species), *Hydascelis* (one), *Madura* (three), and *Maduranoides* (one). These species are distributed from Argentina to the United States. Brailovsky (1988c, 2010a) provides the necessary information to identify genera. *Madura perfida* Stål is reported from grasses and dry corn (references in Brailovsky and Rivera 1979) and from *Annona cherimola* Mill. (Peña and Bennett 1995). A key to the genera known from Neotropical region can be found in Brailovsky (2010a).

Hypselonotini Bergroth (Plates 19.9 and 19.10)

This tribe was first mentioned by Bergroth (1913) as Hypselonotaria, which was also used by Blöte (1935). No description or diagnosis for the tribe was given by Bergroth or Blöte, so a study of the relationships among these genera is badly needed and a careful evaluation of the separation between Hypselonotini and Coreini considered. Several genera belonging to this tribe were the subject of recent revisions, and when mentioned, Coreini is considered as the valid tribe for them (Brailovsky 1983a, 1985, 1988d, 1988e, 1989, 1990c, 1992a, 1995a; Brailovsky and Cadena 1992; Brailovsky and Garcia 1987; Brailovsky and Melendez 1989; Whitehead 1974). Species belonging to this tribe are distributed across the Americas, including Chile, with a considerable number living in subtropical areas. No key for the genera of the tribe is known.

This tribe comprises 34 genera and 352 species: *Acanonicus* Westwood (three species), *Acidomeria* Stål (11), *Althos* Kirkaldy (24), *Anasa* Amyot & Serville (76), *Arioge* Stål (one), *Astygiton* Berg (one), *Catorhintha* Stål (32), *Cebrenis* Stål (25), *Cebreniscella* Brailovsky (two), *Cebrenistella* Brailovsky (three), *Cimolus* Stål (four), *Collatia* Stål (five), *Daphnasa* Brailovsky (four), *Eldarca* Signoret (two), *Encedonia* Stål (two), *Hypselonotus* Hahn (12), *Microbasis* Dallas (one), *Namacus* Amyot & Serville (four), *Nirovecus* Stål (three), *Nisoscolopocerus* Barber (two), *Paryphes* Burmeister (28), *Petersitocoris* Brailovsky (one), *Petersitocoroides* Brailovsky (four), *Rochrosoma* Reed (one), *Scolopocerus* Uhler (four), *Sethenira* Spinola (five), *Sphictyrtus* Stål (20), *Stenoprasia* Horváth (five), *Stiroptus* Stål (one), *Sundarus* Amyot & Serville (31), *Vazquezitocoris* Brailovsky (14), *Viklundocoris* Brailovsky (one), *Villasitocoris* Brailovsky (1), and *Zicca* Amyot & Serville (19) (CoreoideaSF Team 2015).



1. *Acidomeria sp.*

2. *Althos pericarti*

3. *Anasa litigiosa*

4. *Arioge germanii*

5. *Catorhintha guttula stali*

6. *Cebrenis cauta*

7. *Cimolus luteus*

8. *Daphnasa mucronata*

9. *Encedonia mutica*

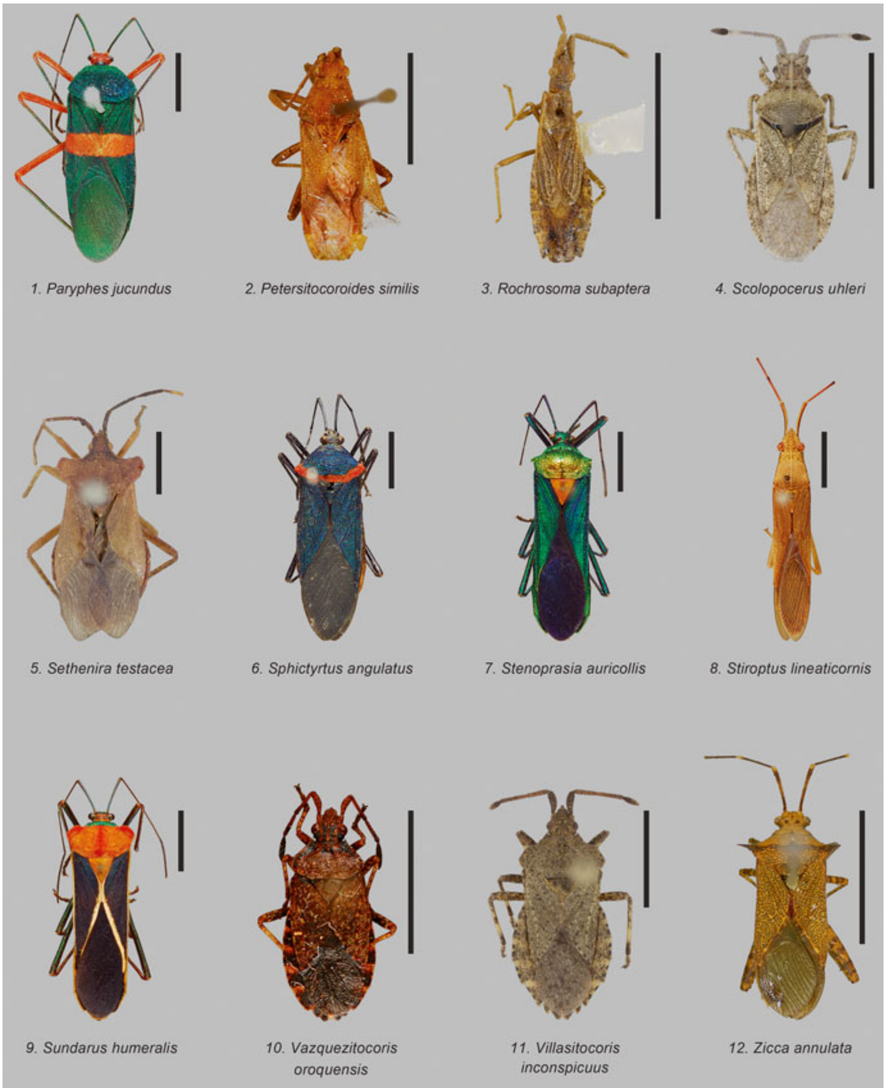
10. *Hypselonotus lineatus*

11. *Namacus prominulus*

12. *Nirovecus claviger*

Plate 9 - Hypselonotini Bergroth, 1913 (Scalebars = 5mm): 1. *Acidomeria sp.* [BMNH]; 2. *Althos pericarti* Brailovsky, 1990 [BMNH]; 3. *Anasa litigiosa* Stål, 1862 [NHMW]; 4. *Arioge germainii* (Signoret, 1863) [NHMW]; 5. *Catorhintha guttula* (Fabricius, 1794) [RNHL]; 6. *Cebrenis cauta* Brailovsky, 1995 [MNHN]; 7. *Cimolus luteus* Brailovsky, 2001 [MNHN]; 8. *Daphnasa mucronata* (Distant, 1881) [MNHN]; 9. *Encedonia mutica* (Signoret, 1863) [NHMW]; 10. *Hypselonotus lineatus* Stål, 1862 [NHMW]; 11. *Namacus prominulus* (Stål, 1860) [ZMHB]; 12. *Nirovecus claviger* Stål, 1860 [BMNH].

Plate 19.9 Coreinae plate—Hypselonotini



1. Paryphes jucundus

2. Petersitocoroides similis

3. Rochrosoma subaptera

4. Scolopocerus uhleri

5. Sethenira testacea

6. Sphictyrtus angulatus

7. Stenoprasia auricollis

8. Stiroptus lineaticornis

9. Sundarus humeralis

10. Vazquezitocoris oroquensis

11. Villasitocoris inconspicuus

12. Zicca annulata

Plate 10- Hypselonotini Bergroth, 1913 (Scalebars = 5mm): 1. *Paryphes jucundus* Horváth, 1913 [HNHM]; 2. *Petersitocoroides similis* Brailovsky, 1992 [RNHL]; 3. *Rochrosoma subaptera* Reed, 1899 [USNM]; 4. *Scolopocerus uhleri* Distant, 1881 [BMNH]; 5. *Sethenira testacea* Spinola, 1837 [MRSN]; 6. Sphictyrtus angulatus Horváth, 1913 [HNHM]; 7. *Stenoprasia auricollis* Horváth, 1913 [HNHM]; 8. *Stiroptus lineaticornis* Stål, 1860 [ZMHB]; 9. *Sundarus humeralis* Horváth, 1913 [HNHM]; 10. *Vazquezitocoris oroquensis* Brailovsky, 1990 [UNAM]; 11. *Villasitocoris inconspicuus* (Herrich-Schäffer, 1842) [BMNH]; 12. *Zicca annulata* (Burmeister, 1835) [NHMW].

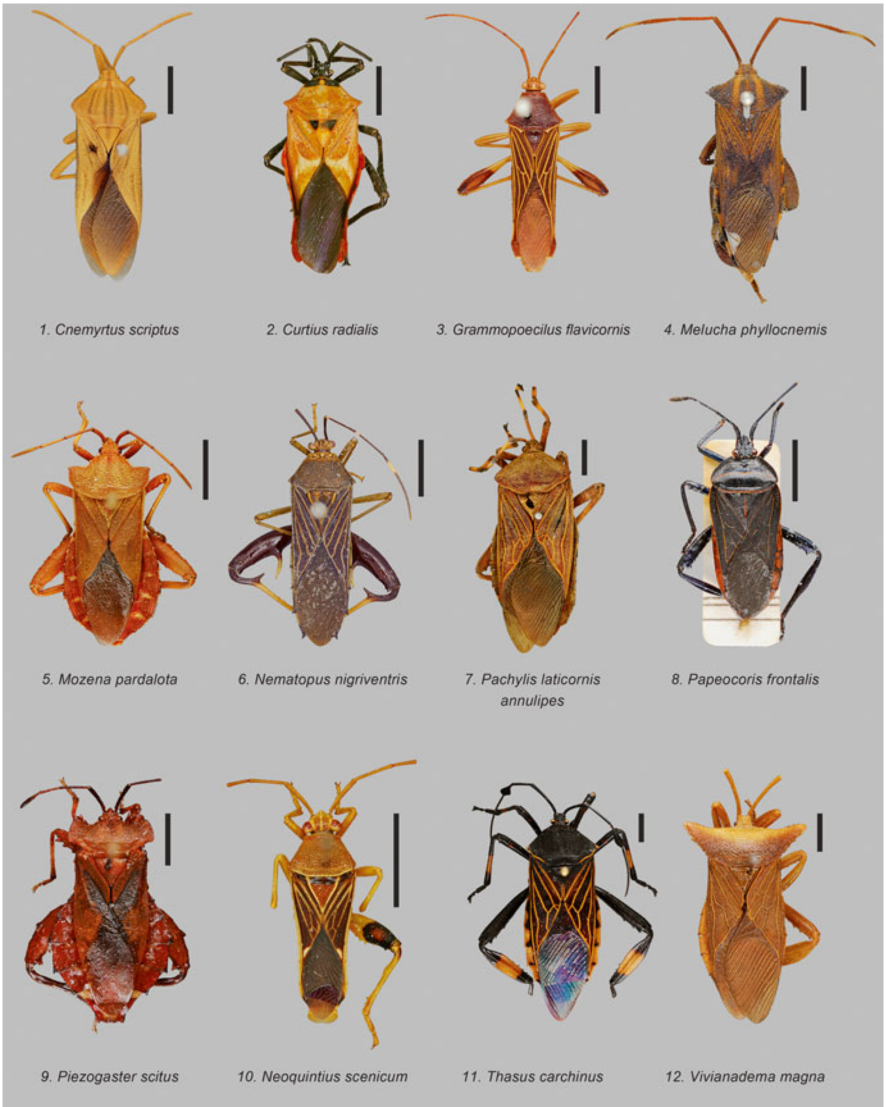
Plate 19.10 Coreinae plate—Hypeslonotini 2

Many *Anasa* spp. feed on cucurbits, and these bugs are by far the most economically important in the tribe; *Anasa tristis* (De Geer) and congeners are treated separately in section "*Anasa* Amyot & Serville". But the Hypselonotini is not linked strongly to Cucurbitaceae; *Paryphes blandus* Horváth feeds on the leaves of a cucurbit vine (Young 1980), but other species of Hypselonotini have been reported from a variety of crops. Adults of *Hypselonotus lineatus* Stål were noted to feed in large numbers on the flowers of physic nut, *Jatropha curcas* L. (Euphorbiaceae), in addition to their usual breeding host, *Waltheria indica* L. (Sterculiaceae) in Nicaragua (Grimm and Maes 1997; Grimm and Führer 1998), and both nymphs and adults of *H. fulvus* (De Geer) (as *H. lanceolatus* Horváth) were observed to pierce the fruits of arazá (*Eugenia stipitata* McVaugh, Myrtaceae) in Peru (Couturier et al. 1996). The latter species also feeds on the euphorb *Julocroton argenteus* (L.) in open pastures in Costa Rica (Solomon and Froeschner 1981) and comes to flowering cotton in Trinidad although mainly found on another malvaceous plant, *Malachra capitata* L. (Urich 1916). Whitehead (1974) provides host plant collection records for several other *Hypselonotus* species. In southern Brazil, *H. interruptus* Hahn was recorded from three native tree species: *Casearia sylvestris* (Flacourtiaceae), *Campomanesia xanthocarpa* Berg (Myrtaceae), and *Myrciaria rivularis* Cambessedes (Myrtaceae) (Thum and Costa 1997). In this same survey, *Zicca nigropunctata* (De Geer) (as *Z. nigropunctulata*) was found on *Patagonula americana L.* (Boraginaceae). *Sphictyrtus chrysis* (Lichtenstein) is reported to feed on *Annona muricata* L. in Venezuela (Peña and Bennett 1995) and is associated with cashew in Brazil (Bleicher and Melo 1996). Known host plants of *Cebrenis supina* are in Asteraceae (*Neurolaena lobata* (L.) R. B. R., *Mikania scandens* (L.) Willd, and *Verbesina* sp.) (Brailovsky 1995, cited in Barcellos et al. 2008). Schaefer and Mitchell (1983) present additional host records and speculated that the food plant preferences of Coreini (s.l.) might aid in determining relationships among genera.

Nematopodini Amyot & Serville (Plate 19.11)

This is the tribe of the bulky bugs; here is found the second largest group of bugs—*Thasus* and *Pachylis* (Plate 19.11). Species large to very large, head subquadrate; tylus projecting slightly beyond juga; antenniferous tubercles unarmed, occupying most of anterior head, ocellar tubercles small; metathoracic scent gland opening placed almost ventrally, peritreme with two completely separated lobes and area between them depressed; femora incrassate, posterior femora markedly incrassate especially in male and armed ventrally, anterior femora distally armed with two ventral spines; tibiae sometimes dilated; abdominal venter unarmed; paramere heavily sclerotized (O'Shea 1980b; Packauskas 1994).

Nematopodini and Acanthocerini were part of the Mictini until O'Shea and Schaefer (1978) reinstated them, separating the Neotropical species of the first two



1. *Cnemyrtus scriptus*
2. *Curtius radialis*
3. *Grammopoecilus flavicornis*
4. *Melucha phyllocnemis*
5. *Mozena pardalota*
6. *Nematopus nigriventris*
7. *Pachylis laticornis annulipes*
8. *Papeocoris frontalis*
9. *Piezogaster scitus*
10. *Neoquintius scenicum*
11. *Thasus carchinus*
12. *Vivianadema magna*

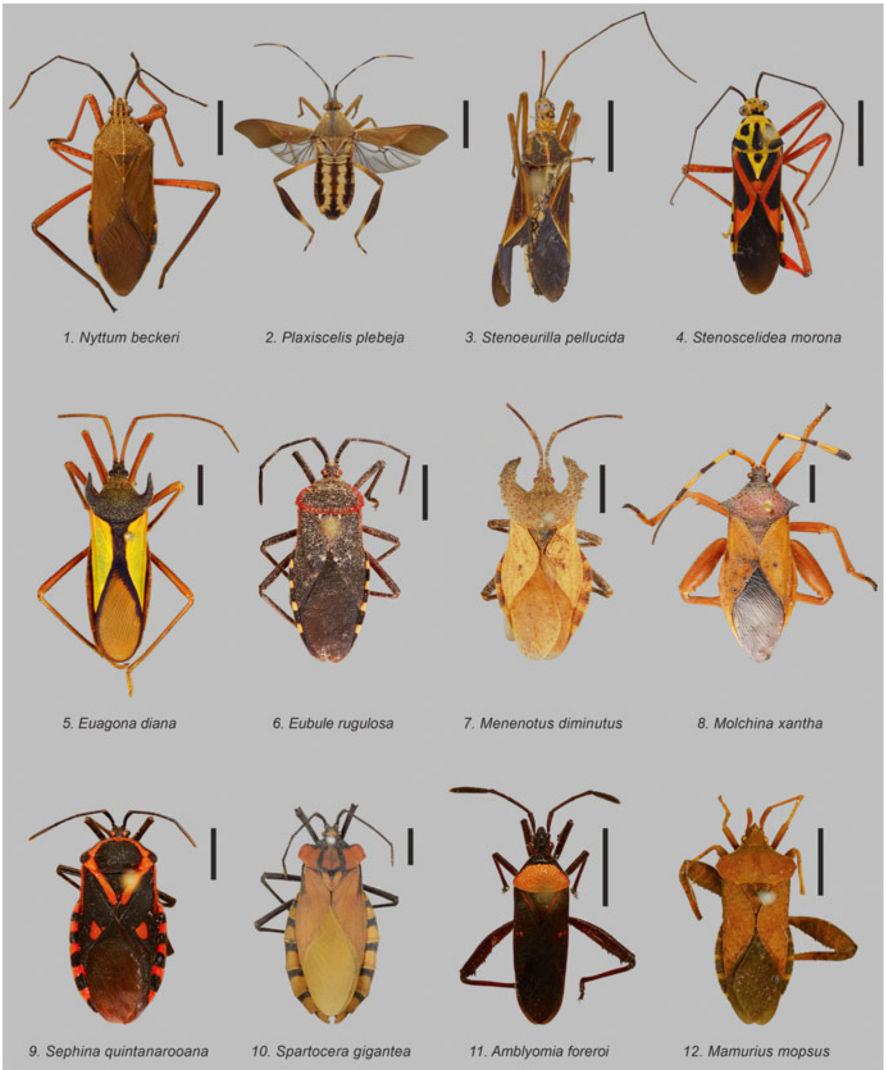
Plate 11 - Nematopodini Amyot & Serville, 1843 (Scalebars = 5mm): 1. *Cnemyrtus scriptus* (Burmeister, 1835) [ZMHB]; 2. *Curtius radialis* Brailovsky, 1986 [NHMW]; 3. *Grammopoecilus flavicornis* (Fabricius, 1803) [ZMUC]; 4. *Melucha phyllocnemis* (Burmeister, 1835) [ZMHB]; 5. *Mozena pardalota* Brailovsky & Barrera, 2001 [UNAM]; 6. *Nematopus nigriventris* Breddin, 1904 [DEI]; 7. *Pachylis laticornis annulipes* Blöte, 1938 [RNHL]; 8. *Papeocoris frontalis* Brailovsky, 2002 [UNAM]; 9. *Piezogaster scitus* Brailovsky & Barrera, 1984 ; 10. *Neoquintius scenicum* (Brailovsky & Barrera, 1986) [RNHL]; 11. *Thasus carchinus* Brailovsky & Barrera, 1994 [UNAM]; 12. *Vivianadema magna* Brailovsky, 1987 [AMNH].

Plate 19.11 Coreinae plate—Nematopodini mentioned tribes and keeping the Old World species in Mictini. Nematopodini comprises 22 genera and 161 species distributed across the Americas, but only 8 genera are represented in Central America and only *Mozena* is predominantly distributed in the northern part of the Neotropical region and the United States. Genera belonging to Nematopodini are: *Cnemyrtus* Stål (two species), *Curtius* Stål (four), *Grammopoecilus* Stål (two), *Himella* Dallas (three), *Melucha* Amyot & Serville (11), *Meluchamixia* Brailovsky (one), *Mozena* Amyot & Serville (31), *Nectoquintius* Brailovsky & Barrera (one), *Nematopus* Berthold (31), *Neoquintius* Brailovsky & Barrera (six), *Ouranion* Kirkaldy (three), *Pachylis* Le Peletier & Serville (10), *Papeocoris* Brailovsky (three), *Piezogaster* Amyot & Serville (33), *Quintius* Stål (three), *Saguntus* Stål (two), *Stentoquintius* Brailovsky & Barrera (two), *Thasopsis* O'Shea (two), *Thasus* Stål (eight), *Tovarocoris* Brailovsky (one), *Vivianadema* Brailovsky (one), and *Wilcoxina* O'Shea (one) (CoreoideaSF Team 2015). Keys to the genera of Nematopodini and additional notes can be found in O'Shea (1980b), Brailovsky (1987a, 1995b), and Brailovsky and Barrera (1986b, 2002, 2009b).

The strong association between Nematopodini and Fabaceae was noted by Schaefer and O'Shea (1979) and is clearly apparent from the known host records; mesquite and acacia are the most frequently reported hosts. All *Mozena* spp. are associated with legumes (*Acacia*, *Prosopis*, *Schrankia*), as are *Thasus* (*Prosopis*), *Pachylis laticornis* (F.) (*Pithecellobium*), *P. hector* Stål (*Mimosa*, *Prosopis*), and *Piezogaster odiosus* (Stål) (*Pachyrrhizus*) (Schaefer and O'Shea 1979; Schaefer and Mitchell 1983; Brailovsky et al. 1995), although *P. laticornis* has also been reported from banana (Musaceae) (Schaefer and O'Shea 1979). Also clear from host records and behavioral observations is a preference for vegetative structures, especially new growth and young shoots, although pods may also be used (Schaefer and Mitchell 1983). Aggregation behaviors of *P. laticornis* (as *Thasus acutangulus*) in Costa Rica are described by Aldrich and Blum (1978), but little is known of the biology of other Neotropical species other than host plant records. Nymphal descriptions and host plant associations for several species in Mexico are given by Brailovsky et al. (1995) and components of the scent fluid have been identified for nymphs of one Mexican species (Noge et al. 2012). The biology of the North American species, *Thasus neocalifornicus* Brailovsky & Barrera, has been thoroughly investigated, including the chemistry of the scent glands (Prudic et al. 2008) and the gut biota (Olivier-Espejel et al. 2011). *Mozena obtusa* Uhler has been extensively studied in Texas as a potential biological control agent for mesquite in Australia and South Africa (Cuda and DeLoach 1998).

Placoscelini Stål (Plate 19.12)

This tribe was proposed by Schaefer (1968) as Stenoscelideini, but only Packauskas (2006) presented a more complete description and the synapomorphies that support this taxon (mostly from the internal genitalia). Brailovsky and Barrera (2012) presented a diagnosis of the tribe and a key for the genera, both reproduced below. Dolling in the Coreoidea Species File (CoreoideaSF Team 2015) commented that



1. *Nyttum beckeri* 2. *Plaxiscelis plebeja* 3. *Stenoeurilla pellucida* 4. *Stenoscelidea morona*

5. *Euagona diana* 6. *Eubule rugulosa* 7. *Menenotus diminutus* 8. *Molchina xantha*

9. *Sephina quintanarooana* 10. *Spartocera gigantea* 11. *Amblyomia foreroi* 12. *Mamurius mopsus*

Plate 12 - Placoscelini Stål, 1868 (Scalebars = 5mm): 1. *Nyttum beckeri* Dolling & Casini, 1988 [BMNH]; 2. *Plaxiscelis plebeja* Stål, 1860 [BMNH]; 3. *Stenoeurilla pellucida* (Brailovsky & Barrera, 1997) [BMNH]; 4. *Stenoscelidea morona* Brailovsky & Barrera, 1996 [USNM];
Spartocerini Amyot & Serville, 1843: 5. *Euagona diana* Dallas, 1852 [BMNH]; 6. *Eubule rugulosa* Brailovsky, 1992 [UNAM]; 7. *Menenotus diminutus* Walker, 1871 [BMNH]; 8. *Molchina xantha* Brailovsky, 2006 [UNAM]; 9. *Sephina quintanarooana* Brailovsky, 1987 [UNAM]; 10. *Spartocera gigantea* Distant, 1892 [BMNH]; **Incertae sedis:** 11. *Amblyomia foreroi* Brailovsky, 1998 [NHMW]; 12. *Mamurius mopsus* Stål, 1862 [UNCB].

Plate 19.12 Coreinae plate—Placoscelini Spartocerini

Placoscelini Stål (as Placoscelida) has priority over Stenoscelideini Schaefer, because *Plaxiscelis* Spinola (= *Placoscelis* Agassiz) is included in this tribe. Head with postclypeal sulcus single or double (with internal ridge); clypeus raised as a short tubercle above deflexed juga; distance between antenniferous tubercles slightly less than width of one tubercle; antennal segment I longer than maximal length of head; antennal segment IV the longest and never longer than II and III together; rostrum reaching posterior margin of mesosternum or anterior third of metasternum; rostral segment III the shortest. Pronotum slightly declivent, bilobate; callar region slightly raised; collar present; humeral angles obtusely rounded or with a tiny spinous projection; metathoracic scent gland peritreme in form of two separate auricles with distinct bridge between them. Macropterous, hemelytra extending beyond apex of last abdominal segment. Connexival segments raised above terga; posterior angle unarmed, never spined postero-apically; abdominal spiracles circular.

This tribe comprises only four genera: *Nyttum* Spinola (10 species), *Plaxiscelis* Spinola (eight), *Stenoeurilla* Brailovsky & Barrera (eight), and *Stenoscelidea* Westwood (13) (CoreoideaSF Team 2015). These taxa are composed of species found basically in South America and previously placed in Acanthocephalini, except those belonging to *Stenoeurilla. Stenoeurilla aenescens* (Stål) (as *Stenoscelidea*) was reported by Solomon and Froeschner (1981) to feed on *Lonchocarpus costaricensis* Pittier. A key can be found in Brailovsky and Barrera (2012).

Spartocerini Amyot & Serville (Plate 19.12)

This tribe was called erroneously Corecorini by several authors that followed van Duzee (1916) considering *Corecoris* Hahn as the valid name instead of *Spartocera* Laporte. Specimens small to large with body robust. Head rectangular and declivent. Antenniferous tubercles close together, unarmed and projected beyond tylus. Antennae short with segments stout. Rostrum short just surpassing procoxae. Pronotum steeply declivent with anterior margin tuberculate or crenulate. Metacoxae separate from each other by the same distance of the metacoxa to the lateral margin. Posterior wing with cubital vein strongly curved anteriorly and hamus reaching the base of the wing. Spur of the third alar sclerite not developed. Trichobothria of the third abdominal segment located before the spiracle. Inner laterotergites of the connexivum fused.

This tribe is exclusively Neotropical and represented by six genera: *Euagona* Dallas (three species), *Eubule* Stål (13), *Menenotus* Laporte (two), *Molchina* Amyot & Serville (six), *Sephina* Amyot & Serville (24), and *Spartocera* Laporte (18). No key for all genera has been produced, and information is spread out in the literature. Only *Euagona* was revised recently (Brailovsky 2010b), but other genera were treated to some extent—*Eubule* (Brailovsky 1992b), *Sephina* (Brailovsky 1983b, 1987a, 2001b; Brailovsky and Sánchez 1983b), and *Molchina* (Brailovsky 2006a, key to the species) (CoreoideaSF Team 2015). Two species of *Sephina* are reported to feed on *Metastelma* spp. (Apocynaceae). *Eubule sculpta* (Perty) is reported from *Morrenia* sp. (Apocynaceae) but also from a cucurbit host (Schaefer and Mitchell 1983). The brightly colored bull's horn bugs, *Euagona* spp., exhibit an unusual trait, in that the dorsal coloration of the abdomen of nymphs appears to resemble that of the wings of the adults (W.R. Dolling, pers. comm.). Only one genus in this tribe is of major economic importance: *Spartocera* spp. are covered in detail in section "*Spartocera* Laporte".

Incertae sedis (Plate 19.12) Two genera of Neotropical Coreidae were considered *Incertae sedis* by CoreoideaSF Team(2015). The genus *Amblyomia* Stål is composed by three species revised by Brailovsky (1998b) and considered in Leptoscelidini. Species are known from Mexico and Colombia and apparently feed on bromeliads. Packauskas (2008) removed *Amblyomia* from this tribe and considered it *Incertae sedis* based on an uncoiled vesica and absence of a posttylar sulcus.

The genus *Mamurius* Stål is composed by two northern Neotropical species resembling a small *Piezogaster* (Nematopodini). Some diagnostic characteristics were mentioned by Brailovsky (1982) comparing this genus to *Dalmatomammurius*. O'Shea (1979) considered *Mamurius* out of Nematopodini due to the small size, tylus much projected anteriorly and genitalia not similar to those of the nematopodines.

19.5 Main Species

Here we discuss some genera of major importance for which the biology, ecology, behavior, natural enemies, and/or pest status were not covered in detail in Sect. 19.4. Information on many of these economically important species was summarized in Mitchell (2000); rather than repeat information already available in the literature, we refer the reader to *Heteroptera of Economic Importance* (Schaefer and Panizzi 2000) and focus here primarily on more recent research and updates to our knowledge.

19.5.1 Acanthocerini Bergroth

***Crinocerus* Burmeister**

The single species in this genus, *Crinocerus sanctus* (F.) (Plate 19.1), has a quite recognizable dorsal pattern described by O'Shea (1980a) as "a light brown St. Andrew's cross on a darker brown background." Aspects of the life history and photographs of immature stages and adults are provided by Amaral (1986). Photographs of an adult male, illustrating the incrassate femora, declivent pronotum, and distinctive markings, may also be found in Pall and Coscarón (2013).

These bugs have a wide host range, including leaves, green stems, and nuts of cashew (Bleicher and Melo 1996); oranges, limes, cotton, and leaves and fruit of guava (Amaral 1986); and new shoots and green fruit of acerola (*Malpighia* spp.) (Soglia et al. 1998). On the latter host, wilting of shoots and deformation of fruit are reported. However, *C. sanctus* is most commonly a pest of legumes, including *Canavalia ensiformis*, guandu bean, *Dolichos* sp., and particularly cowpea, on which bugs cause serious losses, feeding on stems, new foliage, and pods. (Bosq 1937; Amaral 1986; Daoust et al. 1985). In northern Brazil (Pará, Amazonas, Acre), this species is considered a principal pest of cowpea, forming part of a pod-sucking bug complex that includes the pentatomid *Piezodorus guildinii* (Westwood) (Daoust et al. 1985). Laboratory rearing studies using cowpea plus acerola or guandu bean leaves plus cowpea have shown nymphal development to range from 56 days at 27 ± 2 °C (Soglia et al. 1998) to 58.41 ± 1.25 days at 22 ± 2 °C (Amaral 1986).

19.5.2 Anisoscelini Laporte

***Anisoscelis* Latreille**

Bugs in this genus feed on *Passiflora* spp.; flower buds and fruits of cultivated passion fruit damaged by feeding may wither or drop from the vine (Polaszek and Kolberg 2008). *Anisoscelis foliaceus* (F.) has been the most extensively studied, particularly in southern Brazil where it overlaps and shares host plants with *Holhymenia clavigera* Herbst (Rodrigues and Moreira 2005). Eggs are ovoid, golden initially but later turning brown; nymphs are green in the early instars, darkening to ochre in the fifth instar. The expansion of the hind tibia becomes visible in third instars and continues to enlarge during development. Eggs and juveniles of both species were described and compared (Rodrigues and Moreira 2005) and were found to be remarkably similar through the fourth instar except in size and tibial foliation; *H. clavigera* are larger and lack the broad, leaflike expansions characteristic of Anisoscelini. Rearing experiments showed the wild host, *P. suberosa*, to be optimal for growth and development compared with cultivated passion fruit, *P. edulis*. A mix of vegetative and reproductive structures is used, and plant part preference changes over the course of development (Rodrigues et al. 2007b, 2008). Detailed histological studies of feeding sites showed mainly penetration to xylem in mature leaves, whereas several sites within the fruit were targeted, including pericarp, aril (pulp), endosperm, and embryo (Rodrigues et al. 2007a). *Anisoscelis flavolineatus* Blanchard is listed as a pest of cultivated passion fruit in Columbia (Urueta-Sandino 1975), but the genus is not mentioned for Venezuela (Aguiar-Menezes et al. 2002). Only low densities of *A. foliaceus* were found on cultivated passion vines in southeastern Brazil (Caetano et al. 2000, cited in Rodrigues et al. 2007b). Egg parasitoids of *A. foliaceus* include *Gryon chrysolaum* Walker and *G. vitripenne* Masner (Polaszek and Kolberg 2008).

Holhymenia Lepeletier & Serville

These unusual-looking bugs, with black and white markings and clear wings, are thought to be Batesian mimics of ichneumonid wasps (Rodrigues and Moreira 2005) (Plate 19.1). Two very similar species, *Holhymenia histrio* (F.) and *H. clavigera* (Plate 19.6, #6), cause extensive damage to cultivated passion fruit by feeding on stems, floral buds, and fruits. Feeding and consequent damage by *Holhymenia* spp. resembles that of *A. foliaceus*; xylem is probed on leaves, but feeding occurs on pericarp, aril, and seeds. First instars fed on tendrils of *P. edulis* and terminal buds and leaves of the native host, *P. suberosa*; fruit was preferred by later instars. Adults preferred green fruits over purple fruits (Rodrigues et al. 2007a, 2008). The egg and immatures of *H. clavigera* were described in detail by Rodrigues and Moreira (2005) and closely resemble those of *A. foliaceus* until the fifth instar, when the foliated antennal segments of *H. clavigera* develop a brown margin and the legs are strikingly banded. Two platygastrid parasitoids have been reared from eggs of *H. rubiginosus* Breddin: *G. chrysolaum* and *G. vitripenne* (Polaszek and Kolberg 2008).

Leptoglossus Guérin-Menéville

Primarily Neotropical with some Nearctic species, this large genus includes some of the more damaging and most extensively studied of the coreid economic pests. The majority of species are primarily found in South America (Allen 1969), but two species have achieved considerably wider distribution. The range of *Leptoglossus gonagra* (F.) extends well beyond the Neotropics, to Africa, Asia, and Australia. The North American conifer pest, *L. occidentalis* Heidemann, recently invaded Europe, Turkey, and East Asia; it represents a potential threat to commercial seed orchards and European alpine forest ecosystems (Lesieur et al. 2014). In the Neotropics, however, the most damaging species is unquestionably the highly polyphagous *L. zonatus* (Dallas), distributed from Argentina north to the southern United States.

Leptoglossus spp. are characterized by an elongate body shape, head porrect, humeral angles of the pronotum slightly to greatly expanded, hind femora slightly incrassate in males, and hind tibiae foliated, although the shape of the inner and outer dilations varies among species. Sexual dimorphism of the tibial dilations has been reported for a few species (Schaefer et al. 2008). A transverse fascia may be present on the corium; its color varies from bright white to pale, and shape varies in width and in the appearance of the margin: straight or zigzag (Allen 1969). Presently, 61 species are placed in the genus (CoreoideaSF Team 2015), although information on biology is available for relatively few species, primarily those with economic importance or unusual feeding habits.

Some species are host specific at the genus level; others are highly polyphagous, but there appear to be no evolutionary patterns of relatedness among the preferred host plants. Two species are associated with Amazonian palms, *L. hesperus*

Brailovsky in Brazil and *L. lonchoides* Allen in Peru (Couturier et al. 1991; Brailovsky and Couturier 2003). In North America, two species breed exclusively on mistletoe, and two are associated with conifers (Schaefer and Mitchell 1983). The conifer-feeding species are related to one another and to a more broadly feeding species that includes gymnosperms in the diet; together they constitute the *corculus* group of Allen (1969) and belong to the *zonatus* group of Packauskas and Schaefer (2001). Similarly, the mistletoe feeders are closely related (Allen 1969). However, the three specialists on Magnoliaceae (L. *katiae* Schaefer & Packauskas, *L. fulvicornis* (Westwood), and *L. dilaticollis* Guérin) are divided between two species groups (Schaefer et al. 2008). Similarly, the various cactus feeders (*L. subauratus* Distant, *L. dentatus* Berg, and *L. cinctus* Herrich-Schäffer) are divided among three species groups (Packauskas and Schaefer 2001); thus, host plant relationships do not always reflect taxonomic relationships.

The more generalist feeders, pests on a variety of crops, are primarily in the *zonatus* group. Species with exceptionally broad host plant ranges include *L. phyllopus* (L.) (Mitchell 2006), *L. zonatus* (Dallas) (Fernandes and Grazia 1992), *L. stigma* (Herbst) (Amaral and Cajueiro 1977), and *L. gonagra* (F.) (Mitchell 2000). Other Neotropical species mentioned as being crop pests are *L. conspersus* Stål on tomato and passion fruit (Urueta-Sandino 1975; Mitchell 2000); *L. balteatus* (L.) on guava, loofah, oranges, tomatoes, and legumes (Barber and Bruner 1947; Schaefer and Mitchell 1983); *L. chilensis* (Spinola) on various fruits; and *L. cinctus* on various fruits in addition to cacti (Faúndez and Carvajal 2011; Schaefer and Mitchell 1983). The latter species has the distinction of being the only coreid ever reported to bite a human, presumably to acquire fluids (Faúndez and Carvajal 2011). Allen (1969) notes that damage to guava, cashew, lychee, and annatto attributed to *L. stigma* probably refers to the very similar *L. concolor* (Walker).

Several species of *Leptoglossus* are known to transmit or facilitate the transmission of plant diseases, including fungal pathogens and fruit-inhabiting trypanosomatids. Two fungal diseases of pistachio, botryosphaeria panicle and shoot blight and stigmatomycosis, are transmitted by *L. clypealis* Heidemann in North America. Among the Neotropical species, *L. gonagra* transmits citrus diseases, *L. zonatus* transmits stigmatomycosis from pomegranate to citrus, and puncture wounds on fruit caused by *L. stigma* facilitate the entry of fungi. *Phytomonas* spp. are carried internally (salivary glands, alimentary canal) in *L. gonagra*, *L. ingens* (Mayr), and *L. stigma* (Mitchell 2004 and references therein). The ability of *L. zonatus* to harbor and transmit *Phytomonas mcgheei* to corn seeds has been studied experimentally; this species is considered a potential trypanosomatid vector because trypanosomes from bug salivary glands could infect corn in laboratory studies (Jankevicius et al. 1993).

Mitchell (2000) reviews the biology, life history, and distribution of *L. stigma*. This species, similar to *L. concolor* (Walker) but with a more steeply declivent pronotum and smooth pronotal calli, ranges from Mexico through South America east of the Andes, as far south as Paraguay and Brazil (Allen 1969; Packauskas 2010). An irregular fascia is usually, but not always, present on the corium. Food plants include pumpkin, guava, starfruit, cashew, oranges, mango, pomegranate, and tangerine. Adults attack the fruits and buds of guava (Amaral and Cajueiro 1977 and references therein). The development and behavior of *L. stigma* (as *Veneza stigma*) was observed and documented in the laboratory (Amaral and Cajueiro 1977). Nymphs could be reared on a diet of guava, pumpkin, and chayote, although mortality was high. Durations of the egg stage and nymphal stadia were determined and adult reproductive behavior described.

The distribution of *L. phyllopus* extends from the United States south through much of Central America, but it has only been considered to be of economic importance in the United States. These bugs have a broad, straight transverse fascia on the corium and bicolored hind wings (Allen 1969). The natural history, seasonal dispersal, host plant preference, feeding behavior, and tissue preference were examined by Mitchell (2006), using mark-release-recapture, field censuses, laboratory rearing experiments, and histological techniques. Stylets penetrated to xylem on vegetative tissue and to developing seeds and xylem on pods of green bean and tomato fruit. Nymphs developed equally well on reproductive structures from plants from different families, but could not survive on vegetative tissue alone. In the field, host-switching occurred frequently; teneral adults moved from the nymphal host to another plant species shortly after emergence, suggesting that the observed polyphagy is sequential rather than concurrent and the ability to develop on a variety of plants allows versatility in locating hosts in the appropriate reproductive condition.

Allen (1969) confirmed the synonymy of *L. membranaceus* (F.) with *L. australis* (F.). Baranowski and Slater (1986) then synonymized the Eastern Hemisphere *L. australis* with the Neotropical *L. gonagra s.s.*, thereby expanding the range of this species nearly worldwide. There is great variability in tibial dilations and humeral angles, but the orange-red to yellow lunate transverse fascia on the pronotal disk and the variegated antennae are quite recognizable in this species (Plate 19.6, #8) (Allen 1969; Baranowski and Slater 1986). Mitchell (2000) summarized the Eastern Hemisphere literature under *australis* and that of the Western Hemisphere under *gonagra*. In the Neotropics, *L. gonagra* damages citrus throughout its range, with damage reported in Florida, Puerto Rico, Argentina, and Brazil; however, this insect is highly polyphagous, and other crops attacked include pumpkin, chayote, loofah, cucumber, bitter gourd, watermelon, guava, araçá, passion fruit, papaya, mango, pomegranate, tobacco, physic nut, and corn. However, breeding hosts are more limited; bitter gourd, loofah, watermelon, and citron support nymphal populations (Mitchell 2000). Damage to citrus fruit has been described in detail: fruit drop, necrotic spots and lesions, dried, damaged, and bitter pulp, and secondary fungal infections are characteristic of *L. gonagra* infestations (Calza et al. 1964; Albrigo and Bullock 1977).

Extensive studies of the biology of *L. gonagra*, including egg stage duration and hatching success, nymphal development on leaves and fruit of pumpkin, and adult reproductive cycle were conducted in the lab under varying conditions of temperature and humidity (Amaral and Storti 1976). High mortality occurred during the second stadium on both pumpkin and bitter gourd, the wild host. Duration of the total life cycle was 80.7 ± 1.12 days. Development times (in days) were 8.2 for eggs and 3.6, 13.9, 10.3, 11.2, and 15.4 for the five nymphal instars, respectively.

Nymphal development and growth under controlled laboratory conditions were compared among five species of *Passiflora* (Caetano and Boiça 2000). Nymphs could not complete development on fruits alone. When provided branches, buds, flowers, and fruits, nymphs failed to complete development on *P. nitida* and showed the lowest adult weight on *P. giberti*. *P. laurifolia* was judged to be the most susceptible species, based on development time, adult weight, and longevity.

The literature on *L. zonatus* has grown substantially in recent years, due to increased interest in its economic importance on a variety of crops in South America and its spread across the southern United States. This species is typically characterized by two large whitish-yellow spots on the pronotal disk and a wide irregular fascia across the corium (Plate 19.1), but the fascia may vary in width or be missing entirely (Allen 1969). The eggs and immatures are described and illustrated by Fernandes and Grazia (1992), with observations on adult behavior. Mitchell (2000) summarizes older information in the literature on biology, host plants, economic damage, and control.

In the southern United States, satsuma mandarin oranges are damaged directly by bug feeding and indirectly by transmission of the yeast, *Nematospora coryli*; *L. zonatus* is considered to be a key pest (Henne et al. 2003; Xiao and Fadamiro 2010). The latter authors evaluate damage to satsumas (2010) and provide developmental data for nymphs and adult life history and reproductive parameters (2009). Preferences were tested between ripened and unripened fruit and among tomato, satsumas, kumquats, lemons, and peach; tomato was highly preferred, but *L. zonatus* can survive and develop on a diet entirely composed of satsuma fruit. Fruit maturity did not affect preference (Xiao and Fadamiro 2009). Among the wild hosts in the United States is Chinese tallow, an invasive euphorb (Johnson and Allain 1998).

Development of *L. zonatus* and the reproductive parameters of adults have also been studied on sorghum and corn (Matrangolo and Waquil 1994) and on corn, soybean, and green bean (Panizzi 1989). Corn seeds were far preferable for rearing than pods of either legume, and this insect is abundant in corn fields in Brazil (de Souza and Amaral 1999a; Panizzi 2004b). An African tree widely planted in greenbelts, *Spathodea campanulata* Beauv (Bignoniaceae), supports adults and nymphs and may serve as an alternate host (de Souza and Amaral 1999a). The entire life cycle can also be completed on physic nut; instar duration data, nymphal measurements, and reproductive parameters have been determined for this host plant (Grimm and Somarriba 1999). *L. zonatus* is the second most common heteropteran on this crop in Nicaragua (Grimm and Maes 1997) and also occurs on physic nut in Mexico (Tepole-García et al. 2012). Damage to pomegranate (Raga et al. 1995) and guava (Pires et al. 2013) has also been described, and occurrence of this insect on *Annona* spp. (Peña and Bennett 1995), *Malpighia emarginata* Sessé & Moc, *Morus nigra* L., and *Mangifera indica* L. (Pires et al. 2013) has been recorded.

Omnivory has also been observed in *L. zonatus*; egg masses of fall armyworm, *Spodoptera frugiperda*, were consumed by adults in maize fields in Brazil (Menezes-Netto et al. 2012). *L. zonatus* has also been observed to orient toward and land on humans and on plastic cylinders hung from poles in corn fields, possibly representing either territorial or recognition behavior (Panizzi 2004b). Natural enemies include *Trichopoda pennipes* F. and egg parasitoids including *Gryon* sp. (de Souza and Amaral 1999b). Control using entomopathogens (*Beauveria bassiana* (Bals.) Vuil. and *Metarhizium anisopliae* (Metsch.) Sorok) appears promising in laboratory and field trials and was more effective than treatment with neem seed (Grimm and Guharay 1998).

***Narnia* Stål**

Narnia spp. inhabit primarily the desert areas of North America; however, the distribution of *N. femorata* Stål extends to Guatemala (Brailovsky 1975). Various cacti are hosts for *Narnia* spp., including *Opuntia* spp. (Brailovsky 1975), but unlike the cactus pad specialists in Chelinideini, these bugs preferentially feed on fruits. Brailovsky et al. (1994) provide detailed descriptions of the egg, nymphal stadia, and life cycle of *N. femorata* in Mexico. Eggs are laid on the spines and pads, and the life cycle is dependent on the fruiting and flowering cycle of the host. First instars are gregarious, but do not feed; late instars disperse. Recent behavioral studies of *Narnia femorata* Stål have added substantially to our understanding of coreid feeding and mating. Adults reared exclusively on pads survive, but development is delayed and body size is smaller compared with individuals with access to fruits (Nageon de Lestang and Miller 2009). In the presence of cactus fruit, females prefer the odor of males who developed on fruit although no preference is exhibited in the absence of fruit odors (Addesso et al. 2014). Both male-male competition and female choice operate in this species; enlarged femora in males are used in combat (Miller 2013) to defend territories on cactus, but male body size and leg area only strongly affect the outcome of male-male competition in the presence of females (Procter et al. 2012).

***Phthia* Stål**

The genus *Phthia* Stål was recently revised by Brailovsky (2009c) with the erection of four new genera. Of the 13 species originally in *Phthia s.l.*, *Phthia picta* (Drury) has been placed alone in the genus *Phthiacnemia* Brailovsky, while *P. lunata* (F.) remains, along with three other species, in *Phthia s.s.* Three additional species were placed in *Phthiadema* Brailovsky, four in *Phthiarella* Brailovsky, and one in *Rhytidophthia* Brailovsky. Brailovsky (2009c) provides a key to genera, which may be distinguished from one another by the development of the humeral angles and the extent of metallic iridescence on the head, clavus, and corium. Although all are Neotropical, only the widely distributed *P. picta* has received any mention in the economic literature; this species may be distinguished by the dull, non-metallic body surface and the truncate (non-acute) humeral angles. A narrow orange-red transverse band may be present on the posterior portion of the pronotum (see illustration in Brailovsky 2009c), and other orange markings may be variably present (Baranowski and Slater 1986), but unlike *Phthia s.s.*, no yellow transverse fasciae occur on the anterior lobe or on the corium (Brailovsky 2009c). Literature records for this species may be found under *Dallacoris* Osuna in addition to *Phthia* and *Phthiacnemia*.

Host plant records are available for *P. picta*, *P. lunata*, and *Rhytidophthia splendens* (Valdés). The latter, endemic to Cuba, was collected from *Taonabo* (=*Ternstroemia*) *parviflora* Krug & Urban (Theaceae) (Barber and Bruner 1946). *P. lunata* is reported from Cucurbitaceae (*Citrullus* and *Cucurbita*) (Maes and Goellner-Scheiding 1993). Published host plant records for *P. picta* are summarized by Schaefer and Mitchell (1983), Baranowski and Slater (1986), and Mitchell (2000). Serantes (1973) lists the known hosts in Argentina. *Solanum nigrum* L. is the common wild breeding host in Florida, and occurrence on tomato has been reported throughout the range of *P. picta*, from the Caribbean to Argentina (Baranowski and Slater 1986; Serantes 1973). However, the species is not always considered an economically important pest (Mitchell 2000), and despite the common names, "chinche de tomate" and "percevejo do tomate," it is not restricted to Solanaceae. This species is in fact highly polyphagous, feeding on cultivated cucurbits and legumes in addition to tomato and eggplant; plants from 11 families are reported as feeding or breeding hosts (Schaefer and Mitchell 1983). Feeding punctures cause direct damage resulting in deformed fruit; indirect damage includes entry pathways for fungal pathogens (Amaral 1980) and transmission of a trypanosomatid of tomatoes, *Phytomonas serpens* (Gibbs) (Jankevicius et al. 1989; Freymuller et al. 1990; Fiorini et al. 1993). Flagellates of *P. serpens* were found in the digestive tract of field-collected insects and appear in hemocoel and salivary glands 1 week following acquisition in the laboratory. Transmission in both directions (from *P. picta* to tomato fruit and from tomato fruit to insect) was documented. The nature of the relationship between tomato and *P. serpens* is not known with certainty; fruit-dwelling trypanosomatids may not actually be pathogenic although phloem-inhabiting trypanosomatids, also transmitted by bugs, cause serious disease and economic losses (e.g., hartrot of coconut transmitted by *Lincus lobuliger* Breddin (Sgrillo et al. 2005).

The eggs of *P. picta*, like those of *Leptoglossus* and *Narnia*, are hemicylindrical and laid in a single row, end to end. The juvenile stages are described by Serantes (1973) with illustrations of the egg and first and fifth instars. Detailed measurements, descriptions, and illustrations of all five instars are provided by da Silva et al. (2001). Younger instars, brightly colored and gregarious, develop faster when reared in aggregations (Amaral 1981a). Life history and behavioral observations are given by Serantes (1973) for Argentine populations and Amaral (1980, 1981a, b) for Brazil and reviewed by Mitchell (2000) and da Silva and Carvalho (2001). More recent studies of development under controlled laboratory conditions (da Silva and Carvalho 2001) showed total nymphal development time to be 34.39 ± 0.67 days on tomato at 26 ± 1 °C, 70 ± 10 % RH, and 14: [L:D] photoperiod, with 56 % mortality.

For females, the pre-oviposition period was 62.83 ± 9.86 days, with 9.37 ± 1.48 days between egg batches. Data are also provided on clutch size, adult longevity, and development time for eggs and each instar.

19.5.3 Hypselonotini Bergroth

Anasa **Amyot & Serville**

This large genus comprises 76 species (CoreoideaSF Team 2015) with distributions ranging from Canada to northern Argentina and Uruguay (Brailovsky 1985; Packauskas 2010), although the majority of species are Neotropical. These medium-sized bugs are elongate-oval, with the pronotum strongly declivent; the connexivum widely exposed; the antennae, femora, and tibiae slender; and the beak extending at least to the middle coxae (Blatchley 1926). Although several species have been noted as injurious to cucurbit crops, only *Anasa tristis* (De Geer) is currently considered a serious economic pest. Reports of other *Anasa* spp. feeding on cultivated cucurbits include *A. trilineata* Stål in Venezuela; *A. incompta* Brailovsky in Colombia; *A. costalis* Stål , *A. litigiosa* Stål, *A. maculipes* Stål, *A. ruficornis* Stål, and *A. uhleri* Stål in Mexico; and *A. guttifera* Berg in Argentina (Brailovsky 1985; Brailovsky et al. 1994). The widely distributed *A. scorbutica* (F.) is reported from loofah, squash, gourds, maize, tomato, and physic nut in various parts of its range (Mitchell 2000 and references therein), but cucurbits are the only hosts on which breeding was noted (Barber and Bruner 1947). *A. andresii* (Guérin-Méneville), distributed from the southern United States and the Caribbean to Colombia and Ecuador (Packauskas 2010), is reported from cucurbits, including *C. pepo* (L.) and *C. ficifolia* Bouché, cotton, tomatoes, and bromeliads (Brailovsky 1985) and was described in Cuba to be "at times a pest on squash" (Barber and Bruner 1947). On squash, these bugs cluster on the leaf underside, causing wilting and death, and may also feed on fruits (Mitchell 2000 and references therein). Interestingly, a number of *Anasa* spp. have been collected from bromeliads: *A. litigiosa* (Plate 19.9, #3) occurs on *Tillandsia* in addition to wild and cultivated cucurbits (Brailovsky 1985), and *A. costalis* has been reported from both *C. pepo* and two species of *Tillandsia* (Brailovsky 1985; Brailovsky et al. 1994), whereas *A. capaneodes* Stål and *A. impictipes* Stål may be more strictly associated with *Tillandsia* spp. (Brailovsky 1985). Brailovsky (1985) compiled a thorough list of all known host plants and habitats for *Anasa* spp., adding more Mexican host plants subsequently (Brailovsky et al. 1994). Of the 17 species for which host plants are known, 13 feed on cucurbits (although not always exclusively), with stem, leaf, and fruit all mentioned as feeding sites. With the exception of *A. tristis* and two strictly North American species (*A. armigera* (Say) and *A. repetita* Heidemann), virtually nothing is known of the natural history of *Anasa* species (Brailovsky 1985).

The notorious "squash bug," *A. tristis*, occurs from Canada to Brazil and is a pest of squash and pumpkin in the United States and Mexico. A vast amount of research has been dedicated to understanding the biology of *A. tristis*, the damage it causes, and potential control methods. Mitchell (2000) reviewed this primarily North American literature, including life cycle, behavior, feeding and oviposition preferences, histological studies of feeding damage, insecticidal control methods, cultural controls, natural enemies, and tritrophic interactions. More recent studies have revealed that, in addition to direct damage to vascular tissues, the squash bug transmits a phloem-colonizing bacterium, *Serratia marcescens* Bizio, the causative agent of cucurbit yellow vine disease (Bruton et al. 2003). This disease was first described in 1988 in Texas and Oklahoma and subsequently spread eastward in the United States. The pathogen can be acquired in the nymphal stage and transmitted after the bug reaches adulthood; transmission appears to be propagative rather than noncirculative. No bacteria are found in the cibarium, suggesting that the likely location for retention of the bacterium is the hemocoel (Wayadande et al. 2005). Overwintering infected adults can transmit *S. marcescens* to cucurbit crops the following spring (Pair et al. 2004). The pathway of transmission from insect to phloem sieve tube cells is not yet understood (Wayadande et al. 2005; Maskey 2010); wilting caused by *A. tristis* has been attributed to xylem blockage (Neal 1993), but stylets do penetrate to the phloem tissue. However, the diameter of the stylets is too large to permit direct insertion into phloem sieve tube elements in the manner of aphid or leafhopper feeding (A. Wayadande, personal communication), and despite several studies of squash bug feeding using electrical penetration graphing (Bonjour et al. 1991; Cook and Neal 1999; Maskey 2010), the mode of feeding and the mode of pathogen transmission in *A. tristis* remain uncertain (Maskey 2010). Nonetheless, the economic importance of the squash bug, and possibly other *Anasa* spp. as well, has increased with the recognition of its vector competence.

19.5.4 Spartocerini Amyot & Serville

Spartocera Laporte (Plate 19.1)

Much of the older literature on this group, especially the species of economic importance, was published under the synonym *Corecoris* Hahn. These bugs are characteristically large and ovoid, with a broad abdomen and prominent connexivum. Of the 18 species distributed from the southern United States through South America, six have been noted as injurious to crops. In the United States, *Spartocera diffusa* (Say) damages potato; Chittenden (1927) provides nymphal descriptions and information on natural history and host plants. A preference for solanaceous crops also characterizes the Neotropical species, but sweet potato (*Ipomoea batatas* (L.), Convolvulaceae) is also attacked. *Solanum nigrum* L. is reported as a wild host for several pest species, including *S. diffusa*, *Spartocera brevicornis* (Stål), *Spartocera batatas* (F.), and *Spartocera fusca* (Thunberg) (Chittenden 1927; Bosq

1937; Costa Lima 1940; Halbert 2003). Little is known of the natural history of species that pose no economic threat, with one exception. *Spartocera lativentris* Stål feeds on the leaves and stems of *Solanum sisymbriifolium* L., with two generations per year in southern Brazil. No feeding on fruits was observed, and first instars were not observed to feed (Becker and Prato 1982). These authors also provide detailed information on the eggs of this species, including a description, oviposition sites, egg clusters, female reproductive organs, and egg mortality, hatching success, and parasitism.

Spartocera batatas (F.) feeds on sweet potato in Jamaica, Cuba, Puerto Rico, and other Caribbean islands; it is currently considered to reach minor pest status only in Puerto Rico. One infestation in Florida has also been reported (Halbert 2003 and references therein). Adults are parasitized by the tachinid fly, *Trichopoda pennipes* (F.) in the Caribbean and in Brazil (Amaral and Vieira 1978). Both *S. brevicornis* and *S. fusca* are associated with various cultivated solanaceous crops; tobacco and tomato, respectively, are mentioned by Costa Lima (1940) for Brazil. However, *S. fusca* has been noted elsewhere in its broad range to feed on a variety of hosts including *Capsicum annuum* (chili peppers) and *Physalis* sp. and has been collected from citrus. In Florida, it breeds on *Solanum americanum* P. Mill (Blatchley 1926; Brailovsky and Sánchez 1983b; Baranowski and Slater 1986). *Spartocera granulata* Stål is also registered in Brazil as a pest of cultivated solanaceous crops (Becker and Prato 1982).

By far the most damaging species in the genus, and the best studied, is *Spartocera dentiventris* Berg, a pest of tobacco in Brazil. Feeding causes the tobacco leaves to twist and wilt, causing economic losses. Detailed information on the biology of this species is provided by Caldas et al. (1998, 1999, 2000) including a description of the immatures, reproductive biology, longevity of adults, and cage studies of life history in tobacco. Mark-release-recapture in tobacco fields (Jesus et al. 2002) documented the population dynamics of the bug over the tobacco growing season, showing an aggregated pattern of distribution and predation by the reduviid *Cosmoclopius nigroannulatus* Stål on the second generation of nymphs Canto-Silva & Romanowski (2003). This assassin bug shows a type II functional response when feeding on first instar *S. dentiventris* (da Rocha and Redaelli 2004). Reported parasitoids of both *S. dentiventris* and *S. lativentris* include the eurytomid wasp *Neorileya ashmeadi* Crawford and the platygastrid *Gryon gallardoi* (Brèthes) (Becker and Prato 1982; Santos et al. 2001). Extensive studies have been conducted on the behavior of *G. gallardoi* as a potential biological control agent for *S. dentiventris* (da Rocha et al. 2007, 2008).

19.6 Concluding Remarks

Two recently compiled catalogs (Packauskas 2010; CoreoideaSF Team 2015) provide an invaluable resource for continued and expanded study of the Neotropical Coreidae. Catalogs of the North American fauna (e.g., Baranowski and Slater 1986; Henry and Froeschner 1988) have been available for some time, but only recently has information on the entire New World Coreidae become easily accessible. As Packauskas (2010) noted, studies of New World coreids, and especially the Neotropical genera, languished for over 100 years. The higher classification of the Coreoidea has received attention (e.g., Schaefer 1964) and Stål's (1867) key to New World subfamilies and tribes has been updated (Packauskas 1994), but no modern comprehensive key to genera exists. The voluminous contributions of Brailovsky and his collaborators (see References for an appreciation of the extent of these works) include keys to genera for five Neotropical tribes discussed herein; papers by Yonke (1972) and O'Shea (1980a, b) provide information and keys for another three tribes. However, keys are lacking for some of the largest Neotropical coreid tribes and those with the most economically damaging members (e.g., Hypselonotini). Furthermore, keys to species exist for fewer than half the described genera in most tribes (see listings in Packauskas 1994). The Coreidae of the Neotropical region form an impressive and complex assemblage, with striking, often bizarre, characters and spectacular coloration. It is hoped that the advent of the newly launched Coreoidea Species File Online (CoreoideaSF Team 2015) will stimulate further, much needed, work on these elegant bugs.

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Chapter 20
Scentless Plant Bugs (Rhopalidae)

**Trevor M. Fowles, Maria del C. Coscarón, Antônio R. Panizzi,
and Scott P. Carroll**

Abstract Rhopalidae are closely related to the much more speciose Coreidae, and like them are plant feeders, although more associated with reproductive tissues and seeds. The two rhopalid subfamilies, Rhopalinae and Serinethinae, occur worldwide, with the latter more restricted to tropical latitudes. About 38 % of the ca. 210 rhopalid species and 38 % of the 21 genera have at least partially Neotropical distributions. The serinethine genus *Jadera* Stål is particularly associated with the Neotropics and like other members of the subfamily feeds on seeds of Sapindaceae (soapberry family). Most Neotropical rhopalid species are unstudied, and few appear to have major economic importance. However, serinethines are important models in insect reproductive life history, behavior, and human-induced evolution. Rhopalids are not scentless, and a more accurate family name is needed.

20.1 Introduction

The rhopalids are a small worldwide family of approximately 200 species of plant-feeding bugs in 21 genera and 209 species (Henry 2009). Formerly treated as a subfamily of the Coreidae, usually with the name Corizinae, Schaefer (1965) ended a century of taxonomic controversy with his definitive elevation of these insects to family Rhopalidae, with subfamilies Rhopalinae and Serinethinae. Chopra (1967)

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Table 20.1 Summary of the known number of Rhopalidae genera and species for the Australian (1), Nearctic (2), Neotropical (3), Palearctic (4) and regions and the world (5)

Australian		Nearctic		Neotropical		Palearctic		World	
Genus	Species	Genus	Species	Genus	Species	Genus	Species	Genus	Species
2	6	10	39	9	81	14	69	21	209

(1) Based on Cassis and Gross (2002)
(2) Based on chapters in Henry (1988)
(3) Based on this chapter
(4) Based on chapters in Aukena and Rieger (1995–2006)
(5) Based on Henry (2009)

extensively revised the tribal classification of the family and included keys to subfamilies, tribes, and genera. Göllner-Scheiding (1983) published a world catalog of the family. In Rhopalinae there are approximately 150 species in six tribes and 17 genera, while the Serinethinae (soapberry bugs) consist of about 65 species in three genera.

For the Neotropical region, four of the six rhopaline tribes are present (Table 20.1), with none of these being exclusive to the New World. Likewise, two of the three serinethine genera are present, and the genus *Jadera* Stål is exclusive to the New World.

