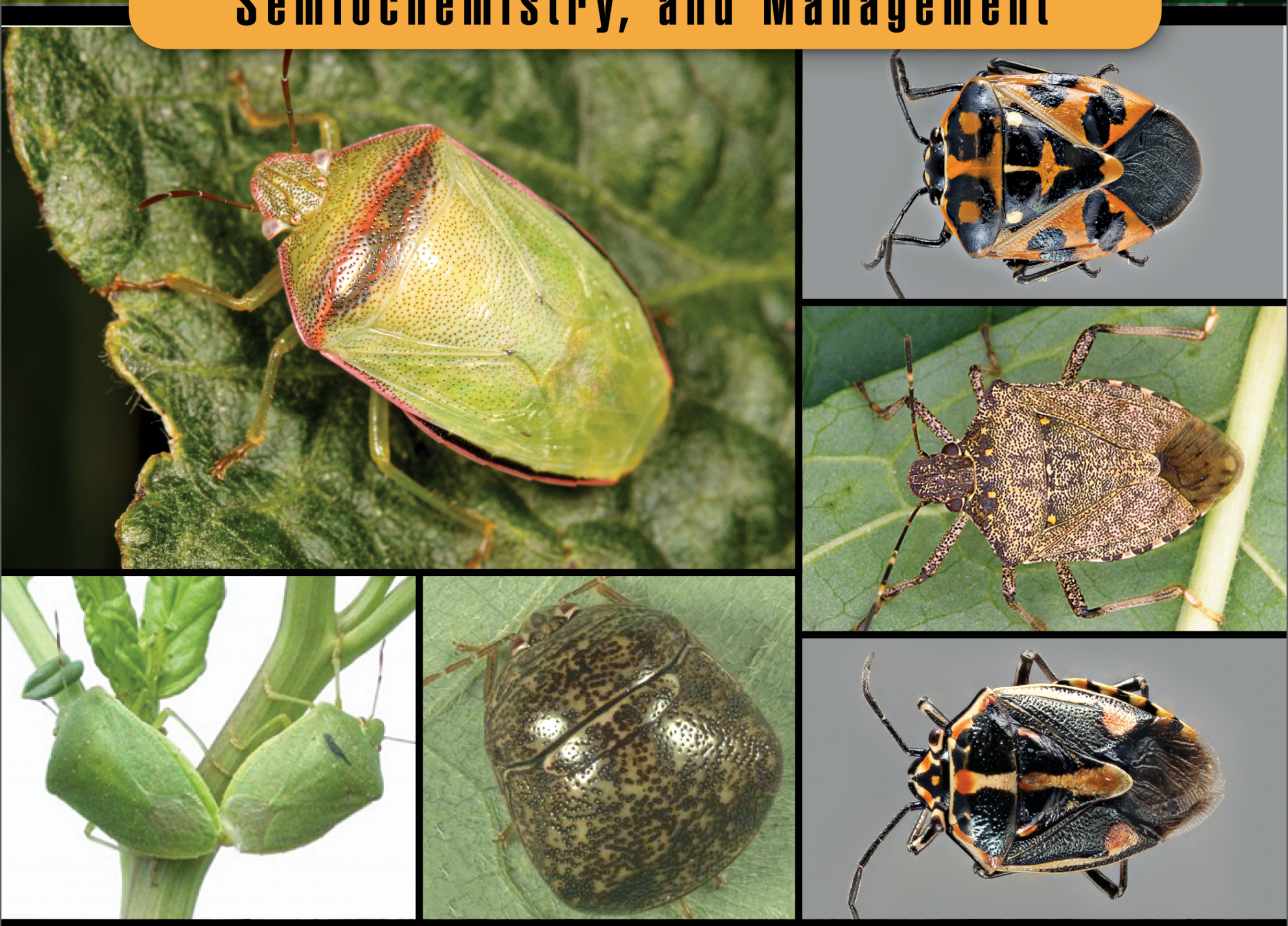
Invasive Stink Bugs and Related Species (Pentatomoidea)

Biology, Higher Systematics, Semiochemistry, and Management



Edited by

J. E. McPherson

CRC Press
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CRC Press
Taylor & Francis Group
Boca Raton London New York

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Adult of *Piezodorus guildinii* (Westwood), Photograph by Ted C. MacRae; Adult of *Murgantia histrionica* (Hahn), Photograph by C. Scott Bundy; Adult of *Halyomorpha halys* (Stål), Photograph by George C. Hamilton; Adult of *Bagrada hilaris* (Burmeister), Photograph by C. Scott Bundy; Adult of *Megacopta cribraria* (F.), Photograph by J. E. Eger; Mating pair of *Nezara viridula* (L.), Photograph by Jesus F. Esquivel. Used with permission. All rights reserved.

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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Printed on acid-free paper

International Standard Book Number-13: 978-1-4987-1508-9 (Hardback)

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Library of Congress Cataloging-in-Publication Data

Names: McPherson, J. E. (John Edwin), 1941- , author.
Title: Invasive stink bugs and related species (Pentatomoidea) : biology, higher systematics, semiochemistry, and management / J.E. McPherson.
Description: Boca Raton : Taylor & Francis, 2017. | Includes index.
Identifiers: LCCN 2016048509 | ISBN 9781498715089 (hardcover : alk. paper)
Subjects: LCSH: Stink bugs. | Hemiptera. | Agricultural pests.
Classification: LCC QL523.P5 M37 2017 | DDC 595.7/54--dc23
LC record available at https://lccn.loc.gov/2016048509

Visit the Taylor & Francis Web site at
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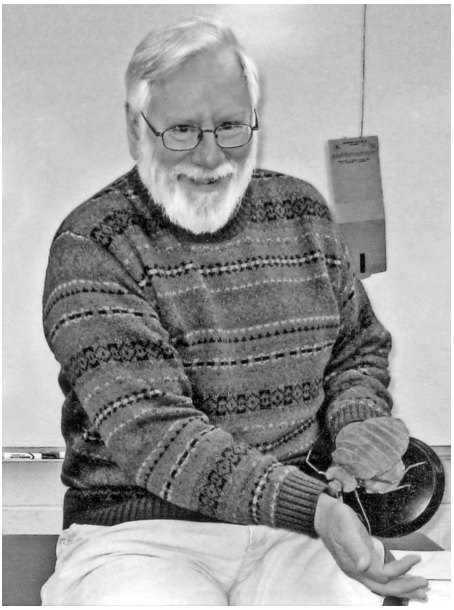

This book is dedicated to the late Carl W. Schaefer, Professor Emeritus at the University of Connecticut, Storrs. Dr. Schaefer was a friend and colleague to many of us and a recognized world leader in the study of Hemiptera-Heteroptera. He was a prolific researcher and writer, authoring over 240 journal articles and editing or co-editing seven books. He began "The Heteropterists' Newsletter" in 1973, which he edited and produced for over 20 years. He also was editor of the Annals of the Entomological Society of America (ESA) for 25 years (1973–1998) and served in several additional leadership positions in the Society, including President of the Eastern Branch. In recognition of his outstanding career, he was elected by the ESA as an Honorary Member in 1996 and as a Fellow in 2006. In 2014, he was elected for Honorary Life Membership by the International Heteropterists' Society, one of the first two individuals ever to have received this award. Truly, his contributions during his career were outstanding and certainly are worthy of this dedication.

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Preface

This book began with Tom Miller, University of California-Riverside, in his position as editor of the series “Contemporary Topics in Entomology,” produced by CRC Press and Taylor & Francis Group, with John Sulzycki as senior editor with the publisher. The series results from people and symposium titles Tom encounters at various meetings and is centered on topics of current interest. Thus far, the series has published the following titles: *Insect Symbiosis* (3 volumes); *Insect Sounds and Communication: Physiology, Behaviour, Ecology, and Evolution; Food Exploitation by Social Insects: Ecological, Behavioral, and Theoretical Approaches; Molecular Biology and Genetics of Lepidoptera*; *Honey Bee Colony Health: Challenges and Sustainable Solutions; Forensic Entomology: International Dimensions and Frontiers*; and *Greenhouse Pest Management*.

The idea for this book began with Tom’s involvement with Global Knowledge Initiative, a Washington D.C.-based non-profit organization dedicated to helping developing countries address science and technology problems. The first project of this organization in 2012 was to help solve a defect associated with Arabica coffee from East Africa. This defect is called “Potato Taste Defect” (PTD) because a few out of 100 cups of brewed coffee taste and smell like rotten potatoes. PTD is attributed to contamination of coffee cherries by microbes left from feeding by stink bugs of the genus *Antestiopsis*; occurrence of these bugs is centered in Rwanda and Burundi and, to a lesser extent, in Uganda, Kenya, Congo, and Tanzania. Coffee exports represent about 25% of Rwanda’s income, and although the coffee industry is thriving there, solving PTD would be of great benefit.

During this same period, Tom also became familiar with the biology of the brown marmorated stink bug and the southern green stink bug and learned of their association with microbes. He found the information so interesting that he organized a symposium, “Pentatomids and Microbes,” for the European Congress of Entomology that was held in York, United Kingdom, 3–8 August 2014. The contributors for that symposium constituted the starting core for designing the book on stink bug biology. Shortly thereafter, Tom asked me to serve as editor of the section on invasive stink bug species plus the *Antestiopsis* complex (antestia bugs).

I soon realized that serving as editor for the invasive stink bugs and *Antestiopsis* was going to be difficult because the other chapters involved Pentatomoidea in general (e.g., Higher Classification, Pathogens, Semiochemistry) and there was no underlying theme to pull the information together. After consulting with Tom about my concerns, he asked me to serve as editor for the entire book. Oh, well!

My first task was to select an individual for each chapter who, based on my knowledge or on recommendations from others, was highly qualified and willing to serve as chair. Then, I asked each chair to select contributors for his/her chapter who also were highly qualified and enthusiastic about contributing their expertise. The net result was the selection of 60 contributors from 13 countries (15, if you include the native countries of two authors whose current locations are elsewhere), giving the book a cosmopolitan flavor.

The contributors for each chapter were asked to submit the most recent information of which they were aware and to treat it as though they were preparing an article for the *Annual Review of Entomology*. All were highly enthusiastic about the project, each group of contributors considering their chapter to be an excellent opportunity to present the most comprehensive and up-to-date treatment of their specialties. As a result, this book encompasses a wide-ranging series of topics that are connected, sometimes loosely, by the underlying theme of the invasive species (even with the inclusion of the *Antestiopsis* complex, **Chapter 10**).

The book is divided into **10 sections**, reflecting the breadth of coverage among the **16 chapters**. **Section I (Chapter 1)** discusses introductory information including a brief classification overview of the Pentatomoidea, general biology of this superfamily, predators, parasites, chemical defenses, and brief information on the invasive species. **Section II (Chapter 2)** presents a thorough treatment of the higher classification of the Pentatomoidea, primarily at the tribal level. **Section III (Chapters 3–8)** provides a detailed discussion of each of the six recognized invasive species, including three that recently have been introduced into the United States [*Bagrada hilaris* Burmeister, *Halyomorpha halys* (Stål), and *Megacopta cribraria* (F.)]. **Section IV (Chapter 9)** deals with potentially invasive species in the United States and includes only three species, *Oebalus insularis* (Stål), *O. ypsilongriseus* (De Geer), and *Arvelius albopunctatus* (De Geer). The two species of *Oebalus*, which are noted pests of rice, are widely distributed in South and Central America but have been recorded in the United States only from Florida; potentially, they appear capable of spreading to adjacent states but, thus far, have not done so. *A. albopunctatus* apparently prefers wild and cultivated species of Solanaceae. It occurs throughout most of South America north through Baja California (Mexico) to Arizona, Texas, and Florida; it has not, as yet, become a pest in the United States. **Section V (Chapter 10)** discusses the *Antestiopsis* complex in Africa and Asia, a taxon noted as a pest of coffee that has not spread further although other pests of coffee are present today wherever coffee is grown. **Section VI (Chapters 11–12)** discusses diapause and seasonal cycles of Pentatomoidea. **Section VII (Chapter 13)** deals with Pentatomoidea as vectors of plant pathogens and **Section VIII (Chapter 14)**, symbiotic microorganisms associated with this superfamily. **Section IX (Chapter 15)** presents a detailed discussion of the semiochemistry of Pentatomoidea including pheromones, allomones, and kairomones. And, finally, **Section X (Chapter 16)** considers general management practices (both historical and current controls) from a broad perspective.

Serving as editor of this book was a challenging task, and I agreed to do it with some trepidation. Dealing with numerous contributors from several countries could have proven to be an unpleasant experience. But, such was not the case. All participants were so cooperative and enthusiastic about their contributions that my role was both exciting and rewarding. I want to extend my thanks to all of the contributors and hope that readers of this book will find it beneficial, rewarding, and a great tool for their own research and teaching and for increasing their own general knowledge of these areas of entomology.

J. E. McPherson
Carbondale, Illinois, U.S.A.

Acknowledgments

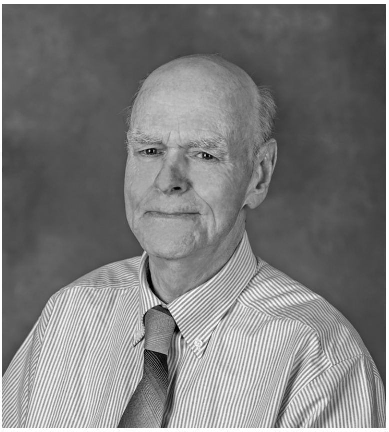
With a book of this size and breadth of topics, it is obvious that many individuals had to be involved in its development. Those who were not authors but contributed valuable information are acknowledged after the various chapters. However, others were involved with the development of the book as a whole. I am grateful to John Sulzycki, our editor at CRC Press, who provided me with his expertise and encouragement throughout the development of the book and always was willing to listen to my suggestions and ideas, adopting them when possible or carefully explaining why they were not possible. I am grateful to Jill Jurgensen, Project Coordinator, formerly at CRC Press, who worked with me on a day-to-day basis and was a joy to deal with. Her expertise on preparation of the chapters, tables, figures, and copyrights was outstanding and made my work much easier. Jill's responsibilities for the book were assumed by Jennifer Blaise, Editorial Assistant, CRC Press, who continued the same high quality of its preparation for publication. Jill and Jennifer's outstanding professionalism was continued by Marsha Hecht, Project Editor, CRC Press; and Adel Rosario, Project Manager, Manila Typesetting Company, both of whom were responsible for preparation of the galley proofs and final copyediting. I feel fortunate to have had the opportunity to work with such a dedicated group of individuals. I also owe a special thanks to Dmitry Musolin, co-chair of Chapters 11 and 12 and a contributing author to Chapter 7, who volunteered to help proofread the entire book manuscript and did an outstanding job.

I thank Tom J. Henry (Systematic Entomology Laboratory, U.S. Department of Agriculture-Agricultural Research Service [USDA-ARS], c/o National Museum of Natural History, Washington, DC) for his advice on various taxonomic problems. I also thank Michael T. Madigan (Department of Microbiology, Southern Illinois University, Carbondale) who provided invaluable expertise in the preparation of the microorganism index and assistance with the proper citing of these organisms in the text.

Doreen S. Hees (Office Administrator, Department of Zoology, SIUC) spent considerable time photocopying literally thousands of manuscript pages of this book for my copyediting (because I do not like to edit on the screen) and completed each job quickly. Her help was invaluable.

Lastly, I am pleased to acknowledge my wife, Jean, who tolerated a moody husband who used her as a sounding board for 4 years as the book was evolving. She provided the calming atmosphere that I needed, and I want her to know how much I appreciate her understanding and patience.

Editor



J. E. McPherson is Professor Emeritus of Zoology at Southern Illinois University, Carbondale (SIU). He obtained his Ph.D. in entomology from Michigan State University in 1968 and joined SIU in 1969 as Assistant Professor. He was promoted to Associate Professor in 1974 and to Professor in 1979. He retired in July 2012 but has continued to conduct research, maintaining the same office and laboratory space he had during his employment, and still is managing the entomology collection.

Dr. McPherson has written broadly on the ecology and systematics of the Heteroptera, particularly the Pentatomoidea, Reduvioidea, and various aquatic and semiaquatic taxa. He has authored or co-authored 200 refereed journal articles and three books, presented papers at both national and regional meetings, and given invited lectures at various universities. He has received several research grants, primarily from the USDA Forest Service.

Dr. McPherson is a member of the Entomological Society of America (ESA) and has served on numerous ESA national and branch committees. He was the recipient of an ESA National Service Award in 1991 for his work on the Editorial Board of the *American Entomologist*, the society's flagship publication, and served as editor of that publication from 1993 through 2001. He was the 1993 recipient of the Distinguished Achievement Award in Teaching, the 1997 recipient of the C. V. Riley Achievement Award, and the 2006 Award of Merit, all from the ESA North Central Branch. He also was the 1996 recipient of the Outstanding Teacher in the College of Science, SIU. He served 6 years on the ESA Governing Board, 3 (1994–1996) as Section A (now Systematics, Evolution, and Biodiversity) representative and 3 as an officer (Vice-President, 2001; President, 2002; Past-President, 2003). He was elected an Honorary Member in 2004 and a Fellow in 2007 of the ESA. Recently, he received the 2017 Michigan State University Entomology Distinguished Alumnus Award.

Dr. McPherson is a member of several additional societies including the Entomological Society of Washington, Florida Entomological Society, Michigan Entomological Society, and the New York Entomological Society. A Festschrift issue of the *Great Lakes Entomologist* was dedicated to him in 2012 by the Governing Board of the Michigan Entomological Society and was comprised of a series of papers, primarily on the Pentatomidae, contributed by colleagues including some former graduate students.

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Section I

Introduction

1

Overview of the Superfamily Pentatomoidea[1,2]

J. E. McPherson, C. Scott Bundy, and Alfred G. Wheeler, Jr.

CONTENTS

1.1 General Information

The superfamily Pentatomoidea (stink bugs and their relatives) comprises 18 families worldwide (including two fossil families) with over 8,000 species, the largest of which is the Pentatomidae (about 5,000 species) (**Table 2.2**). Six families are represented in America north of Mexico: Acanthosomatidae (acanthosomatids or parent bugs), Cydnidae (burrower bugs), Pentatomidae (stink bugs), Scutelleridae (shieldbacked

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[1] This chapter was modified and updated (in part) from Stink bugs of economic importance in America north of Mexico by J. E. McPherson and R. M. McPherson. Copyright 2000 CRC Press.

[2] Statements describing content of **Chapters 2 and 9–16** were contributed by one or more authors of those chapters.

or jewel bugs), Thyreocoridae (black bugs or ebony bugs), and, recently, Plataspidae (plataspids). Most species in these families are phytophagous, the major exception being the asopine pentatomids, which are predaceous. Within each of these families are species that cause economic injury to crops in the New World, Old World, and worldwide (Schuh and Slater 1995, Schaefer and Panizzi 2000, Eger et al. 2010, Ruberson et al. 2013). The Pentatomidae, largest of the six pentatomoid families, contains the highest number of economically important species (Schuh and Slater 1995, Schaefer and Panizzi 2000).

1.2 Classification Overview

The Pentatomoidea are members of the order Hemiptera and suborder Heteroptera (true bugs). The Heteroptera are recognized by a segmented beak that arises from the front of the head; and wings that, when present and well developed, have the first pair leathery basally and membranous distally (**Figure 1.1A**), the second pair membranous, with both pairs lying flat on the abdomen. The other suborders (i.e., Auchenorrhyncha, Sternorrhyncha, Coleorrhyncha) have the segmented beak appearing to arise ventrally from the rear of the head or between the front coxae; and wings, that when present and well developed, usually are held rooflike over the abdomen with both pairs of uniform texture throughout.

As with most other insect groups, the higher classification of the Pentatomoidea has changed considerably over time. Various families and subfamilies have been raised, lowered, then raised again between those two categories on a number of occasions. With few exceptions, the family and subfamily classification now seems relatively stable (see Grazia et al. 2008). However, the tribal classification remains in a state of chaos and requires a thorough phylogenetic analysis. The higher classification of the Pentatomoidea is discussed in **Chapter 2**. A list of the families, subfamilies, and tribes currently in use is presented along with notes concerning how these taxa are defined. The generic groups of Gross (1975, 1976) and Linnavuori (1982) also are discussed. Keys are provided to the families of the Pentatomoidea and subfamilies and tribes of the Pentatomidae. Some preliminary speculation is given on the validity of these taxa and their phylogenetic relationships.

1.3 Biology

As noted above, most pentatomoids are phytophagous. Phytophagous pentatomoids feed on a wide variety of fruit, vegetable, nut, and grain crops as well as wild hosts. Generally, the bugs feed on roots, stems, and leaves but most often are associated with developing seeds, fruits, or growing shoots. Adults and nymphs obtain nutrients by piercing the plant tissues with their mandibular and maxillary stylets.

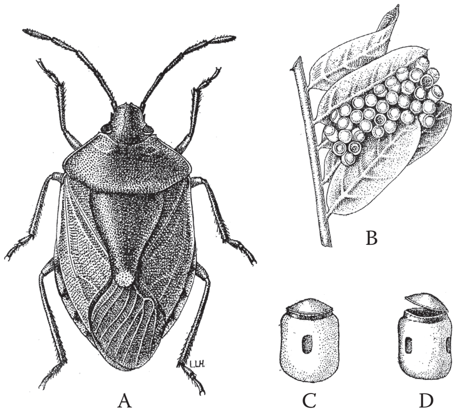

FIGURE 1.1 Adult and eggs of a typical stink bug, *Chlorochroa ligata*. A, Adult; B, Egg mass; C, Individual egg; D, Empty egg showing displaced pseudoperculum. (Modified from Morrill 1910).

Although all stages feed on plant material (often excluding the first instars), adults and/or fifth instars cause the most injury, at least to soybeans. Often, the bug leaves a salivary sheath at the feeding site (see discussion in McPherson and McPherson 2000, p. 3).

Many phytophagous insects, including aphids, sharpshooters, and weevils, possess symbiotic microorganisms; these symbionts play major roles in the lives of their hosts including provision of essential nutrients, digestion of food materials, and protection of their hosts from parasites, pathogens, and/or chemical pesticides. Among phytophagous insects, the Pentatomoidea exhibit extraordinary diversity in their symbiotic system, including morphology of the symbiotic organ, mechanism of symbiont transmission, and host-symbiont interdependency. The current biological knowledge of the diverse stink bug-microbe associations is reviewed in **Chapter 14**, highlighting the role of symbiotic microorganisms in the evolution of pentatomoid species. Injury can be associated with microbial symbionts, which can affect the taste of the crop (e.g., coffee, tea; see **Chapter 10**).

Compounding the detrimental effects of feeding is the ability to transmit plant pathogens. Pentatomids are known or suspected to transmit a variety of disease-causing plant pathogens including the causal pathogens for seed and boll rot, yeast spot, leaf spot and vein necrosis, stem canker, stigmatomycosis, panicle and shoot blight, witches' broom, hartrot, and marchitez. Affected crops range from pistachio and oil palms to cotton, soybean, and cowpea. Organized by vector-borne diseases, the relationships between various pentatomid species and fungi, bacteria, phytoplasmas, viruses, and trypanosomatids are explored and reviewed in **Chapter 13**, including an examination of feeding, transmission, and vector-pathogen interactions.

1.4 General Life History

Adults (sometime nymphs, rarely eggs) overwinter beneath leaf litter and other ground debris, usually remaining inactive. Some species [e.g., *Murgantia histrionica* (Hahn), *Nezara viridula* (L.)] can become active during milder temperatures with feeding, copulation, and oviposition possible. In fact, *N. viridula* will even feed when in reproductive diapause and, apparently, feeding during this time seems to enhance overwintering survival (see McPherson and McPherson 2000). In some instances, when winters are mild, species remain active throughout the winter. Examples include *Bagrada hilaris* (Burmeister) (Taylor al. 2015) (**Chapter 3**) and *Mecidea minor* Ruckes (Bundy and McPherson 2011), which are found in southern North America.

Diapause and related phenomena in the Pentatomidae and other pentatomoid families are reviewed in **Chapter 11**. Using pentatomoids as examples, the consecutive stages of the complex dynamic process of diapause (such as diapause preparation, induction, initiation, maintenance, termination, post-diapause quiescence, and resumption of direct development) are described and discussed.

Adults emerge in the spring as temperatures rise and begin feeding and reproducing on grasses, herbaceous plants, shrubs, and trees, depending on the species. As noted above, they are attracted most often to the developing seeds, fruits, or growing shoots. In fact, they will move from host to host as earlier hosts pass peak suitability and that of later hosts approaches (McPherson and McPherson 2000). Reproduction of the bugs begins shortly thereafter. For those few species that overwinter as eggs or nymphs, the patterns of their life cycles in spring are somewhat different.