Several partial catalogs have been developed for South America: Argentina (five species in two genera, Pennington 1920–1921, and 35 species in five genera, Coscarón 2014), mainland Ecuador (10 species in four genera, Froeschner 1981), the Galápagos Islands (three species in three genera, Froeschner 1985), Nicaragua (12 species in six genera, Maes and Göllner-Scheiding 1993), and Panama (14 species in four genera, Froeschner 1999). In addition, for Brazil, Grazia et al. (2012) refer to five genera with 26 species, namely, the rhopalines *Niesthrea* Spinola (six spp.), *Liorhyssus* Stål (one sp.), *Harmostes* Burmeister (eight spp.), and *Xenogenus* Berg (two spp.), and the serinethine *Jadera* (nine spp.).

Only a few species of Neotropical rhopalids have been studied in any detail, and scientific knowledge of the general biology and ecology of this fauna is largely incomplete. In-depth information is available for a few *Jadera* species, though mainly at the margins of the Neotropical region in southern Florida and southern Brazil (e.g., Carroll et al. 2003a, b; Panizzi et al. 2005). To encourage further study, Carroll and Loye (2012) reviewed host associations of *Jadera* with plant species in the soapberry family (Sapindaceae). Much remains to be learned about the systematics of Neotropical rhopalids, as well as their potential economic importance (Gonzáles 1989). While there are no comprehensive keys for identification of the Neotropical rhopalid species, Pall and Coscarón (2012) have provided one for the Argentinian taxa, along with photographs and range maps. The Web site "Soapberry Bugs of the World" (www.soapberrybugs.org) is a center for information on serinethines.

20.2 General Characteristics and Diagnosis

Rhopalids have four-segmented mouthparts and antennae. They may resemble coreids but are generally narrower and smaller bodied (although a few Neotropical serinethines reach or exceed 15 mm in body length). Most rhopalines are much smaller than most serinethines and generally dull brownish in color. In contrast, many serinethines have contrasting coloration with bright red, orange, and black. Rhopalids are often misidentified, and other insects are likewise mistaken for rhopalids. The distinct paired ocelli between the eyes (Fig. 20.1a) distinguish serinethines from Pyrrhocoridae such as *Dysdercus* Guérin-Méneville, which lack ocelli. The rhopalid forewing membrane has close to 20 slender parallel veins arising from a transverse basal vein (Fig. 20.1a), further distinguishing serinethines from Pyrrhocoridae and the superficially similar lygaeine Lygaeidae and rhopalines from the similar Orsillinae Lygaeidae, all of which have just 4–5 major veins in the membrane. Adult rhopalids lack the scent glands on the thorax between the middle and hind coxae present in Coreidae and Lygaeidae and are also unusual in retaining functional dorsal abdominal glands between the 4–5 and 5–6 terga (Fig. 20.1b).

The commonly applied name for this family, "scentless plant bugs," reflects the absence of metathoracic scent glands in serinethines. However, this name is misleading and inappropriate because these and other rhopalids commonly produce redolent compounds from scent glands (Aldrich et al. 1990a). Members of the more diverse subfamily, Rhopalinae, in fact possess fully functional metathoracic scent glands as adults, in common with other hemipterans (Aldrich et al. 1990a; Davidova-

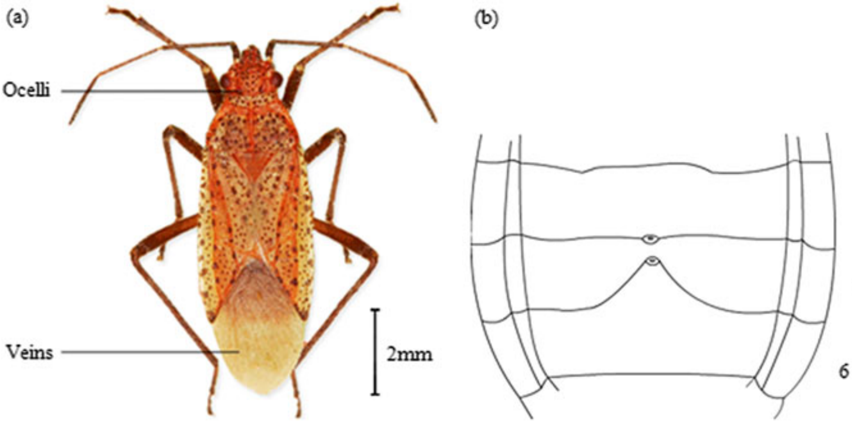

Fig. 20.1 (**a**) *Jadera choprai* Göllner-Scheiding; the ocelli distinctly raised. The front wing membrane has many veins of similar size. (**b**) *Liorhyssus hyalinus*. Image adapted from Davidova-Vilímová et al. (2000). The dorsal abdominal glands between 4–5 and 5–6 ; the terga are unusual among Hemiptera because they remain functional in the adult stage

Vilímová et al. 2000). Moreover, both subfamilies retain the anterior dorsal abdominal gland usually found only in immature Heteroptera (Davidova-Vilímová et al. 2000), and adult males also secrete fragrances from glands in the genitalia (Aldrich 1988; Aldrich et al. 1990a). If the vestigial metathoracic scent glands of Serinethinae indeed indicate a reduced capacity for synthesis of de novo chemical defense, it may have evolved in association with their conversion of toxic cyanogens from the seeds of their host plants (Braekman et al. 1982). They can secrete, excrete, and bleed these toxins to defend against predators (Aldrich et al. 1990b). Ribeiro (1989) found that predatory birds and toads rejected *J. haematoloma* (Herrich-Schäffer) after initially ingesting them. However, glandular secretions may have an additional function in rhopalids. Schwartz et al. (2009) reported that the odorous monoterpene secretions from the dorsal abdominal glands of *Boisea* Kirkaldy, which the insects actively spread across their cuticles with the legs, inhibit the germination and halt the growth of the fungal pathogen *Beauveria bassiana* (Bals.), which is potentially lethal to serinethines (Reinert et al. 1999). Accordingly, the redolent glandular products and vascular toxins of rhopalids likely serve multiple important functions in these insects.

20.3 General Biology and Ecology

To varying extents, rhopalids specialize on particular host plant taxa as food resources for growth and reproduction. In consequence, many aspects of the general biology and ecology may be predicted from knowledge of host plant range, phenology, morphology, and chemical characteristics. In some cases there is evidence of host–rhopalid coevolution, as in the variably inflated fruits of balloon vines coupled with variation in the mouthpart lengths of their specialist serinethine seed predators (e.g., Carroll 1988). Even specialists may take water or nutriment from other sources, however, including flowers, sweet fruits, and dead insects, which may sometimes lead to confusion about the definitive host on which they depend for growth and reproduction. In addition, probably well under 1 % of museum specimens have reliable host records, making it challenging to determine host relations without focused field studies (Carroll and Loye 2012). In this section we treat development and reproduction in further detail, organized around subfamily, tribe, and host relations.

20.3.1 Eggs and Oviposition

Rhopalids typically lay their eggs on or near host plants. The most extensive analysis of rhopalid eggs was undertaken by Vilímová and Rohanová (2010). They found that the differences in egg characteristics between tribes supported Schaefer and Chopra's (1982) treatment of Rhopalidae. Detailed studies of eggs and oviposition have not been made for most Neotropical rhopalids, so that we have included observations from temperate and subtropical congeners and conspecifics to describe some key attributes.

All rhopaline eggs have two micropylar processes, and this conformation is regarded as the ancestral state by Vilímová and Rohanová (2010). Tribe Rhopalini, with characters such as poorly defined pseudopercula, appears to be the most primitive. The widely distributed rhopaline *Liorhyssus hyalinus* (F.) typically lays eggs on host sepals or nearby stems and leaf midribs.

Until now, contributions on instars included *Arhyssus hirtus* (Torre-Bueno) (Wheeler and Henry 1984), *A. lateralis* (Say) (Paskewitz and McPherson 1983), *Esperanza texana* Barber (Wheeler and Henry 1984), *Harmostes* (*Harmostes*) *reflexulus* (Say) (Yonke and Walker 1970a, b), *Liorhyssus hyalinus* (F.) (Cornelis et al. 2012), *Niesthrea louisianica* Sailer (Wheeler 1977), *Rhopalus* (*Brachycarenus*) *tigrinus* (Schilling) (Wheeler and Hoebeke 1988) and *R.* (*Rhopalus*) *parumpunctatus* Schill. (Stroyan 1954), and *Xenogenus gracilis* Reed (Diez and Coscarón 2015).

Eggs may be parasitized by Hymenoptera in the *Telenomus podisi* (Ashmead) group (Cornelis et al. 2012).

In tribe Harmostini, the attachment stalk is not developed. *Harmostes reflexulus* (Say) lays one to four eggs on the floral pappi of Asteraceae. Eggs require about 8 days to hatch over an average month-long oviposition period (Yonke and Walker 1970a, b).

The ovoid eggs of Niesthreini are deposited in small loose clusters (Vilímová and Rohanová 2010) and have hexagonal surface reticulation on the chorion (Paskewitz and McPherson 1983). Within this group the pseudoperculum ranges from well defined (e.g., *Niesthrea louisianica* Sailer) to poorly defined [e.g., *Arhyssus* Stål and *N. sidae* (F.)]. Each egg is attached by a thin, short strand protruding from the dorsal side; whether this is homologous with egg stalks in Chorosomatini is uncertain (Paskewitz and McPherson 1983; Vilímová and Rohanová 2010). Overwintered *N. louisianica* oviposit on the undersides of leaves in spring; successive generations oviposit on flower pedicels as buds develop and fruits and seeds become more abundant. As many as 1,000 eggs may be laid by a single female (Wheeler 1977).

Vilímová and Rohanová (2010) regard the egg characteristics of subfamily Serinethinae as derived relative to the Rhopalinae. Rather than just two micropylar processes, 6–45 are present, arranged in one or two broad circles. At least two *Jadera* species, *J. choprai* Göllner-Scheiding and *J. haematoloma* (Herrich-Schaeffer), exhibit a rare oviposition behavior, burying their nearly round eggs in a hole they dig in the soil using their forelegs (Carroll 1988, 1991; Panizzi et al. 2002). *J. choprai* nymphs are able to emerge even when extra soil is deposited on top of the eggs (Panizzi et al. 2002). These authors speculated that burying may deter predation and prevent desiccation. Burying eggs may be more widespread within the genus, but is not universal. For example, *J. obscura* (Westwood) and *J. coturnix* (Burmeister) feeding on host vines in the canopy drop their eggs to the ground. This oviposition coincides with the dehiscence of host seeds from the canopy to the forest floor [Wolda and Tanaka 1987; Tanaka and Wolda 1987 (as *J. aeola*)].

20.3.2 Nymphal Feeding and Development

Little is known about the biology of juvenile tropical rhopalines. In the Nearctic, bivoltine *Arhyssus lateralis* (Say) develops during the summer months and requires about 40 days to mature (Paskewitz and McPherson 1983). *Niesthrea louisianica* matures in about 25 days (Wheeler 1977), and *Harmostes reflexulus* requires 22 days to eclose after hatching, with most time in the 1st and 5th instars (4.7 and 6.7 days, respectively; Yonke and Walker 1970a, b).

More is known about nymphal feeding and development in Neotropical serinethines. Nymphs of *Jadera choprai* in southern Brazil feed and develop on the sapindaceous weedy balloon vine, *Cardiospermum halicacabum* (L.) (Panizzi and Hirose 2002; Panizzi et al. 2002, 2005), which is common among row crops (Lorenzi 2000). In the laboratory more than 75 % of nymphs complete development on mature balloon vine seeds, with nymphs reared in groups surviving better. Group rearing also speeds development time (average 35 days in groups, 40 days alone; Panizzi et al. 2005). Often, groups of nymphs are found feeding on a single seed, forming a cluster around the seed; the many stylet sheaths left behind after each feeding session are visible on the seed surface (Fig. 20.2a, b). These authors also provide a detailed description of the eggs and nymphs of this species. Similarly, *J. obscura* on Barro Colorado Island in Panama develop over a 5–6-week span, feeding on seeds of sapindaceous canopy and light gap lianas in aggregations that may exceed a million individuals in number (Wolda and Tanaka 1987; Carroll and Loye 1987). Wolda and Tanaka (1987) described nymphal development of this species in detail.

Jadera haematoloma, which ranges from the United States to South America and has been accidentally introduced to Hawaii and Taiwan, develops on ten or more native and introduced sapinds (Carroll and Loye 2012). Development time is similar

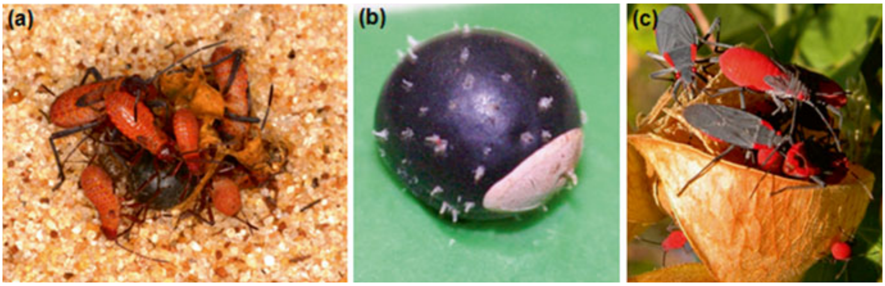

Fig. 20.2 Rhopalid bug nymphs and adults feeding on a single mature host fruit or seed; (**a**) nymphs of *Jadera choprai* feeding on a mature seed of the balloon vine *Cardiospermum halicacabum*; (**b**) mature seed of *C. halicacabum* showing stylet sheaths left on the seed integument after each feeding session (Photos AR Panizzi); (**c**) nymphs and adults of *Jadera haematoloma* on the dehiscent fruit of the balloon vine *Cardiospermum corundum.* Clusters of feeding nymphs may completely cover a seed, forming a bright red "ball of bugs" around it (Photo SP Carroll)

to that reported for other *Jadera.* In Florida, USA, this native insect, after adopting an invasive Asian ornamental tree as a host in Florida in the mid-twentieth century, has evolved to a remarkable degree in many traits, including egg size, developmental ability, and the length of mouthparts used in feeding on host seedpods (Carroll and Boyd 1992; Carroll et al. 1997, 1998, 2003a). Experiments rearing bugs from both hosts on either native or nonnative host seeds indicate that the offspring of early colonists from the native balloon vine host probably survived and developed poorly on the introduced tree at the time they first colonized it but now exploit that host with an efficiency similarly to which their ancestors from the native host showed on the native host. The derived population on the tree has, however, lost its ability to perform well on the native host (Carroll et al. 1998). Ironically, the most detailed description of the nymphal stadia of this species is in a beautifully complete review of the species by Tsai et al. (2013), based on observations of the recently introduced population in Taiwan. Nymphs and adults of *J. haematoloma* cluster on seeds of the balloon vine *Cardiospermum corundum* (L.) forming a bright red “ball of bugs” around it (Fig. 20.2c).

20.3.3 Adult Feeding and Reproduction

In contrast to rhopalines, fewer serinethines enter temperate latitudes, although the two New World *Boisea* are largely temperate (Carroll and Loye 2012). *Boisea trivittata* (Say) enters tropical latitudes in eastern Mexico, where its patchy highland distribution matches that of its otherwise north temperate host tree, *Acer negundo* L. Globally, sapinds in the widely distributed balloon vine genus *Cardiospermum* L. are the most commonly used, though many others among the over 150 sapind genera and close to 2,000 species are also exploited, particularly in the Paleotropics, by the third serinethine genus *Leptocoris* Hahn (Carroll and Loye 2012). The Neotropical sapind flora is distinctive in that the 500 species of sapind lianas in the five genera *Cardiospermum*, *Paullinia* L., *Serjania* Mill., *Thinouia* Planch. & Triana, and *Urvillea* Kunth constitute 60 % of regional family diversity and >25 % of the world family diversity (Acevedo-Rodríguez et al. 2011). The majority of the native host records for *Jadera* (the principal Neotropical serinethine) are from these genera, suggesting that much of the diversification of *Jadera* has occurred in association with these host radiations (Carroll and Loye 2012).

Adult feeding and reproduction of *J. choprai* has been extensively studied. In the laboratory, on mature seeds of the balloon vine *C. halicacabum*, males lived on average for 86.6 days, while females lived for 47.7 days; average fecundity (number of eggs/female) was 146.4 eggs and egg hatchability 85.3 % (Panizzi et al. 2005). *J. haematoloma* in Florida has similar vital statistics, but lays about twice as many eggs in captivity (Carroll et al. 1998, 2003b). Both species are flight and wing polymorphic. In *J. haematoloma*, there are four types, which in females are long-winged flyers that retain the flight muscles after mating (and presumably feeding), long-winged flyers that histolyze the muscles after feeding and mating, long-winged bugs that do not develop flight muscles, and short-winged bugs that do not develop flight muscles (Dingle and Winchell 1997). The flight morphs differ in life history, with flying individuals, which tend to be larger, having a much later age of first reproduction, while flightless bugs become reproductive within a few days of eclosion if food is present. Histolyzing bugs represent an intermediate state in terms of reproductive options, and flight morph frequencies appear to be evolving in populations on introduced hosts that differ from the native hosts in the spatial and temporal availability of seeds (Carroll et al. 2003b).

A risk of flightlessness in *J. haematoloma* and likely other *Jadera* is that flightless individuals are not capable of physiological diapause in the absence of food (Carroll et al. 2003b). Thus, the reproductive life span of congenitally flightless individuals depends on the persistence of seeds within a highly circumscribed locale. Temperate populations of this species in the central United States enter a photoperiodic diapause as day length declines in advance of the winter season. In subtropical Florida, seeds of *Cardiospermum* are available most of the year but are locally sporadic depending on plant phenology and the activities of the multi-taxon community of seed predators (Carroll et al. 2003b; Carroll and Loye 2006). Flight-capable adults there do not diapause in response to shortening day length but, in addition to being able to fly in search of more productive sites, are also able to enter a starvation-based diapause that will be advantageous during periods of low seed availability at local and regional scales (sensu Dingle 1972; Dingle and Arora 1973).

On Barro Colorado Island in Panama, *J. obscura* and *J. coturnix* diapause during much of the year due to rather synchronous seed predation in their primary liana hosts (Wolda and Tanaka 1987; Tanaka and Wolda 1987). During this period, *J. obscura*, which is entirely volant, travels the understory in swarms that may exceed 100,000 individuals, taking moisture from the leaves of small nonhost trees. *J. coturnix* (which is often referred to by the invalid name *J. aeola*) similarly diapauses and then produces two generations during the late dry season (Tanaka and Wolda 1987). The first generation is produced by volant adults coming out of a 10-month dormancy. They aggregate on newly mature host seeds and oviposit around those hosts. The developing offspring then consume much of that year's seed crop, and upon emerging as adults many fly to sheltered locations, aggregating beneath understory leaves to await for the next year's seeds. A subset of the bugs however emerges as small, short-lived, but highly fecund flightless and short-winged individuals that will neither migrate nor diapause, but instead quickly feed on remnant seeds, mate, and oviposit. All resulting offspring in laboratory trials were long winged, suggesting that the risky tactics of producing a subset of obligatorily reproductive individuals that are incapable of diapausing are coordinated to produce diapausing offspring (Tanaka and Wolda 1987). Circumstances permitting lineages that succeed in completing this extra cycle could potentially greatly out-reproduce lineages constrained to the more conservative tactic with a single annual generation.

In summary, diapausing aggregations that may reach enormous numbers are a common feature of volant adult serinethines, whether the diapause is induced by photoperiod in cold winter areas, by predictable food shortages when host seed production is highly seasonal, or during periods of food shortage that are not as predictable (Fig. 20.3). Both New World *Jadera* and Old World *Leptocoris* commonly cluster beneath the green leaves of hosts or other nearby plants for weeks to many months in advance of the next period of seed production (Tanaka and Wolda 1987; Wolda and Tanaka 1987; Tanaka et al. 1987; Carroll et al. 2005; Zych 2010). Densities may reach up to 500 bugs/leaf (Wolda and Tanaka 1987). These and especially the third soapberry bug genus, *Boisea*, are renowned nuisance pests in many regions based on their propensity to aggregate and to enter homes in large numbers (e.g., Schowalter 1986, Fig. 20.3). This behavior of serinethines may not have been reported in the Neotropics.

While diapause is less well studied in the subfamily Rhopalinae, there is evidence of diapause in temperate populations of rhopalines with partially Neotropical ranges. In the Niesthreini, this includes *N. louisianica* Wheeler (1977) and *A. lateralis*, Readio (1928), and in the Harmostini *H. reflexulus* (Yonke and Walker 1970a).

Fig. 20.3 Adult *Boisea trivittata* aggregate during nonreproductive periods and may inhabit buildings in large numbers (Photo courtesy of Jodi Green under Creative Commons https://creativecommons.org/licenses/by-nc-nd/2.0/)

20.4 Classification and Diversity

A key to the subfamilies, tribes, and genera of Rhopalidae in the Neotropics is shown below (Chopra (1967), revised by Froeschner (1981) and used by Pall and Coscarón (2012); authors have added *Stictopleurus*).

1 Lateral margin of the pronotum with a distinct notch delimiting the collar posteriorly. Suture between visible abdominal segments III and IV as strong and deep as suture between sternites IV and V. Subfamily Serinethinae ....*Jadera* Stål

Lateral margins of the pronotum not notched immediately posterior to collar. Suture between visible abdominal segments III and IV much shallower and weaker than other sutures. Subfamily Rhopalinae Amyot and Serville................2

2(1) Posterior femur thicker than the median or anterior femora, ventrally with several strong spines..3

Posterior femur not thicker than the anterior or median femora, no spines ventrally..4

3(2) Anterolateral angle of the pronotum produced anteriorly as an acute tooth. Clypeus acutely projecting beyond the juga. Tribe Harmostini Stål ....*Harmostes* Burmeister

Anterolateral angle of the pronotum not produced. Clypeus bluntly rounded apically, not or slightly (less than own width) surpassing the juga. Tribe Chorosomini Douglas and Scott..*Xenogenus* Berg

4(3). Phragma at junction of the first and second abdominal terga poorly developed in males, absent in females; the apodeme of the seventh sternum very small in males, absent in females. Phallus with one dorsomedian lobe on theca. Rhopalini Amyot and Serville..5

Phragma at junction of the first and second abdominal terga moderately developed in males, absent in females; the apodeme of the seventh sternum well developed in males, absent in females. Phallus with a pair of dorsolateral lobes on the theca. Niesthreini Chopra...6

5(4) Metapleura divided and metathoracic scent gland openings not reduced. Three pairs of asymmetrical, sclerotized, lateral, conjunctival appendages*Liorhyssus* Stål

Metapleura undivided and reduced metathoracic scent gland openings, absence of the left distal lateral conjunctival appendage.....................*Stictopleurus* Stål

6(5) Last connexival segment dorsally with an inconspicuous oblique suture setting off lateral basal angle (generally, the membrane must be lifted to see this suture). Labium not surpassing the posterior coxae.....................*Arhyssus* Stål

Last connexival segment without a dividing suture. Labium reaching or surpassing the third abdominal sternite................................*Niesthrea* Spinola

The number of rhopalid species in the different ecoregions is referred on Table 20.1 (Göllner-Scheiding 1997). For the Neotropics, the following eight genera and 80 species are recorded (Table 20.2 lists references and resident countries for each species below):

Table 20.2 References and resident countries for nine genera and 81 species and three subspecies of rhopalids from the Neotropics

Subfamily: Rhopalinae
Tribe: Chorosomatini (Fieber)
Genus: *Xenogenus* Berg
gracilis (Reed)
Distribution: Argentina, Chile, South America
References: Göllner-Scheiding (1983), Pall and Coscarón (2012), Pall et al. (2013), Diez and Coscarón (2015)
picturatum Berg http://heteroptera.myspecies.info
Distribution: Argentina, Bolivia, Cuba, Mexico, Nicaragua, Puerto Rico, Saint Vincent, Uruguay, Central and South America
References: Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Coscarón (1998), Carpintero and De Biase (2011), Dellapé and Carpintero (2012), Pall and Coscarón (2012), Pall et al. (2013), Diez and Coscarón (2015)
Tribe: Harmostini
Genus: *Aufeius* Stål
impressicollis Stål
Distribution: Guatemala, Mexico
References: Göllner-Scheiding (1983)
Genus: *Harmostes* Burmeister
Subgenus: *Harmostes* Burmeister
angustatus Van Duzee
Distribution: Mexico
References: Göllner-Scheiding (1983), Henry (1988)
bilobatus Melo & Montemayor
Distribution: Argentina
References: Melo and Montemayor (2011)
brevispinus Blöte
Distribution: Argentina, Bolivia
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
disjunctus Barber
Distribution: Ecuador
References: Göllner-Scheiding (1983)
dorsalis Burmeister
Distribution: Argentina, Guatemala, Mexico, Nicaragua, Peru, from British Columbia to Argentina/Peru

(continued)

Table 20.2 (continued)

References: Blöte (1934), Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Pall and Coscarón (2012)
enatus Brailovsky & Soria
Distribution: Mexico
References: Brailovsky and Soria (1981)
formosus Distant
Distribution: Mexico
Reference: Göllner-Scheiding (1983)
fraterculus (Say)
Distribution: Mexico, Central and South America
References: Göllner-Scheiding (1983), Henry (1988)
fusiformis Harris
Distribution: Peru
References: Göllner-Scheiding (1983)
gravidator (F.)
Distribution: Argentina, Mexico, Central and South America (Argentina, Bolivia, Brazil, Colombia, Peru, Venezuela)
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
incisuratus Distant
Distribution: Brazil, Chile, Colombia, Peru
Göllner-Scheiding (1983)
nebulosus Stål
Distribution: El Salvador, Guatemala, Mexico, Nicaragua, Panama, Central America
References: Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993)
parafraterculus Göllner-Scheiding
Distribution: Argentina, Brazil
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
paraprolixus Göllner-Scheiding
Distribution: Bolivia
References: Göllner-Scheiding (1998)
prolixus Stål
Distribution: Argentina, Bolivia, Brazil, Mexico, Paraguay, Peru, Uruguay, South America (Argentina, Bolivia, Brazil, Paraguay, Peru, Uruguay)
References: Göllner-Scheiding (1983), Melo et al. (2011), Dellapé and Carpintero (2012), Pall and Coscarón (2012), Pall et al. (2013)
reflexulus (Say)
Distribution: Cuba, Mexico
References: Göllner-Scheiding (1983)
rubrum Melo & Montemayor http://heteroptera.myspecies.info
Distribution: Argentina
References: Melo and Montemayor (2011)
serratus (F.)

(continued)

Table 20.2 (continued)

Distribution: Argentina, Bolivia, Brazil, Costa Rica, Cuba, Dominican Republic, Ecuador, El Salvador, Guatemala, Honduras, Jamaica, Lesser Antilles, Mexico, Nicaragua, Panama, Paraguay, Puerto Rico, Venezuela, West Indies, Central and South America
References: Blöte (1934), Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Melo et al. (2011), Dellapé and Carpintero (2012), Pall and Coscarón (2012)
signoreti Reed
Distribution: Argentina, Chile
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
splendens Harris
Distribution: Argentina, Bolivia, Brazil, Paraguay
References: Göllner-Scheiding (1983) (Melo and Montemayor, personal communication)
Subgenus: *Neoharmostes* Göllner-Scheiding
apicatus Stål
Distribution: Mexico, South America (Argentina, Bolivia, Brazil, Chile, Paraguay, Uruguay)
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
bergi Göllner-Scheiding
Distribution: Argentina, Bolivia
References: Göllner-Scheiding (1998), Melo and Montemayor (personal communication)
confinis Harris 1942
Distribution: Chile
References: Göllner-Scheiding (1983)
corazonus Distant
Distribution: Argentina, Chile, Ecuador, Peru
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
corizoides Jensen-Haarup
Distribution: Argentina, Uruguay
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
imitabilis Harris
Distribution: Argentina
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
insitivus Harris
Distribution: Argentina, Chile
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
marmoratus (Blanchard)
Distribution: Argentina, Bolivia, Chile, Peru
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
minor (Spinola)
Distribution: Argentina, Chile
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
petulans Harris
Distribution: Argentina, Bolivia, Peru, Uruguay

(continued)

Table 20.2 (continued)

References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
procerus Berg http://heteroptera.myspecies.info
Distribution: Argentina, Brazil, Peru, Uruguay, Patagonia
References: Göllner-Scheiding (1983), Coscarón (1998), Marrero et al. (2008), Carpintero (2009), Carpintero and De Biase (2011), Melo et al. (2011), Cava et al. (2012), Dellapé and Carpintero (2012), Pall and Coscarón (2012)
Tribe: Niesthreini
Genus: *Arhyssus* Stål
confusus Chopra
Distribution: Mexico
References: Göllner-Scheiding (1983)
lateralis (Say)
Distribution: Guatemala, Mexico
References: Göllner-Scheiding (1983), Henry (1988)
parvicornis (Signoret)
Distribution: Costa Rica, Mexico, Paraguay, Utah to Costa Rica
References: Nickel (1958), Göllner-Scheiding (1983), Henry (1988)
peruensis Chopra, 1968
Distribution: Peru
References: Göllner-Scheiding (1983)
pilosus (Signoret)
Distribution: Venezuela
References: Göllner-Scheiding (1983)
punctatus (Signoret)
Distribution: Guatemala, Honduras, Mexico, Nicaragua, Panama, Colorado to Honduras
References: Göllner-Scheiding (1983), Henry (1988), Maes and Göllner-Scheiding (1993)
slateri Chopra
Distribution: Mexico
References: Göllner-Scheiding (1983)
tricostatus (Spinola)
Distribution: Argentina, Chile
References: Göllner-Scheiding (1983), Melo and Montemayor (personal communication)
validus (Uhler)
Distribution: Mexico
References: Göllner-Scheiding (1983)
Genus: *Niesthrea* Spinola
agnes Chopra
Distribution: Argentina
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
ashlocki Froeschner

(continued)

Table 20.2 (continued)

Distribution: Ecuador
References: Froeschner (1989), Henry and Wilson (2004)
brevicauda Chopra
Distribution: Peru
Göllner-Scheiding (1983)
dentatus Chopra
Distribution: Brazil
References: Göllner-Scheiding (1983)
dignus Chopra
Distribution: Brazil
References: Göllner-Scheiding (1983)
fenestratus (Signoret)
Distribution: Chile
References: Göllner-Scheiding (1983)
josei Göllner-Scheiding
Distribution: Argentina
References: Pall and Coscarón (2012)
louisianica Sailer
Distribution: Mexico
References: Göllner-Scheiding (1983)
pictipes (Stål)
Distribution: Argentina, Brazil, Ecuador, Mexico, Paraguay
References: Froeschner (1981), Göllner-Scheiding (1983), Carpintero and De Biase (2011), Dellapé and Carpintero (2012), Pall and Coscarón (2012)
pictipes casinii Göllner-Scheiding
Distribution: Argentina, Uruguay
References: Göllner-Scheiding (1984)
sidae (F.)
Distribution: Columbia, Ecuador, Mexico, Nicaragua, Panama, Puerto Rico, Venezuela, Caribbean, Central America, South America, and West Indies
References: Blöte (1934), Göllner-Scheiding (1983), Maes and Tellez (1988), Henry (1988), Maes and Göllner-Scheiding (1993), Henry and Wilson (2004)
similis Chopra
Distribution: Argentina, Brazil
References: Göllner-Scheiding (1983), Melo et al. (2011), Pall and Coscarón (2012)
ventralis (Signoret)
Distribution: Guatemala, Mexico, Nicaragua, Texas to Guatemala
References: Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993)
vincentii (Westwood)
Distribution: Argentina, Brazil, Paraguay, Venezuela, West Indies
References: Blöte (1934), Göllner-Scheiding (1983), Pall and Coscarón (2012)
Tribe: Rhopalini
Genus: *Liorhyssus* Stål

(continued)

Table 20.2 (continued)

hyalinus (F.)
Distribution: Argentina, Chile, Cuba, Guatemala, Mexico, Nicaragua, Venezuela, Patagonia, all the world
References: Dallas (1852) as *Rhopalus ruber* Dallas, Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Hernandez (1994), Cermeli et al. (2004), Werner (2009), Carpintero and De Biase (2011), Dellapé and Carpintero (2012), Pall and Coscarón (2012)
kaltenbachi Göllner-Scheiding
Distribution: Bolivia, Brazil, Paraguay
References: Göllner-Scheiding (1983)
lineatoventris (Spinola)
Distribution: Argentina, Chile, Ecuador
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
Genus: *Stictopleurus* Stål
knighti Harris
Distribution: Mexico
References: Göllner-Scheiding (1983)
punctiventris (Dallas)
Distribution: Mexico
References: Henry (1988)
Subfamily: Serinethinae
Genus: *Jadera* Stål
aeola (Dallas)
Distribution: Brazil, Antilles, from Mexico to Argentina
References: Göllner-Scheiding (1983), Barcellos et al. (2008), Pall and Coscarón (2012)
Note: see *coturnix*
aeola aeola (Dallas)
Distribution: Argentina, Guatemala, Mexico, Nicaragua, Caribbean, from Mexico to Argentina
References: Göllner-Scheiding (1979), no distributional information Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Carpintero and De Biase (2011), Melo et al. (2011), Pall and Coscarón (2012)
aeola rufoculis (Kirby, 1890)
Distribution: Brazil
References: Göllner-Scheiding (1983)
antica (Walker)
Distribution: Dominican Republic, West Indies
References: Göllner-Scheiding (1983)
bayardae Göllner-Scheiding
Distribution: British Honduras, Guatemala, Mexico, Panama, from Mexico to Panama
References: Göllner-Scheiding (1983), Henry (1988), Colombia SPC personal observation (2011)
choprai Göllner-Scheiding
Distribution: Argentina, Bolivia, Brazil, Paraguay, Uruguay, South America

(continued)

Table 20.2 (continued)

References: Göllner-Scheiding (1979), Göllner-Scheiding (1983), Carpintero and De Biase (2011), Pall and Coscarón (2012)
coturnix (Burmeister)
Distribution: Brazil, Uruguay
Note: According to Göllner-Scheiding (1979) *coturnix* (Burmeister) is a synonym of *aeola* (Dallas). Henry (1988) lists each as separate species; we have followed Henry (1988) and the Coreoidea Species File which consider *coturnix* a valid species
decipiens Göllner-Scheiding
Distribution: Argentina, Brazil, West Indies
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
diaphona Göllner-Scheiding
Distribution: Mexico, Nicaragua, Panama
References: Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993)
golbachi Göllner-Scheiding
Distribution: Argentina, Bolivia, Ecuador
References: Göllner-Scheiding (1983), Pall and Coscarón (2012)
haematoloma (Herrich-Schäffer)
Distribution: Argentina, Belize, Cuba, Colombia, Guatemala, Mexico, Nicaragua, Uruguay, from Central America to Colombia and Venezuela, West Indies
References: Göllner-Scheiding (1983), Maes and Téllez (1988), Maes and Göllner-Scheiding (1993), Bressa et al. (2001), Pall and Coscarón (2012)
harrisi Göllner-Scheiding
Distribution: Bolivia, Brazil
References: Göllner-Scheiding (1979)
obscura (Westwood)
Distribution: Argentina, Brazil, Costa Rica, from Mexico to Argentina/Peru
References: Blöte (1934), Göllner-Scheiding (1983), Carroll and Loye (1987), Pall and Coscarón (2012)
parapectoralis Göllner-Scheiding
Distribution: Argentina, Brazil
References: Göllner-Scheiding (1983), Schaefer (2001), Carpintero and De Biase (2011), Pall and Coscarón (2012)
pectoralis Stål
Distribution: Bolivia, Brazil, Uruguay
References: Göllner-Scheiding (1983)
peruviana Göllner-Scheiding
Distribution: Peru
References: Göllner-Scheiding (1983)
pyrrholoma Stål
Distribution: Bolivia, Brazil, Colombia, Ecuador
References: Göllner-Scheiding (1983)
sanguinolenta (F.)
Distribution: Argentina, Belize, Cuba, Ecuador, Nicaragua, Paraguay, Puerto Rico, St. Croix, Culebra, St. John, St. Thomas, Uruguay
References: Heidemann (1901), Barber (1923) as *Jadera rubrofusca*, Göllner-Scheiding (1983), Maes and Göllner-Scheiding (1993), Bressa et al. (2001), Carpintero (2009), Pall and Coscarón (2012), personal observation Scott Carroll (1987)

(continued)

Table 20.2 (continued)

schuhi Göllner-Scheiding
Distribution: Venezuela
References: Göllner-Scheiding (1983)
silbergliedi Froeschner
Distribution: Galápagos Islands
References: Froeschner (1985)
similaris Göllner-Scheiding
Distribution: Ecuador
References: Göllner-Scheiding (1983)
Genus: *Boisea* Stål
trivittata (Say)
Distribution: Mexico
References: Scott Carroll personal observation (2011) (new record for the Neotropical region)

Note: Geographic distribution was taken into account from Göllner-Scheiding (1983) and posterior publications. The classification follows Coreoidea Species File (http://Coreoidea.SpeciesFile.org/)

Family: Rhopalidae
Subfamily: Rhopalinae
Tribe: Chorosomatini (Fieber)
Genus: *Xenogenus* Berg
gracilis Reed
picturatum Berg
Tribe: Harmostini
Genus: *Aufeius* Stål
impressicollis Stål
Genus: *Harmostes* Burmeister
Subgenus: *Harmostes* Burmeister
angustatus Van Duzee
bilobatus Melo & Montemayor
brevispinus Blöte
disjunctus Barber
dorsalis Burmeister
enatus Brailovsky & Soria
formosus Distant
fraterculus (Say)
fusiformis Harris
gravidator (F.)
incisuratus Distant
nebulosus Stål
parafraterculus Göllner-Scheiding

(continued)

- *paraprolixus* Göllner-Scheiding
- *prolixus* Stål
- *reflexulus* (Say)
- *rubrum* Melo & Montemayor
- *serratus* (F.)
- *signoreti* Reed
- *splendens* Harris
- Subgenus: *Neoharmostes* Göllner-Scheiding
  - *apicatus* Stål
  - *bergi* Göllner-Scheiding
  - *confinis* Harris
  - *corazonus* Distant
  - *corizoides* Jensen-Haarup
  - *imitabilis* Harris
  - *insitivus* Harris
  - *marmoratus* (Blanchard)
  - *minor* (Spinola)
  - *petulans* Harris
  - *procerus* Berg
- Tribe: Niesthreini
  - Genus: *Arhyssus* Stål
    - *confusus* Chopra
    - *lateralis* (Say)
    - *parvicornis* (Signoret)
    - *peruensis* Chopra
    - *pilosus* (Signoret)
    - *punctatus* (Signoret)
    - *slateri* Chopra
    - *tricostatus* (Spinola)
    - *validus* (Uhler)
  - Genus: *Niesthrea* Spinola
    - *agnes* Chopra
    - *ashlocki* Froeschner
    - *brevicauda* Chopra
    - *dentatus* Chopra
    - *dignus* Chopra
    - *fenestratus* (Signoret)
    - *josei* Göllner-Scheiding
    - *louisianica* Sailer
    - *pictipes* (Stål)
    - *pictipes casinii* Göllner-Scheiding
    - *sidae* (F.)
    - *similis* Chopra
    - *ventralis* (Signoret)

(continued)

- *vincentii* (Westwood)
- Tribe: Rhopalini
  - Genus: *Liorhyssus* Stål
    - *hyalinus* (F.)
    - *kaltenbachi* Göllner-Scheiding
    - *lineatoventris* (Spinola)
  - Genus: *Stictopleurus* Stål
    - *punctiventris* (Dallas)
    - *knighti* Harris
- Subfamily: Serinethinae
  - Genus: *Jadera* Stål
    - *aeola* (Dallas)
    - *aeola aeola* (Dallas)
    - *aeola rufoculis* (Kirby)
    - *antica* (Walker)
    - *bayardae* Göllner-Scheiding
    - *choprai* Göllner-Scheiding
    - *coturnix* (Burmeister)
    - *decipiens* Göllner-Scheiding
    - *diaphona* Göllner-Scheiding
    - *golbachi* Göllner-Scheiding
    - *haematoloma* (Herrich-Schäffer)
    - *harrisi* Göllner-Scheiding
    - *obscura* (Westwood)
    - *parapectoralis* Göllner-Scheiding
    - *pectoralis* Stål
    - *peruviana* Göllner-Scheiding
    - *pyrrholoma* Stål
    - *sanguinolenta* (F.)
    - *schuhi* Göllner-Scheiding
    - *silbergliedi* Froeschner
    - *similaris* Göllner-Scheiding
  - Genus: *Boisea* Stål
    - *trivittata* (Say)

20.4.1 Main Species

***Harmostes reflexulus* (Say)**

This is considered the most common *Harmostes* in the Nearctic by Blatchley (1926). In Göllner-Scheiding's (1978) revision of the genus, she lists its range as extending into Mexico and Cuba.

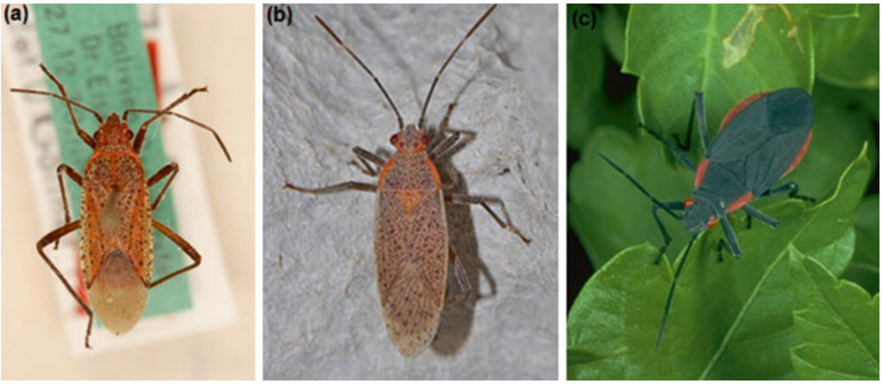

Fig. 20.4 (**a**) Adult of *Jadera choprai*, (**b**) *Jadera coturnix*, and (**c**) *Jadera haematoloma*

In Missouri it is a bivoltine species that feeds on many Asteraceae, and its seasonal migration follows a procession of maturing blooms throughout the summer (Yonke and Walker 1970a). Of their field-captured adults, 15.7 % were parasitized by the fly *Leucostoma acirostre* Reinhard.

Relevant literature: Van Duzee (1909) distribution in Florida, Yonke and Walker (1970a) life history, and Yonke and Walker (1970b) description of the egg and nymphs.

Jadera choprai Göllner-Scheiding (Fig. 20.4a)

An abundant species in the Neotropics. Many museum specimens have been misidentified as *J. sanguinolenta*. About 8–12 mm in length. They are larger and more orange in color than *J. sanguinolenta*, *J. decipiens*, and *J. goldbachi*. They are recognized by ocher-orange dorsal sides marked with irregular spots. The head and scutellum are orange (the head sometimes brown). The ventral side is ocher. Appendages are dark brown.

J. choprai preys on the seeds of *Cardiospermum corindum* as well as *Cardiospermum halicacabum* var. *halicacabum*. Like *J. haematoloma*, they have been observed carrying seeds (Panizzi and Hirose 2002).

Distribution: Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

Relevant literature: Göllner-Scheiding (1979) description, Panizzi et al. (2002) oviposition, and Panizzi and Hirose (2002) seed-carrying behavior.

Jadera coturnix (Burmeister) (Fig. 20.4b)

Most twentieth-century literature refers to this species as *aeola* after being designated by Kirby in 1852. However, Burmeister had already named it *coturnix* in 1835, giving the latter name priority. Göllner-Scheiding considers this species to be the most widely distributed *Jadera* (Göllner-Scheiding 1979). *J. coturnix* varies in size and color, typically brown with numerous dark spots and red lateral margins of the head and pronotum. Spots may form vertical lines, especially near the center of the head. Spots may be bigger on veins of hemelytra and on part of the membrane. About 8–13 mm in length. Appendages are brown. *J. coturnix* ocelli are much closer together than those of *J. hinnulea. J. coturnix* is a seed predator of sapindaceous vines and has been observed feeding on *Cardiospermum grandiflorum* L., *Paullinia sessiliflora* Radlk., *P. turbacensis* Kunth, *Serjania decaplueria* (Croat), *S. mexicana* L., and *Thinouia myriantha* (Tr. & Planch.).

Distribution: Mexico, Nicaragua, Panama, Ecuador, Brazil, Argentina, Puerto Rico, and Virgin Islands.

Relevant literature: Göllner-Scheiding (1979) description, (1983) general catalog, Tanaka and Wolda (1987) flight and life history polymorphism, and Carroll and Loye (2012) host records.

Jadera haematoloma (Herrich-Schäffer) (Fig. 20.4c)

This rhopalid is about 10–14 mm in length. It has a charcoal dorsal ground color with broad red lateral stripes on the sides of the head and pronotum (most distinct on the pronotum); the eyes are also red. The ventral side is dark except for margins of the abdomen and posterior segment, which are red. Appendages are black.

The red lateral margins on the pronotum and black dorsum resemble *J. diaphona* and *J. pyrrholoma*. The head of *J. haematoloma* is relatively wider than *J. pyrrholoma. J. haematoloma* is intermediate in size between these two species. Its charcoal and red abdomen help distinguish it from the uniformly orange-red abdominal venter of *J. diaphona*. The best diagnostic feature is the male genitalia, illustrations and descriptions for which are provided by Göllner-Scheiding (1979).

In addition to feeding on seeds, *J. haematoloma* also feeds opportunistically on vulnerable conspecifics (Carroll and Loye 1987). Comprehensive tables of host records are provided by (Carroll and Loye 2012). *J. haematoloma* aggregates in large numbers around hosts, competing for food and mates. Males guard their mates, by copulating until the onset of oviposition. During oviposition a male may stand on top of a female, fending off other males and re-copulating after all eggs are laid (Carroll 1988). Some populations are rapidly evolving in adaptation to introduced host plants (discussed above).

Distribution: Mexico, Guatemala, Nicaragua, Belize, Panama, Colombia, Venezuela, Uruguay, Argentina, Cuba, Puerto Rico, United States, Hawaii, and Taiwan (Tsai et al. 2013).

Relevant literature: Schaefer (1965), 10 (morphology, genitalia, figures); Göllner-Scheiding (1979), 57 (redescription, lectotype, genitalia, figures, distribution); Schaefer and Chopra (1982), 226 (morphology, host plants); Schaefer and Mitchell (1983), 593 (host plants); Mead (1985) (diagnostic characters, wing polymorphism, larva, photos, host plant, distribution, map, phenology, aggregation, impact on human, control); Carroll and Loye (1987), 373 (host plants, feeding, coevolution with host plants, aggregation, ecology, distribution, map); Carroll (1988), 54 (records, distribution, host plants, phenology, development, reproductive behavior, and ecology); Ribeiro (1989), 466 (records, host plant, aggregation, aposematism, development); Aldrich et al. (1990a), 200 (laboratory rearing, chemical ecology); Carroll (1991), 510 (reproductive behavior and ecology); Carroll and Boyd (1992), 1,053 (intraspecific variability, evolution); Carroll (1993), 156 (reproductive ecology); Carroll and Dingle (1996), 210 (records, host plants, feeding, intraspecific variability, evolution); Dingle and Winchell (1997), 365 (genetic and physiological control of wing polymorphism); Carroll et al. (1998), 956 (records, host plants, reproductive ecology, adaptation); Reinert et al. (1999), 469 (pest status, biological control); Winchell et al. (2000), 1,365 (wing polymorphism, physiology); Carroll et al. (2003b), S80 (genetic variation, selection); Carroll et al. (2003a), 135 (host plants, records, polymorphism); Dingle et al. (2009), 2,031 (genetic architecture, intraspecific variability, selection); Carroll and Loye (2012), 675 (host plants); Zych et al. (2012) (stridulation); and Tsai et al. (2013) (the most comprehensive review of the species and the source of this redacted reference list).

Liorhyssus hyalinus (F.) (Fig. 20.5a)

Worldwide and throughout the Neotropics (Göllner-Scheiding 1983), this species is distinguished by a hyaline membrane of the hemelytra extending beyond the abdomen. Its length is 5.5–6.5 mm and width 1.8–2.5 mm. Eggs are usually deposited in groups of 20–30 (Vilímová and Rohanová 2010). Early instars aggregate. Cornelis et al. (2012) detail nymphs, parasites, and hosts.

All life stages of *L. hyalinus* feed on *Sorghum vulgare* Pers., damaging crops in Venezuela (Cermeli et al. 2004). Cage experiments showed no significant damage to lettuce seed yield and germination until unnatural numbers of insects (400) and their nymphs fed on a single plant (Carlson 1959).

Distribution: Mexico, Guatemala, Nicaragua, Colombia, Venezuela, Ecuador, Chile, Argentina, Cuba, Grenada, and Puerto Rico.

Relevant literature: Readio (1928) (eggs, life history, host plants), Cermeli et al. (2004) (sorghum crop damage), Cornelis et al. (2012) (life history, nymphs, host plants, parasites), Davidova-Vilímová et al. (2000) (scent glands, systematics), and Carlson 1959 (effects on lettuce seed production).

Harmostes serratus F. (Fig. 20.5b)

Primarily a Neotropical species with range extending into the Southern United States (Göllner-Scheiding 1978, 1983). When viewed laterally it can be distinguished from other Harmostes by ventrally indented antenniferous tubercles. It can be distinguished from other *Harmostes* by the crenulate to serrate lateral margins of the thorax. The head is long with lateral spinous processes between the eyes and antennae, size 7–8 mm. long, and width 2.3–2.5 mm (Gibson 1917).

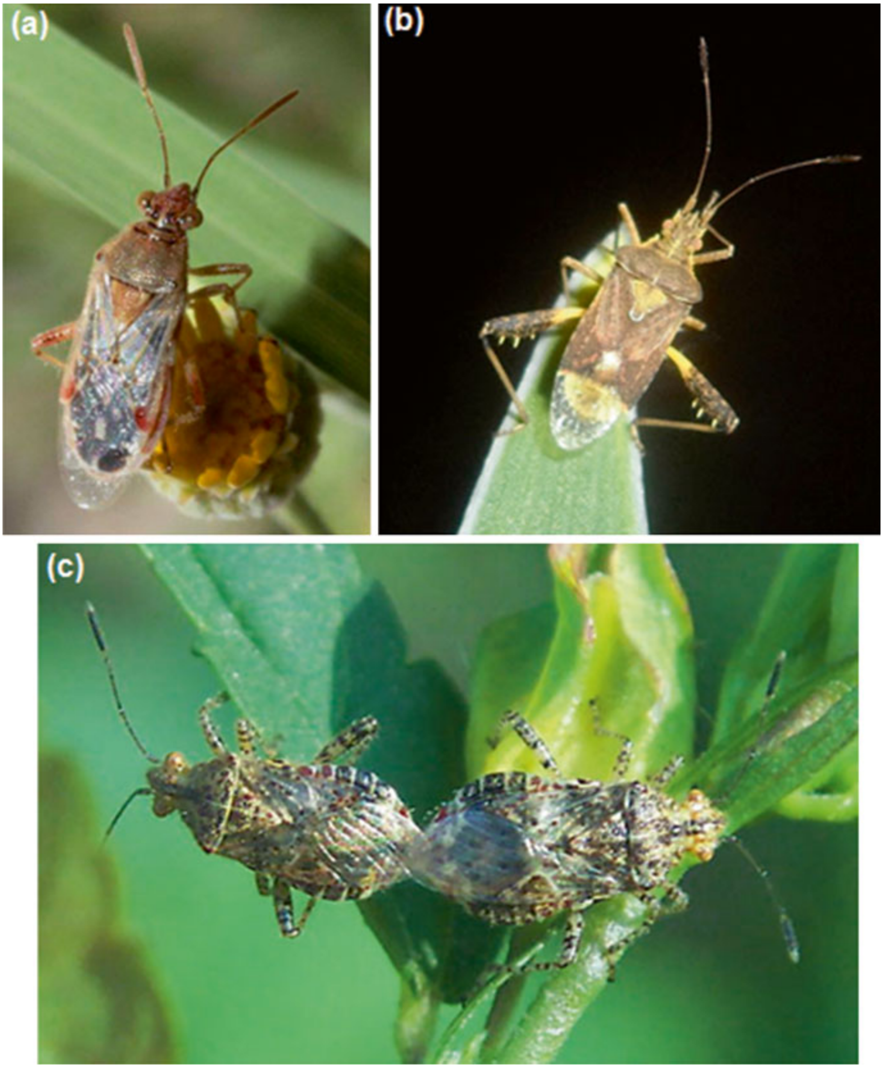

Fig. 20.5 (**a**) Adult of *Liorhyssus hyalinus* (Photo courtesy of L. Brehmer and E. Flores-Guevara), (**b**) *Harmostes serratus*, and (**c**) *Niesthrea sidae* (Courtesy of Hannah Mason)

H. serratus has been found feeding on *Dahlia* Cav. in several locations in Puerto Rico (Wolcott 1948).

Distribution: Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Brazil, Peru, Bolivia, Paraguay, Argentina, Cuba, Dominican Republic, Puerto Rico, Jamaica, and Trinidad and Tobago.

Relevant literature: Göllner-Scheiding (1978) (revision of the genus) and Gibson (1917) (the genus *Harmostes* Berm).

Niesthrea sidae (F.) (Fig. 20.5c)

This is the most widespread species in the genus and widely distributed in the Neotropics (Henry and Wilson 2004). Sailer (1961) first identified *N. sidae* and established it as the type specimen for the genus. He noted many museum specimens, and descriptions in the literature erroneously identify with *N. louisianica*, to which it is very similar. Chopra (1973) considers it a complex of highly variable local populations, which may contribute to the confusion. It is distinguished from *N. ashlocki* by the shorter parameres, by the less deeply convex apex of the medioventral lobe, and by the longer, denser pubescence of the head, pronotum, and legs (Sailer 1961; Henry and Wilson 2004).

It has been observed feeding on the malvaceous plants *Abutilon* Mill. and *Sida* L. (Wheeler 1977; Schaefer and Chopra 1982), as well as the fruit of the euphorb *Jatropha curcas* L. (Grimm and Führer 1998). Collections of *N. sidae* have been made on the leaves of *Lantana* L. and *Prosopis* L. (Palmer and Pullen 1995; Smith and Ueckert 1974), though these may be coincidental landings and not hosts.

Distribution: Mexico, Nicaragua, Panama, Colombia, Venezuela, Ecuador, Galápagos Islands, Brazil, Peru, Bolivia, Paraguay, Puerto Rico, and Grenada.

Relevant literature: Sailer (1961) designated lectotype, Chopra (1973) revised genus, Henry and Wilson (2004) description, and Galápagos record.

20.5 Concluding Remarks

Rhopalids belong to a small but widespread family that is important in both applied and basic entomology. Yet very little is known about the biology of most of its approximately 200 species. Ironically, while members the subfamily Serinethinae are commonly noted as nuisance pests because many species form large aggregations in domestic settings (e.g., Mead 1985), they are little studied from a practical perspective and instead are more commonly the subject of theoretically motivated studies in evolution and ecology (reviewed by Tsai et al. 2013). Genus *Jadera* is speciose and common throughout the Neotropics but has not been actively studied at low latitudes since the 1980s. In addition to the value that might derive from more pragmatically motivated studies of serinethines, investigations of contemporary evolution on introduced sapindaceous host plants, for which *Jadera* is well known in North America, could be logically expanded to South America.

Subfamily Rhopalinae is more diverse than Serinethinae at higher levels of classification (Chopra 1967), and four of the six rhopaline tribes occur in the Neotropics: Harmostini, Chorosomini, Rhopalini, and Niesthreini. Many of the species feed on reproductive tissues of Asteraceae, and others are associated with Malvaceae and Poaceae. In contrast to Serinethinae, none of the Rhopalinae are known to use sapindaceous plants as hosts.

The negative economic impacts of rhopalids appear to be limited. In Serinethinae they are related mainly to the nuisance of diapausing aggregations entering structures and occasional fruit spotting. Panizzi et al. (2002) suggested that the seed predation by *Jadera* species on weedy *Cardiospermum halicacabum* in cultivated soybean could be beneficial, and Carroll (2011) suggested that adaptation to this same plant in northern Australia wildlands by the serinethine *Leptocoris tagalicus* (Burmeister) could supply genotypes for the control of the congeneric Neotropical environmental weed *C. grandiflorum* in eastern Australia. Such considerations would benefit from further development. In Rhopalinae, *Liorhyssus* has been recognized as a pest of sorghum in Venezuela (Cermeli et al. 2004). Many rhopalines are small, cryptically colored, and furtive. It is possible that their presence on crops is underappreciated, and this too deserves additional consideration in field agriculture in the Neotropics.

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Chapter 21
Burrower Bugs (Cydnidae)

Cristiano F. Schwertner and Cristiane Nardi

Abstract Burrower bugs are typical pentatomoid insects, small to medium in size, recognized by the morphological adaptations for digging. However, some cydnids live aboveground or on vegetation, feeding on falling seeds or even plant tissues.

The family has a worldwide distribution, being well represented in tropical and temperate regions, known in the fossil record since at least the Late Cretaceous. Cydnidae includes more than 750 species in 93 genera, divided in six subfamilies. In the Neotropical region, 145 species are recorded and included in the subfamilies Amnestinae (38 spp.), Cephalocteinae (eight), Cydninae (97), and Sehirinae (one). The monophyly of the Cydnidae and phylogenetic relationships with other pentatomoid families are still controversial. Among the subfamilies, only Cephalocteinae has a strong support in a phylogenetic context. Burrower bugs are phytophagous and seem to be polyphagous, and although the group has been considered of little economic importance, damage to crops in the Neotropical region has been growing in the last 15 years. Because of the burrowing habits and small size of most of the species, people unnoticed its presence, limiting taxonomic characterization, host plants records, as well as damage and symptoms to cultivated plants. In this chapter, an overview of the group in the Neotropical region is presented, including an identification key for subfamilies and genera with the characterization of the commonest species.

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21.1 Introduction

The burrower bugs are typical pentatomoid insects, small to medium in size, and with a unique life habit among true bugs. Most of the species are recognized by the morphological adaptations for digging: wide and flattened head, legs with strong and long spines, and modified tibia and tarsi. These characteristics are more conspicuous in the species with fossorial habitats that feed on roots. However, some cydnids live aboveground or on vegetation, feeding on falling seeds or even plant tissues (Schuh and Slater 1995; Schaefer 2009).

The family has a worldwide distribution, being well represented in tropical and temperate regions (Froeschner 1960; Lis 1999a, 2002). It includes more than 750 species in 93 genera, divided in six subfamilies (Table 21.1) (Grazia et al. 2008; Pluot-Sigwalt and Lis 2008).

Cydnids were considered to be primitive pentatomoids (Schaefer 1968, 1981), despite the derived features associated with fossorial habits. Fossil Cydnidae have been assigned from the Mesozoic to Lower Miocene (Shcherbakov and Popov 2002; Grimaldi and Engel 2005). At least one extant cydnid subfamily, Amnestinae, is known from the Late Cretaceous and Early Jurassic (Yao et al. 2007) and represents part of the dominant land bug fauna during the Cretaceous (Shcherbakov and Popov 2002).

The monophyly of the group has been questioned (Grazia et al. 2008; Pluot-Sigwalt and Lis 2008), and the phylogenetic position among pentatomoids is still uncertain (Lis 2010). Some cydnids show maternal care of eggs and young (Agrawal et al. 2001, 2004; Nakahira and Kudo 2008; Filippi-Tsukamoto et al. 2008), a behavior also found in other related families (Filippi-Tsukamoto et al. 1995; Tallamy and Schaefer 1997).

Burrower bugs are phytophagous, and most of the species seems to be polyphagous (Froeschner 1960; Lis et al. 2000). Although the group has been considered of

Table 21.1 Number of extant genera and species of Cydnidae by subfamilies and tribes for the world and Neotropical region

	World		Neotropical (total[a])		Neotropical (endemic[b])	
Subfamily/Tribe	Gen	sp	Gen	sp	Gen	sp
Amaurocorinae	3	5	0	0	0	0
Amnestinae	2	38	2	38	1	35
Cephalocteinae	8	32	2	8	1	7
Cephalocteini	2	4	0	0	0	0
Scaptocorini	6	28	2	8	1	7
Cydninae	65	576	11	97	5	76
Cydnini	11	114	1	1	0	0
Geotomini	54	462	11	97	5	78
Garsauriinae	3	17	0	0	0	0
Sehirinae	12	72	1	1	0	0
Total	93	742	16	131	7	118

[a] Includes species with Nearctic distribution

[b] Includes species found only in the Neotropical region

little economic importance (Lis et al. 2000), damage to crops in the Neotropical region has been growing in the last 15 years (Oliveira et al. 2000, 2013). Lis et al. (2000) reviewed the species of economic importance, and since then, several studies have added new knowledge about the biology of the species associated to crops (e.g., Chapin and Thomas 2003; Oliveira and Malaguido 2004; Riis et al. 2005b; Chapin et al. 2006; Nardi et al. 2008; Vivan et al. 2013).

21.2 General Characteristics and Diagnosis

Size varying from 2 to 25 mm, color black or brown, usually with a glossy or shining surface (Figs. 21.1, 21.2, 21.3, 21.4, 21.5, and 21.6). Body ovoid and convex. Head quadrate or semicircular, wide, and often explanate (Figs. 21.7, 21.8, 21.9, and 21.10). Antenna 5-segmented. Scutellum never surpassing the middle of the

Fig. 21.1 *Amnestus pusio* (Stål) (Cydnidae: Amnestinae), dorsal view (Photo CF Schwertner)

Fig. 21.2 *Amnestus pusio* (Stål) (Cydnidae: Amnestinae), frontal view (Photo CF Schwertner)

Fig. 21.3 *Scaptocoris castanea* Perty (Cydnidae: Cephalocteinae: Scaptocorini), dorsal view (Photo CF Schwertner)

Fig. 21.4 *Scaptocoris castanea* Perty (Cydnidae: Cephalocteinae: Scaptocorini), lateral view (Photo CF Schwertner)

Fig. 21.5 *Cyrtomenus mirabilis* (Perty) (Cydnidae: Cydninae: Geotomini), dorsal view (Photo CF Schwertner)

Fig. 21.6 *Sehirus cinctus cinctus* (Palisot de Beauvois) (Cydnidae: Sehirinae), dorsal view (Photo CF Schwertner)

Fig. 21.7 *Amnestus pusio*, detail of the head (frontal view) (Photo CF Schwertner)

Fig. 21.8 *Scaptocoris castanea*, detail of the head (frontal view) (Photo CF Schwertner)

Fig. 21.9 *Cyrtomenus mirabilis*, detail of the head (dorsal view) (Photo CF Schwertner)

Fig. 21.10 *Sehirus cinctus cinctus*, detail of the head (frontal view) (Photo CF Schwertner)

Fig. 21.11 *Scaptocoris castanea*, median tibia (Photo CF Schwertner)

abdomen. Distal margins of coxae with a row of setae or bristles, known as coxal combs. Tibia with strong and long spines in all extension (Figs. 21.11, 21.12, 21.13, 21.14, and 21.15), anterior tibia usually compressed (Figs. 21.12, 21.14, 21.15);

Fig. 21.12 *Cyrtomenus teter*, anterior tibia (Photo CF Schwertner)

Fig. 21.13 *Sehirus cinctus cinctus*, posterior tibia (Photo CF Schwertner)

tarsi 3-segmented; in Cephalocteinae, anterior and posterior tibiae are strongly modified, and tarsi may be reduced or absent (Figs. 21.14, 21.15, 21.29). Abdominal trichobothria on sterna 3–7 oblique, longitudinal, or transversal to the spiracle line, usually 2 + 2. Nymphal scent glands present between abdominal terga 3/4, 4/5, and 5/6.