Precopulatory and copulatory behaviors have been reported for several species (e.g., McPherson 1982), and certain patterns are apparent. Mating usually begins with the male antennating various parts of the female's body but eventually concentrating on or near the tip of her abdomen. If she is receptive, she will raise the tip of her abdomen for aedeagal insertion. If she is not receptive, the male may replace or combine antennating with head butting and may attempt to lift her abdomen with his head. If he is successful in stimulating the female to lift the tip of her abdomen, he will turn 180°, elevate his abdomen, and attempt to insert his aedeagus. If he is successful in doing so, copulation may last for several hours in this end-to-end position. Both adults may feed during this time, the female sometimes dragging the male along. When the female is not receptive, she may not elevate her abdomen, or may kick at the male with her hind legs, or simply walk away (McPherson 1982, McPherson and McPherson 2000).

Eggs of the Pentatomoidea, though superficially similar as a group, are variable in their morphology depending upon the family, features of which are helpful in their identification (see Southwood 1956, Hinton 1981, Javahery 1994). A ring of micropylar processes of various shapes and sizes is present at the cephalic end of the pentatomoid egg. Members of the Pentatomidae, Plataspidae, Scutelleridae, and Tessaratomidae have a thick chorion (thinner in the Plataspidae) with a pseudoperculum, a caplike structure through which the hatching nymph emerges (Hinton 1981, McPherson 1982) (**Figure 1.1C, D**). However, members of the Acanthosomatidae, Cydnidae, and Thyreocoridae have a thin chorion, which splits irregularly when the nymph hatches (McPherson 1982). An egg burster, which aids in emergence from the egg, is present in embryos of at least some species in all these families (Hinton 1981, McPherson 1982).

In most Pentatomoidea, eggs are laid on the host plants in round or subhexagonal clusters on the leaves or in longitudinal rows generally on the leaves and stems; the eggs adhere to the plant and to each other by a sticky secretion (**Figure 1.1B**). Members of the Plataspidae deposit their eggs in two rows along with fecal pellets containing bacterial symbionts that enhance survival of the nymphs (Hosokawa et al. 2007, Ruberson et al. 2013; see **Chapter 5**). In rare instances, the eggs are laid singly in the soil although the sticky secretion is still evident (e.g., *Bagrada hilaris*, Taylor et al. 2014b; see **Chapter 3**). In the Thyreocoridae, eggs are laid singly on the host plant; and in the Cydnidae, eggs are laid in loose clusters in the soil (McPherson 1982). In the closely-related Parastrachiidae, *Parastrachia japonensis* Scott lays its eggs in clusters of up to 100 in shallow nests in the leaf litter (Filippi et al. 2001). Recently, Cervantes et al. (2013) reported that the cydnid *Melanaethus crenatus* (Signoret), lays its eggs singly in the soil, usually close together.

The eggs usually are abandoned immediately after oviposition but members of most pentatomoid families contain species in which females exhibit parental care (e.g., Acanthosomatidae, Pentatomidae, Scutelleridae, Cydnidae, and Parastrachiidae), guarding the eggs and young nymphs (e.g., Eberhard 1975, McPherson 1982, Sites and McPherson 1982, Tallamy and Schaefer 1997, Peredo 2002, Costa 2006).

Pentatomoids have five nymphal instars (**Figure 1.2**). The first instars generally are gregarious, inactive, and remain atop or near the egg shells during the stadium. If they are disturbed, the cluster begins to break up and the individuals seem unable to reaggregate. Although first instars of pentatomids generally are thought not to feed (McPherson 1982), they may acquire symbionts by sucking the secretions covering the shells of the unhatched eggs (McPherson 1982, McPherson and McPherson 2000). In some species

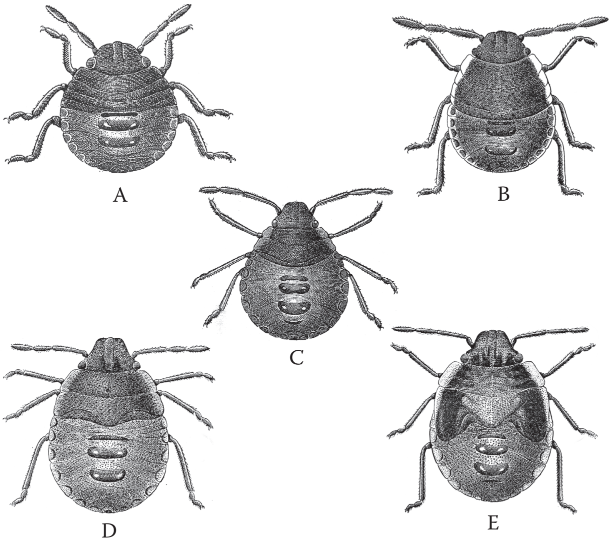

FIGURE 1.2 Nymphal instars of a typical stink bug, *Chlorochroa ligata*. A-E, First through fifth instars, respectively. (Modified from Morrill 1910).

[e.g., *Halyomorpha halys* (Stål)], the female defecates on the egg, and the first instars acquire symbionts by feeding on her feces (Taylor et al. 2014a). Also, the first instars of *Nezara viridula* apparently do feed (Esquivel and Medrano 2014), although the probing may be for water rather than nutrient uptake. Among the other families of pentatomoids, the first instars of at least some species of Thyreocoridae and Cydnidae are active and feed on the host plants (McPherson 1982, Sites and McPherson 1982, Bundy and McPherson 2009, Cervantes et al. 2013).

For those species that aggregate during the first stadium, the later instars begin to gradually and progressively disperse. This tendency to remain clustered in earlier instars may provide some protection from predation (Lockwood and Story 1986).

As the nymphs pass through the various stadia, subtle morphological changes are evident, particularly in the fourth and fifth instars. These two older instars can be distinguished from younger instars by the lengths of the wing pads, which are longest in the fifth instars. The eggs and nymphal instars have been described for many pentatomoid species, including the six invasive species discussed in this book (e.g., Moizuddin and Ahmad 1975, McPherson 1982, McPherson and McPherson 2000, Hoebeke and Carter 2003, Zhang et al. 2012, Leslie et al. 2014, Taylor et al. 2015).

Species of pentatomoids in northern and central North America generally are uni- or bivoltine with the number increasing to five in the extreme south (McPherson 1982, McPherson and McPherson 2000). The diversity of seasonal cycles known in the Pentatomoidea, mostly from the Temperate Zone, including those that are uni-, bi-, multi-, and semivoltine, is reviewed in **Chapter 12**. Further discussion focuses on the ecological importance of photoperiodic and thermal responses in natural or artificial expansions of pentatomids outside their original ranges.

1.5 Predators and Parasitoids

Pentatomoids are attacked by numerous invertebrate and vertebrate species, both parasitoids and predators. The parasitoids consist primarily of hymenopteran egg parasitoids (e.g., Scelionidae) and tachinid flies (Tachinidae). Numerous predators have been recorded, including predaceous stink bugs (e.g., *Podisus*). Among vertebrates, birds often have been reported as predators of pentatomoids (McPherson 1982). Native fungal pathogens, nematodes, and other parasitic organisms also have been recorded from invasive stink bugs (e.g., Sosa-Gómez and Moscardi 1998).

As with most other invasive insect pests, alien pentatomoids have arrived in new geographic areas without their most important coevolved natural enemies, and, thus, some have been targets for classical biological control. One of the best-known projects against an invasive pest insect was the introduction of the egg parasitoid *Trissolcus basalis* (Wollaston) (Platygastridae) for management of the southern green stink bug, *Nezara viridula*, across five continents (Walker A. Jones, personal communication).

Tachinid flies attacking pentatomids include certain parasitic species that have been subjects of classical projects. The recent invasions of the brown marmorated stink bug, *Halyomorpha halys*; the painted bug, *Bagrada hilaris* (Pentatomidae); and the bean plataspid or kudzu bug, *Megacopta cribraria* (F.) (Plataspidae) into North America have triggered projects that are in various stages of progress (Walker A. Jones, personal communication).

1.6 Chemical Defenses of Pentatomoids

Pentatomoids, like many other heteropterans, have a rich array of semiochemical compounds that function as pheromones, allomones, synomones, and kairomones. Although probably best known for their allomonal scent-gland secretions, pentatomoids have many semiochemical intra- and interspecific interactions that are just being uncovered. Among the increasingly evident complex chemistry and relationships are defenses against parasitoids and predators, eavesdropping by these natural enemies, cross-species attraction, and intraspecific variation in production of and response to semiochemicals based on life stage and physiology. The exciting discoveries in this area and the potential and actual uses of these chemicals in pest detection, monitoring, and management are addressed in **Chapter 15**.

1.7 Management Practices

Management tactics are considered in detail in **Chapter 16**. Beginning with a brief overview of the types of control, the history of these tactics is discussed. The earliest control practice apparently was the use of sulfur by the Sumerians in 2500 B.C. to control insects and mites. Following were reports of cultural, botanical, and biological control, the practices of which moved from the Old World to the New World and continued to become more sophisticated. The dramatic effect of the introduction of the synthetic organic insecticides for insect control in the 1940s, the resulting detrimental effects of their widespread use, the resurgence of research in biological control, and the development of integrated pest management are discussed in detail. Following is a detailed discussion of control practices in the modern era ending with a discussion of future management practices.

1.8 Pentatomoid Fauna: Potential Impact of Invasive Insects on Noninvasive Species

1.8.1 Terminology

Invasion biology (ecology, science), the study of organisms that become established in areas outside their native ranges, assumed prominence in the 1980s. Since the late 1990s, the number of books and journal articles on nonnative species has exploded. Those who consider themselves invasion biologists represent numerous disciplines and work with disparate taxa. The controversies that pervade the literature on nonnative species (e.g., Simberloff 2012, Richardson and Ricciardi 2013, Valéry et al. 2013) might have been anticipated in a field characterized by practitioners from dissimilar backgrounds and interests. Some of invasion biology's critics represent disciplines other than biology or ecology, such as history, philosophy, and sociology (Simberloff 2003). An unfounded criticism is that invasion biologists are xenophobes who regard all nonnative species as "bad" when, in fact, the benefits of such species often are mentioned (e.g., Simberloff 2003, Wheeler and Hoebeke 2009). Helping to fuel controversy is the emotionalism that infects the language of invasion biology, which shares certain military metaphors (e.g., invader, invasion) used by L. O. Howard in the late nineteenth and early twentieth century to promote the importance of economic entomology (Russell 1999). Especially contentious among invasion biologists has been use of the terms "invasion" and "invasive species" (e.g., Colautti and MacIsaac 2004, Colautti and Richardson 2009).

Attempts to standardize terminology involving plant and animal invasions, as noted by Davis (2009), Blackburn et al. (2011), and Heger et al. (2013), have met with minimal success. The term "invasive species" continues to be used inconsistently; it can refer to any nonnative organism (Wheeler and Hoebeke 2009, Simberloff 2011) and be used with or without consideration of impact. Simberloff (2013) prefers a biologically based definition of organisms that become invasive: "species that arrive with human assistance [intentionally, as well as inadvertently], establish populations, and spread." Similarly, Pyšek and Richardson (2006) would restrict invasive species to those that spread rapidly, regardless of any ecological harm or economic loss that might accrue. Definitions that incorporate harm or impact are subjective because they introduce human perception and values, which can vary regionally (Lodge et al. 2006). Moreover, the addition of impact in defining "invasive" tends to obscure an ecological and evolutionary appreciation of the invasion process (Colautti and Richardson 2009).

Yet, it is unrealistic for entomologists to avoid using the value-based term "pests" in referring to insects that adversely affect human well-being. In addition, reference to harm or impacts of invasive species seems unavoidable when considering the potential risks that nonnative species pose for natural ecosystems (Ward et al. 2008) or assessing the ecological and economic consequences of alien insects (e.g., Pimentel et al. 2005, Kenis et al. 2009, Kenis and Branco 2010, Aukema et al. 2011, Vinson 2013, Herms and McCullough 2014). Davis (2009), even though he preferred other terminology, acknowledged the absurdity of omitting the word "invasion" from his book on invasion biology. Regulatory agencies likewise are compelled to introduce human values in defining impacts (Jeschke et al. 2014). Similarly, we need to include harm in our definition of invasive species, which, as Davis (2009) pointed out, is consistent with usage adopted by the Global Invasive Species Program, International Convention on Biological Diversity, and the United States National Invasive Species Council. Thus, contributors throughout this book will use the following definition for their chapters: ***invasive pentatomoids are nonnative species whose populations become established and spread, sometimes exhibiting uncontrolled population growth and displacing native populations, and cause adverse socioeconomic, environmental, or human-health effects***.

Species not considered invasive can be termed adventive, immigrant, introduced, and native (Wheeler and Hoebeke 2009). Adventive is an inclusive term that refers to any species that is not native. Adventives can be immigrants, that is, species not deliberately or intentionally introduced; or they can be purposeful introductions, such as natural enemies used in biological control. All remaining species, then, represent the native fauna. Native species also can become invasive (Buczkowski 2010, Davis et al. 2011), but for the purposes of this book, all invasive species are adventive, but not all adventive species are invasive.

1.8.2 What Factors Allow Species to Become Invasive?

Researchers long have attempted to identify attributes that enable plants and animals to be successful invaders and, independently, to determine environmental conditions that favor invasion. The invasion process, however, is best understood by appreciating the interconnectedness of environmental conditions and organisms' traits as well as the significance of propagule pressure (Lockwood et al. 2005, Pyšek and Richardson 2006, Davis 2009, Su 2013, Jeschke 2014). Several characteristics, however, tend to facilitate invasiveness, although not all insect species possessing these traits become invasive (Su 2013). Traits that can favor invasiveness include: (1) ability to move readily in commerce; (2) tolerance of multiple habitat conditions, such as tolerance of temperature and humidity; (3) ability to reproduce rapidly with a concomitant increase in population size; (4) ability to compete successfully for resources; (5) lack of natural enemies; and (6) ability to fly.

1.8.3 Harmful Effects of a Successful Invasion by Insects

Wheeler and Hoebeke (2009) listed several harmful effects including (1) transmission of animal (and plant) diseases, (2) extreme crop damage, (3), severe damage to forests, homes, and gardens, (4) elimination of competing native species, and (5) effects on evolution. To these can be added effects on recreational areas and ecosystem processes and the insects becoming nuisance urban pests.

1.9 Invasive Pentatomoids

Invasive insect species worldwide consist primarily of Hymenoptera (Formicidae, Vespidae) but also many include other groups such as Coleoptera, Isoptera, Lepidoptera, and Hemiptera (e.g., Anonymous 2014). Within the Hemiptera, one such group is the Pentatomoidea. In Europe and Asia, only two pentatomoid species are listed as invasive, *Halyomorpha halys* and *Nezara viridula* (Rabitsch 2008). However, six invasive species are found in North America, including *H. halys* and *N. viridula*. The additional four species include *Bagrada hilaris*, *Murgantia histrionica*, *Piezodorus guildinii* (Westwood), and *Megacopta cribraria*.

Certain biological characteristics and environmental factors enhance the ability of pentatomoids to become invasive species, Panizzi (2015) discusses both topics under the following categories: (1) polyphagy (feeding on a wide range of host plants), (2) ability to survive unfavorable conditions, and (3) climate change. In addition, specifically concerning the Neotropics (but also the impact of pentatomoids on a worldwide basis), other factors include changes in cultivation practices, growth of agribusiness, and increased trade.

In the United States, injury caused by stink bugs in the native fauna has increased for one major reason, at least for cotton – "a reduction in the frequency of foliar, broad-spectrum insecticide applications" (Greene et al. 2006). This reduction in pesticide use may have played a role in the dramatic increase in populations of the three most recent invasive pentatomoids, *Bagrada hilaris*, *Halyomorpha halys*, and *Megacopta cribraria*.

1.9.1 History of Invasive Pentatomoids in America North of Mexico

1.9.1.1 Bagrada hilaris (Burmeister), Bagrada Bug or Painted Bug

This species (**Chapter 3**) was described by Burmeister as *Cimex hilaris* in 1835 (p. 368). Although the locality was not given, and the type was lost, Fabricius had described the same species in 1775. But the name he proposed, *Cimex pictus*, was invalid because it was a primary homonym of *Cimex pictus* Drury (1770). The locality of this specimen was given as India.

This stink bug, which somewhat resembles a small harlequin bug, has an Old World distribution of Asia (including India), Africa, southern Europe, and the Middle East (Taylor et al. 2015). First reported in the United States from southern California in June 2008, *Bagrada hilaris* has extended its range north and south in California and east to Nevada, Utah, Arizona, New Mexico, and western Texas (Reed et al. 2013).

Bagrada hilaris prefers cruciferous crops (Halbert and Eger 2010, Reed et al. 2013) and has reached economic importance in California and Arizona (Palumbo and Natwick 2010). It attacks broccoli, cabbage, cauliflower, kale, collards, and radish but also will injure sunflower, corn, and cotton, among others (Reed et al. 2013).

1.9.1.2 Halyomorpha halys (Stål), Brown Marmorated Stink Bug

This Asian species (**Chapter 4**) was described by Stål as *Pentatoma halys* in 1855 from China (p. 182) and now is considered a recent invasive in Europe (Rabitsch 2008, Milonas and Partsinevelos 2014) and North America (Hoebeke and Carter 2003, Fogain and Graff 2011). It first was reported in the United States by Hoebeke and Carter in 2003 from sightings in Allentown, PA, in fall 1996 (Adams Island), September 1998, and January 1999. It has spread rapidly in the intervening years and now occurs in more than 41 states and the District of Columbia (Leskey et al. 2012, Wallner et al. 2014) and in Ontario and Quebec, Canada (Fogain and Graff 2011). It is highly polyphagous, feeding on a wide variety of agricultural and nonagricultural plants including ornamentals, hardwood trees, field crops, tree and small fruits, vegetables, and wild plants (Nielsen and Hamilton 2009, Wallner et al. 2014). It also is considered a significant nuisance because it overwinters in houses, garages, offices, and other similar enclosures (Inkley 2012, Leskey et al. 2012).

1.9.1.3 Megacopta cribraria (F.), Kudzu Bug

This species (**Chapter 5**), although not a stink bug, is member of the pentatomoid family Plataspidae. Described by Fabricius as *Cimex cribraria* in 1798 from India (p. 531), it later was reported from various localities in Asia and the Indian subcontinent (Eger et al. 2010). It first was reported in the United States in 2009 from Georgia and, as of 2012, had spread to seven states in the Southeast (Ruberson et al. 2013) and, as of 2013, as far north as Maryland and the District of Columbia (Leslie 2014). The preferred host plants are kudzu and soybeans, both of which are legumes.

1.9.1.4 Murgantia histrionica (Hahn), Harlequin Bug

This species (**Chapter 6**) apparently was the first invasive stink bug for the United States and certainly the first for which substantial records are available. Described by Hahn as *Strachia histrionica* in 1834 from Mexico (p. 116), it first was reported in the United States by Walsh (1866) from specimens collected in 1864 from Washington Co., TX. Its spread was monitored closely after its detection because of its potential to injure crucifers. Today, it ranges in the continental United States primarily from New England south to Florida and west to Minnesota, South Dakota, Nebraska, and California but occurs primarily in the South (McPherson 1982). It is an established immigrant in Hawaii (Froeschner 1988).

1.9.1.5 Nezara viridula (L.), Southern Green Stink Bug

This species (**Chapter 7**) was described by Linnaeus as *Cimex viridulus* in 1758 from India (p. 444). It subsequently was reported from other parts of Asia and Europe and the New World including the West Indies, Jamaica, St. Domingo, Cuba, and Venezuela (DeWitt and Godfrey 1972). The earliest record for the United States was by Distant (1880) (p. 78), who reported it from the southern states, including Texas. Today, it occurs primarily from Virginia to Florida west to Texas and Oklahoma and also occurs in California (McPherson and McPherson 2000) and Washington (see **Chapter 7**). It feeds on a wide variety of plants including soybeans, tomatoes, vegetables, row crops, cruciferous vegetation, and leguminous weeds (McPherson and McPherson 2000).

1.9.1.6 Piezodorus guildinii (Westwood), Redbanded Stink Bug

This species (**Chapter 8**) was described by Westwood as *Rhaphigaster guildinii* in 1837 from St. Vincent Island (p. 31) and today ranges from the West Indies to South America and north to the southern United States (Panizzi et al. 2000). The earliest records for the United States of which we are aware are southern Florida (Uhler 1894) and New Mexico (Van Duzee 1904). This species previously was collected primarily in Florida but now has extended its range to include South Carolina, Tennessee, Georgia, Alabama, Mississippi, Arkansas, Missouri, Louisiana, Texas, and New Mexico (Van Duzee 1904, McPherson and McPherson 2000, Bundy 2012, Davis 2012, Temple et al. 2013, Vyavhare et al. 2014) (Bundy 2012 noted that the bug's presence in New Mexico needs to be verified). It seems to prefer soybeans but will attack many other plants such as alfalfa, clover, cotton, kidney bean, lentil, peanut, strawberry, and others (McPherson and McPherson 2000, Panizzi et al. 2000). It has reached economic importance in Louisiana and Texas (Temple et al. 2013, Vyavhare et al. 2014). The important question is why does it now appear to be expanding its range and increasing in numbers in the southern states.

1.10 Potentially Invasive Pentatomoids

1.10.1 *Oebalus* spp.

The genus *Oebalus* Stål (1862) (**Chapter 9**) contains three species that occur in the United States including *O. pugnax* (F.), *O. insularis* Stål (1872), and *O. ypsilongriseus* (De Geer) (1773). Although *O. pugnax* is widely distributed in the United States (Froeschner 1988), *O. insularis* and *O. ypsilongriseus* have been recorded only from Florida. All three species are noted pests of rice.

1.10.2 *Arvelius albopunctatus* (De Geer), Tomato Stink Bug

This species occurs from South America north to Arizona, Texas, and Florida in the United States. It is a pest of several economically important crops in Brazil and Mexico but has been reported to feed only on solanaceous weeds in the United States.

1.10.3 Other Species

Recently, Panizzi (2015) authored a paper on the invasive species of the pentatomids in the United States, which includes a section on species of potential invaders from the Neotropics. This list includes the following five species, all of which are of major economic importance in South America: *Dichelops* *furcatus* (F.), *Dichelops melacanthus* (Dallas), *Edessa meditabunda* (F.), *Euschistus heros* (F.), and *Tibraca limbativentris* Stål.

1.11 Noninvasive Group (A Comparison)

A group of pentatomids, commonly known as antestia bugs, has been the object of many studies as important pests of Arabica coffee in Africa. They currently attract interest because they are supposed to be the cause of potato taste defect (PTD), which significantly downgrades the value of the coffee crop, especially in the Great Lakes region of Africa. The specific linkage between PTD and stink bugs is not known, although symbiotic microorganisms might be involved. The current knowledge of the distribution, life history, and natural enemies of antestia bugs, as well as their injury, role in coffee potato taste defect, economic impact, and control is reviewed in **Chapter 10**. Also discussed are their current ecological range and distribution on coffee. These bugs are particularly interesting because they appear capable of becoming invasive species wherever coffee is grown but have remained limited to Africa and Asia. Yet other major coffee pests, such as the coffee berry borer, which also originated in Africa, are found wherever coffee is grown. Possible reasons are offered to explain the geographical differences between antestia bugs and other coffee pests.

1.12 Key to Families of Pentatomoidea in America North of Mexico[3]

1. Tarsi 2-segmented (**Figure 1.3**).. 2
1’. Tarsi 3-segmented (**Figure 1.4**).. 3
2. Scutellum U-shaped, greatly enlarged, covering wings and most of abdomen; abdomen widest subapically (**Figure 1.5**)..Plataspidae
2’. Scutellum subtriangular, small, not covering wings and most of abdomen; abdomen not widest subapically (**Figure 1.6**).. Acanthosomatidae
3. Pronotum expanded posteriorly, covering base of scutellum (**Figure 1.7**).......Tessaratomidae[4]
3’. Pronotum not expanded posteriorly, not covering base of scutellum.. 4
4. Scutellum U-shaped, greatly enlarged, covering wings and most of abdomen (**Figures 1.8 and 1.9**).. 5
4’. Scutellum usually subtriangular, not greatly enlarged, not covering most of abdomen (**Figures 1.10 and 1.11**); if scutellum large and U-shaped, then colors bright and contrasting or prominent tooth present either side of each anterolateral angle of pronotum.. 6
5. Tibiae with strong spines (**Figure 1.12**); color basically shiny black (**Figure 1.9**)..Thyreocoridae
5’. Tibiae without strong spines (**Figure 1.13**); color variable but never shiny black (**Figure 1.8**)..Scutelleridae
6. Tibiae with strong spines (**Figure 1.10**); front legs fossorial (**Figure 1.14**) or cultrate (**Figure 1.15**)..Cydnidae
6’. Tibiae without strong spines (**Figure 1.16**); front legs not fossorial or cultrate ... Pentatomidae

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[3] Modified from Eger et al. (2010).

[4] Represented by *Piezosternum subulatum* (Thunberg), which occurs from Mexico to Brazil and the West Indies but has not yet been found in the United States (Froeschner 1988).

FIGURE 1.3 Two-segmented tarsus of *Megacopta cribraria* (Plataspidae). (Courtesy of J. E. Eger)

FIGURE 1.4 Three-segmented tarsus of *Apoecilus cynicus* (Pentatomidae). (Courtesy of J. E. Eger)

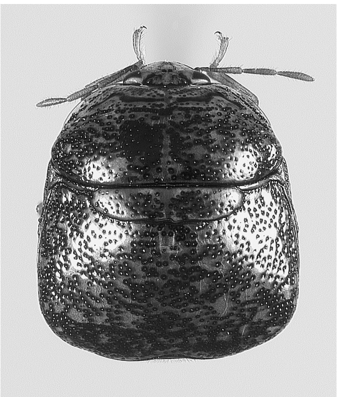

FIGURE 1.5 Habitus of *Megacopta cribraria* (Plataspidae). (Courtesy of J. E. Eger)

FIGURE 1.6 Habitus of *Elasmucha* sp. (Acanthosomatidae). (Courtesy of J. E. Eger)

FIGURE 1.7 Habitus of *Catacanthus* sp. (Tessaratomidae). (Courtesy of C. Scott Bundy)

FIGURE 1.8 Habitus of *Augocoris* sp. (Scutelleridae). (Courtesy of J. E. Eger)

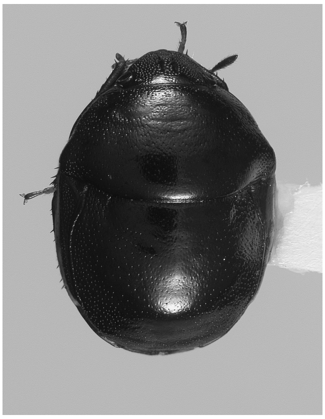

FIGURE 1.9 Habitus of *Corimelaena* sp. (Thyreocoridae). (Courtesy of J. E. Eger)

FIGURE 1.10 Habitus of *Pangaeus* sp. (Cydnidae). (Courtesy of J. E. Eger)

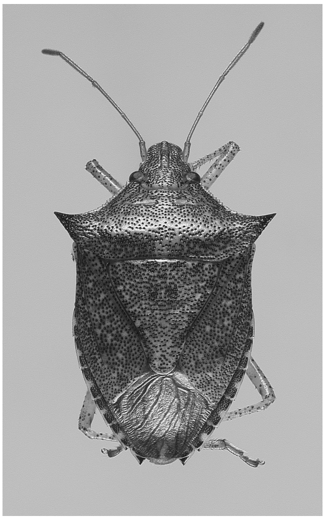

FIGURE 1.11 Habitus of *Euschistus quadrator* (Pentatomidae). (Courtesy of J. E. Eger)

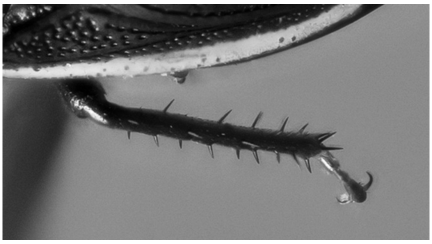

FIGURE 1.12 Hind tibia of *Corimelaena lateralis* (Thyreocoridae). (Courtesy of C. Scott Bundy)

FIGURE 1.13 Hind tibia of *Tetyra robusta* (Scutelleridae). (Courtesy of C. Scott Bundy)

FIGURE 1.14 Fossorial foretibia of *Cyrtomenus* sp. (Cydnidae). (Courtesy of J. E. Eger)

FIGURE 1.15 Cultrate foretibia of *Atarsocoris* sp. (Cydnidae). (Courtesy of J. E. Eger)

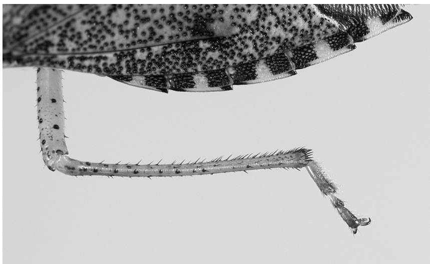

FIGURE 1.16 Hind tibia of *Euschistus servus* (Pentatomidae). (Courtesy of J. E. Eger)

1.13 Chapters 2–16

In the following chapters, we summarize and update the knowledge of the extent of problems associated with invasive pentatomoids worldwide including economic importance (feeding injury, nuisance problems, transmission of pathogens, role of symbionts); research on their biology (including diapause and voltinism), behavior, chemical ecology, monitoring, and control. We discuss why these species have become invasive and what the future holds for their continued geographic expansion and the resulting direct and indirect effects of these bugs on the human population.

1.14 Acknowledgments

We thank J. E. Eger (Dow Agrosciences, Tampa, FL) for providing many of the images used in this chapter.

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Section II

Systematics

2

Higher Systematics of the Pentatomoidea

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CONTENTS

2.1 Introduction

The Pentatomoidea – What a wonderful and diverse assemblage of insects! Members of this superfamily occur in nearly all parts of the World and occupy virtually all terrestrial habitats. They range greatly in size with the smallest species not much larger than a pin head (e.g., *Megaris* Stål in Megarididae and *Sepontia* Stål in the Pentatomidae) to some of the largest and most robust species in the Heteroptera (e.g., many Tessaratomidae). Most species are phytophagous, and several are known to cause economic damage to various crops; however, some species are predatory (Pentatomidae: Asopinae), preying mainly on other insects, and a few groups are at least suspected to be fungivores (Canopidae, Megarididae, some Plataspidae). Nearly all species have scent glands, both in the immatures and the adults, which emit a foul odor, presumably to ward off predators. Even so, many species also rely on crypsis to avoid predators as many are various shades of greens, tans, and browns, allowing them to blend in with the vegetation, soil, or whatever substrate they live on. There are, however, some species that seem to advertise their repugnant qualities; that is, they are aposematically colored with reds, yellows, oranges, and blues, sometimes with a brilliant metallic sheen. Certain groups have evolved elaborate stridulatory mechanisms involving the legs, abdomen, and/or wings. Additionally, some groups (e.g., some Acanthosomatidae; some Cydnidae; some Dinidoridae; Parastrachiidae; Phloeidae; some Discocephalinae, Edessinae, and Pentatominae in the Pentatomidae; some Plataspidae; some Scutelleridae; and some Tessaratomidae) exhibit parental care with the females, and, perhaps, sometimes the males, standing guard over the egg masses and early instars.

In this chapter, we provide a taxonomic history for each family and subfamily (if applicable) and, in addition, for the tribes and generic groups within the Pentatomidae, that, perhaps, will give some perception of the taxonomic position of each group. We also discuss the systematic classification within each of these groups and provide general diagnoses and descriptions for all families within the Pentatomoidea and for the subfamilies, tribes, and generic groups within the Pentatomidae. We also have summarized some of the biological information for each group. Keys to aid in the identification of the various taxa are included, but it should be understood that to build keys that work for all taxa all the time would become long and tedious. We have chosen to present keys that will work for most of the commonly encountered taxa but, perhaps, not for some of the exceptional taxa. Most of these exceptional taxa are discussed as they arise in the body of the chapter. The present treatise is not meant as the last word in the phylogenetic study of this superfamily. Rather, it is a work in progress and reflects the current state of knowledge on the higher classification of the Pentatomoidea. We discuss potentially important characters and point out problems in the existing classification. It is our intention to provide information on the currently recognized or disputed taxa, their defining characters, and their relationships. We recognize that with further study the classification presented herein will change greatly.

There are several characteristics that we believe are of paramount importance for the classification of the Pentatomoidea. For example, in females belonging to several pentatomoid families, the spermathecal duct has a large membranous dilation around its middle. In members of the Pentatomidae, there is an elongate, sclerotized, double-walled tube (sclerotized rod) projecting from the distal orifice of the dilation into its lumen. All known members of the family Pentatomidae have this structure, save one, the genus *Trichopepla* Stål (**Figure 2.20G**) (currently a member of the Carpocorini), which we consider to be a secondary loss. Although a similar structure is also found in some members of other pentatomoid families (e.g., Cydnidae, Thyreocoridae) (Štys and Davidová-Vilímová 1979, Pluot-Sigwalt and Lis 2008), sometimes with an analogous projection of the proximal orifice (e.g., some Scutelleridae) (Tsai et al. 2011), its presence in the Pentatomidae can be regarded as a synapomorphy of the family (Gapud 1991, Grazia et al. 2008). Accordingly, we tentatively include the Aphylinae, Cyrtocorinae, and Serbaninae as subfamilies within the Pentatomidae, and exclude the Lestoniidae and the Phloeidae, based on the presence or absence of the dilation, respectively, but stress that the evolution of this character is not fully understood. Additionally, there are, undoubtedly, several important characters in the male genitalia that have phylogenetic significance. For example, Gross (1976) stated that the presence of the so-called "median penial plates" (mesal, sclerotized portions of the second pair of conjunctival processes fused along their midline and closely associated with the distal portion of the vesica) is strictly a pentatomid character. Further study of the phallus and aedeagus of the males will be necessary to determine which characters are informative and which are homoplastic.

Another character that we feel may be of primary importance is the structure of the thoracic sterna (Gross 1975b), at least for the classification within the Pentatomidae. Most pentatomid genera have the mesosternum medially carinate, or at least with a weak, raised line. There are, however, several small groups of genera that have the mesosternum medially sulcate without any sign of a medial carina. The significance of this character is yet to be determined, but it could lend support to an eventual splitting of the Pentatominae as presently conceived. The absence of the mesosternal carina is especially common in certain Australian and African groups of genera. We also believe the structure of the base of the abdomen (rounded or produced), and the structure of the ostiole and its associated structures, will be important. They are difficult to interpret, however, as certain characteristics have arisen multiple times, and some have been lost secondarily. The form of the ostiolar structure has been especially well-studied (Kment and Vilímová 2010b).

2.2 Pentatomoidea

As with many other superfamilies, heteropteran or not, the Pentatomoidea has a long and complicated taxonomic history. Through time, each of the included families, subfamilies, and tribes has been transferred across the family level ranks as often as there have been heteropterists working on the classification of these taxa (see **Table 2.1**). Although the recognition of the most important families (and subfamilies) has more or less stabilized, their evolutionary relationships are still poorly understood; therefore, the current classification is certainly tentative even at the family and subfamily levels. The tribal classification of most families, and particularly within the Pentatomidae remains chaotic at best.

The superfamily Pentatomoidea is a member of the insect order Hemiptera, suborder Heteroptera, and infraorder Pentatomomorpha. Typically, this infraorder has been divided into six superfamilies: Aradoidea, Idiostoloidea, Pentatomoidea, Lygaeoidea, Pyrrhocoroidea, and Coreoidea. The Aradoidea lack the trichobothria that are present in the other superfamilies; as such, those five superfamilies are grouped together as the Trichophora, a group first proposed by Tullgren (1918). Most workers since that time have supported the monophyly of the Trichophora (Schuh and Slater 1995). Although it was not a focus of their study, the phylogenetic analysis of Grazia et al. (2008) also generally supported the Trichophora as a monophyletic group. Their study also supported the monophyly of the Pentatomoidea based primarily on four characters: (1) the enlarged scutellum, the apex of which usually reaches or surpasses an imaginary line uniting the posterolateral angles of abdominal connexiva III, (2) the claval commissure that is usually obsolete (i.e, the clavi usually do not surpass the apex of the scutellum), (3) the trichobothria (usually paired but sometimes singular) located laterally near the spiracular line on abdominal sternites II through VII, and (4) tergite VIII covering tergite IX in females. Additionally, the five-segmented antennae may be a significant synapomorphy. Several other recent studies based on molecular markers, including Grazia et al. (2008), also support the monophyly of the Pentatomoidea and most of the included families. Relationships among families, subfamilies, and tribes within the Pentatomoidea are mostly unsettled, and the available information will be discussed under each corresponding section. The pentatomoid family and subfamily classification used in this chapter is outlined in **Table 2.2**. We also are developing a catalog of the Pentatomoidea of the World; this work has led directly to a series of nomenclatural changes throughout the superfamily (Rider and Rolston 1995; Rider 1998a,b, 2007; Rider and Fischer 1998; Rider and Kment 2015). At present, there are 1410 genera and 8042 species described in the Pentatomoidea (**Table 2.2**). A tentative list of pentatomoid genera, and their placement to family, subfamily, and tribe can be found on the internet (Rider 2015b).

2.2.1 Key to the Families of Pentatomoidea

1 Large to medium-sized species with body strongly dorsoventrally flattened; lateral margins of juga, pronotum, and base of coria greatly enlarged, foliaceous (**Figures 2.1A, 2.16F**); each compound eye divided into a dorsal and a ventral section by foliaceous lateral margin of head, cryptic, bark-dwelling species (**Figures 2.25G, 2.27K**)............ 2

1’ Size and shape variable, usually not conspicuously flattened; lateral margins of juga, pronotum, and base of coria not foliaceous; if body somewhat flattened, then compound eyes not divided into two sections 3

2(1) Antennae 3-segmented (**Figure 2.1A**); spermatheca lacking a sclerotized rod; South America (**Figures 2.16F, 2.25G**) .... Phloeidae

2’ Antennae 4-segmented; spermatheca with a sclerotized rod; Southeast Asia (Borneo) (**Figure 2.27K**)... Pentatomidae (part: Serbaninae)

3(1) Body tortoise-shaped, greatly convex dorsally, flat ventrally; margins of head, lateral margins of pronotum, part of costal margins of coria, and lateral margins of abdomen laminately produced ventrally (**Figure 2.25D**); abdominal venter of female with one or two pairs of disc-shaped organs; Australia .... Lestoniidae

TABLE 2.1

Historical Classifications

Amyot & Serville 1843	Stål, 1870s	Atkinson, Late 1880s	Distant, 1900s
Family Longiscutes	Subfamily Cimicina	Subfamily Plataspina	Subfamily Plataspidinae
Tribe Orbiscutes	Division Elvisuraria	Subfamily Cydnina	Subfamily Scutellerinae
Race Anguleux	Division Sphaerocoraria	Section Cydnides	Division Elvisuraria
Group Scutellérides	Division Scutelleraria	Section Séhirides	Division Sphaerocoraria
Group Pachycorides	Division Tetyraria	Subfamily Scutellerina	Division Scutelleraria
Group Tétyrides	Division Odontotarsaria	Division Elvisuraria	Division Tetyraria
Group Eurygastrides	Division Eurygastraria	Division Sphaerocoraria	Division Odontotarsaria
Group Podopides	Division Odontoscelaria	Division Scutellaria	Division Eurygastraria
Group Oxynotides	Subfamily Asopina	Division Tetyraria	Division Odontoscelaria
Race Globuleux	Subfamily Tessaratomina	Division Odontotarsaria	Subfamily Graphosomatinae
Group Thyréocorides	Division Oncomerina	Division Eurygastraria	Subfamily Cydninae
Group Odontoscelides	Division Tessaratomina	Division Odontoscelaria	Subfamily Pentatominae
Group Canopides	Division Eusthenina	Subfamily Pentatomina	Division Halyaria
Tribe Coniscutes	Division Prionogastrina	Division Podoparia	Division Sciocoraria
Libertirostres	Division Cyclogastrina	Division Halyaria	Division Dorpiaria
Longirostres	Subfamily Dinidorina	Division Sciocoraria	Division Dymantaria
Race Spissirostres	Subfamily Oxynotina	Division Myrocharia	Division Mecidaria
Group Stirétrides	Subfamily Phloeina	Division Odiaria	Division Amyntaria
Group Asopides	Subfamily Discocephalina	Division Tropicorypharia	Division Carpocoraria
Ténuirostres	Subfamily Pentatomina	Division Cappaearia	Division Aeschrocoraria
Race Spinipèdes	Division Tarisaria	Division Carpocoraria	Division Eusarcocoriaria
Group Cydnides	Division Trigonosomaria	Division Diploxyaria	Division Hoplistoderaria
Group Séhirides	Division Graphosomaria	Division Eysarcoriaria	Division Antestiaria
Group Pododides	Division Podoparia	Division Agonosceliaria	Division Eurydemaria
Race Nudipèdes	Division Halyaria	Division Strachiaria	Division Compastaria
Inermiventres	Division Sciocoraria	Division Hoplistoderaria	Division Tropicaria
Sulciventres	Division Aeliaria	Division Catacantharia	Division Rhynchocoraria
Group Halydes	Division Eysarcoraria	Division Nezaria	Division Nezaria
Group Phléides	Division Pentatomaria	Division Hyllaria	Division Menidaria
Pléniventres	Division Strachiaria	Division Plautiaria	Division Diplostiraria
Group Sciocorides	Subfamily Acanthosomina	Division Axiagastaria	Division Euryaspisaria
Group Pentatomides	Subfamily Plataspina	Division Euryasparia	Subfamily Asopinae
Armiventres	Subfamily Cydnina	Division Menidaria	Subfamily Tessaratominae
Group Rhaphigastrides	Subfamily Urolabidina	Division Piezodoraria	Division Tessaratomaria
Race Brévirostres	Subfamily Phyllocephalina	Division Bathycoeliaria	Division Eusthenaria
Group Edessides		Division Rhynchocoraria	Subfamily Dinidorinae
Group Phyllocéphalides		Division Tropicoraria	Subfamily Phyllocephalinae
Canalirostres		Subfamily Asopina	Subfamily Urostylinae
Mégyménides		Subfamily Acanthosomina	Subfamily Acanthosomatinae
		Subfamily Urostylina	
		Subfamily Tessaratomina	
		Division Tessaratomaria	
		Division Eusthenaria	
		Division Oncomeraria	
		Subfamily Dinidorina	
		Subfamily Phyllocephalina	

3’ Body not as in 3(1), if somewhat tortoise-shaped with convex dorsum and flat venter, then margins of head, pronotum, coria, and abdomen not laminately produced ventrally, abdominal venter of both sexes lacking disc-shaped organs.......... 4

4(3) Scutellum subtriangular, leaving apices of clavi exposed at rest; apices of clavi either meeting in a single point or forming a distinct claval commissure (**Figures 2.3C; 2.15F; 2.16J; 2.25I, L; 2.31B**).......... 5

4’ Scutellum or at least its extreme tip projecting posteriad beyond frena, concealing apices of clavi at rest; apices of clavi separated.......... 9

5(4) Length less than 3.5 mm; body elongate; scutellum short, not surpassing posterior margin of metanotum (**Figure 2.16J**); scent gland ostiole situated close to lateral margin of metapleuron, with long vestibular scar; ocelli, if present, placed relatively far from each other; resembling lygaeoids in appearance; southern and northern Africa, southwest Asia (**Figure 2.16J**).......... Thaumastellidae

5’ Size usually greater, body broader; scutellum usually longer, surpassing posterior margin of metanotum; scent gland ostiole, if present, situated close to acetabula; ocelli, if present, placed close to each other.......... 6

6(5) Ant-mimic (**Figures 2.14E, 2.31B**); black, marked with white, with large spines; clavi extending beyond apex of scutellum and meeting at a single point; Thailand.......... Pentatomidae (part: Pentamyrmecini)

6’ Not an ant mimic; color variable, but usually not black with white markings, may have bristles or small spines or pegs, but not large spines; clavi extend beyond apex of scutellum and form a claval commissure.......... 7

7(6) Lateral and anterior margins of head with strong, peg-like setae (**Figure 2.1B**); tibiae provided with spines along length (**Figure 2.1C**); ocelli placed closer to compound eyes than to each other; reddish-brown to blackish-brown species; Western Hemisphere except for one species introduced into Iran (**Figure 2.15F**).......... Cydnidae (part: Amnestinae)

7’ Head and tibiae unarmed; ocelli, if present, placed closer to each other than to compound eyes; color variable, but usually not red-brown or black-brown.......... 8

8(7) Larger (usually more than 10 mm in length), variously colored (**Figure 2.25L**); scent gland ostiole present; spiracles III-VII situated far from lateral margins of abdomen; Eastern Hemisphere (Oriental region and neighboring areas of temperate East Asia).......... Urostylididae

8’ Smaller (usually less than 4.5 mm); generally of pale color (**Figure 2.25I**); scent gland ostiole strongly reduced or lacking; spiracles III-VII situated close to lateral margins of abdomen; Oriental region.......... Saileriolidae

9(4) Coxal combs (a row of strong, frequently broadened and flattened setae along apical margin of coxa) present on all legs (**Figure 2.1D**); tibiae frequently with distinct spines along their length (**Figures 2.1E-H**).......... 10

9’ Coxal combs absent; tibiae may have hairs, but not distinctly spinose (except in a few exceptional cases).......... 12

10(9) Scutellum usually subtriangular (**Figures 2.15K, L; 2.25E**), sometimes enlarged but if so, not nearly covering all of abdomen (**Figures 2.15G, I**).......... 11

10’ Scutellum greatly enlarged, nearly covering entire abdomen; worldwide (**Figure 2.25K**).......... Thyreocoridae

11(10) Tibiae without distinct spines; medium-sized, aposematically black and red species; Africa, India through China to Japan (**Figures 2.25E, F**).......... Parastrachiidae

11’ Tibiae with distinct, frequently strong spines; of various colors but not aposematically black and red; worldwide.......... Cydnidae (part)

TABLE 2.2

Pentatomoidea Classification and Diversity (as of April 2017)

Family	Subfamily	Tribe	Genera[1]	Species[1]
Acanthosomatidae			**57**	**287**
	Acanthosomatinae		17	211
	Blaudusinae		23	47
		Blaudusini	10	22
		Lanopini	13	25
	Ditomotarsinae		17	29
		Ditomotarsini	13	22
		Laccophorellini	4	7
Canopidae			**1**	**9**
Cydnidae			**111**	**852**
	Amaurocorinae		3	5
	Amnestinae		8	59
	Cephalocteinae		8	31
		Cephalocteini	2	4
		Scaptocorini	6	27
	Cydninae		75	659
		Cydnini	11	160
		Geotomini	64	499
	Garsauriinae		5	16
	Sehirinae		12	82
Dinidoridae			**17**	**109**
	Dinidorinae		13	82
		Amberianini	1	2
		Dinidorini	9	76
		Thalmini	3	4
	Megymeninae		4	27
		Byrsodepsini	1	2
		Megymenini (including Eumenotini)	3	25
Lestoniidae			**1**	**2**
Megarididae			**2**	**18**
Mesopentacoridae[3]			**2**	**3**
Parastrachiidae			**2**	**8**
Pentatomidae[2]			**940**	**4949**
	Aphylinae		2	3
	Asopinae		63	303
	Cyrtocorinae		4	11
	Discocephalinae		81	325
	Edessinae		15	338
	Pentatominae		660	3484
	Phyllocephalinae		45	214
	Podopinae		68	269
	Serbaninae		1	1
	Stirotarsinae		1	1

(*Continued*)

TABLE 2.2 (CONTINUED)

Pentatomoidea Classification and Diversity

Family	Subfamily	Tribe	Genera[1]	Species[1]
Phloeidae			**3**	**4**
Plataspidae			**66**	**606**
Primipentatomidae[3]			**4**	**5**
Saileriolidae			**3**	**4**
Scutelleridae			**100**	**531**
	Elvisurinae		7	29
	Eurygastrinae		10	37
		Eurygastrini	2	21
		Psacastini	8	16
	Hoteinae		7	24
	Odontoscelinae		5	29
	Odontotarsinae		11	78
		Odontotarsini	6	39
		Phimoderini	5	39
	Pachycorinae		26	120
	Scutellerinae		33	212
		Scutellerini	29	196
		Sphaerocorini	4	16
	Tectocorinae		1	2
Tessaratomidae			**62**	**252**
	Natalicolinae		9	18
	Oncomerinae		18	62
	Tessaratominae		35	172
		Prionogastrini	1	1
		Sepinini	5	17
		Tessaratomini	29	154
Thaumastellidae			**1**	**3**
Thyreocoridae			**30**	**223**
	Corimelaeninae		28	217
	Thyreocorinae		2	6
Urostylididae			**8**	**172**
TOTAL			**1410**	**8042**

[1] Numbers of genera and species are compiled from the World Catalog of Pentatomoidea (David A. Rider, unpublished), and include subgenera, subspecies, and fossil genera and species.

[2] For a list of the tribes in the pentatomid subfamilies with numbers of included genera and species, see **Table 2.3**.

[3] Fossil family.