Fig. 21.14 *Atarsocoris giselleae* (Carvalho), anterior tibia (Photo CF Schwertner)

Fig. 21.15 *Scaptocoris castanea*, anterior tibia (Photo CF Schwertner)

21.3 General Biology and Ecology

The biology of the Cydnidae is relatively well known for species that live above the ground, especially species of the subfamily Sehirinae, e.g., *Sehirus cinctus* (Palisot).

On the other hand, the Neotropical species of the family are predominantly excavators and spend most of their lives in the soil. The subterranean habit hampers knowledge of their biology, ecology, and behavior, and such studies are scarce.

Most of the nymphs and adults of Cephalocteinae and Cydninae are sap-feeding through the roots of the hosts, although some species, e. g., *Pangaeus bilineatus* (Say), were observed sucking the content of ground pods of *Arachis hypogaea* L. (Chapin et al. 2006). For Sehirinae and Amnestinae, feeding occurs in aboveground structures of the host plants. The species *Sehirus cinctus* consumes mature fallen seeds from several host plants (Froeschner 1960; Sites and McPherson 1982), while *Amnestus* spp. were found feeding on fruits and seeds of *Ficus colubrinae* Standl. in Mexico (Mayorga and Cervantes 2001).

21.3.1 Eggs and Oviposition

The females of Cephalocteinae and Cydninae lay single eggs, belowground (García and Bellotti 1980; Riis et al. 2005b). In Sehirinae, females lay egg masses in shallow cracks on the soil surface (Sites and McPherson 1982). At least one species of Amnestinae, *Amnestus ficus* Mayorga and Cervantes, lays eggs inside the fruits of *Ficus* (Moraceae) (Mayorga and Cervantes 2001).

Maternal care is observed in those species that lay egg masses, i.e., *Sehirus cinctus cinctus* and *Adomerus triguttulus* (Motschulsky). The females guard the eggs until the nymphs leave the place after hatching (Southwood and Hine 1950; Nakahira et al. 2013). This behavior was not observed in species of other subfamilies than Sehirinae.

When oviposition occurs in the soil, eggs are usually deposited near the host plant. This behavior probably increases the efficiency of food location by the offspring, which typically have limited ability to move. The moisture and soil texture seem to determine the depth of the oviposition site (Willis and Roth 1962; Riis and Esbjerg 1998; Riis et al. 2005b). In times of prolonged drought in Brazilian Cerrado, eggs of *Scaptocoris* spp. were found about 1.5 m deep (Nardi et al. 2008).

Eggs of Cydnidae are characterized by corium smooth, uniform creamy coloration and no conspicuous projections (Fig 21.16a) (García and Bellotti 1980; Mayorga and Cervantes 2001; Vivan et al. 2013). Incubation time can vary from one week (García and Bellotti 1980; Sites and McPherson 1982; Riis et al. 2005b) up to 4 weeks (Sales and Medeiros 2001).

21.3.2 Nymph Feeding and Development

The nymphal stage of the Neotropical species of Cephalocteinae and Cydninae lives within the soil, feeding in the roots of the hosts. Typically polyphagous, it is likely that nymphs feed on plants closer to the site hatching.

The newly hatched nymphs measure from 1.0 to 2.5 mm in length (García and Bellotti 1980; Sites and McPherson 1982; Riis et al. 2005b) and move around in the soil alone. Like most of the terrestrial Heteroptera, postembryonic development occurs in five instars (Fig. 21.16), visually characterized by the morphology of the individuals. The last three instars have wing pads, which become more evident in the 5th instar (Fig. 21.16f). Time of postembryonic development remains unknown for most of the species, especially those that do not have established methods for laboratory rearing. Laboratory studies found that adults of *Cyrtomenus bergi* Froeschner, under 23.9 ± 1.1 °C and gravimetric moisture of 24 %, emerge in 112 days on average (García and Bellotti 1980; Riis et al. 2005a). For other species of Cydnidae, the development period can be shorter, as in *S. cinctus cinctus* (54 days) (Sites and McPherson 1982), although many still remain unknown. Field experiments

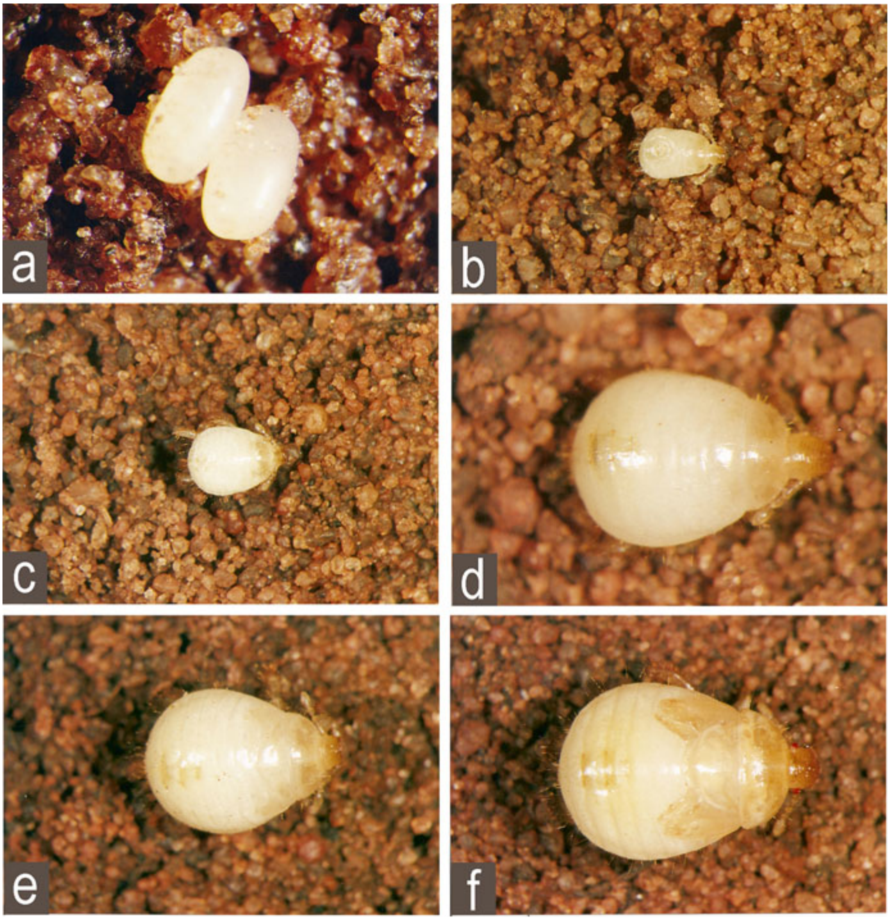

Fig. 21.16 Immature stages of *Scaptocoris carvalhoi*. (**a**) Eggs; (**b**) first instar; (**c**) second instar; (**d**) third instar; (**e**) fourth instar; (**f**) fifth instar (Photos C Nardi)

in pasture areas in Mato Grosso State, Brazil, conducted by Sales Jr. and Medeiros (2001) verified that egg-adult period of *Scaptocoris carvalhoi* Becker is 150–180 days.

As for insects in general, immature stage in cydnids is extremely sensitive to temperature changes, humidity, population density, and food availability (Tauber et al. 1986). For some nymphs (e.g., *Scaptocoris* spp.), dry periods may determine their location at greater depths in the soil, apparently in search for higher humidity (Oliveira and Malaguido 2004; Nardi et al. 2007; Pereira et al. 2012).

It remains unknown the occurrence of diapause in Neotropical populations. However, *P. bilineatus* from Texas (USA) showed diapause during the winter, when overwinter individuals remained inactive at 6–8 inches belowground (Cole 1988).

21.3.3 Adult Feeding and Reproduction

Most of the biological aspects of Cydnidae are difficult to be determined, but it is known that adults may live from 100 to 300 days (García and Bellotti 1980; Sales and Medeiros 2001). Observations from Riis et al. (2005b) and García and Bellotti (1980) showed that the preoviposition in *C. bergi* is 10.5 days and the female can lay at least 250 eggs. Similar reports for other species of Neotropical cydnids are unknown from the literature.

As for the nymphal stage, adults of most Cydnidae (subfamilies Cephalocteinae and Cydninae) occur in the soil, where they remain during much of life. The structure and physical conditions of the soil are extremely important for their survival. Generally, the burrower bug exhibits preference for sandy soils, to the detriment of clay soils (Riis and Esbjerg 1998; Riis et al. 2005a; Oliveira and Malaguido 2004), probably due to the lower water accumulation and lower compression, features that facilitate excavation (Willis and Roth 1962). In fact, the moisture seems to be determinant in the distribution of insects in the soil, since in times of drought, adults of Cephalocteinae seem to avoid dry areas and the surface of the soil, and individuals can be found more than 2 m deep where the soil is wetter (Nardi et al. 2007). The search for ideal conditions of temperature and soil moisture also has been related to persistence of some underground Cydnidae as tenants in nests of *Atta* spp., i.e., *Atarsocoris giselleae* (Carvalho) and *Amnestus* spp. (Froeschner 1960, 1975; Moser 1963; Soares et al. 2006).

Most of the Neotropical Cydnidae is polyphagous, and plants of several families have been reported as hosts (Becker 1967; Riis et al. 2005b; Timonin 1958; Mayorga and Cervantes 2001; Chapin et al. 2006) (Table 21.2). Host plants include small size plants, such as *A. hypogaea*, to larger-sized *Eucalyptus* spp. Very often these insects are reported as agricultural pests, and, depending on the population level, the symptoms of their occurrence can be checked on the shoots, whose leaves turn yellow and dry (Gallo et al. 2002; Riis et al. 2005b; Oliveira and Malaguido 2004; Pereira et al. 2012).

Burrower bugs have the ability to leave the ground during a period of adult life. Typically, this behavior is associated with flight capacity, which allows individuals to reach long distances and colonize new environment. The ability to fly and leave the soil is associated with the development of wings, which may vary between species and even between individuals of a population. According to Froeschner (1988), adults of *Tominotus caecus* (Van Duzee) are brachypterous, which prevents these individuals to leave the soil by flying. Nardi et al. (2008) studied *S. carvalhoi* of the Brazilian Cerrado and described the occurrence of brachypterous and macropterous individuals. The brachypterous adults are unable to move the wings and have no fly ability, while macropterous ones have high mobility and ability to fly. The flight behavior of aggregates of *S. carvalhoi* is called swarm, which occurs at the end of the day, usually after rain events. During these swarms, the insects fly about 3 ft high and can reach distances of several kilometers, often attracted by light. However, contrary to what occurs in other groups of insects, flight activity does not seem to be related to mating and is only associated with colonization of new areas, location of food and finding new sexual partners (Willis and Roth 1962; Oliveira and

Table 21.2 Host plants related to Neotropical species of Cephalocteinae and Cydninae

Species	Host plant family	Host plants	References
Scaptocoris buckupi	Asteraceae	*Senecio brasiliensis* Less	Becker (1967)
	Poaceae	*Brachiaria* spp.	Oliveira et al. (2003)
Scaptocoris carvalhoi	Fabaceae	*Glycine max* L.	Becker (1967)
		Phaseolus vulgaris L.	Becker (1996)
	Malvaceae	*Gossypium* sp.	Souza Fo et al. (1997)
	Poaceae	*Zea mays* L.	
		Pastures (several species)	
	Solanaceae	*Nicotiana tabacum* L.	
Scaptocoris castanea	Arecaceae	*Cocos nucifera* L.	Moreira (1923)
	Asteraceae	*Helianthus annuus* L.	Costa Lima (1940)
	Euphorbiaceae	*Manihot esculenta* Crantz	Hayward (1943)
	Fabaceae	*Arachis hypogaea* L.	Andrade and Puzzi (1953)
		Glycine max L.	Silva et al. (1968)
		Lupinus albus L.	Brewer (1972)
		Medicago sativa L.	Brisolla et al. (1985)
		Phaseolus vulgaris L.	Salvadori (1999)
		Pisum sativum L.	Oliveira et al. (2000)
	Malvaceae	*Gossypium* sp.	Matias et al. (2011)
	Meliaceae	*Azadirachta indica* A. Juss.	
	Myrtaceae	*Eucalyptus* spp.	
	Musaceae	*Musa* sp.	
	Poaceae	*Brachiaria* spp.	
		Oryza sativa L.	
		Panicum sp.	
		Pennisetum glaucum L.	
		Saccharum officinarum L.	
		Sorghum bicolor L.	
		Triticum vulgare Vill.	
		Zea mays L.	
	Portulacaceae	*Portulaca oleracea* L.	
	Rubiaceae	*Coffea* sp.	
	Solanaceae	*Capsicum annuum* L.	
		Lycopersicon esculentum Mill.	
		Nicotiana tabacum L.	
Scaptocoris divergens	Musaceae	*Musa* sp.	Roth (1961)
Scaptocoris talpa	Musaceae	*Musa* sp.	Timonin (1961a, b)
Atarsocoris giselleae	Amaranthaceae	*Telanthera maritima* (Mart.) Moq.	Becker (1967)
	Chenopodiaceae	*Chenopodium ambrosioides* L.	
	Palmae	*Diplothemium maritimum* Mart.	
	Poaceae	Several species	

(continued)

Table 21.2 (continued)

Species	Host plant family	Host plants	References
Cyrtomenus bergi	Euphorbiaceae	*Manihot esculenta* Crantz	CIAT (1981, 1989)
Cyrtomenus mirabilis	Fabaceae	*Arachis hypogaea* L.	Cividanes et al. (1981)
		Phaseolus vulgaris L.	Lacerda (1983)
		Pisum sativum L.	Herrera (1988)
	Liliaceae	*Allium cepa* L.	
		Allium fistulosum L.	
	Poaceae	*Saccharum officinarum* L.	
		Sorghum bicolor (L.) Moench	
		Zea mays L.	
		Pastures (several species)	
		Weeds (several species)	
	Palmae	*Elaeis guineensis* Jacq.	
	Solanaceae	*Solanum tuberosum* L.	
	Rubiaceae	*Coffea arabica* L.	
	Umbelliferae	*Coriandrum sativum* L.	
Pangaeus bilineatus	Amaranthaceae	*Spinacia* sp.	Gould (1931)
	Fabaceae	*Arachis hypogaea* L.	Cole (1988)
	Malvaceae	*Gossypium* sp.	Smith and Pitts (1974)
	Rosaceae	*Fragaria vesca* L.	Otten (1956)
	Solanaceae	*Capsicum* sp.	Froeschner (1988)
			Lis et al. (2000)
Tominotus communis	Fabaceae	*Arachis hypogaea* L.	Smith and Pitts (1974)
Sehirus cinctus cinctus	Anacardiaceae	*Toxicodendron radicans* (L.) Kuntze	Stoner (1920)
	Apiaceae	*Chaerophyllum procumbens* (L.) Crantz	Hart (1919)
	Apocynaceae	*Apocynum cannabinum* L.	Froeschner (1941)
		Asclepias spp.	Blatchley (1926)
		Ageratina altissima (L.) King and H.E. Rob.	McPherson and Mohlenbrock (1976)
		Antennaria plantaginifolia (L.) Richards.	
		Erigeron philadelphicus L.	
		Helianthus spp.	
		Solidago spp.	
		Verbesina alternifolia (L.)	
	Ebenaceae	*Diospyros virginiana* L.	

(continued)

Table 21.2 (continued)

Species	Host plant family	Host plants	References
	Lamiaceae	*Lamium purpureum* L.	
		Melilotus spp.	
		Monarda punctata L.	
		Perilla frutescens (L.) Britt.	
		Physostegia virginiana (L.) Benth.	
		Stachys spp.	
		Teucrium canadense L.	
	Poaceae	*Elymus virginicus* L.	
		Phleum pratense L.	
		Poa spp.	
	Polygonaceae	*Rumex crispus* L.	
	Rosaceae	*Prunus* spp.	
		Rubus spp.	
	Scrophulariaceae	*Verbascum thapsus* L.	

Malaguido 2004; Nardi et al. 2008). Swarming behavior is also mentioned for other species of the Neotropical Scaptocorini (Becker 1967).

Although little is known about the reproduction of Neotropical cydnids, for those species that live in the soil, mating occurs in this habitat, as showed for *Scaptocoris divergens* Froeschner (Willis and Roth 1962) and *S. carvalhoi* (Nardi 2005). During copulation males and females remain connected by the genitalia and in opposite directions (Willis and Roth 1962). Whereas Cydnidae present solitary behavior, finding sexual partners may be difficult, since the environment where these bugs live restricts large-scale communication between individuals.

Like other Heteroptera, it is likely that copulation in Cydnidae is mediated by chemicals and sound signals. Studies by Gogala et al. (1974), Gogala (1984), and Cokl et al. (2006) show that the morphology of the stridulatory apparatus of males and females is different in some species (Fig. 21.17); consequently, sound production also differs between the sexes. However, there are no detailed studies on the implications of these differences in the encounter between sexual partners. Vibrational signals have a low propagation capacity, reaching distances of a few centimeters. Thus, structures to amplify such signals and allow it to spread to greater distances would be necessary; the root of the host plants would be one of those structures (Drašlar and Gogala 1976; Cokl and Virant-Doberlet 2003).

With respect to chemical signals in Cydnidae, few studies have been conducted. Pluot-Sigwalt (2008) identified basi-abdominal glands in males of tribes Cydnini and Geotomini (Cydninae) that produced pheromones. This pheromone is probably associated with the location of sexual partners, courtship, and copulation, since the secretion of the gland is associated with increased sexual activity. However, this characteristic appears to be unique to the subfamily Cydninae; basi-abdominal glands are absent in male of Amaurocorinae, Cephalocteinae, and Sehirinae (Pluot-Sigwalt 2008). No species of Amnestinae and Garsauriinae was analyzed to date with respect to this characteristic.

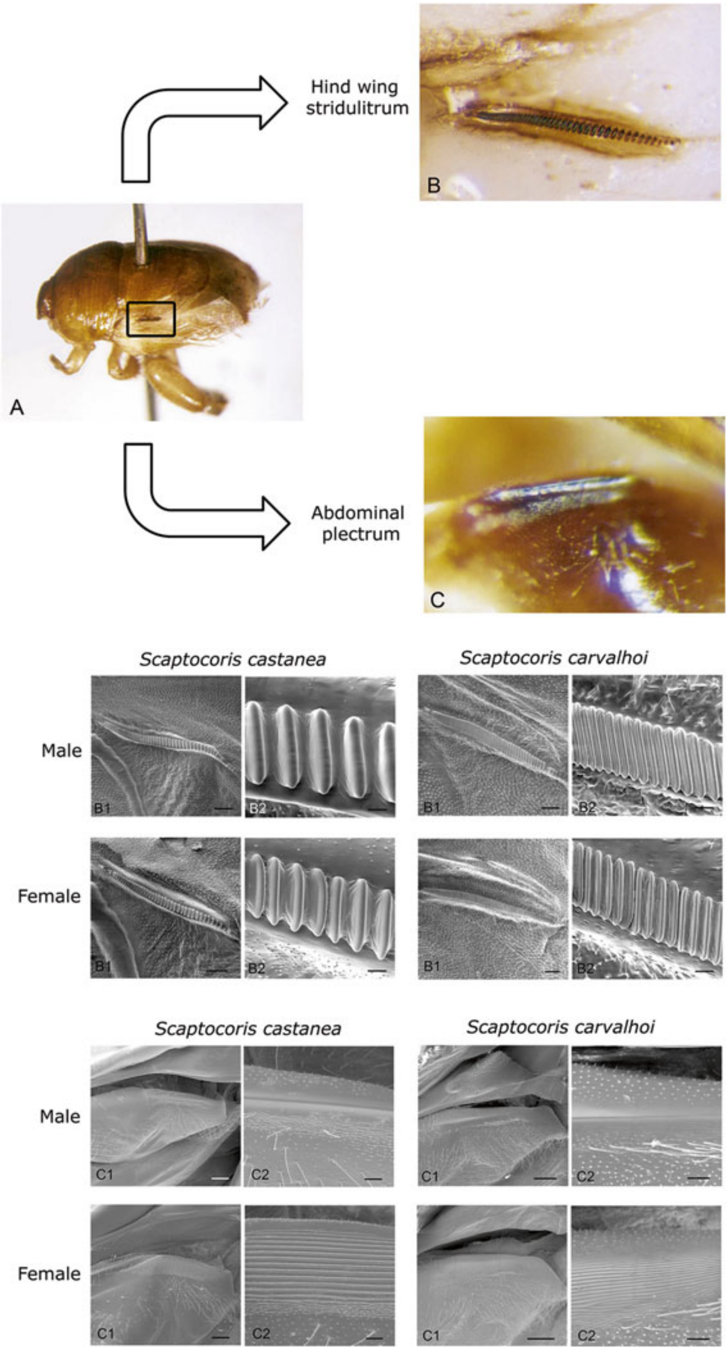

Fig. 21.17 Male and female stridulatory apparatus of burrower bugs, *Scaptocoris castanea* and *Scaptocoris carvalhoi*. (**a**) Adult body showing the stridulatory apparatus location; (**b**, **b1**) stridulitrum situated on the postcubital vein of the hind wings (scale bar = 100 µm); (**b2**) middle third of the stridulitrum, showing teeth detail (scale bar = 10 µm); (**c**, **c1**) stridulatory plectrum situated on both lateral sides of the frontal edge of the tergal plate (scale bar = 100 µm); (**c2**) middle third of stridulatory plectrum (scale bar = 20 µm) (Photos C Nardi)

21.4 Classification and Diversity

Six subfamilies are recognized in Cydnidae, and four of them are recorded in the Neotropical region (Table 21.1). The subfamilies Amaurocorinae and Garsauriinae are restricted to the Eastern hemisphere (Lis 1999a, 2002). The subfamily Sehirinae is predominantly Palearctic, with only one species occurring in North America and reaching the neotropics (Froeschner 1960; Mayorga 2002).

The monophyly of the Cydnidae and phylogenetic relationships with other pentatomoid families are still controversial (Grazia et al. 2008; Pluot-Sigwalt and Lis 2008; Lis 2010). Two of the typical characteristics of the Cydnidae (i.e., coxal combs and spinose tibiae) are shared with the related families Parastrachiidae, Thaumastellidae, and Thyreocoridae, sometimes included as subfamilies in a more inclusive taxon (Dolling 1981; Schuh and Slater 1995). The classification of this group of families has been intensively studied (Pluot-Sigwalt and Lis 2008; Lis 2010), and general conclusions remain unsettled. Among the subfamilies, only Cephalocteinae has a strong support in a phylogenetic context (Lis 1999b), while the non-monophyly of the taxa Geotomini (Cydninae) and Sehirinae is suggested (Pluot-Sigwalt and Lis 2008; Lis 2010).

Froeschner (1960) reviewed the Cydnidae in the Western Hemisphere and included identification keys to all genera and species known at that time to the neotropics. Becker (1967) monographed the Scaptocorini of the Neotropical region, described new species of *Scaptocoris* Perty, and proposed the new genus *Atarsocoris* to include *A. giselleae*. Froeschner (1975) and Mayorga and Cervantes (2001, 2005, 2009) described new species of Amnestinae and Cydninae from the Neotropical region, while Eger (2008) described a new genus and three new species for Amnestinae. Grazia et al. (2004) updated the taxonomy of the Cephalocteinae, and Marco and Coscarón (2011) summarized the literature of the group in the Neotropical region after the publication of Froeschner (1960).

Identification key to subfamilies of Cydnidae of the Neotropical region (based on Froeschner 1960, 1981):

1. Scutellum short, not surpassing the middle length of the abdomen, claval commissure present, almost as long as the scutellum (Fig. 21.22)..... Amnestinae
– Scutellum usually surpassing the middle length of the abdomen, claval commissure never present 2
2. Tibiae strongly modified, anterior tibia cultrate in shape (Figs. 21.14, 21.15, 21.29), posterior tibia club shaped, posterior tarsi always absent (Figs. 21.18, 21.19) ....Cephalocteinae
– Tibiae usually cylindrical, sometimes strongly compressed and modified (Fig. 21.12), but never as described above... 3
3. Pronotum with a lateral, submarginal row of setigerous punctures (Fig. 21.5); tarsal segment II subequal in diameter than I and III (Fig. 21.20)..........Cydninae
– Pronotum without a row of setigerous punctures; tarsal segment II distinctly narrower than I and III (Fig. 21.21) .... Sehirinae

Fig. 21.18 *Atarsocoris giselleae* (Carvalho), posterior tibia (Photo CF Schwertner)

Fig. 21.19 *Scaptocoris castanea*, posterior tibia (Photo CF Schwertner)

Fig. 21.20 *Cyrtomenus mirabilis*, anterior tarsus (Photo CF Schwertner)

Fig. 21.21 *Sehirus cinctus cinctus*, anterior tarsus (Photo CF Schwertner)

Fig. 21.22 *Amnestus pusio*, scutellum and hemelytra in detail (Photos CF Schwertner)

21.4.1 Subfamily Amnestinae

These very small bugs (1.6–4.5 mm) are reddish brown to blackish brown in color and easily recognized by the presence of the claval commissure (Fig. 21.22). Other unique characteristics include clypeus and juga with marginal pegs (Fig. 21.7), posterior margin of pronotum sinuate laterally near humeral angles, short scutellum, and anterior tibia compressed. Amnestinae is predominantly Neotropical (Table 21.1), with two species endemic to the Nearctic region. One species, *Amnestus pusillus* Uhler, is well established in the Iran (Province of Gilan), probably introduced by man (Mayorga et al. 2012).

Species of Amnestinae are among the oldest fossils of true bugs, dated at least from the Cretaceous/Jurassic (Shcherbakov and Popov 2002; Yao et al. 2007). Distribution of this subfamily was widespread during the Mesozoic, and species were found in localities included today in Neotropical and Palearctic regions

(Shcherbakov and Popov 2002). Other Amnestinae fossils were recorded in amber from Mexico (Chiapas) and the Dominican Republic (Thomas 1988, 1994).

The two extant genera of Amnestinae can be separated by the development of the hemelytral membrane and the presence of ocelli (Eger 2008). In *Amnestus*, the hemelytral membrane is developed, occupying 1/3 of the hemelytral length (Fig. 21.1), and the ocelli are present; in *Lattinestus*, the hemelytral membrane is reduced, occupying 1/7 or less of the hemelytral length, and the ocelli are absent (Eger 2008).

Adults of Amnestinae were recorded in litter of humid forest (Eger 2008; Mayorga and Cervantes 2001), low vegetation in moist areas (Van Duzee 1894; Blatchley 1926 in McPherson and Mohlenbrock 1976), bluegrass on sandy knolls (*Andropogon furcatus* Muhl. consortia) (McPherson and Mohlenbrock 1976), and beach drift (Torre-Bueno 1915; Froeschner 1960). Nymphs and adults of *A. ficus* were found belowground, 10 cm deep in the soil, or inside of the *Ficus* fruit, feeding on freshly fallen fruits and seeds of *Ficus cotinifolia* H.B.K., *F. insipida* Willd, *F. trigonata*, and *F. colubrinae* Standley (Mayorga and Cervantes 2001). Furthermore, Caudell (1924, in Mayorga and Cervantes 2001) found *Amnestus subferrugineus* (Westwood) associated with guano in bat caves, suggesting that this species feed on the seeds contained in the excrements.

The species of Amnestinae are poorly studied, and most of the recent publications include descriptions of new species, morphology, and host plant records (Lis 1998; Lis and Hohol-Kilinkiewicz 2001; Lis and Pluot-Sigwalt 2002; Yao et al. 2007; Pluot-Sigwalt and Lis 2008; Eger 2008; Lis 2010; Mayorga et al. 2012; Mayorga-Martinez and Brailovsky 2012). The most complete work about *Amnestus* biology and behavior was done by Mayorga and Cervantes (2001). These authors showed that female of *A. ficus* laid single eggs inside the fruits of *Ficus* or inside the soil. Nymphs and adults are diurnal and disperse from one tree to another, probably attracted to fresh fruit volatiles. According to Froeschner (1960), these insects are attracted to light, although Mayorga and Cervantes (2001) collected only a few specimens with light traps. Life cycle of *A. ficus* takes ca. 25 days, and in this short period, individuals need to find suitable fruits and seeds before rain falls and competitors (e. g., ants and crabs) remove the seeds (Laman 1996; Mayorga and Cervantes 2001).

21.4.2 Subfamily Cephalocteinae

Besides the strongly modified tibiae, the species of Cephalocteinae are also recognized by having globular and strongly convex body (Figs. 21.3 and 21.4), coloration varying from yellow amber to dark brown, and length between 4 and 10 mm (Schuh and Slater 1995; Lis 1999b; Grazia et al. 2004). Two tribes are recognized, and their distribution includes all biogeographical regions (Lis 1999b). Two genera are found in the neotropics: *Atarsocoris* Becker (1967) (monotypic) and *Scaptocoris* Perty (1833) with seven species. Species of Scaptocorini are related to several host plants, including many crops (Becker 1967, 1996; Souza Fo et al. 1997; Oliveira et al. 2003; Grazia et al. 2004) (Table 21.2).

The genus *Atarsocoris* is characterized by the apex of tylus bifid (Figs. 21.23 and 21.24), ostiole exposed (Fig. 21.26), and anterior tarsi absent. In the genus

Scaptocoris, the apex of the tylus is entire (Figs. 21.8, 21.25, and 21.27), the ostiole covered (Fig. 21.28), and the anterior tarsi present or reduced, but always with tarsal insertion present (Fig. 21.29; see also Grazia et al. 2004). Lis and Hohol-Kilinkiewicz (2001) showed that the number and arrangement of trichobothria can also be used to differentiate *Atarsocoris* and *Scaptocoris* (one trichobothria on each side of the abdominal segment in the first, two in the second).

Fig. 21.23 *Atarsocoris giselleae*, head in frontal view (Photo CF Schwertner)

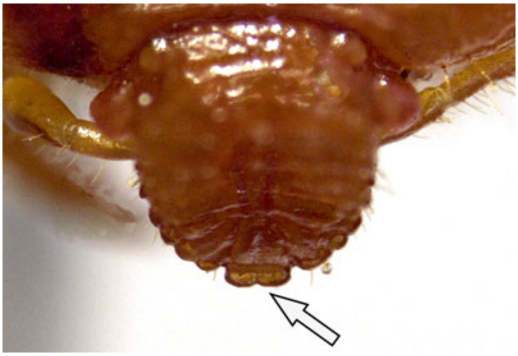

Fig. 21.24 *Atarsocoris giselleae*, detail of the head in dorsal view, showing apex of tylus (Photo CF Schwertner)

Fig. 21.25 *Scaptocoris carvalhoi*, head in dorsal view (Photo CF Schwertner)

Fig. 21.26 *Atarsocoris giselleae*, evaporatorium (Photo CF Schwertner)

Fig. 21.27 *Scaptocoris divergens*, head in dorsal view (Photo CF Schwertner)

Fig. 21.28 *Scaptocoris minor*, evaporatorium (Photo CF Schwertner)

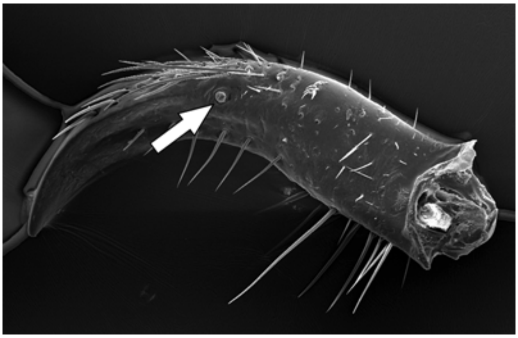

Fig. 21.29 *Scaptocoris carvalhoi*, anterior tibia (Photo C Nardi)

In the Western Hemisphere, Scaptocorini is distributed from the USA to Argentina, although it is more common in Brazil, where large populations cause significant damage to crops. *Scaptocoris buckupi* Becker, *S. carvalhoi*, and *S. castanea* Perty are the main species associated to damage (Froeschner 1960; Becker 1967; Grazia et al. 2004) and can be differentiated by the shape and arrangement of corbicles present in the posterior tibiae and presence of tarsus or tarsal insertion in the anterior and median leg (Grazia et al. 2004).

Damage caused by brown burrower bugs in crops and pastures is due to the feeding of adults and nymphs, sucking the sap of plants through the roots (Souza 2002; Gallo et al. 2002). According to Souza (2002), the initial symptom of the attack is a slight number of nearby plants with yellowish leaves, withered and dry aspect. However, during severe infestations, these symptoms may occur in plants distributed in several acres.

21.4.3 Main Species

Scaptocoris carvalhoi Becker (= _Atarsocoris brachiariae_ syn. jr.) (Figs. 21.16, 21.17, 21.25, 21.29, 21.30, and 21.31a)

Adults and nymphs (Fig. 21.16) of *S. carvalhoi* have anterior tarsi absent, but tarsal insertion present, like a small knob (Fig. 21.29), and the discal tubercles of the corbicle (Fig. 21.30) distinctly elongated (Becker 1967; Grazia et al. 2004). The synonym between *S. buckupi* and *Atarsocoris brachiariae* Becker was defined recently (Grazia et al. 2004).

Vivan et al. (2013) published the first detailed morphological record of immatures belonging to *Scaptocoris*, describing *S. carvalhoi*. Eggs of *S. carvalhoi* are elliptical and have 1.60 mm length and 0.90 mm width, a smooth chorion surface, and no visible aero-micropylar processes (Fig. 21.16a). Nymphal stage of *S. carvalhoi* presents five instars, an elliptical body, and fossorial scythe-like forelegs. The tarsi are absent as in adults, and the prototarsal insertion region becomes visible only in the 4th instar. Nymphs from the 1st to 4th instar of *S. carvalhoi* showed the presence of 1 + 1 trichobothria in urosternites III to VII, close to the anterior margin

Fig. 21.30 *Scaptocoris carvalhoi*, posterior tibia (Photo CF Schwertner)

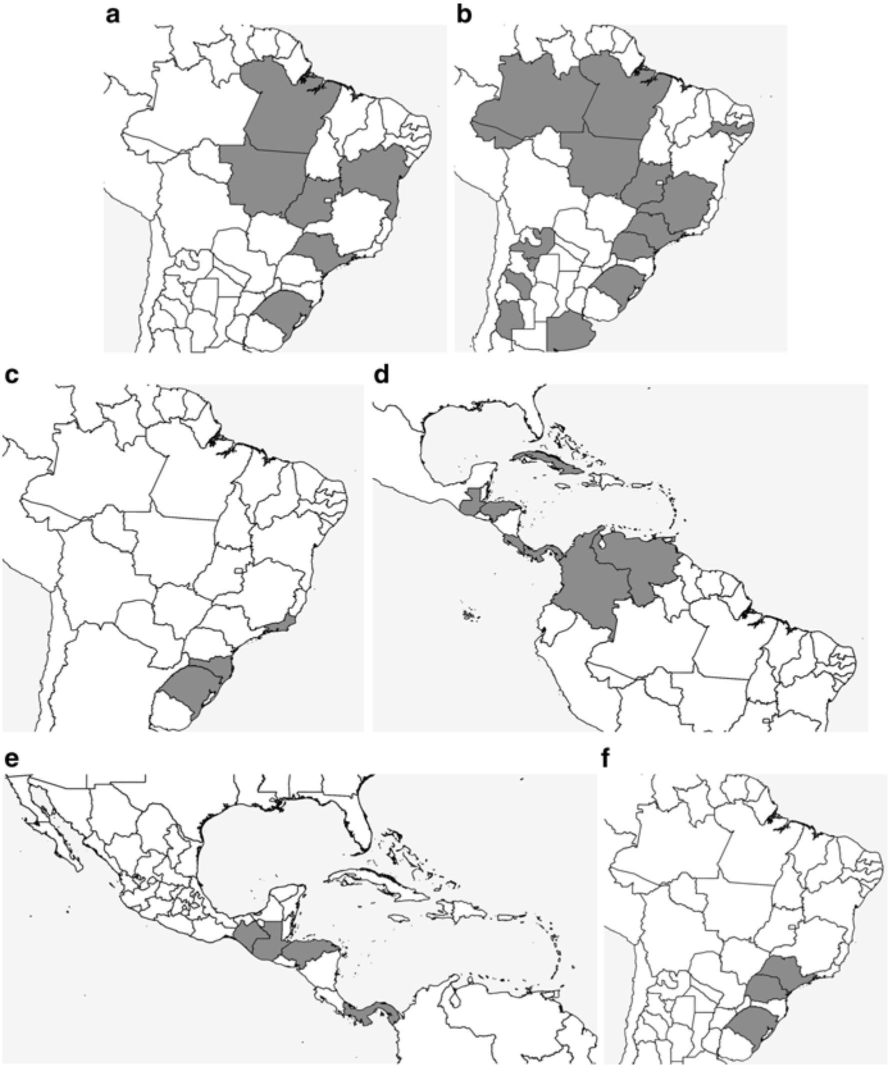

Fig. 21.31 Distribution maps of Cephalocteinae in the Neotropical region. (**a**) *Scaptocoris carvalhoi*; (**b**) *Scaptocoris castanea*; (**c**) *Scaptocoris buckupi*; (**d**) *Scaptocoris divergens*; (**e**) *Scaptocoris talpa*; (**f**) *Atarsocoris giselleae*

and inside the spiracles; besides these trichobothria, fifth instars presented 1 + 1 pre-trichobothria in urosternites III to V located posteriorly, almost in the row of spiracles close to the posterior margin of the urosternites.

Although frequently related with plants of Poaceae (Becker 1967), nymphs and adults of *S. carvalhoi* are polyphagous and occur on plants of several families (Table 21.2). Furthermore, this species is frequently mistaken with other brown burrower bugs, and all symptoms and damages to crops are generally attributed to *S. castanea* (Lis et al. 2000).

Sales Jr. and Medeiros (2001) estimated that the egg-adult period takes 150 to 180 days, adult longevity is about 150 days, and preoviposition period takes 18.2 days. The egg and nymphal stages take 30 and 145 days, respectively. Nevertheless, these biological data are approximate and obtained without any control of the population, temperature, or soil moisture. It is necessary to develop methods for rearing these insects and to define exactly their biological aspects.

Behavioral aspects of *S. carvalhoi* are poorly understood. Male and female of *S. carvalhoi* emit stridulatory signals, which are produced by a stridulatory system located at the dorsum of the abdomen and at the basal area of the hind-wing vein (Cokl et al. 2006). The morphology of stridulatory apparatus is different between males and females (Fig. 21.17), as well as the signals produced by them.

In field conditions, the population of *S. carvalhoi* is found stratified in the soil, and the distribution of individuals depends mainly on rainfall conditions and soil moisture. Nardi et al. (2007) showed that nymphs and adults were located in the top layer of the soil during the rainy season and were found deeper during rainless period in the Brazilian Cerrado region (16° 51′ 50″ S, 50° 33′ 43″ W). Nardi et al. (2008) described some ecological aspects of the adults of *S. carvalhoi*, which swarm in the beginning of the rainy season, after a prolonged drought period in the Brazilian Cerrado region. In these swarms, part of the population leaves the soil, performing long flights to locations with more abundant vegetation. These authors demonstrated that adults of *S. carvalhoi* have wing polymorphism and macropterous individuals have greater flight capacity than brachypterous individuals. Also, the study supported that increased number of macropterous belowground and the simultaneous swarming could be a seasonal-related event and that rainless period could influence the formation of polymorphic adults (Nardi et al. 2008).

Since *S. carvalhoi* is pointed as an important species of crop plants in Brazil, biological and ecological data are extremely important to develop methods for integrated management of these insects. According to Nakano et al. (2001), *S. carvalhoi* feeds through the roots of the hosts, causing developmental delay, wilting, and death of plants. In areas where the soil is degraded, the damage caused by these insects is more severe (Oliveira et al. 2000).

Scaptocoris castanea Perty (Figs. 21.3, 21.4, 21.8, 21.11, 21.15, 21.19, 21.31b)

Adults of *S. castanea* are characterized by the presence of anterior and median tarsi; median tibia with dorsal area flat and glabrous; surface of corbicle flattened (Fig. 21.19); discal tubercles arranged in irregular row, extending from the base to near the apex of the corbicle.

Cokl et al. (2006) demonstrated that males and females of *S. castanea* emit stridulatory signals, which were registered when the adults were on the roots of soybean. Males and females also show distinct stridulatory tergum system, with one ridge in male and 13 ridges in female. Furthermore, differences between male and female emissions were expressed significantly in syllable repetition time, in the repetition time of the first and second pulse train, and in the interval between them, in the number of pulses per pulse train, and in their repetition rate.

Although cited as the most frequent species in Brazil and Argentina, Becker (1967) and Lis et al. (2000) commented that possibly many reports of occurrence assigned to species are mistaken. *Scaptocoris castanea* cause damage in a wide range of host plants, and apparently populations occur in areas previously cultivated with pastures (Puzzi and Andrade 1957).

The damage caused by nymphs and adults of *S. castanea* occurs by sucking the sap of the plants through the roots, causing withering, drying, and even the death of plants (Oliveira et al. 2000). In the Southeast and Midwest of Brazil, population peak of these insects occurs in late spring and summer, while the greatest number of adults in the soil is observed in summer (from December to February) (Oliveira and Malaguido 2004). Nymphs and adults remain in the upper soil layers (above 20 cm) during rainy seasons, going down deep when water availability is low. Based on this, Oliveira and Malaguido (2004) suggest that sampling for population estimates should be made at depths of 30–50 cm in order to reach the population throughout the year. Furthermore, these authors suggested that the best time for the application of control measures is the period when the bugs are more accessible, i.e., closer to the soil surface.

The population density of *S. castanea* also appears to vary with the cultural agricultural practices. Pereira et al. (2012) showed that *S. castanea* population is larger in integrated crop-livestock system (corn associated with *Brachiaria decumbens* Stapf), with no tillage. Both nymphs and adults of *S. castanea* were more numerous in areas where corn was cultivated for two consecutive years and where pasture was renewed every 2 years. Moreover, lower insect population densities were observed in plots that remained only with *Brachiaria* pasture.

Despite the importance of *S. castanea* in agriculture, few results have been obtained with the management of the populations in the field, due to the difficulty to target these insects by conventional control. Thus, we emphasize the need for more basic studies, aiming to recognize aspects of their biology, ecology, and behavior, to improve the strategies for their management.

Secondary Species

Scaptocoris buckupi Becker (Figs. 21.31c)

Adults of *S. buckupi* are characterized by the presence of tarsal insertion in the anterior leg (shared with *S. carvalhoi*) and median tibiae with the dorsal area uniformly convex and bristly, and tubercles of the corbicle in a median regular row, except for two of them in the middle third, arranged obliquely (Becker 1967).

Scaptocoris buckupi is understudied with respect to their biology and behavior. Since the description of the species by Becker (1967), the occurrence of nymphs and adults associated with *Senecio brasiliensis* (Spreng.) is the only available information about these insects (treated as *Atarsocoris* sp. in Oliveira et al. 2003). Grazia et al. (2004) reviewed the taxonomy of the species associated to pastures in Brazil and identified them as *S. buckupi*.

This insect is more abundant at the base of the weed plants where they probably found the favorable conditions to survive (Oliveira et al. 2003). Moreover, populations of *S. buckupi* seem to follow the general behavior of other *Scaptocoris*, living in sandy-textured, low-level organic matter soil.

Scaptocoris divergens (Figs. 21.27 and 21.31d)

S. divergens is found in Guatemala, Honduras, Costa Rica, Panama, Trinidad, Colombia and Venezuela. This species is characterized by having the clypeus distinctly surpassing the apex of jugae, greatly expanding forward (Fig. 21.27) (Becker 1967). Host plant records include roots of banana (Roth 1961) (Table 21.2). Willis and Roth (1962) commented on the occurrence of swarms of *S. divergens* in Colombia, during six or seven nights for a month, with several individuals collected in light traps. In this study, the authors illustrate the mating behavior in *Scaptocoris* for the first time, an extremely difficult task because this behavior occurs belowground (Willis and Roth 1962; Nardi 2005).

Roth (1961) described the morphology of the scent gland of *S. divergens* and identified the secretion as a compound of seven aldehydes, two furans, and two quinones. These compounds showed fungistatic and fungicidal activity against *Fusarium* and repellent activity against ants (*Pheidole* sp.).

Scaptocoris talpa (Fig. 21.31e)

Scaptocoris talpa is the largest species within *Scaptocoris*, reaching 8.8 mm in length, with corbicle tubercles flattened and with approximately 25 setigerous punctures in the lateral margin of the pronotum (Becker 1967). This species was found feeding on the roots of banana (Timonin 1958) and sugarcane (Champion 1900 cited in Becker 1967) in Honduras and Guatemala, respectively.

Timonin (1961a, b) showed that the scent gland volatiles released by these insects reduced the population of four isolates of *Fusarium oxysporum* Schlecht. f. sp. *cubense* and 14 other isolated soil-inhabiting fungi, associated with banana cultivation. These compounds proved to be important for the protection of banana and tomato plants against soil fungi and pathogenic nematodes (Timonin 1961a).

Atarsocoris giselleae (Figs. 21.14, 21.18, 21.23, 21.24, 21.26, and 21.31f)

This is the only species included the genus *Atarsocoris* Becker (Grazia et al. 2004). According to Becker (1967), individuals of this species were collected in coastal dune vegetation, where prevailed grasses, shrubs, and small trees. Label records indicated that this species also swarms in some periods of the year. No other information is available about this peculiar species.

21.4.4 Subfamily Cydninae

This group represents the most speciose subfamily of Cydnidae (Table 21.1). The size ranges from 3 to 20 mm, and body coloration is usually black or dark brown (Figs. 21.5, 21.38, and 21.39). Despite the morphological variation found among the subfamily, species can be recognized by the more compressed body, presence of setigerous punctures in the lateral margins of pronotum and hemelytra, anterior tibia never cultrate, and tarsi always arising at or near the apex of tibia (Froeschner 1960, 1981). In the Neotropical region, only species of the tribe Geotomini are indigenous. The species *Cydnus aterrimus* (Foster) (Cydnini) found in the neotropics is considered an accidental introduction in the Western Hemisphere (Froeschner 1960; Lis 1996); *C. aterrimus* was recorded in the USA and Tobago by a single specimen in each locality (Froeschner 1960).

The Neotropical fauna of Cydninae, Geotomini, is predominantly endemic, with some species reaching the Nearctic region (Table 21.3). Only the genus *Microporus* Uhler is found outside the Western Hemisphere, with species also found in the

Table 21.3 Species of subfamily Cydninae by genera in the Neotropical region

Taxon	World	Neotropical (total)	Neotropical (endemic)
Cydnini	114	1	0
Cydnus[a]	7	1	0
Geotomini	443	96	78
Cyrtomenus[b]	8	7	6
Dallasiellus[b]	31	27	23
Ectinopus	3	3	3
Melanaethus	18	10	7
Microporus[a]	16	3	2
Onalips	3	3	3
Pangaeus[b]	23	22	17
Prolobodes	3	3	3
Rhytidoporus[b]	6	6	4
Tominotus[b]	14	14	10
Total	557	97	78

[a] Genera with species outside the Western Hemisphere

[b] Genera predominantly Neotropical, with species reaching the Nearctic region

Afrotropical, Australian, Oriental, and Palearctic regions (Lis 1999a, 2002). Fossil of the extant genus *Dallasiellus* is known from Dominican amber of Lower Miocene (Thomas 1994).

Economically important species in the Neotropical region are included in the genera *Cyrtomenus* Amyot and Serville and *Pangaeus* Stål. Nymphs and adults of these taxa feed on roots, tubers (Riis et al. 2005b), and ground pods (Riis et al. 2005b; Chapin et al. 2004, 2006), reducing productivity and facilitating infection by soil pathogens such as *Fusarium*, *Aspergillus*, *Pythium*, and *Genicularia* (Riis et al. 2005b), as well as the development of aflatoxins (Chapin et al. 2004). At least one species of *Tominotus* is recorded feeding on peanuts (Lis et al. 2000), but this species was never studied in detail, and the damage level was unknown. Biological information about other genera of Neotropical Cydninae is still limited.

21.4.5 Key to Some of the Genera of Cydninae: Geotomini of the Neotropical Region (Modified From Froeschner 1960).

We include in the key those genera with species discussed in this chapter (*Cyrtomenus*, *Dallasiellus*, *Pangaeus*, *Prolobodes*, and *Tominotus*). All of them have the anterior part of the peritreme without an enlarged, differentiated apical structure (Fig. 21.32) and were separated by Froeschner (1960) from the remaining genera in the first step of his key. To identify those genera with the anterior part of the peritreme modified (*Ectinopus* Dallas, *Macroporus* Uhler, *Melanaethus* Uhler, *Microporus* Uhler, and *Onalips* Signoret), the works of Froeschner (1960, 1981) and Mayorga (2002) are appropriate references:

1. Pronotum anteriorly with deep, sharply impressed line paralleling anterior margin from side to side (Figs. 21.33a and 21.38)..*Pangaeus*
– Pronotum anteriorly without this impressed line, rarely with a partial, vague line laterally, sometimes with a row of punctures in the same area.................... 2
2. Posterior tibia conspicuously compressed (Fig. 21.34), anterior and posterior faces glabrous, not spined; spines of the posteroventral margin conspicuously longer, thinner, and more tapering than those of dorsal margin...........................3
– Posterior tibia not or only weakly compressed (Figs. 21.35); dorsal and ventral spines equally developed... 4
3. Labial segment II with a large, semicircular, foliaceous lobe (Fig. 21.36)..*Prolobodes*
– Labial segment II without large foliaceous lobe ....*Cyrtomenus*
4. Margin of each jugum with a complete row (extending from the eye to the apex of jugum) of coarse, more or less contiguous punctures giving rise to numerous long hairs and usually also to a row of pegs (Fig. 21.39) ....*Tominotus*
– Margin of each jugum without a complete row of coarse setigerous punctures, which can be absent or, if present, not extending more than ¾ of way to apical angle of jugum; pegs never present (Fig. 21.37)................................*Dallasiellus*

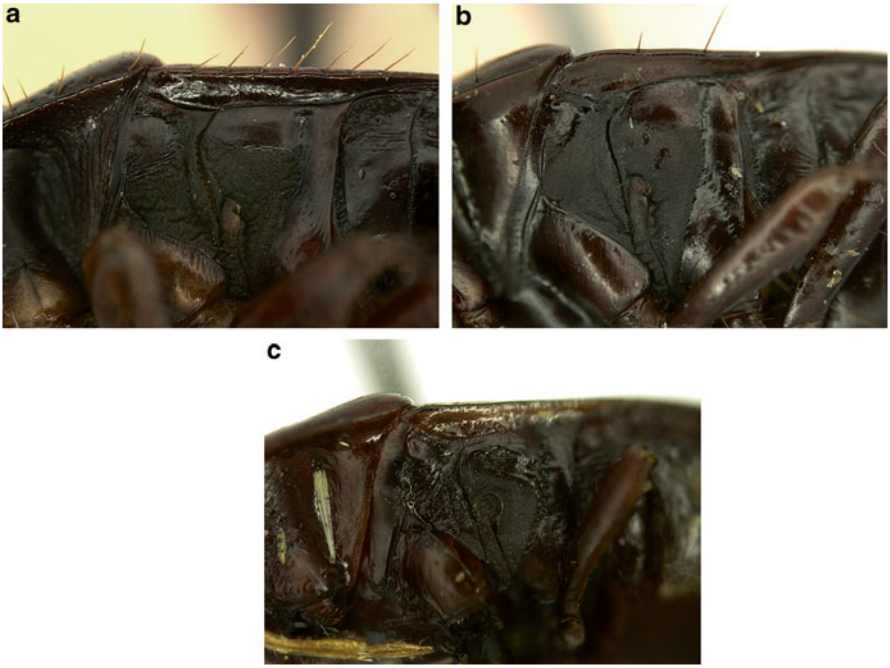

Fig. 21.32 Evaporatoria in Cydninae. (**a**) *Cyrtomenus mirabilis*; (**b**) *Pangaeus neogeus*; (**c**) *Melanaethus spinolae* (Photos CF Schwertner)

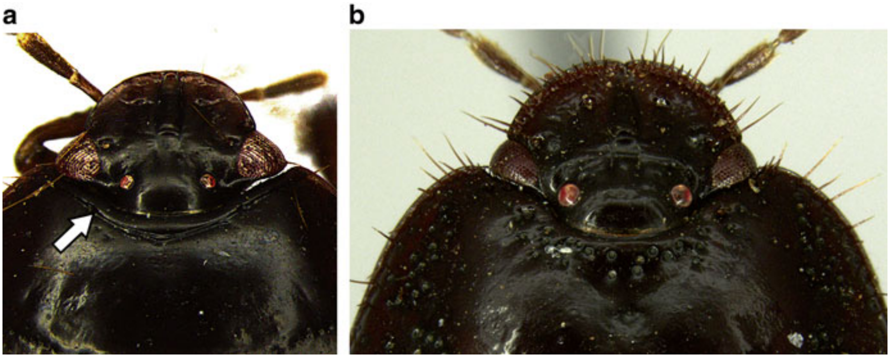

Fig. 21.33 Detail of pronotum in dorsal view. (**a**) *Pangaeus neogeus*; (**b**) *Cyrtomenus mirabilis* (Photos CF Schwertner)

Fig. 21.34 Posterior tibia, *Cyrtomenus mirabilis*. (**a**) Lateral view; (**b**) dorsal view (Photos CF Schwertner)

Fig. 21.35 Posterior tibia, *Dallasiellus longulus* (Photo CF Schwertner)

Fig. 21.36 Rostrum of *Prolobodes giganteus* (second segment in detail) (Photo CF Schwertner)

Fig. 21.37 *Dallasiellus longulus*, head in dorsal view (Photo CF Schwertner)

21.4.6 Main Species

***Cyrtomenus bergi* Froeschner (Fig. 21.40a) and *Cyrtomenus mirabilis* (Perty) (Figs. 21.5, 21.9, 21.20, 21.32a, 21.33b, 21.34, and 21.40a)**

The species *Cyrtomenus bergi* and *C. mirabilis* were included in the subgenus *Cyrtomenus* by Froeschner (1960) that can be differentiated from the subgenus *Syllobus* by the mesopleural evaporatorium entire, not posteriorly interrupted by a shining, submarginal band (Fig. 21.32a). Among species of the subgenus, the absence of a transverse row of prominent setigerous punctures in the urosternites IV to VI and posterior tibia not so compressed as the anterior tibia (Figs. 21.12 and 21.34) allow the recognition of both species. Becker and Galileo (1982) suggested that *C. bergi* and *C. mirabilis* may be the same species; indeed, they are morphologically identical, and the characters proposed to separated them (Froeschner 1960) are difficult to ascertain (CF Schwertner, unpublished data).

Eggs of *C. bergi* have a cream hyaline coloration, are oval shaped, and have an average size of 1.35 mm (length) and 0.92 mm (width); the incubation time is 13.6 days; at hatching, nymphs have whitish-yellowish coloration and are about 1.7 mm and at the fifth instar reach 6.2 mm on average (García and Bellotti 1980).

Cyrtomenus bergi is polyphagous and considered an agricultural pest in several countries, causing damage in plants of numerous families (Riis et al. 2005b) (Table 21.2). Most of the damage was reported in cassava (*Manihot esculenta* Crantz) and peanuts (*A. hypogaea*) (CIAT 1989; García and Bellotti 1980; Arias and Bellotti 1985; Bellotti et al. 1999; Riis et al. 2005b). In peanuts, *C. bergi* pierce the pods and feed on the kernels. A less severe attack will cause yellow to brownish dry rot spots (ca. 1.5 mm diameter) on the kernels of both mature and immature pods, while a more severe attack can cause a complete loss of the harvest (Riis et al. 2005b). In cassava, the damage caused by *C. bergi* is due to the stylet insertion in the epidermis of the roots, allowing infection by soil microorganisms such as *Fusarium*, *Aspergillus*, *Genicularia*, *Pythium*, *Diplodia*, and *Phytophthora* (CIAT 1989), deteriorating the root system of the plant, reducing the content of starch, and affecting the quality of cassava. According to Arias and Bellotti (1985), 20–30 % of roots affected result in 100 % commercial loss.

Biological parameters of *C. bergi* may vary according to the food consumed by nymphs and adults (García and Bellotti 1980, Riis et al. 2005b). In cassava, egg to adult development time is ca. 90 days, whereas in peanut was ca. 60 days; longevity of females reared on peanuts was significantly higher (316.1 days) than females reared on maize (199.1 days) or cassava (111.7 days) (Riis et al. 2005b).

Cyrtomenus bergi is one of the most studied species of Cydnidae. Basic biological aspects are well known (García and Bellotti 1980; Riis et al. 2005b), as well as information about behavior, population dynamics, and food preference (Riis 1997; Riis et al. 2005a, b). Chemical, biological, and cultural control was discussed in several works (e.g., Bellotti and Riis 1994; Calcedo and Bellotti 1994; Sánchez and Bellotti 1997; Barberena and Bellotti 1998; Riis et al. 2003; Jaramillo et al. 2005).

Cyrtomenus mirabilis is considered an important species in cultivated peanuts in Peru, Paraguay, Argentina, and Brazil (Froeschner 1960; Zucchi et al. 1993; Gallo et al. 2002). Damage is the same as described for *C. bergi*. In Brazil, Waquil et al. (2003) reported the occurrence of individual feeding on roots of *Sorghum bicolor* L.

Pangaeus bilineatus (Say) (Figs. 21.38 and 21.40b)

Within the genus, *P. bilineatus* can be recognized by the presence of three or more submarginal setigerous punctures on each jugum and the absence of two key characters used to diagnose other species of *Pangaeus*: ventral surface of posterior femora without tubercles and subapical line of the pronotum without punctures (Froeschner 1960). *Pangaeus bilineatus* lives in the soil and feeds on the roots or underground pods. Females lay single eggs in the soil near plant structures, where newly hatched immatures can rapidly access the roots (Smith and Pitts 1974). Nymphs and adults of this species are considered pest of peanuts in the USA (Chapin and Thomas 2003; Chapin et al. 2006) and have been recorded in other crops (Gould 1931; Otten 1956; Smith and Pitts 1974; Lis et al. 2000) (Table 21.2).

Fig. 21.38 *Pangaeus bilineatus*, habitus dorsal view (Photo CF Schwertner)

In spinach crops, *P. bilineatus* attack newly germinated seeds (Gould 1931; Smith and Pitts 1974), and sucking the stem results in plant wilting and dying (Smith and Pitts 1974).

In peanut, feeding of *P. bilineatus* in the kernels reduces the flavor and the oil quality besides the increment of seed contamination by aflatoxin (Chapin et al. 2006). The damage of nymphs and adults of this species is called "pitting," which is recognized by light yellow to dark brown lesions as a result of this burrower-bug feeding. According to Chapin et al. (2004), 98 % of all aflatoxin contamination in peanut seeds was related to *P. bilineatus* feeding. Overwintering adults were present in conservation tillage of peanut field before planting, and two to three subsequent generations were observed (Chapin and Thomas 2003). These authors demonstrated that peanuts strip-tilled into corn or wheat residue had greater *P. bilineatus* populations and kernel feeding than conventional tillage or strip tillage into rye residue. The control of this species has been carried out by chemical methods, besides conventional tillage practices and crop rotation system (Smith and Pitts 1974; Chapin and Thomas 2003).

In peanut crop areas, Highland and Lummus (1986) used white light traps and captured numerous individuals of *P. bilineatus* (Say). According to these authors, peaks of adult catches can be closely related to field infestations, indicating that light traps are useful tools in an integrated pest management program for this species.

Although the species had been pointed as a vector of certain plant virus disease in the USA (Sailer 1958 in McPherson and Mohlenbrock 1976), there is no detailed account about plant-virus-insect interaction.

Secondary Species

Tominotus communis (Uhler) (Figs. 21.39 and 21.40c)

T. communis is distributed in Nicaragua, British West Indies, Cuba, Haiti, the Dominican Republic, Puerto Rico, the Bahamas, and the USA. The genus *Tominotus* Mulsant and Rey is distributed from the USA to Argentina, but knowledge about the species is scarce. *T. communis* is widespread in Central and North America (Fig. 21.40c) and can be recognized by the narrower scutellar apex and polished dorsum (Froeschner 1960).

This species was recorded in peanut crops associated with a *P. bilineatus* population in Texas. In these areas, nymphs and adults of *T. communis* caused decrease of seed quality, deforming the kernels and turning them badly flavored (Smith and Pitts 1974).

21.4.7 Subfamily Sehirinae

Species of the subfamily Sehirinae are easily recognized among Neotropical Cydnidae by the absence of the row of setigerous punctures in the lateral margin of pronotum and the shape of the tarsal segment II distinctly narrower than I and III. Froeschner (1960) also called attention to the presence of narrow, creamy white margins of the pronotum, corium, and abdomen (Fig. 21.6), a unique pattern among cydnids in the Neotropical region.

Fig. 21.39 *Tominotus communis*, habitus dorsal view (Photo CF Schwertner)

Fig. 21.40 Distribution maps of Cydninae (**a**, **b**, and **c**) and Sehirinae (**d**) in the Neotropical region. (**a**) *Cyrtomenus bergi* and *C. mirabilis*; (**b**) *Pangaeus bilineatus*; (**c**) *Tominotus communis*; (**d**) *Sehirus cinctus cinctus*

Sehirinae is predominantly Palearctic (Lis 1999a, 2002); only the genus *Sehirus* Amyot and Serville has been found in the Western Hemisphere (Table 21.1). The single endemic New World species, with three recognized subspecies, range from southern Canada to Mexico (Froeschner 1960). *S. cinctus cinctus* is well distributed in Mexico (Fig. 21.40d), reaching the Neotropical region.

Although most of the cydnids seem to live close to the soil or belowground, individuals of Sehirinae are commonly collected in aboveground parts of host plants. Nymphs and adults of *Sehirus* are often caught in various herbs, especially mint species (Lamiaceae). McDonald (1968) reared *S. cinctus albonotatus* Dallas on *Stachys palustris* L. (Lamiaceae), while Rider (2012) found this species in *Physostegia parviflora* Nutt. (Lamiaceae). Besides the phytophagous habit of *Sehirus* spp., individuals of this species were found feeding on the beebread discarded from honeybee colonies. According to Van Engelsdorp and Donovall (2009), several adults of *S. cinctus* were found associated with the beebread, probably feeding on a mixture of pollen and honey stored in the colony cells. These authors also observed *S. cinctus* nectaring on *Physostegia virginiana* (L.) Bentham (Lamiaceae).