12(9) Tarsi 2-segmented; antennae clearly 5-segmented (Plataspidae) or appear to be 4-segmented (subdivision of pedicel indistinct) (Megarididae); scutellum greatly enlarged, nearly covering entire abdomen (**Figures 2.16E, G, I; 2.25H**)......................................13

12’ Not with the above combination of characters...14

13(12) Evaporatoria of scent glands covering nearly entire ventral surfaces of prothorax, mesothorax, and metathorax (**Figure 2.1I**); Eastern Hemisphere, except two introduced species (southeastern North America, and Panama) (**Figures 2.16G-I; 2.25H**).............Plataspidae

13’ Evaporatoria of scent glands small, never on ventral surface of prothorax; Neotropics (**Figure 2.16E**)...Megarididae

14(12) Scutellum greatly enlarged, nearly covering entire abdomen (**Figures 2.16A; 2.26A-L**) ... 15

14’ Scutellum usually subtriangular in shape, sometimes enlarged, but usually leaving lateral and sometimes apical portions of abdomen uncovered (exceptions: Pentatomidae: Aphylinae, *Sepontia* and *Sepontiella*, and several other Oriental and Austro-Papua genera) 16

15(14) Anterior margin of pronotum meeting lateral margins in rounded arc; forewing with secondary transverse fold at apex of corium; ventral abdominal intersegmental sutures obscured laterally; dorsum strongly convex, venter flat, body uniformly black, usually shining; Neotropics (**Figure 2.16A**) .... Canopidae

15’ Anterior and lateral margins of pronotum angulate; forewing not folded transversely; ventral abdominal intersegmental sutures complete, reaching lateral margins; shape and color variable, but if dorsum strongly convex and venter flat, then body usually not totally black; worldwide (**Figures 2.26A-L**) .... Scutelleridae

16(14) Tarsi 2-segmented; mesosternum often with a large compressed median keel (**Figures 2.1J, K**) posterior margin of abdominal sternite VII deeply excised in males, leaving abdominal segment VIII exposed (**Figure 2.1L**); worldwide (**Figures 2.15A-E; 2.25A**) .... Acanthosomatidae

16’ Tarsi 3-segmented (exceptions: Dinidoridae: Dinidorinae: Thalmini; Tessaratomidae: Natalicolinae; Pentatomidae: Pentatominae: Nealeriini, Opsitomini, *Phalaecus*, *Rolstoniellus*, *Prionocompastes*); abdominal sternite VII of male not as above 17

17(16) Bucculae elongate, uniformly elevated along length, forming ridge on each side of first rostral segment (**Figures 2.1M, N**); worldwide .... Pentatomidae (in part)

17’ Bucculae much shorter, arcuately elevated, forming short, flap-like structure on each side along anterior portion of first rostral segment (**Figures 2.1O, 2.2A**) 18

18(17) Spiracles on abdominal segment II (first visible segment) partially or fully exposed, not completely concealed by posterior margin of metapleuron (**Figure 2.2B**) 19

18’ Spiracles on abdominal segment II (first visible segment) usually completely concealed by posterior margin of metapleuron; Old World, Neotropics (**Figures 2.18E-H; 2.27F-H**) .... Pentatomidae (part: Edessinae and Phyllocephalinae)

19(18) Metasternum usually produced laterally between coxae, and anteriorly onto mesosternum (**Figure 2.2C**); antennae usually 4-segmented, if 5-segmented, then segment III quite short, segments more or less cylindrical (**Figure 2.2D**); pronotum often extended posteriorly over base of abdomen (**Figure 2.2E**); ostiolar ruga in form of anterior and posterior lobes (Natalicolinae and Tessaratominae) (**Figure 2.4C**) or spout-shaped (Oncomerinae) (**Figure 2.4D**); veins in hemelytral membrane usually subparallel (**Figure 2.2E**); Old World, except one genus in Neotropics (**Figures 2.16K, L; 2.25J**) .... Tessaratomidae

19’ Metasternum usually not produced laterally or anteriorly; antennae 4- or 5-segmented, but usually with segment III not distinctively short, some segments often flattened (**Figure 2.2F**); pronotum not produced posteriorly over base of abdomen (**Figure 2.25C**); ostiolar ruga always spout-shaped (**Figures 2.4A, B**); veins of hemelytra may be reticulate; Old World with one genus in Neotropics (**Figures 2.16B-D; 2.25C**) .... Dinidoridae

2.2.2 Acanthosomatidae Signoret, 1863

The family Acanthosomatidae has had a typical pentatomoid taxonomic history. It, as well as many other families of Pentatomoidea, has been treated by most early workers as a subfamily of a broadly-defined Pentatomidae. Although China (1933) accorded it family status, it would be another 20-30 years before most workers accepted it as a valid family. In his generic revision of the group, Kumar (1974a) recognized this taxon as a valid family.

Fischer (1994) and Grazia et al. (2008) provided support for the monophyly of the family; however, the phylogenetic relationships of the Acanthosomatidae within the Pentatomoidea are still unsettled (Kment 2006, Carvajal and Faúndez 2013). Gapud (1991) established the family as an intermediate lineage

FIGURE 2.1 A, *Phloeophana longirostris*, antennae, ventral view; B, *Amnestus pusio*, head, dorsal view; C, *Amnestus pusio*, anterior tibia, inner view; D, *Cyrtomenus mirabilis*, middle and posterior coxae, ventral view; E, *Cyrtomenus mirabilis*, anterior tibia, inner view; F, *Galgupha* sp., anterior tibia, inner view; G, *Sehirus cinctus*, anterior tibia, inner view; H, *Sehirus cinctus*, posterior tibia, inner view; I, *Coptosoma* sp., ostiole and evaporatoria, ventral view; J, *Elasmostethus ligatus placidus,* mesosternum, lateral view; K, *Elasmostethus ligatus placidus*, mesosternum, ventral view; L, *Planois gayi*, posterior part of the abdomen, lateral view; M, *Dolycoris baccarum*, head, ventral view; N, *Plautia affinis*, head, ventral view; O, *Basycriptus distinctus*, head, lateral view.

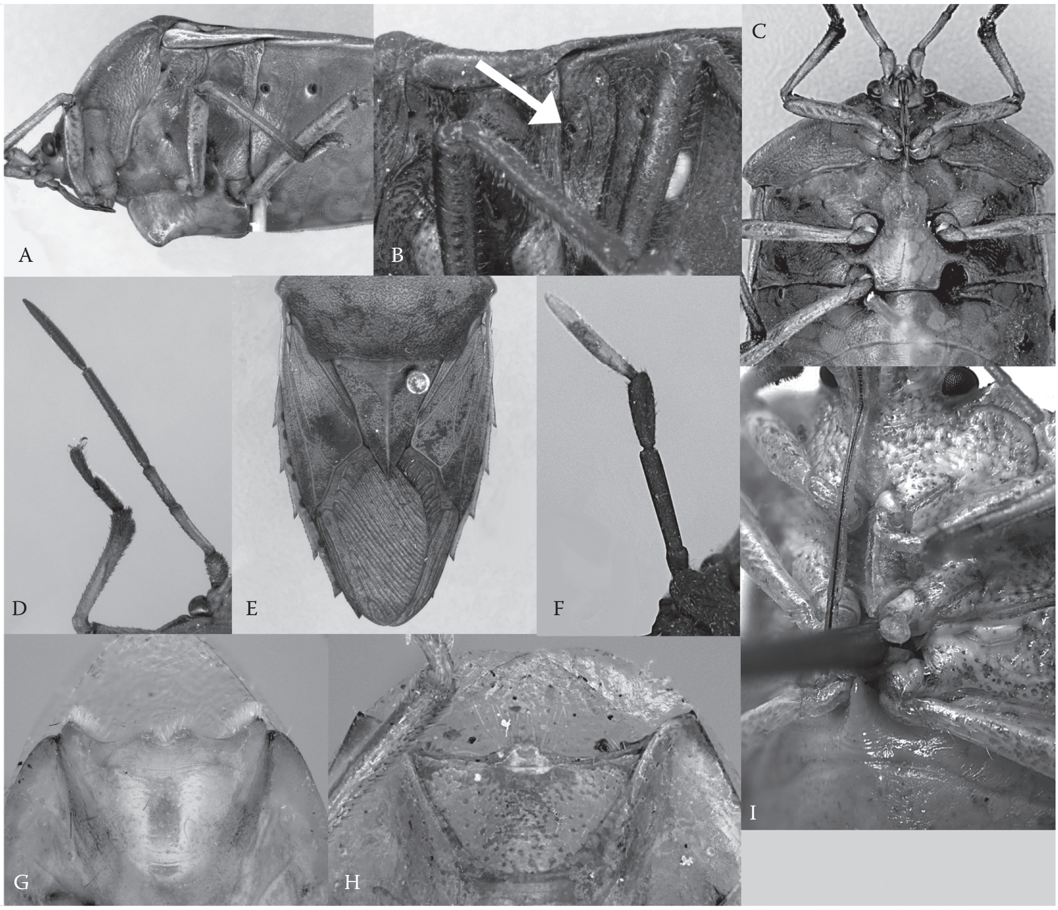

FIGURE 2.2 A, *Piezosternum thunbergi*, thoracic pleura and base of abdomen, lateral view; B, *Dinidor mactabilis*, thorax and anterior abdomen, lateral view; C, *Piezosternum thunbergi,* head and thorax, ventral view; D, *Piezosternum thunbergi*, antennae; E, *Piezosternum thunbergi*, thorax and abdomen, dorsal view; F, *Dinidor mactabilis*, antennae; G, *Nopalis sulcatus*, posterior abdomen, ventral view; H, *Elasmostethus ligatus placidus*, posterior abdomen, ventral view; I, *Lanopis rugosus*, thorax, ventral view.

within the Pentatomoidea. Results in Grazia et al. (2008) varied according to the analysis performed; the morphological evidence pointed to a basal position, whereas molecular data suggested that the family is a derived taxon related to Pentatomidae. Both analyses, as well as another molecular study by Wu et al. (2016) suggested a sister group relationship between the Acanthosomatidae and the Lestoniidae.

Members of this family, in general appearance, resemble pentatomids, being approximately the same size (5-20 mm) and shape and having a more or less triangular scutellum (with the frena extending about three-fourths the lateral distance). They differ from most species of Pentatomidae, however, by their having two-segmented tarsi, the males have the posterior margin of abdominal segment VII broadly emarginated, leaving segment VIII broadly exposed (**Figure 2.1L**), the females usually have Pendergrast's organs [i.e., glandular abdominal organs that are usually rounded or oval in shape and are located on abdominal sternites V through VII, or only on VII in some species; these are usually lacking in species that exhibit maternal care (Fischer 2006, Tsai et al. 2015)], and they lack a dilation and sclerotized rod in the spermathecal duct (Schuh and Slater 1995, Schwertner and Grazia 2015). Except for a small group of Madagascan genera that has four-segmented antennae (Kment 2006), they have five-segmented antennae. The mesosternum is often strongly carinate medially (**Figures 2.1J, K**) (subfamily Acanthosomatinae), and abdominal sternite III is often armed with an anteriorly directed spine or tubercle. The trichobothria on abdominal sternites III through VII are transverse in position. The tibiae lack distinct spines or bristles. Females usually have the posterior margin of abdominal sternite VII deeply emarginated medially. Twelve species of acanthosomatids have been karyotyped, of which nine have a diploid number of 10 + XY (Ueshima 1979, Kerzhner et al. 2004, Rebagliati et al. 2005).

Kumar (1974a) divided the Acanthosomatidae into three subfamilies: the Blaudusinae (spelled Blaudinae by some authors), the Ditomotarsinae, and the Acanthosomatinae, with the Blaudusinae further subdivided into two tribes (the Blaudusini and Lanopini), and the Ditomotarsinae also divided into two tribes (the Ditomotarsini and Laccophorellini) (see **Table 2.2**). Separation into subfamilies was based primarily on differences in the sternal structure of the thorax and the presence or absence of a spine or tubercle at the base of the abdomen. The resulting classification is controversial and leaves the character evolution unclear; as Kment (2006) pointed out, even Kumar (1974a) realized that there were many exceptions and that some genera were not easily placed in these subfamilies or tribes. Currently, there are 57 genera and 287 species in the Acanthosomatidae (**Table 2.2**).

The distribution of the Acanthosomatidae is predominantly in the Southern Hemisphere, especially Argentina, Chile, South Africa, and Australia. Only a few genera of Acanthosomatinae (i.e., *Acanthosoma* Curtis, *Cyphostethus* Fieber, *Elasmostethus* Stål, *Elasmucha* Stål, and *Sastragala* Amyot and Serville) have representatives in the Northern Hemisphere but there has been remarkable species radiation in East and Southeast Asia. Kumar (1974a) monographed the World fauna, Kment (2006) reviewed the fauna of Madagascar, and Rolston and Kumar (1974) provided keys to the genera occurring in the Western Hemisphere. The Australian, Iranian, Nearctic, and Palearctic species have been catalogued by Cassis and Gross (2002), Ghahari et al. (2014), Froeschner (1988a), and Göllner-Scheiding (2006a), respectively. Knowledge on the Neotropical species was summarized by Schwertner and Grazia (2015). There have been five fossil species named in the genus *Acanthosoma* (Heer 1853, Förster 1891, Piton and Théobald 1935), and one named in *Elasmostethus* (Popov 1968a). Also, Fujiyama (1987) recognized but did not name a fossil species in *Acanthosoma* and another in *Elasmucha*. Additionally, another fossil genus and species, *Suspectocoris grandis* Jordan (1967), were originally described in the Acanthosomatidae, but was later transferred to the Pentatomidae (Popov 2007).

Ahmad and Moizuddin (1990) reviewed the family for the Indo-Pakistan region, and Kment (2006) reviewed those species occurring in Madagascar. Recent revisions, either in part or in whole, include *Acanthosoma* (Tsai and Rédei 2015a,b,c), *Acrophyma* Bergroth (Faúndez 2009), *Archaeoditomotarsus* Faúndez, Carvajal, and Rider (Faúndez et al. 2014a), *Cyphostethus* (Ahmad and Önder 1993), *Duadicus* Dallas (Wang et al. 2014), *Elasmostethus* (Thomas 1991, Ahmad 1997, Yamamoto 2003), *Elasmucha* (Thomas 1991), *Eupolemus* Distant (Jensen-Haarup 1931b), *Hellica* Stål (Froeschner 2000), *Lindbergicoris* Leston (Zheng and Wang 1995), *Mahea* Distant (Kment 2006), *Noualhieridia* Breddin (Kment 2007), *Panaetius* Stål (Wang et al. 2015), *Rhopalimorpha* Dallas (Pendergrast 1950, 1952), and *Tolono* Rolston and Kumar (Carvajal et al. 2015b).

Acanthosomatids are herbivorous bugs that are usually polyphagous with some species being monophagous or oligophagous (Schaefer and Ahmad 1987; Faúndez 2007a, 2009). Host plants includes trees and shrubs (Kumar 1974a; Schaefer and Ahmad 1987; Faúndez 2007b, 2009), and feeding sites include young tissues and reproductive parts of the hosts (Schaefer and Ahmad 1987; Faúndez 2007a,b). Casual records of feeding on decaying organic matter and predation are known (Miller 1971) and are probably related to a shortage of suitable host plants (Schaefer and Ahmad 1987).

Maternal care is relatively common in species of the subfamily Acanthosomatinae (Schuh and Slater 1995, Hanelová and Vilímová 2013, Tsai et al. 2015). Faúndez and Osorio (2010) described maternal care behavior for *Sinopla perpunctatus* Signoret (subfamily Blaudusinae); they also reported coloration change in the female associated with the reproductive period and the guarding of eggs and nymphs. Maternal care in the Acanthosomatidae does not represent phylogenetic conservatism; the results of a recent study (Tsai et al. 2015) do not support the hypothesis of Tallamy and Schaefer (1997) that parental care is a plesiomorphic relict in Hemiptera, which has been lost repeatedly due to high carrying cost. Maternal care has arisen four times independently in the subfamily Acanthosomatinae: common ancestor of the genus *Elasmucha*, common ancestor of *Sastragala*, in *Acanthosoma firmatum* (Walker), and in *Sinopla perpunctatus* (Tsai et al. 2015).

2.2.2.1 Key to the Subfamilies of Acanthosomatidae (modified from Kumar 1974a)

1 Abdominal spine absent; posterolateral angles of abdominal segment VII rounded or angulate, not spinose (**Figure 2.2G**); anterolateral pronotal margins thick; Australia, Africa, South America (**Figures 2.15D, E**) .... Ditomotarsinae

1' Abdominal spine usually present but if absent, then either posterolateral angles of last connexival segments spinose (**Figure 2.2H**) or anterolateral pronotal margins thin 2

2(1) Mesosternal carina usually absent, but if present, it is only a short raised wedge at juncture of pro- and mesosterna (may extend slightly forward and backward); when both pro- and mesosternal carinae present then invariably poorly developed (**Figure 2.2I**) and never continuous (in such cases abdominal spine well-developed and sometimes reaching anterior end of prosternal carina); Australia, southern Africa, South America (**Figures 2.15C, 2.25A**) .... Blaudusinae

2' Mesosternal carina usually well-developed and receiving at its posterior end the generally distally concave abdominal spine, latter closely apposed to sternal carina on left-hand side (or extending over it, or completely fused with it) (**Figures 2.1J,K**); worldwide (**Figures 2.15A, B**) .... Acanthosomatinae

2.2.3 Canopidae Amyot and Serville, 1843

The family Canopidae is a small family, both in size (5-7 mm) and number of included taxa with one genus, *Canopus* F., and nine species (**Table 2.2**). Interestingly, twice this many species have been described, but most were based on nymphal specimens that are now considered to be of unknown identity (McAtee and Malloch 1928). As with many pentatomoid families, this group was treated as a subfamily of an inclusive Pentatomidae. Horváth (1919) proposed tribal status for this group (as Canoparia), and described two new species. The first major monograph of the group (McAtee and Malloch 1928) treated it as such. It was elevated to family status by McDonald (1979) where it has remained. The only included genus was described by Fabricius in 1803 to include the species *C. obtectus* F., the type specimens of which are all nymphs, thus the type species for *Canopus* is now considered to be *incertae sedis* (McAtee and Malloch 1928). A key to the species was provided by McAtee and Malloch (1928).

Diagnostic characters (Schuh and Slater 1995, Schwertner and Grazia 2015) for this family include the following: the bugs have a circular or obovate shape, are strongly convex dorsally, rather flattened ventrally, and generally are shiny black in color, sometimes with purple or greenish reflections (**Figure 2.16A**). The length of the head anterior to the compound eyes is almost as long as the width between the compound eyes, and the jugal margins are narrowly reflexed. The antennae are five-segmented with segment II short, subequal to its diameter. The scutellum is greatly enlarged, nearly covering the entire abdominal dorsum; only a small fraction of the hemelytra is exposed. The hemelytra are quite elongate, usually twice the length of the abdomen, with a line of weakness for folding the wing near the apex of the costa; the wing membrane has at least five parallel veins. The hind wings have lobate posterior margins; they possess a stridulatory mechanism composed of a strigil on the posterior anal vein (postcubitus in several earlier papers) of the hind wing and a plectrum located on abdominal tergum I. The tibiae may be setose, but they are not distinctly bristled or spined; the tarsi are three-segmented. The abdominal sutures become obsolete laterad of the spiracles; the abdominal trichobothria are longitudinally placed mesad of the spiracular line on abdominal sterna III through VII. 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 are twice the width of the other two; sterna II and III are divided mesally.

The general habitus, development of the scutellum, and some abdominal and wing characters may suggest a relationship with the Megarididae and Plataspidae; however, other morphological and molecular evidence are conflicting (Grazia et al. 2008). Schaefer (1981a, 1988) considered the families Canopidae, Cydnidae, Cyrtocoridae, Lestoniidae, Megarididae, Plataspidae, and Thaumastellidae as primitive groups within the Pentatomoidea because of the plesiomorphic characters they have in common (e.g., structure of the spermatheca, stridulatory structures).

The biology and ecology of the canopids are poorly known. McHugh (1994) found two species of *Canopus* on sporophores of certain fungi in different localities in Bolivia and Costa Rica, giving evidence that canopids may be mycetophagous in habit. Schaefer (1988) provided some information on plant associations of the Canopidae.

2.2.4 Cydnidae Billberg, 1820

This family, in contrast to most of the pentatomoid families, generally has been considered to be a valid family almost from its conception. Billberg (1820) proposed the group Cydnides with a similar concept as the family Pentatomidae of Leach (1815). Amyot and Serville (1843) recognized the 'race Spinipèdes' to include the groups Cydnides, Séhirides, and Pododides, the latter currently included in the Pentatomidae under the tribe Sciocorini. Dallas (1851) treated the Cydnides and Séhirides of Amyot and Serville in his concept of the Cydnidae. The main instability pertaining to this family has been associated with its contents; that is, the taxa included within the Cydnidae have changed often. Both Fieber (1860) and Stål (1876) considered the genera *Corimelaena* White and *Thyreocoris* Schrank, both herein included in the Thyreocoridae, to be members of the Cydnidae. Uhler (1872) and Lethierry and Severin (1893) treated the Cydnidae and Thyreocoridae as separate entities. More recently, however, Dolling (1981) held a rather broad view of the family, defined by the presence of setal combs on the coxae and a strigil on the ventral surface of the hind wings; he included eight subfamilies within the Cydnidae, three of which are not included within the family in this treatise (Corimelaeninae, Thaumastellinae, and Thyreocorinae), and at least one or two others may be raised to family status in the future (see below).

Important monographs of the Cydnidae include that of Froeschner (1960) for the New World; Linnavuori (1993) for west, central, and northeast Africa; and Lis (1994) for the Oriental Region. Lis provided a catalog of the Old World taxa (1999a) as well as an updated version of the Palearctic species (2006a). Recent regional catalogs or checklists of North American (Froeschner 1988b), Old World (Lis 1999a), Palearctic (Lis 2006a), Austro-Papuan (Lis 1995) and Australian (Cassis and Gross 2002) faunas are available. Information regarding the Neotropical members of this family has been provided by Schwertner and Nardi (2015).

The Cydnidae is arguably the morphologically most diverse family of the Pentatomoidea. Accordingly, although it is easy to recognize small, apparently monophyletic subgroups within it, the monophyly of the family as a whole is questionable, and its phylogenetic relationships within Pentatomoidea are unknown (Grazia et al. 2008, Pluot-Sigwalt and Lis 2008, Lis 2010). Most modern authors exclude Thyreocoridae, *Thaumastella* Horváth, *Parastrachia* Distant, and *Dismegistus* Amyot and Serville from the Cydnidae, but there is little doubt that all of these taxa (particularly the latter two) are closely related to some cydnid subgroups; a comprehensive study of the whole complex is needed to elucidate their relationships. All of these groups possess coxal combs, and Thyreocoridae and *Thaumastella* have spine-like setae on the tibiae (albeit very weak in the latter). Some or all of these taxa are sometimes considered as subfamilies in a more broadly defined Cydnidae (Dolling 1981, Schuh and Slater 1995).

Any morphological definition of the Cydnidae will greatly overlap at least with *Parastrachia* and *Dismegistus*. The diagnostic characters (Schuh and Slater 1995, Schwertner and Nardi 2015) for the Cydnidae, in a narrow sense, include small to medium in size (2-25 mm), usually somewhat ovoid in shape, and usually glossy or shiny black or brown (some sehirines are bluish with white markings) in color. Cydnids are usually somewhat convex dorsally and distinctly convex ventrally. The head may be somewhat quadrate or more often semi-circular, relatively wide, often somewhat explanate. The antennae are five-segmented, rarely four-segmented (e.g., *Schiodtella* Signoret, *Geopeltus* Lis, and *Adrisa* Amyot and Serville). The scutellum is usually subtriangular in shape, but sometimes may be somewhat enlarged, apically broadly rounded, and usually reaching less than three quarters of the length of the abdomen. The subfamily Amnestinae has the clavi extending beyond and meeting caudad of the scutellar apex, forming a distinct claval commissure (**Figures 2.3C, 2.15F**). Most cydnids possess a stridulatory mechanism composed of a strigil on the posterior anal vein (postcubitus in several earlier papers) of the hind wing and a plectrum located on abdominal tergum I. The distal margins of the coxae are provided with a row of setae or bristles, known as coxal combs (**Figure 2.1D**). The legs are adapted for digging in soil and leaf litter, having strong spine-like setae on the tibiae (**Figures 2.1C, E-H**), sometimes set on distinct wart-like projections; the anterior tibiae often are compressed. The tarsi are three-segmented except in the Cephalocteinae where the anterior and posterior tibiae are strongly modified and, thus, the accompanying tarsi may be reduced or absent (**Figures 2.3D, E**). Abdominal trichobothria usually are present on segments III through VII and arranged longitudinally or transversely (**Figures 2.3A, B**), usually laterad of the spiracular line. Nymphal scent glands are present between abdominal terga III and IV, IV and V, and V and VI. The female spermatheca is diverse, and the spermathecal duct is either simple or is provided with a dilation of various sizes, shapes, and inner structure; sclerotized tubular projections of the distal orifice are also not rare (Pluot-Sigwalt and Lis 2008). Fourteen species of Cydnidae have been karyotyped, of which eight and four have a diploid number of 10 + XY, and 12 + XY, respectively (Ueshima 1979, Kerzhner et al. 2004, Rebagliati et al. 2005).