Like the related group Parastrachiidae, burrower bugs of the Sehirinae (i.e., *S. cinctus* and *Adomerus* spp.) present subsocial behavior (maternal care), which includes production of trophic eggs, egg guarding, protection of nymphs, and progressive provisioning (Sites and McPherson 1982; Mukai et al. 2010, 2012; Nakahira et al. 2013). The subsocial behavior in Sehirinae always occurs in the ground (see description for *S. c. cinctus* below).

Sehirus cinctus cinctus **Palisot (Figs. 21.6, 21.10, 21.13, 21.21, and 21.40d)**

Sites and McPherson (1982) described the life history of Illinois populations of *S. c. cinctus*. According to these authors, adults emerged from overwintering sites and walk near the base of host plants. After oviposition, the female remains atop of round clusters of eggs, which are deposited into a shallow hole in the soil. This maternal care behavior is widely studied, in which females brood and provision eggs and gregarious nymphs. The incubation period is 10.2 days and the egg-adult period is 53.2 days, in average. Females remain with the eggs and early instar larvae for several weeks, guarding them against ants and other predators and feeding them by carrying mint seeds from the surface to the chamber (Southwood and Hine 1950; McDonald 1968). The time duration of maternal care in this species can be affected by maternal age and physiological status (i.e., first vs. second reproduction), with older females showing a decreased amount of care earlier than younger females (Kligh 1997).

Populations of *S. c. cinctus* live in open habitats and show aggregate behavior, feeding on leaves or fallen seeds of mint and other species of plants (Sites and McPherson 1982; Van Engelsdorp and Donovall 2009) (Table 21.2). Although *S. c. cinctus* has been related to some economic important plants (*Prunus* spp., *Helianthus* spp.) (Table 21.2), this species is not considered an agricultural pest in the Neotropical region.

21.5 Concluding Remarks

The cydnids are a diverse and widely distributed group of bugs and in the Neotropical region represent an important part of the true bug fauna. Remarkable features include the unique burrower habit and morphological adaptations for digging, subsocial behavior, important fossil records, and damage to cultivated plants.

Because to the burrowing habits and small size of most of the species, people unnoticed its presence, limiting taxonomic characterization, host plants records, as well as damage and symptoms to cultivated plants.

More comprehensive investigations must be conducted about the biology, ecology, and behavior of cydnids. It is essential to establish methodologies to study this group of heteropterans in natural habitats and under laboratory conditions. Furthermore, the influence of environmental conditions on field populations, dispersal, and seasonal adaptations may also be useful for improving integrated management.

Although the taxonomy of the Cydnidae is considered well understood (Schuh and Slater 1995), still much work on the Neotropical taxa needs to be done. For some species, several reports have been mistaken [e.g., occurrence and damage attributed to *S. castanea* are actually due to the attack of *S. carvalhoi*, Lis et al. (2000)], and a correct identification is essential to define and delineate studies about each species, as well as control and management measures. In some cases, the taxonomy at the species level still awaits revision (e.g., *Cyrtomenus bergi* and *C. mirabilis*), and it is probable that new species will be found (*Amnestus* spp.) (Mayorga and Cervantes 2001, 2005). In addition to the species already reported as economically important, other cydnids might become agricultural pests, and monitoring natural populations of these insects may help to understand such potential.

Finally, studies on the evolution of these bugs are still lacking, and a phylogenetic classification of the group awaits better resolution. Investigations on the phylogenetic relationships of the Neotropical taxa will be crucial to test current classification and evolutionary hypothesis, helping to improve knowledge on this diverse group of true bugs.

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Chapter 22
Stink Bugs (Pentatomidae)

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Abstract The Pentatomidae, representing the fourth largest family within Heteroptera, are one of the most diverse groups with about 800 genera and more than 4,700 species in the world. In the Neotropics, about 230 genera and 1,400 species are included in seven subfamilies of the world's nine subfamilies; four subfamilies are exclusively of the Neotropics. In this chapter, for each subfamily, a diagnosis, an overview of the classification, and information on life history, ecology, and economic importance are given. Comprehensive keys and diagnosis to the subfamilies, tribes, and genera for the Neotropical Region, including Mexico, Central and South America, and the West Indies, are also given.

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22.1 Introduction

Pentatomidae is the fourth most numerous family within Heteroptera including more than 4,700 species in more than 800 genera (Table 22.1). Pentatomids are represented in all zoogeographical regions although the tropical and subtropical faunas are more diverse; they are commonly known as stink bugs. Rolston and McDonald (1979), Rolston (1981, 1984), and Rolston et al. (1980) provided keys to the identification of subfamilies, tribes, and genera of the Western Hemisphere. The subfamilies Asopinae, Cyrtocorinae, Discocephalinae, Edessinae, and Pentatominae are widely represented in the Neotropical Region, while Podopinae and Stirotarsinae only have one species each. The subfamilies Cyrtocorinae, Discocephalinae, and Stirotarsinae are exclusively of the Neotropics. The Edessinae, with the exception of two species found in the Southern United States of America (McPherson 1982), occur in the Neotropics.

The asopines have predacious habits and the incrassate rostrum is the morphological feature common to the group as an adaptation to predatory behavior. They are found in all zoogeographical regions.

Table 22.1 Number of genera and species in the subfamilies and tribes of Pentatomidae of the Neotropical region

	World		Neotropics	
Subfamily/tribe	Genera	Species	Genera	Species
Asopinae	63	357	23	100
Cyrtocorinae	4	11	4	11
Discocephalinae	76	315	76	315
Discocephalini	43	192	43	192
Ochlerini	33	123	33	123
Edessinae	7	>300	7	>300
Pentatominae	380	>2,803	116	>667
Carpocorini	106	>800	53	>223
Catacanthini	7	53	5	32
Halyini	82	>390	2	13
Mecideini	1	17	1	4
Menidini	27	>100	2	23
Nezarini	20	150	3	>70
Pentatomini	65	>900	30	>200
Piezodorini	4	>25	1	1
Procleticini	11	33	11	23
Sciocorini	11	>150	1	3
Strachiini	14	>100	1	13
Unplaced	32	92	6	53
Podopinae	62	255	1	1
Stirotarsinae	1	1	1	1
Total			228	>1,400

Cyrtocorinae is a small subfamily, cryptically colored with the tree bark substratum where they live; the scutellum with a median, long, and tough spine is a morphological feature found in all species. They are distributed from Mexico to Argentina.

Discocephalinae includes two tribes, Discocephalini and Ochlerini, with more than 300 species almost all medium sized and dark colored. The morphology of the immatures and the biology within the group are poorly known. Exceptions are found in Discocephalini, the genus *Antiteuchus* Dallas which is a natural host of cacao (*Theobroma cacao*) in the Amazon region and shows maternal care habits, and Ochlerini, the genera *Lincus* Stål and *Macropygium* Spinola of which some species are important vectors of *Phytomonas* spp. (Trypanosomatidae) in palms in South America.

Edessinae includes the most colored and largest stink bugs, with great diversity in the Amazon region, and more than 300 known species. They have in common the strong development of the metasternum. For more than a century, the group was treated as a tribe of Pentatominae but studies in the last two decades raised the taxon to subfamily rank and increased the number of genera to seven.

The subfamily Pentatominae is the most diverse within the Pentatomidae and includes species recorded in all the zoogeographical regions in numbers higher than 3,000 distributed in about 600 genera. About 1/4 of this diversity is present in the Neotropics. They are all phytophagous and many species are economically important as pests of cultivated crops. Pentatominae is not a monophyletic group and does not have a definition based on phylogenetic studies. Different authors consider the classification within Pentatominae as having from 8 to more than 40 tribes. Following Rider's tentative classification, 11 tribes are registered in the Neotropics: Catacanthini Atkinson, Carpocorini Mulsant & Rey, Halyini Amyot & Serville, Mecideini Distant, Menidini Atkinson, Nezarini Atkinson, Pentatomini Leach, Piezodorini Atkinson, Procleticini Pennington, Sciocorini Amyot & Serville, and Strachiini Mulsant & Rey.

The subfamily Podopinae has worldwide distribution but is poorly represented in the Neotropics, with only one species. The subfamily Stirotarsinae was recently erected to include *Stirotarsus abnormis* Bergroth, only known from the northern region of South America.

22.2 Subfamily Asopinae

22.2.1 Introduction

Species of the subfamily Asopinae are predaceous, a secondary condition among pentatomids. More than 350 species and 60 genera are known worldwide (Thomas 1992, 1994). Asopines are easily recognized by the incrassate rostrum (Fig. 22.1), and some species are useful as biocontrol agents (De Clercq 2000, 2008).

Fig. 22.1 *Apateticus lineolatus* (Herrich-Schaeffer), lateral showing detail of the incrassate rostrum (Photo by CF Schwertner)

22.2.2 General Characteristics and Diagnosis

The general morphology of the species is similar to other groups of pentatomids. Diagnostic characteristics include modifications of the head associated to the feeding habits: rostrum strongly incrassate, insertion of the labium very close to the base of labrum, and posterior margins of buccula merged (Gross 1975; Gapud 1991). The group also shared the presence of the genital plates of the male pygophore and presence of thecal shield (Gapud 1991; Gapon and Konstantinov 2006).

22.2.3 General Biology and Ecology

Asopines predate insects and other small organisms, usually slow and soft-bodied individuals, i.e., larvae of Lepidoptera, Diptera, and Hymenoptera (Schuh and Slater 1995; De Clercq 2008). Most species seems to be generalists, but some may have a more restricted diet (i.e., oligophagous) or may be related to specific habitats (De Clercq 2000, 2008). Nymphs and adults are observed sucking plant fluids and water, probably to acquire the basic needs during periods of prey scarcity. However, asopines do not develop unless they have access to nutrients of animal origin, required from the 2nd instar on. Early nymphs (2nd and 3rd instars) tend to attack and feed together, while the late instars and adults tend to attack alone; nymphs and adults may show cannibalism when preys are not available (De Clercq 2000, 2008).

Life cycle of the asopines is similar to that of the phytophagous pentatomids. Adults emerge and start to feed and reproduce using different preys; some species may live up to 3 months. They use visual, chemical, and tactile cues to locate and recognize their prey. Mating behavior is similar to phytophagous species, with males starting courtship by antennal movement. Eggs are laid in masses, on different parts of plants used by adults or on nearby structures. The number of eggs per clutch varies between species, between individuals, or between clutches of the same female. There are five nymphal instars. First instars are not predatory and only need moisture for survival. From the 2nd instar on, they need to feed on prey for survival. Initial nymphs are gregarious and tend to attack in groups; gregarious behavior decreases with the development, and nymphs disperse in search for prey. Incubation period, nymphal development time, prereproductive period, and longevity are quite variable; influence of food and abiotic conditions (temperature and humidity) impact the expression of these traits. Egg parasitoids (Hymenoptera: Scelionidae) are recorded as natural enemies.

Although highlighted as potential agents for pest control, the use of asopines in biological control programs is still limited. Only about 10 % of the species have been the focus of such studies (De Clercq 2008). In the Neotropical Region, species of the genera *Alcaeorrhynchus* Bergroth, *Apateticus* Dallas, *Euthyrhynchus* Dallas, *Brontocoris* Thomas, *Perillus* Stål, *Podisus* Herrich-Schäffer, *Stiretrus* Laporte, *Supputius* Distant, and *Tylospilus* Stål have been the focus of recent studies. Two species, *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas), show great potential in controlling populations of phytophagous insects (Saini 1994; De Clercq 2000). *P. maculiventris* is the only asopine commercially available for augmentative biological control (De Clerq 2008).

22.2.4 Classification and Diversity

In the Neotropical Region, 23 genera and 100 species are known (Table 22.2). Taxonomy of the subfamily Asopinae was revised by Thomas (1992), which includes identification keys to all genera and species of the Western Hemisphere.

Table 22.2 Checklist of genera and species of Neotropical Asopinae (distribution as available in the literature)

Species	Distribution
Alcaeorrhynchus grandis (Dallas)	USA, MEX, TRI, CO, BR, UR, ARG, ECU, BOL, CU, JAM, CR, HON, VEN
Alcaeorrhynchus phymatophorus (P. de B.)	PR, HT, DOR, CU, USA (Florida Keys)
Andrallus spinidens (F.)	USA, MEX, NIC, CR, CU, HON, DOR
Apateticus lineolatus (Herrich-Schaeffer)	USA, MEX, CR, ESAL, PAN, HON, CO, VEN, NIC, ECU,
Apateticus marginiventris (Stål)	USA, MEX
Apoecilus invarius (Walker)	USA, MEX
Brontocoris nigrolimbatus (Spinola)	CHI
Brontocoris tabidus (Signoret)	CHI, PAR, ARG, BR
Colpothyreus flavolineatus (Blanchard)	BOL
Comperocoris roehneri (Philippi)	CHI, ARG
Coryzorhaphis leucocephala Spinola	BR
Coryzorhaphis carneolus Erichson	GUY, BR, PER, BOL, ECU, FG
Coryzorhaphis cruciata Stål	MEX, BEL, HON, PAN, CO, VEN, BR

(continued)

Table 22.2 (continued)

Species	Distribution
Coryzorhaphis superba Breddin	PER, BOL, ECU
Coryzorhaphis egeri Thomas	MEX, CR, HON
Coryzorhaphis dollingi Thomas	ECU
Discocera caynnensis Laporte	BR, PER, SUR, FG
Discocera coccínea (F.)	BR, PER, COL, ECU, SUR, PAR, BOL
Euthyrhynchus floridanus (L.)	USA, MEX, GUA, ESAL, HON, CR, PAN, ECU, BR, BOL, NIC
Heteroscelis servillei Laporte	BR, PER, BOL, ARG, PAR, VEN, GUY, FG, SUR, TRI
Heteroscelis lepida (Stål)	USA, MEX, GUA, PAN, CO, VEN, FG, ECU, HON
Heteroscelis bimaculata (Walker)	BOL, BR, PER, PAN
Heteroscelis robustus Thomas	BR, PAR
Marmessulus nigricornis Bergroth	BR, ARG, URU
Marmessulus brasilianus Schouteden	BR
Oplomus dichrous (Burmeister)	USA, MEX, HON
Oplomus catena (Drury)	BR, FG, ARG, URU, PAR, ECU
Oplomus cruentus (Burmeister)	ARG, BR, PER, URU
Oplomus mutabilis Stål	MEX, GUA, HON
Oplomus ebulinus (Herrich-Schaeffer)	BR, PER, BOL, PAR, ECU
Oplomus salamandra (Burmeister)	COL, VEN, SUR, ECU, BOL, PER, BR
Oplomus marginalis (Westwood)	BR, PAN, COL, ECU, PER, BOL, ARG, VEN, SUR, PAR
Oplomus mundus Stål	USA, MEX, GUA, CR, PAN, NIC, HON
Oplomus pulcher Dallas	MEX, CR, PAN, HON
Oplomus annotatus Uhler	CU
Oplomus punctatus Montandon	ARG
Oplomus pulchiventris Horvath	ARG
Ornithossoma rivieri Kormilev	ARG
Parajalla sanguineosignata (Spinola)	CHI
Perillus confluens (Herrich-Schaeffer)	USA, MEX, GUA, ELS, CR, HON
Perillus circumcintus Stål	USA, CAN, MEX
Perillus bioculatus (F.)	USA, CAN, MEX
Perillus splendidus (Uhler)	USA, MEX
Podisus aenescens (Stål)	MEX, GUA, HON, CR, PAN, CO, ECU, BOL, PER, ARG, BR, FG, PAR
Podisus sculptus Distant	CR, PAN, PER, BOL
Podisus formosus Costa Leite	BR
Podisus mucronatus Uhler	USA (Florida), CU, PUR, DOR
Podisus falcatus Distant	GUA, HON, CR
Podisus semialbus (Walker)	BR, VEN
Podisus curvispina Bergroth	BR

(continued)

Table 22.2 (continued)

Species	Distribution
Podisus cornutus (Dallas)	CO, BR
Podisus gundlachii (Guérin-Méneville)	CU
Podisus borinquensis Barber	PUR
Podisus congrex (Stål)	MEX, GUA, CR, ESAL, PAN, VEN, ECU, HON
Podisus crassimargo (Stål)	BR, ECU, COL, VEN, CHI, PAN
Podisus volxemi Distant	BR, ECU
Podisus tinctus (Dallas)	COL, ECU
Podisus subferrugineus Barber & Bruner	CU, JAM
Podisus sagitta (F.)	USA (Texas), MEX, GUA, ESAL, HON, NIC, CR, PAN, VEN, JAM, GRE, DRE, HAI, DOR, PUR, TRI, Curacao, CU, BAH
Podisus nigrispinus (Dallas)	BR, PAN, CR, BOL, ARG, PER, ECU, SUR, COL, GUY, PAR
Podisus distinctus (Stål)	ECU, BOL, COL, BR, VEN, FG, PAR, ARG, PER
Podisus maculiventris (Say)	USA, MEX, CAN, HAI, DRE, BAH
Podisus neglectus Westwood	USA, MEX
Podisus affinis Distant	MEX, GUA, HON, PAN
Podisus mexicanus Distant	MEX
Podisus nigriventris Distant	MEX, GUA, NIC, HON, CR, PAN, COL
Podisus insignis Distant	GUA
Podisus trucidatus Thomas	MEX, HON, CR, PAN
Podisus ventralis (Dallas)	VEN, BR, ECU, PER, ARG
Podisus sordidus (Stål)	ECU (Galapagos)
Podisus rostralis (Stål)	BR, BOL
Podisus pallipes (Dallas)	VEN, BR, ECU, ARG
Podisus mactans Thomas	ECU
Podisus serieventris Uhler	CAN, USA, MEX
Stiretrus quinquepunctatus Germar	HAI, DOR
Stiretrus decemguttatus (Lepeletier & Serville)	BRA, SUR, BOL, PAR, URU, ARG, PER
Stiretrus decastigmus (Herrich-Schaeffer)	ARG, BRA, BOL, PAR
Stiretrus erythrocephalus (Lep. & Serville)	ARG, BRA, BOL, PAR, URU
Stiretrus anchorago (F.)	USA, MEX, GUA, ESAL, CR, HON, PAN, NIC
Stiretrus bifrenatus Breddin	COL, ECU, PER, BRA, URU
Stiretrus loratus Germar	BR, BOL
Stiretrus cinctellus Germar	BR, ARG
Supputius typicus Distant	MEX, CR, PAN, VEM, COL, ECU, BR, HON
Supputius cincticeps (Stål)	BR, VEN, PR, CHI, BOL, ARG
Supputius pulchricornis (Stål)	MEX
Tylospilus armatus Thomas	ARG
Tylospilus cloelia (Stål)	MEX, HON, PAN, COL, BOL, BR, PAR, ARG
Tylospilus chilensis (Spinola)	CHI, ARG

(continued)

Table 22.2 (continued)

Species	Distribution
Tylospilus nigrobinotatus (Berg)	ARG, BRA, URU
Tylospilus acutissimus Stål	USA, MEX, NIC, COL, ANT, DOR
Tylospilus megaspilus (Walker)	BR
Tylospilus distans Bergroth	BR, CHI
Tylospilus peruvianus (Horvath)	PERU, SUR, BR
Tynacantha marginata Dallas	BR, ARG, BOL, PER, COL, ECU, PAR, URU
Tynacantha splendes Distant	PAN, CR
Tyrannocoris rex Thomas	BR, VEN
Tyrannocoris nigriceps Thomas	BR, ARG
Tyrannocoris rideri Thomas	PUR
Tyrannocoris jole (Stål)	MEX, HON, CU, HAI, RDO
Zicrona americana Thomas	USA, MEX

Since then, studies about morphology, biology, and distribution records of some of the Neotropical species have been published (see Sects. 2.5 and 2.6).

Key to the genera of subfamily Asopinae with species included in biological control studies in the Neotropical Region (adapted from Thomas 1992). Number in superscript indicates Neotropical genera that are keyed in the same step (see list at the end of the key).

1. Scutellum greatly enlarged, covering most of the abdomen, apex surpassing coria in length, almost attaining apex of abdomen (Fig. 22.2) .... *Stiretrus* Laporte[1,2]

1′. Scutellum not covering most of the abdomen, usually shorter than coria (Figs. 22.3 and 22.4) 2

2. Apical part of the scutellum enlarged, equal in length or longer than the frenal margin of the scutellum, and about as wide as the corium (Figs. 22.3 and 22.5) .... 3[3]

2′. Apical part of the scutellum small, shorter than the frenal margin and much narrower than the corium (Fig. 22.4) 4

3. Frenal margin of the scutellum shorter than the postfrenal scutellum; protibia usually expanded... *Oplomus* Spinola (Fig. 22.5)

3′. Frenal margin of the scutellum longer than postfrenal scutellum; protibia always prismatic, never expanded.. *Perillus* Stål (Fig. 22.3)

4. Scent gland with elevated peritreme, surrounded by evaporatoria (Fig. 22.6) 5

4′. Ostiole of scent gland without elevated peritreme, terminating in short or long sulcus not surrounded by evaporatoria (Fig. 22.7) .... *Alcaeorrhynchus* Bergroth[4] (Fig. 22.8)

5. Protibiae dilated, expanded... *Euthyrhynchus* Dallas[5]

5′. Protibiae not dilated.. 6

6. Base of the abdomen with anteriorly directed tubercle or spinous process (Fig. 22.9).. 7

6′. Base of the abdomen may be prominent but without forwardly directed tubercle or spinous process ....*Supputius* Distant (in part)[6] (Fig. 22.10)

7. Rostral segment II distinctly longer than III and IV combined ....*Supputius* Distant (in part)[7]

7′. Rostral segment II shorter or subequal in length to III and IV combined .... 8[8]

8. Abdominal spine long, extending to mesocoxae; posterior tibiae terete; most or all of the dorsal surface of the head with pale colorless punctuation 9

8′. Abdominal spine usually short, not surpassing metacoxae; posterior tibia usually sulcate; dorsal surface of the head densely punctuate 10

9. Scent gland peritreme long, reaching more than half way to pleural edge; anterolateral pronotal margin dentate to spinulose .... *Brontocoris* Thomas

9′. Scent gland peritreme short, reaching less than halfway to the pleural edge; anterolateral pronotal margin rugulose, smooth (Fig. 22.11) ....*Tylospilus* Stål (Fig. 22.12)

10. Inner margins of jugae distinctly convergent (Fig. 22.13); males with glandular patches of silk hairs on abdominal venter..........*Apateticus* Dallas[9] (Fig. 22.14)

10′. Inner margins of jugae parallel or concave but never convergent (Fig. 22.15); males without glandular patches of silk hairs on abdominal venter ....*Podisus* Herrich-Schäffer (Figs. 22.4, 22.16, and 22.17).

1, *Colpothyreus* Stål; 2, *Discocera* Laporte; 3, *Heteroscelis* Laporte, *Coryzorhaphis* Spinola, *Comperocoris* Stål, *Marmessulus* Bergroth; 4, *Parajalla* Distant, *Rhacognathus* Fieber, *Zicrona* Amyot & Serville; 5, *Eocanthecona* Bergroth; 6, *Ornithosoma* Kormilev, *Andrallus* Bergroth; 7, *Picromerus* Amyot & Serville; 8, *Thynacantha* Dallas, *Tyrannocoris* Thomas; 9, *Apoecilus* Stål

22.2.5 Main Species

De Clercq (2000) reviewed the most studied species of asopines (main and secondary) in a world basis and discussed information available for each one. In this and the next section, we present a brief characterization for some of the common Neotropical species that have been the focus of recent studies.

Fig. 22.2 *Stiretrus anchorago* (F.), dorsal view (Courtesy of G. Fauske)

Fig. 22.3 *Perillus bioculatus* (F.), dorsal view (Courtesy of G. Fauske)

Fig. 22.4 *Podisus maculiventris* (Say), dorsal view (Photo by CF Schwertner)

Brontocoris tabidus (Signoret)

The genus *Brontocoris* included only two species, and *B. tabidus* differs from *B. nigrolimbatus* (Spinola) by the anterolateral pronotal margin crenulate and connexivum with a black spot in each anterolateral and posterolateral angles (Thomas 1992; Rider 2014); in *B. nigrolimbatus* the pronotal margin is spinulose and the connexivum uniformly pale yellow. Considering a promising biological agent in Brazil (Zanuncio et al. 1994; De Clercq 2000), it has been the focus of several studies (e.g., Oliveira et al. 2005; Zanuncio et al. 2006; Lemos et al. 2009, 2010; DeMenezes et al. 2013; Pires et al. 2011).

Perillus bioculatus (F.) (Fig. 22.3)

Among the species included in the genus, *P. bioculatus* can be recognized by the following suite of characters: presence of an ante-apical spine or tubercle in the profemur, pronotum tumid and without lunate black mark on the anterior half, abdominal spiracles enclosed within black area, and dorsal punctuation widely spaced (Thomas 1992). The two-spotted stink bug is one of the main predators of the Colorado potato beetle (*Leptinotarsa decemlineata*, Chrysomelidae); the biology and other aspects of

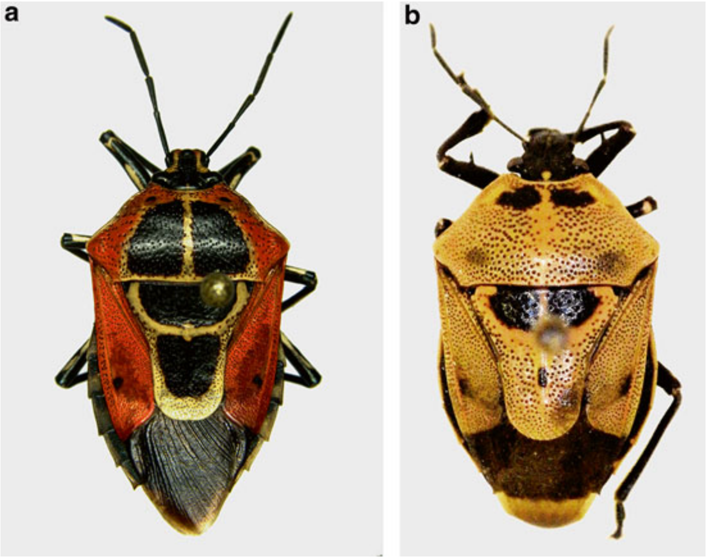

Fig. 22.5 (**a**) *Oplomus catena* (Drury), dorsal view (Photo by CF Schwertner). (**b**) *Oplomus dichrous* (Burmeister), dorsal view (Courtesy of G. Fauske)

Fig. 22.6 *Supputius cincticeps* (Stål), ventral view showing detail of the evaporatorium (Photo by CF Schwertner)

Fig. 22.7 *Alcaeorrhynchus grandis* (Dallas), ventral view showing detail of the evaporatorium (Photo by CF Schwertner)

Fig. 22.8 *Alcaeorrhynchus grandis* (Dallas), dorsal view (Photo by CF Schwertner)

Fig. 22.9 *Apateticus lineolatus* (Herrich-Schaeffer), ventral view (Photo by CF Schwertner)

Fig. 22.10 *Supputius cincticeps* (Stål), dorsal view (Photo by CF Schwertner)

Fig. 22.11 *Tylospilus distans* Bergroth, head in dorsal view (Photo by CF Schwertner)

this asopine have been investigated by several authors (reviewed in De Clercq 2000; see also Adams 2000, 2001; Wittmeyer and Coudron 2001; Coudron et al. 2002; Coudron and Kim 2004; Matlock 2005; Greenstone et al. 2010).

Podisus maculiventris (Say) (Figs. 22.4 and 22.15)

Thomas (1992) recognized several groups of species within *Podisus*, including the *maculiventris* group of species. Species included in this group can be recognized by the dorsal surface of pronotum without *calli*; anterolateral margins of the pronotum

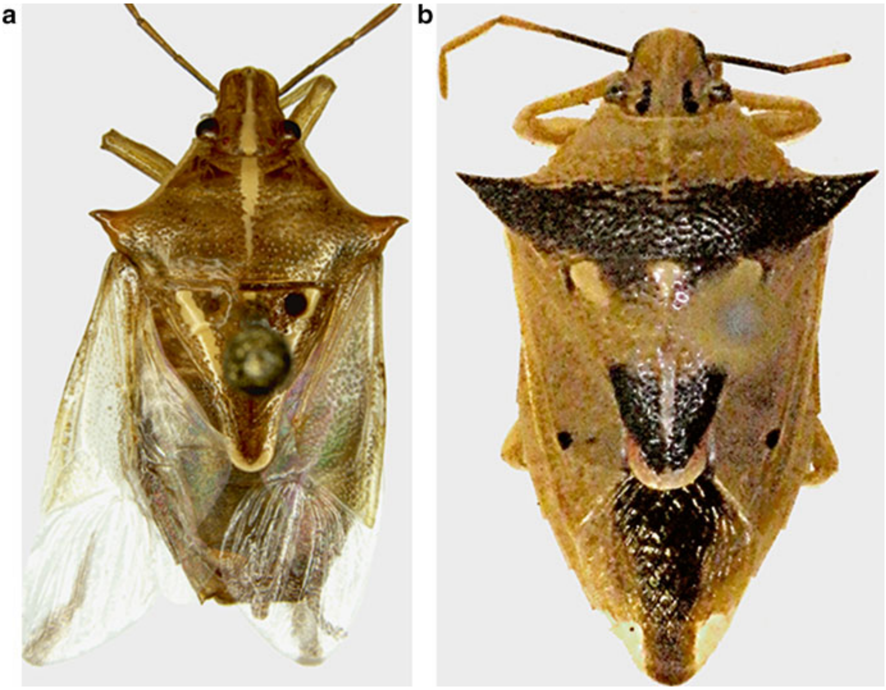

Fig. 22.12 (**a**) *Tylospilus distans* Bergroth, dorsal view (Photo by CF Schwertner). (**b**) *Tylospilus acutissimus* Stål, dorsal view (Courtesy of G. Fauske)

not inflated and dentate, crenulate, or rugulose; and humeral angles simple and directed laterad, not elongately produced (Thomas 1992). Within the group, *P. maculiventris* is the only species with humeral angles laterally produced in acuminate angles (Fig. 22.4) and with the abdominal spine reaching between metacoxae. It is the most common species in North America, also known as spined soldier bug, and extensive literature about its biology, role, and potential use in biological control programs has been published (De Clercq 2000, 2008).

Podisus nigrispinus **(Dallas) (Fig. 22.16)**

Species included in the *sagitta* group, which is similar to the *maculiventris* group (see above diagnosis of *P. maculiventris*), however, have the humeral angles distinctly bifid or emarginate (Fig. 22.16) (Thomas 1992). Within the group, *P. nigrispinus* can be recognized by the last rostral segment darker than the others and by the anterolateral margins of pronotum paler than the pronotal disk. One of the most common species in the Neotropical Region, *P. nigrispinus* has been found attacking several pest insects (De Clercq 2000). Several studies has been carried out regarding

Fig. 22.13 *Apateticus lineolatus* (Herrich-Schaeffer), head in dorsal view (Photo by CF Schwertner)

Fig. 22.14 *Apateticus lineolatus* (Herrich-Schaeffer), dorsal view (Photo by CF Schwertner)

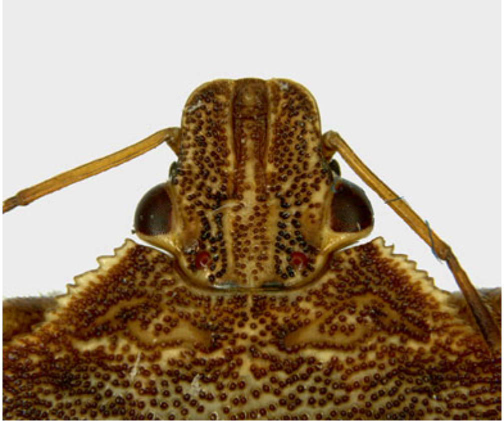

Fig. 22.15 *Podisus maculiventris* (Say), head in dorsal view (Photo by CF Schwertner)

Fig. 22.16 *Podisus nigrispinus* (Dallas), dorsal view (Photo by CF Schwertner)

the biology, predation potential in different agroecosystems, and rearing methods of this species, also known as the Brazilian soldier spined bug (De Clercq 2000; Vivan et al. 2003; Lemos et al. 2003, De Medeiros et al. 2004; Sousa-Souto et al. 2006; Torres et al. 2006; Neves et al. 2009; Rodrigues et al. 2009; De Bortoli et al. 2011; Soares et al. 2011; Laumann et al. 2013; Vacari et al. 2013).

Fig. 22.17 *Podisus sagitta* (F.), dorsal view (Photo by CF Schwertner)

***Supputius cincticeps* (Stål) (Figs. 22.6 and 22.10)**

The genus *Supputius* include three species, and *S. cincticeps* can be recognized by rostral segment II as long as III and IV combined, apex of scutellum concolorous with the disk and abdominal tubercle strongly produced, reaching between metacoxae (Thomas 1992). Although not so common as *P. nigrispinus*, this species is also found attacking several pests in South America (De Clercq 2000; Zanuncio et al. 2004, 2005a, b; De Castro et al. 2013).

22.2.6 Secondary Species

The species included in this section are far less studied than the species included in the previous section, and little is known about them besides their distribution and morphological aspects. However, they represent common Neotropical asopines and potential control agents in biological control programs.

***Alcaeorrhynchus grandis* (Dallas) (Figs. 22.7 and 22.8)**

This is the most common and widespread species of *Alcaeorrhynchus*, the only one found in the continental Americas (Thomas 1992). The genus include only two species, which can be identified by the direction of the spined humeral angle: it is bent somewhat forward in *A. grandis* and directed laterad in *A. phymatophorus*. The species *A. grandis* is the largest Neotropical asopine and is associated to several cultivated ecosystems, attacking lepidopterous larvae (Malaguido and Panizzi 1998a; De Clercq 2000).

Apateticus lineolatus (Herrich-Schaeffer) (Figs. 22.1, 22.13, and 22.14)

The genus *Apateticus* include two species, and *A. lineolatus* can be recognized by the posterior angle of the pronotum without a tooth and the basal abdominal spine robust, protruding between metacoxae (Thomas 1992). There are few studies about this species (De Clercq 2000); in Mexico, *A. lineolatus* was found feeding in larvae of the beetles *Epilachna varivestis* (Coccinellidae) and *Leptinotarsa* spp. (Chrysomelidae), pests of important crops as beans and potatoes.

Euthyrhynchus floridanus (L.)

This genus is monotypic, despite the high color polymorphism found in *E. floridanus*; Thomas (1992) mentioned that North and South American populations represent distinct lineages (forms) of this species. A very conspicuous species, with red and metallic blue coloration, with extensive literature on bionomics under laboratory conditions is available (De Clercq 2000; Briceño 2014). However, only a few notes about its life history on the field are known (Avila-Núñez et al. 2009).

Oplomus dichrous (Burmeister) (Fig. 22.5b)

The genus *Oplomus* includes 12 species, and *O. dichrous* can be recognized by two unique characters: prosternum expanded between procoxae and juga longer than tylus, contiguous and deflexed anteriorly in males (Thomas 1992). A common species within it distribution range, it seems to be an important predator of *L. decemlineata* Mexico (De Clercq 2000), but laboratory and field tests showed that *O. dichrous* has little potential as control agent in cool climates.

Podisus spp.

Podisus sagitta (F.) (Fig. 22.17) and *P. distinctus* (Stål)

Both species belong to the *sagitta* group (Thomas 1992), together with *P. nigrispinus* (see diagnose for *P. nigrispinus* above). They can be separated by the coloration of the rostral segments: the last rostral segment darker than the three preceding segments in *P. sagitta* and the first rostral segment distinctly paler than the three succeeding segments in *P. distinctus*. Besides, both species have the anterolateral margin of pronotum concolor, which allows separating these species from *P.*

nigrispinus. The biology of *Podisus* spp. is similar, and *P. sagitta* and *P. distinctus* have been studied as control agents of different pests in North and South America (De Clercq 2000; Matos Neto et al. 2004).

Podisus rostralis (Stål)

This species is included in the *maculiventris* group, together with *P. maculiventris* (see diagnosis above) and another eight species of *Podisus* (Thomas 1992). The group is widely distributed in the American continent; however *P. rostralis* has a more restricted distribution (Table 22.2). It can be recognized among other species of *Podisus* by a unique set of characters: dorsum of the head densely punctuated, hemelytral membrane transparent with a mesial dark blotch, and basal rostral segment contrastingly pale to three dark succeeding segments. In Brazil, *P. rostralis* was found attacking pests of *Eucalyptus* spp. and information about its biology under laboratory conditions are available (Molina-Rugama et al. 1998; Matos Neto et al. 1999; Lemos et al. 2005).

***Stiretrus* spp.**

The genus includes eight species; *S. anchorago* (F.) (Fig. 22.2) and *S. decemguttatus* (Lepeletier & Serville) can be recognized by the protibia distinctly dilated, anterolateral margins of the pronotum concavely sinuate to subrectilineal (never convex), and basal abdominal spine long, protruding between mesocoxae (Thomas 1992). The species can be separated by the length of the ostiole: *S. anchorago* has the ostiole long, reaching at least halfway to the pleural margin; in *S. decemguttatus* it is short, reaching one-third the distance to the pleural margin.

The distribution of both species does not overlap, and *S. anchorago* is the only species within the genus that occurs in the north of Panama (all the other species of *Stiretrus* are known from South America). More data on the bionomics and life history of *S. anchorago* are available (De Clercq 2000), but its effectiveness in agroecosystems still needs more attention. More recently, Paleari (2013) studied the development, the polymorphism, and some ecological aspects of *S. decemguttatus*.

***Tylospilus acutissimus* (Stål) (Fig. 22.12b)**

This species can be recognized within the genus *Tylospilus* by humeral angle spinose, often slightly directed forward and without a post-apical tooth on the posterior edge; base of the scutellum with only indistinct calluses at basal angles, never elongated; ostiole extending halfway to the pleural margin; and basal abdominal spine reaching almost to the mesocoxae (Thomas 1992). Although considered a common species in some parts of the United States, this species has received minor attention and only scattered data about its biology is known (De Clercq 2000).

22.2.7 *Remarks*

The subfamily Asopinae includes a diverse group of species, with worldwide distribution and relatively well-known taxonomy (Thomas 1992, 1994). However, studies in a phylogenetic context are still lacking for the group. The monophyly of the subfamily and included genera was never questioned, but its position within Pentatomidae and the phylogenetic relationships within the subfamily are unresolved.

The unique feeding habits within the superfamily Pentatomoidea make the group an exciting subject of study in many distinct research areas such as evolutionary biology, comparative physiology, and crop protection.

Knowledge about the Neotropical asopines is mostly restricted to species related to agroecosystems. Details about species distribution, life history traits, comparative morphology, and molecular data are still scarce and will be crucial to understand the diversity and evolution of the group in the Neotropical Region.

22.3 Subfamily Cyrtocorinae

22.3.1 *Introduction*

This exclusively Neotropical taxon was revised by Packauskas and Schaefer (1998); it includes four genera and 11 species. Besides the record of *Cyrtocoris trigonus* (Germar) from California (Banks 1910; Horváth 1916; Brailovsky et al. 1988), Packauskas and Schaefer (1998) agreed with Henry and Froeschner (1988) that the lack of any subsequent discovery of *Cyrtocoris* White in the United States makes Bank's record suspect. According to Packauskas and Schaefer (1998), Kormilev (1955) appears to have been the first author to present evidence for raising Cyrtocorinae to family rank as distinct from the Pentatomidae allying Cyrtocoridae with Cydnidae.

22.3.2 *General Characteristics and Diagnosis*

Length 6–10 mm. Body black to brown in ground color, often covered with brown-tan and/or white scalelike setae, giving the bug a lighter brown color dorsally and ventrally. Ventral covering usually variegated with areas of deep brown and yellow-white. Body broadly rectangular in dorsal view, in lateral view convex above, and nearly flat below; trapezoidal to rectangular in posterior view. Head subquadrate, angles rounded in front of the eyes; mandibular plates developed, flattened, and depressed on either side of clypeus. Apex of clypeus at base of rostrum expanded laterally beyond bucculae. Bucculae extending past eyes. Antennae arising from below eyes; V segment longest, slightly swollen distally; II shortest (very short). Rostrum and antennae fitting into midventral sulcus on thoracic sterna. Pronotum broadly trapezoidal; humeri greatly expanded and directed downward anterolaterally. Scutellum broadly U-shaped, extending to end of the abdomen; most of corium and sometimes part of membrane exposed. Tarsi 2-segmented; 2nd segment 2–4 times as long as 1st. Metathoracic scent gland opening sustained by an auricle peritreme. Abdominal segments II–IV exposed dorsally, strongly extended laterally and angled ventrally. Each abdominal spiracle closer to preceding segment than to lateral edge of its own segment or to posterior segment; 2nd abdominal spiracle on membranous anterior of segment. Abdominal sterna III–VII laterally with one pair of trichobothria side by side, those on anterior sterna lateral to spiracle; trichobothria all of equal size.

22.3.3 General Biology and Ecology

Cyrtocorines are of minor economic importance and they are not commonly found. As a consequence little is known about their biology. *C. trigonus* were found feeding on stems of the weed plant arrowleaf sida, *Sida rhombifolia* L. (Malvaceae), in Londrina, Paraná State, Brazil. Despite egg deposition in the laboratory, nymphs did not develop on this plant. Nymphs and adults of *Cyrtocoris egeris* Packauskas & Schaefer were observed feeding on immature soybean pods in Argentina (Reconquista, Santa Fé Province). Under laboratory conditions, nymphs of neither species could be reared beyond the 3rd instar (Schaefer et al. 2005). Adult and nymphal *C. egeris* fed gregariously on the stems of *Acalypha diversifolia* Jacquin (Euphorbiaceae) and moved to the leaves when these became available; adults could also feed on *Piper* sp. (Piperaceae) (Brailovsky et al. 1988). *Cyrtocoris gibbus* (F.) is reported to feed on stems of other legume plants such as the trees *Acacia* sp. and "bracatinga" (*Mimosa scabrella* Bentham), in Rio de Janeiro (Costa Lima 1940; Silva et al. 1968). Adults of *C. trigonus* feed on *Syngonium podophyllum* Schott (Araceae), *Acalypha* sp. (Euphorbiaceae), *Piper* sp., and *Pothomorpha umbellatum* (L.) Miquel (Piperaceae) (Brailovsky et al. 1988, as *C. obtusus* Horváth).

Not many studies have been published focusing on Cyrtocorinae immatures. Brailovsky et al. (1988) described the egg and nymphs of *C. egeris* [as *Cyrtocoris trigonus* (Germar)] from Mexico, including notes on the biology of the species. Schaefer et al. (1998) described the last three instars of *C. egeris* from Ecuador. Bianchi et al. (2011) studied under SEM the egg and the 1st and 5th instars of *C. egeris*; their results corroborate the hypothesis of Schaefer et al. (1998) on the absence of spiracles on urosternite I of nymphs and the trichobothrial arrangement (1 + 1 trichobothria on 1st instar and 2 + 2 trichobothria on following instars) contrary to Brailovsky et al. (1988). Also, the placement of the trichobothria relative to the spiracle on different sterna, becoming more medial posteriorly, described for the later instars and adult of *C. egeris* in Schaefer et al. (1998) were confirmed by Bianchi et al. (2011). The presence of three irregular rows of aero-micropylar processes in the egg stage and the large amount of dorsal abdominal sclerotization in the nymphal stage, as stated by Schaefer et al. (1998), seem to be distinctive features of Cyrtocorinae, comparable to the degree of modification of the adult stage. On the other hand, barrel-shaped eggs and the pattern of the nymphal morphology are shared by Cyrtocorinae and other subfamilies of the Pentatomidae (Bianchi et al. 2011).

22.3.4 Classification and Diversity

Cyrtocorinae includes four genera, three of them monotypic and one with eight species: *Ceratozigum* Horváth, monotypic with *C. horridum* (Germar) (Fig. 22.18a, b) registered for Brazil, Panama, Peru, and Venezuela; *Cyphothyrea* Horváth, monotypic, with *C. erosa* Horváth, from Peru and Brazil; *Cyrtocoris* White, the most diverse genus, including eight species – *C. andicola* Horváth (Peru), *C. egeris* Packauskas & Schaefer (Mexico through Brazil), *C. gibbus* (F.) (widely distributed), *C. montanus* Horváth (Peru), *C. obtusus* Horváth (Brazil), *C. paraensis* Pirán (Southern Brazil), *C. simplex* Horváth (Brazil), and *C. trigonus* (Germar) (Mexico through Argentina) – and *Pseudocyrtocoris* Jensen-Haarup, monotypic with *P. laceratus* (Herrich-Schäffer) from Argentina and Brazil.

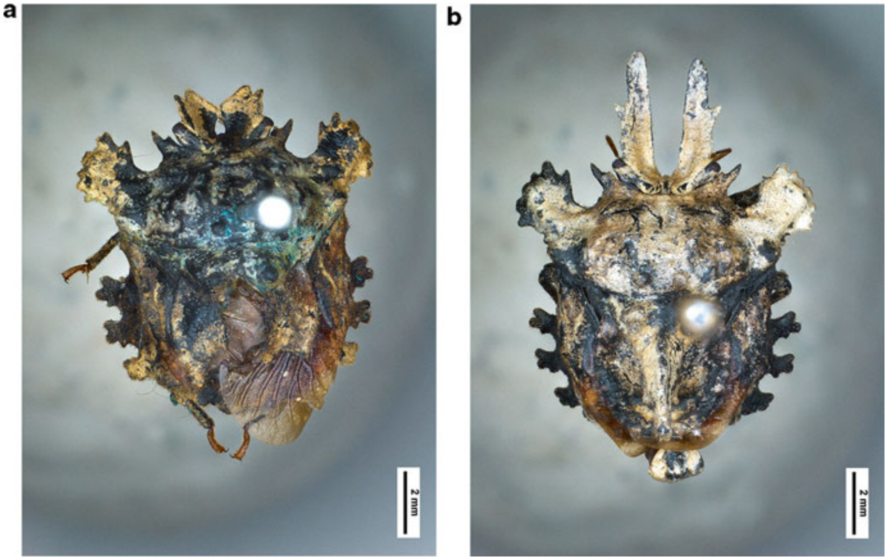

Fig. 22.18 *Ceratozigum horridum* (Germar): (**a**) female; (**b**) male (Photos by A Ferrari)

Packauskas and Schaefer (1998) provided detailed redescriptions of the taxa and keys to separate the genera and the *Cyrtocoris* species, beside the intraspecific variability found in this genus; they also discussed the peculiar sexual dimorphism found in *Ceratozigum horridum* (Germar). There are two forms of the head in the males themselves, one form resembling the female mandibular plates (greatly produced anteriorly) and another form (but in no female) where the mandibular plates extend far forward.

Kormilev (1955) appears to have been the first author to present evidence for raising Cyrtocorinae to family rank as distinct from the Pentatomidae allying Cyrtocoridae with Cydnidae. Kormilev's arguments persuaded Rolston and McDonald (1979) to raise Cyrtocorinae, and for the most part Cyrtocoridae has been recognized since. Gapud (1991) separated Cyrtocorinae (as a pentatomid subfamily) from the rest of Pentatomidae by the absence of a triangulin, 2nd valvifers with a distinct median fusion line, and male phallotheca relatively flexible. Packauskas and Schaefer (1998) considered the presence of a triangulin, 2nd valvifers completely fused, and a rigid phallotheca as apomorphies of Pentatomidae minus Cyrtocoridae. Gapud (1991) placed the Cyrtocorinae + Pentatomidae sensu stricto as the most apical taxa, "strongly separated from the rest of Pentatomoidea" by the loss of first valvulae, the absence of the gonangulum, the invagination and dilation on the spermathecal duct, the retention of membranous flaps of the 2nd valvulae, and the presence of an anteroposterior pair of basal sclerites on the spermathecal base. In Grazia et al. (2008) the morphological characters that consistently support the recognition of a broadly conceived Pentatomidae [Cyrtocorinae (Aphylinae + Pentatomidae sensu stricto)] are the loss of gonapophyses 8 and the first *rami*, gonapophyses 9 reduced and fused to gonocoxites 9, gonangulum absent, and the ductus receptaculi dilated and invaginated, forming three distinct walls.

22.4 Subfamily Discocephalinae

22.4.1 Introduction

Discocephalinae (Fig. 22.19) is a group of phytophagous species (77 genera; 307 species) restricted to the Neotropical Region. This subfamily was proposed by Fieber (1860) as the family "Discocephalida." It was treated as a subfamily for the first time by Stål (1868) and considered by Kirkaldy (1909) as a tribe of Pentatominae. More recently, Rolston and McDonald (1979) followed Stål and regarded the group as a subfamily, providing diagnosis and including 23 American genera removed from Halyini (Pentatominae). These 23 genera were later grouped in the tribe Ochlerini by Rolston (1981), and the remaining genera were placed within the nominal tribe Discocephalini. This tribe arrangement of Discocephalinae was followed by subsequent authors.

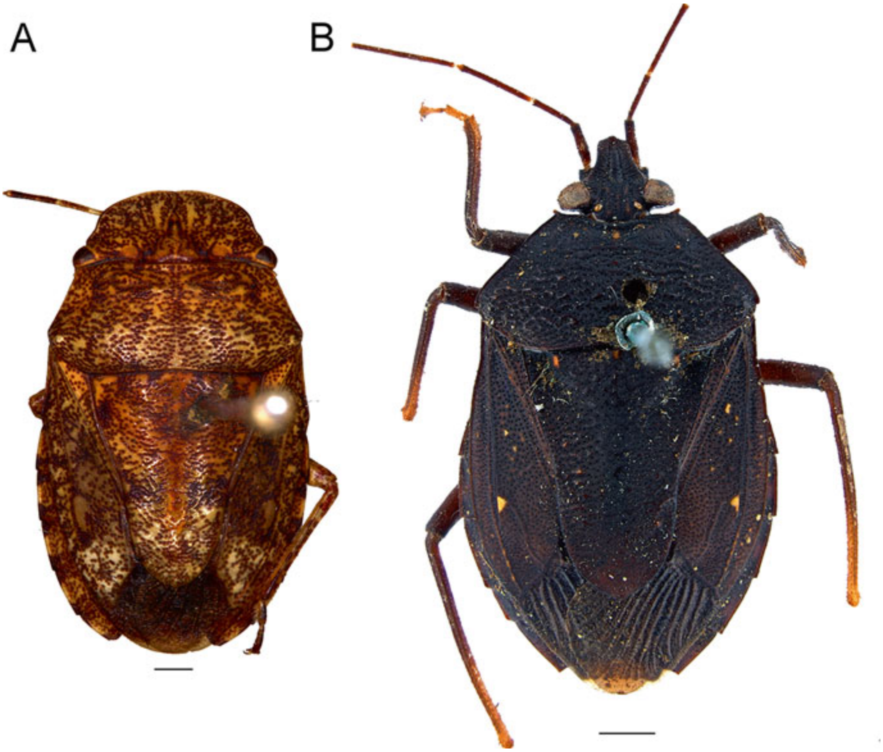

Fig. 22.19 Representative species of Discocephalinae; (**a**) *Discocephala marmorea* Laporte (Discocephalini); (**b**) *Ochlerus signoreti* Breddin (Ochlerini). Scale bars = 1 mm (Photos by LA Campos & TA Garbelotto)

22.4.2 General Characteristics and Diagnosis

This subfamily includes species usually with flattened body, small to medium sized, mottled brown, and black or fuscous. They can be diagnosed primarily by the insertion of the labium, usually arising on or posterior to the anterior limit of the eyes (Fig. 22.20), and the pairs of abdominal trichobothria usually laterad of the imaginary line connecting the spiracles (Fig. 22.21) – in other subfamilies the trichobothria are usually in line with spiracles (Rolston and McDonald 1979; Rolston 1981).

The two tribes of Discocephalinae, Discocephalini and Ochlerini, can be distinguished from one another by the general aspect, color, and the structure of the dorsal surface of the third tarsal segment of the hind legs of females, convex in Discocephalini and shallowly depressed or flattened in Ochlerini (Fig. 22.22) (Rolston 1981).

Fig. 22.20 Ventral view of the head of *Tetragonotum megacephalum* Ruckes, depicting the insertion of the 1st rostral segment (*i*) placed posterior to the anterior limit of eyes (*dashed line*). Scale bar = 1 mm (Photo by LA Campos & TA Garbelotto)

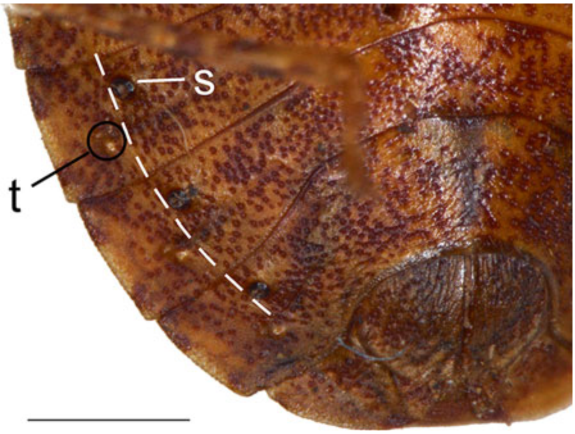

Fig. 22.21 Ventral view of part of the abdomen of *Opophylax extenebratus* Bergroth, depicting the trichobothria (*t*) placed laterad of imaginary line (*dashed line*) connecting spiracles (*s*). Scale bar = 1 mm (Photo by LA Campos & TA Garbelotto)

22.4.3 General Biology and Ecology

Discocephalinae are all phytophagous, considered to be phloem feeders (Waldkircher et al. 2004; Guerra et al. 2011). Some species of *Antiteuchus* Dallas (Discocephalini) are natural hosts of cacao (*Theobroma cacao*) in the Amazon region and in the Brazilian state of Bahia, and some species of *Lincus* Stål and *Macropygium* Spinola

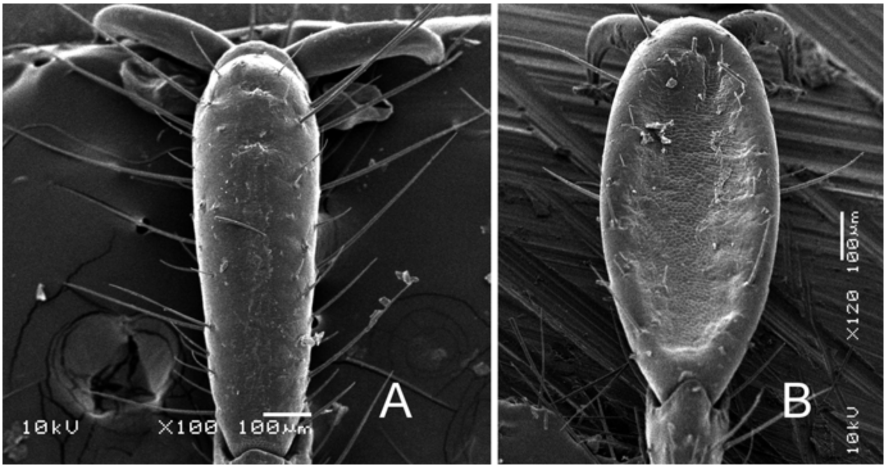

Fig. 22.22 Scanning electron micrographs, third tarsomere of female hind legs of representative species of Discocephalinae, dorsal; (**a**) *Antiteuchus tripterus* (F.); (**b**) *Schraderiellus cinctus* (Ruckes) (Photos by LA Campos & T Roell)

(Ochlerini) are important vectors of *Phytomonas staheli* (Trypanosomatidae) in palms in tropical South America (Costa Lima 1940; Desmier-De-Chenon 1984; Couturier and Kahn 1989; Llosa et al. 1990; Dollet et al. 1993).

The morphology of the immatures and the biology within the group is poorly known; a few studies mention immatures without describing them. Maternal care is recorded in Discocephalini for species of *Antiteuchus* (Eberhard 1975; Santos and Albuquerque 2001a, b) with female bugs protecting both egg masses and immatures; trophobiosis with ants is recorded for an unidentified species of *Lincus* (Stahel 1964) and for *Eurystethus* (*H.*) *microlobatus* Ruckes (Guerra et al. 2011). Field observations by LA Campos and TA Garbelotto indicate that parental care and trophobiosis with ants also occur in *Dinocoris rufitarsus* Ruckes and *Catulona pensa* Rolston, respectively.

22.4.4 Classification and Diversity

Systematics of Discocephalinae is yet in a very early stage. Although a first cladistic approach is available for Ochlerini (Fig. 22.23) (Campos and Grazia 2006), hypotheses of relationship among genera of Discocephalini are based on morphological interpretation by classic authors (e.g., Ruckes, Rolston), although lacking at all for several genera. The relationship among Discocephalinae and other pentatomid subfamilies is also obscure. Campos and Grazia (2006) recovered the monophyly of the subfamily sustained by two exclusive synapomorphies, first segment of labium reaching the prosternum and the dorsal surface of the male proctiger membranous

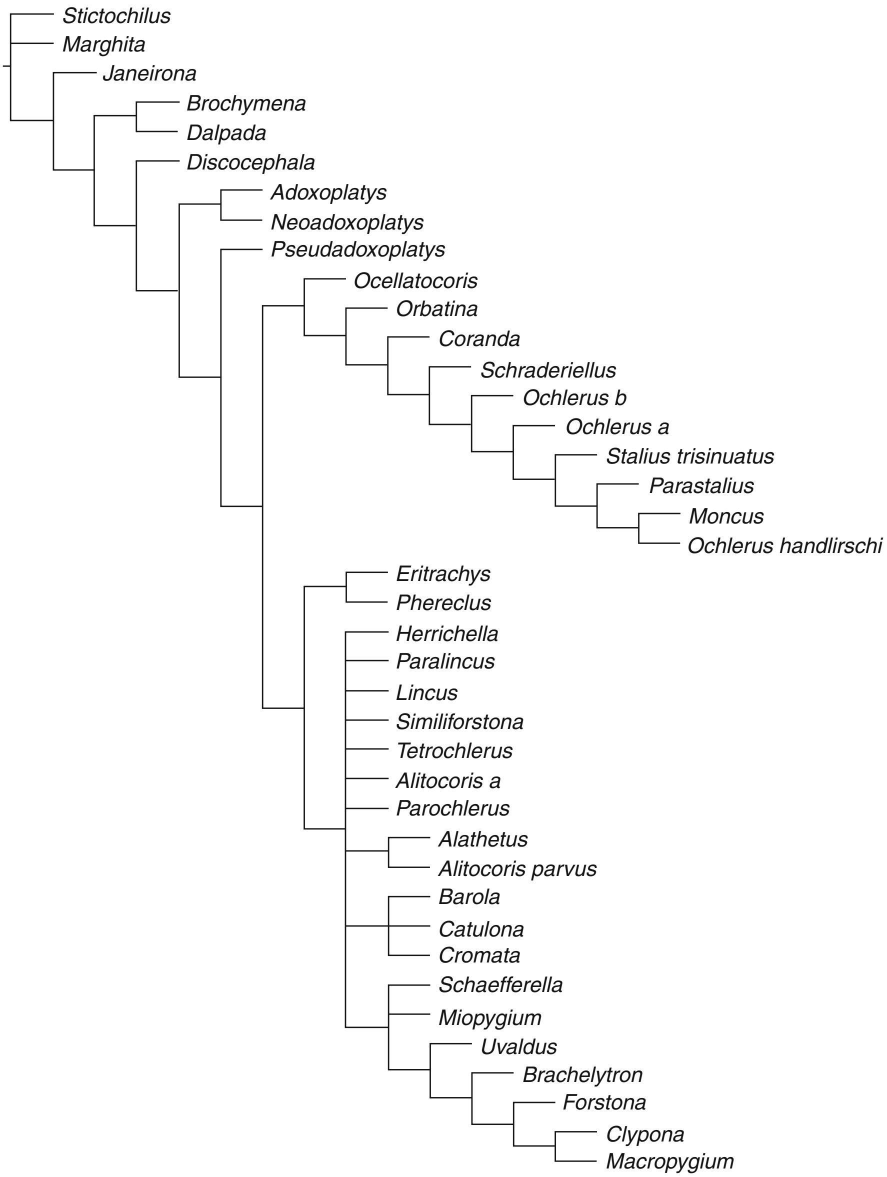

Fig. 22.23 Phylogeny of Ochlerini depicting the relationship between genera; strict consensus tree after successive weighting (Redrawn from Campos and Grazia (2006))

at basal third and one homoplastic synapomorphy, metasternum with median carina. But, as mentioned before, the tribe arrangement adopted for Discocephalinae (with two tribes, Discocephalini and Ochlerini) is the same since Rolston and McDonald (1979) and Rolston (1981).

Discocephalini

Discocephalini comprises 43 genera and 192 species (Table 22.3), including the monotypic fossil genus *Acantocephalonotum* Petrulevičius & Popov. Members of this tribe are brown, often mottled with black or shiny black (Figs. 22.19a and 22.24), although a formal diagnosis for this tribe has never been published. A phylogeny for

Table 22.3 Checklist of genera and species of Discocephalini (distribution as available in the literature)

Genera	Species
Abascantus Stål	*A. grandis* Becker – BRA
	A. lobatus Stål (type) – BRA
	A. pubescens Becker – PER
Ablaptus Stål	*A. amazonus* Stål (type) – BRA
	A. bolivianus Becker & Grazia – BOL
	A. brevirostrum Rolston – COL; CRI; PAN
	A. costaricensis Grazia & Zwetsch – CRI
	A. phoenix Grazia & Zwetsch – CRI
	A. simillimus Becker & Grazia – BOL
	A. tavakiliani Rolston – GUF
	A. varicornis (Walker) – BRA
Acanthocephalonotum Petrulevičius & Popov[a]	*A. martinsnetoi* Petrulevičius & Popov – ARG[a]
Acclivilamna Ruckes	*A. vicina* (Signoret) (type) – BRA
Agaclitus Stål	*A. australis* Becker & Grazia – BRA
	A. dromedarius Stål (type) – BOL; BRA; GUF; PER
	A. fallenii Stål – BRA?; GUF
Alcippus Stål	*A. reticulatus* (Stål) (type) – BRA
Allinocoris Ruckes	*A. nubilus* (Dallas) (type) – BRA
Alveostethus Ruckes	*A. latifrons* (Dallas) (type) – BRA
	A. politus (Signoret) – BRA; COL; PER; VEN
	A. pseudopolitus (Ruckes) – PRY
	A. regulosus (Fieber) – BRA
Antiteuchus Dallas	*A. amapensis* Fernandes & Grazia – BRA
	A. amplus (Walker) – BOL; BRA; ECU; GUF; PER

(continued)

Table 22.3 (continued)

Genera	Species
	A. bartletti Ruckes – GUY
	A. beckerae Fernandes & Grazia – BOL; BRA
	A. confinium Ruckes – ECU; PER
	A. costaricensis Ruckes – CRI; PAN
	A. cuspidatus Ruckes – COL; PAN
	A. doesburgi Fernandes & Grazia – BRA; SUR
	A. exiguus Fernandes & Grazia –BRA
	A. fulvescens Ruckes – PER
	A. geometricus Engleman – BRA
	A. graziae Engleman – BOL; BRA; COL; ECU; PER
	A. guianensis Ruckes – BRA; GUF; GUY
	A. innocens Engleman – BLZ; GTM; MEX
	A. kerzhneri Rider –PER
	A. ledeburi Fernandes & Grazia – BRA
	A. macraspis (Petry) – BRA; COL; CRI; GUF; PAN; PER; SUR; VEN;
	A. maculosus Ruckes – ECU
	A. marini Fernandes & Grazia – BRA
	A. marmoratus (Erichson, 1848) – GUY
	A. melanicus Fernandes & Grazia – PER
	A. melanoleucus (Westwood) – BOL; BRA; GUY; PER; SUR; VEN
	A. mimeticus Ruckes – BRA; PER
	A. mixtus (F.) (type) – ARG; BOL; BRA; GUF; GUY; SUR; TTO; VEN
	A. nebulosus Ruckes – BRA
	A. nigricans Ruckes – COL; ECU
	A. pallescens Stål – BRA; GUY; SUR
	A. panamensis (Ruckes) – PAN
	A. peruensis Ruckes – PER
	A. pictus Ruckes – ECU; PER
	A. punctissimus Ruckes – BRA
	A. radians Ruckes – BRA
	A. rideri Rolston – BRA
	A. rolstoni Engleman – COL; ECU
	A. ruckesi Rolston – PER
	A. rufitasus Rolston – VEN
	A. schuhi Engleman – BRA; ECU
	A. sepulcralis (F.) – BOL; BRA; SUR; TTO; VEN
	A. simulatus Fernandes & Grazia – BRA
	A.tatei (Ruckes) (*species inquirenda*) – VEN
	A. tesselatus (Westwood) – BRA

(continued)

Table 22.3 (continued)

Genera	Species
	A. tripterus (F.) – ARG; BOL; BRA; COL; ECU; PAN; PRY; TTO; VEN
	A. variegatus Dallas – BOL; BRA; PER
Callostethus Ruckes	*C. guattatopunctatus* (F.) (type) – BRA; PER
	C. flavolineatus Fernandes & Grazia – BRA
Cataulax Spinola	*C. annulicornis* Walker (*insertae sedis*) – BRA
	C. eximius (Stål) (type) – BRA *C. froeschneri* Grazia, Campos & Becker – BRA
	C. pudens (Distant) – PAN; VEN *C. punctipes* Walker (*insertae sedis*) – BRA
	C. radians Grazia, Campos & Becker – PER
	C. subtiliterconspersus Grazia, Campos & Becker – BRA; GUF *C. subvittatus* Walker (*insertae sedis*) - BRA
Colpocarena Stål	*C. complanata* (Burmeister) (type) – BRA; SUR; VEN
Coriplatus White	*C. depressus* White – BRA; COL; CUB; GUF; GUY; VEN
Dinocoris Burmeister	
Dinocoris Burmeister	*D.* (*D.*) *antennatus* (Dallas) – BOL; BRA; PER
	D. (*D.*) *corrosus* (Herrich-Schäffer) – ARG; BRA; PAR
	D. (*D.*) *fabricii* Becker & Grazia – unknown
	D. (*D.*) *gibbosus* (Fallou) – BRA; PAN; VEN
	D. (*D.*) *gibbus* (Dallas) – ARG; BRA; PRY VEN
	D. (*D.*) *histrio* (L.) – GUY
	D. (*D.*) *maculatus* Laporte – BRA; COL; PER; VEN
	D. (*D.*) *nigroantennatus* Becker & Grazia – COL; PER
	D. (*D.*) *ramosus* (Walker) – MEX
	D. (*D.*) *reticulatus* Becker & Grazia – BRA
	D. (*D.*) *rufitarsus* Ruckes – BRA; COL; HND; NIC; PAN
	D. (*D.*) *variolosus* (L.) (type) – GUF; PAN; TTO
Praedinocoris Becker & Grazia	*D.* (*P.*) *lineatus* (Dallas) (type) – BRA; GUF; GUY; PER; SUR; VEN
	D. (*P.*) *nigrodecoratus* Becker & Grazia – BRA
	D. (*P.*) *prolineatus* Becker & Grazia – ARG; BRA; PRY; URY
Discocephala Laporte	*D. carvalhoi* Becker & Grazia – BRA
	D. deplanata Walker – BRA
	D. marmorea Laporte (type) – BRA
Discocephalessa Kirkaldy	*D. andina* (Breddin) – ECU
	D. humilis (Herrich-Schäffer) – COL
	D. notulata (Stål) (type) – CRI; MEX
	D. sordida (Walker) – BRA; GUF
	D. terminalis (Walker) – BOL; BRA

(continued)

Table 22.3 (continued)

Genera	Species
Dryptocephala Laporte	*D. asperula* Perty – ?BRA
	D. brullei Laporte (type) –BRA
	D. crenata Ruckes – PER
	D. cydnoides (Perty) – ?BRA
	D. dentata Fieber – BRA; URY
	D. dentifrons (Latreille) –PER
	D. integra Walker – BRA
	D. latiloba Stål – BRA
	D. lipoloba Ruckes – BRA
	D. lurida (Erinchson) – ARG; BRA; COL; GUY
	D. maculosa Ruckes – BRA
	D. nigricornis Ruckes – BRA
	D. obtusiceps Stål – BRA; COL; ECU; PER
	D. punctata Amyot & Serville – BRA; PER; VEN
	D. spinosa Mayr – BRA
Eurystethus Mayr	*E. deplanatus* Becker – BRA
	E. goianensis Becker – BRA
Eurystethus Mayr	*E.* (*E.*) *ellipsoidalis* Ruckes – PAN
	E. (*E.*) *macroconus* Ruckes – BRA
	E. (*E.*) *nigropunctatus* Mayr (type) – BRA
	E. (*E.*) *ornatus* Ruckes – BRA
	E. (*E.*) *ovalis* Ruckes – BOL; PER
	E. (*E.*) *pallescens* Ruckes – SUR
	E, (*E.*) *parvulus* Ruckes –BRA
	E. (*E.*) *sordidus* Ruckes – GUF
	E. (*E.*) *spurculus* Ruckes – GUF
Hispidisoma Ruckes	*E.* (*H.*) *fulvescens* Ruckes – BRA
	E. (*H.*) *microlobatus* Ruckes – BRA; SUR
	E. (*H.*) *nigricornis* Ruckes – ECU
	E. (*H.*) *nigroviridis* Ruckes – BRA
	E. (*H.*) *punctissimus* Ruckes – BRA
	E. (*H.*) *sacculatus* Ruckes – BRA
	E. (*H.*) *variegatus* Ruckes (type) – BOL; BRA
Glyphuchus Stål	*G. sculpturatus* Stål (type) – BRA
Grassatorama Rider	*G. nigroventris* (Ruckes) (type) – CRI
	G. reticulatus (Ruckes) – VEN
	G. sinuatus (Ruckes) – CRI
Harpogaster Kormilev	*H. willineri* Kormilev (type) – ARG; BRA
Ischnopelta Stål	*I. luteicornis* (Walker) – BRA
	I. oblonga (Fieber) – BRA
	I. scutellata (Signoret) (type) – BRA; PRY; VEN
Lineostethus Ruckes	*L. clypeatus* (Stål) (type) – MEX
	L. graziae Hildebrand & Becker – MEX

(continued)

Table 22.3 (continued)

Genera	Species
	L. marginellus (Stål) – MEX; USA
	L. tenebricornis (Ruckes) – MEX; USA
Mecistorhinus Dallas	*M. amplus* (Walker) – BRA
	M. complanatus (Distant) – PAN
	M. coralium Ruckes – PER
	M. guatemalensis (Distant) – GTM
	M. josephi (Stål) – GUF
	M. obscurus (Dallas) – MEX
	M. rufescens Dallas (type) – BRA
	M. semilugens Bergroth – GUF
	M. tesselatus (Westwood) – BRA
	M. tibialis Ruckes – CRI; PAN
	M. variegatus Ruckes – ECU
Oncodochilus Fieber	*O. integer* Breddin – BRA
Oncodochilus Fieber	*O.* (*O.*) *aradiformis* (Herrich-Shäffer) (type) – BRA
	O. (*O.*) *patruelis* (Stål) –BRA
Oncoeochilus Breddin	*O.* (*O.*) *taschenbergi* (Breddin) (type) – BRA
	O. (*O.*) *cruciatulus* Breddin –BOL
Opophylax Bergroth	*O. extenebratus* Bergroth (type) – BRA
	O. signoreti (Distant) – PAN
Pandonotum Ruckes	*P. bergrothi* Becker – BRA
	P. puncticentris Ruckes (type) – BRA
Paralcippus Becker & Grazia	*P. dimidiatus* (Ruckes) (type) –ECU
Parantiteuchus Ruckes	*P. hemitholus* Ruckes (type) – GUF
Parvamima Ruckes	*P. bicolor* Ruckes (type) – PAN
	P. mexicana Rolston – MEX
Patronatus Ruckes	*P. binotatus* Ruckes (type) – COL; PAN
	P. flavierus Ruckes – VEN
	P. punctissimus Ruckes – GUY
Pelidnocoris Stål	*P. haglundi* Ruckes – BRA
	P. majusculus Ruckes – PAN
	P. stalii Haglund (type) – COL; CRI; PAN; MEX
Phineus Stål	*P. fucopunctatus* Stål (type) – MEX
Phoeacia Stål	*P. erubescens* (Distant) – GTM; PAN
	P. gibba (Fieber) – BRA
	P. lineaticeps (Stål) (type)– BRA
Placidocoris Ruckes	*P. bivittatus* Ruckes (type) – ARG
Platycarenus Fieber	*P. umbraculatus* (Fieber) (type) – BRA; COL; ECU;GUF; GUY; PAN; PER; SUR; VEN
Priapismus Distant	*P. costaricensis* Rolston – CRI
	P. ecuadorensis Rolston – ECU

(continued)

Table 22.3 (continued)

Genera	Species
	P. foveatus Distant (type) – CRI; PAN
	P. maculatus Distant – PAN
	P. pini Rolston – HND
Psorus Bergroth	*P. cassidiformis* Bergroth (type) –BRA; PER; TTO
	P. paraensis Fernandes, Grazia & Lobo – BRA
	P. manauara Fernandes, Grazia & Lobo – BRA
Ruckesiocoris Rider	*R. nitidus* (Ruckes) (type) – PAN
Sympiezorhincus Spinola	*S. punctipes* Dallas – BRA
	S. tristis Spinola (type) – BRA; GUF; PRY
Tetragonotum Ruckes	*T. megacephalum* Ruckes (type) – BRA
Uncinala Ruckes	*U. tau* Ruckes (type) – BRA
Uncicrus Ruckes	*U. kollarii* (Fieber) (type) – BRA
Insertae sedis and *species inquirenda*	*Empicoris marmoreus* Spinola (see Fernandes and Grazia 2006)

[a] Fossil

[b] The monotypic genera *Anhanga* Distant and *Braunus* Distant (previously included in Discocephalini) are being transfered to Pentatominae (TdeA Garbelotto, personal communication, and Barão et al. in press)

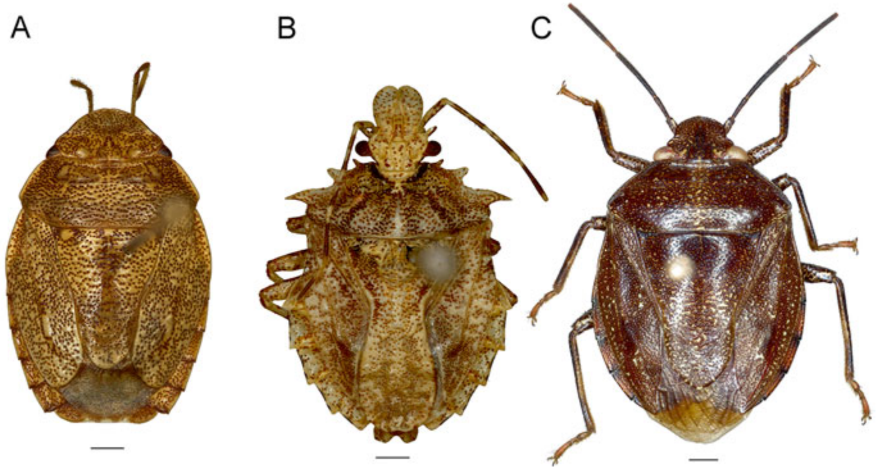

Fig. 22.24 Representative species of Discocephalini; (**a**) *Acclivilamna vicina* (Signoret); (**b**) *Coriplatus depressus* White; (**c**) *Antiteuchus rideri* Rolston. Scale bars = 1 mm (Photos by LA Campos & TA Garbelotto)

this group is being prepared by TdeA Garbelotto, but groups of genera were recognized by some authors based on morphological similarity, as detailed below.

The genera *Abascantus* Stål, *Coriplatus* White, *Eurystethus* Mayr, *Paralcippus* Becker & Grazia, and *Pelidnocoris* Stål shared the form and proportions of the metasternum and the spatial relationships of the mesocoxae and metacoxae – where a metasternum broadly hexagonal, somewhat wider than long (Fig. 22.25), causes

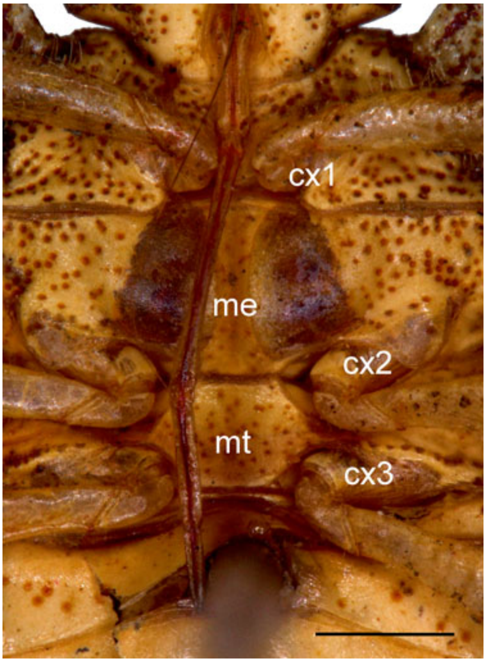

Fig. 22.25 Ventral view of thoracic sternites of *Paralcippus dimidiatus* (Ruckes). *cx1* procoxae, *cx2* mesocoxae, *cx3* metacoxae, *me* mesosternum, *mt* metasternum. Scale bar = 1 mm (Photos by LA Campos & TA Garbelotto)

the metacoxae to be placed much farther apart from each other than they are distant from the respective mesocoxae, the shape of pronotum, and the widely exposed connexivum (last two not in *Eurystethus* Mayr) (Ruckes 1966a; Ruckes and Becker 1970; Becker 1977; Becker and Grazia 1986). Also, *Abascantus* Stål, *Coriplatus* White, and *Pelidnocoris* Stål have in common the shape of scutellum and gonocoxites VIII of external female genitalia much enlarged, covering reduced laterotergites IX. *Paralcippus* Becker & Grazia and *Eurystethus* Mayr share a shorter scutellum (Becker 1977; Becker and Grazia 1986). The genus *Alcippus* Stål shares with *Paralcippus* Becker & Grazia and *Eurystethus* Mayr the presence of the laterotergites IX and the shorter scutellum, and though the general facies of *Alcippus* is similar to that of *Paralcippus* it has the meso and metacoxae mutually equidistant (Becker and Grazia 1986, 1989). *Pandonotum* Ruckes was also placed near *Eurystethus* by the shape of the head and scutellum, the labium with an intercalary unit between the two basal segments, and the reticulate venation of hemelytral membrane (Ruckes 1965).

Ablaptus Stål, *Agaclitus* Stål, *Cataulax* Spinola, *Sympiezorhincus* Spinola, and *Uncinala* Ruckes are considered related especially because of the sexual dimorphic hemelytral membrane, with sclerotized areas and a transversal furrow in males (Fig. 22.26), less clearly differentiated in *Cataulax*. Species of these genera except *Ablaptus* also have the apical angle of corium reaching the apex of the abdomen (Ruckes 1965; Becker and Ruckes 1969; Becker and Grazia 1989, 1992, 1995; Grazia et al. 2000).

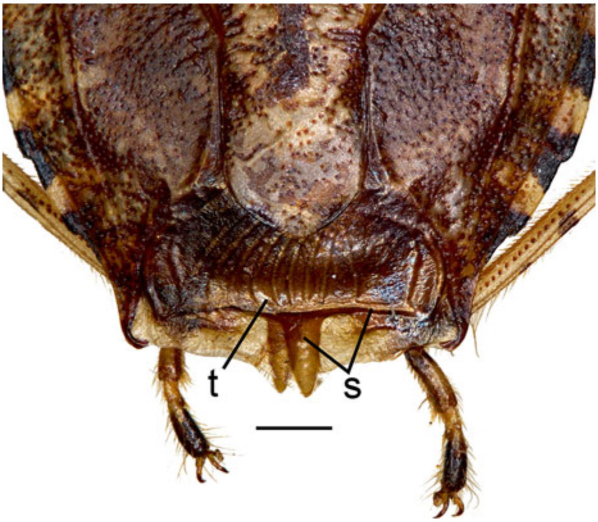

Fig. 22.26 Hemelytral membranes of male of *Uncinala tau* Ruckes. *s* sclerotized areas, *t* transversal furrow. Scale bar = 1 mm (Photo LA Campos & TA Garbelotto)

The larger group of genera within Discocephalini is known as “broadheaded discocephalines”; it includes 14 genera whose species have the interocular width equal to or greater than the length of the head (Figs. 22.19a and 22.24a), the basal segment of the rostrum projecting onto the prosternum, and the base of abdominal venter unarmed (Ruckes 1966b; Becker 1977; Rolston 1990).

Keys for two of these groups of genera are available, one for the broadheaded discocephalines (Rolston 1990) and another to separate *Antiteuchus* Dallas of similar genera (Ruckes 1964). Keys for species of several genera are also available (Ruckes 1966a for *Eurystethus*, 1966b for *Alveostethus* and *Lineostethus*, 1966c for *Dryptocephala*, 1966d for *Pelidnocoris*; Rolston 1984 for *Priapismus*; Becker and Grazia 1989 for *Ablaptus*, 1992 for *Agaclitus*; Grazia et al. 2000 for *Cataulax*; Grazia and Zwetsch 2000 for *Ablaptus*; Fernandes and Grazia 2006 for *Antiteuchus*), but some of them (Ruckes 1966a, b for *Lineostethus*, Rolston 1984, and Fernandes and Grazia 2006) are out to date since new species were described after the publication of the keys.

Ochlerini

Ochlerini was raised by Rolston (1981) and presently includes 32 genera and 115 species (Table 22.4) (Garbelotto et al. 2013; Cervantes-Peredo and Ortega-León 2014; Simões and Campos 2014). Species of Ochlerini are, with few exceptions, recognizable by their dull black or fuscous coloration, and primarily by the shallowly excavated or flattened superior surface of the third tarsal segment of the hind legs in females (Fig. 22.22b) and sometimes in males as well (Rolston 1981).

Table 22.4 Checklist of genera and species of Ochlerini (distribution as available in the literature)

Genera	Species
Adoxoplatys Breddin	*A. brasiliensis* Kormilev – BRA
	A. bridarollii Kormilev – BOL
	A. comis Breddin – PER; BOL
	A. gallardoi Kormilev – ARG
	A. giaii Kormilev – ARG
	A. minax Breddin (type) – PER; BOL
	A. panamensis Kormilev – PAN
	A. willineri Kormilev – BOL
Alathetus Dallas	*A. haitiensis* Rolston – HAI
	A. rufitarsis Dallas (type) – JAM
Alitocoris Sailer	*A. grandis* Garbelotto & Campos – PAN
	A. lateralis Garbelotto & Campos – CRI
	A. ornatus Garbelotto & Campos – PAN
	A. schraderi Sailer (type) – CRI; GTM; HND; PAN
	A. maculosus Sailer (*sedis mutabilis*)[a] – GTM; HND
	A. brunneus Sailer (*sedis mutabilis*)[a]
Barola Rolston	*B. farfala* Rolston (type) – PAN
Brachelytron Ruckes	*B. angelicus* Ruckes (type) – BRA
Catulona Rolston	*C. apaga* Rolston – BRA
	C. lucida Campos & Grazia – BRA
	C. pensa Rolston (type) – BRA
Clypona Rolston	*C. aerata* Rolston (type) – ARG
Coranda Rolston	*C. castana* Rolston – ECU
	C. picipes (Stål) (type) – COL; PER
Cromata Rolston	*C. ornata* Rolston (type) – BRA
	C. graziae Campos – VEN; BRA
Eritrachys Ruckes	*E. bituberculata* Ruckes (type) – CRI; PAN
	E. brailovskyi Ortega-León & Thomas – ECU
Forstona Rolston	*F. speciosa* Rolston (type) – BRA
Herrichella Distant	*H. thoracica* Distant (type) – COL
Hondocoris Thomas	*H. cavei* Thomas (type) – HND
Lincus Stål	*L. anulatus* Rolston – PAN; BRA
	L. apollo Dolling – FRG
	L. armiger Breddin – BOL
	L. bipunctatus (Spinola) – GUY; FRG; BRA
	L. breddini Rolston – SUR
	L. convexus Rolston – PER
	L. dentiger Breddin – PER; ECU
	L. discessus (Distant) – CRI; GUY
	L. fatigus Rolston – SUR
	L. hebes Rolston – PER
	L. incisus Rolston – SUR

(continued)

Table 22.4 (continued)

Genera	Species
	L. lamelliger Breddin – COL; FRG; SUR
	L. laminatus Rolston – PER
	L. lethifer Dolling – ECU
	L. leviventris Rolston – PER
	L. lobuliger Breddin – BRA
	L. malevolus Rolston – PER
	L. manchus Rolston – BOL
	L. modicus Rolston – ECU
	L. operosus Rolston – VEN
	L. parvulus (Ruckes) – PER; BRA
	L. repizcus Rolston – PER
	L. rufospilotus (Westwood) (type) – COL; GUY; SUR; PER; BRA
	L. securiger Breddin – BOL; PER; BRA
	L. singularis Rolston – PER
	L. sinuosus Rolston – PER
	L. spathuliger Breddin – PER
	L. spurcus Rolston – PER
	L. styliger Breddin – COL; PER
	L. substyliger Rolston – COL
	L. subuliger Breddin – COL; VEN
	L. tumidifrons Rolston – PAN; TTO; VEN
	L. vallis Rolston – PER
	L. vandoesburgi Rolston – SUR
	L. varius Rolston – PER
Macropygium Spinola	*M. reticulare* (F.) (type) – BRA[b]
Miopygium Breddin	*M. cyclopeltoides* Breddin (type) – BRA
	M. grossa Ruckes – BRA
Moncus Stål	*M. obscurus* (Dallas) (type) – BRA
	M. monachus Bergroth – FRG
Neoadoxoplatys Kormilev	*N. haywardi* Kormilev – ARG
	N. longirostra Ruckes – COL
	N. saileri Kormilev (type) – MEX
	N. thomasi Cervantes & Ortega – MEX
Ocellatocoris Campos & Grazia	*O. dasys* Campos & Grazia (type) (MNRJ) – BRA
Ochlerus Spinola	*O. bergrothi* Breddin – UNKNOWN
	O. bistillatus Breddin – PER; BOL
	O. cinctus Spinola (type) – ?BRA
	O. coriaceus Herrich-Schäffer – COL; VEN
	O. circummaculatus Stål – BRA
	O. communis Breddin – UNKNOWN
	O. cotylophorus Breddin – COL; ?PER

(continued)

Table 22.4 (continued)

Genera	Species
	O. dentijugis Breddin – PER
	O. handlirschi Breddin – MEX; HND
	O. incisulus Breddin – VEN
	O. lutosus Herrich-Schäffer – BRA
	O. notatulus Breddin – BRA
	O. profanus Breddin – PER
	O. rusticus Breddin – BRA
	O. signoreti Breddin – FRG
	O. stylulatus Breddin – PER
	O. tenuicornis Breddin – VEN
Orbatina Ruckes	*O. fuligina* Ruckes (type) – PAN; COL; BOL
Paralincus Rolston	*P. bimaculatus* (Ruckes) – GUY
	P. silvae Rolston – SUR; BRA
	P. terminalis (Walker) (type) – BRA
	P. sordidus (Herrich-Shäffer) (*nomen dubium*) – BRA
Parastalius Matesco, Grazia, & Campos	*P. trisinuatus* (Rolston) (type) – CRI; PAN
	P. rolstoni Matesco, Grazia & Campos – CRI
Parochlerus Breddin	*P. latus* Breddin (type) – PER; BRA
Phereclus Stål	*P. pluto* Stål (type) – COL
	P. punctatus (Dallas) – COL
	P. antennatus Distant – COL
Pseudadoxoplatys Rolston	*P. mendacis* Rolston (type) – PER; BOL
Schaefferella Spinola	*S. fusca* Rolston – ECU; PER
	S. incisa (Herrich-Schäffer) (type) – BRA
Schraderiellus Rider	*S. cinctus* (Ruckes) (DBTC) – CRI
	S. hughesae (Ruckes) (type) – CRI
Similiforstona Campos & Grazia	*S. bella* Campos & Grazia (type) – BRA
Stalius Rolston	*S. castaneus* (Distant) – NIC
	S. leonae Ortega – MEX, GUA
	S. scutellatus Thomas – CRI
	S. tartareus (Stål) (type) – MEX; HND; COL
Tetrochlerus Breddin	*T. fissiceps* Breddin (type) – ECU
Uvaldus Rolston	*U. concolor* Rolston (type) – BRA
Xynocoris Garbelotto & Campos	*X. calosus* Garbelotto & Campos – BOL
	X. crinitus Garbelotto & Campos – BRA
	X. cupreus Garbelotto & Campos – BRA
	X. egeri Garbelotto & Campos – CRI, BRA
	X. insularis Garbelotto & Campos – TTO
	X. lucidus Garbelotto & Campos – BRA
	X. meridionalis Garbelotto & Campos – BRA, PAR

(continued)

Table 22.4 (continued)

Genera	Species
	X. parvus (Distant) (type) – CRI, PAN, VEN, SUR, BRA, ECU
	X. recavus Garbelotto & Campos – VEN, BRA
	X. tuberculatus Garbelotto & Campos – VEN, BRA

[a] See Garbelotto et al. (2013)

[b] There are several undescribed species of *Macropygium* occurring in different countries, from Mexico to Argentina

The most comprehensive systematic work for Ocherini was made by Rolston (1992a), including the description of nine genera, diagnosis for the tribe, and key and diagnosis for its genera. The phylogeny of genera of Ochlerini and its sister-group relationship to Discocephalini were recently the theme of a cladistic study (Campos and Grazia 2006) (Fig. 22.23). Unambiguous synapomorphies of Discocephalinae are the long first segment of labium, reaching prosternum, and the male segment X largely membranous at least on its basal third (Campos and Grazia 2006, characters 13 and 37). Unambiguous synapomorphy of Ochlerini is the presence of a dorsal depression of the third tarsal segment of the hind legs of females (Campos and Grazia 2006, character 30).

The most basal genera within Ochlerini are *Adoxoplatys* Breddin, *Neoadoxoplatys* Kormilev, and *Pseudadoxoplatys* Rolston, whose species can be easily distinguished from other ochlerines by a usually long and flattened body, light-brown colored and of somewhat glossy aspect (Fig. 22.27a). All other genera were grouped into two clades, named *Ocellatocoris* and *Herrichella* clades by Campos and Grazia (2006). The first includes the type genus *Ochlerus* Spinola and seven other genera (Fig. 22.19b), and the later includes the remaining 20 genera known by that time (Fig. 22.27b), except *Hondocoris* Thomas that was not included in the cladistic analysis. The *Herrichella* clade was subject of another cladistic analysis that aimed to give a phylogeny-based classification of the genus *Alitocoris* Sailer and related species (Fig. 22.28) (Garbelotto et al. 2013).

The checklist for genera and species of Ochlerini provided by Campos and Grazia (2006) is updated here, with the inclusion of taxonomic information from several sources (Arismendi and Thomas 2003; Matesco et al. 2007; Ortega-León and Thomas 2010; Garbelotto et al. 2011, 2013; Simões and Campos 2014; Cervantes-Peredo and Ortega-León 2014) (Table 22.4).

22.4.5 Remarks

The study of Discocephalinae remains a challenging issue, since species of most genera are poorly represented in scientific collections and their natural history is virtually unknown. The description of life cycles and morphology of immatures are

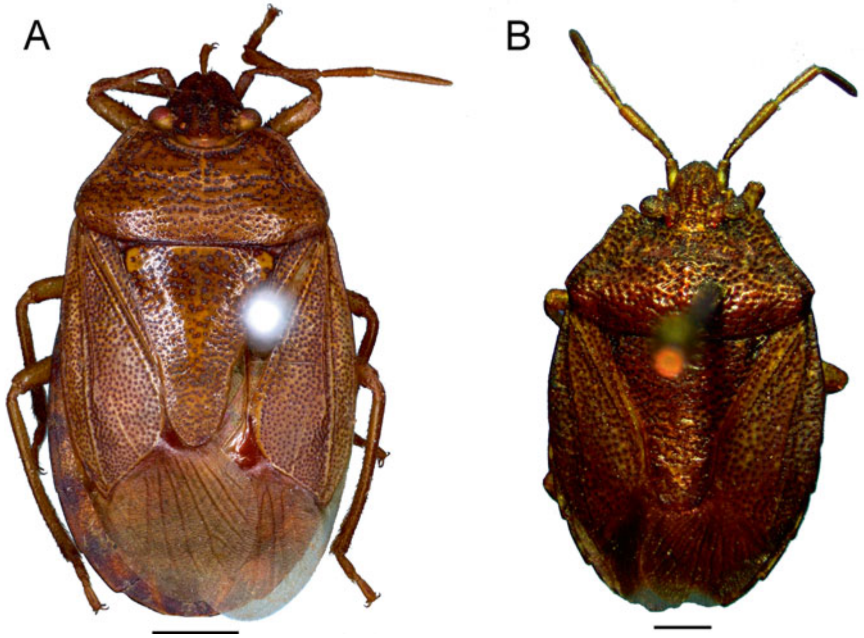

Fig. 22.27 Representative species of Ochlerini; (**a**) *Adoxoplatys comis* Breddin; (**b**) *Xynocoris parvus* (Distant). Scale bars = 1 mm (Photos by LA Campos & TA Garbelotto)

strongly needed. Behaviors registered for a few species such as parental care and trophobiosis with ants are interesting research themes, as well as feeding relationship with plants especially of Ochlerini. Phylogeny and systematics of Discocephalinae are also in need for investigation, focusing the review and modern taxonomic treatment of genera, use of molecular data in cladistic analyses, and relationship with other subfamilies of Pentatomidae.

22.5 Subfamily Edessinae

22.5.1 Introduction

Edessinae is one of the largest subfamilies of Pentatomidae with about 300 species (Schuh and Slater 1995; da Silva et al. 2013) distributed only in Neotropical Region, except for two species found in the Southern United States of America [*Edessa bifida* (Say) and *E. florida* Barber] (McPherson 1982). This subfamily includes seven genera without tribal division. Edessinae was until recently treated as a tribe of Pentatominae but was raised to subfamily by Rolston and McDonald (1979). This taxon has well-established limits but they are quite similar to the limits of the genus *Edessa*, causing a lot of confusion and turning the latter a depot of species.

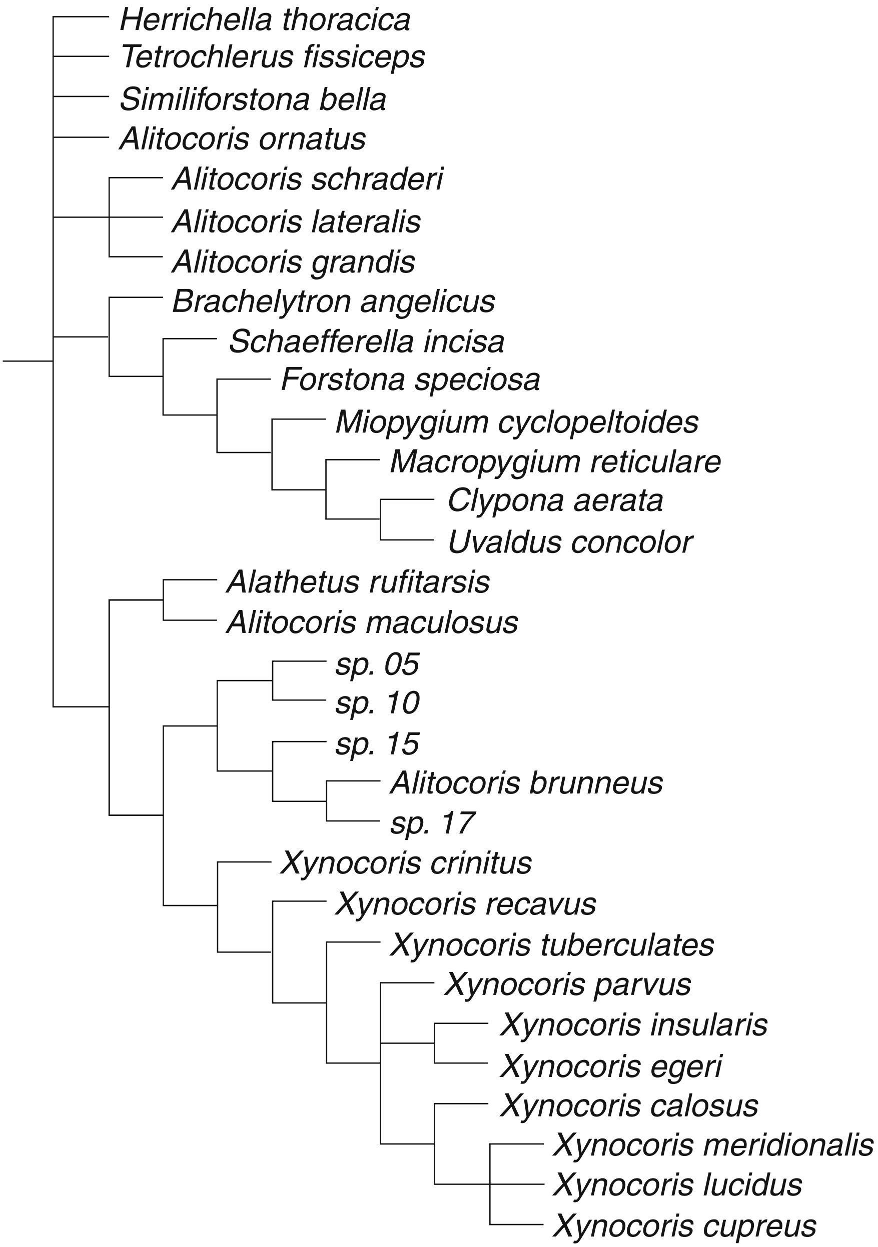

Fig. 22.28 Phylogeny of the *Herrichella* clade depicting the relationship between species of the *Alitocoris* group; strict consensus tree after implied weighting (Redrawn from Garbelotto et al. (2013))

22.5.2 General Characteristics and Diagnosis

Medium to large size bugs (1–3 cm long). Very attractive bugs with color ranging from light green to greenish-brown with highly contrasting connexivum and ventral surface. Head short and wide. Antennae 4 or 5 segmented. Humeral angles ranging from not to highly developed conical or flat, apex rounded, or acute. Metasternum strongly produced anteriorly onto mesosternum (prosternum in *Pantochlora* Stål) and usually bifid except for *Pantochlora* and *Doesburgedessa* that show a single projection. First rostral segment short, reaching anterior notched part. Posterior part of metasternal process also notched, receiving medial abdominal tubercle (Stål 1872; Rolston and McDonald 1979; Schuh and Slater 1995). Distal angle of the abdominal segment VII range from before the level of genital plates to surpassing them by far (Stål 1872). Dorsal rim of pygophore with a superior process. Ventral surface of the body usually lighter than dorsal with dark stripes at least on abdominal intersegmentar areas (Figs. 22.29, 22.30, 22.31, 22.32, 22.33, and 22.34).

Female internal genitalia: Description is almost the same of Pentatominae but capsula seminalis with 3 digitiform processes and a beak-like projection on the thickening of the vaginal intima (Barcellos and Grazia 2003b).

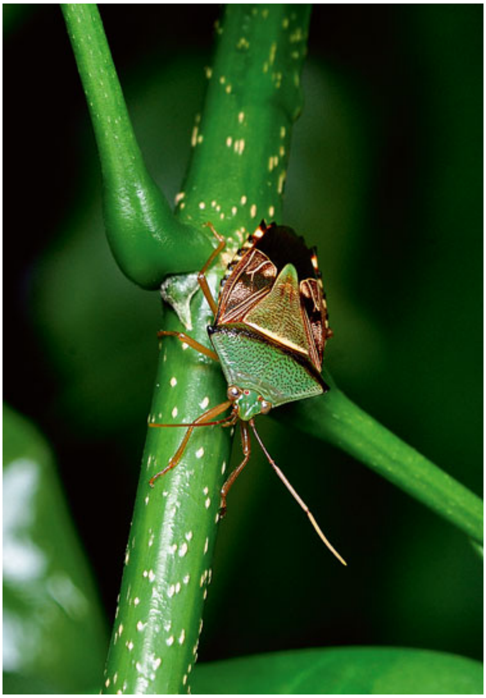

Fig. 22.29 *Edessa oxyacantha* Breddin (Photo by F Carvalho-Filho)

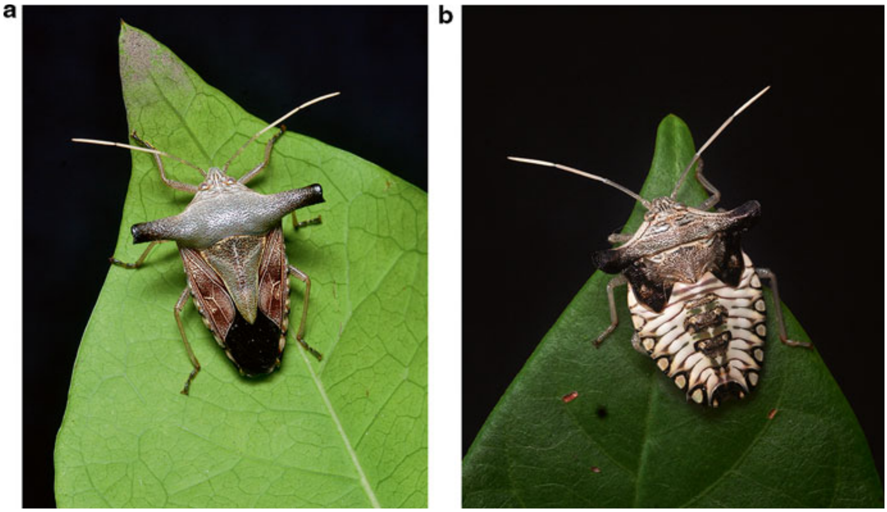

Fig. 22.30 *Edessa laticornis* Stål: (**a**) adult; (**b**) 5th instar nymph (Photo by F Carvalho-Filho)

Fig. 22.31 *Edessa bifida* (Say) (Photo by F Carvalho-Filho)

Fig. 22.32 *Edessa elaphus* Breddin (Photo by F Carvalho-Filho)

Fig. 22.33 *Edessa dolichocera* Burmeister, lateral view (Photo by F Carvalho-Filho)

Fig. 22.34 *Edessa dolichocera* Burmeister, frontal view (Photo by F Carvalho-Filho)

Male internal genitalia: The phallus of Edessinae is quite simple; phalloteca is strongly esclerotized, tubular to pear-like, and elongated; conjunctiva absent; vesica small, elliptical in lateral view; and *ductus seminis distalis* short, not or slightly surpassing the apex of vesica.

22.5.3 General Biology and Ecology

Edessinae are all plant feeder bugs, and only one species is economically important as pests of cultivated crops – *Edessa meditabunda* (F.) (Fig. 22.35), particularly on soybean and on tobacco (Silva et al. 1968; Rizzo 1971; Lopes et al. 1974; Panizzi et al. 2000). Another species is recognized as a secondary pest – *Edessa rufomarginata* (De Geer) – that feeds on Leguminosae but is more often found on Solanaceae, causing damage to tomato (Silva et al. 1968; Rizzo and Saini 1987; Panizzi et al. 2000). The species mentioned before are very common throughout South and Central Americas due to their capability to invade areas modified by man and are well studied with several registers over time. On the other hand, others may have local importance and are barely or not studied so far– e.g., a not described species that is an important pest in camu camu (Myrtaceae) crops in Pucallpa, Peru (Iannacone et al. 2007). Several other species can be found on cultivated or native plants of economical or ornamental interest but cause no apparent damage: *Edessa scabriventris* Stål on guava and Brazilian cherry (Lima et al. 2010) and *Paraedessa stolida* (L.) on acerola (JAM Fernandes, personal observation).

Only a few works concentrated on economically important species were produced so far. Rizzo (1971) presented detailed information on the biology, immature stages, field ecology, and host plants of *Edessa meditabunda*. This species has been the subject of studies regarding its association with and damaging potential to soy-

Fig. 22.35 *Edessa meditabunda* (F.) (Courtesy of JJ Silva)

bean (Silva et al. 2012) and sunflower (Malaguido and Panizzi 1998b) and nymph development and feeding behavior (Panizzi and Machado-Neto 1992); also, the behavior of newly hatched nymphs on the corions has been recently studied in detail (Calizotti and Panizzi 2014).

Rizzo and Saini (1987) presented biology data on *Edessa rufomarginata*. This species was subject of another study focused on the description of the immature stages (Fortes and Grazia 1990) under controlled laboratorial conditions. The same species was observed and studied in the field revealing several interesting ecological data including trophobiotic interaction between nymphs of *E. rufomarginata* and ants (Silva and Oliveira 2010). A species not recognized as pest – *Edessa scabriventris* – had some ecological and biological characteristics revealed in Lima et al. (2010). A probably new species considered pest in camu camu crop had its biology, immature stages, and field ecology studied (Iannacone et al. 2007).

22.5.4 Classification and Diversity

The subfamily Edessinae Amyot & Serville has seven genera: *Edessa* F. (about 280 species), *Brachystethus* Laporte (10 species), *Peromatus* Amyot & Serville (seven species), *Olbia* Stål (three species), *Pantochlora* Stål (one species), *Doesburgedessa* Fernandes (five species), and *Paraedessa* Silva & Fernandes (nine species). The genus *Brachystethus* is recognized by the short metasternal process and anterior apex slightly notched. *Peromatus* has only four antennal segments. *Olbia* has a pair of spines on the posterior margin of the pronotum, near the scutellum base.

Pantochlora is characterized by the anterior apex of the metasternal process not bifurcate, projected between procoxae, laterally flattened, and attached to the sternum. *Doesburgedessa* is recognized by the metasternal process with a single conical anterior projection which is detached from the mesosternum. *Paraedessa* has a reduction of the genital plates of the females plus a remarkable esclerotization of the gonapophyses 8; males show a lateral expansion of the proctiger and a dark crest covering base of the paramere. *Edessa* is composed of several groups of species with the metasternal process clearly bifurcating anteriorly but variable in many other characteristics (Fernandes 2010). Edessinae is a monophyletic group Barcellos and Grazia 2003a) supported by several characteristics, but its composition at supra-specific level is still not clear due to *Edessa* that is hiding the real diversity of the subfamily. Studies are revealing different groups of species (e.g., Fernandes and Van Doesburg 2000; Fernandes and Campos 2011; da Silva and Fernandes 2012) and also new genera *Doesburgedessa* (Fernandes 2010) and *Paraedessa* (da Silva et al. 2013). The heterogeneity of *Edessa* can be confirmed by its confusing taxonomical and nomenclatural history that culminates with Kirkaldy's catalog (1909) where he listed the subgenera but considered himself unable to include the species in them (footnote p. 153). Genus *Edessa* despite its size still has hundreds of new species to be described. New taxonomical studies probably will split *Edessa* in different taxa. A phylogenetic study is also important to present a hypothesis of relationship among taxa and confirm or not that *Edessa* is a paraphyletic taxon. In this book the genera *Lopadusa*, *Mediocampus*, *Neopharnus*, *Pharnus*, *Platistocoris*, and *Praepharnus* are included in Pentatomini (Pentatominae).

Key to genera of Edessinae and species group of *Edessa*. The concept of Stål (1872) dividing the genus in species groups is adopted here; genus in italic and group of species in bold.

1. Body rounded; apex of metasternal process level with mesocoxae, anteriorly raised, and sulcated but not clearly bifurcated .... *Brachystethus* Laporte
– Body with different shapes but usually elongated, lateral margins subparallel, metasternal process not as above 2
2. Metasternal process anteriorly clearly bifurcated 4
– Metasternal process projected anteriorly in a simple process............................ 3
3. Metasternal process long, reaching mesocoxae, laterally compressed, and fused with sterna, and apex widely rounded; humeral angle slightly projected and acute; found in Central America .... *Pantochlora* Stål
– Metasternal process short, not reaching procoxae, conical, not in contact with sterna, apex truncate; humeral angle projected laterally or dorsolaterally, conical, apex sharp; found in Amazon region............*Doesburgedessa* Fernandes
4. Four segmented antennae; second antennal segment very long, at least three times longer than the first; humeral angle truncate or globose; paramere robust and large; specimens usually bigger than 2 cm........*Peromatus* Amyot & Serville
– Five segmented antennae; second antennal segment short, at most twice longer than the first; humeral angle and paramere strongly variable in shape; specimens usually smaller than 2 cm.. 5

5. Posterior margin of the pronotum with a large pair of spines overlapping basal angles of scutellum; humeral angles long, sinuous, and laterally directed; pronotal disk with green and yellow stripes connecting humeral angles .... *Olbia* Stål
– Posterior margin of the pronotum without large spines or other projections; humeral angles variable in shape; pronotal disk not as above (*Edessa*) 6
6. Humeral angles rounded or sharp but not laterally developed more than the distance between the eyes 7
– Humeral angles variable in shape and laterally developed more than the distance between the eyes 11
7. Species elongate; abdominal segment VII projected posteriorly and contrastingly dark at least in distal half 8
– Species elliptical; abdominal segment VII not posteriorly projected and concolorous with connexivum 10
8. Corium brown with yellow veins; dark rounded spots below the spiracles; seventh abdominal segment mostly contrastingly dark dorsally, ventrally concolorous, posterior projection at least 1.5 times longer than wide at base .... **Pygoda** Amyot & Serville
– Corium brown variegate with whitish and blackish spots; without dark spots below spiracles; abdominal segment VII contrastingly dark dorsally only in distal half, ventrally with spots or stripes contrastingly dark, posterior projection at most 1.2 times longer than wide at base 9
9. Posterior part of proctiger expanded laterally; behind this part bristles short and sparse; pygophore with a rough ridge on each side of proctiger; gonocoxites 8 slightly to strongly reduced, leaving visible part of gonapophyses 8; gonapophyses 8 strongly developed and sclerotized .... *Paraedessa* Silva & Fernandes
– Posterior part of proctiger not expanded laterally at most with a small carina and dense tuft of long bristles; pygophore without ridge close to proctiger; gonocoxites 8 not reduced and leaving visible a tiny part of gonapophyses 8 at most; gonapophyses 8 not developed and membranous .... *Hypoxys* Amyot & Serville
10. Pronotal disk tumid; costal margin of corium uniformly colored and punctured; connexivum with punctures dark .... *Ascra* Say
– Pronotal disk not tumid. Costal margin of corium with punctures and usually color distinct from the rest; connexivum with punctures concolor .... **Aceratodes** Amyot & Serville
11. Humeral angle long, apex acute. Abdominal segment VII with apex twisted, strongly projected posteriorly, surpassing considerably the genital plates. Pygophore with a yellow spot on the base of each genital cup process .... **Dorypleura** Amyot & Serville
– Humeral angle long or short; apex acute, truncate, or globose, black or yellow contrasting with general coloration. Abdominal segment VII with apex not twisted projected posteriorly but not or slightly surpassing the genital plates. Pygophore without any spot on the base of genital cup process .... *Edessa* F.

22.5.5 Remarks

Edessinae was treated as a tribe of Pentatominae and was raised to subfamily by Rolston and McDonald (1979). This taxon has well-established limits; nevertheless its concept is quite similar to the genus *Edessa*. They are well represented in scientific collections, and modern taxonomical studies probably will split *Edessa* in different taxa. Recent studies are revealing different groups of species and also new genera within *Edessa*, a probably a paraphyletic taxon, deserving a phylogenetic study to establish the relationships within the subfamily and among the Pentatomidae.

22.6 Subfamily Pentatominae

22.6.1 Introduction

Pentatominae is the most diverse subfamily of Pentatomidae and includes species distributed in all the regions of the world (Schuh and Slater 1995; Grazia et al. 1999). The exact number of groups (tribes, genera, and species) gathered in Pentatominae is uncertain, since the definition of the subfamily is still under discussion. Nonetheless, it is possible to estimate that between 400 and 600 genera and 2,700 and 3,300 species are included in Pentatominae (Grazia et al. 1999; Cassis and Gross 2002; Rider 2014). In the Neotropical Region, approximately 120 genera and about 680 species occur.

22.6.2 General Characteristics and Diagnosis

Extremely variable in color, form, and size. First segment of labium arising anterior to the line of anterior margin of the eyes, with variable length in relation to the bucculae. Humeral angles frequently with process (acute or not); scutellum not reaching the apex of the abdomen, with frenal region extending from 2/5 to 2/3 the length of the scutellum. Metasternum rarely produced anteriorly. Abdominal segments III to VII with two pairs of trichobothria, near the spiracular line (Rolston and McDonald 1979; Schuh and Slater 1995) (Figs. 22.36, 22.37, 22.38, 22.39, 22.40, 22.41, 22.42, and 22.43).

Female internal genitalia: vesicular region of ductus receptaculi membranous, invaginated into a sclerotized rod; capsula seminalis with anterior and posterior annular flanges, bearing or not processes of variable number (Rolston and McDonald 1979; Schuh and Slater 1995). Male internal genitalia: conjunctiva usually membranous, sometimes absent; vesica usually as a sclerotized tube, with variable length (Rolston and McDonald 1979; Schuh and Slater 1995).

Fig. 22.36 *Oenopiella punctaria* Stål (Photo by A Ferrari)

Fig. 22.37 *Agroecus scabricornis* Herrich-Schaeffer (Photo by L Barros)

22.6.3 General Biology and Ecology

Pentatominae are all phytophagous and many species are economically important as pests of cultivated crops (Grazia et al. 1999; Panizzi et al. 2000). In the Neotropics the Pentatominae cause damage mainly in Leguminosae and Gramineae crops. *Nezara viridula* (L.) (Fig. 22.40), *Piezodorus guildinii* (Westwood) (Fig. 22.44), and *Euschistus heros* (F.) (Fig. 22.45) are important pests of soybean (Panizzi et al. 2000),

Fig. 22.38 *Euschistus irroratus* Bunde, Grazia, & Mendonça Jr. (Photo by J Grazia)

Fig. 22.39 *Pellaea stictica* (Dallas) (Courtesy of CSRibeiro-Costa)

Fig. 22.40 *Nezara viridula* (L.) (Photo by A Ferrari)

Fig. 22.41 *Phalaecus* sp. (Photo by J Grazia)

Fig. 22.42 *Roferta marginalis* (Herrich-Schaeffer) (Photo by JAM Fernandes)

Fig. 22.43 *Stictochilus tripunctatus* Bergroth (Photo by R Lupoli)

and species of *Arvelius* Spinola, *Loxa* Amyot & Serville, *Agroecus* Dallas, *Dichelops* Spinola, and *Chinavia* Orian also occur in this crop, sometimes causing damage (Panizzi and Slansky 1985; Panizzi et al. 2000; Schwertner and Grazia 2007).

Mormidea v-luteum (Lichtenstein), *Oebalus poecilus* (Dallas), *Oebalus ypsilon-griseus* (De Geer) (Fig. 22.46), and *Tibraca limbativentris* Stål (Fig. 22.47) cause

Fig. 22.44 *Piezodorus guildinii* (Westwood) (Courtesy of JJ Silva)

Fig. 22.45 *Euschistus heros* (F.) (Courtesy of JJ Silva)

damage to rice and wheat (Panizzi et al. 2000). Also, *Glyphepomis* Berg species are rice pests (Campos and Grazia 1998; Farias et al. 2012) and *Dichelops melacanthus* (Dallas) (Fig. 22.48) is considered an important problem in wheat (Chocorosqui and Panizzi 2004; Manfredi-Coimbra et al. 2005) and corn crops (Ávila and Panizzi 1995) in Brazil.

Loxa spp. and *Arvelius albopunctatus* (De Geer) (Fig. 22.49) cause damage in Solanaceae plants in Brazil (Panizzi et al. 2000). The last one is also reported to feed in tobacco in Brazil (Marques et al. 2006).

Pentatominae are, in general, highly polyphagous, and their life history includes several host plant sequences. For some species this has been investigated in details in the Neotropics, as illustrated by the studies conducted by Panizzi (1997).

Fig. 22.46 *Oebalus ypsilongriseus* (De Geer) (Courtesy of H. Prando)

Fig. 22.47 *Tibraca limbativentris* Stål (Courtesy of H. Prando)

Fig. 22.48 *Dichelops melacanthus* (Dallas) (Courtesy of JJ Silva)

Fig. 22.49 *Arvelius albopunctatus* (De Geer) (Courtesy of JJ Silva)

22.6.4 Classification and Diversity

Pentatominae is not a monophyletic group (Gapud 1991; Grazia et al. 2008) and does not have a definition based on phylogenetic studies. Therefore, authors diverge about composition of the subfamily (Cassis and Gross 2002). Schuh and Slater (1995), for example, included eight tribes in Pentatominae, from which only Pentatomini is registered in the Neotropical Region. Rider (2014) considers 42 tribes in Pentatominae, 11 registered in Neotropics: Catacanthini Atkinson, Carpocorini Mulsant & Rey, Halyini Amyot & Serville, Mecideini Distant, Menidini Atkinson, Nezarini Atkinson, Pentatomini Leach, Piezodorini Atkinson, Procleticini Pennington, Sciocorini Amyot & Serville, and Strachiini Mulsant & Rey. The relationship among tribes is unknown; also most of the tribes do not have diagnostic characteristics to define them, which make the establishment of the exact composition of these groups difficult. Six genera of the Neotropical Region are considered as unplaced in Rider's classification (Table 22.5).

Table 22.5 Checklist of Neotropical Pentatominae genera (distribution as available in the literature)

Carpocorini	
Acledra Signoret	BRA, CHI, ARG, URU
Agroecus Dallas	PER, ECU, BOL, GUY, FGU, COL, VEZ, BRA, PER, BOL, ARG, PAR
Amauromelpia Fernandes & Grazia	CR, FGU, BRA, BOL, COL, PER
Berecynthus Stål	MEX, CR, PAN, COL, VEZ, SUR, BRA, PER
Braunus Distant	CR, VEZ, COL, ECU, PER, BOL
Bucerocoris Mayr	BRA
Caonabo Rolston	BRA
Caribo Rolston	BAH, JAM, IS. VIR
Caracia Stål	VEZ
Copeocoris Mayr	BRA, ARG
Cosmopepla Stål	USA, MEX, ELS, CR, VEZ, COL, ECU
Cradia Bergroth	BRA
Curatia Stål	BRA
Dichelops Spinola	PAN, BRA, ECU, PAR, VEZ, BRA, PER, BOL, PAR, ARG, URU
Epipedus Spinola	BRA
Euschistus Dallas	USA, MEX, NIC, GTM, ELS, HON, CR, PAN, COL, VEZ, W.I. (ALL), GUY, BRA, ECU, BOL, FGU, PER, CUB, JAM, CURAÇAO, BLZ, ARG, URU,
Galedanta Amyot & Serville	CR, GUY, COL, BRA
Glyphepomis Berg	BRA, ARG, URU
Hypanthracos Grazia & Campos	BRA, URU
Hypatropis Bergroth	HON, NIC,CR, PAN, TTO, COL, VEZ, SUR, BRA, ARG, URU
Lattinidea Rider & Eger	CR, PAN, COL, VEZ, FGU, BRA, ECU, PER
Lattinellica Rider & Eger	COL, BRA, ECU, PER
Ladeaschistus Rolston	BRA, BOL, PAR, ARG, URU
Luridocimex Grazia, Fernandes & Schwertner	BRA
Mathiolus Distant	GTM
Mecocephala Dallas	BRA, ARG, URU
Menudo Thomas	PUR
Mormidea Amyot & Serville	CAN, USA, MEX, NIC, PUR, CUB, HIS, DRE, COL, GUY, FGU, PER, BOL, SUR, BRA, ECU, TRI, PAN, ARG, URU, VEZ, JAM, PAR, GRE, TRI

(continued)

Table 22.5 (continued)

Carpocorini	
Oebalus Stål	USA, MEX, W.I. (ALL), SUR, BRA, PER, PAR, ARG, URU, TRI, COL, GUY, ECU, BOL, HIS, PUR, CUB
Oenopiella Bergroth	BRA, CHI, ARG, URU
Ogmocoris Mayr	BRA
Padaeus Stål	USA, MEX, GTM, NIC, HON, CR, ECU, COL?
Parahypatropis Grazia & Fernandes	BRA, ARG
Paramecocephala Benvegnú	SUR, GUY, GUF, BRA, ECU, ARG, URU
Paratibraca Campos & Grazia	PAN, TTO, SUR, COL, BRA, PER, BOL
Parentheca Berg	BRA, PAR, ARG, URU
Pedinonotus Fernandes & Grazia	BRA
Pentatomiana Grazia & Barcellos	BRA (RJ, SP, SC)
Poriptus Stål	TTO, COL, BRA, BOL, ARG
Prionotocoris Kormilev	BOL, ARG
Proxys Spinola	USA, MEX, DRE, CUB, GTM, NIC, FGU, BLZ, CR, GRE, PAN, COL, VEZ, BRA, ARG, URU
Sibaria Stål	MEX, ALL CENTRAL AM., COL, VEZ, FGU, GUY, SUR, TTO, BRA, ECU, PER, BOL, PAR, ARG
Spinalanx Rolston & Rider	COL, PER, ECU, BOL
Stysiana Grazia, Fernandes & Schwertner	COL, SUR, TTO, GUY, BRA, PER, ARG, PAR
Tibraca Stål	DRE, CUB, CR, COL, VEZ, BRA, PER, BOL, ARG, URU
Trichopepla Stål	CAN, USA, MEX
Catacanthini	
Arocera Spinola	MEX, BLZ, HON, CR, PAN, CUB, JAM, PUR, DRE, TTO, VEZ, FGU, GTM, CR, COL, GUY, SUR, FGU, BRA, ECU, BRA, BOL, ARG
Boea Walker	CR, BRA
Rhyssocephala Rider	MEX, BLZ, GTM, CR, PAN, JAM, COL, VEZ, ECU, BRA, PER, BOL
Runibia Stål	USA, JAM, Virgen Is, COL, VEZ, ECU, BRA, PER, BOL, GUF, ARG, PAR, URU
Vulsirea Spinola	USA, MEX, HON, HAI, JAM, CR, CUB, PAN, COL, VEZ, BRA, BOL
Halyini	
Brochymena Amyot & Serville	USA, MEX, HON, CR, BAH, CUB
Parabrochymena Larivière	USA, MEX, GTM, CR
Mecideini	
Mecidea Dallas	USA, MEX, NIC, HON, CR, PUR, ANTIGUA, ARG

(continued)

Table 22.5 (continued)

Carpocorini	
Menidini	
Elanela Rolston	SUR, BRA, PER
Rio Kirkaldy	MEX, GTM, ELS, CR, PAN, VEZ, SUR, BRA, ARG
Nezarini	
Chinavia Orian	CAN, USA, MEX, BLZ, CR, CUB, DRE, PUR, JAM, Grenada, Guadeloupe, Dominica, St. Croix, VIR IS., GTM, NIC, HAI, HON, BAH, COL, VEZ, SUR, FGU, GUY, BRA, ECU, PER, BOL, CHI, PAR, ARG, URU
Chlorochroa Stål	CAN, USA, MEX
Nezara Amyot & Serville	MEX, NIC, HON, CUB, DRE, PAN, VEZ, BRA, CHI, ARG, URU
Roferta Rolston	BLZ, PUR, PAN, TRI, CUB, BRA, ARG
Pentatomini	
Adevoplitus Grazia & Becker	MEX, GTM, CR, PAN, VEZ
Arvelius Spinola	DRE, GUP, MAR, BAR, SVI, USA, MEX, ELS, GTM, HON, CUB, DRE, PUR, VIR, ANT, BAH, NIC, JAM, CR, PAN, COL, VEZ, SUR, GUY, TTO, HAI, ECU, BRA, BOL, PAR, ARG, URU, GUY
Banasa Stål	USA, MEX, ALL CENTRAL AM., ALL W.I., COL, ECU, VEZ, PER, BOL, BRA, PAR, SUR, GUY, GUF, ARG, URU,
Brasilania Jensen-Haarup	BRA
Chlorocoris Spinola	USA, MEX, BLZ, NIC, HON, GTM, JAM, CR, PAN, COL, VEZ, SUR, TRI, ECU, BRA, PER, BOL, PAR, ARG
Chloropepla Stål	BRA, BOL, VEZ, CR, PER, GUY, FGU,
Disderia Bergroth	MEX, GTM, BLZ
Elsiella Froeschner	ECU
Eludocoris Thomas	CR
Evoplitus Amyot & Serville	BRA
Fecelia Stål	PUR, HAI, DRE
Glaucioides Thomas	HON, CR, PAN, VEZ, SUR, GUY, BRA
Grazia Rolston	MEX, CUB, DRE, PAN, VEZ, BRA, PAR
Janeirona Distant	BRA, PER, PAR, ARG
Kermana Rolston	USA, MEX, CR, HON, PAN, BRA, ARG, URU
Lopadusa Stål	PAN, VEZ, GUY, BRA, ECU, PER, BOL, PAR, ARG
Loxa Amyot & Serville	USA, MEX, CUB, DRE, BAH, PUR, DOMINICA, GUADALOUPE, CURAÇAO, GRENADINIES, ST. LUCIA, JAM, HON, NIC, PAN, COL, GUY, VEZ, SUR, FGU, BRA, PER, ARG
Marghita Ruckes	BRA, ARG
Mayrinia Horváth	NIC, CR, COL, VEZ, GUY, BRA, PER, BOL, PAR, ARG
Mediocampus Thomas	DOR
Modicia Stål	CUB
Myota Spinola	BRA

(continued)

Table 22.5 (continued)

Carpocorini	
Neopharnus Van Duzee	EUA, CUB
Neotibilis Grazia & Barcellos	MEX, CR, PAN, COL, VEZ, GUY, GUF, BRA, ECU, PER, BOL
Nocheta Rolston	SUR, BRA
Pallantia Stål	MEX, GTM, PAN, VEZ, PER, BRA, PAR, ARG
Paratibilis Ruckes	MEX, PER
Pellaea Stål	USA, MEX, NIC, HON, CR, PAN, COL, VEZ, GUY, BRA, ECU, ARG, URU
Phalaecus Stål	GUY, SUR, GUF, BRA, COL
Pharnus Stål	CUB
Pharypia Stål	MEX, HON, GTM, CR, PAN, COL, VEZ, FGU, BRA, ARG
Placocoris Mayr	BRA, ARG
Platistocoris Rider	BRA
Praepharnus Barber & Bruner	CUB
Pseudevoplitus Ruckes	VEZ, BRA, PER, BOL, ARG
Ramosiana Kormilev	MEX, CR, PAN, PER, BOL
Rhyncholepta Bergroth	PAN, VEZ, GUF, VEZ, BRA, BOL
Rideriana Grazia & Frey-da-Silva	BRA, PER, BOL
Serdia Stål	CR, PAN, VEZ, BRA, PER, BOL, PAR, ARG
Similliserdia Fortes & Grazia	BRA
Stictochilus Bergroth	ARG, BRA
Taurocerus Amyot & Serville	MEX, GTM, CR, PAN, COL, GUY, BRA, PER, BOL
Tibilis Stål	BRA, ECU, PER, BOL
Vidada Rolston	PER
Piezodorini	
Piezodorus Fieber	USA, TRI, PUR, GTM, HON, NIC, JAM, CUB, DRE, St. Vincent, Grenada, PAN, VEZ, BRA, ECU, PAR, ARG
Procleticini	
Aleixus McDonald	BRA
Brepholoxa Van Duzee	USA, MEX, W.I.
Dendrocoris Bergroth	USA, MEX, GTM,
Lobepomis Berg	ARG
Neoderoploa Pennington	BOL, ARG
Odmalea Bergroth	GUF, TTO, PAN, VEZ, COL, BRA, BOL, ARG, URU
Parodmalea Rider	BRA
Procleticus Berg	ARG
Pseudobebaeus Distant	BRA, PER
Terania Pirán	ARG
Thoreyella Spinola	BRA, PAR, ARG, URU

(continued)

Table 22.5 (continued)

Carpocorini	
Strachiini	
Murgantia Stål	USA, MEX, GTM, ANT, CR, PAN, BRA, PER, BOL
Sciocorini	
Trincavellius Distant	ECU, CHI, PER
Unplaced	
Capivaccius Distant	MEX, HON, PAN, BRA, ARG
Cyptocephala Berg	USA, CENTRAL AM. (ALL), BAH, CUB, DRE, JAM, VIR IS., DRE, PUR, BRA, PER, BOL, ARG, URU
Patanius Rolston	BRA
Senectius Rolston	PER
Tepa Rolston & McDonald	USA, CURAÇAO
Thyanta Stål	USA, MEX, GTM, BLZ, ELS, HON, NIC, CR, PAN, BAH, CUB, JAM, DRE, HAI, PUR, VIR IS., BARBADO, BRITISH W.I., FRENCH W.I., CURAÇAO, TTO, VEZ, COL, SUR, FGU, BRA, PER, ECU, CHI, BOL, PAR, ARG, URU

Catacanthini was established by Atkinson (1888) to include *Catacanthus* Spinola (15 spp.) and *Chalcocoris* Dallas (two spp.), both genera not known in the Neotropical Region. More five Neotropical genera were added since then (Table 22.5). Some of the most colorful species of Pentatominae are included in Catacanthini. Keys for identification of species are available for *Arocera* (Rider 1992), *Rhyssocephala* (Rider 1991), and *Runibia* (Zwetsch and Grazia 2001). A study of the relationships within Catacanthini using morphologic characters is under development (J. Grazia, unpublished).