The Cydnidae currently contains 111 genera and 852 species. They are classified into six subfamilies (**Table 2.2**), but the Amaurocorinae are sometimes considered to be a tribe of the Sehirinae (e.g., Lis 1994). The Amaurocorinae and Garsauriinae are restricted to the Eastern Hemisphere (Lis 1999a, 2002), the Amnestinae is predominantly Neotropical, and the Sehirinae is predominantly Palearctic (Froeschner 1960, Lis 1999a, Mayorga 2002); species of the subfamilies Cephalocteinae and Cydninae are distributed worldwide. As the family is potentially non-monophyletic, it may be necessary to remove some of the included taxa.

The classification of this group has been studied thoroughly, but general conclusions remain unsettled (Pluot-Sigwalt and Lis 2008, Lis 2010). Concerning the classification at the subfamilial and tribal level, only Cephalocteinae is supported in a phylogenetic context (Lis 1999b), whereas the non-monophyly of the Cydninae and Sehirinae is suggested by some authors (Pluot-Sigwalt and Lis 2008, Lis 2010).

The biology is well-known for some members of this family and not so well-known for others (Schwertner and Nardi 2015). Species that live above ground, especially those in the subfamily Sehirinae [e.g., *Sehirus cinctus* (Palisot de Beauvois)] have been the subject of a number of studies. Others, however, that spend most of their time underground as excavators (subfamilies Cephalocteinae and Cydninae) are more difficult to study in their subterranean habitats. Nymphs and adults of the subterranean species are thought to feed on the sap of roots, although some species [e.g., *Pangaeus bilineatus* (Say)] have been observed feeding on ground pods of *Arachis hypogaea* L. (Chapin et al. 2006). Sehirines and amnestines usually feed on above-ground structures of their host plants. For example, *Sehirus cinctus cinctus* feeds on mature seeds that have fallen from several different host plants (Froeschner 1960, Sites and McPherson 1982), whereas species of *Amnestus* Dallas feed on the fruits and seeds of *Ficus colubrinae* Standley in Mexico (Mayorga and Cervantes 2001).

The females of Cephalocteinae and Cydninae lay eggs singly below the ground surface (García and Belotti 1980, Riis et al. 2005a,b). In contrast, sehirine females lay egg masses in shallow cracks in 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* L. (Moraceae) (Mayorga and Cervantes 2001). Maternal care has been observed in some of those species that lay egg masses [e.g., *Sehirus cinctus cinctus* and *Adomerus triguttulus* (Motschulsky)]. The females guard the eggs until the nymphs disperse after hatching (Southwood and Hine 1950, Nakahira et al. 2013). Within the entire Pentatomoidea, an active provisioning of food by females to the nymphs is known only in the Cydnidae and the Parastrachiidae. When oviposition occurs in the soil, eggs usually are deposited near the host plant. The moisture and soil texture seem to determine the depth of oviposition (Willis and Roth 1962, Riis and Esbjerg 1998a,b, Riis et al. 2005a,b). In times of prolonged drought in the Brazilian Cerrado, eggs of *Scaptocoris* Perty species have been found as deep as 1.5 meters (Nardi et al. 2008). The eggs of cydnid species are characterized by a smooth corium, a uniform creamy coloration, and no conspicuous projections (García and Belotti 1980, Mayorga and Cervantes 2001, Vivan et al. 2013). Incubation time can vary from 1 week (García and Belotti 1980, Sites and McPherson 1982, Riis et al. 2005a,b) up to 4 weeks (Sales and Medeiros 2001). Several sehirine species (e.g., *Adomerus triguttulus* and *Canthophorus niveimarginatus* Scott), are known to produce trophic eggs (i.e., inviable eggs that are usually used for food for offspring) (Nakahira 1994; Kudô and Nakahira 2004, 2005; Kudô et al. 2006; Filippi et al. 2008).

Burrower bug nymphs live within or near the surface of the soil, feeding on the roots or fallen seeds of their hosts. They are typically oligophagous or polyphagous, feeding on the plants near the site where they hatched from the eggs. As with most terrestrial Heteroptera, cydnids go through five nymphal instars. The majority of cydnid species seems to be polyphagous with several plant families reported as hosts (Timonin 1958, Becker 1967a, Mayorga and Cervantes 2001, Riis et al. 2005a,b, Chapin et al. 2006, Schwertner and Nardi 2015). On occasion, the bugs are reported as agricultural pests (Gallo et al. 2002, Riis et al. 2005a,b, Schwertner and Nardi 2015).

Some species, and some individuals within other species, are brachypterous and, thus, are unable to fly. Those that can fly seem to take wing mostly for dispersal, but flying could also be for colonization of new areas, location of food, and finding new mates (Willis and Roth 1962, Oliveira and Malaguido 2004, Nardi et al. 2008). Little is known about cydnid reproductive behavior. Soil-dwelling species mate in the soil (Willis and Roth 1962, Nardi 2005). Similar to other Heteroptera, it appears that copulation in the Cydnidae is mediated by chemicals and sound communication (Gogala et al. 1974, Gogala 1984, Čokl et al. 2006, Pluot-Sigwalt 2008).

As expected from a group whose members live primarily on or near the ground, there are several fossil genera and species known. Also, at least three family-level names have been proposed within the Cydnidae. For example, Pinto and Ornellas (1974) erected two fossil families, the Pricecoridae for *Pricecoris beckerae* Pinto and Ornellas and the Latiscutellidae for *Latiscutella santosi* Pinto and Ornellas. Additionally, Popov (1986) proposed the subfamily Clavicorinae for two fossil genera, *Clavicoris* Popov and *Cretacoris* Popov. Later, Popov and Pinto (2000) placed all three of these family-groups as junior synonyms of the Amnestinae. Within the subfamily Amnestinae, there are six genera and nine fossil species (Pinto and Ornellas 1974, Popov 1986, Thomas 1988, 1994a, Yao et al. 2007); within the subfamily Cydninae, there are three genera and 41 fossil species (Heer 1853; Oustalet 1874; Novák 1877; Scudder 1878, 1890; Förster 1891; Cockerell 1909; Henriksen 1922; Piton 1933; Théobald 1937; Statz and Wagner 1950; Jordan 1967; Kinzelbach 1970; Popov 1986, 2007; Schaefer and Crepet 1986; Thomas 1994a); and within the Sehirinae, there are five fossil species (Statz and Wagner 1950, Vršanský et al. 2015). There are currently six genera and 25 fossil species that have not been placed to subfamily. Another fossil genus and species, *Ovalocoris parvis* Jordan, was originally described in the Lygaeidae but later (Popov 2007) transferred to the Cydnidae. Additionally, there are three fossil species that were originally placed in the Cydnidae that have now been placed elsewhere. That is, *Cydnopsis affinis* Jordan and *C. ventralis* Jordan have both been transferred to the nepomorphan family Aphelocheiridae (Popov 2007), and the third species, *Cydnopsis nigromembranacea* Jordan (1967) has been transferred to the Coleoptera (Popov 2007).

2.2.4.1 Key to the Subfamilies of Cydnidae (modified from Schuh and Slater 1995)

1 Clavi reaching beyond and meeting in a straight line beyond apex of scutellum, forming claval commissure (**Figure 2.3C**); New World (except one species introduced into Old World) (**Figure 2.15F**) .... Amnestinae

1’ Claval commissure absent 2

2(1) Fore tibiae falcate or cultrate, much produced beyond tarsal insertion, therefore tarsi appearing to arise at middle of tibial length (except in *Cephalocteus* where tarsus is inserted apically or subapically) (**Figures 2.3D, E**); posterior tibiae strongly broadened; worldwide (**Figures 2.15G, H**) .... Cephalocteinae

2’ Fore tibiae not cultrate, tarsi arising at or near apices of tibiae (**Figures 2.1E, G**).......... 3

3(2) A submarginal row of setigerous punctures present along each lateral pronotal margin (**Figure 2.3F**); diameter of tarsal segment II subequal to diameters of tarsal segments I and III (**Figure 2.1E**); worldwide (**Figures 2.15J, K; 2.25B**) .... Cydninae

3’ Pronotum lacking submarginal row of setigerous punctures along lateral margins; diameter of tarsal segment II distinctly narrower than diameters of tarsal segments I and III (**Figures 2.1G, H**).......... 4

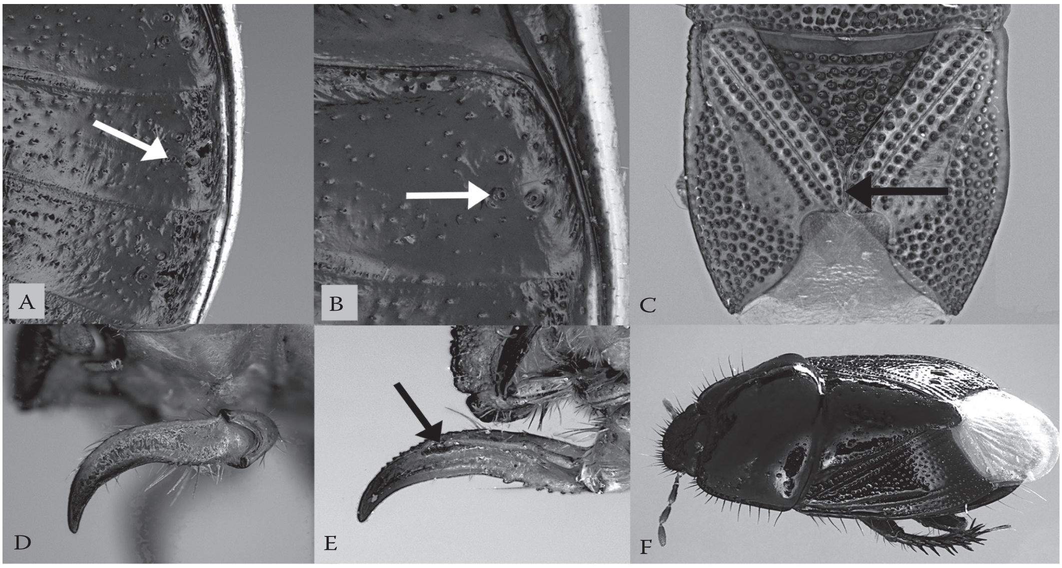

FIGURE 2.3 A, *Sehirus cinctus*, lateral abdomen, ventral view; B, *Sehirus cinctus*, detail of the second abdominal segment, ventral view; C, *Amnestus pusio*, scutellum and hemelytra, dorsal view; D, *Scaptocoris castaneus*, anterior tibia, lateral view; E, *Scaptocoris castaneus*, anterior tibia, inner view; F, *Cyrtomenus mirabilis*, habitus, dorsolateral view.

4(3) Pronotum with a fine, distinctly impressed subapical groove paralleling anterior margin; abdominal trichobothria on segments III through VII arranged in longitudinal pairs; body conspicuously flattened and coarsely punctured; Old World .... Garsauriinae

4’ Pronotum without distinctly impressed subapical groove paralleling anterior margin; abdominal trichobothria on segments III through VII arranged in transverse pairs (**Figures 2.3A, B**); body not conspicuously flattened.. 5

5(4) Long setae present at least on lateral margins of head, pronotum, and corium (**Figure 2.15I**); female spermatheca composed of a long, coiled, simple, non-differentiated tube; Old World (**Figure 2.15I**) .... Amaurocorinae

5’ Long setae not present along lateral margins of head, pronotum and corium (**Figure 2.15L**); female spermatheca more complex, possessing a spermathecal bulb and pump region; worldwide (**Figure 2.15L**)... Sehirinae

2.2.5 Dinidoridae Stål, 1868

The Dinidoridae represents another family that was treated by most early workers as a subfamily of the Pentatomidae. Amyot and Serville (1843) recognized the group Mégyménides, including only *Megymenum* Guérin-Méneville, as a group within their tribe Coniscutes. Stål (1868) proposed the group Dinidorida to include the genera *Aspongopus* Laporte (= *Coridius* Illiger), *Atelides* Dallas (= *Sagriva* Spinola), *Dinidor* Latreille, and *Megymenum*; he later (Stål 1870) gave the group subfamilial status, a classification that most workers followed until the 1950s. The main exception was Lethierry and Severin (1893) who catalogued this group as a family. Cachan (1952), in his monograph of the Madagascar fauna, treated this group as a family. Although the name Megymeninae has priority over the Dinidoridae, the latter family has been well established and should not be supplanted (see article 35.5 of the International Code of Zoological Nomenclature [ICZN]); the Megymeninae is retained as a subfamily within the Dinidoridae.

The most recent authoritative work on the family was by Durai in 1987 who also treated this group at the family level; earlier, this family was treated in a still useful paper by Schouteden (1913). Durai (1987) established the presently used classification (with a couple updates - see below), and provided diagnoses and keys for identifying all genera and species. A checklist of Old World taxa was provided by Lis (1990), a World catalog was provided by Rolston et al. (1996), and the Palearctic species also have been catalogued (Lis 2006b). Information on the Neotropical species have been compiled by Schwertner and Grazia (2015).

There are at least two fossil pentatomoids possibly belonging to this family: *Dinidorites margiformis* described from Eocene deposits in Colorado (Cockerell 1921) and an unnamed fossil reported from deposits in British Columbia (Archibald and Mathewes 2000), Canada, which was originally placed in the subfamily Megymeninae.

Diagnostic characters of the family (Schuh and Slater 1995, Schwertner and Grazia 2015) include the lateral margins of the head, which are usually carinate; and the bucculae, which are short and elevated, almost flap-like. The antennae may be four or five-segmented, some segments may be flattened (**Figure 2.2F**), and the rostrum usually reaches to or beyond the middle coxae. The humeral angles of the pronotum are rounded, almost never developed, but the lateral margin usually bears an anteriorly directed projection in the Megymeninae (**Figure 2.16D**). The scutellum is usually somewhat triangular in shape, with the basal width subequal to the medial length, and it never covers the corium; the apex is usually rounded. The hemelytral membrane usually has reticulate venation. The tarsi may be two- or three-segmented; the tibiae lack distinct bristles or spines, and the coxae lack the coxal combs evident in the Cydnidae and related families. The female spermatheca lacks a dilation and sclerotized rod. Eight of twelve species that have been karyotyped have a diploid number of 12 + XY (Ueshima 1979, Kerzhner et al. 2004, Rebagliati et al. 2005).

Typically, this family is divided into two subfamilies (i.e., Dinidorinae and Megymeninae) (**Table 2.2**), each with quite different facies. The dinidorines are somewhat rounded to oval, colored in browns, blacks, and tans, occasionally with red or yellow, but are relatively smooth surfaced with typical pentatomoid punctures. The megymenines are usually gray to dark grey or almost black, not quite so smoothly ovoid in shape, and their dorsal surface is rather rough or granulated (**Figure 2.16D**). *Eumenotes* Westwood (**Figure 2.16C**) and *Afromenotes* Kment and Kocorek, which superficially resemble members of the Megymeninae, are of uncertain placement. It may be justified to place them in a third subfamily, the Eumenotinae, or keep them as a tribe in either of the other two subfamilies.

The family Dinidoridae includes 17 genera and 109 species in two subfamilies and five tribes (**Table 2.2**), distributed mostly in the Old World. The only representative in the New World is the nominotypical genus, *Dinidor*, with six endemic species. The classification used in this chapter was established by Durai (1987), followed by Rolston et al. (1996) in their World catalog of the group, and includes updates from Kocorek and Lis (2000) and Lis et al. (2015). In the first work, Kocorek and Lis (2000) proposed a new tribe (Byrsodepsini [**Figure 2.16B**]) within the Megymeninae and placed the Eumenotini as a junior synonym of the Megymenini. The Eumenotini has had a complex taxonomic history, at one time or another, having been classified within the Aradidae, Pentatomidae, Tessaratomidae, Dinidoridae, or as a distinct family, the Eumenotidae (see Kment and Kocorek 2014). The molecular analysis by Lis et al. (2012a) revealed that the Eumenotini is more closely related to the Dinidorinae than to the Megymeninae, which resulted in its removal from the synonymy of the Megymeninae and restoring it as a tribe without subfamily assignment. In the second work, Lis et al. (2015) conducted a molecular investigation of the Madagascan genus *Amberiana* Distant. Interestingly, the molecular data indicated that *Amberiana* was related to the cydnid subfamily Sehirinae or the family Parastrachiidae, but the authors stated that the morphology was typical dinidorid; they ultimately decided to leave *Amberiana* in the Dinidoridae, but they erected a new tribe, the Amberianini, for this single genus.

Gapud (1991) considered the Dinidoridae and Tessaratomidae as sister groups based on two synapomorphies: the spiracles on abdominal segment II at least partially exposed (**Figure 2.2B**) and laterotergites IX quite large in females. Grazia et al. (2008) found similar results, although they felt that the Dinidoridae could be paraphyletic or monophyletic according to the analyses they performed (morphological, molecular, or combined analyses). The sister-group relationship of Dinidoridae and Tessaratomidae was supported morphologically (Kment and Vilímová 2010a) and by molecular data (Lis et al. 2012a,c). The two families together certainly form a single monophyletic assemblage, but the monophyly of each of them, particularly the Tessaratomidae, needs further support.

Only a few species of this family have had their biology studied; most of the available information is limited to label data or other field observations (Schaefer and Ahmad 1987, Schaefer et al. 2000). All species studied to date are exclusively phytophagous, feeding on both the reproductive and vegetative parts of the host plant. The data indicate that polyphagy is widespread, but oligophagy in some species is likely. Some species seem to show a preference for certain plant families (e.g., *Coridius* Illiger species prefer plants of the family Cucurbitaceae and can be pests on melons and squash; *Eumenotes* species are frequently found on Convolvulaceae). All species studied are univoltine and usually use more than one host plant during their life cycles (Schaefer et al. 2000). Some species exhibit gregarious behavior at certain times of the year, being found in large quantities together on their host plants. Dinidorids only lay one or two clutches of eggs per female, each containing 14-28 eggs (Schaefer et al. 2000). At least one species, *Cyclopelta parva* Distant, has been reported to exhibit parental care of the immature forms (Hoffmann 1936).

Various species of dinidorids have been used for human consumption (Strickland 1932, Hoffmann 1947). For example, in the Sudan, gelatin has been extracted from *Coridius viduatus* (F.), which has been used in making ice cream (Mariod and Fadul 2014). Dinidorids also are thought to have medicinal value, especially in oriental regions. For example, *C. chinensis* (Dallas), once popular in China as an aphrodisiac (Hoffman 1947), still it is in use as a traditional Chinese medicine; it is believed that it can regulate breath and relieve pain (Zhang and You 2002, Yao 2006); Hoffmann (1947) stated that "this species is very commonly used in China in an aphrodisiacal medicine and is on sale in Chinese medicine shops throughout China. It is called 'Chu Shan Chung' or 'Hai Tao Chung' and was written about in 1590 by Li Shih Chen and in 1890 by Fang Shui." *Coridius nepalensis* (Westwood) is used similarly in India; again Hoffmann (1947) stated "the natives of Assam are very fond of these bugs which they pound up and mix with foods that are made of rice to improve the taste." In Sudan, oils have been extracted from *C. viduatus*, which were found to have anti-bacterial properties (Mustafa et al. 2008).

2.2.5.1 Key to the Subfamilies of Dinidoridae (modified from Schuh and Slater 1995)

1 Basal angles of scutellum without fovea; posterolateral angles of abdominal connexiva neither tuberculate nor lobed; Old World except one genus (*Dinidor*) in New World tropics (**Figures 2.16B, 2.25C**)........................Dinidorinae

1' Basal angles of scutellum each with a fovea; posterolateral angles of abdominal connexiva either tuberculate or lobed........................2

2(1) Abdominal spiracles arranged along a line; trichobothria paired; Old World (**Figure 2.16D**)..........................Megymeninae

2' Spiracles of abdominal segment II situated close to lateral margin, not in line with spiracles of remaining segments (**Figure 2.4E**); trichobothria unpaired; Old World (**Figure 2.16C**)........................Eumenotini (of uncertain placement)

2.2.6 Lestoniidae China, 1955

This endemic Australian family contains a single genus (*Lestonia* China [**Figure 2.25D**]) and two species (*L. haustorifera* China and *L. grossi* McDonald) (**Table 2.2**). This group originally was described as a subfamily of the Plataspidae (China 1955) but subsequently was elevated to family status by China and Miller (1959). Because of the enlarged scutellum, this family has been associated at one time or another with the Plataspidae, Scutelleridae, or the pentatomid subfamily Aphylinae. Fischer (2000) proposed a possible relationship with the Acanthosomatidae, based on the two-segmented tarsi, and the supposed homology of the Pendergrast's organs in the Acanthosomatidae with the pair of unusual, small, disc-shaped organs located on the abdominal venter of female specimens of this family. A relationship with the Aphylinae can be dismissed by the presence of a sclerotized rod in the female spermatheca of the aphylines (lacking in the Lestoniidae). Studies by McDonald (1969a, 1970), Gross (1975b), Gapud

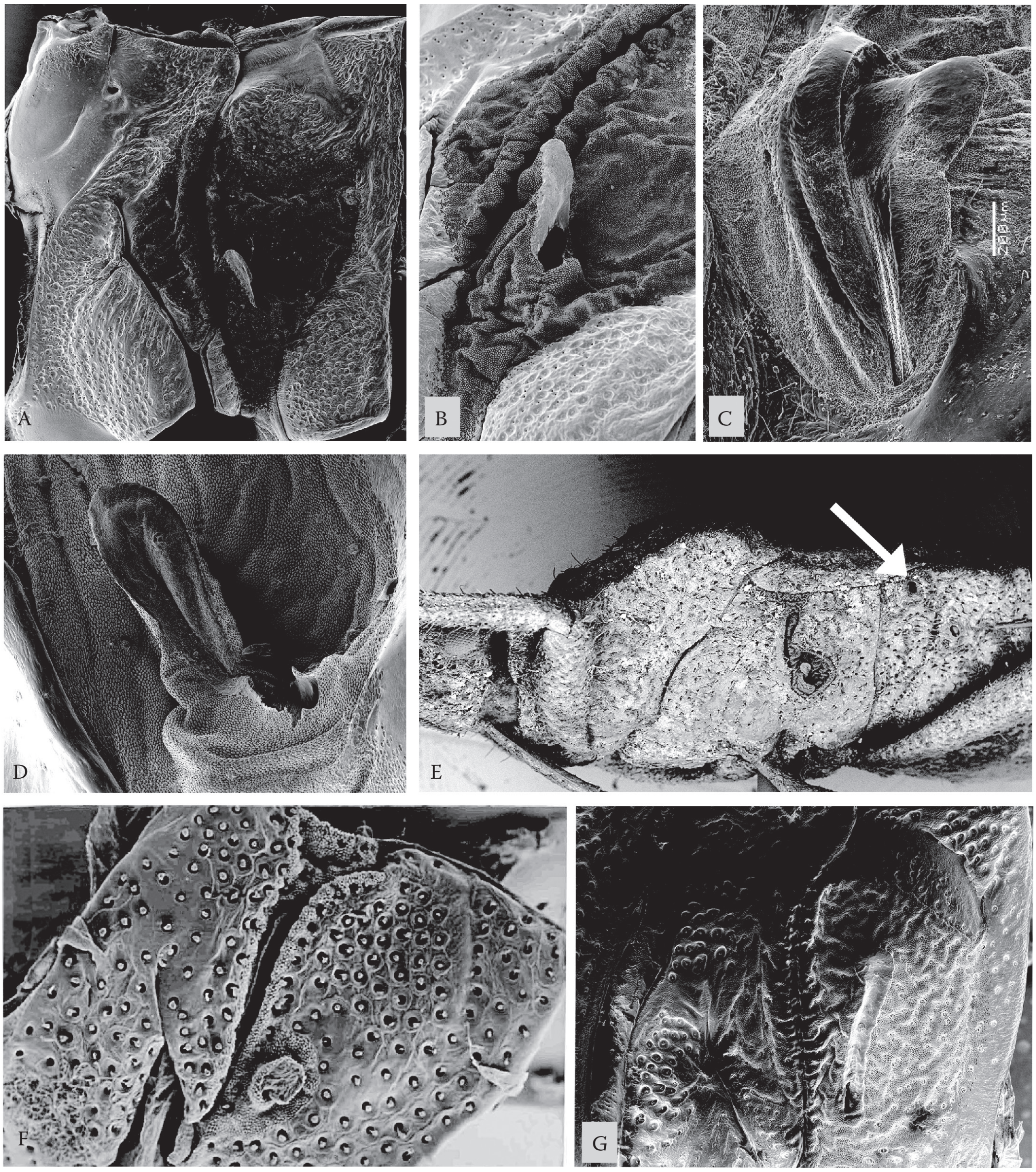

FIGURE 2.4 A, *Coridius viduatus*, evaporatorium, ventral view; B, *Coridius viduatus*, ostiolar ruga, ventral view; C, *Tessaratoma papillosa*, ostiolar ruga, ventral view; D, *Oncomeris flavicornis*, ostiolar ruga, ventral view; E, *Eumenotes obscura*, thorax and anterior abdomen, lateral view; F, *Kayesia parva*, evaporatorium, ventral view; G, *Eurygaster maura*, evaporatorium, ventral view.