Carpocorini was first defined by Mulsant and Rey (1866), including *Carpocoris* Kolenati, *Dryocoris* Mulsant & Rey (junior synonym of *Holcostethus*), and *Peribalus* Mulsant & Rey (junior synonym of *Holcostethus*). This tribe is one of the most diverse in the subfamily (Cassis and Gross 2002) and includes many of the species of economic importance as *Euschistus heros* (F.), *Oebalus poecilus* (Dallas), and *Tibraca limbativentris* Stål. In the Neotropical Region, 53 genera are included in Carpocorini. A phylogenetic analysis based on morphology and DNA sequences is under development (J. Grazia, unpublished).

The tribe Halyini was established by Amyot and Serville (1843) to include a heterogeneous group of 16 genera, which currently included different families of Pentatomoidea and subfamilies and tribes of Pentatomidae. Dallas (1851) considered the group as a separate family; however the Halyini as currently circumscribed share all synapomorphies of the Pentatomidae. The tribe includes 82 genera with worldwide distribution, with great diversity in the Afrotropical and Australian regions (Linnavuori 1982; Gross 1975). Two genera are recorded in the Western Hemisphere (Table 22.5), with species found in the northern Neotropical Region.

Distant (1902) propose Mecideini to include *Aenaria* Stål and *Mecidea* Dallas. The proposal was questioned by Bergroth (1905), and *Mecidea* was grouped with other seven genera today included in the tribe Diemeniini Kirkaldy. Mecideini was accepted as a separated tribe (i.e., Rolston and McDonald 1979) but remains monotypic. The genus *Mecidea* includes 16 species distributed in all biogeographic regions except the Australian region (Sailer 1952). In the Neotropics, *Mecidea* has a disjunct distribution, with 4 described species (Sailer 1952; Thomas 2000; Grazia and Schwertner 2008).

Menidini was described to include four genera: *Cresphontes* Stål, *Antestia* Stål (currently Antestiini), *Apines* Dallas, and *Menida* Motschulsky (Atkinson 1888). The definition of the tribe and relationship among the genera, however, are in need of phylogenetic studies (Rider 1998). In the Neotropical Region, only two genera occur from the 28 actually assigned to the tribe (Table 22.5). Keys to the identification of the species of the Neotropical genera, *Rio* Kirkaldy and *Elanela* Rolston are available (Fortes and Grazia 2000; Grazia and Greve 2011) and *Rio* was revised (Grazia and Fortes 1995).

The tribe Nezarini is represented by four genera in the Neotropical Region: *Chinavia*, *Chlorochroa* Stål, *Roferta* Rolston, and *Nezara* Amyot & Serville. The last one is represented only by *N. viridula* (L.), which has a cosmopolitan distribution (Ferrari et al. 2010). The group was proposed to include species of *Nezara* and *Acrosternum* Fieber (Atkinson 1888). Cladistic analyses in the genus and group of species level were published recently (Ferrari et al. 2010; Genevcius et al. 2012; Genevcius and Schwertner 2014); however, the tribe lacks a formal definition, based on phylogenetic studies. A pictorial key for the Brazilian species of *Chinavia*, which include some secondary pests in South America, is presented in Schwertner and Grazia (2007).

Pentatomini is the most diverse tribe of Pentatominae. The original description brings as the only character defining the group, the scutellum not covering the wings or elytra (Leach 1815). No further definition was elaborated and the scattered phylogenetic evidences indicate that Pentatomini is not a monophyletic group (Gapud 1991; Hassan and Kitching 1993; Campos and Grazia 2006). Nonetheless, several studies using cladistic methodology at genus level for Neotropical groups put some light on to the relationships, especially among groups of species and genus level (Grazia 1997; Fortes and Grazia 2005; Simões et al. 2012; Greve et al. 2013). A phylogenetic analysis based in morphology and DNA sequences testing the *Chlorocoris* group was recently developed (Greve, personal communication), and the results derived from the total evidence analysis and the morphological analysis alone are not in complete agreement. The differences among the two hypotheses of relationship prevent the proposal of a unified classification for the taxa studied, not supporting the group as a monophyletic clade.

In the Neotropical Region, Piezodorini is represented only by the genus *Piezodorus* Fieber, with the species *P. guildinii* (Westwood) being a major pest of soybean in South America (Panizzi et al. 2000). The original description was based in species of *Piezodorus* and *Ambiorix* Stål and defines the tribe by “tibiae generally rounded, rarely furnished above with a narrow and obsolete furrow, or flat and emarginate; venter spinose at the base, spine sometimes extended to the head; apical angles of the sixth abdominal segment sometimes produced in a large acute tooth” (Atkinson 1888).

The tribe Procleticini was described to include two monotypic genera: *Lobepomis* Berg and *Procleticus* Berg (Pennington 1920). Currently it includes 11 genera (Table 22.5) almost exclusively Neotropical (Rider 1994; Bernardes et al. 2009; Schwertner and Grazia 2012). Only *Brepholoxa* and *Dendrocoris* have species occurring in the Nearctic region (Rider 1994). The group is considered monophyletic and is supported by metasternum sulcate, ventral rim of pygophore with a medial U-shaped emargination and with 1 + 1 process with different degrees of development, and gonocoxites 8 smaller than laterotergites 9 (Schwertner and Grazia 2012).

Amyot and Serville (1843) proposed the group Sciocorides to include genera currently in different subfamilies of Pentatomidae. A more restricted concept of the taxon was applied by Stål (1876), who restricted the group to *Dyroderes* Spinola, *Mennacarus* Amyot & Serville, *Pododus* Amyot & Serville, and *Sciocoris* Fállen. The tribe includes currently 11 genera distributed in all biogeographic regions, although poorly represented in the Neotropics, with only one genus (Table 22.5).

The group Strachiaries (Mulsant and Rey (1866)) included originally only the genus *Strachia* Hahn. Stål (1876) expanded the group to include *Agaeus* Dallas, *Bagrada* Stål, *Cinxia* Stål, *Eurydema* Laporte, and *Stenozygum* Dallas. Currently the tribe contains 14 genera worldwide, with only the genus *Murgantia* with representatives in the Neotropical Region (Brailovsky and Barrera 1889).

Other six genera treated as unplaced in Rider (2014) are registered in the Neotropical Region (*Capivacius* Distant, *Cyptocephala* Berg, *Patanius* Rolston, *Senectius* Rolston, *Tepa* Tolston & McDonald, and *Thyanta* Stål). With the exception of *Cyptocephala* (4 spp.) and *Thyanta* (27 spp.), the remaining genera are monotypic.

Key to the genera of Pentatominae of economic importance (modified from Rolston 1974 and Rolston and McDonald 1984):

1. Third urosternite with medial process.. 2
1′. Third urosternite without process.. 5
2. Specimens not longer than 9 mm, yellowish brown in color *Piezodorus* Fieber
2′. Specimens with at least 10 mm, green in life, or reddish brown or pale yellow in dry preserved.. 3
3. Mandibular plates surpassing clypeus in length; mandibular plates apex acute; lateral margin of pronotum partially crenulated ....*Arvelius* Spinola
3′. Mandibular plates not surpassing clypeus, rounded at apex; lateral margin of pronotum not ornamented.. 4
4. Wide colored band in the margins of the head, pronotum, or basal third of hemelytra; spiracle sometimes surrounded by yellow callus, without any other macula.. *Chinavia* Orian
4′′. Margins of the head, pronotum, and basal third of hemelytra concolor with the body or with a thin yellow band; spiracle without callus and green macula may be present..*Nezara* Amyot & Serville
5. Distal apex of the femora bearing a strong spine; specimens green in vivo (can be reddish brown or pale yellow in dry preserved specimens) ....*Loxa* Amyot & Serville

5′. Distal apex of the femora unarmed, specimens usually brown or dark 6

6. Two rows of small tubercles present on inferior surface of femora .... *Agroecus* Dallas

6′. Inferior surface of the femora lacking tubercles 7

7. Small specimens, at most10 mm length, usually not reaching this length 8

7′. Specimens length over 10 mm 10

8. Specimens' dorsum uniform brown to dark in color, without ornamentation of different colors; insects shorter than 7 mm.......................... *Glyphepomis* Berg

8′. Pronotum and scutellum frequently with ivory callous; insects around 10 mm in length 9

9. Apex of first rostral segment projecting past bucculae .... *Mormidea* Amyot & Serville

9′. First rostral segment lying entirely between bucculae.......................... *Oebalus* Stål

10. Mandibular plates conspicuously longer than clypeus, with apices usually acute .... *Dichelops* Spinola

10′. Mandibular plates nearly equal to clypeus in length, sometimes a little longer or shorter 11

11. Peritreme long, evanescent.......................... *Thyanta* Stål

11′. Peritreme short 12

12. First antennal segment reaching and sometimes slightly surpassing the apex of the head; anterolateral margins of pronotum distinctly undulating, denticulate, or vertically rugose .... *Euschistus* Dallas

12′. First antennal segment not attaining the apex of the head; anterolateral margins entire .... *Tibraca* Stål

22.6.5 Remarks

The Pentatominae is the most speciose subfamily within Pentatomidae and are represented in all geographic regions. New characters should be investigated and analyzed in all Pentatominae groups, in order to help in the clarification of infra-subfamily relations. Cladistics studies at genus and species levels in the subfamily are needed.

22.7 Subfamilies Podopinae and Stirotarsinae

22.7.1 Introduction

The subfamilies Podopinae and Stirotarsinae are represented by only one species each in the Neotropical Region. The subfamily Podopinae is distributed worldwide; most of its diversity can be found in the Afrotropical, Oriental, and Palearctic regions (Davidová-Vilímová and Štys 1994; Rider 2014). The Stirotarsinae was erected recently (Rider 2000) to include *Stirotarsus abnormis* Bergroth, a species known only by a female specimen collected in Peru (Fig. 22.50a, b).

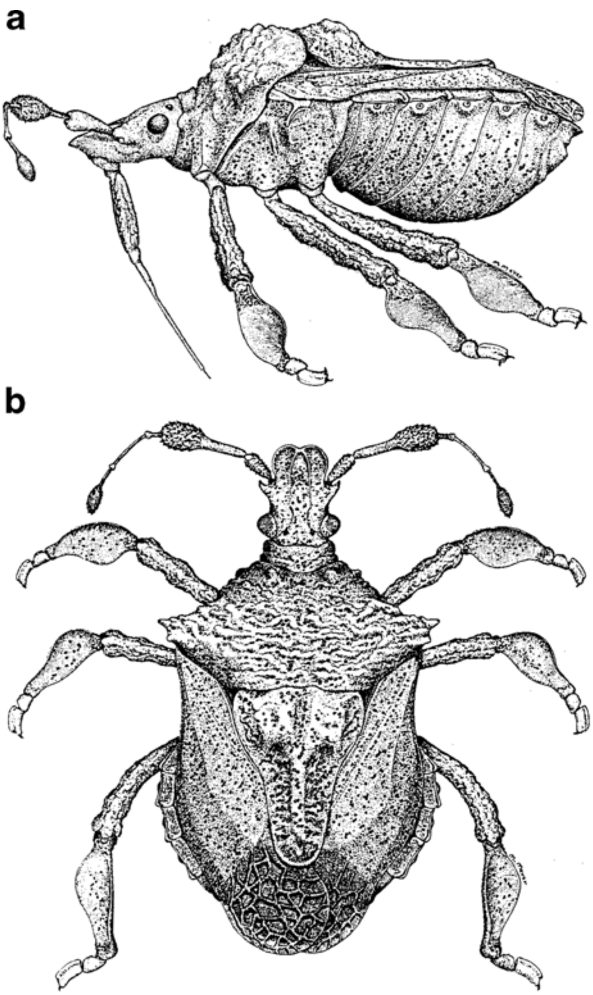

Fig. 22.50 *Stirotarsus abnormis* Bergroth, dorsal view (**a**) and ventral view (**b**) (From Rider (2000), with permission of the Annals of Entomological Society of America)

22.7.2 General Characteristics and Diagnosis

Characteristics of Podopinae include antenniferous tubercle visible in dorsal view; scutellum usually elongated, surpassing 2/3 the abdominal length; lateral rim of pygophore well developed, projecting on the ventral rim; ventral wall of pygophore with a median depression; lateral lobes of the conjunctiva strongly sclerotized (Schaefer 1981; Gapud 1991; Gapon and Konstantinov 2006).

The subfamily Stirotarsinae can be recognized by the antennal segments I, II, and V distinctly inflated; rostrum three-segmented, without apparent segmentation and anterior half enlarged; tarsi two-segmented, enlarged and with a longitudinal carina; tibiae foliate, dorsally concave. Other diagnostic characteristics, like the general body surface wrinkly, head longer than wide, sternum sulcated, and peritreme and evaporatorium reduced, are found in several groups of Pentatomidae and Pentatomoidea (i.e., Cyrtocorinae and some Podopinae).

22.7.3 Classification and Diversity

The Podopinae was first recognized by Stål (1876) as a group of genera. Lethierry and Severin (1893) gave status of subfamily to the group. The current classification was established by Davidová-Vilímová and Štys (1994), with five tribes: Brachycerocorini, Deroploini, Graphosomatini, Podopini, and Tarisini (Rider 2014). The monotypic genus *Neoleprosoma* was described by Kormilev and Pirán (1952) to include the Neotropical species *N. argentinensis* Kormilev & Pirán (Fig. 22.51). The authors considered *Neoleprosoma* related to *Leprosoma* Baerensprung and other similar genera of Podopinae from the Palearctic region, although the classification of the species was never reviewed. Davidová-Vilímová and Štys (1994) included *Neoleprosoma* in the tribe Graphosomatini. Distribution records of *N. argentinensis* include Argentina (Buenos Aires, Córdoba, and Santa Fé) and Uruguay (Artigas), in the southern region of South America.

Fig. 22.51 *Neoleprosoma argentinensis* Kormilev & Pirán (Photo by CF Schwertner)

The monotypic *Stirotarsus* was proposed by Bergroth (1911) to include *S. abnormis* from Peru, but because of its aberrant features, the classification among Pentatomidae was unsettled (Rider 2000). Based on the presence of a *ductus receptaculi* dilated and invaginated with three distinct walls in the female spermatheca and the unique set of characters found in *S. abnormis*, Rider (2000) proposed to place the genus in a separate subfamily. Poorly represented in collections (only one female), this taxon is probably endemic to the northern region of South America. No biological information is available; however previous hypothesis placed this taxon related to the asopines.

22.8 Concluding Remarks

The Pentatomidae, though predominantly herbivorous, includes predacious species and some economically important species of Heteroptera, such as the green stink bugs and the brown bugs. The group represents the second largest family of the infraorder Pentatomomorpha, with nine subfamilies, about 850 genera, and 4.700 species worldwide. The Neotropical fauna treated in this chapter comprises about 230 genera and more than 1,400 species, in seven subfamilies, representing 23 % of the world's genera and about 33 % of the species, suggesting that the number of new taxa awaiting description is immense. We hope this review of the family, which includes information on hosts, habits, economic importance, classification, checklists of species and/or genera, and keys to many of the Neotropical genera, will provide information to stimulate new interest in this large and diverse group of taxonomically and ecologically important insects.

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Chapter 23
Shield Bugs (Scutelleridae)

Joseph Eger Jr., Aline Barcellos, and Luciana Weiler

Abstract Scutelleridae Leach includes three subfamilies, 25 genera, and almost 100 species in the Neotropics. Both subfamilies Scutellerinae and Elvisurinae are represented by a single genus, and Pachycorinae contains the majority of the species. Neotropical shield bugs are usually dull colored, but polymorphisms and sexual dimorphisms have caused a considerable confusion in their taxonomy. Several genera need revision, and many new taxa are awaiting formal descriptions. Biological and ecological data are scarce, with a few species reported as minor pests.

23.1 Introduction

The family Scutelleridae Leach is global in distribution and quite diverse in size and appearance. These bugs have typically been referred to as "shield bugs," but recent papers on Old World representatives have used the term "jewel bugs" (Cassis and Vanags 2006; Tsai et al. 2011) because of their bright colors. However, this term does not accurately describe all scutellerids as many are rather dull colored. The Palearctic Scutelleridae are fairly well known and were recently catalogued by Göllner-Scheiding (2006). Australian and Taiwanese representatives have been revised by Cassis and Vanags (2006) and by Tsai et al. (2011), respectively. Neotropical shield bugs tend to be rather cryptic in coloration and poorly known

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taxonomically and biologically. Species numbers are probably greatly underestimated. Polymorphism in several species has contributed to a considerable degree of nomenclatural confusion as well. Overall, these little studied bugs are in need of taxonomic, ecological, and biological studies in the Neotropics.

Contributing to the lack of research on Neotropical Scutelleridae is the fact that there are few economically important species in this area. In the Middle East, species of *Eurygaster* Laporte are major pests of wheat, while *Calidea* spp. and *Tectocoris diophthalmus* (Thunberg) are pests of cotton in Africa and Australia, respectively (Javahery et al. 2000). A number of other species are minor pests in the Old World, but New World species tend to be minor pests of minor crops.

23.2 General Characteristics and Diagnosis

Shield bugs represent a diverse pentatomoid family, with 80 genera and about 500 species worldwide (Tsai et al. 2011). They are recognized by the beetle-like appearance, due to the great development of mesoscutellum (scutellum), which covers almost the entire abdomen. An enlarged scutellum occurs in a number of other pentatomoid families, including Aphylidae and Lestoniidae which are found only in Australia. In the New World, Thyreocoridae, Cyrtocoridae, and some Pentatomidae (primarily in the subfamilies Asopinae and Podopinae) have an enlarged scutellum. The tibiae of thyreocorids possess strong spines, much like cydnids, whereas scutellerids have strong setae at most. Cyrtocorids have a quadrate body shape and a spinose to quadrate projection on the scutellum which is lacking in scutellerids, while asopine pentatomids have an enlarged rostrum not found in scutellerids. Finally, the trichobothria of podopines are single while those of scutellerids are paired. Scutellerids vary greatly in shape, color, and size, but they are usually medium-sized pentatomoids (10–20 mm). Most of the species diversity occurs in the tropics (Lattin 1964).

Besides the enlarged scutellum, other diagnostic, but not always present, characters are rostrum attaining at least mesocoxae, prosternal keel well developed, hemelytra weakly sclerotized, legs usually unarmed, paired trichobothria, external genitalia visible or concealed by seventh sternite, spermathecal bulb with simple wall, genital capsule with a ringlike 8th segment, phallus often with two or three pairs of well-developed conjunctival projections, and parameres commonly uncinate (Schuh and Slater 1995; Tsai et al. 2011; Barcellos et al. 2014).

The location of the metathoracic ostiole, the presence or absence of the ostiolar peritreme, and the length and shape of the latter are diagnostic characters useful for identifying the different genera of Neotropical scutellerids and may be helpful in the separation of species in a limited number of genera. The external genitalia within Scutelleridae are usually simple but may be diagnostic for separation of species. Specifically, the shape of the posterior margin of the genital cup, the parameres, and the female genital plates may offer valuable taxonomic characters at the species level, depending on the genus. Internal genitalia, especially the development and shape of the conjunctival projections and phallotheca, are usually diagnostic. Variations in the spermatheca, including the shape of the spermathecal bulb, and distal and proximal flanges are important as described by authors such as McDonald (1966), Kumar (1965), and Candan et al. (2007, 2010).

Unlike the Afrotropical and Oriental shield bugs, those from Neotropics are usually dull brown, with only a few aposematic, and frequently polymorphic, species (e.g., species of *Agonosoma* Laporte, *Augocoris* Burmeister, *Pachycoris* Burmeister, and *Tiridates* Stål). Sexually dimorphic species are also found at least in three genera (*Agonosoma*, *Lobothyreus* Mayr, and *Crathis* Stål). Both polymorphism and sexual dimorphism have caused many synonymies and considerable confusion in the taxonomy of this group.

In the Neotropics, 25 genera are recorded, some of them also distributed in Nearctic region along with several undescribed genera. About 112 species are recorded in this region; however, as most of the genera need revision, this number is probably underestimated.

23.3 General Biology and Ecology

For Neotropical fauna, there are studies on the biology of *A. flavolineata* Laporte (Paleari 1992b), *P. klugii* Burmeister (Cervantes-Peredo 2002), *P. torridus* (Scopoli) (Rodrigues et al. 2011), and *Dystus puberulus* Stål (Cervantes-Peredo 2004).

Scutellerids are generally considered to be exclusively phytophagous, although some authors consider these bugs generalists (Javahery et al. 2000). Host plant records in Neotropical shield bugs are scarce (Table 23.1). Chérot et al. (1998) reported *Chrysocoris* (*Fitha*) *fascialus* (White) feeding on a decomposing snake in Thailand, while Eger et al. (2015) have collected large numbers of New World scutellerids at butterfly traps baited with putrefied fish carrion.

Maternal care has been described for *A. flavolineata* (Paleari 1992b), *P. torridus* (Hussey 1934; Santos et al. 2005), *P. klugii* (Cervantes-Peredo 2002), and also *P. stallii* Uhler (Williams et al. 2005). Females guard their eggs and first instar nymphs and may transmit aggregation semiochemicals to first instar nymphs. Nymphs become less aggregated as they develop, and fifth instars disperse totally.

Aposematism is usually associated with acquisition of toxic compounds by shield bugs from their host plants, providing protection against predation. Such strategy has been described for *Pachycoris*, whose species are known to feed preferentially on euphorbs. Williams et al. (2001) studied the chemical compounds of exocrine glands of *P. stallii*, a shield bug occurring in northwestern Mexico. This bug feeds on *Croton californicus* Muell. Arg., a Euphorbiaceae toxic to vertebrates. *Pachycoris stallii* uses toxic compounds obtained from this host plant to prevent predation by other invertebrates. The mostly South American *P. torridus* has the euphorb *Cnidoscolus pubescens* Pohl as its supposed preferential host plant (Santos et al. 2005) although there are several other records of host plants for this species. *Agonosoma flavolineata*, *Chelycoris haglundi* (Montandon), *C. lethierryi*

Table 23.1 Distribution and biology of Neotropical Scutelleridae[a]

Species	Distribution	Biology and notes
Scutellerinae		
Augocoris ehrenbergii Germar	Mexico, Guatemala, Venezuela*, Brazil*, Argentina*	
Augocoris gomesii Burmeister	USA (Arizona) and Mexico, South to Brazil	Attracted to light (Torre-Bueno 1914)
Augocoris illustris (F.)	USA (Florida), Mexico South to Argentina, and Brazil	Host plants: Phyllanthaceae, *Phyllanthus epiphyllanthus* L.; Sapotaceae, *Chrysophyllum cainito* L., *C. oliviforme* L., *Manilkara zapota* (L.) van Royen, *Mimusops elengi* L., *Sideroxylon foetidissimum* Jacq. (Barber and Bruner 1932; Wolcott 1923, 1936; Bruner et al. 1945).
		Attracted to light (Callan 1948; Hussey 1956)
Augocoris nigripennis Dallas	Venezuela	
Augocoris poeyi Uhler	Cuba	
Augocoris rufus Dallas	Colombia	
Augocoris rugulosus Herrich-Schaeffer	Brazil	
Pachycorinae		
Acantholomidea porosa (Germar)	Southern USA, Cuba, Mexico, Guatemala, Colombia	Host plant: Fabaceae, *Phaseolus vulgaris* L. (Maes 1994)
Agonosoma bicolor (Westwood)	Brazil	
Agonosoma flavolineata Laporte	Grenada, French Guyana, Brazil, Paraguay	Host plants: Convolvulaceae, *Ipomoea batatas* (L.) Lam.; Euphorbiaceae, *Croton glandulosus* L., *Jatropha gossypifolia* L.; Malvaceae, *Gossypium hirsutum* L. (Quintanilla et al. 1976; Paleari 1992b; Smith and Heard 2003; Rider 2014).
		Life history: Paleari (1992b)
Agonosoma trivittata (Panzer)	Grenada, Panama, Colombia, Venezuela, French Guyana, Brazil	Host plant: Euphorbiaceae, *Cnidoscolus urens* (L.) Arthur (Hallman 1979)
Ascanius atomarius (Germar)	Mexico*, Brazil, Bolivia, Argentina	Host plant: Rosaceae, *Ascanius* sp. collected on *Rubus erythrocladus* Mart. (Barcellos et al. 2014)
Ascanius hirtipes (Herrich-Schaeffer)	Brazil, Paraguay, Argentina	

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Camirus brevilinea (Walker)	Brazil	
Camirus conicus (Germar)	Mexico and Trinidad, S. to Colombia, Venezuela, Guyana, Brazil	
Camirus divergens (Walker)	Brazil, "Amazon region"	
Camirus impressicollis Stål	Brazil	
Camirus moestus (Stål)	USA (Arizona), Mexico, Nicaragua	Host plants: Asteraceae, *Ambrosia ambrosioides* (Cav.) Payne; Malvaceae, *Gossypium* sp. (Maes 1994; Rider 2014)
Camirus socius (Stål)	Mexico	
Chelycoris haglundi (Montandon)	Brazil, Peru, Paraguay, Argentina	Host plant: Euphorbiaceae, *Croton* sp. (Barcellos et al. 2014)
Chelycoris lethierryi (Montandon)	Brazil, Peru, Argentina, Uruguay	Host plant: Euphorbiaceae, *Croton* sp. (Barcellos et al. 2014)
Chelycoris scitulus (Walker)	Brazil, Peru, Bolivia, Paraguay, Argentina	
Chelycoris vittatus Distant	Brazil, Paraguay	
Chelyschema incarnata (Germar)	Brazil	
Chelyschema leucotelus (Walker)	Brazil	
Chelyschema trinotata (Walker)	Guatemala, French Guyana, Brazil	
Coptochilus ferrugineus Amyot & Serville	Ecuador, Brazil, Bolivia, Argentina	
Coptochilus lentiginosus Berg	Brazil, Paraguay, Argentina	
Coptochilus Neotropicsis Distant	French Guyana, Brazil	Collected at light (Eger et al. 2015)
Crathis ansata (Distant)	Belize, Costa Rica, Panama, Bolivia*	
Crathis longifrons Stål	French Guyana, Colombia, Brazil, Peru	Collected at fish carrion-baited butterfly traps (Eger et al. 2015)
Diolcus cassidoides (Walker)	Hispaniola	

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Diolcus disjunctus Barber	Puerto Rico	
Diolcus irroratus (F.)	USA (Florida), Cuba, Hispaniola, Puerto Rico, Jamaica, Antigua, Saint Vincent	Host plants: Combretaceae, *Conocarpus erectus* L.; Malvaceae, *Gossypium* sp. (Eger et al. 2015, Wolcott 1941)
Diolcus pusillus Berg	Argentina, Uruguay	
Diolcus variegatus (Herrich-Schaeffer)	Cuba, Hispaniola, Jamaica, adventive in Florida	Host plant: Malvaceae, *Malvastrum corchorifolium* (Desc.) Britt., *Sida acuta* Burm. (cited as *Sida carpinifolia* L.) (Bruner et al. 1945; Eger and Baranowski 2002)
Dystus puberulus Stål	Mexico, Costa Rica, Brazil, Bolivia	Host plant: Moraceae, *Ficus* spp. (Cervantes-Peredo 2004)
		Life history, immatures (Cervantes-Peredo 2004)
Ephynes brevicollis Stål	Brazil	
Galeacius crowleyi Distant	Brazil	
Galeacius martini Schouteden	French Guyana, Brazil	Host plant: Melastomataceae, *Miconia sellowiana* Naudin (Bianchi et al. 2011).
		Immatures described (Bianchi et al. 2011)
Galeacius simplex Breddin	Peru	
Galeacius tessellatus Distant	Panama	
Homaemus proteus Stål	Southern United States, Mexico, Jamaica*, Costa Rica, Colombia	
Lobothyreus brasiliensis Schouteden	Brazil	
Lobothyreus breviceps Breddin	Peru	
Lobothyreus illex Bergroth	French Guyana, Brazil,	
Lobothyreus lobatus (Westwood)	Colombia, Brazil	
Misippus spinolae (Signoret)	Brazil, Chile, Argentina, Uruguay	Host plant: Poaceae, *Oryza sativa* L. and *Sorghum bicolor* (L.) (Quintanilla et al. 1976)

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Orsilochides glirina (Bergroth)	Brazil	
Orsilochides leucoptera (Germar)	Brazil, Peru, Bolivia, Paraguay, Argentina	Host plants: Euphorbiaceae, *Croton* sp.; Malvaceae, *Gossypium hirsutum* L. Moench; Poaceae, *Sorghum bicolor* (L.) Moench (Quintanilla et al. 1976; Barcellos et al. 2014)
Orsilochides scurrilis (Stål)	Mexico, Guatemala, El Salvador, Nicaragua, Bolivia*	
Orsilochides stictica (Dallas)	USA (Texas), Mexico, Guatemala, Honduras	
Orsilochides variabilis (Herrich-Schaeffer)	Mexico, Belize, Guatemala, Nicaragua, Costa Rica, Colombia, Argentina*, Uruguay*	
Pachycoris chrysomelinus Walker	Ecuador	
Pachycoris fabricii (L.)	Caribbean, Mexico* to Brazil*	Host plants: Boraginaceae, *Cordia nitida* Vahl.; Euphorbiaceae, *Croton discolor* (Willd.) Raf., *Croton humilis* L., *Croton* sp.; Verbenaceae, *Lantana involucrata* L., *Lantana* sp. (Barber 1939; Wolcott 1923, 1941)
Pachycoris klugii Burmeister	Mexico, northern Central America, Colombia*, Brazil*, Paraguay*	Host plant: Euphorbiaceae, *Jatropha curcas* L. (Cervantes-Peredo 2002; Martínez-Herrera et al. 2010; Tepole-García et al. 2012)
		Immatures described, maternal care, field observations (Cervantes-Peredo 2002)
Pachycoris nitidiventris Breddin	Costa Rica	
Pachycoris obscuratus Herrich-Schaeffer	South America	
Pachycoris stallii Uhler	Mexico	Host plant: Euphorbiaceae, *Croton californicus* Muell. Arg. (Williams et al. 2005)
		Immatures described, maternal care, life history, egg parasite *Telenomus pachycoris* (Costa Lima) (Hymenoptera: Scelionidae) and predator *Dorymyrmex bicolor* (Hymenoptera: Formicidae) Wheeler (Williams et al. 2005)

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Pachycoris torridus (Scopoli)	Mexico and California* south to Argentina and Brazil	Host plants: Anacardiaceae, *Anacardium occidentale* L., *Mangifera indica* L., *Schinus terebinthifolius* Raddi; Aquifoliaceae, *Ilex paraguariensis* St. Hil.; Boraginaceae, *Cordia* sp.; Euphorbiaceae, *Aleurites fordii* Hemsley, *Cnidoscolus pubescens* Pohl, *Croton californicus* Müll. Arg., *Jatropha curcas* L., *Jatropha* sp., *Manihot esculenta* Crantz, *Sapium haematospermum* Müll. Arg.; Malpighiaceae, *Malpighia glabra* L.; Myrtaceae, *Eucalyptus* sp., *Psidium guajava* L., *P. guineense* Sw. (cited as *P. araca* Raddi); Poaceae, *Oryza sativa* L.; Rubiaceae, *Coffea* sp. (Hussey 1934; Bosq 1937, 1940; Costa Lima 1940; Callan 1948; Silva et al. 1968; Maes 1994; Sánchez-Soto and Nakano 2002; Sánchez-Soto et al. 2004; Santos et al. 2005; Michelotto et al. 2006; Rodrigues et al. 2011; Souza et al. 2012; Rider 2014)
		Egg parasitoid, *Paratelenomus pachycoris* Costa Lima (Costa Lima 1928) (Hymenoptera: Scelionidae); parasitoids, *Trichopoda pennipes* (F.), *T. pilipes* (F.) (Diptera: Tachinidae) (Guimarães 1977); parental care, ecology, field observations (Hussey 1934; Santos et al. 2005). Collected at fish carrion-baited butterfly traps (Eger et al. 2015)
Polytes bicolor Distant	Peru	
Polytes bimaculatus Eger	Peru	Collected at fish carrion-baited butterfly traps (Eger et al. 2015)
Polytes bullocki Eger	Peru	
Polytes confusus Eger	Peru	
Polytes discrepans (Uhler)	Peru	
Polytes fenestra Breddin	Colombia, Peru, Bolivia, Argentina	
Polytes granulatus (Walker)	Colombia, Ecuador, Peru, Bolivia, Argentina	
Polytes lattini Eger	Peru	
Polytes leopardinus Distant	Peru	
Polytes lineolatus (Dallas)	Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia	

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Polytes obscurus (Dallas)	Colombia, Brazil*, Peru, Bolivia, Argentina	
Polytes nigrovittatus Eger	Peru	
Polytes propinquus (Walker)	Venezuela	
Polytes rubromaculatus Distant	Ecuador	
Polytes ruth (Breddin)	Peru, Bolivia	
Polytes similis Eger	Peru	
Polytes speculiger Breddin	Peru	
Polytes tigrinus (Vollenhoven)	Colombia, Peru	
Polytes velutinus (Dallas)	Colombia, Venezuela, Ecuador, Peru, Bolivia	
Sphyrocoris obliquus (Germar)	Southern USA throughout the Caribbean and Central America into Colombia and Venezuela	Host plants: Asteraceae, *Bidens bipinnata* L., *Bidens* sp.; Fabaceae, *Glycine max* L. Merrill; Lamiaceae, *Salvia mellifera* Greene; Malvaceae, *Gossypium barbadense* L. (Callan 1948; Eger 2012)
		Egg parasitoid, *Trissolcus trinidadensis* Crawford (Hymenoptera: Scelionidae) (Crawford 1913; Callan 1948)
Symphylus affinis (F.)	South America, Antilles*	
Symphylus albomaculatus Distant	Panama	
Symphylus caribbeanus Kirkaldy	USA (Texas, Florida), Mexico, Caribbean, Central America	Host plants: Anacardiaceae, *Mangifera indica* L.; Clusiaceae, *Clusia major* L. (as *C. rosea* Jacq.); Fabaceae, *Phaseolus lathyroides* L.; Lamiaceae, *Salvia mellifera* Greene; Myricaceae, *Myrica cerifera* L.; (Blatchley 1926; Bruner et al. 1945; Callan 1948; Lattin 1964)
		Attracted to light (McPherson 1977)
Symphylus cyphonoides (Walker)	Mexico, Panama, Ecuador, Brazil, Bolivia,	Collected at fish carrion-baited butterfly traps (Eger et al. 2015)
Symphylus deplanatus (Herrich-Schaeffer)	Mexico, Guatemala, Belize, Jamaica, Saint Vincent, Grenada, Trinidad y Tobago, Panama, Ecuador, Brazil, Paraguay, Argentina	Host plant: Boraginaceae, *Cordia macrostachya* (Jacquin) Roemer & Schultes (Rider 2014)
		Attracted to light (Uhler 1894; Torre-Bueno 1914)

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Symphylus devexus Walker	Brazil	
Symphylus enac Breddin	Bolivia	
Symphylus infamatus Uhler	Mexico	
Symphylus lativittatus Breddin	Ecuador	
Symphylus leucospilus (Walker)	Amazon Region, Brazil	
Symphylus luminosus (Germar)	Mexico	
Symphylus modestus Distant	Guatemala, Panama	
Symphylus obtusus Dallas	Mexico, Panama, Colombia	
Symphylus poecilus Dallas	Brazil	
Symphylus ramivitta Walker	Belize, Ecuador, Brazil, Peru, Bolivia, Paraguay, Argentina	Collected at fish carrion-baited butterfly traps (Eger et al. 2015)
Symphylus rivulosus (Walker)	Mexico, Guatemala, Nicaragua, Trinidad y Tobago, Panama, Brazil	
Symphylus signoretti Distant	Mexico	
Testrina wolfii (Fabricius)	Brazil, South America	
Tetyra antillarum Kirkaldy	USA (Florida), Mexico, Antilles	Attracted to light (Wolcott 1941)
Tetyra pinguis (Germar)	Mexico, Guadalupe, Guatemala, Jamaica, Honduras, Colombia, French Guyana, Brazil, Bolivia	Host plant: Rubiaceae, *Coffea* sp. (Maes 1994)
Tetyra poecila Berg	Brazil, Argentina	Host plants: Fabaceae, *Acacia caven* (Mol.) Mol. (cited as *A. cavenia*), *A. farnesiana* (L.) Willd., *Gleditsia triacanthos* L.; Solanaceae, *Solanum bonariense* L. (Berg 1879)
		Immatures described (Berg 1879)
Tiridates mexicanus (Herrich-Schaeffer)	Mexico	

(continued)

Table 23.1 (continued)

Species	Distribution	Biology and notes
Tiridates rubrocinctus rubrocinctus (Herrich-Schaeffer)	Mexico	
Tiridates rubrocinctus schaffneri Eger	Mexico, Honduras	
Elvisurinae		
Nesogenes boscii (Fabricius)	Greater Antilles, Saint Vincent	

[a]Species treated in this table are those treated as valid by Kirkaldy (1909) unless more recent work has modified the status of these species. Subspecies treated by Kirkaldy are not treated here. *Localities followed by an asterisk are probably the result of a misidentification and are considered questionable

(Montandon), and *Orsilochides leucoptera* (Germar) were observed feeding on *Croton* spp. in Brazil (Eger et al. 2015).

Adult diapause has been reported for *A. flavolineata* during the dry season in southeastern Brazil (Paleari 1992b). Also, adults of *Pachycoris torridus* were found, apparently in diapause, inside terrestrial bromeliads during the winter in southern Brazil (Barcellos et al. 2014).

23.3.1 Eggs and Oviposition

Scutellerid eggs are spherical or barrel-shaped, similar to those of other pentatomoids, with small aero-micropylar processes variable in number among species, and hatching occurs through a triangular or T-shaped egg burster. The eggs of the Neotropical *Dystus puberulus* have a smooth surface, with 6–7 aero-micropylar processes (Cervantes-Peredo 2004). In *Galeacius martini* Schouteden, eggs are reddish brown, with the surface of the chorion translucent, nearly smooth under light stereomicroscope, and with a mean of 24 aero-micropylar processes (Bianchi et al. 2011). Studies employing scanning electron microscopy (SEM) for Neotropical fauna are available for *Pachycoris stallii* (Williams et al. 2005) and *Galeacius martini* (Bianchi et al. 2011).

Scutellerid eggs are laid in two (more often) or more rows, on several parts of the host plant. Egg masses vary in number, averaging from 14 (*Agonosoma flavolineata*, Paleari 1992b; *D. puberulus*, Cervantes-Peredo 2004) to almost a hundred eggs (75–92) in *P. torridus* (Santos et al. 2005) and 81.4 on average in *P. klugii* (Cervantes-Peredo 2002). Under laboratory conditions, individuals of *P. torridus* reared on the physic nut, *Jatropha curcas* L., showed a preoviposition period twice as long as, and laid more eggs than, those fed on strawberry guava – *Psidium cattleianum* Sabine (Myrtaceae) (Borges Filho et al. 2013).

23.3.2 Nymph Feeding and Development

A few Neotropical species have had their biological cycle studied. Life cycle is highly variable in length. For *Agonosoma flavolineata* reared on *Croton glandulosus* L. (Euphorbiaceae), a mean total development time of about 42 days was recorded, including a 7-day incubation period (Paleari 1992b). Cervantes-Peredo (2004) observed a total life cycle of 60 days in *D. puberulus* reared on fruits of *Ficus* spp. The nymphal stage of *P. torridus* is about 55 days long when fed on *J. curcas* or strawberry guava, under laboratory conditions (Borges Filho et al. 2013). First stadium nymphs, as in other pentatomoids, do not feed, using only reserves from embryonic stage. Apparently, this fact contributes to the low mortality observed in this instar, as food availability is not a constraint. Conversely, the role of aggregation is considered crucial for the survival of the first instar.

23.3.3 Adult Feeding and Reproduction

Shield bugs are broadly phytophagous, although there are some observations of necrophagy or at least attraction to carrion as mentioned previously (Chérot et al. 1998, J. Eger et al. 2015). Stems, leaves, and flowers may be used as food although fruit and seeds seem to be most commonly used. Data on the known host plants are still scarce (Table 23.1), but some patterns may be pointed out. *Pachycoris torridus* has a wide range of reported host plants of different botanical families, but shows preference for euphorbs, similar to its congeners. *Symphylus* spp. are recorded mostly on Malvaceae and Lamiaceae. *Sphyrocoris obliquus* (Germar) also seems to be polyphagous.

The sex ratio in collections is sometimes puzzlingly biased. Eger (1990) observed that specimens of *Polytes* Stål in collections were overwhelmingly males. Genera such as *Crathis* and *Lobothyreus* have many more males than females sampled, and we do not know the reason for that. However, some scutellerids attracted to fish carrion are primarily males (Eger et al. 2015), so collection method may have more to do with sex ratio differences in collections and this bias may not be indicative of a bias in natural populations.

23.4 Classification and Diversity

The higher classification of scutellerids has not been well studied historically, but recent work has helped clarify the subfamily status of various taxa. Cassis and Vanags (2006) provide a detailed discussion of the infrafamilial groups. There are currently eight subfamilies, only three of which are further divided into tribes. The subfamilies Tectocorinae McDonald and Cassis, Odontoscelinae Amyot and

Serville, and Hoteinae Carapezza are exclusively Old World. New World representatives of Odontotarsinae Mulsant and Rey and Eurygastrinae Amyot and Serville occur only in the Nearctic region, leaving the Neotropics with three subfamilies, Elvisurinae Stål, Pachycorinae Amyot and Serville, and Scutellerinae Leach.

Pachycorinae was historically characterized by stridulatory areas on the abdominal sterna associated with a tibial plectrum and also by the presence of a single interclaval vein in the hind wing (Fischer 2001). Included in the subfamily were three genera with Old World distribution (*Deroplax* Mayr, *Hotea* Amyot and Serville, and *Tectocoris* Hahn) (Kumar 1965). Lattin (1964) and others contested the monophyly of Pachycorinae, as the stridulatory areas appeared to have evolved more than once within the family (Lattin 1964). McDonald and Cassis (1984) placed *Tectocoris* in a monotypic subfamily, Tectocorinae, based primarily on genitalic characters and the presence of abdominal sternal glands in males. Carapezza (2009) described genitalic differences between the Old World genera *Hotea* and *Deroplax* and the New World genera of Pachycorinae and erected a new subfamily, Hoteinae, for these two genera. He also pointed out that species of *Ellipsocoris* Mayr (Odontotarsinae) possess stridulatory patches on the abdominal sterna. Cassis and Vanags (2006) mentioned that stridulatory areas occur in *Nesogenes* (Elvisurinae) as well (see discussion below). Moreover, the interclaval vein is also shared with Odontotarsinae and Eurygastrinae (Czaja 2007). The removal of *Deroplax*, *Hotea*, and *Tectocoris* from the subfamily makes the Pachycorinae exclusively New World in distribution. Based on these characters, associated with the absence of a unique pattern of genitalia morphology, Tsai et al. (2011) suggested a non-monophyly of Pachycorinae, a hypothesis that is currently under investigation (Weiler et al. in prep.).

Scutellerinae is primarily an Old World subfamily which contains two tribes, Sphaerocorini Stål and Scutellerini Leach. The Scutellerinae are represented in this hemisphere by only a single genus, *Augocoris*, which belongs in the tribe Scutellerini. The subfamily Elvisurinae is also represented by a single genus in the Neotropics. Horvath (1921) placed his new genus *Nesogenes* in the Elvisurinae based on the developed thoracic sterna. The type and only species is *Cimex boscii* F. which was previously placed in the genus *Diolcus* Mayr. This species is distributed in the Greater Antilles, where most of the species of *Diolcus* are found, and the thoracic sterna are developed into relatively thick carinae (Fig. 23.53), not at all like the thin platelike lobes of the Elvisurinae. *Nesogenes* appears to be more closely related to species of *Diolcus* than to any of the Elvisurini and probably should be removed from Elvisurini and placed back in the Pachycorinae, if not back into the genus *Diolcus* (Eger et al. 2015).

The Neotropical scutellerid fauna, the poorest known of the zoogeographic regions, currently includes three subfamilies, Pachycorinae with 23 genera, Scutellerinae, represented in the region only by *Augocoris*, and Elvisurinae represented by the probably misplaced genus, *Nesogenes*. With the exception of *Stethaulax* Uhler, all remaining pachycorine genera are recorded in the Neotropics, with a few occurring in both the Nearctic and Neotropical Regions (*Acantholomidea*, *Diolcus*, *Homaemus*, *Orsilochides*, *Sphyrocoris*, and *Tetyra*). However, it is likely that some species currently assigned to *Symphylus* may actually belong to *Stethaulax*, which would extend the range of this genus into the Neotropics as well (Lattin 1964). There are 112 recorded species, but this number is certainly underestimated.

The scutellerine genus *Augocoris* includes six species, of which *A. illustris* and *A. gomesii* are the best known in Neotropics. Both are polymorphic, ranging from almost entirely white dorsally to black or blue with red markings (Lattin 1964).

The taxonomic knowledge of the Neotropical pachycorine fauna is incipient. There are revisions only for *Agonosoma* (Paleari 1992a), *Tiridates* (Eger 1987), *Polytes* (Eger 1990), and *Sphyrocoris* Mayr (Eger 2012) although Eger and Lattin (1995) reviewed the generic placement and synonymy of types of New World scutellerids found in the British Museum. Most of the remaining genera are known only from their original descriptions. Some of them are particularly problematic. *Symphylus* is a "catch-all" genus which probably represents a non-monophyletic group in need of revision. Some species currently placed in *Symphylus* may belong to related genera (*Ephynes* Stål, *Galeacius* Distant, and *Stethaulax*) or may require the establishment of new genera and there appear to be a large number of undescribed species in this group. Additionally, there are many apparently undescribed species in genera such as *Camirus* Stål, *Diolcus*, and *Tetyra* F.

23.4.1 Main Species, Economic Aspects

Pachycoris torridus (Scopoli) (Fig. 23.27) and *P. klugii* Burmeister, both highly polymorphic species, are reported as pests of *J. curcas* (Grimm and Maes 1997; Cervantes-Peredo 2002; Rodrigues et al. 2011; Souza et al. 2012), damaging the seeds. *P. torridus* occurs from southern Mexico to Argentina, but is more abundant in South America and is the only species considered to be of economic importance in Brazil. Besides *J. curcas*, *P. torridus* is reported on several host plants, causing damage to strawberry guava and tung, *Vernicia fordii* (Hemsl.) (Euphorbiaceae) (Borges Filho et al. 2013). *Pachycoris klugii* is distributed from Mexico into Central America.

Augocoris illustris (F.) (Fig. 23.2) – this representative of the only scutellerine genus in the Neotropics – is highly variable in color, species varying from light, almost white with variable dark spots, to black with red markings. Barber and Bruner (1932) provided illustrations of the variability in this species. Reported hosts are *Chrysophyllum oliviforme* L. and other species of Sapotaceae.

Augocoris gomesii Burmeister (Fig. 23.1) – this species is a little larger and more ovate than the preceding but also shows a great deal of variability in color. Host plants are not known, but it can be abundant at lights in some parts of South America.

Agonosoma flavolineata (Laporte) (Fig. 23.13) and *A. trivittata* (Panzer) – these species are widely distributed in South America. Females of the former species and both sexes of the latter are polymorphic (Paleari 1994). *Agonosoma trilineatum* was introduced to Australia as a biological control agent for the introduced weed *Jatropha gossypifolia* L. (Smith and Heard 2003).

Symphylus deplanatus (Herrich-Schaeffer) – this species is very common in collections and is a medium-sized (10–12 mm) shield bug. It is also polymorphic, showing different patterns of black to brown markings. There is one synonym and two subspecies of this species, but based on genitalia, there is probably a complex of species that may be misidentified in collections.

Tetyra pinguis Germar – described from Brazil, this species is recorded for all Neotropics. This wide distribution, together with variable size and color patterns, might indicate that it represents a complex of several species.

23.4.2 Secondary Species

Crathis ansata (Distant) – this is a Central American species which differs from its congeners by the anterior part of scutellum conspicuously more elevated than pronotum.

Crathis longifrons Stål (Fig. 23.9) – this species is widely distributed in South America, and the southern limit of its range is Central Brazil. Curiously, there are large series of male specimens contrasting with very few females in collections. It has been collected at fish carrion-baited traps.

Tetyra poecila Berg – this species is very commonly found in collections from southern Brazil and Argentina. It was recorded on Fabaceae and Mimosaceae.

Symphylus spp. (Fig. 23.17) – the genus as currently conceived contains a large number of mostly brown mottled species that are frequently collected at light and at fish carrion-baited traps.

Symphylus ramivitta Walker (Fig. 23.19) – its color pattern, consisting of longitudinal stripes, is very distinctive among its congeners. This species is broadly distributed in the Neotropics.

Symphylus cyphonoides (Walker) (Fig. 23.18) – this is one of the smallest species within the genus, is yellowish brown, has rounded shape, and distributed from Central America to Brazil. Adults have been collected on fruits of *Cervantesia* sp. (Santalaceae) in Peru.

Galeacius martini Schouteden (Fig. 23.23) – this bug is a very distinctive pachycorine, with humeri strongly produced. The immature stages were described by Bianchi et al. (2011).

Camirus spp. (Fig. 23.4) – these brown nondescript species are frequently collected when sweeping secondary growth along trails or roadways.

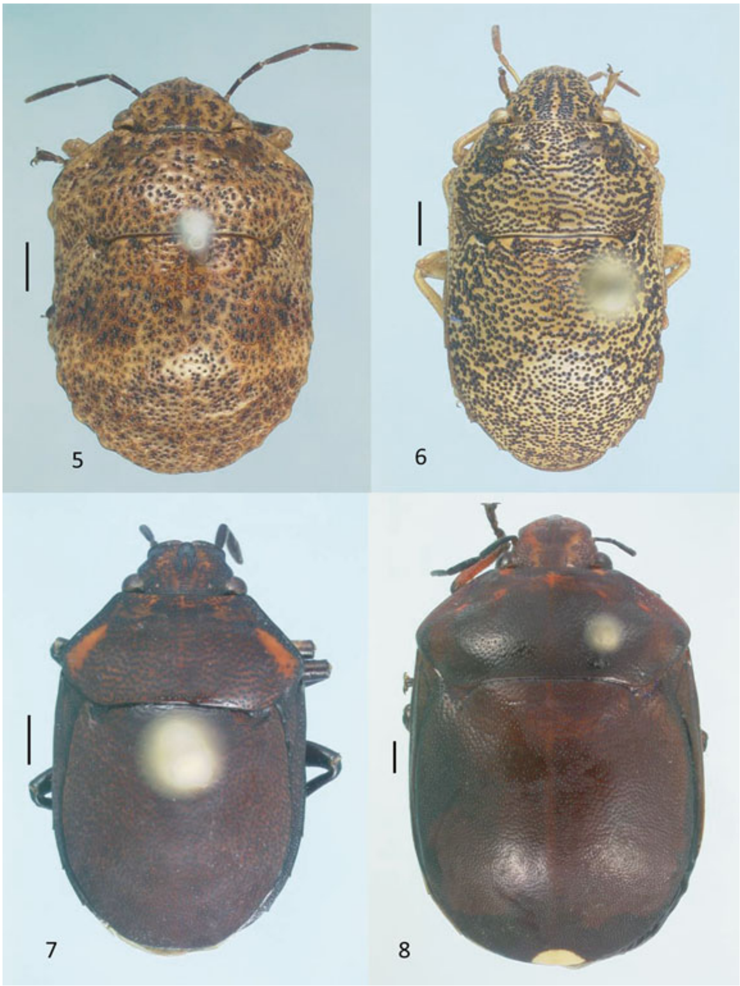
Homaemus spp. (Fig. 23.15) and *Sphyrocoris obliquus* (Germar) (Fig. 23.16) – these are also dull brown insects with some darker patterning. As with *Camirus* spp., they are commonly swept from vegetation in disturbed areas, the latter taxa being reported from *Bidens* spp. (Eger 2012). Distribution for both species ranges from the United States into northern South America.

Natural enemies include invertebrate predators such as the ant *Dorymyrmex bicolor* Wheeler on *P. stallii* (Williams et al. 2001); egg parasitoids such as the platygastrid wasps *Trissolcus trinidadensis* Crawford and *Telenomus pachycoris*

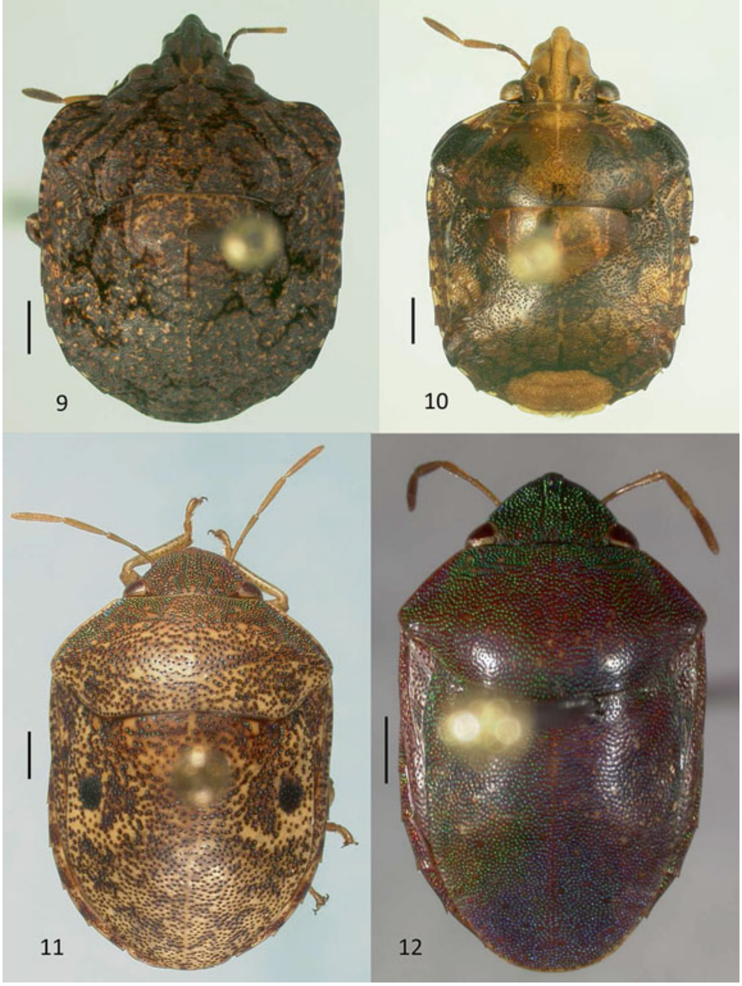
Figs. 23.1–23.4 Dorsal habitus. 1: *Augocoris gomesii*; 2: *Augocoris illustris*; 3: *Acantholomidea porosa*; 4: *Camirus* sp. Dimensional lines equal 1.0 mm (Photos by J Eger)

(Costa Lima) (as *Pseudotelenomus pachycoris*) (Gabriel et al. 1988), respectively, on *Sphyrocoris obliquus* (Germar) and *P. torridus*; and adult parasitoids such as the tachinids *Trichopoda pennipes* (F.) on *P. klugii* (Cervantes-Peredo 2002) and *T. pilipes* (F.) and *T. pilipes* on *P. torridus* (Guimarães 1977).

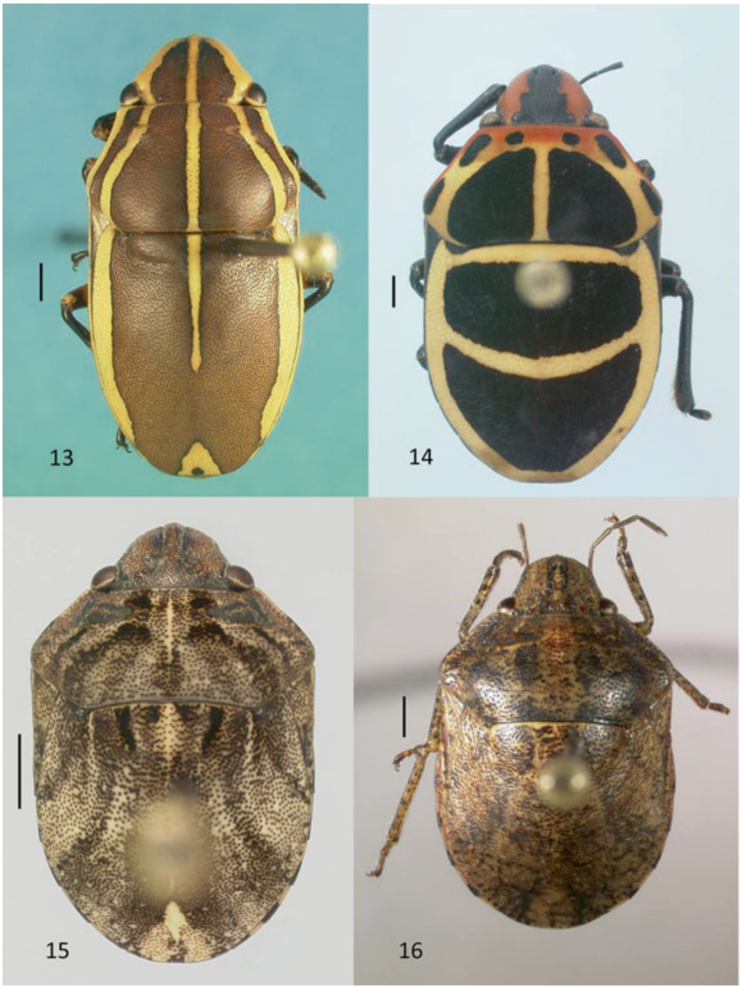
Key to Neotropical genera of Scutelleridae [adapted from Schouteden (1904), Lattin (1964), and Barcellos et al. (2014)]



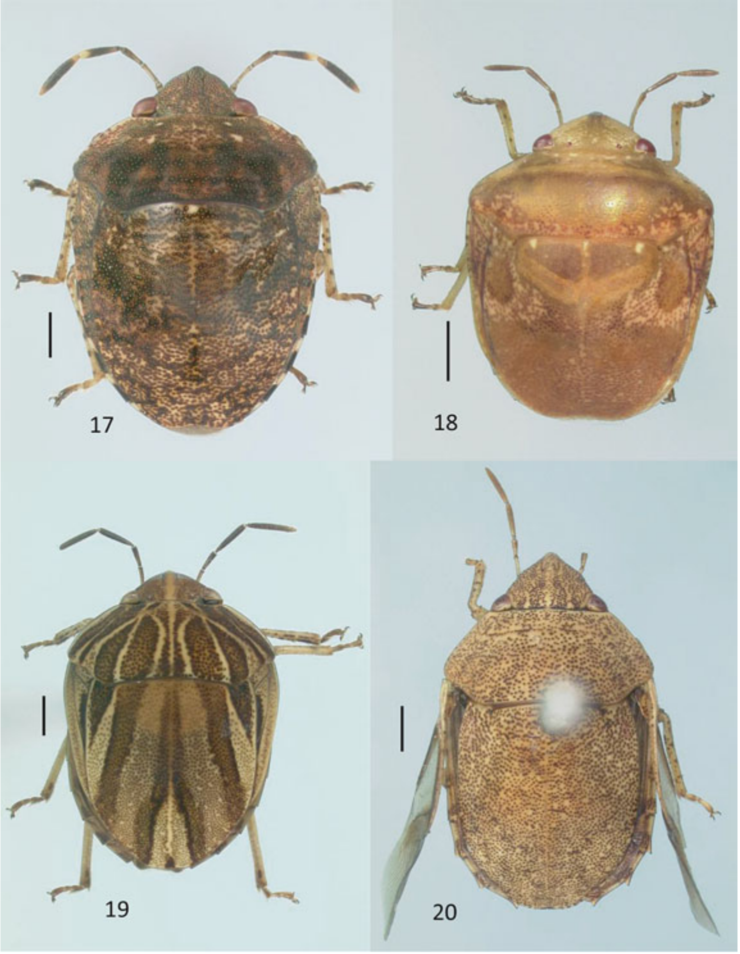
Figs. 23.5–23.8 Dorsal habitus. 5: *Ascanius hirtipes*; 6: *Chelycoris haglundi*; 7: *Coptochilus ferrugineus*; 8: *Chelyschema* sp. Dimensional lines equal 1.0 mm (Photos by J Eger)



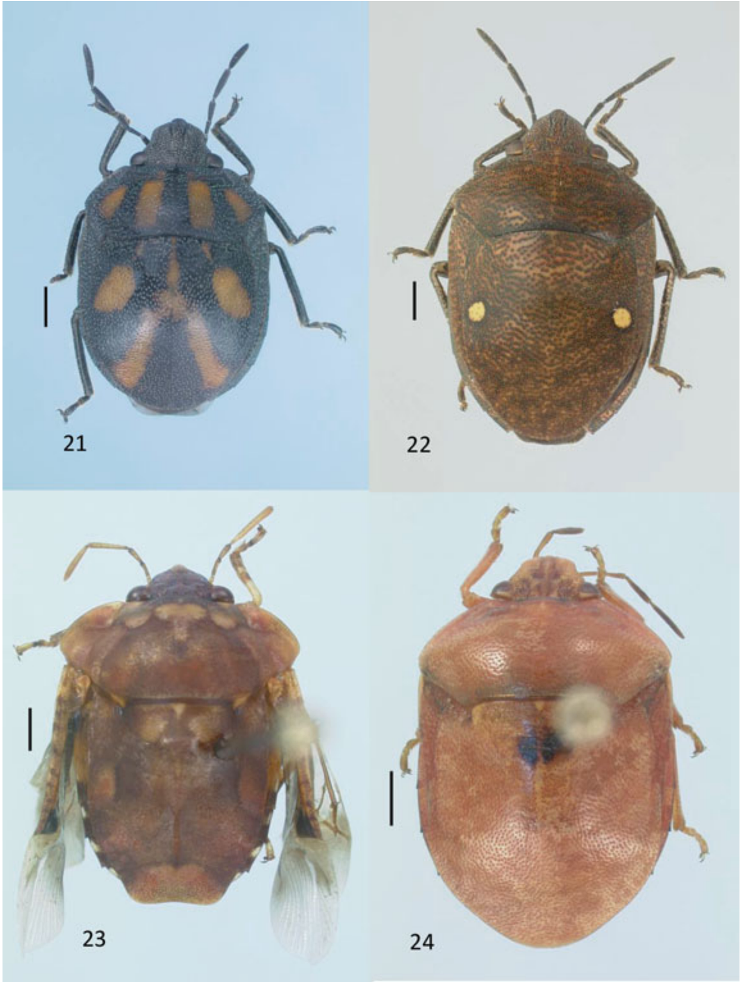
Figs. 23.9–23.12 Dorsal habitus. 9: *Crathis longifrons*; 10: *Lobothyreus brasiliensis*; 11: *Diolcus chrysorrhoeus*; 12: *Nesogenes boscii*. Dimensional lines equal 1.0 mm (Photos by J Eger)



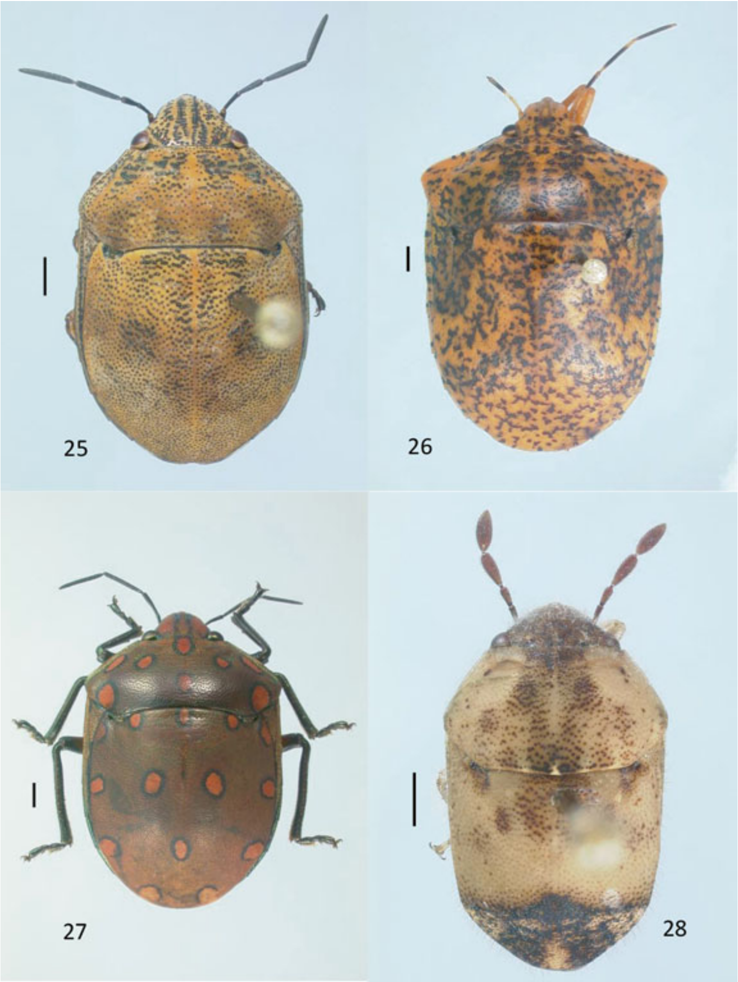
Figs. 23.13–23.16 Dorsal habitus. 13: *Agonosoma flavolineata*; 14: *Tiridates rubrocinctus*; 15: *Homaemus proteus*; 16: *Sphyrocoris obliquus*. Dimensional lines equal 1.0 mm (Photos by J Eger)



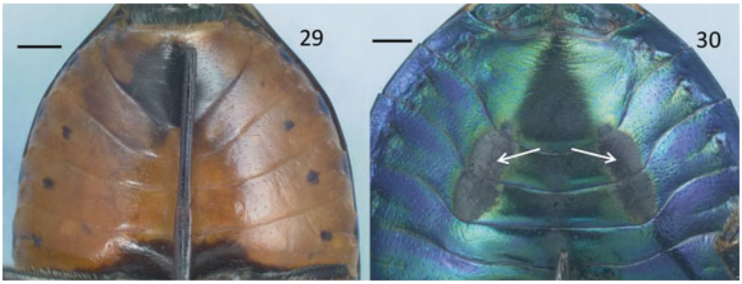
Figs. 23.17–23.20 Dorsal habitus. 17: *Symphylus* sp.; 18: *Symphylus cyphonoides*; 19: *Symphylus ramivitta*; 20: *Ephynes brevicollis.* Dimensional lines equal 1.0 mm (Photos by J Eger)



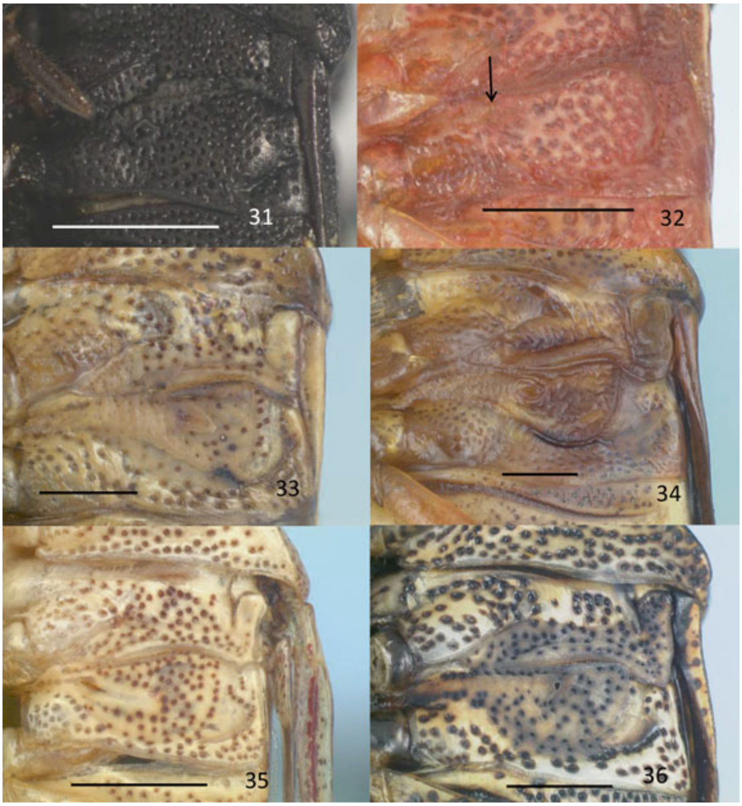
Figs. 23.21–23.24 Dorsal habitus. 21: *Polytes fenestra*; 22: *Polytes bimaculatus*; 23: *Galeacius martini*; 24: *Misippus spinolae*. Dimensional lines equal 1.0 mm (Photos by J Eger)



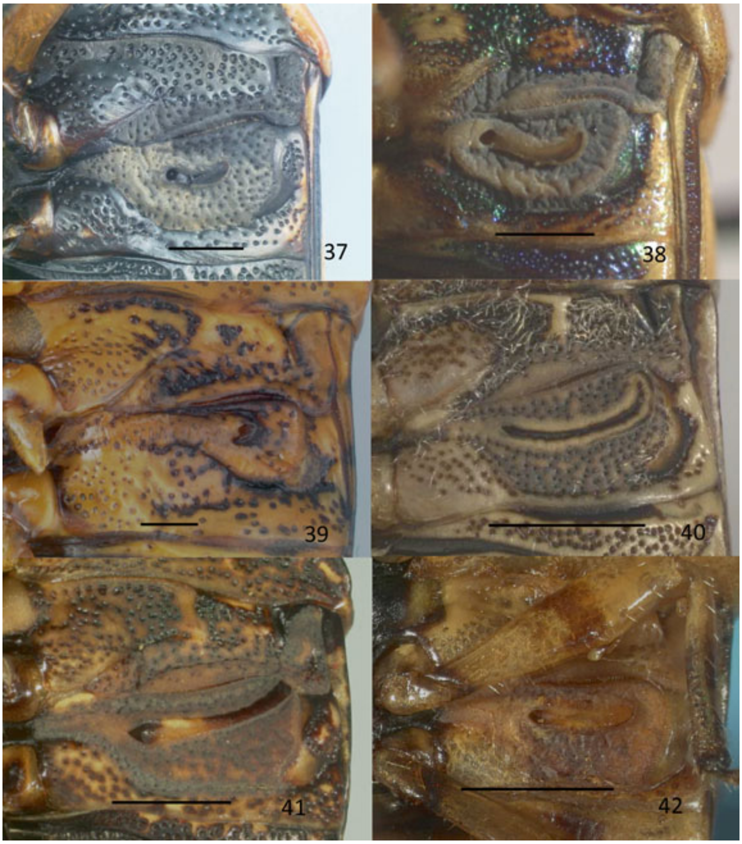
Figs. 23.25–23.28 Dorsal habitus. 25: *Orsilochides leucoptera*; 26: *Tetyra* sp.; 27: *Pachycoris torridus*; 28: *Dystus puberulus*. Dimensional lines equal 1.0 mm (Photos by J Eger)



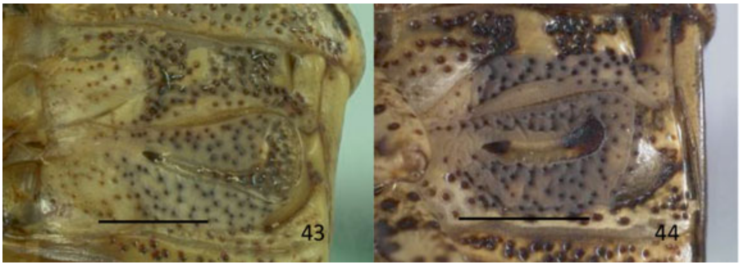
Figs. 23.29–23.30 Abdominal venter. 29: *Augocoris gomesii*; 30: *Pachycoris torridus*, *arrows* indicate striated areas. Dimensional lines equal 1.0 mm (Photos by J Eger)



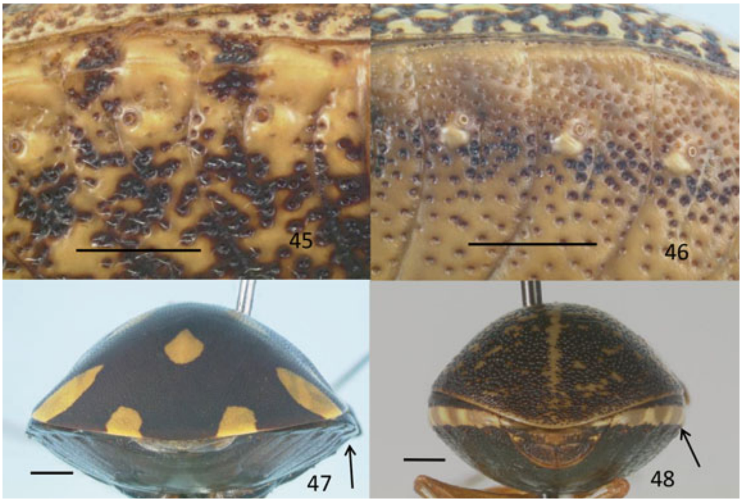
Figs. 23.31–23.36 External efferent system. 31: *Acantholomidea porosa*; 32: *Misippus spinolae*, *arrow* indicates location of ostiole; 33: *Chelycoris lethierryi*; 34: *Chelyschema* sp.; 35: *Ephynes brevicollis*; 36: *Polytes obscurus*. Dimensional lines equal 1.0 mm (Photos by J Eger)



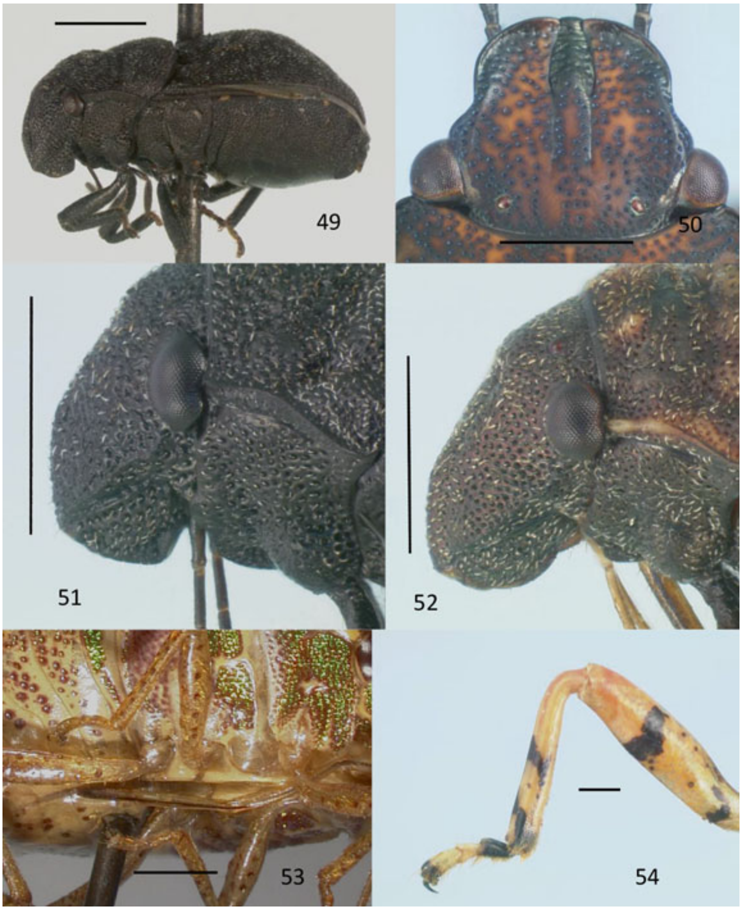
Figs. 23.37–23.42 External efferent system. 37: *Tiridates rubrocinctus*; 38: *Agonosoma flavolineata*; 39: *Tetyra* sp.; 40: *Homaemus proteus*; 41: *Crathis longifrons*; 42: *Galeacius martini*. Dimensional lines equal 1.0 mm (Photos by J Eger)



Figs. 23.43–23.44 External efferent system. 43: *Sphyrocoris obliquus*; 44: *Symphylus caribbeanus*. Dimensional lines equal 1.0 mm (Photos by J Eger)



Figs. 23.45–23.48 45–46: Lateral view of abdomen showing spiracles. 45: *Ascanius hirtipes*; 46: *Chelycoris lethierryi*. 47–48: Caudal view of abdomen. 47: *Pachycoris torridus*; 48: *Orsilochides guttata*. *Arrows* indicate lateral compression in *P. torridus* and lateral convexity in *O. guttata*. Dimensional lines equal 1.0 mm (Photos by J Eger)



Figs. 23.49–23.54 49: *Acantholomidea porosa*, lateral view; 50: *Coptochilus ferrugineus*; 51–52: Lateral view of head. 51: *Acantholomidea porosa*; 52: *Camirus* sp. 53: Thoracic sterna of *Nesogenes boscii*; 54: Proleg of *Tetyra* sp. Dimensional lines equal 1.0 mm (Photos by J Eger)

1. Stridulatory areas absent on abdominal venter (Fig. 23.29); antennae three-segmented (Scutellerinae) .... *Augocoris* (Figs. 23.1, 23.2)

1'. Stridulatory areas present on both sides of midline on each of at least abdominal sternites 5–6 (Fig. 23.30); antennae five-segmented (Pachycorinae) 2

2. Head with anterior margins and anterior portion of lateral margins elevated (Fig. 23.50).. *Coptochilus* (Fig. 23.7)

2'. Head with anterior and lateral margins not elevated 3

3. Distance from metacoxa to ostiole shorter than distance from ostiole to lateral margin of metapleuron (Figs. 23.31, 23.32, 23.34, 23.35, 23.37, 23.38, 23.40, 23.41, 23.42, 23.43, and 23.44) 4

3'. Distance from metacoxa to ostiole longer than or subequal to distance from ostiole to lateral margin of metapleuron (Figs. 23.33, 23.36, 23.39) 19

4. Pronotum with a median transverse impression, this usually conspicuous (Fig. 23.49); head usually declivent (Figs. 23.51, 23.52); coloration brown to black, frequently mottled; punctures usually provided with short, decumbent setae.. 5

4'. Pronotum not impressed transversely; head usually porrect; coloration variable; punctures rarely provided with setae and if so, setae generally long and erect 6

5. Head strongly declivent; bucculae with distinct lobe anteriorly, lobe strongly truncate posteriorly (Fig. 23.51); coloration black (Fig. 23.3); stridulatory areas not extending onto seventh sternite .... *Acantholomidea*

5'. Head moderately to slightly declivent; bucculae smoothly rounded, not truncate posteriorly (Fig. 23.52); coloration brown, usually mottled (Fig. 23.4); stridulatory areas frequently extending onto seventh sternite .... *Camirus*

6. Ostiole not attended by peritreme or attending structure less than twice as long as the width of ostiole (Figs. 23.32, 23.34) 7

6'. Ostiole attended by peritreme that is much more than twice as long as width of ostiole (Figs. 23.35, 23.37, 23.38, 23.40, 23.41, 23.42, 23.43, and 23.44)... 10

7. Ostiole less than one third of distance from metacoxa to lateral margin of metapleuron (Fig. 23.32) (southern South America).......*Misippus* (Fig. 23.24)

7'. Ostiole distinctly more than one third of distance from metacoxa to lateral margin of metapleuron (Fig. 23.34)... 8

8. Located in South America into southern Central America .... *Chelyschema* (Fig. 23.8)

8'. Located in the Caribbean and North America into Mexico............................... 9

9. Thoracic sterna sulcate, sulcus bordered by well-developed carina (Fig. 23.53)... .... *Nesogenes* (Fig. 23.12)

9'. Thoracic sterna only shallowly sulcate, carina not developed............................ .... *Diolcus* (Fig. 23.11)

10. Ostiolar peritreme reaching anterolateral corner of metathoracic evaporative area or separated from anterolateral corner by less than its width at that point (Figs. 23.40, 23.41, 23.43).. 11

10’. Apex of ostiolar peritreme separated from anterolateral corner of metathoracic evaporative area by at least its width at that point (Figs. 23.35, 23.37, 23.38, 23.42, 23.44) 14

11. Peritreme greatly expanded apically (Fig. 23.43) .... *Sphyrocoris* (Fig. 23.16)

11’. Peritreme roughly parallel sided, groove-like (Figs. 23.40, 23.41) 12

12. Peritreme scar-like, its sides elevated (Fig. 23.40) .... *Homaemus* (Fig. 23.15)

12’. Peritreme an elevated groove (Fig. 23.41) 13

13. Anterolateral pronotal margins straight or slightly sinuous (Fig. 23.10) .... *Lobothyreus*

13’. Anterolateral pronotal margins concave (Fig. 23.9) .... *Crathis*

14. Length of peritreme less than ½ distance from ostiole to lateral margin of metapleuron (Fig. 23.37) 15

14’. Length of peritreme more than ½ distance from ostiole to lateral margin of metapleuron (Figs. 23.35, 23.38, 23.42, 23.44) 16

15. Posterior margin of last abdominal sternite convex, covering male and female genitalia; antennae mostly black .... *Tiridates* (Figs. 23.14, 23.37)

15’. Posterior margin of last abdominal sternite concave mesially, exposing male and female genitalia; antennae dark with white annulations .... *Tetyra antillarum*

16. Peritreme spout shaped, curved anterad (Fig. 23.38)..... *Agonosoma* (Fig. 23.13)

16. Peritreme relative straight, may be curved anterad only at apex 17

17. Pronotum twice as wide as long, anterolateral margins strongly developed; posterior margin of scutellum strongly concave (Fig. 23.23) .... *Galeacius*

17’. Pronotum less than twice as wide as long, anterolateral margins rounded, not developed; posterior margin of scutellum rounded, truncate, or shallowly concave (Figs. 23.17–23.20) 18

18. Posterolateral angles of last three abdominal sternites strongly developed into distinct spines (Fig. 23.20); ostiolar peritreme angled posterad (Fig. 23.35) .... *Ephynes*

18’. Posterolateral angles of last three abdominal sternites developed at most into small spines (Figs. 23.17–23.19); ostiolar peritreme extended laterad, slightly curved anterad (Fig. 23.44) .... *Symphylus*

19. Ostiole not attended by ruga, sulcus, or auricle or attending structure shorter than the diameter of ostiole (Fig. 23.36) 20

19’. Ostiole attended by distinct ruga, sulcus, or auricle at least as long as the diameter of ostiole (Figs. 23.33, 23.39) 21

20. Head broadly rounded anteriorly; anterolateral pronotal margins moderately developed .... *Testrina*

20’. Head usually narrowing anteriorly, mostly triangular; anterolateral pronotal margins not developed (Figs. 23.21, 23.22) .... *Polytes*

21. Antennal segments 4 and 5 distinctly flattened; dorsum with conspicuous erect setae (Fig. 23.28) .... *Dystus*

21’. Antennal segments 4 and 5 cylindrical or, at most, slightly flattened; dorsum usually lacking setae or at most with short, decumbent setae 22

22. Each abdominal spiracle within or subtended by callus; tylus surpassing juga by at least diameter of second antennal segment (Figs. 23.45,23.46).................. 23
22'. Abdominal spiracles not within or subtended by calli.................................. 24
23. Each abdominal spiracle located in dorsal edge of concolorous callus (Fig. 23.45); body shape oval (Fig. 23.5)..*Ascanius*
23'. Each abdominal spiracle subtended by or adjacent to pale callus (Fig. 23.46); body shape elongate oval (Fig. 23.6)..*Chelycoris*
24. Distance from metacoxa to ostiole about 1.5 times the distance from ostiole to lateral margin of metapleura (Fig. 23.39); if less than that, femora provided with black annulus or ring of black macules (Fig. 23.54)............. *Tetyra* (Fig. 23.26)
24'. Distance from metacoxa to ostiole subequal to or slightly greater than distance from ostiole to lateral margin of metapleuron; femora uniformly colored..... 25
25. Abdominal sternites compressed near lateral margins (Fig. 23.47).................... ....*Pachycoris* (Fig. 23.27)
25'. Abdominal sternites not compressed laterally (Fig. 23.48)................................ ....*Orsilochides* (Fig. 23.25)

23.5 Concluding Remarks

The knowledge on Neotropical shield bugs is still an open field of investigation. We need to make serious efforts to study their taxonomy, systematics, and bioecology. Phylogenies of the group, at any taxonomic level, should include larger samples, if possible, with representatives of all biogeographic areas, especially those regarding molecular characters. Polymorphism also deserves further studies, from the molecular and phylogeographical approaches. For that, collections in sampled areas should be emphasized with special attention to under explored microhabitats.

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Chapter 24
Negro Bugs (Thyreocoridae)

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Abstract The Thyreocoridae, usually known as "negro bugs," includes 212 species in 12 genera distributed in two subfamilies Thyreocorinae (seven species in three genera) which are not represented in the neotropics and Corimelaeninae (205 species in nine genera) with a worldwide distribution. Relatively small and dark colored, often shiny, this is a poorly studied family within Pentatomoidea and its relationships still being debated. They are exclusively herbivorous, and, at least, 23 Mexican and Neotropical species have some record of associated plant. Besides that, in the literature, there is no information about damage caused by these bugs. Immature stages are known only for eight species occurring in Mexico and Neotropical region, including descriptions of eggs and/or nymphs and/or life history. The only known key for the Neotropical representatives of the family is that found in McAtee and Malloch (Ann Carnegie Mus 21:191–411, 1933).

24.1 Introduction

The Thyreocoridae Amyot & Serville (=Corimelaenidae Uhler) is a common but poorly studied group in the Pentatomoidea. It includes the Thyreocorinae, with seven species in three genera, and Corimelaeninae, with 205 species in nine genera (McAtee and Malloch 1933; Sailer 1940, 1941; Kormilev 1956a, b; McPherson and Sailer 1978; Stys and Davidová 1979; Dolling 1981; Ahmad and Moizuddin 1982; Lis 2006). Previous authors considered the Thyreocorinae (= Corimelaeninae) as a subfamily of Cydnidae (i.e., Gapud 1991) by the presence of coxal fringes and tibial spines. Grazia et al. (2008), in a cladistic analysis of the Pentatomoidea, suggested

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that the Parastrachiinae Schaefer, Dolling, and Tachikawa should be treated as part of a more broadly conceived Thyreocoridae.

Only the subfamily Corimelaeninae is represented in the Neotropical region. Basic information (e.g., life cycle, geographical distribution) for many species is either incomplete, inaccurate, or lacking (McPherson 1974), especially in the neotropics. Keys to the genera, subgenera, and species are found in McAtee and Malloch (1933). *Galgupha* Amyot & Serville is the most diverse Neotropical genus with 155 species in 15 subgenera. Table 24.1 shows the number of Thyreocoridae species registered in the world, in Mexico, and in the Neotropical region. Table 24.2 provides the number of Mexican and Neotropical species in each genus and subgenus of the Corimelaeninae.

24.2 General Characteristics and Diagnosis

Negro bugs (Figs. 24.1, 24.2, 24.3, 24.4, 24.5, 24.6, 24.7, and 24.8) have a size from 3 to 8 mm, body oval-elongate, dorsally convex, and ventrally flat. Dark color (castaneous or black), usually shiny. Head declivent, subtriangular in dorsal view. Antennae five segmented. Scutellum strongly convex recovering most of hemelytra. Corium reduced, some species with the visible part of corium in yellow. In the Corimelaeninae, hind wings with jugal lobe perforated. Tibiae with setae and spines in all their extension; tarsi 3-segmented.

24.2.1 Immatures

Thyreocoridae immatures have been broadly overlooked, probably due to their minute size, somewhat secretive habits, and lack of knowledge about host plants, which is required for nymphal development (Yonke 1991). General features of the eggs and nymphs of thyreocorid species have been briefly described (Southwood 1956; Cobben 1968; Hinton 1981; Yonke 1991). Immature stages are known only for eight species occurring in Mexico and Neotropical region, including descriptions of eggs and/or nymphs and/or life history (Table 24.3).

Southwood (1956) and Cobben (1968) discussed the egg characters of two thyreocorid species, *Corimelaena* sp. and *Thyreocoris scarabaeoides* (L.), respectively. At least five Nearctic Corimelaeninae species have their immature described

Table 24.1 Number of genera and species of the subfamilies of the Thyreocoridae (Hemiptera) occurring in the world, Mexico, and Neotropical region

	World		Mexico		Neotropics	
	Genera	Species	Genera	Species	Genera	Species
Thyreocoridae	12	212	6	42	9	159
Corimelaeninae	9	205	6	42	9	159
Thyreocorinae	3	7	0	0	0	0

Table 24.2 List of genera and subgenera included in Thyreocoridae: Corimelaeninae and its respective number of species occurring in Mexico and Neotropical region

Genus	Subgenus	Total number of species	Number of Mexican species	Number of Neotropical species
Alkindus Distant		2	1	2
Amyssonotum Horváth		1	1	1
Corimelaena White		31	16	13
Cydnoides Malloch		9	4	3
	Cydnoides Malloch	3	2	0
	Sayocoris McAtee & Malloch	3	2	0
	Cosmarioides McAtee & Malloch	3	0	3
Eumetopia Westwood		1	0	1
Galgupha Amyot & Serville		155	19	133
	Acritophleps McAtee & Malloch	1	0	1
	Acrotmetus Horváth	6	1	6
	Astiroderma Horváth	2	0	2
	Bonaria McAtee & Malloch	1	0	1
	Charoda McAtee & Malloch	1	0	1
	Ctenopoda McAtee & Malloch	2	0	2
	Euryscytus Horváth	38	4	34
	Galgupha Amyot & Serville	8	4	1
	Gyrocnemis McAtee & Malloch	37	5	33
	Micrcompsus Horváth	3	0	3
	Nothocoris McAtee & Malloch	27	4	22
	Orocoris McAtee & Malloch	1	0	0
	Psestophleps McAtee & Malloch	18	1	17
	Pteronomos McAtee & Malloch	9	0	9
	Trepocnemis McAtee & Malloch	1	0	1
Godmania Horváth		1	1	1
Pericreps Horváth		4	0	4
Pruhleria McAtee & Malloch		1	0	1

McAtee and Malloch (1933), Sailer (1940, 1941), Kormilev (1956a, b), McPherson and Sailer (1978), and Dolling (1981)

Fig. 24.1 *Eumetopia fissipes* Westwood, adult, *dorsal view*

Fig. 24.2 *Alkindus crassicosta* Horváth, adult, *dorsal view*

Fig. 24.3 *Corimelaena lateralis* (F.), adult, *dorsal view*

Fig. 24.4 *Eumetopia fissipes* Westwood, female, head and pronotum, *dorsal view*

Fig. 24.5 *Eumetopia fissipes* Westwood, male, head and pronotum, *dorsal view*

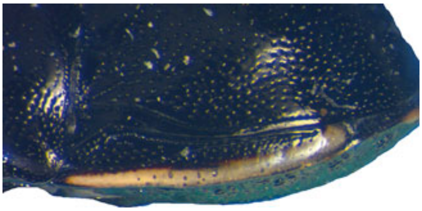

Fig. 24.6 *Corimelaena lateralis* (F.), corium, *dorsolateral view*

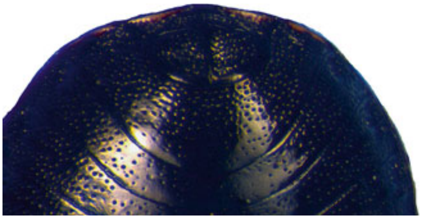

Fig. 24.7 *Corimelaena lateralis* (F.), female, abdomen, *ventral view*

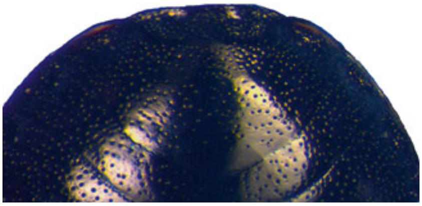

Fig. 24.8 *Corimelaena lateralis* (F.), male, abdomen, *ventral view*

Table 24.3 List of thyreocorid species occurring in Mexico and Neotropical region with described immature stages (eggs and/or nymphs) and/or immature biology

Species	Eggs		Nymphs	Biology
	SEM[a]	SM[a]		
Corimelaena (*Corimelaena*) *lateralis* (F.)		McPherson (1972)	McPherson (1972)	McPherson (1971, 1972)
Corimelaena (*Parapora*) *extensa* Uhler		Lung and Goeden (1982)	Lung and Goeden (1982)	Lung and Goeden (1982)
Corimelaena (P.) incognita (McAtee & Malloch)	Bundy and McPherson (2009)		Bundy and McPherson (2009)	Bundy and McPherson (2009)
Galgupha (Euryscytus) difficilis (Breddin)	Matesco et al. (2012)			
Galgupha (Galgupha) atra Amyot & Serville		Javahery (1994)		
Galgupha (*G.*) *ovalis* Hussey		Biehler and McPherson (1982)	Biehler and McPherson (1982)	Biehler and McPherson (1982)
Galgupha (Gyrocnemis) fossata McAtee & Malloch	Matesco et al. (2012)			

[a] *SEM* scanning electron microscopy, *SM* stereomicroscopy

(McPherson 1972; Biehler and McPherson 1982; Lung and Goeden 1982; Bundy and McPherson 1997, 2009). Matesco et al. (2012) described the egg ultrastructure of two Neotropical species *Galgupha* (*Euryscytus*) *difficilis* (Breddin) and *Galgupha* (*Gyrocnemis*) *fossata* McAtee & Malloch.

The eggs are elongate with rounded poles. Corium is thin, apparently smooth, but wrinkled when observed in scanning electron microscopy (Bundy and McPherson 1997, 2009; Matesco et al. 2012). Initially white, the eggs become reddish or dark red with the embryo development; the translucent chorion allows viewing the structures inside the egg. Aero-micropylar processes around the apical pole are pedunculated, curved inward, varying in numbers from 4 to 10, and differing in the peduncle size. Operculum is absent and the eclosion line irregular and transversal (Javahery 1994). Bundy and McPherson (2009) described the egg burster of *Corimelaena incognita* (McAtee & Malloch) as rhomboid, with a short median process; Southwood (1956) and Cobben (1968) mentioned the egg burster is reduced in both subfamilies. In thyreocorid eggs, no pattern has been recognized yet at the generic level. Egg characters in the family are scarce – the egg structure is simple – and basic information is available for only a few species.

Matesco et al. (2012), based on the egg morphology of ten Corimelaeninae species, outlined a consistent pattern: eggs are laid singly on parts of the host plants; each egg is cylindrical with rounded ends and white before embryonic development; the chorion is thin and shiny with a few (2–10) short, stalked aero-micropylar processes around the anterior pole; lengths of eggs and micropylar processes are 0.65–1.08 and 0.03–0.05 mm, respectively.

Nymphs are similar to the adults in body and head shapes. In general, nymph morphological characters are similar to the other Pentatomoidea families. Most of the body is dark, black, or castaneous; the abdomen varies from yellow to reddish always with dark punctures. The body is strongly convex with punctures uniformly distributed. Tibiae spines are present. Median dorsal abdominal plates present in all abdominal segments, segments I and II with paired plates; scent glands ostiole paired and placed between segments III–IV, IV–V, and V–VI; and lateral abdominal plates subquadrangular. Other characters, apparently unique to this family, are metanotum partially fused on 1st to 3rd instars; posterior and anterior margins of the dorsal abdominal plates of segments IV and V, respectively, are contiguous.

24.3 General Biology and Ecology

Negro bugs are exclusively herbivorous, generally associated to bushes, feeding and living in the host plant reproductive parts as flowers and developing or ripe fruits. McPherson (1971, 1972) registered the preference of *Corimelaena lateralis* (F.) for mature plants of *Daucus carota* L. (Apiaceae), instead of inflorescences of the same plant. *Corimelaena pulicaria* (Germar) does not show this preference (McPherson 1972). The latter species is registered in distinct host plants up to 10 different plant families (Table 24.2). Nevertheless, all species studied used, along their life cycle in the same area, only one (i.e., Biehler and McPherson 1982) or two (i.e., Bundy and McPherson 1997) plant families as preferential sites for feeding, mating, and oviposition.

Schaefer (1988) compiled data on the host plants for several Pentatomoidea families, including Thyreocoridae. The data do not point to any preference for host plant at subfamily or genus level. Most species feed on the reproductive parts, rich in nitrogen (especially *Corimelaena* spp.); a few occur over the soil (especially *Cydnoides* spp.) (Schaefer 1988). Rider (2013) provided a list of several published records of host plants of Thyreocoridae. At least, 23 Mexican and Neotropical species have some record of associated plant in the literature (Table 24.4).

All studies of thyreocorids at field were developed in the northern hemisphere; the life cycle corresponds in general to the pentatomid life cycle (Grazia and Schwertner 2008). They could be uni-, bi-, or multivoltine: in low latitudes, a higher number of generations per year occur, whereas in higher latitudes, only one generation per year is possible (McPherson 1972; Lung and Goeden 1982; Bundy and McPherson 1997, 2009). The adults show dormancy, and during this period, they could be found under litter, soil, and also rocks; they leave the dormancy sites at late winter or early spring and then move to the host plants and start feeding. Precopula behavior was described by Bundy and McPherson (1997): the male stands behind the female and starts the contact by antennation; after the female acceptance, the copula takes place with the individuals positioned in opposite directions, just touching genitalic structures; copulation can last hours.

Thyreocorids lay eggs singly and glued laterally to the substrate, often in the host plant reproductive parts, less frequently in branches or leaves. Egg development varies between eight and 11 days, depending on the species and also the temperature and humidity. First instar nymphs are actives, differing from other Pentatomoidea families' nymphs, feeding and not showing gregarious behavior. Nymphs' development varies from 30 to 45 days, probably influenced by the diet and also by the local temperature and humidity. Tachinidae (Diptera) and Scelionidae (Hymenoptera) egg parasitoids are the major natural enemies recorded.

24.4 Classification and Diversity

The evolution of Thyreocoridae within Pentatomoidea has been discussed (Gapud 1991; Grazia et al. 2008; Lis et al. 2012, and Matesco et al. in prep.), usually suggesting a close relationship with the Cydnidae.

The hypothesis of Gapud (1991) of the relationships within Pentatomoidea based on morphology recognizes that the Cydnidae and Thyreocoridae are strongly related by the presence of coxal fringes and tibial spines. However, the Cydnidae can be separated from the Thyreocoridae by setigerous punctures in the head and pronotum. Thyreocoridae shares weak characters with other families, such as the broad scutellum, covering the abdomen; short frenum; and laterotergites nine contiguous.

Table 24.4 List of species of Thyreocoridae: Corimelaeninae occurring in Mexico and Neotropical region and its respective potential host plants and geographical distribution

Species	Plant family	Plant species	Distribution
Alkindus atratus Distant	Fabaceae	*Glycine* sp.[24]	Mexico and Neotropical (Guatemala[27], Honduras[24], El Salvador[24], Nicaragua, Aruba, Curaçao, Venezuela, Costa Rica, Colombia, Panama, Brazil[27])
		Phaseolus sp.[24]	
	Malvaceae	*Gossypium* sp.[24]	
		Sida sp.[24]	
	Moraceae	*Ficus* sp.[27]	
	Musaceae	*Musa* sp.[24]	
	Myrtaceae	*Eucalyptus* sp.[24]	
	Poaceae	*Cenchrus* sp.[24]	
		Echinochloa sp.[24]	
		Oryza sp.[24]	
		Sorghum sp.[24]	
		Zea mays L.[2]	
	Rubiaceae	*Coffea* sp.[24]	
	Sterculiaceae	*Theobroma* sp.[24]	
A. crassicosta Horváth	Poaceae	*Andropogon bicornis* L.[20]	Neotropical (Brazil)
Amyssonotum rastratum (Stål)			Mexico and Neotropical (Belize, Guatemala, Costa Rica, Trinidad, Colombia, Panama, Suriname, Brazil, Peru, Bolivia)
Corimelaena alticola (Horváth)			Mexico
C. barberi (McAtee & Malloch)			Mexico and Neotropical (Costa Rica)
C. championi (Distant)			Neotropical (Belize, Guatemala)
C. cognata (Van Duzee)	Loasaceae	*Eucnide* sp.[47]	Mexico and Neotropical (Cuba, Jamaica, Nicaragua, Colombia, Venezuela[2])

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
C. contrasta (McAtee & Malloch)			Mexico
C. corallina (McAtee & Malloch)			Mexico and Neotropical (Guatemala)
C. digitata (McAtee & Malloch			Mexico
C. elegans (McAtee & Malloch)			Mexico and Neotropical (Guatemala, Costa Rica, Panama, Trinidad)
C. extensa Uhler	Asteraceae	*Baccharis salicifolia* (Ruiz & Pav.) Pers.[9]	Mexico[16]
	Scrophulariaceae	*Linaria vulgaris* Mill.[40]	
	Solanaceae	*Nicotiana glauca* Graham[23]	
C. incognita (McAtee & Malloch)	Chenopodiaceae	*Atriplex* sp.[6]	Mexico
	Scrophulariaceae	*Leucophyllum frutescens* (Berland.) I.M.Johnst.[10]	
	Solanaceae	*Nicotiana glauca* Graham[19]	
		Nicotiana obtusifolia Martens & Galeotti[19]	
C. interrupta Malloch			Mexico and Neotropical (Guatemala, Honduras, Costa Rica)
C. lateralis (F.)	Apiaceae	*Chaerophyllum procumbens* (L.) Crantz[31]	Mexico and Neotropical (Guatemala[16])
		Chaerophyllum tainturieri Hook[42]	
		Daucus carota L.[29, 30, 31, 42]	
		Torilis japonica (Houtt.) DC.[42]	

	Asteraceae	*Erigeron philadelphicus* L.[31]	
		Solidago altissima L.[30]	
	Geraniaceae	*Geranium carolinianum* L.[31, 42]	
		Geranium maculatum L.[25]	
	Juglandaceae	*Juglans nigra* L.[33]	
	Poaceae	*Bromus tectorum* L.[42]	
		Elymus hystrix L.[31]	
	Ranunculaceae	*Ranunculus macranthus* Scheele[19]	
	Rubiaceae	*Galium aparine* L.[1, 42]	
	Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	
C. micans (McAtee & Malloch)			Neotropical (Guatemala)
C. minuta Uhler			Neotropical (Cuba, Haiti, Dominican Republic, Puerto Rico, Jamaica)
C. minutissima Malloch			Mexico
C. nigra Dallas	Ranunculaceae	*Ranunculus* sp.[22]	Mexico
C. palmeri (McAtee & Malloch)			Mexico
C. parana McAtee & Malloch			Neotropical (Brazil)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
C. pulicaria (Germar)	Anacardiaceae	*Rhus glabra* L.[15]	Mexico[13] and Neotropical (Guatemala, Martinique, Venezuela[2])
	Apiaceae	*Daucus carota* L.[30,31,42]	
		Chaerophyllum procumbens (L.) Crantz[31]	
		Torilis japonica (Houtt.) DC.[42]	
	Apocynaceae	*Apocynum cannabinum* L.[31,42]	
	Asclepiadaceae	*Asclepias incarnata* L.[31]	
	Asteraceae	*Antennaria plantaginifolia* (L.) Richardson[31]	
		Baccharis neglecta Britton[34]	
		Cirsium arvense (L.) Scop.[28]	
		Erigeron philadelphicus L.[31]	
		Erigeron strigosus Muhlenberg[33,42]	
		Eupatorium sp.[43]	
		Iva frutescens L.[21]	
	Geraniaceae	*Geranium maculatum* L.[25]	
	Juglandaceae	*Juglans nigra* L.[32,33]	
	Liliaceae	*Uvularia* sp.[15]	
	Plantaginaceae	*Veronica peregrina* L.[14,44]	
	Poaceae	*Sorghum halepense* L. (Pers.)[42]	
	Polygonaceae	*Polygonum* sp.[15]	
	Rhamnaceae	*Ceanothus americanus* L.[14,44]	
	Rubiaceae	*Galium verum* L.[1]	
	Scrophulariaceae	*Linaria vulgaris* Mill.[28,40]	
		Verbascum thapsus L.[31]	

C. signoretii (McAtee & Malloch)			Neotropical (Brazil)
C. tibialis (F.)			Mexico and Neotropical (Jamaica, Costa Rica, Panama, Colombia, Saint Vincent and the Grenadines, Grenada, Venezuela, Trinidad, Guiana, Suriname, French Guiana, Brazil, Ecuador, Bolivia)
Cydnoides (*Cydnoides*) *ciliatus* (Uhler)	Euphorbiaceae	*Euphorbia* sp.[44]	Mexico
	Fabaceae	*Cassia marilandica* L.[8,44]	
C. (*C.*) *confusus* McAtee & Malloch	Euphorbiaceae	*Euphorbia* sp.	Mexico
C. (*Sayocoris*) *obtusus* (Uhler)	Euphorbiaceae	*Euphorbia polycarpa* Benth.[44]	Mexico[16]
C. (*S.*) *peregrinus* McAtee & Malloch			Mexico[44]
C. (*Cosmarioides*) *nitens* McAtee & Malloch			Neotropical (Brazil)
C. (*C.*) *reticulatus* McAtee & Malloch			Neotropical (Brazil)
C. (*C.*) *setiventris* McAtee & Malloch			Neotropical (Bolivia, Paraguay)
Eumetopia fissipes Westwood			Neotropical (Brazil)
Galgupha (*Acritophleps*) *luteomarginata* McAtee & Malloch			Neotropical (Brazil, Bolivia)
G. (*Acrotmetus*) *brasilianus* (Jensen-Haarup)			Neotropical (Brazil, Bolivia, Paraguay)
G. (*A.*) *crassa* McAtee & Malloch			Neotropical (Brazil)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
G. (*A.*) *grossa* McAtee & Malloch			Neotropical (French Guiana, Brazil, Paraguay[17])
G. (*A.*) *minuenda* McAtee & Malloch			Neotropical (Brazil)
G. (*A.*) *schulzii* (F.)	Rubiaceae	*Spermacoce verticillata* L.[11]	Mexico e Neotropical (Panama, Trinidad[11], French Guiana, Brazil, Argentina)
	Solanaceae	*Solanum tuberosum* L.[36]	
G. (*A.*) *tucumanus* (Horváth)			Neotropical (Brazil, Argentina)
G. (*Astiroderma*) *albipennis* (Eschsholtz)			Neotropical (Guatemala, French Guiana, Brazil, Argentina, Uruguay)
G. (*A.*) *breddini* McAtee & Malloch			Neotropical (Brazil, Argentina[17])
G. (*Bonaria*) *longirostris* (Berg)			Neotropical (Argentina)
G. (*Charoda*) *simplex* McAtee & Malloch			Neotropical (Brazil, Chile, Argentina[17])
G. (*Ctenopoda*) *castor* McAtee & Malloch			Neotropical (Brazil)
G. (*C.*) *maculosa* (Berg)			Neotropical (Brazil, Paraguay, Argentina[3])
G. (*Euryscytus*) *aliena* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *apicata* McAtee & Malloch			Neotropical (Suriname, French Guiana)
G. (*E.*) *assimilis* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *australis* McAtee & Malloch			Neotropical (Brazil, Bolivia, Paraguay, Argentina)
G. (*E.*) *basalis* (Germar)	Moraceae	*Ficus* sp.[12]	Neotropical (Jamaica[46], Brazil)

G. (*E.*) *caudata* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *caudiculata* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *contra* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *contracta* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *corvina* (Horváth)			Neotropical (Brazil, Argentina)
G. (*E.*) *cruenta* (Horváth)			Mexico
G. (*E.*) *curvata* McAtee & Malloch			Neotropical (Brazil, Bolivia[17])
G. (*E.*) *curvatula* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *difficilis* (Breddin)	Scrophulariaceae	*Buddleja Brasiliensis* Jacq. ex Spreng.[26]	Neotropical (Brazil, Argentina)
G. (*E.*) *foveolata* (Jensen-Haarup)			Neotropical (Brazil)
G. (*E.*) *insula* McAtee & Malloch			Neotropical (Paraguay, Argentina)
G. (*E.*) *jaczewskii* McAtee & Malloch			Neotropical (Brazil, Argentina[17])
G. (*E.*) g*labrata* McAtee & Malloch			
G. (*E.*) *laevis* (Stål)			Neotropical (Brazil)
G. (E.) lucretia McAtee & Malloch			Mexico e Neotropical (Guatemala)
G. (*E.*) *mammula* McAtee & Malloch			Neotropical (Brazil)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
G. (*E.*) *nitida* McAtee & Malloch			Neotropical (Panama)
G. (*E.*) *obesa* McAtee & Malloch			Neotropical (Paraguay)
G. (*E.*) *opacifrons* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *opercula* McAtee & Malloch			Mexico
G. (*E.*) *parae* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *parallela* McAtee & Malloch			Neotropical (Brazil, Bolivia)
G. (*E.*) *punctata* McAtee & Malloch			Mexico
G. (*E.*) *rasilis* (Horváth)			Neotropical (Colombia, Guiana, Suriname, French Guiana, Brazil, Bolivia)
G. (*E.*) *regularis* McAtee & Malloch			Neotropical (Argentina)
G. (*E.*) *romana* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *rostrata* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *sahlbergi* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *signatipennis* (Germar)			Neotropical (Brazil, Paraguay, Argentina)
G. (*E.*) *smidtii* (F.)			Neotropical (Brazil)

G. (*E.*) *valvata* McAtee & Malloch			Neotropical (French Guiana)
G. (*E.*) *variipennis* McAtee & Malloch			Neotropical (Brazil)
G. (*E.*) *vulnerata* (Horváth)			Neotropical (Brazil, Paraguay)
G. (*Galgupha*) *atra* Amyot & Serville	Asteraceae	*Helianthus decapetalus* L.[31]	Mexico
	Euphorbiaceae	*Euphorbia maculata* L.[48]	
	Juglandaceae	*Juglans nigra* L.[33]	
	Plantaginaceae	*Plantago aristata* Michaux[41, 44]	
	Rosaceae	*Rubus allegheniensis* Porter[31]	
	Scrophulariaceae	*Castilleja sessiliflora* Pursh[41]	
		Verbascum thapsus L.[31]	
G. (*G.*) *denudata* (Uhler)			Mexico
G. (*G.*) *monostira* Horváth			Mexico
G. (*G.*) *ovalis* Hussey	Asteraceae	*Vernonia interior* Small[39]	Mexico and Neotropical (Guatemala)
	Juglandaceae	*Juglans nigra* L.[32]	
	Plantaginaceae	*Plantago aristata* Michaux[7]	
G. (*Gyrocnemis*) *acuta* McAtee & Malloch			Neotropical (Brazil)
G. (*G.*) *basigrapha* (Horváth)			Neotropical (Peru, Bolivia[17])
G. (*G.*) *bicornis* McAtee & Malloch			Neotropical (Brazil)
G. (*G.*) *concava* McAtee & Malloch			Neotropical (Brazil, Bolivia, Paraguay, Argentina)
G. (*G.*) *cruralis* (Stål)	Aquifoliaceae	*Ilex paraguariensis* A. St. Hil.[37]	Neotropical (Brazil, Bolivia, Argentina)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
	Poaceae	*Sorghum bicolor* L. Moench[36]	
		Oryza sativa L.[36]	
		Zea mays L.[5]	
	Rutaceae	*Citrus* sp.[36]	
	Solanaceae	*Solanum tuberosum* L.[4, 5]	
G. (*G.*) *cydnoidea* McAtee & Malloch			Neotropical (Colombia, Venezuela)
G. (*G.*) *differentialis* McAtee & Malloch			Neotropical (Brazil, Peru, Bolivia, Paraguay)
G. (*G.*) *dimorpha* McAtee & Malloch			Neotropical (Bolivia, Paraguay)
G. (*G.*) *diversa* McAtee & Malloch			Neotropical (Paraguay, Argentina)
G. (*G.*) *durionei* Kormilev			Neotropical (Bolivia[17])
G. (*G.*) *fossata* McAtee & Malloch	Scrophulariaceae	*Buddleja brasiliensis* Jacq. ex Spreng.[26]	Neotropical (Brazil, Paraguay, Argentina)
G. (*G.*) *geayi* McAtee & Malloch			Neotropical (Venezuela)

G. (*G.*) *guttiger* (Stål)	Arecaceae	*Elaeis* sp.[24]	Mexico and Neotropical (Cuba, Haiti, Dominican Republic, Jamaica, Belize[13], Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Bolivia)
	Brassicaceae	*Brassica* sp.[24]	
	Cucurbitaceae	*Cucurbita* sp.[24]	
	Fabaceae	*Cajanus* sp.[24]	
		Phaseolus sp.[24]	
	Lauraceae	*Persea* sp.[24]	
	Malvaceae	*Gossypium* sp.[24]	
		Sida sp.[24]	
	Nyctaginaceae	*Boerhavia* sp.[24]	
		Bougainvillea sp.[24]	
	Pedaliaceae	*Sesamum* sp.[24]	
	Poaceae	*Oryza* sp.[24]	
		Sorghum sp.[24]	
		Zea sp.[24]	
	Rubiaceae	*Coffea* sp.[24]	
	Solanaceae	*Lycopersicon* sp.[24]	
		Nicotiana sp.[24]	
		Solanum sp.[24]	
G. (*G.*) *impressa* (Horváth)			Neotropical (Venezuela, Brazil, Peru, Bolivia, Argentina)
G. (*G.*) *inaequalis* McAtee & Malloch			Neotropical (Colombia, Venezuela, Bolivia)
G. (*G.*) *intermedia* McAtee & Malloch			Neotropical (Brazil, Argentina[17])
G. (*G.*) *lineata* McAtee & Malloch			Neotropical (Brazil, Argentina)
G. (*G.*) *maculipennis* (Germar)			Neotropical (Brazil[3], Paraguay, Argentina)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
G. (*G.*) *morbiloci* McAtee & Malloch			Mexico
G. (*G.*) *nitens* (Breddin)			Neotropical (Brazil, Colombia, Peru, Bolivia)
G. (*G.*) *nitidipennis* McAtee & Malloch			Neotropical (Venezuela)
G. (*G.*) *notha* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *novatra* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *novella* McAtee & Malloch			Neotropical (Brazil)
G. (*G.*) *occulta* McAtee & Malloch			Neotropical (Brazil)
G. (*G.*) *omissa* McAtee & Malloch			Neotropical (Brazil)
G. (*G.*) *parva* McAtee & Malloch			Neotropical (Brazil, Paraguay)
G. (*G.*) *punctifer* McAtee & Malloch			Mexico and Neotropical (Belize, Guatemala, Costa Rica, Panama, Colombia, Bolivia)
G. (*G.*) *quadrisignata* (Stål)	Verbenaceae	*Lantana* sp.[35]	Mexico and Neotropical (Belize, Guatemala, Honduras, El Salvador, Costa Rica)
G. (*G.*) *reinhardtii* (Jensen-Haarup)			Neotropical (Venezuela, Brazil)
G. (*G.*) *singularis* McAtee & Malloch			Neotropical (Argentina)
G. (*G.*) *soror* McAtee & Malloch			Mexico

G. (*G.*) *torresi* Kormilev			Neotropical (Argentina[17])
G. (*G.*) *triconcava* McAtee & Malloch			Neotropical (Brazil, Bolivia, Paraguay, Argentina)
G. (*G.*) *unica* McAtee & Malloch			Neotropical (Colombia)
G. (*Microcompsus*) *daldorfii* (Fabricius)			Neotropical (Brazil)
G. (*M.*) *haywardi* Kormilev			Neotropical (Argentina[18])
G. (*M.*) *vinculata* (Germar)	Rubiaceae	*Spermacoce verticillata* L.[11]	Neotropical (Colombia, Venezuela, Trinidad, Suriname, French Guiana, Brazil, Bolivia, Paraguay, Argentina)
G. (*Nothocoris*) *akarna* McAtee & Malloch			Neotropical (Argentina)
G. (*N.*) *alutacea* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *boliviano* McAtee & Malloch			Neotropical (Brazil, Bolivia)
G. (*N.*) *brevis* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *brunnipennis* (Germar)			Neotropical (Brazil, Paraguay)
G. (*N.*) *caracasana* McAtee & Malloch			Neotropical (Venezuela)
G. (*N.*) *chilocoroides* (Walker)			Mexico and Neotropical (French Guiana, Brazil)
G. (*N.*) *chrostowski* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *coccineloides* Horváth			Neotropical (French Guiana, Brazil, Bolivia, Paraguay, Argentina)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
G. (*N.*) *fossula* McAtee & Malloch			Mexico
G. (*N.*) *grenadensis* McAtee & Malloch			Neotropical (Colombia)
G. (*N.*) *inornata* McAtee & Malloch			Neotropical (Argentina)
G. (*N.*) *juno* McAtee & Malloch			Neotropical (Argentina)
G. (*N.*) *magna* Sailer			Mexico[38]
G. (*N.*) *marginalis* McAtee & Malloch			Neotropical (Colombia)
G. (*N.*) *marginicollis* Horváth			Neotropical (Colombia, Venezuela, Grenada)
G. (*N.*) *microphthalma* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *nitiduloides* (Wolff)	Asteraceae	*Helenium* sp.	Mexico and Neotropical (Guatemala, Nicaragua[24], Costa Rica, Brazil)
	Fabaceae	*Glycine* sp.[24]	
	Malvaceae	*Gossypium* sp.	
	Plantaginaceae	*Plantago patagonica* Jacq.[44, 45]	
	Poaceae	*Saccharum* sp.	
	Verbenaceae	*Lantana* sp.[35]	
G. (*N.*) *oculata* McAtee & Malloch			Neotropical (Paraguay)
G. (*N.*) *parvula* Horváth			Neotropical (Peru)
G. (*N.*) *repetita* McAtee & Malloch			
G. (*N.*) *semilimbata* Horváth			Neotropical (Brazil, Paraguay)

G. (*N.*) *stramineipennis* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *surda* McAtee & Malloch			Neotropical (Brazil)
G. (*N.*) *terminalis* (Walker)			Neotropical (Brazil, Bolivia, Paraguay, Uruguay)
G. (*Psestophleps*) *altera* McAtee & Malloch			Neotropical (Brazil)
G. (*P.*) *bergiana* McAtee & Malloch			Neotropical (Brazil, Peru, Paraguay, Argentina)
G. (*P.*) *bisignata* McAtee & Malloch			Neotropical (Brazil, Argentina)
G. (*P.*) *carbonata* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *casta* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *costomaculata* McAtee & Malloch			Neotropical (Brazil, Paraguay)
G. (*P.*) *denieri* Kormilev			Neotropical (Argentina[17])
G. (*P.*) *fimbriata* McAtee & Malloch			Neotropical (Venezuela, Suriname)
G. (*P.*) *imitans* McAtee & Malloch			Neotropical (Venezuela[2], Brazil)
G. (*P.*) *inops* McAtee & Malloch			Neotropical (Brazil)
G. (*P.*) *mayana* McAtee & Malloch			Neotropical (Honduras)
G. (*P.*) *media* McAtee & Malloch			Neotropical (Guiana, Suriname)

(continued)

Table 24.4 (continued)

Species	Plant family	Plant species	Distribution
G. (*P.*) *mexicana* McAtee & Malloch			Mexico
G. (*P.*) *neobisignata* McAtee & Malloch			Neotropical (French Guiana, Brazil, Paraguay, Argentina, Uruguay)
G. (*P.*) *obovata* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *pallipennis* McAtee & Malloch			Neotropical (Brazil)
G. (*P.*) *porcata* Horváth			Neotropical (Brazil, Paraguay, Argentina)
G. (*P.*) *tabellula* McAtee & Malloch			Neotropical (Suriname)
G. (*Pteronomos*) *amitta* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *china* McAtee & Malloch			Neotropical (Brazil, Peru, Bolivia, Argentina)
G. (*P.*) *fritzi* Kormilev			Neotropical (Chile[17])
G. (*P.*) *meridiana* McAtee & Malloch			Neotropical (Paraguay, Argentina)
G. (*P.*) *oblonga* McAtee & Malloch			Neotropical (Brazil, Paraguay, Argentina)
G. (*P.*) *punctifrons* McAtee & Malloch			Neotropical (Argentina)
G. (*P.*) *ruficornis* (Dallas)			Neotropical (Colombia)
G. (*P.*) *vianai* Kormilev			Neotropical (Argentina[18])
G. (*P.*) *vittifrons* McAtee & Malloch			Neotropical (Bolivia, Argentina)

G. (*Trepocnemis*) *anomala* McAtee & Malloch			Neotropical (Argentina)
Godmania aterrima Horváth			Mexico and Neotropical (Guatemala)
Pericrepis afer McAtee & Malloch			Neotropical (Argentina)
P. bergi Kormilev			Neotropical (Argentina[18])
P. bosqui Kormilev			Neotropical (Argentina[18])
P. callosula Horváth			Neotropical (Brazil, Paraguay[17], Argentina)
Pruhleria incerta (Uhler)	Musaceae	*Musa* sp.	Neotropical (Cuba, Nicaragua[13])

All data were taken from McAtee and Malloch (1933), except when indicated by the superscript numbers that correspond to references

Referências: 1. Batra (1984), 2. Becker and Grazia-Vieira (1971), 3. Berg (1891). 4. Bertels (1962), 5. Bertels and Baucke (1966), 6. Bibby (1961), 7. Biehler and McPherson (1982), 8. Blatchley (1926), 9. Boldt and Robbins (1990), 10. Bundy and McPherson (2009), 11. Callan (1948), 12. Costa Lima (1936), 13. Distant (1880), 14. Forbes (1905), 15. Froeschner (1941), 16. Froeschner 1988, 17. Kormilev (1956a), 18. Kormilev (1956b), 19. Jones (1993), 20. Klein et al. (2013), 21. Lago and Testa (2000), 22. Linsley and MacSwain (1959), 23. Lung and Goeden (1982), 24. Maes (1994), 25. Martin (1965), 26. Matesco et al. (2012), 27. Matesco and Grazia (2013), 28. Maw (1976), 29. McPherson (1971), 30. McPherson (1972), 31. McPherson and Mohlenbrock (1976), 32. McPherson and Weber (1990), 33. Nixon et al. (1975), 34. Palmer (1987), 35. Palmer and Pullen (1995), 36. Quintanilla et al. (1976), 37. Quintanilla et al. (1981), 38. Sailer (1941), 39. Schwitzgebel and Wilbur (1942), 40. Smith (1959), 41. Stoner (1920), 42. Tecic and McPherson (2005), 43. Uhler (1894), 44. Torre-Bueno 1939, 45. van Duzee (1904), 46. van Duzee (1907), 47. van Duzee (1923)

Grazia et al. (2008) analyzed the relationships within the Pentatomoidea, using 135 terminal taxa, 57 morphological characters, and sequence data from genetic regions of rDNA 18S, rDNA 16S, rDNA 28S, and COI. The study supports the monophyly of the Corimelaenidae (=Thyreocoridae), represented by *Thyreocoris* Schrank + *Allocoris* McAtee & Malloch (=*Corimelaena* White) based on seven homoplasious synapomorphies. Those are posterior and humeral angles of pronotum not developed; hind wings with A1 stridulitrum; prosternum deeply sulcate; prosternum strongly carinate; coxae with a fringe of setae, bristles, or scales; fore tibiae with a row of stout setae on lateral margin; and gonocoxites 9 joined medially by membrane.