(1991), and Schaefer (1993) seemed to support a relationship with the Plataspidae, but they ultimately decided that there were enough differences to maintain separate family status. The phylogenetic studies by Grazia et al. (2008) and Wu et al. (2016) provide further support for the recognition of Lestoniidae as the sister group of the Acanthosomatidae.

Members of this family are relatively small (5-6 mm), ovoid, dorsally convex, and ventrally flattened (Schuh and Slater 1995). The scutellum is large in *Lestonia haustorifera* (**Figure 2.25D**) covering much, but not all, of the dorsum but usually reaching to near the apex of the abdomen; it is much shorter and more triangular in *L. grossi*. The margins of the head, pronotum, and basal areas of the coria, in both species, are laminately produced, giving the insect the appearance of a small tortoise beetle or scale. The pronotum is relatively large with the anterior angles reaching beyond the anterior margin of the compound eyes. The ocelli are quite small and widely separated. The antennae are relatively short, four-segmented. They have two-segmented tarsi, which has been used to link them with the Acanthosomatidae. Similarly, the females have a pair of small disclike organs located on abdominal sternite VI just anterior to and laterad of the external genitalia; again, these have been considered to be homologous to the Pendergrast's organs in the Acanthosomatidae; China (1955) speculated that they may help specimens adhere to the substrate. The two species possess a pair of small, transversely arrayed trichobothria (initial studies by China 1955 indicated that there was only a single trichobothrium on each segment; this was later corrected by China 1963) with the ental trichobothrium of each pair in line with the spiracular line. The female spermathecal duct lacks a dilation and a sclerotized rod; the spermathecal bulb is ball-shaped, without diverticula; Schuh and Slater (1995) indicated that *L. haustorifera* lacks flanges near the bulb, but they indicated such a flange is present near the spermathecal bulb in *L. grossi*.

Little is known about the biology of lestoniids. They have only been found near the growing tips of trees of the genus *Callitris* Ventenat (Cupressaceae) in mostly arid conditions, where they resemble small scales or tortoise beetles (Gross 1975b, Cassis and Gross 2002).

2.2.7 Megarididae McAtee and Malloch, 1928

Members of the Megarididae are rare in collections, probably due to their small size (less than 5 mm), and their secretive habits. It is also a small family in number of taxa, including a single extant genus (i.e., *Megaris*) and currently 18 species (**Table 2.2**), all occurring in the Neotropics (McDonald 1979). A second genus with one species (*Minysporops dominicanus* Poinar and Heiss) has been described from Dominican amber (Poinar and Heiss 2013). This group was not recognized as a family-level taxon until McAtee and Malloch (1928) proposed the subfamily Megaridinae within the Pentatomidae; they also provided a key to species known at that time. Kormilev (1954) elevated it to family status, a position that nearly all recent workers have recognized.

Members of this family, in general appearance, are quite similar to the Canopidae and some members of the Plataspidae, only much smaller (**Figure 2.16E**). Diagnostic characters (Schuh and Slater 1995, Schwertner and Grazia 2015) include the rounded shape, the convex dorsum, the flattened venter, and the usual shiny black color, occasionally with reddish spots or markings. The anterolateral margins of the head and pronotum are carinate; the bucculae are undeveloped. The antennae are four-segmented, with many long setae that are about the same length as the diameter of the antennal segment in females, and much longer in males. The scutellum is enlarged and nearly covers the abdominal dorsum (**Figure 2.16E**). Similar to the Canopidae, the forewings are longer than the abdomen, but they have a thin, weak area at about the middle of the costa, thus allowing the wings to fold up underneath the scutellum. The wing membrane lacks veins or has a single longitudinal vein. The tibiae lack spines or bristles; the tarsi are two-segmented. The coxal combs are absent. The female spermathecal duct lacks a dilation and sclerotized rod.

In the study by Grazia et al. (2008), the Megarididae are placed near the Plataspidae in their morphological studies. They did indicate that this placement was inconclusive because it was based heavily on the similar shape and structure of the scutellum. They stated that "body shape alone is misleading with regard to the establishment of phylogenetic affinities." Unfortunately, they were not able to obtain fresh material to do DNA studies, so the phylogenetic placement of this family within the Pentatomoidea remains unclear.

The biology and ecology of the megaridids are poorly known. It is believed that all species are exclusively phytophagous. *Megaris puertoricensis* Barber and *M. semiamicta* McAtee and Malloch have been recorded feeding on flowers of *Eugenia* L. species (Myrtaceae) (Schuh and Slater 1995). More recently, a specimen of an unknown species of *Megaris* was collected in a light trap placed inside a plot of cultivated species of *Eucalyptus* L'Héritier de Brutelle (Myrtaceae) in the state of São Paulo, Brazil (Cristiano F. Schwertner, unpublished data).

2.2.8 Mesopentacoridae Popov, 1968

Popov (1968b) erected a new fossil family, the Mesopentacoridae, to contain a single genus and species, *Mesopentacoris costalis* Popov. Superficially, this genus and species are similar in appearance to modern day urostylidids or the fossil coreoid family Pachymeridiidae (Yao et al. 2008). Popov (1989) added a second species, *M. orientalis*, and then in 1990, he added another genus and species, *Corienta transbaicalica*. Finally, in 1996, Ren et al. added a third genus with another new species, *Pauropentacoris macruratus*.

2.2.9 Parastrachiidae Oshanin, 1922

This family presently contains two genera (and eight species), *Dismegistus* (**Figure 2.25F**) and *Parastrachia* (**Figure 2.25E**) (**Table 2.2**), which have had similar but separate taxonomic histories. Distant (1883) originally placed *Parastrachia* in the Pentatomidae "somewhere between the genera *Strachia* Hahn [currently Strachiini] and *Catacanthus* Spinola [currently Catacanthini]." Oshanin (1922) placed *Parastrachia* in its own tribe, but still within the Pentatomidae. In the first thorough study of the group, Schaefer et al. (1988) established the subfamily Parastrachiinae within the family Cydnidae solely for the genus *Parastrachia*. Schaefer later (Sweet and Schaefer 2002) admitted that he had "private reservations" about this placement and felt that the Parastrachiinae probably deserved family status, a move that was made by Sweet and Schaefer (2002). This position has been supported by more recent studies (Grazia et al. 2008, Lis 2010).

Originally, *Dismegistus* was placed in the cydnid subfamily Sehirinae (Amyot and Serville 1843), a position that was supported by Stål (1876). Signoret (1880) transferred this genus to the Pentatomidae, placing it near the genus *Strachia* (currently Strachiini). Interestingly, Bergroth (1923) moved *Dismegistus* to the pentatomid subfamily Asopinae. Leston (1956a) returned the genus to its original placement as a member of the Sehirinae in the Cydnidae. Dolling (1981), in his thorough study of the Cydnidae and related families, removed *Dismegistus* from the Cydnidae, but he did not know where to place it. It remained in limbo until Pluot-Sigwalt and Lis (2008) noticed similarities with the genus *Parastrachia* (mainly in the structure of the spermatheca); at about the same time, Grazia et al. (2008) determined that *Dismegistus* and *Parastrachia* had similar DNA sequences. Consequently, *Dismegistus* only recently has been transferred into the Parastrachiidae.

A couple of factors may have contributed to the two genera having separate taxonomic histories. For example, they have different distributions, the two species of *Parastrachia* occurring from India through China, and into Japan, and the six species of *Dismegistus* being confined to the African continent. Furthermore, although members of both genera are usually red and black in coloration, their size and shape are different. Species of *Parastrachia* are somewhat larger, more slender, and somewhat similar in shape to some Largidae or Pyrrhocoridae (**Figure 2.25E**). Species of *Dismegistus* are smaller and much more ovoid in shape (**Figure 2.25F**). This also may help explain why few papers have been recently published on *Dismegistus* as compared to *Parastrachia*. Schaefer et al. (1991) reviewed the genus *Parastrachia*. The species have recently been catalogued (Lis 2006c).

Members of this family are small to medium in size and usually colored red and black; species of *Parastrachia* (**Figure 2.25E**) are larger and more slender, whereas species of *Dismegistus* (**Figure 2.25F**) are smaller and more broadly oval. The bucculae meet posteriorly, similar to that seen in the pentatomid subfamily Asopinae, but the rostrum is not particularly crassate, and these species are not typically predatory (united bucculae are also found elsewhere in the Pentatomoidea, including the pentatomid subfamily Edessinae, see **Section 2.2.10.6**). The antennae are five-segmented. The prosternum is medially sulcate; the sternal thoracic structure is similar to that seen in the Sehirinae, but parastrachiines have tibiae that are not adorned with bristles or spines. Both *Parastrachia* and *Dismegistus* possess coxal combs composed of an irregular series of long, narrow setae. The ostiolar rugae and associated evaporative areas are well developed in *Parastrachia*, but strongly reduced, obsolete in *Dismegistus*. Abdominal segment VIII is broadly exposed, similar to that seen in the Acanthosomatidae and the Urostylididae, but the bugs lack the claval commissure of the urostylidids; also, they have three-segmented tarsi, thus differing from the acanthosomatids. The female spermatheca is relatively simple, the duct lacking the dilation and sclerotized rod; the spermathecal bulb is simple, ball-shaped, with a pair of flanges present.

Virtually nothing is known about the biology of members of *Dismegistus*. On the other hand, much is known about *Parastrachia japonensis* Scott. Females of this species exhibit parental care as they will excavate an egg chamber in the soil or leaf litter, provision it with seeds, and stand guard over the eggs and early instars (Nomakuchi et al. 1998, 2001, 2005; Filippi et al. 2000a,b, 2001, 2002, 2005; Hironaka et al. 2003a,b, 2007a-c, 2008a,b). They are known to produce trophic eggs, that is eggs that are not viable but are used for food by offspring (Hironaka et al. 2005). The known host plant of *P. japonensis* is *Schoepfia jasminodora* Siebold and Zuccarini (Schoepfiaceae).

2.2.10 Pentatomidae Leach, 1815

The Pentatomidae is the largest family in the Pentatomoidea, containing 940 genera and 4,949 species in ten subfamilies (**Table 2.2**) with many new taxa still awaiting description. The total number of species undoubtedly will reach 5,000 in the near future and perhaps even 6,000 eventually. As with any large and diverse group, it is difficult to provide defining characters that work for all members. The Pentatomidae was proposed by Leach (1815) as a family group; he included it together with the Scutelleridae in a taxon currently equivalent to the Pentatomoidea. Burmeister (1835) referred to this group as the Scutata.

Amyot and Serville (1843) presented one of the first classifications of the Pentatomoidea (**Table 2.1**). Their "famille Longiscutes" (long scutellum) is essentially equivalent to our present day Pentatomoidea. Amyot and Serville divided this 'family' into two large groups, the Orbiscutes for those taxa with a scutellum that covered most of the abdomen, and the Coniscutes for those taxa in which the scutellum did not nearly cover the entire abdomen. They further divided the Orbiscutes into two "races" based on body shape: the Anguleux contained those taxa that were somewhat more flattened (our present day scutellerids, podopines, and cyrtocorines), and the Globuleux contained those taxa that were rounded and more globular in shape (our present day thyreocorids, canopids, and some scutellerids). The remaining Coniscutes were separated into smaller groups using some of the same characters we use today (e.g., size and length of rostrum, the armature of the venter, and whether the legs had spines or not).

Dallas (1851) recognized many of the same taxa but now at the family level (Asopidae, Edessidae, Halydidae, Oxynotidae, Pentatomidae, Phyllocephalidae and Podopidae) within the group Scutelleroidea. Fieber (1861) recognized two more family groups, the Macropeltidae and Discocephalidae. Stål (1865) considered only the subfamilies Asopida, Pentatomida, and Phyllocephalida in a more inclusive Pentatomidae. He refined his classification in later works (Stål 1870-1876), treating also Discocephalina and Oxynotina as subfamilies and dividing the Pentatomina into several groups of genera (see comment below in the Pentatominae section); current genera included in Podopinae were recognized as a distinct group within Pentatomina. The taxa recognized in the Stål-based classification (**Table 2.1**) were largely followed by subsequent workers (e.g., Lethierry and Severin 1893, Kirkaldy 1909, Oshanin 1912, Leston 1952a, China and Miller 1955, Linnavuori 1982). The works of Singh-Pruthi (1925) and Pendergrast (1957) helped establish the current limits of the family. Based on the male and female genitalia, the results of these two authors supported the recognition of a single group including five of Stål's subfamilies (Asopinae, Discocephalinae, Pentatominae, Phyllocephalinae, and Podopinae). This arrangement has been refined and expanded (Leston 1958; McDonald 1966; Gross 1975b; Rolston and McDonald 1979; Gapud 1991; Rider 2006a, 2015c; Cassis and Gross 2002; Grazia et al. 2008).

The family Pentatomidae represents a well-supported group among the Pentatomoidea, based on both morphology and molecular data (Gapud 1991; Henry 1997; Li et al. 2005; Xie et al. 2005; Grazia et al. 2008; Li et al. 2012; Yao et al. 2012). Morphological synapomorphies include gonapophyses 8 and first rami lost (non-homoplastic); gonapophyses 9 reduced, fused to gonocoxites 9, second rami lost (non-homoplastic); and spermathecal duct dilated, its distal orifice provided with a sclerotized invagination (slerotized rod) (homoplastic) (Gross 1975b, Gapud 1991, Grazia et al. 2008). However, with such a large group, there is much variation in size, shape, and coloration, thus making it difficult to give a precise diagnosis for the family.

Some of the smallest species (*Sepontia*) are only a couple of millimeters in length, whereas some species of *Alcaeorrhynchus* Bergroth (**Figure 2.17B**), *Catacanthus* (**Figure 2.29C**), *Porphyroptera* China, *Mustha* Amyot and Serville, and *Xiengia* Distant are quite large, approaching or surpassing 25-35 millimeters. The body is usually broad and ovate, but some grass-feeding species are quite long and slender (e.g., *Acoloba* Spinola [**Figure 2.21D**], *Aelia* F. [**Figure 2.28A**], *Mecidea* Dallas [**Figure 2.30F**]). All variations of coloration exist, from browns and greens allowing the individuals to blend in with their surroundings, to bright reds, oranges, and blues, sometimes in metallic hues (**Figures 2.27A-2.32L**). The family is characterized further (Schuh and Slater 1995, Grazia et al. 2015) by the antennae usually having five segments, although some subfamilies (Cyrtocorinae, Serbaninae) and species only have four, and at least one halyine genus, *Omyta* Spinola, has only three. The scutellum is usually large and subtriangular, although it may be enlarged in some groups, and even cover a large portion of the abdomen in some asopines, podopines, and pentatomines. Frena are present, and they usually extend beyond the middle of the scutellar margins; the clavi usually do not extend beyond the apex of the scutellum, so the claval commissure is lacking. In many groups, the thoracic sterna are sulcate medially, whereas in more advanced groups, the sulcus has been replaced by a medial carina. The tarsi are usually three-segmented, but they are only two-segmented in the Cyrtocorinae, Stirotarsinae, and in some minor pentatomine tribes or isolated genera. The abdominal trichobothria are usually transverse, and located near the spiracular line. In some species, there are areas on the abdominal venter on each side that appear to be thinner, somewhat opaque; these "cuticular patches" were studied in a series of papers (Staddon 1992, 1998, 2000; Staddon and Ahmad 1994; Staddon et al. 1994). The female spermathecal duct has a dilation with a long, slender, sclerotized rod evaginated from the distal orifice; the spermathecal pump is well-developed with both a proximal and a distal flange; the spermathecal bulb may be simple, digitoid, or ball-shaped, often with one to three tubular diverticula. The eggs are usually barrel-shaped with a pseudoperculum. Nearly 300 species of Pentatomidae have been karyotyped; the diploid number varies from 10 + XY up to 24 + XY, but the most common diploid number by far is 12 + XY (Ueshima 1979, Kerzhner et al. 2004, Rebagliati et al. 2005).

Almost all subfamilies of Pentatomidae are well-defined by unique apomorphies, supporting the monophyly of these taxa (Rolston and McDonald 1979, Gapud 1991, Konstantinov and Gapon 2005, Campos and Grazia 2006, Gapon and Konstantinov 2006). The only exception is the subfamily Pentatominae, a 'catch-all' taxon that includes several genera and groups of genera not recognized in any of the other subfamilies (Cassis and Gross 2002).

The phylogenetic relationships among pentatomid lineages have been almost completely ignored. Leston (1953a, 1954a) was the first to document and discuss the monophyly and phylogenetic relationships within the Pentatomidae. McDonald (1966), Gross (1975b), and Linnavuori (1982) expanded these studies and suggested good apomorphic characters for the recognition of several monophyletic groups within the family. Gross (1975b) and Linnavuori (1982) also discussed possible phylogenetic relationships among those groups. Gapud (1991) and Hasan and Kitching (1993) were the first authors to discuss phylogenetic relationships with the Pentatomidae based on phylogenetic trees.

More recently, studies under a phylogenetic framework have been conducted at different taxonomic levels. The monophyly of the subfamily Edessinae was tested in part by Barcellos and Grazia (2003b); they also proposed hypotheses concerning the relationships among the included genera. The work of Campos and Grazia (2006) supported the monophyly of the tribe Ochlerini (Discocephalinae); Garbelotto et al. (2013) and Roell and Campos (2015) expanded the knowledge about phylogenetic relationships within this tribe. Concerning the subfamily Pentatominae, phylogenetic studies at the tribal (Schaefer and Ahmad 1987, Memon et al. 2011, Schwertner and Grazia 2012), groups of genera (Grazia 1997, Bernardes et al. 2009), and genera levels (Thomas 1985, Fortes and Grazia 2005, Ferrari et al. 2010, Greve et al. 2013) have been published. But most of the subfamilies, tribes, and groups of genera have never been studied in a phylogenetic framework, and the relationships within the Pentatomidae remain unknown. The results of Gapud (1991) and Grazia et al. (2008) suggest that the Aphylinae and Cyrtocorinae may be basal lineages, but a definitive conclusion and better resolution at the family and tribal levels in the phylogenetic hypothesis presented were limited by the scope of the study conducted. The pentatomid subfamilial and tribal classification used in this book is outlined in **Table 2.3**.

We will not go into the biology of the Pentatomidae here. Some notes on biology, habitats, etc., will be discussed under the subfamily and tribal sections, and also in many of the chapters throughout this book. The Australian, Iranian, North American, and Palearctic species have recently been catalogued by Cassis and Gross (2002), Ghahari et al. (2014), Froeschner (1988c), and Rider (2006a), respectively. Salini and Viraktamath (2015) provided keys for the identification of the South Indian genera. Grazia et al. (2015)

TABLE 2.3

Pentatomidae Classification and Diversity

							Total	
Subfamily	**Tribe**	**Genera[1]**	**Species[1]**	**Tribe**	**Genera[1]**	**Species[1]**	**Genera[1]**	**Species[1]**
Aphylinae							2	3
Asopinae							63	303
Cyrtocorinae							4	11
Discocephalinae							81	325
	Discocephalini	46	195	Ochlerini	35	130		
Edessinae							15	338
Pentatominae							660	3484
	Aeliini	4	28	Hoplistoderini	7	35		
	Aeptini	8	19	Lestonocorini	4	20		
	Aeschrocorini	8	20	Mecideini	1	16		
	Agaeini	2	11	Memmiini	1	7		
	Agonoscelidini	1	26	Menidini	28	164		
	Amyntorini	6	8	Myrocheini	25	75		
	Antestiini	29	171	Nealeriini	2	4		
	Axiagastini	4	12	Nezarini	26	272		
	Bathycoeliini	1	32	Opsitomini	1	1		
	Cappaeini	24	151	Pentamyrmecini	1	1		
	Carpocorini	127	503	Pentatomini	56	316		
	Catacanthini	11	63	Phricodini	1	7		
	Caystrini	14	66	Piezodorini	5	21		
	Chlorocorini	10	77	Procleticini	11	36		
	Coquereliini	4	5	Rhynchocorini	18	106		
	Degonetini	1	2	Rolstoniellini	6	19		
	Diemeniini	14	55	Sciocorini	16	126		
	Diplostirini	2	2	Sephelini	10	34		
	Diploxyini	5	29	Strachiini	20	142		
	Eurysaspini	3	25	Triplatygini	4	9		
	Eysarcorini	19	230	Unplaced	29	108		
	Halyini	91	430					
Phyllocephalinae							**45**	**214**
	Cressonini	6	12	Phyllocephalini	32	167		
	Megarrhamphini	3	12	Tetrodini	4	23		
Podopinae							**68**	**269**
	Brachycerocoris group	3	13	*Podops* group	28	135		
	Deroploa group	9	20	*Tarisa* group	3	22		
	Graphosoma group	19	70	Unplaced	6	9		
Serbaninae							**1**	**1**
Stirotarsinae							**1**	1
TOTAL							**940**	**4949**

[1] Numbers of genera and species are compiled from the World Catalog of Pentatomoidea (David A. Rider, unpublished, as of April, 2017) and include subgenera, subspecies, and fossil genera and species.

compiled information for the Neotropical species. A key to the subfamilies and tribes of American Pentatomidae was provided by Rolston and McDonald (1979). Local monographs and checklists are available for several countries or larger geographic areas.

2.2.10.1 Key to the Subfamilies of Pentatomidae (modified from Schuh and Slater 1995)

1 Tarsi 2-segmented, longitudinally carinate dorsally (**Figures 2.14A, B**); rostrum apparently 3-segmented, flattened (**Figure 2.14C**); antennae 5-segmented, with antennal segments II and V enlarged, inflated, segment III small; Neotropics (**Figures 2.13F, 2.14D, 2.27L**).... Stirotarsinae

1’ Tarsi usually 3-segmented, if 2-segmented then lacking longitudinal carina dorsally; rostrum clearly 4-segmented, rounded (not flattened); antennae may be 3 to 5 segmented, but never with both segments II and V enlarged or inflated and segment III small 2

2(1) Scutellum enlarged, covering most of abdomen (lateral margins uncovered) (**Figure 2.27A**); pronotum curves downward and posteriorly, forming a large posterolateral lobe on each side, with a large, distinct posterolateral notch that leaves a 3-4 sclerite portion of the mesopleural region exposed (exponium); head rather short, not extending much beyond eyes (**Figure 2.5A**); Australia (**Figures 2.17A, 2.27A**) .... Aphylinae

2’ Scutellum usually subtriangular, sometimes more expansive; pronotum not as described above, exponium absent; head usually more elongate 3

3(2) Rostrum rather short, exceeding at most slightly beyond procoxae (**Figures 2.10, 2.5B**); Old World (**Figures 2.18H; 2.27G, H**) .... Phyllocephalinae

3’ Rostrum more elongate, extending well beyond procoxae 4

4(3) Rostrum distinctly thickened, especially segment I which does not lie entirely between bucculae (**Figures 2.5C-E**); worldwide (**Figures 2.17B-F; 2.27B**) .... Asopinae

4’ Rostrum not distinctly thickened, segment I lying entirely between bucculae or only slightly beyond posterior buccal margins of bucculae 5

5(4) Antennae 3- or 4-segmented 6

5’ Antennae 5-segmented 8

6(5) Bucculae obsolete, shorter than first rostral segment; body extremely flattened; Borneo (**Figure 2.27K**) .... Serbaninae

6’ Bucculae well developed, nearly as long, subequal, or longer than first labial segment; body not extremely flattened, more robust 7

7(6) Scutellum produced dorsad into a robust thorn-like projection medially (**Figure 2.17G**); tarsi two-segmented; body usually gray to dark gray, covered by a very dense pubescence composed of short and thick setae, dorsal surface rather rough; New World tropics (**Figures 2.17G, 2.27C**) .... Cyrtocorinae

7’ Scutellum usually not produced into a robust thorn-like projection, if projection is present, then tarsi three-segmented, coloration and vestiture different and dorsal surface not roughened (the New World edessine genus *Peromatus* will also key here, but it has the mesosternum produced anteriorly as a bifurcate process [**Figure 2.5G**]); worldwide ...... Pentatominae (in part)

8(5) Metasternum produced anteriorly onto mesosternum or rarely prosternum (**Figures 2.5F-H**); rostrum not surpassing mesocoxae (**Figures 2.5F-H**); New World (**Figures 2.18E-G; 2.27F**) .... Edessinae

8’ Metasternum rarely produced anteriorly onto mesosternum but if so, then rostrum extending onto abdomen or at least to metacoxae 9

9(8) Trichobothrium nearest spiracle on sternum 7 laterad of spiracular line by distance at least equal to greatest diameter of spiracular opening (**Figures 2.5I, J**) 10

9’ At least one trichobothrium on sternum 7 on or mesad of spiracular line (**Figure 2.5K**) 11

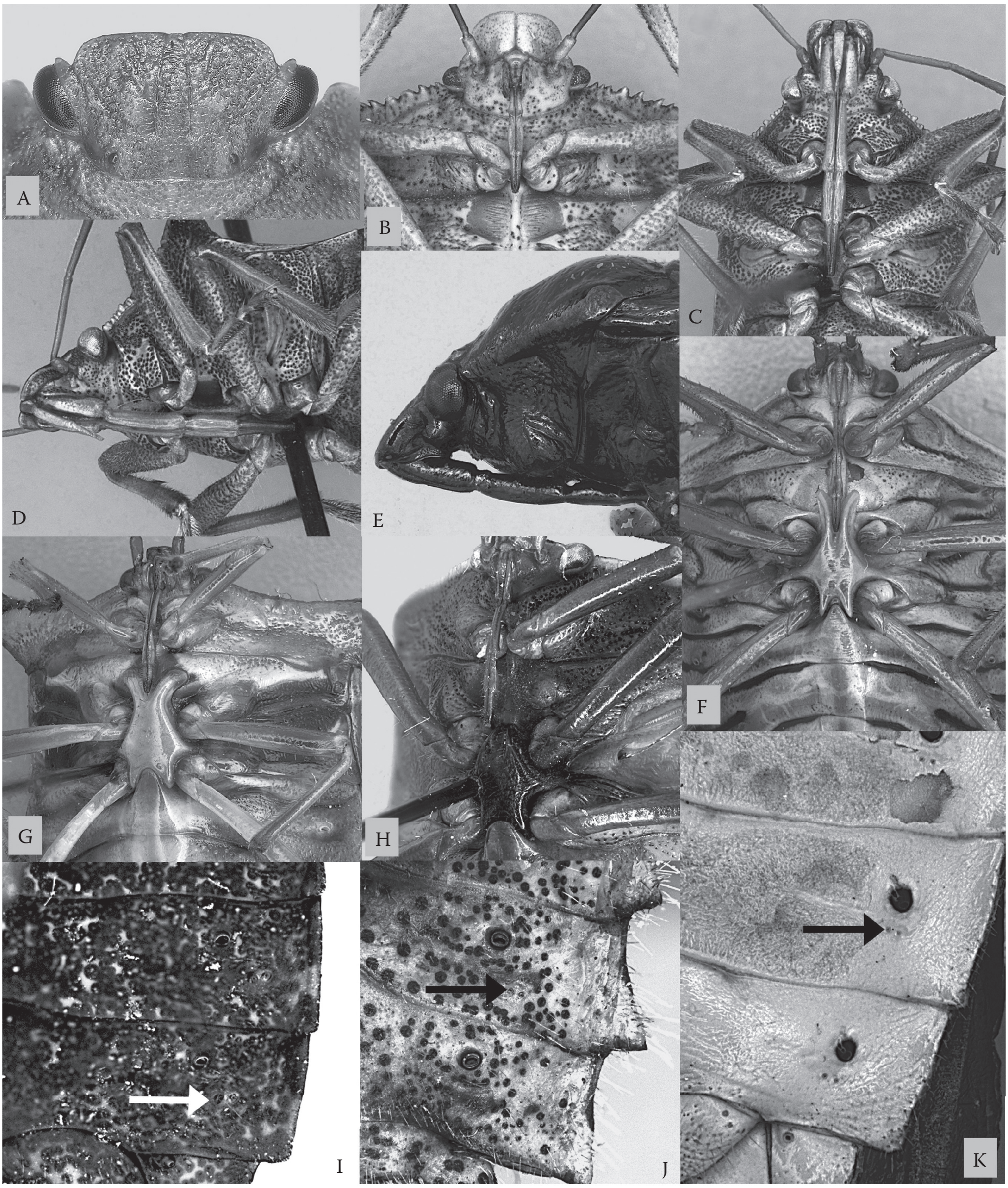

FIGURE 2.5 A, *Aphylum syntheticum*, head, anterodorsal view; B, *Basycriptus distinctus*, head and anterior thorax, ventral view; C, *Picromerus bidens*, head and thorax, ventral view; D, *Picromerus bidens*, head and thorax, ventrolateral view; E, *Zicrona caerulea*, head and thorax, lateral view; F, *Edessa rufomarginata*, thoracic sterna, ventral view; G, *Peromatus notatus*, head and thorax, ventrolateral view; H, *Brachystethus geniculatus*, thorax, ventrolateral view; I, *Macropygium reticulare*, lateral margins of abdominal segments VI and VII, ventral view; J, *Dryptocephala spinosa*, lateral margins of abdominal segments VI and VII, ventral view; K, *Pellaea stictica*, lateral margins of abdominal segments VI and VII, ventral view.

10(9) Base of abdominal venter with mesal tubercle; metasternum produced, flattened; worldwide .... Pentatominae (in part)

10' Base of abdominal venter rarely tuberculate but if so, then metasternum thinly carinate mesally; New World .... Discocephalinae (in part)

11(9) Rostrum arising on or posterior to an imaginary line traversing head at anterior limit of eyes (**Figures 2.6A, B**) and/or superior surface of tarsal segment III of hind legs shallowly excavated in females (**Figure 2.6C**); New World .... Discocephalinae (part)

11' Rostrum arising anterior to an imaginary line traversing head at anterior limit of eyes (**Figures 2.1M, N; 2.6E**); superior surface of tarsal segment III of hind legs convex or flattened in both sexes 12

12(11) Tibiae usually sulcate on outer surface (**Figure 2.6D**); rostral segment I often longer than bucculae (**Figure 2.6E**); trichobothria paired; scutellum not reaching apex of abdomen; frena one-third or more length of scutellum (**Figure 2.6F**) worldwide .... Pentatominae (in part)

12' Tibiae not sulcate on outer surface; rostral segment I usually not longer than bucculae; trichobothria single (**Figure 2.6G**) or paired; scutellum usually reaching apex of abdomen (**Figure 2.6H**); frena short, less than one-third length of scutellum (**Figure 2.6H**), but if one-half length of scutellum, then scutellum not reaching apex of abdomen; worldwide (**Figures 2.18I-L; 2.27I, J**) .... Podopinae

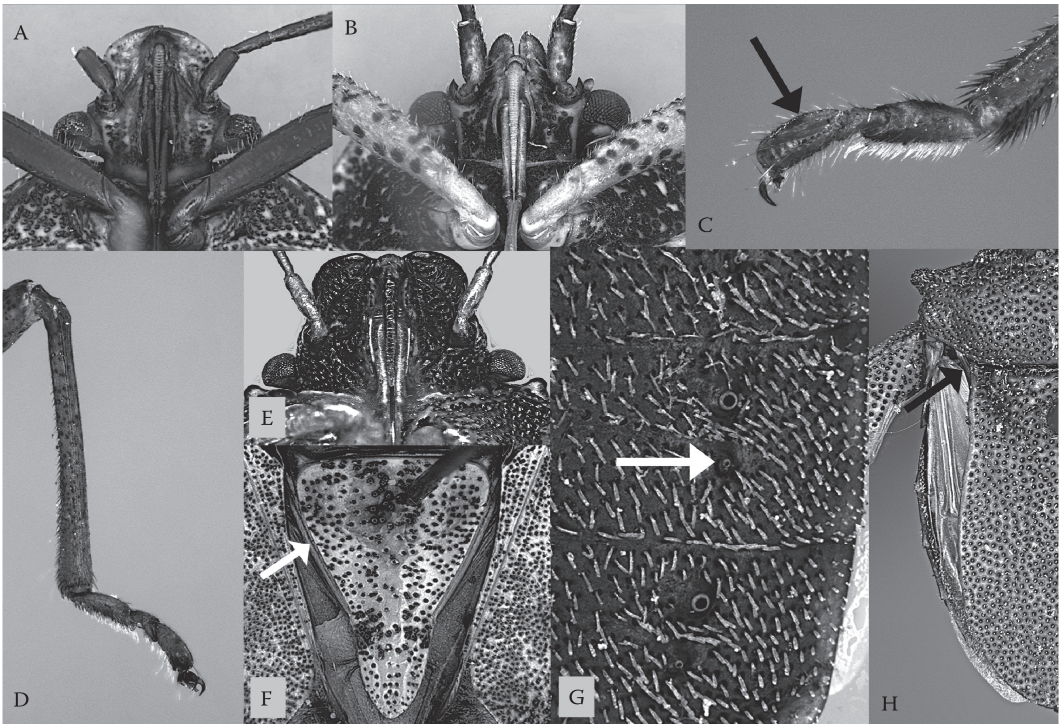

FIGURE 2.6 A, *Antiteuchus mixtus*, head, ventral view; B, *Macropygium reticulare*, head, ventral view; C, *Miopygium cyclopeltoides*, tarsus, dorsolateral view; D, *Pentatoma rufipes*, tibia, inner view; E, *Eysarcoris aeneus*, head, ventral view; F, *Rhaphigaster nebulosa*, scutellum, dorsal view; G, *Amaurochrous dubius*, lateral margins of abdominal segments V, VI and VII, ventral view; H, *Amaurochrous dubius*, detail of scutellum, dorsal view.

2.2.10.2 Aphylinae Bergroth, 1906

This is a small group (two genera, three described and several undescribed species) endemic to Australia (**Tables 2.2, 2.3**). As with other pentatomine taxa, it has had an interesting taxonomic history. Originally, it was described as a subfamily of the Pentatomidae (Bergroth 1906b); that same year, Schouteden published a detailed monograph of the subfamily (Schouteden 1906). Reuter (1912) and China and Miller (1959) treated this group as a family; Gross (1975b) lowered it back to a subfamily, indicating that it might be related to the podopine genus *Tarisa* Amyot and Serville. In their review of the World Heteroptera, Schuh and Slater (1995) once again treated this group as a family, a position which was followed by Cassis and Gross (2002) and Kment et al. (2012). Recently, as a result of their cladistic analysis, Grazia et al. (2008) concluded that for now, it should be treated as a pentatomid subfamily. The genitalia of both sexes, particularly the presence of a distinct pentatomid-type sclerotized rod within the dilation of the female spermathecal duct, support this placement.

Members of this subfamily are relative small (usually less than 5 mm), oval, with the dorsal surface strongly convex and the pleural and abdominal areas flattened or concave (Schuh and Slater 1995) (**Figure 2.17A**). The scutellum, somewhat enlarged, usually extends to the apex of the abdomen but leaves the connexiva and lateral portions of the coria exposed (**Figure 2.27A**). The pronotum curves downward and posteriorly forming a large posterolateral lobe on each side, with a large, distinct posterolateral notch, which in turn leaves three to four sclerites of the mesopleural region exposed (normally covered by the forewings in other pentatomoids); this region has been given the term exponium by Štys and Davidová-Vilímová (2001). Its function is to draw the defensive secretion from the metathoracic scent glands upwards to the outer surface of the body (Kment et al. 2012). The head is relatively short and broad, barely extending anteriorly beyond the compound eyes. The parameres, at least in the genus *Aphylum* Bergroth, have two articulating sections. The female spermathecal duct has a distinct sclerotized rod that is narrowed apically and hooked; the spermathecal bulb is globose with two finger-like diverticula (McDonald 1970).

This subfamily contains two genera, *Aphylum* (**Figures 2.17A, 2.27A**) with two described species distributed in eastern Australia, and the recently described *Neoaphylum* Štys and Davidová-Vilímová with a single species only known from western Australia. The only known biological information is that some specimens have been collected from under the bark of the River Red Gum, *Eucalyptus camaldulensis* (Myrtaceae) (Cassis and Gross 2002). Štys and Davidová-Vilímová (2001) stated that the spiracular structure in *Neoaphylum* (with a "stopper"-like structure located in each spiracle) indicated that this species might be adapted to live in dry, arid regions.

2.2.10.3 Asopinae Amyot and Serville, 1843

The asopines are considered and recognized as a natural (e.g., monophyletic) taxon, having as a defining synapomorphy a crassate rostrum (**Figures 2.5C-E**) (Gapud 1991). An adaptation for predation, the "beak" consists of barbed stylets strengthened by the thickened rostrum are used to "spear" their prey and hold it at beaks-length, thus limiting potential injury when the prey, typically larvae of holometabolous insects, thrashes in an effort to escape. Additionally, the bucculae are united behind the oral groove, not open as in the Pentatominae. United bucculae is likely a plesiomorphic character as it is found in other pentatomid groups (e.g., Edessinae) as well. In many, but not all, genera, the forelegs seem to be adapted for predation with spurs on the profemora and a foliate expansion of the protibiae (also seen in several phytophagous species) (**Figure 2.27B**), possibly to ward off counter-attacks by the prey. Barão et al. (2013) cite the protibiae of asopines as unique and a defining apomorphy for the subfamily. Many asopines have the evaporatoria reduced compared to the typical non-predatory stink-bugs and such reduction would presumably minimize the problem of the scent giving away their presence to potential prey.

Predatory behavior is not limited to the asopines. Insectivory by species in the halyine genus *Brochymena* Amyot and Serville has been observed with sufficient frequency to conclude that they are at least adventitious predators. They have a non-crassate rostrum and, thus, lack specific adaptations for predation unless one counts the foliate protibiae and reduction in the external structures of the metathoracic scent gland apparatus. Reductions in the scent gland apparatus occurs in some unrelated pentatomines and podopines (e.g., *Braunus* Distant, *Murgantia* Stål, *Tornosia* Bolívar) but is likely a convergent adaptation for avoidance of parasitoids that are known to key on the scent to find their hosts. Moreover, at least one genus of asopines, *Tylospilus* Stål, has species that are at least partially, and presumably secondarily, herbivorous (Stoner et al. 1974), and this latter genus has the least crassate rostrum in the subfamily.

Although predation, and its accompanying adaptations, could result from convergence, important synapomorphies of the genitalia strongly support asopine monophyly. Although neither feature, the thecal shield (apical part of theca *sensu* Gapon and Konstantinov 2006) or the genital plates (parandria *sensu* Tuxen 1970) is unique to the asopines, these bugs are the only pentatomids that have both in combination (McDonald 1966).

Members of the Asopinae are found in both the Old and New World and also in the Pacific islands. The Old World fauna consists of 40 genera (Thomas 1994b) and the New World 26 (Thomas 1992b), with four genera found in both. Gapon (2010a) added a new New World genus bringing the total to 63 genera, with 303 species worldwide (**Tables 2.2, 2.3**). The exact number of species is in doubt because many of the larger Old World genera have not been revised recently. Nomenclatural notes and a checklist of the Chinese species was provided by Rider and Zheng (2002). When making identifications of asopine specimens, the two monographs by Thomas should be consulted. His 1992b publication provides keys to the genera and species of the New World taxa; his 1994 work provides keys to the Old World genera and checklists of the known species. Also, the Euro-Mediterranean taxa were treated by Péricart (2010). Two older papers that still provide very useful information for identifying taxa are those by Schouteden (1905a, 1907). The Chinese species of the genera *Amyotea* Ellenrieder and *Picromerus* Amyot and Serville have been reviewed by Zhao et al. (2011, 2013) respectively. Other genera that have been reviewed, either in part or in whole, include *Anasida* Karsch (Ahmad and Rana 1991), *Arma* Hahn (Ahmad and Önder 1990a, Zheng 1981), *Blachia* Walker (Ahmad and Rana 1994), *Canthecona* Amyot and Serville (Ahmad and Rana 1988, Khuong and Lam 2001), *Oechalia* Stål (Usinger 1941, 1942), *Perillus* Stål (Knight 1952), *Picromerus* (Ahmad and Önder 1990b), and *Rhacognathus* Fieber (Josifov and Kerzhner 1978).

The tribal classification is unresolved. Various suprageneric names have been proposed but not in the context of a formal classification. The oldest name applied to the group, Spissirostres, by Amyot and Serville (1843) was not based on a genus name and, therefore, has no significance in tribal classification. Kirkaldy (1909) used the name "Cimicinae" for the group based on the genus *Cimex*, but a subsequent ICZN decision restricted this name to the bed bugs and, thus, cannot apply to Asopinae. The name Asopinae, based on the genus *Asopus* Burmeister, was proposed by Amyot and Serville (1843) as "Asopides." Tribal names that have been proposed, and their type genera, are provided in **Table 2.4**.

When Amyot and Serville (1843) divided their "Spissirostres" into two subordinate taxa (i.e., Asopides and Stirétrides), they were following Burmeister's (1835) Handbuch that recognized three genera: *Stiretrus* Laporte, *Discocera* Laporte, and *Asopus*. Their "Asopides" included only *Asopus*, and their "Stirétrides" included *Stiretrus* and *Discocera*. Thus, Kirkaldy's (1909) selection of *Asopus gibbus* Burmeister, a junior synonym of *Discocera cayennensis* Laporte, as the type-species of *Asopus*, was unfortunate as it rendered Asopini, Stiretrini, and Discocerini as synonymous. Kirkaldy was a strict priorist and his selection serves as an excellent example for not always adhering to strict priority.

TABLE 2.4

Proposed Asopine Tribal Names, Authority and Nominate Genus

Asopini Amyot & Serville (1843) based on *Asopus* Burmeister
Stiretrini Amyot & Serville (1843) based on *Stiretrus* Laporte
Armini Bergroth (1904) based on *Arma* Hahn
Discocerini Schouteden (1907) based on *Discocera* Laporte
Amyotini Schouteden (1907) based on *Amyotea* Ellenreider
Jallini Dupuis (1949) based on *Jalla* Hahn
Stilbotini Gapud (2015) based on *Stilbotes* Stål

As Amyot and Serville (1843) and Schouteden (1907) perceived, there does appear to be a natural dichotomy within the asopines. Although many of the genera are coarsely punctate and cryptically colored in earth-tones (i.e., brown, tan, gray or black), about an equal number are glabrous and aposematic (i.e., brightly colored or even metallic). There is circumstantial evidence that the bright colors are meant to mimic the colors of the prey, typically chrysomelid beetles (van Doesburg 1970, Schaefer 1996); this could be aggressive mimicry allowing the pentatomids to move closer to their prey without being noticed, but it could also be a form of protective mimicry as both the pentatomids and the chrysomelids probably taste bad to predators. But there is only weak support from the other character states that would suggest that aposematic coloration is synapomorphic. Given the limited material at hand, it is likely that Amyot and Serville's concept of the "Asopides" was meant for the dull-colored forms and would be most exemplified by *Asopus argus* (F.), [now *Amyotea malabarica* (F.)], which Bergroth (1911) argued should be the type species for the asopines. This led to Leston's (1953a) proposal to replace the subfamily name with Amyotinae, which would have had as its nominate tribe Amyotini. But the oldest name for this tribe is Armini, based on the genus *Arma*, as proposed by Bergroth (1904), leaving the nominate tribe Asopini typified by the genus *Discocera*.

The most striking apomorphy in the group is the presence of a pair of pilose glands on the abdominal sternum of males. It has been shown that this gland secretes an aggregative pheromone that is released when the males find prey. This attracts other members of the species including potential mates (Aldrich 1988, Aldrich and Lusby 1986). Of the 62 genera for which males are known (*Australojalla* Thomas is known from a single female), 23 have the abdominal glands. The glands are present in *Afrius* Stål (except the subgenus *Subafrius* Schouteden), *Andrallus* Bergroth, *Apateticus* Dallas, *Apoecilus* Stål, *Blachia* Walker, *Bulbostethus* Ruckes, *Canthecona*, *Cazira* Amyot and Serville, *Coryzorhaphis* Spinola, *Discocera*, *Eocanthecona* Bergroth, *Heteroscelis* Latreille, *Hoploxys* Dallas, *Leptolobus* Signoret, *Macroraphis* Dallas (except the subgenus *Megarhaphis* White), *Mecosoma* Dallas, *Montrouzierellus* Kirkaldy, *Oplomus* Spinola, *Perillus*, *Platynopiellus* Thomas, *Platynopus* Amyot and Serville, *Stilbotes* Stål, and *Stiretrus*. Because of its complexity, function, and, most importantly, the constant nature of its morphology among genera, there is little likelihood that its presence is the result of convergence rather than relationship. Its absence in two subgenera of genera that possess them would be explainable as a secondary loss. Because the above 23 genera include *Asopus*, they would constitute the nominotypical tribe Asopini.

Species with reduced or suppressed glands are known at least in the genera *Afrius*, *Cazira* (**Figure 2.27B**), and *Macroraphis*. This indicates that the glands could have been lost multiple times. The non-glandular genera would constitute a sister clade, an arrangement consistent with the dichotomy envisioned by early workers, Amyot and Serville (1843), Schouteden (1907) and Bergroth (1904, 1911). But, inasmuch as it is defined by a plesiomorphy, the resulting clade, functionally the Armini, may well be polyphyletic. Within this group, a second tribe has been proposed by Dupuis (1949). The Jallini was erected to include *Jalla* Hahn and *Zicrona* Amyot and Serville, but there is no reason to suspect that *Jalla* and *Zicrona* are related. Dupuis cited the extension of the seventh abdominal tergite; however, the extension is found also in the genus *Dorycoris* Mayr, which shares no apomorphic characters with either of the two genera included by Dupuis and thus there is minimal support for the tribe as proposed. We suspect that *Jalla* more likely is related to the genera *Amyotea*, *Anasida*, and *Pseudanasida* Schouteden (but not *Jalloides* Schouteden or *Australojalla*) based on a similarly broad but flattened body form and the scent-gland ruga is gutter-like. Without a formal phylogenetic analysis to define its relationships, we consider that Dupuis' Jallina is no more than a subclade of Armini, moreover with *Zicrona* excluded.

Similarly, within the clade of male-gland possessing genera, the monotypic tribe Stilbotini has been proposed by Gapud (2015) based on *Stilbotes*, from the Philippines. Based on a suite of shared characteristics, *Stilbotes* is related to the African genus *Leptolobus*. Both genera have pedunculated eyes distant from the cervix (i.e., a membranous area between the head and thorax), a bilobed thorax, and spinous humeri. Both genera also have the male abdominal glands and therefore fall within the Asopini; thus, Stilbotini is probably a subclade of the latter tribe. Until a formal phylogenetic analysis can confirm its validity, we propose that Gapud's name should be treated as a synonym of the Asopinae, being a subclade of Asopina, including *Leptolobus*.

In a study of the aedeagus of the Asopinae, Gapon and Konstantinov (2006) found three more or less distinct patterns; however, one genus (*Euthyrhynchus* Dallas) was difficult to place into any of the categories. As only 18 of the 63 asopine genera were studied, and no studied genus included more than one species (which might have provided information on how plastic or consistent the characteristics are), the results of this work should be tested on a larger sample. The three groups outlined by Gapon and Konstantinov did not correspond to the groups possessing or lacking male abdominal glands. This lack of congruent pattern might suggest that either the male genital characters, or the abdominal glands, or perhaps both are subject of convergent/homoplastic evolution. Gapon and Konstantinov wisely eschewed proposing tribal designations for their schemes, a decision we support.

Only two fossil species have been described in the Asopinae, one of which has been transferred into the Pentatominae. The species still treated as an asopine is *Asopus puncticollis* Piton (1940). The other species, *Arma contusa* Förster (1891), was later placed as a synonym of *Eysarcoris mammillata* Förster (Théobald 1937), which is a member of the Pentatominae: Eysarcorini.