In the morphological analysis of Grazia et al. (2008), Corimelaenidae shows up as a basal group within Cydnidae. In some trees of the molecular analysis, *Allocoris* is the sister group of Parastrachiidae (*Parastrachia* Distant + *Dismegistus* Amyot & Serville). Grazia et al. (2008) suggest that Parastrachiidae should be given a subfamily rank and treated as part of a broadly conceived Thyreocoridae.

The analysis of Lis et al. (2012) tests the monophyly of the Dinidoridae and its systematic position within Pentatomoidea, based on sequence data of rDNA 12S and 16S. Although the analysis of Thyreocoridae was not one of the authors' aims and the results about the family were not discussed, three terminal taxa were included: *Galgupha difficilis* (Breddin), *Strombosoma impictum* (Stål), and *Thyreocoris scarabaeoides* (L.). In any of the analysis (rDNA 12S, rDNA 16S, and the combined analysis), Thyreocoridae was not recovered as monophyletic. In the combined analysis, *S. impictum* and *T. scarabaeoides* show up as sister groups (supporting Thyreocorinae), and *G. difficilis* comes on a distantly related branch.

Matesco et al. (in prep.) made considerations on the phylogeny of the Thyreocoridae, emphasizing the relationships among species of *Corimelaena*. They included 40 terminal taxa and 114 morphological characters of the adult and immature stages. According to the consensus tree, *Corimelaena* has been recovered as monophyletic, but not its subgenera. The monophyly of Thyreocoridae, Corimelaeninae, *Strombosoma* Amyot & Serville, and the subgenus *Galgupha* was also corroborated. The monophyly of the Thyreocorinae and the genera *Alkindus* Distant and *Galgupha*, however, was not supported by the results. The authors suggested the maintenance of family status to Thyreocoridae (not including the Parastrachiidae) and the abandonment of the subgenera of *Corimelaena*.

In Matesco et al. (in prep.), the monophyly of Thyreocoridae is supported by six synapomorphies, which are a high density of the head punctation, presence of punctation on the area between the eye and the ocellus, presence of the pseudoperitreme on mesopleuron, anterior margin of the sternite VII angulate in the male, absence of the carina on the internal face of the dorsal rim of the pygophore, and parameres partially exposed.

Thyreocoridae was first established by Amyot and Serville (1843) as Thyréocorides. Uhler (1872) suggested the name Corimelaenidae to include the genera *Galgupha* and *Corimelaena*. Lethierry and Severin (1893) considered the subfamily Corimelaenidae within the Pentatomidae, removing it from the subfamily Cydnidae. Horváth

(1919) treated the group as the subfamily Thyreocorinae of the Cydnidae and recognized two tribes: Canoparia and Thyreocoraria. McAtee and Malloch (1928) excluded the Canoparia from Thyreocorinae. McAtee and Malloch (1933) considered Thyreocorinae as a subfamily of Pentatomidae, being equivalent to the current family status within Pentatomoidea (Rolston and McDonald 1979; Ahmad and McPherson 1990). Froeschner (1960), following McAtee and Malloch (1933), separated Thyreocoridae from the Cydnidae, giving it a status of family. Dolling (1981) recognized Thyreocorinae and Corimelaeninae as two independent subfamilies within the Cydnidae. Thyreocoridae is currently given a family status by Stys and Davidová (1979). Lis (2006) considered both Thyreocorinae and Corimelaeninae as subfamilies of Thyreocoridae.

The status (family vs. subfamily) and the name of the group (Thyreocoridae vs. Corimelanidae) have been intensely disputed (Leston 1953; Rolston and McDonald 1979; Dolling 1981; Ahmad and Moizuddin 1982; Froeschner 1988), but its composition has remained almost unchanged (McAtee and Malloch 1933; Dolling 1981; Lis 2006). Within the Corimelaeninae, the only genus whose position has been disputed is *Eumetopia* Westwood, excluded from Thyreocoridae by McAtee and Malloch (1933), but later included in the Corimelaeninae by Dolling (1981).

Taxonomic studies of the Neotropical thyreocorids are scarce. Only the genus *Alkindus* (Matesco and Grazia 2013) has been revised after the broad revision of the group by McAtee and Malloch (1933). The genus is associated with at least 15 species of plants. Its distribution is restricted to forest areas in the Neotropical region, and there is a large gap between the distributions of both species: *Alkindus atratus* Distant occurs from Mexico to northern Brazil, and *A. crassicosta* Horváth is restricted to southern and southeastern Brazil (Matesco and Grazia 2013).

In diversity studies and directed searches, bugs of this family are collected in abundance (McPherson 1974). In recent diversity analysis in southern Brazil, Thyreocoridae is an especially rich and diverse group within Pentatomoidea, following Pentatomidae (Barcellos 2006; Schmidt and Barcellos 2007; Mendonça et al. 2009).

The current state of knowledge of thyreocorid species, however, prevents the identification of all collected specimens, hindering both the analysis of diversity and the accumulation of information about these insects in nature. Mendonça et al. (2009) attribute the impossibility of identification to the species level to the current lack of knowledge of the group in the Neotropical region.

In the neotropics, several regional studies on the Thyreocoridae are available, for the fauna of Cuba (Barber and Bruner 1932), Puerto Rico (Barber 1939), Jamaica (Van Duzee 1907), Nicaragua (Maes 1994), Grenada (Uhler 1894), Trinidad (Callan 1948), Venezuela (Becker and Grazia-Vieira 1971), French Guiana (Becker and Grazia-Vieira 1977), Brazil (McAtee and Malloch 1928; Grazia et al. 1999; Barcellos 2006; Schmidt and Barcellos 2007; Mendonça et al. 2009; Grazia and Schwertner 2011), Ecuador (Froeschner 1981), Chile (Porter 1933), and Argentina (Berg 1879, 1884, 1891; Grazia et al. in press).

24.5 Economic Importance

Although several thyreocorid species have been recorded in crops, there is no information about damage caused by these bugs (Lis et al. 2000). Schuh and Slater (1995) just mentioned that some species of Corimelaeninae could be secondary pests to orchards and flowers. There are scattered reports of noticeable damage to cultivated and ornamental plants; more often, reference is made to the unpleasant taste given to the small berries in which these insects occur (Froeschner 1988). However, none of thyreocorid species are mentioned among the Heteroptera of economic importance (Schaefer and Panizzi 2000).

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Chapter 25
Less Diverse Pentatomoid Families (Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae)

Cristiano F. Schwertner and Jocélia Grazia

Abstract The superfamily Pentatomoidea comprises about 7,000 species worldwide divided in 15 families and shows a remarkable diversity. In the Neotropical region, more than 1,900 species in 10 families are recorded. In this chapter, the knowledge about the families Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae, which include 66 species in 28 genera in the region, is summarized. Although representing less diverse lineages within the superfamily Pentatomoidea, studies about these families will be fundamental to understand the evolution and natural history of the true bugs in the Neotropical region. Some of them are endemic to the Neotropics (i.e., Canopidae and Megarididae) or have relict distribution (i.e., Acanthosomatidae, Phloeidae, and Tessaratomidae). Characteristics like cryptic coloration (Phloeidae) and maternal care behavior (Acanthosomatidae) make these bugs good models for evolutionary and ecological studies. However, little information is available for most of the species. Identification keys for all families of Pentatomoidea found in the Neotropics as well as characterization of all families and genera treated in this chapter are provided.

25.1 Introduction

The superfamily Pentatomoidea includes mainly phytophagous bugs, recognized by the developed scutellum, 2 + 2 abdominal trichobothria lateral to the spiracle line, opening of the genital capsule in males (the pygophore) directed posteriorly, and

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eggs barrel shaped (Schuh and Slater 1995; Grazia et al. 2008). The group comprises about 7,000 species worldwide and shows a remarkable morphological diversity (Fig. 25.1), separated in 15 families (Grazia et al. 2008). In the Neotropical region, more than 1,900 species in ten families are recorded (Table 25.1).

Fig. 25.1 Morphological diversity of Pentatomoidea families. (**a**) *Canopus* sp. (Canopidae); (**b**) *Dinidor mactabilis* Perty (Dinidoridae); (**c**) *Phloea subquadrata* Spinola (Phloeidae), male and female in copula (Photos: (a) D Ellyahu (b) CF Schwertner (c) JC Bernardes)

Table 25.1 Number of genera and species of Pentatomoidea families for the world and for the Neotropical Region

		World		Neotropical Region	
Family	Subfamily	Genera	Species	Genera	Species
Acanthosomatidae		57	183	22	34
	Acanthosomatinae	16	132	1	1
	Blaudusinae	25	30	12	21
	Ditomotarsinae	16	21	9	12
Canopidae	[a]	1	8	1	8
Cydnidae	[b]	93	742	16	131
Dinidoridae		13	115	1	6
	Dinidorinae	10	68	1	6
	Megymeninae	3	17	0	0
Lestoniidae	[a]	1	2	0	0
Megarididae	[a]	1	16	1	16
Parastrachiidae	[a]	2	4	0	0
Pentatomidae	[b]	900	4.700	240	>1,500
Phloeidae	[a]	3	4	2	3
Plataspididae	[a]	59	560	0	0
Scutelleridae	[b]	81	450	25	112
Tessaratomidae		55	240	1	3
	Natalicolinae	8	14	0	0
	Oncomerinae	14	60	1	3
	Tessaratominae	32	166	0	0
Thyreocoridae	[b]	12	212	9	159
Thaumastellidae	[a]	1	3	0	0
Urostylididae	[a]	4	80	0	0

[a] Without classification at subfamilial or tribal level

[b] For the classification and diversity at subfamilial/tribal level, see corresponding chapter in this book

In this chapter, the knowledge about the families Acanthosomatidae, Canopidae, Dinidoridae, Megarididae, Phloeidae, and Tessaratomidae in the Neotropical region is summarized, which include 66 species in 28 genera in the region (Table 25.2). Canopidae and Megarididae are exclusively found in the Neotropics (McAtee and Malloch 1928, 1933), while Phloeidae has a relic distribution, with one species found in the Australian region (Grazia et al. 2008). To help identify the families treated here, an identification key to all families of Pentatomoidea found in the Neotropics is provided.

Table 25.2 Checklist of the species and country distribution of the less diverse families of the Pentatomoidea in the Neotropical Region

Family/Subfamily	Species	Distribution
Acanthosomatidae		
Acanthosomatinae	*Elasmucha lateralis* (Say)	CAN, USA, MEX
Blaudusinae		
Blaudusini	*Bebaeus punctipes* Dallas	CO, PAR, VEM, BOL
	Blaudus ruficornis Stål	COL
Lanopini	*Acrophyma bicallosa* (Stål)	COL, BRA
	Acrophyma cumingii (Westwood)	CHI, ARG
	Cochabambia martinezi Pirán	BOL
	Ea australis Distant	CHI, ARG
	Ea septentrionalis Carvajal, Fáundez, and Rider	CHI
	Hellica johni Froeschner	ARG, URU
	Hellica johnpolhemi Froeschner	BOL, ARG
	Hellica nitida Haglund	BR (AM?, SC, RS), ARG
	Lanopis algescens Bergroth	ARG
	Lanopis chubuti Distant	ARG
	Lanopis rugosus Signoret	CHI, ARG
	Lanopis splendens Distant	ARG
	Mazanoma variada Rolston and Kumar	CHI
	Phorbanta variabilis (Signoret)	CHI, ARG
	Pseudosinopla canaliculus (Reed)	CHI
	Sinopla humeralis Signoret	CHI
	Sinopla perpunctatus Signoret	CHI, ARG
	Sniploa obsoletus Signoret	CHI
	Sniploa shajovskoii Kormilev	ARG
Ditomotarsinae		
Ditomotarsini	*Archaeoditomotarsus* Fáundez, Carvajal, and Rider	CHI

(continued)

Table 25.2 (continued)

Family/Subfamily	Species	Distribution
	Cylindrocnema plana Mayr	CHI, ARG
	Ditomotarsus punctiventris Spinola	CHI, ARG
	Hyperbius geniculatus Signoret	CHI, ARG
	Nopalis sulcatus Signoret	CHI
	Planois patagonus Distant	ARG
	Planois gayi (Spinola)	CHI, ARG
	Praesus incarnatus Stål	COL
	Rolstonus rolstoni Froeschner	COL
	Tolono decoratus Rolston and Kumar	COL, ECU
	Tolono confusus Carvajal, Rider, and Faúndez	COl, ECU
	Tolono pallidus Carvajal, Rider, and Faúndez	COL
Canopidae	*Canopus andinus* Horváth	PER
	Canopus burmeisteri McAtee and Malloch	BRA (AM), BOL
	Canopus caesus (Germar)	BR (PA)
	Canopus fabricii McAtee and Malloch	CR, PAN, BR
	Canopus germari McAtee and Malloch	CR, PAN, COL, ECU
	Canopus globosus Horváth	BRA, PER, BOL
	Canopus impressus F.	BR
	Canopus orbicularis Horváth	GUI, BRA
Dinidoridae		
Dinidorinae	*Dinidor braziliensis* Durai	BRA, PAR
	Dinidor impicticollis Stål	COL, ECU
	Dinidor mactabilis Perty	BRA, ARG
	Dinidor pulsator (Schouteden)	PER
	Dinidor rufocinctus Stål	PAN, COL, BRA, ECU, BOL
	Dinidor saucius Stål	BRA
Megarididae		
	Megaris antennata McAtee and Malloch	GUA
	Megaris atratula Stål	BLZ
	Megaris constricta McAtee and Malloch	GUA
	Megaris hemisphaerica McAtee and Malloch	GUY, VEN, BRA
	Megaris laevicollis Stål	BRA, PAR, ARG, VEN?
	Megaris longula McAtee and Malloch	BRA
	Megaris majuscula McAtee and Malloch	CUB

(continued)

Table 25.2 (continued)

Family/Subfamily	Species	Distribution
	Megaris nigritula Stål	BRA
	Megaris peruviana Horváth	PER
	Megaris puertoricensis Barber	PUR
	Megaris punctulata Horváth	TRI
	Megaris rotunda McDonald	BRA
	Megaris semiamicta McAtee and Malloch	GUA, PAN
	Megaris stalii McAtee and Malloch	BRA
	Megaris trinotata Distant	PAN
	Megaris vianai Kormilev	ARG
Phloeidae		
	Phloea corticata (Drury)	BRA
	Phloea subquadrata Spinola	BRA
	Phloephana longirostris (Spinola)	BRA
Tessaratomidae		
Oncomerinae		
Piezosternini	*Piezosternum subulatum* (Thunberg)	MEX, NIC, CUB, RDO, PUR, GDE (Guadeloupe), MAR, PAN, VEM, COL, FGU, GUY, SUR, BRA, ECU
	Piezosternum thunbergi Stål	BRA, BOL, PAR, ARG, URU
	Piezosternum venezolanum Pirán	VEN

Key to the families of Neotropical Pentatomoidea (modified from Rolston and McDonald 1979):

1. Antennae IV- or V-segmented; MTG opening distant from the lateral margin of metapleura..........2
– Antennae III-segmented; MTG opening near the lateral margin of metapleura (Fig. 25.2) ....Phloeidae
2. Scutellum enlarged covering most of hemelytra (Fig. 25.3)..........8
– Scutellum leaving most of hemelytra exposed even when scutellum attains the apex of abdomen..........3
3. Trichobothria in urosternites III–VII on large callus located mesad of the adjacent spiracle (Fig. 25.4)..........Dinidoridae
– Trichobothria not on large callus, both rarely mesad of spiracles on all urosternites..........4
4. Pronotum extending over the base of scutellum (Fig. 25.43) ....Tessaratomidae
– Pronotum ending at the base of scutellum..........5
5. Tibial spines if present are confined to the apex of tibiae..........6
– Tibial spines along all tibiae in addition to setae (Fig. 25.5)..........7

6. Tarsi 2-segmented; urosternite VIII exposed in males (Fig. 25.6); Pendergrast's organs (Fig. 25.7) usually present in females .... Acanthosomatidae
– Tarsi usually 3-segmented; urosternite VIII always in males concealed; Pendergrast's organs in females always absent................................ Pentatomidae
7. Fore tibiae usually expanded (Fig. 25.8a), sometimes cultrate with tarsi inserted midway of length bearing a lateral row of especially stout spines unless cultrate; the apex of scutellum usually narrowly rounded ....Cydnidae
– Fore tibiae subcylindrical; spines on the lateral margin not notably stout (Fig. 25.9); the apex of scutellum broadly rounded (Fig. 25.10) ....Thyreocoridae
8. Tarsi 2-segmented ....Megarididae
– Tarsi 3-segmented 9
9. Tibial spines numerous, along all tibiae in addition to setae; if weakly spined, lateral margins of the pronotum fringed with long setae ....Thyreocoridae
– Tibial spines if present confined to the apex 10
10. Sutures of abdominal venter complete, reaching lateral margins (Fig. 25.11); the second antennal segment much longer than the diameter..........................11
– Sutures of the abdominal venter obsolete laterad of spiracles; the second antennal segment subequal to the diameter ....Canopidae
11. Trichobothria paired (Fig. 25.12); frena lacking............................ Scutelleridae
– Trichobothria single; short frena present .... Pentatomidae

Fig. 25.2 *Phloeophana longirostris* (Spinola) (Phloeidae), metathoracic gland (MTG) opening (Photo CF Schwertner)

Fig. 25.3 *Galgupha coccineloides* Horváth (Thyreocoridae) dorsal view (Photo CF Schwertner)

Fig. 25.4 *Dinidor mactabilis* Perty (Dinidoridae), detail of the *lateral view* of abdomen (Photo CF Schwertner)

Fig. 25.5 *Cyrtomenus mirabilis* Berg (Cydnidae), posterior tibia in *dorsal view* (Photo CF Schwertner)

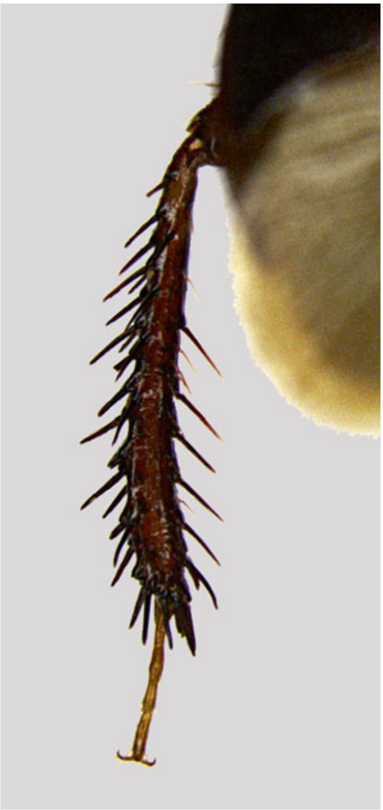

Fig. 25.6 *Planois gayi* (Spinola) (Acanthosomatidae), detail of ventral abdomen showing urosternite VIII exposed in male (Photo CF Schwertner)

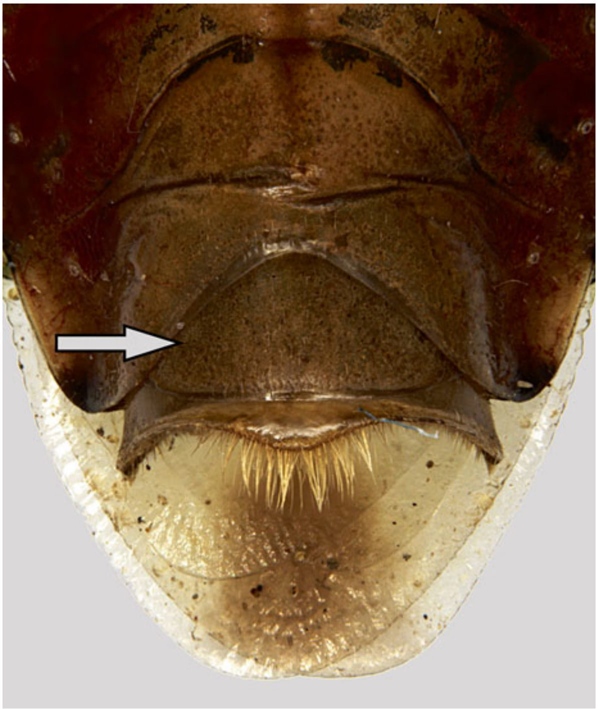

Fig. 25.7 *Planois gayi* (Spinola) (Acanthosomatidae), detail of *lateral view* of abdomen showing Pendergrast's organ (Photo CF Schwertner)

Fig. 25.8 Fore tibia in Cydnidae, lateral view. (**a**) *Cyrtomenus teter* (Spinola), Cydnidae; (**b**) *Scaptocoris castanea Perty*, Cephalocteinae (Photos CF Schwertner)

Fig. 25.9 *Galgupha* sp. (Thyreocoridae), fore tibiae (Photo CF Schwertner)

Fig. 25.10 *Galgupha* sp. Thyreocoridae, *lateral view* (Photo CF Schwertner)

Fig. 25.11 *Tetyra* sp. (Scutelleridae), partial *ventral view* showing sutures of abdominal venter (Photo CF Schwertner)

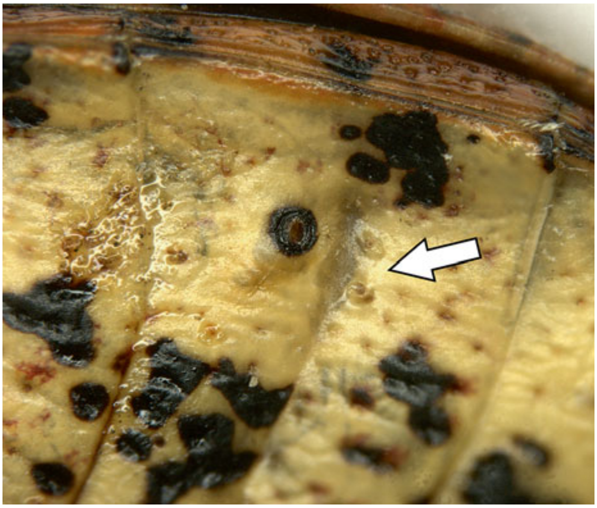

Fig. 25.12 *Tetyra* sp. (Scutelleridae), detail of the *ventral view* (Photo CF Schwertner)

25.2 Acanthosomatidae

Species included in the family Acanthosomatidae resemble median to large pentatomids (i.e., Fig. 25.15) and may be recognized by the shorter scutellum, 2-segmented tarsi, male abdominal segment 8 large and exposed, and Pendergrast's organ present in most of the females. The family includes more than 200 species in 57 genera (Grazia et al. 2008; Faúndez 2014; Carvajal et al. 2015) (Table 25.1), distributed mainly in temperate regions or at high altitudes in the subtropics. All studied species are phytophagous; maternal care is registered for some species (Tallamy and Schaefer 1997).

25.2.1 General Characteristics and Diagnosis

Adults are recognized for having 2-segmented tarsi and short scutellum, never covering the corium; size ranging from 5 to 20 mm in length; antenna 5-segmented, antenniferous tubercles not visible dorsally in most species; mesosternum usually with a conspicuous carina (subfamily Acanthosomatinae); urosternite III often with spine anteriorly developed; 1 + 1 trichobothria in abdominal urosternites III to VII, transversal; males with abdominal segment VIII exposed; females usually with Pendergrast's organs (glandular abdominal organs), rounded or oval, located in the urosternites V to VII (only in the VII in some species); and posterior margin of VII deeply emarginated.

Immatures. Southwood (1956) and Putshkov (1959) provided diagnoses for eggs and nymphs of several families and species of Heteroptera distributed in Europe, including Acanthosomatidae. Four Nearctic species in two genera of the subfamily Acanthosomatinae were described by Cobben (1968), who also discusses the data available so far for the whole group. At least two species have the nymphs formally described (Carter and Hoebeke 2003; Martinez et al. 2003; Faúndez 2007b) and allow us to infer that the immatures of the acanthosomatids share the general aspects of other families of Pentatomoidea (i.e., Grazia and Schwertner 2008).

Characteristics of the immatures include elliptical eggs with narrower anterior pole, smooth corium when observed in optical microscopy, and cup-shaped aero-micropylar processes ("aero-micropylar cup" in Cobben 1968); nymphs with oval body (Fig. 25.13); and anterior openings of scent glands farther apart than the median and posterior openings. In *Sinopla perpunctatus* Signoret, the dorsal plates in the third, fourth, and fifth instars are divided longitudinally, forming paired plates (Martinez et al. 2003, Faúndez 2007a). This feature seems to be unique among immature pentatomoids (Putshkov 1959).

Fig. 25.13 *Sinopla perpunctatus* Signoret, fifth instar nymphs (From Faúndez 2007b. Used with permission from Boletin de la Sociedad Entomológica Aragonesa)

25.2.2 General Biology and Ecology

Few species of Acanthosomatidae have the biology studied in detail to date; most of the investigations were done with Palaearctic species, especially those that present maternal care (Kudo and Nakahira 1993; Kudo 2000). Biological data of Neotropical species include mostly field observations and label records. More recently, studies about the biology of the Neotropical species have been published (Faúndez and Osorio 2010b).

All known acanthosomatids are phytophagous, usually recorded in more than one host, which includes trees and shrubs (Kumar 1974; Schaefer and Ahmad 1987; Faúndez 2007c, 2009). Feeding sites include young tissues of the host and reproductive parts (Schaefer and Ahmad 1987; Faúndez 2007a, c). Casual records of feeding on decaying organic matter and predation including cannibalism are known (Miller 1971), probably related to the shortage of suitable host plants (Schaefer and Ahmad 1987).

Polyphagy seems to be the rule, but specializations can occur at different levels (Schaefer and Ahmad 1987; Faúndez 2007a, 2009). For instance, *Sinopla perpunctatus* is registered only in *Nothofagus* spp. in Chile and is considered a specialized species (Faúndez 2007a; Osorio 2009). Otherwise, *Acrophyma cumingii*

(Westwood) and *Ditomotarsus punctiventris* Spinola are considered generalists (Faúndez 2007b, 2009). Acanthosomatidae species are found feeding in several different host plant families, including Aceraceae, Anacardiaceae, Cornaceae, Apiaceae, Aquifoliaceae, Araliaceae, Asteraceae, Betulaceae, Caprifoliaceae, Casuarinaceae, Cupressaceae, Cyperaceae, Fabaceae, Juncaceae, Moraceae, Myrtaceae, Pinaceae, Poaceae, Proteaceae, Rhamnaceae, Rosaceae, Salicaceae, Nothofagaceae, Polygonaceae, Tiliaceae, and Ephedraceae (Schaefer and Ahmad 1987; Schaefer et al. 2000; Faúndez 2007a, 2008; Osorio 2009). In a survey conducted in riparian forests of the Pampas in southern Brazil (Mendonça et al. 2009), *Hellica nitida* Haglund was one of the most abundant pentatomoids, indicating preference of this species by this type of vegetation.

Life cycle is similar to that described for Pentatomidae (Grazia and Schwertner 2008). Faúndez (2007b) gives a brief description of the life cycle of *D. punctiventris*, providing details of the mating behavior (Faúndez 2007b; Faúndez et al. 2009). Females lay eggs in clutches, corresponding more or less with the number of ovarioles (usually 10–14). Egg and nymphal development time, prereproductive females, and adult longevity have not been studied in any of the Neotropical species.

Maternal care is recorded in species of the subfamily Acanthosomatinae (Schuh and Slater 1995) distributed mainly in Australian, Nearctic, Oriental, and Palearctic regions, including *Elasmucha lateralis* (Say, 1831) which is also recorded in the Neotropical region (Table 25.1). Faúndez and Osorio (2010a, b) described maternal care behavior for the first time in *Sinopla perpunctatus* (Signoret 1864), a species distributed exclusively in the Neotropics. The authors also reported coloration change in the female associated to the reproductive period and guard of eggs and nymphs.

Schaefer et al. (2000) reviewed the species of acanthosomatids with economic importance, and no records of Neotropical species damaging cultivated plants were found in the literature. More recently, *Phorbanta variabilis* (Signoret 1863) was recorded on Magellan barberry, *Berberis microphylla*, Berberidaceae, and *Ditomotarsus punctiventris* (Spinola 1852) is considered as a quarentenary species for the USA (E Fáundez & M Carvajal, personal communication 2014).

25.2.3 Classification and Diversity

Acanthosomatidae was recognized as a higher taxon by Signoret (1864) and treated as a subfamily or tribe of Pentatomidae by different authors (Schuh and Slater 1995). The current classification includes three subfamilies: Acanthosomatinae, Blaudusinae (tribes Blaudusini and Lanopini), and Ditomotarsinae (tribes Ditomotarsini and Laccophorellini) (Kumar 1974; Kment 2005).

Fischer (1994) and Grazia et al. (2008) defined the monophyly of the family. However, relationships of Acanthosomatidae with other Pentatomoidea are still unsettled (Kment 2005; Carvajal and Faúndez 2013). According to Gapud (1991), the family is related to Dinidoridae, Tessaratomidae, and Scutelleridae, in a relatively basal position within Pentatomoidea. Grazia et al. (2008) defined the family in different positions according to the analyses performed: the morphological evidence pointed to a basal position, while molecular data suggest the family as a derived taxon and related to Pentatomidae. Both analyses showed a sister-group relationship between Acanthosomatidae and Lestoniidae, the latter occurring exclusively in Australia.

The distribution of the Acanthosomatidae occurs predominantly in the Southern Hemisphere of the World, including Argentina, Australia, Chile, and South Africa. Only few genera (i.e., *Acanthosoma*, *Elasmucha*, and *Elasmostethus*) have representatives in the Northern Hemisphere. In the Neotropics, at least 22 genera and 34 species are described, and the faunas of Argentina and Chile are more diverse (Table 25.2).

Classical contributions with descriptions of new taxa were made in the nineteenth and early twentieth centuries by Westwood (1837), Spinola (1850, 1852), Signoret (1864), Mayr (1864), Stål (1867, 1872), Haglund (1868), Distant (1911), and Bergroth (1917). The generic world fauna was monographed by Kumar (1974). Keys to the genera found in the Western Hemisphere were provided by in Rolston and Kumar (1975), updated below. More recent studies on the Neotropical fauna include Froeschner (1997, 2000), Faúndez (2007a, b, c, 2009), Faúndez et al. (2009, 2014), Faúndez and Osorio (2010a, b), Carvajal and Faúndez (2013), Carvajal et al. (2014), Faúndez (2014), and Faúndez et al. (2014).

Knowledge about the diversity and the classification of the group in the Neotropical region is currently under revision, including the description of several new taxa (M Carvajal and E Faúndez, personal communication 2014).

Key to the genera of Acanthosomatidae of the Neotropical region (modified from Rolston and Kumar 1975 and Faúndez 2014).

1. Median tubercle or spine present at the base of the abdominal venter 11
1′ Base of the abdominal venter smoothly convex 2
2(1) Distal end of the first antennal segment clearly surpassing the apex of head 3
2′ Distal end of the first antennal segment reaching little if any beyond the apex of head 6
3(2) Longitudinal sulcus on the prosternum before coxae as deep as the diameter of the rostrum, little wider; the distal diameter of the first antennal segment usually about twice the basal diameter .... *Cylindrocnema* Mayr
3′ Longitudinal sulcus on the prosternum absent or much broader than the diameter of the rostrum; the first antennal segment subcylindrical 4
4(3) The length of the first antennal segment more than 4/5 the length of the head measured dorsally .... *Planois* Signoret (Fig. 25.14)
4′ The length of the first antennal segment less than 3/5 the length of the head measured dorsally 5
5(4) The prosternum shallowly depressed lengthwise; humeral angles developed .... *Nopalis* Signoret (Fig. 25.15)

5′ The prosternum transversely convex; humeral angles not developed .... *Ditomotarsus* Spinola (Fig. 25.16)

6(2) Juga far surpassing the anteclypeus, usually contiguous before the anteclypeus 7

6′ Juga not or scarcely surpassing the anteclypeus 8

7(6) The anterior preocular part of the head strongly deflexed, prosternum a strong, mediolongitudinal groove, measuring 8–10 mm .... *Mazanoma* Rolston and Kumar (Fig. 25.17)

7′ The anterior preocular part of the head not strongly deflexed, prosternum without mediolongitudinal groove, measuring 5–6 mm ....*Rolstonus* Froeschner (Fig. 25.18)

8(6) Ostiolar peritreme reaching more than halfway from inner margin of the ostiole to the lateral margin of the metapleuron 10

8′ Ostiolar peritreme short 9

9 The pronotum with anterolateral margins slightly sinuous; mesosternum weakly carinate; female with one pair of Pendergrast's organs; body coloration black, shiny, and marked with shades of yellow, with pronotum having a crescent curving ivory mark, from posterolateral margins to the anterior submargin .... *Tolono* Rolston and Kumar (Fig. 25.19)

9′ The pronotum with anterolateral margins straight; the mesosternum without carina; female with two pairs of Pendergrast's organs; body coloration different from above, pronotum predominantly red .... *Praesus* Stål (Fig. 25.20)

10(8) Juga strongly concave laterally; coloration blackish ....*Hyperbius* Stål (Fig. 25.21)

10′ Juga not strongly concave laterally; coloration not blackish ....*Archaeoditomotarsus* Fáundez, Carvajal, and Rider

11(1) The mesosternal carina greatly produced, extending anteriorly beyond procoxae; the abdominal spine appressed to the right side of the posterior portion of the mesosternal carina 12

11′ The mesosternal carina weakly developed or absent 13

12(11) Ostiolar peritreme reaching a little more than halfway from the inner margin of the ostiole to the lateral margin of the metapleuron ....*Elasmucha* Stål (Fig. 25.22)

12′ Ostiolar peritreme reaching about three-fourth distance from the inner margin of the ostiole to the lateral margin of the metapleuron .... *Elasmostethus* Fieber (Fig. 25.23)

13(11) The abdominal spine surpassing mesocoxae 14

13′ The abdominal spine not reaching mesocoxae 15

14(13) Lateroposterior margins of the pronotum not produced into any spines or processes; the ostiole reaching more than halfway from the inner margin of the ostiole to the lateral margin of the metapleuron; the abdominal spine attaining procoxae .... *Blaudus* Stål (Fig. 25.24)

14′ Humeral angles of the pronotum produced into flat processes; the ostiole reaching about one-third distance from the inner margin of the ostiole to the lateral margin of the metapleuron; the abdominal spine attaining the head .... *Bebaeus* Dallas (Fig. 25.25)

15(13) Juga contiguous before the anteclypeus .... *Sniploa* Signoret

15′ Juga not surpassing the anteclypeus or, if longer than the anteclypeus, neither markedly convergent nor contiguous 16

16(15) Ostiolar peritreme extending much farther than halfway from the inner margin of the ostiole to the lateral margin of the metapleuron .... *Phorbanta* Stål (Fig. 25.26)

16′ Ostiolar peritreme extending halfway or less from the inner margin of the ostiole to the lateral margin of the metapleuron 17

17(16) Ostiolar peritreme reaching halfway from the inner margin of the ostiole to the lateral margin of the metapleuron.............. *Lanopis* Signoret (Fig. 25.27)

17′ Ostiolar peritreme reaching not more than one-third distance from the inner margin of the ostiole to the lateral margin of the metapleuron........................ 18

18(17) The spine at the base of the abdominal venter clearly extending onto the metasternum 19

18′ The base of the abdominal venter tuberculate, with the tubercle not or scarcely surpassing the posterior margin of the metasternum 20

19(18) The apex of head broad, with the anteclypeus and each paraclypeus individually rounded and sides scarcely concave before the eyes .... *Ea* Distant

19′ The apex of the head a narrow smooth parabola, sides distinctly concave before the eyes... *Acrophyma* Bergroth (Fig. 25.28)

20(18) The first antennal segment reaching or slightly surpassing the apex of head 21

20′ The mesosternum without carina; the first antennal segment not reaching the apex of head .... *Hellica* Stål* (Fig. 25.29)

21(20) The ostiolar peritreme narrow and not fleshy (Fig. 25.30)................................ .... *Sinopla* Signoret (Fig. 25.31)

21′ The ostiolar peritreme wide and fleshy .... *Pseudosinopla* Faúndez

* Following Faúndez et al. (2014), the genus *Cochabambia* Pirán will key with *Hellica*. The genus *Cochabambia* from *Hellica* can be separated by more elongated body punctuation denser and shallower, and pronotum trapezoidal in shape.

25.3 Canopidae

Canopids are exclusively distributed in the Neotropical region (Table 25.2), with all eight known species belonging to genus *Canopus* F. that are medium sized (mm), with almost rounded body, dorsally convex and ventrally flat (Fig. 25.32) Coloration black and shiny, with purple and green reflexes. Scutellum enlarged, covering entirely the abdomen and most part of hemelytra (Grazia et al. 2012). The wide scutellum is shared with other pentatomoid families (Aphylidae, Canopidae,

Fig. 25.14 *Planois gayi* (Spinola), *dorsal view* (Photo CF Schwertner)

Fig. 25.15 *Nopalis sulcatus* Signoret, *dorsal view* (Photo CF Schwertner)

Fig. 25.16 *Ditomotarsus punctipes* Spinola, *dorsal view* (Photo CF Schwertner)

Fig. 25.17 *Mazanoma varia* Rolston and Kumar, *dorsal view* (Photo CF Schwertner)

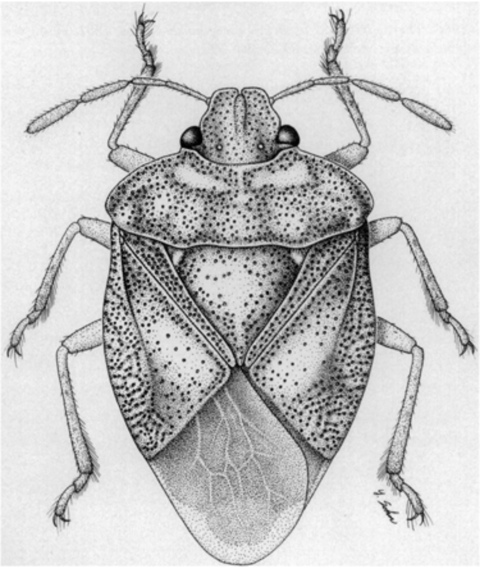

Fig. 25.18 *Rolstonus rolstoni* Froeschner (From Froeschner 2000. Used with permission of Entomologica Americana)

Fig. 25.19 *Tolono decoratus* Rolston and Kumar, *dorsal view* (Photo modified from the original available at http://ihs.myspecies.info/taxonomy/term/94, Copyright American Museum of Natural History licensed under a Creative Commons Attribution CC BY Licence, http://creativecommons.org/licenses/by/3.0/)

Fig. 25.20 *Praesus incarnatus* Stål, *dorsal view* (Photo: Bert Gustafsson. Copyright Swedish Museum of Natural History, Stockholm – NRM)

Fig. 25.21 *Hyperbius geniculatus* Signoret, *dorsal view* (Photo CF Schwertner)

Fig. 25.22 *Elasmucha lateralis* (Say), dorsal view (Photos CF Schwertner)

Fig. 25.23 *Elasmostethus placidus* (Walker), *dorsal view* (Photo CF Schwertner)

Fig. 25.24 *Blaudus ruficornis* Stål, *dorsal view* (Photo: Bert Gustafsson. Copyright Swedish Museum of Natural History, Stockholm – NRM)

Fig. 25.25 *Bebaeus punctipes* Dallas, *dorsal view* (Photo CF Schwertner)

Fig. 25.26 *Phorbanta variabilis* (Signoret), *dorsal view* (Photo CF Schwertner)

Fig. 25.27 *Lanopis rugosus* Signoret, *dorsal view* (Photo CF Schwertner)

Fig. 25.28 *Acrophyma cumingii* (Westwood), *dorsal view* (Photo CF Schwertner)

Fig. 25.29 *Hellica nitida* Haglund, *dorsal view* (Photo CF Schwertner)

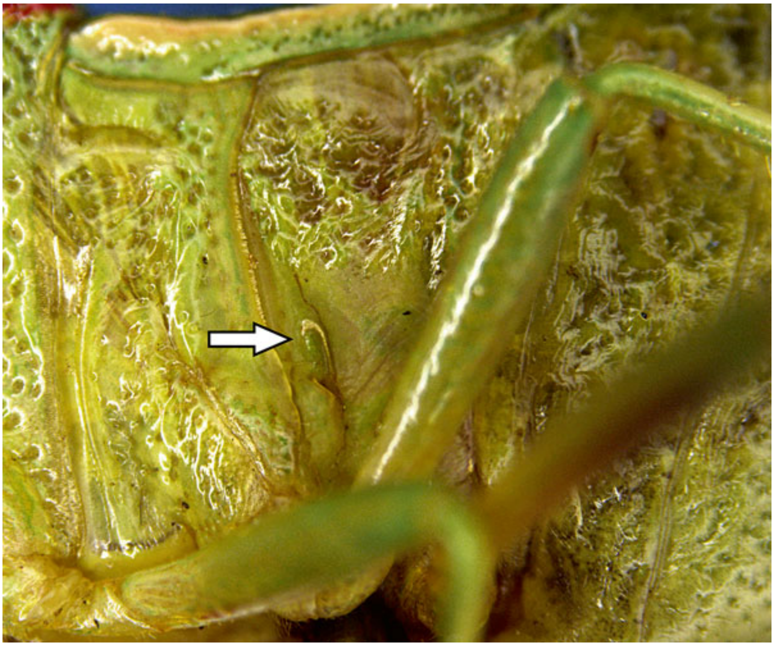

Fig. 25.30 *Sinopla perpunctatus* Signoret, (**b**) *Lanopis rugosus*, detail of ventral view showing ostiolar peritreme (Photo CF Schwertner)

Fig. 25.31 *Sinopla perpunctatus* Signoret, *dorsal view* (Photo CF Schwertner)

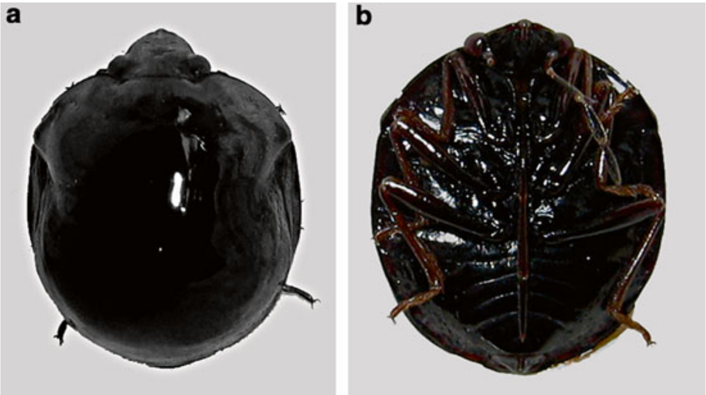

Fig. 25.32 *Canopus* sp. (**a**) *dorsal view*, (**b**) *ventral view* (Photos CF Schwertner)

Lestoniidae, Plataspididae, and Scutelleridae), but the similarity among these families is only superficial (McDonald 1979; Grazia et al. 2008). The family is poorly represented in collections, probably due to the small size and difficult sampling, sometimes being mixed up with Coleoptera. It was recognized as a subfamily of Pentatomidae by McAtee and Malloch (1928).

25.3.1 General Characteristics and Diagnosis

The canopids do not have a common name; they are medium sized (5–7 mm) with obovate outline, slightly narrower posteriorly than anteriorly, strongly convex dorsally, and flattened ventrally; the head is short, length of the head anterior to the eyes almost as long as the eye; margins of mandibular plates slightly reflexed; the prosternal sulcus and strongly laminate propleural carinae present; antennae V-segmented, with segment II reduced, subequal to the diameter; the cutellum covering the abdomen and almost all hemelytra; hemelytra elongated, twice as long as the abdomen with line of weakness for folding at the end of the costa, membrane with at least five parallel veins; hind wings with lobate posterior margins; tibiae setose, tarsi III-segmented; abdomen with obsolete sutures laterad to the spiracles; and trichobothria on sterna III–VII placed longitudinally mesad of the spiracular line. The nymphs are strongly convex and sclerotized, with three pairs of dorsal abdominal scent gland openings between terga III–IV, IV–V, and V–VI, the anterior gland openings twice the width of the other two; nymphal sterna II and III are divided mesally.

25.3.2 General Biology and Ecology

Biology and ecology of the canopids are poorly known. McHugh (1994) registered nymphs and adults of *Canopus* spp. on fungi and found spores in the digestive system, confirming the fungivorous habits of these insects.

25.3.3 Classification and Diversity

A single genus, *Canopus* F., and eight species are known (Table 25.2). The first three species described in the genus were based in nymphs and were not recognized by McAtee and Malloch (1928) in their review of the group. Horváth (1919) proposed the tribe Canoparia and added five new species. McAtee and Malloch (1928) treated Canopinae as a subfamily of Pentatomidae, transferred two previously described species to *Canopus*, synonymized two species described by Horváth (1919), and described three new species, totalizing the eight species so far.

McDonald (1979) recognized Canopidae as a family, describing the morphology of the male and female genitalia of *C. caesus*, *C. orbicularis*, and *C. impressus* and the female genitalia of *C. burmeisteri* and *C. fabricii*. The development of the scutellum may suggest the canopids being related to the Megarididae and Plataspididae, but McDonald (1979) considered them quite clearly as separate families. The only key to the species is found in McAtee and Malloch (1928). Schaefer (1980, 1988) asserted that the families Canopidae, Cydnidae, Cyrtocoridae, Lestoniidae, Megarididae, Plataspididae, and Thaumastellidae consist of a primitive group within the Pentatomoidea, because of the plesiomorphic characters they have in common.

Gapud (1991) considered the Canopidae related to the Scutelleridae. The characters defining the group and the presence of a prosternal sulcus and prosternal carina strong laminate are shared with Megarididae and Thyreocoridae (Grazia et al. 2008). The relationships of the Canopidae with the Cydninae (Cydnidae) were also pointed out by Grazia et al. (2008) in the combined cladistic analysis using morphology and molecular data, but these results are in need of further tests.

25.4 Dinidoridae

Despite its relatively large size (up to 30 mm) and its aposematic coloration, these bugs are poorly represented in collections. The family was reviewed by Durai (1987), which divided it into two subfamilies and four tribes (Table 25.1). Its species are predominantly found in the Afrotropical and Oriental regions. In the Neotropics, only one genus, *Dinidor* Latreille, is recorded, with six species distributed in South America (Table 25.2).

25.4.1 General Characteristics and Diagnosis

Adults have a large size (10–30 mm) body that is ovoid and robust (Fig. 25.33); general color usually dark brown or black, with red/yellow stripes and maculae usually present; head carinate laterally and buccula short and elevated; with 4–5 segments antennae; and rostrum reaching meso and metacoxa. Humeral angles never developed. Scutellum triangular, width subequal to the length, never covering the corium, and apex usually blunt. Hemelytral with venation reticulate. Tarsi 2–3 segments.

Eggs or nymphs of any species of the Neotropical Dinidoridae have not been formally described. Knowledge is restricted to species from other regions (Malipatil and Kumar 1975; Danielczok and Kocorek 2003). Information about the eggs is also provided by Southwood (1956) and Cobben (1968). Eggs and nymphs of *D. mactabilis* were illustrated in Schwertner and Grazia (2014).

Fig. 25.33 *Dinidor mactabilis* Perty, *dorsal view* (Photo CF Schwertner)

In general, the immatures of dinidorids follow the pattern described for those of other families of Pentatomoidea (Cobben 1968; Schuh and Slater 1995; Grazia and Schwertner 2008). Unique characteristics include the shape of the eggs and of the aero-micropylar processes, the aspect of the chorion surface, and the development of some nymph structures.

Eggs are cylindrical, deposited in rows, and horizontally positioned to the substrate (a unique condition among pentatomoids). The chorion can be smooth or ornamented, usually thicker than in other families of Pentatomoidea. Aero-micropylar processes reduced, eccentrically arranged around the egg, with a number of processes variable from 30 to 50. Operculum not apparent, a semicircular line along the upper region, opposite to the region in contact with the substrate. Nymphs with body oval and robust. Openings of the dorsal abdominal glands of nymphs present only between tergites 4/5 and 6/5 (when present between tergites 3/4, the openings are reduced).

25.4.2 General Biology and Ecology

Only a few species of the family Dinidoridae have their biology studied (Schaefer et al. 2000). Most of the available data is limited to label records or other field observations. Schaefer and Ahmad (1987) compiled records of known host plants for four families of Pentatomoidea, including Dinidoridae. Schaefer et al. (2000) reviewed and discussed the data available for the species of economic importance. None of these studies include Neotropical species.

All species studied so far are exclusively phytophagous, feeding both in reproductive and vegetative parts of their hosts. The data indicate that polyphagy is widespread, but monophagy in some species is likely. Schafer and Ahmad (1987) and Schaefer et al. (2000) pointed out that some species can show preference for certain plant families (e.g., *Aspongopus* spp. for plants of the family Cucurbitaceae).

All species studied are univoltine and usually use more than one host plant throughout its life cycle (Schaefer et al. 2000). Some species may exhibit gregarious behavior during part of the year, being found in large quantities together on the host. Dinidoridae species oviposit egg masses averaging 14–28 eggs. Fertility is considered low, not exceeding 1–2 clutches/female (Schaefer et al. 2000).

One Neotropical species, *Dinidor mactabilis* (Dinidorinae), was recorded in *Smilax japecanga* Grisebach (Smilacaceae) in southern Brazil (Grazia et al. 2012). An interesting biological data on this species is the large number of ovipositions grouped on branches of the host plant.

There are no records of crop damage by dinidorids in the Neotropical region. Species in these families considered pests are found in the Oriental and Palearctic regions (*Aspongopus* spp.), associated to cucurbit crops.

25.4.3 Classification and Diversity

Durai (1987) recognized the subfamilies Dinidorinae (with tribes Dinidorini and Thalmini) and Megymeninae (with tribes Megymenini and Eumenotini). Kocorek and Lis (2000) reviewed the Megymeninae, proposed a new tribe (Byrsodepsini), and treated Eumenotini as junior synonym of Megymenini. Keys for identification of all genera and species can be found in Durai (1987). Rolston et al. (1996) summarized the current classification for the family. In the Neotropical region, only the endemic genus *Dinidor* is found, including six species distributed in Central and South Americas (Table 25.2).

Gapud (1991) considered Dinidoridae and Tessaratomidae sister-groups, based on two synapomorphies: presence of spiracles of abdominal segment II, partially exposed, and laterotergites 9 very large in females. Grazia et al. (2008) found similar results, although Dinidoridae may be paraphyletic or monophyletic according to the analyses performed.

25.5 Megarididae

Megaridids are small (5 mm or less in length) and coleopteroid in shape. Strongly convex dorsally, the scutellum is enlarged and covering the abdomen and wings (Fig. 25.34). The distribution is exclusively Neotropical, ranging from Mexico to southern Brazil; one species is endemic to Cuba and another to Puerto Rico. It was recognized as a subfamily of Pentatomidae by McAtee and Malloch (1928) and elevated to family by McDonald (1979). The family is poorly represented in collections, probably due to the small size and difficult sampling.

25.5.1 General Characteristics and Diagnosis

Adults have a body that is ovoid and strongly convex dorsally; dark in color and polished; anterior margins of the head and pronotum carinate and bucculae undeveloped; antennae 4-segmented, with many setae as long as the diameter of segments in females, much longer in males; scutellum almost completely covering hemelytra; forewing longer than the abdomen with thin areas about the middle costa, adapting the wing for folding; membrane with one or none parallel veins; and tibia without spines, tarsi 2-segmented.

Information about immatures are scarce (McAtee and Malloch 1928; Schuh and Slater 1995), and there is no formal description of eggs. General body of nymphs similar to adults in shape and color and heavily sclerotized, with abdominal terga not distinguished.

Fig. 25.34 *Megaris* sp., *dorsal view* (Photo VC Matesco)

25.5.2 General Biology and Ecology

Biology and ecology of the megaridids are completely ignored; it is accepted that all species are exclusively phytophagous. There are records of *Megaris puertoricensis* Barber and *M. semiamicta* McAtee and Malloch em *Eugenia* spp. (Myrtaceae), feeding on flowers of its hosts (references in Schuh and Slater 1995).

25.5.3 Classification and Diversity

A single extant genus, *Megaris* Stål, and 16 extant species are known (McDonald 1979) (Table 25.2). The only key to the species is found in McAtee and Malloch (1928), which should be complemented with the descriptions of Barber (1939), Kormilev (1956), and McDonald (1979). More recently, Poinar and Heiss (2013) described a new genus and species from Dominican amber fossil of Tertiary (age estimated between 45 and 15 mya).

25.6 Phloeidae

Phloeidae is a family of true bugs with peculiar aspect and with unique cryptic morphology. The species are flattened, with the margins of the head, thorax, and abdominal segments expanded into large lobes (Figs. 25.1c, 25.35, 25.36), which make these bugs to be mistaken with the bark of trees they live (Lent and Jurberg 1965; Grazia et al. 2012). They are large in size (20–25 mm). The family is distributed mainly in the Neotropical region and has been better studied since the mid-1960s (Lent and Jurberg 1965). More recently, thorough studies have been conducted on this exquisite group of bugs (Guilbert 2003; Bernardes et al. 2005; Salomão et al. 2012).

25.6.1 General Characteristics and Diagnosis

The body is depressed, with external margins of juga, pronotum, base of corium, and abdomen broadly foliate. Eyes divided into dorsal and ventral portion. The antenna 3-segmented, only partially visible dorsally, hidden below expanded juga; segment 1 very long and segment 3 curved. Peritreme opening near the lateral margin of the pleuron. Hemelytral membrane reticulate. Tarsi 3-segmented. Abdominal sterna 3–7 with trichobothria arranged longitudinally to the spiracular

Fig. 25.35 *Phloeophana longirostris* (Spinola), *dorsal view* (Photo CF Schwertner)

line. Spiracle 2 present and partially exposed. Abdominal scent gland of nymph openings present between terga 3/4, 4/5, and 5/6 (the latter with only one opening).

25.6.2 General Biology and Ecology

The life cycle of these bugs occurs entirely on the trunks of the host (Salomão et al. 2012). Females protect eggs and early nymphs; the latter attach themselves to the abdomen of the mother (Lent and Jurberg 1965; Guilbert 2003) (Fig. 25.37). Nymphs and adults feed on the vascular system of the hosts (Bernardes et al. 2005). Host plants include *Cecropia* sp. (Urticaceae), *Croton floribundus* Spreng (Euphorbiaceae), *Ficus* spp. (Moraceae), *Enterolobium maximum* Ducke (Mimosacea), *Eugenia cauliflora* de Berg (Myrtaceae), *Miconia cubatensis* Hoehne (Melastomataceae), *Machaerium* spp. (Fabaceae), *Myrcia* sp. (Myrtaceae), *Parkia*

Fig. 25.36 *Phloea subquadrata* Spinola, *dorsal view* (Photo CF Schwertner)

multijuga Benth, *Psidium* sp. (Myrtaceae), *Terminalia catappa* L. (Rosaceae), *Sucurinega guaraiva* Kuhlmann (Euphorbiaceae), and *Parkia multijuga* Benth (Mimosaceae). Salomão et al. (2012) gave an excellent account about the group and summarized several studies that have been carried on in the Serra do Japi, São Paulo, Brazil, where the three species occur sympatrically.

25.6.3 Classification and Diversity

The family includes four species in three genera (Grazia et al. 2008), with disjunct distribution in the Southern Hemisphere: *Serbana* Distant (one species) occurs only in Borneo (Leston 1953), while species of the genera *Phloea* Spinola (two species) and *Phloeophana* Leston (one species) occur only in South America, their distribution restricted to Brazil from Pará to Rio Grande do Sul and restricted to Amazon and Atlantic Rainforest regions (Lent and Jurberg 1965). The relationship of the Phloeidae among Pentatomoidea families is still equivocal (Grazia et al. 2008).

Fig. 25.37 *Phloea subquadrata* (Spinola), female ventral view with nymphs attached in the abdomen (Photo CF Schwertner)

25.7 Tessaratomidae

This family of large and robust bugs, sometimes exceeding 40 mm in length, is mainly distributed in the Old World tropics, restricted to the Southern Hemisphere (Schuh and Slater 1995; Grazia et al. 2012). About 45 genera and 235 species are known worldwide (Table 25.1). One genus, *Piezosternum* Amyot and Serville, has wide distribution and includes three endemic species to the Neotropics (Table 25.2).

Similar to large pentatomids, tessaratomids can be distinguished from them by a very small head; antenna usually 4-segmented; short rostrum; metasternum produced anteriorly, generally into a large blade-like projection reaching the anterior coxae; and pronotum extending over the base of the scutellum.

25.7.1 General Characteristics and Diagnosis

Adults are large (10–40 mm) and have a body that is ovoid to elongated and robust (Fig. 25.38). Varied coloration, but the Neotropical species are predominantly green. The head is laterally carinate, relatively small in comparison to the body size;

Fig. 25.38 *Piezosternum thunbergi* Stål, *dorsal view* (Photo CF Schwertner)

buccula is very short. Antennae 4- or 5-segmented (usually 4). The rostrum is short, reaching but not surpassing the anterior coxa. Humeral angles may be developed, a condition found in all Neotropical species; the posterior margin of the pronotum reaching up on the base of the scutellum. The scutellum triangular, longer than broad, never covering the corium, apex usually pointed. Hemelytral membrane without reticulated veins. Hind wing with hamus. The metasternum produced laterad and anteriorly, reaching the anterior coxae; the posterior margin of the metasternum truncate at the junction with the abdomen. Tarsi with 2- or 3-segments.

Knowledge about eggs and nymphs of these families is restricted to species from other regions (Southwood 1956; Cobben 1968; Kumar 1969; McDonald 1969; Malipatil and Kumar 1975; Magnien et al. 2008).

Eggs are spherical, deposited perpendicular to the substrate. Chorion smooth, thinner than in Dinidoridae. Aero-micropylar processes are reduced and knob like, circulating the middle region of the egg, in variable numbers (30 to 60). Operculum not apparent, line of operculum dorsolateral extending basally. Nymphs of the 1st, 2nd, and 3rd instars with oval, flattened body; late instars elongated and more robust body. Fifth instar nymph of *P. thunbergi* is illustrated in Schwertner and Grazia (2014).

25.7.2 General Biology and Ecology

Only a few species of tessaratomids have their biology studied (McDonald 1969; Malipatil and Kumar 1975; Schaefer et al. 2000; Dzerefos et al. 2009); most of the available data is limited to label data or other types of field observation. Schaefer and Ahmad (1987) refer to known host plants, and Schaefer et al. (2000) reviewed and discussed the available data of the species related to crops. None of these studies provided information about the Neotropical species.

All species studied so far are exclusively phytophagous, feeding on both reproductive and vegetative parts of their host. Polyphagy seems to be the rule, but as for Dinidoridae, some species may show host preference [e.g., *Musgraveia sulciventris* (Stål) feeds primarily on plants of the family Rutaceae] (Schaefer and Ahmad 1987; Schaefer et al. 2000).

All species are univoltine and usually use more than one host plant throughout its life cycle (Schaefer et al. 2000; Dzerefos et al. 2009), with biological aspects very similar to Dinidoridae (see item 3.3). Depending on the species, females can lay in masses of four rows (3-4-4-3 formula), with an average of 14–28 eggs per clutch. Fertility is considered low, not exceeding 1–2 clutches/female (Schaefer et al. 2000). Eggs of *Encosternum delegorguei* Spinola took an average of 18 ± 9 days to hatch (temperatures ranging from 11 to 25 °C), while the nymphs took four months to reach adulthood (Dzerefos et al. 2009). Adults of this species overwinter from autumn to late winter. Maternal care has been described for some tessaratomids of the subfamily Oncomerinae in the Australian region (Gogala et al. 1998; Monteith 2006). Three genera show a similar behavior to that described for species of Phloeidae, where the nymphs are carried on the modified body of the female for a period of time after hatching (Monteith 2006).

The Neotropical species *Piezosternum subulatum* (Thunberg) was recorded in *Cucurbita* sp. (Cucurbitaceae), *Coffea* sp. (Rubiaceae), *Hibiscus* sp. (Malvaceae), *Lycopersicon* sp. (Solanaceae), and *Psidium* sp. (Myrtaceae) in Nicaragua (Maes 1994). There are no records of damage to crops in the Neotropical region. A single species of this family is considered pest in the Australian region, *Musgraveia sulciventris* Stål (Schaefer et al. 2000).

25.7.3 Classification and Diversity

In a cladistic analysis, Sinclair (1989) suggested that Tessaratomidae is polyphyletic and raised the Oncomerinae to family status, but recently it was restored as a subfamily (Sinclair 2000). Rolston et al. (1993) catalogued the world fauna. Schuh and Slater (1995) recognized the three subfamilies mentioned above, the Tessaratominae subdivided into five tribes (Eusthenini, Platytatini, Prionogastrini, Sepinini, and Tessaratomini), and the Oncomerinae into two tribes (Oncomerini and Piezosternini). Grazia et al. (2008) found different results concerning the monophyly of the family, according to the analyses performed: the group appears as monophyletic or paraphyletic, but always related to the Dinidoridae. The intrafamiliar classification was recently discussed by Kment and Vilímová (2010). No phylogenetic hypothesis concerning the relationships within the family is available. Identification key to the Neotropical species is available in Pirán (1971).

25.8 Concluding Remarks

The families treated in this chapter represent less diverse lineages of the superfamily Pentatomoidea, although with great importance to understand the evolution and natural history of the true bugs in the Neotropical region. Most of the species found in the Neotropics are endemic taxa (i.e., Canopidae and Megarididae) or have a relict distribution (i.e., Acanthosomatidae, Phloeidae, and Tessaratomidae), and studies in these groups will certainly be helpful to have a better picture of the fauna of the region.

The species found in the Neotropics show remarkable characteristics, like cryptic coloration (Phloeidae) and maternal care behavior (Acanthosomatidae), and may be good models for evolutionary and ecological studies. For some families, like Canopidae and Megarididae, there is little information available despite scattered distribution records. Future research in these families should include more detailed studies on the distribution of the species, phylogenetic relationships, morphology and natural history.

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