2.2.10.4 Cyrtocorinae Distant, 1880

The Cyrtocorinae is a small subfamily containing four genera and eleven species, all restricted to the New World tropics (**Tables 2.2, 2.3**). They have bounced back and forth in being considered a subfamily within the Pentatomidae or being a separate family. For example, historically, Dallas (1851) and Walker (1867a) (using the synonymic preoccupied name Oxynotidae) treated this group as a family, Distant (1880) as a subfamily, Lethierry and Severin (1893) as a family, Kirkaldy (1909) as a subfamily, and so on. More recently, Schuh and Slater (1995) treated it as a subfamily, but Packauskas and Schaefer (1998), in their revision of the group, treated it as a family. The cladistic study of Grazia et al. (2008) supported the treatment of this group as a subfamily within the Pentatomidae. We also treat it as a subfamily, supported heavily by its members having a dilation and a sclerotized rod in the female spermathecal duct. Amyot and Serville (1843) first recognized this taxon as a family level group under the name Oxynotides; this name, however, was based on a preoccupied generic name, *Oxynotus* Laporte. Family names based on preoccupied generic names are not allowed, so White (1842) proposed *Cyrtocoris* as a replacement generic name, but it was Distant (1880) who first used Cyrtocorinae as a family-level name.

Members of this family are small to medium in size (6-10 mm), somewhat squarish in shape (**Figure 2.27C**), sometimes with long spine-like projections in various directions. They are usually dark grey to black in color, but often appear somewhat lighter because of the presence of many small brown-tan or white scale-like setae (Rolston and McDonald 1979, Packauskas and Schaefer 1998). Their dorsal surface is quite roughened, irregular, and almost granulate (**Figures 2.17G, 2.27C**). They are characterized by the flattened expansions of the juga; the form of the scutellum, which usually reaches the apex of the abdomen; and the presence of a rather robust dorsal thorn-like protuberance on the scutellum (**Figure 2.17G**). The antennae are four-segmented. The tarsi are two-segmented.

Brailovsky et al. (1988) described life history traits of two species, *Cyrtocoris egeris* Packauskas and Schaefer and *C. trigonus* (Germar), which are summarized here. The eggs are deposited in grooves in the bark of hosts in masses of variable number (usually more than ten eggs). The nymphs are gregarious and remain on the same host during their entire development, which can last about 45 days. There is one generation per year, and the insects hibernate as adults. These species are exclusively phytophagous, and feeding sites mainly include the branches of the hosts. Host plant associations include species of Araceae, Euphorbiaceae, Fabaceae, Malvaceae, and Piperaceae (Brailovsky et al. 1988, Schaefer et al. 2005). The eggs and first-fifth nymphal instars of *C. egeris* have been recently studied by Bianchi et al. (2011).

2.2.10.5 Discocephalinae Fieber, 1860

The Discocephalinae presently contains 81 genera and 325 species, all endemic to the New World tropics (**Tables 2.2, 2.3**). Fieber (1860) proposed Discocephalidae to include *Discocephala* Laporte, *Dryptocephala* Laporte, and *Platycarenus* Fieber. The taxon was treated as a subfamily by Stål (1868), a classification followed by most subsequent authors (Stål 1872, Distant 1880, Lethierry and Severin 1893, Schuh and Slater 1995), although Kirkaldy (1909) and McDonald (1966) treated the group as a tribe (Discocephalini). The current classification was defined by Rolston and McDonald (1979), transferring to the Discocephalinae most of the New World genera formerly placed in the Halyini (Pentatominae). Rolston (1981) divided this subfamily into two tribes (i.e., Discocephalini and Ochlerini), erecting the Ochlerini for those genera that have the third tarsal segment of the hind legs in females excavate or flattened. More recently, Campos and Grazia (2006) supported the monophyly of this subfamily. Grazia et al. (2015) presented an updated checklist for the group.

Most members are yellows, greys, browns, and/or blacks, often mottled, helping them blend in with their environment. The body is sometimes somewhat flattened (many genera in the Discocephalini) or more robust and convex ventrally (many genera in the Ochlerini). The labium arises on or posterior to an imaginary line traversing the head at the anterior margins of the eyes (**Figures 2.6A, B**); the first rostral segment usually extends onto the anterior region of the prosternum. The antennae may be four or five-segmented. The metasternum is not produced anteriorly onto the mesosternum. The tarsi are three-segmented; in females in the Ochlerini, the dorsal surface of tarsal segment III of the hind legs usually is excavated and concave (**Figure 2.6C**). The trichobothrium nearest the spiracle on abdominal sternite VII usually arises laterad of the spiracular line (**Figures 2.5I, J**). Males of both tribes have the basal portion of abdominal segment X membranous; the conjunctiva are reduced; the phallotheca, ejaculatory duct, median penial lobes, and conjunctival appendages (when present) are strongly sclerotized; and the vesica is undifferentiated from the conjunctiva (Rolston and McDonald 1979, Schuh and Slater 1995, Konstantinov and Gapon 2005, Campos and Grazia 2006).

As mentioned above, this subfamily is endemic to the New World. There are, however, several Old World genera that are quite similar in habitus to the discocephalines. For example, the Australian genus *Cephaloplatus* White (**Figure 2.19I**) (currently in Caystrini) and *Discimita* Kment and Garbelotto (2016) from Central Africa (tentatively placed in the Myrocheini) are similar in appearance to the discocephaline genus *Dryptocephala*. Also, several genera from Southeast Asia and New Guinea [e.g., *Aednus* Dallas (currently in Myrocheini), *Goilalaka* Ghauri (currently in Halyini), and *Mimikana* Distant (currently in Halyini)] are quite similar in general appearance to some ochlerine genera. These similarities however, probably are due to convergence.

All species, as far as known, are phytophagous. There are not many host plant records available. The dull black ochlerines have been found under dead tree trunks where they may be feeding on fungi. Other ochlerine species, especially in the genus *Lincus* Stål, are known to vector a flagellate disease of cultivated palms (Dolling 1984, Asgarali and Ramkalup 1985, Louise et al. 1986, Resende et al. 1986, Resende and Bezerra 1990, Alvarez 1993, Mitchell 2004; also see **Chapter 13**). Several species, especially from the discocephaline genus *Antiteuchus* Dallas (**Figure 2.17H**), exhibit maternal care with the adults guarding the eggs and early instar nymphs (Rau 1918, Fennah 1935, Callan 1944, Eberhard 1975, Melber and Schmidt 1977, Santos and Albuquerque 2001a,b). In the Discocephalini, maternal care also has been recorded for species of *Dinocoris* Burmeister (**Figure 2.17I**), *Eurystethus* Mayr (**Figure 2.17J**), and *Mecistorhinus* Dallas (Tallamy and Schaefer 1997). More recently, Guerra et al. (2011) recorded for the first time trophobiosis between ants and a pentatomid species, *Eurystethus microlobatus* Ruckes. Rolston (1990, 1992) provided keys to the "broad-headed" genera of the Discocephalini (**Figures 2.12F, 2.17K, L; 2.27D**) and the genera of Ochlerini (**Figures 2.18A-D; 2.27E**), respectively. There is one fossil genus and species described in the Discocephalinae: *Acanthocephalonotum martinsnetoi* Petrulevičius and Popov (2014), however, its placement is based merely on external characters, and the genus could fit into the Pentatominae: Triplatygini as well.

Recently revised Discocephalini genera include: *Abascantus* Stål (Becker 1977), *Ablaptus* Stål (Rolston 1988a, Becker and Grazia 1989a), *Agaclitus* Stål (Becker and Grazia 1992), *Alcippus* Stål (Becker and Grazia 1989b), *Alveostethus* Ruckes (Ruckes 1966b), *Antiteuchus* (Ruckes 1964, Engleman and Rolston 1983, Rolston 1993, Fernandes and Grazia 2006), *Callostethus* Ruckes (Fernandes et al. 2011), *Cataulax* Spinola (Grazia et al. 2000), *Dinocoris* (Becker and Grazia 1985), *Dryptocephala* (Ruckes 1966c), *Eurystethus* (Ruckes 1966a), *Lineostethus* Ruckes (Ruckes 1966b), *Mecistorhinus* (Ruckes 1961, 1966e), *Parantiteuchus* Ruckes (Fernandes and Grazia 2002), *Pelidnocoris* Stål (Ruckes 1966d), and *Priapismus* Distant (Rolston 1984a). *Colpocarena* Stål (**Figures 2.12F, 2.27D**) and *Phoeacia* Stål (**Figures 2.13B,**

2.17L) are currently being revised (David A. Rider, unpublished data). Also, the genus *Anhanga* Distant recently has been transferred from the Discocephalini to the Pentatominae: Carpocorini, near the genus *Galedanta* Amyot and Serville (Bianchi et al. 2016a). The Discocephalini presently contains 46 genera and 195 species (**Table 2.3**).

Recent taxonomic work in the Ochlerini includes: Dellapé and Dellapé (2016), including a key to the species of *Adoxoplatys* Breddin, modified from Kormilev (1955); *Alitocoris* Sailer (Sailer 1950, Garbelotto et al. 2013); *Lincus* (Rolston 1983c, 1989); *Ochlerus* Spinola (Simões and Campos 2014, 2015); and *Paralincus* Distant (Rolston 1983d). Recent work by colleagues in Brazil and North America also has resulted in the descriptions of several new ochlerine genera: *Candeocoris* (Roell and Campos 2015), *Hondocoris* (Thomas 2003), *Ocellatocoris* (Campos and Grazia 2001), *Parastalius* (Matesco et al. 2007), *Pseudocromata* (Ortego-León and Thomas 2016), *Stapecolis* (Garbelotto and Campos 2016), and *Xynocoris* (Garbelotto and Campos 2014). The Ochlerini presently contains 35 genera and 130 species (**Table 2.3**).

2.2.10.5.1 Key to the Tribes of Discocephalinae

1 Dull black or fuscous coloration; dorsal surface of hind tarsal segment concave (**Figure 2.6C**) or flattened in females and sometimes in males (**Figures 2.18A-D; 2.27E**)................Ochlerini

1’ Brown, often mottled with black, or shiny black; hind tarsal segment cylindrical in both sexes, not concave or flattened (**Figures 2.12F, G; 2.13B; 2.17H-L**)............................Discocephalini

2.2.10.6 Edessinae Amyot and Serville, 1843

The exclusively New World subfamily Edessinae has undergone significant changes of late. Until recently, this subfamily was considered to contain only four genera: *Edessa* F. (**Figure 2.27F**), *Olbia* Stål, *Pantochlora* Stål, and *Peromatus* Amyot and Serville (**Figure 2.18G**). Now, several genera usually placed in the Pentatominae have been transferred to the Edessinae (e.g., *Brachystethus* Laporte [**Figure 2.18E**], *Lopadusa* Stål [**Figure 2.18F**]) (Barcellos and Grazia 2003b, Rider 2015a), and the extremely speciose genus *Edessa* is being split into several smaller genera (e.g., *Ascra* Say, *Grammedessa* Correia and Fernandes) (Santos et al. 2015, Correia and Fernandes 2016). Currently, this subfamily contains 15 genera and about 338 species (**Tables 2.2, 2.3**), but this undoubtedly will increase as there are still many known species of *Edessa* that are undescribed.

In its early taxonomic history, this group was often included in, or at least confused with, the family Tessaratomidae. Amyot and Serville (1843) included in Edessides the genera related to *Edessa* and also some genera currently included in the Tessaratomidae. Dallas (1851) treated the group as a family, but the recognition of edessines as a distinct group was virtually ignored after the proposition of the Tessaratomidae by Stål (1865). For example, Horváth (1900) erected the family-level name Pantochloraria within the Tessaratomidae to hold the edessine genus *Pantochlora*. Kirkaldy (1909) recognized *Edessa* and related genera in the tribe Edessini, but left the Pantochlorini in the Tessaratomidae. McDonald (1966) also treated this group as a tribe, the Edessini, within the Pentatomidae. Rolston and McDonald (1979) raised the group to subfamily level, which has been followed by subsequent workers (Gapud 1991, Schuh and Slater 1995, Grazia and Schwertner 2008b, Grazia et al. 2015). Even though Leston (1955b) indicated that *Pantochlora* might be related to the edessines, it was not formally transferred to the Edessinae until 1969 by Kumar (1969a), but he said that *Pantochlora* might deserve its own tribal status. Barcellos and Grazia (2003b) supported the placement of *Pantochlora* within the Edessinae.

Members of this subfamily are medium to large in size, often green in color with dark markings, and, occasionally some may have some brighter markings; they tend to be ovoid to ovaloid but narrowing posteriorly. The bucculae are rather short, arcuately elevated, almost flap-like. The most diagnostic character is the prominantly elevated, tumid metasternum, that in many species is produced forward onto or beyond the mesosternum (**Figure 2.5H**) and, in the genus *Edessa* (and related genera), bifurcates anteriorly (**Figures 2.5F, G**). The rostrum is short and, usually, in *Edessa*, the apex fits into the notched metasternal process (Rolston and McDonald 1979, Barcellos and Grazia 2003a,b). Similar appearing processes are known from several pentatomine groups, but they usually are abdominal or mesosternal in origin. The humeral angles are sometimes rather prominent, spinously or truncately produced.

At quick glance, the edessines have a similar appearance to the rhynchocorines (Pentatominae), but they are actually quite different. In the rhynchocorines, the base of the abdomen, the metasternum, and the mesosternum are all produced ventrad and tightly contact each other (nearly appearing fused); it is the mesosternum that protrudes forward over the prosternum and often onto the base of the head (**Figure 2.7E**). In the edessines, only the base of the abdomen and the metasternum are produced ventrad; it is the metasternum that is produced forward over the mesosternum, often becoming bifid anteriorly over the prosternum (**Figures 2.5F-H**). Additionally, the rostrum is much shorter in the edessines, and the bucculae are shorter and flap-like.

Several edessine genera have been reviewed recently, either in part or in whole: *Ascra* (Santos et al. 2015), *Brachystethus* (Barcellos and Grazia 2003a), *Doesburgedessa* Fernandes (Fernandes 2010), *Grammedessa* (Correia and Fernandes 2016), *Lopadusa* (Becker and Grazia 1970), and *Paraedessa* Silva and Fernandes (Silva et al. 2013). Several species groups within *Edessa* have been the subject of revisionary work (Fernandes and van Doesburg 2000a-c; Fernandes et al. 2001; Silva et al. 2004, 2006; Fernandes and Campos 2011; Silva and Fernandes 2012; and Santos et al. 2014).

Various species may feed on a variety of plant hosts, but there seems to be some preference for members of the plant family Solanaceae among the economically important species (Panizzi et al. 2000). Several members of this subfamily (e.g., *Lopadusa augur* Stål and *Edessa nigropunctata* Berg) have been reported to exhibit parental care of the young (Requena et al. 2010). There is one fossil species described in the Edessinae, *Edessa protera* Poinar and Thomas (2012).

2.2.10.7 Pentatominae Leach, 1815

This is, by far, the most diverse subfamily in the Pentatomidae, containing 660 genera and 3,484 species (**Tables 2.2, 2.3**). Its members occur worldwide. A taxon similar to our current Pentatominae was proposed by Stål (1865) and included genera of the groups Halydes, Pentatomides, Pododides, Podopides, Rhaphigastrides, and Sciocorides of Amyot and Serville. Later, the subfamily was divided into groups of genera (Stål 1872, 1876). These groups eventually were rearranged and named by different authors (Atkinson 1888, Distant 1902, Cachan 1952), and were followed partially until recently (Uhler 1886; Kirkaldy 1909; Van Duzee 1917; Cachan 1952; Gross 1975b; Rolston and McDonald 1979; Rider 2006a, 2015a). However, depending on the characters considered important for the classification proposed, the organization and hierarchy of the groups differ considerably (**Table 2.1**).

The lack of unique diagnostic characters hampers the identification of this subfamily, making it difficult to construct a useful and stable classification. As with any large group, it is difficult to find characters that all members possess. In general, pentatomines can be quite small (*Sepontia* and *Sepontiella* Miyamoto species are only a few mm in length) to quite large (*Catacanthus* species are nearly as large as most tessaratomids). Many of its members are dull yellows, tans, greens, browns, and blacks, colored so as to blend in with their surroundings; others, however, may be brilliantly colored in reds, yellows, and oranges, sometimes with a metallic sheen, perhaps aposematically colored to advertise their repugnant odors. Most species have five-segmented antennae, but some species only have four segments, and at least one Australian genus (*Omyta*) has only three segments. The humeral angles are often simple and rounded, but, in some species, they are quite prominent and spinuously produced. The scutellum is usually subtriangular but, in a few species, it is more spatulate; if spatulate, it usually does not reach the apex of the abdomen. The frena usually extend at least two-fifths the length of the scutellum (**Figure 2.6F**). The tarsi are usually three-segmented, but a couple of tribes (Nealeriini, Opsitomini) and at least two genera included in other separate tribes (*Phalaecus* Stål, *Rolstoniellus* Rider) have two-segmented tarsi.

The classification within this subfamily has been chaotic at best. The number of tribes recognized has varied dramatically from worker to worker. For example, various workers from various parts of the world still recognize over 40 different tribes (e.g., Cassis and Gross 2002, Derjanschi and Péricart 2005, Rider 2006a, Salini and Viraktamath 2015), and another 15-20 generic groups have been proposed (Gross 1975b, 1976; Linnavuori 1982). And yet, Schuh and Slater (1995) only recognized eight valid tribes.

There are no recent keys to all of the known tribes or genera, except on a regional basis. For example, there are several important works covering the fauna of various Old World regions: West Palearctic

(Derjanschi and Péricart 2005, Ribes and Pagola-Carte 2013), Central Asia (Putshkov 1965), Far East of Russia (Vinokurov et al. 1988), China (Hsiao et al. 1977), South India (Salini and Viraktamath 2015), West and Central Africa (Linnavuori 1975, 1982), Madagascar (Cachan 1952), and South Australia (Gross 1975b, 1976). Rider et al. (2002) provided nomenclatural notes and a checklist of the Chinese species. In the New World, Lawrence H. Rolston headed up a small group who authored a series of four papers that provided keys for all known pentatomine genera (Rolston and McDonald 1979, 1981, 1984; Rolston et al. 1980). The focus of this series of papers was not to reflect phylogeny or even to hint at a practical classification, but was more utilitarian - it was meant to give workers a means to identify their specimens to genus. This series set the stage for further work in the New World including a number of generic revisions, a book on the Pentatomoidea of northeastern North America (McPherson 1982), a set of regional treatments for various states in the United States in honor of J. E. McPherson's contributions (Bundy 2012, O'Donnell and Schaefer 2012, Packauskas 2012, Rider 2012, Sites et al. 2012, Swanson 2012, Zack et al. 2012), and a separate contribution on the fauna of Ontario (Paiero et al. 2013). More recently, Barão et al. (2017) published a review of the metathoracic scent glands in the Carporcorini; this information will undoubtedly be useful in future phylogenetic studies.

Because one of the primary purposes of this chapter is to provide a framework for future phylogenetic studies, we have chosen to discuss every tribe unequivocally that is still considered valid by someone somewhere, and also any generic groups proposed by Gross (1975b, 1976) and Linnavuori (1982) that do not fit easily into one of the existing tribes. As such, the following key is only tentative at best, with some tribes keying out multiple times. Hopefully, this will still be of some benefit to some workers, but the user should be aware of many exceptional genera (and some genera that have never been placed in a tribe), many of which are discussed under the tribal headings. Obviously, there will be drastic changes in our treatment of the various taxa, particularly the tribal classification, but this chapter should help facilitate the efficiency of future phylogenetic studies as well as provide basic information for identification.

Nearly all Pentatominae are phytophagous (see comments in Asopinae section), usually oligophagous, but a few species are known from many host plants. There are some reports of facultative feeding on dung or carrion (Adler and Wheeler 1984, Eger et al. 2015b). A number of species are known economic pests of various crops (e.g., *Nezara viridula* L. [**Figure 2.22K**], *Euschistus* Dallas spp. [**Figure 2.20A**], *Eurydema* Laporte spp. [**Figure 2.32E**], etc.) (McPherson and McPherson 2000, Panizzi et al. 2000). In some parts of the world (e.g., southern Mexico), pentatomines are used as human food.

2.2.10.7.1 Tentative Key to the Tribes of Pentatominae

1 Sublateral, lunate stridulatory structure present on each side of the abdominal venter (**Figures 2.7A, B**), corresponding stridulatory pegs on inner surface of hind femora....... 2

1' Abdominal venter lacking lunate stridulatory structures (*Neomazium* [Carpocorini] has stridulatory structures, but they form a rather narrow band along lateral margins of abdominal venter), hind femora lacking pegs.. 3

2(1) Elongate, slender, coloration pale yellowish to tan; occurs in arid areas of the New World and in the Middle East, Africa, and India (**Figure 2.30F**) .... Mecideini

2' Variously shaped, but never elongate and slender; coloration usually not yellowish); occurring in Australia and adjacent areas (**Figures 2.12D; 2.21B, C; 2.29I**)............ Diemeniini

3(1) Ant mimic, black with white markings on corium giving it a constricted appearance; pronotum elongate, distinctly constricted in middle; many spines along edges of pronotum, on base and apex of scutellum, and one on each side of abdomen, many of which are oriented dorsad; Southeast Asia (**Figures 2.14E, F; 2.31B**) .... Pentamyrmecini

3' Not an ant mimic; coloration variable, not as above; usually lacking numerous spines along pronotal margins and on scutellum and abdomen, if some spines are present then light brown in color (*Phricodus*) or quite larger (*Mustha*)... 4

4(3) Small, pale brownish species, with numerous spines along margins of pronotum, and base of coria; antennae 4-segmented, segment II long and gradually thickened towards apex, the distal two segments thickened, spindle-shaped; Old World (**Figure 2.31I**) .... Phricodini

4’ Size and coloration variable, but not a combination of pale brownish with numerous spines on pronotum and coria; antennae usually 5-segmented, if 4-segmented, then they are not as above 5

5(4) Ostiole obsolete (**Figure 2.9A**), at most, represented by small opening between the bases of the mid- and hind-coxae, rugae short, merging with surrounding smooth pleuron, associated evaporative area also obsolete, V-shaped, confined to metapleuron (black brachypterous *Trochiscocoris* [Strachiini] has ostioles completely reduced; *Otantestia* [Antestiini] will key here) 6

5’ Ostiole and associated external structures may be reduced and small, but always distinct, sometimes ostiole, rugae, and evaporative areas quite large (**Figures 2.9B-F**) 7

6(5) Large species, body length usually 20 mm or greater; body elongate-oval; head narrowly triangular, tylus distinctly surpassing apices of juga; Afrotropical and Oriental (**Figure 2.28D**) .... Agaeini

6’ Usually smaller and broader; head much broader than its length, tylus never surpassing apices of juga; worldwide (**Figures 2.12H; 2.32D-G**) .... Strachiini

7(5) Mesosternum longitudinally carinate, sometimes carina is low and indistinct (**Figure 2.7C**) or in a shallow sulcus, but is usually visible 8

7’ Mesosternum longitudinally sulcate, not carinate (**Figures 2.7F, G**), occasionally a low, indistinct carina may be visible just near anterior margin 39

8(7) Mesosternal carina large and robust, produced anteriorly over prosternum and often onto base of head as a spine or flattened wedge (**Figures 2.7E, H**) 9

8’ Mesosternal carina usually less elevated, not robust, at most protruding just onto posterior margin of the prosternum (**Figure 2.7D**); may have large spine or wedge produced forward, but these originate from metasternum or abdomen 10

9(8) Usually green in color when alive, but often fades to yellowish after death; India through China, Southeast Asia, and Australia to Oceania (**Figures 2.13D, E; 2.23L; 2.24A, B; 2.31L**) .... Rhynchocorini

9’ Usually brown or mottled brown and pale; New World (**Figures 2.13A, 2.31E**) .... Pentatomini (part, *Evoplitus* group)

10(8) Antennae 4-segmented; abdominal venter in females nearly covered with large, opaque areas which are provided with a dense layer of hairs (several genera of Halyini may key here); Madagascar (**Figure 2.30G**) .... Memmiini

10’ Antennae with 3-5 segments, but usually 5-segmented; abdominal venter in females lacking large opaque areas, not covered with hairs 11

11(10) Abdominal venter with distinct medial, longitudinal sulcus, the rostrum often elongate with at least the apex lying in sulcus (**Figure 2.8A**); usually green or greyish-green in color; Old World tropics (**Figures 2.19F, 2.28J**) .... Bathycoeliini

11’ Abdominal venter usually lacking medial sulcus, or if sulcus present, then usually brown or grey in color 12

12(11) Abdominal venter armed basally with a forwardly directed spine or tubercle (**Figures 2.8B, C**) 13

12’ Abdominal venter unarmed basally 18

13(12) Large species, body length usually around or above 20 mm; body colorful, marked with reds, yellows, oranges, and sometimes metallic blues or greens; dorsal surface of head often nearly impunctate, but with oblique transverse ridges or wrinkles (**Figure 2.8F**); worldwide (except Europe) (**Figures 2.20I, J; 2.29C, D**) .... Catacanthini (part)

13’ Small to medium sized, if larger, then usually not colorfully marked, if colorfully marked, then head usually distinctly punctate 14

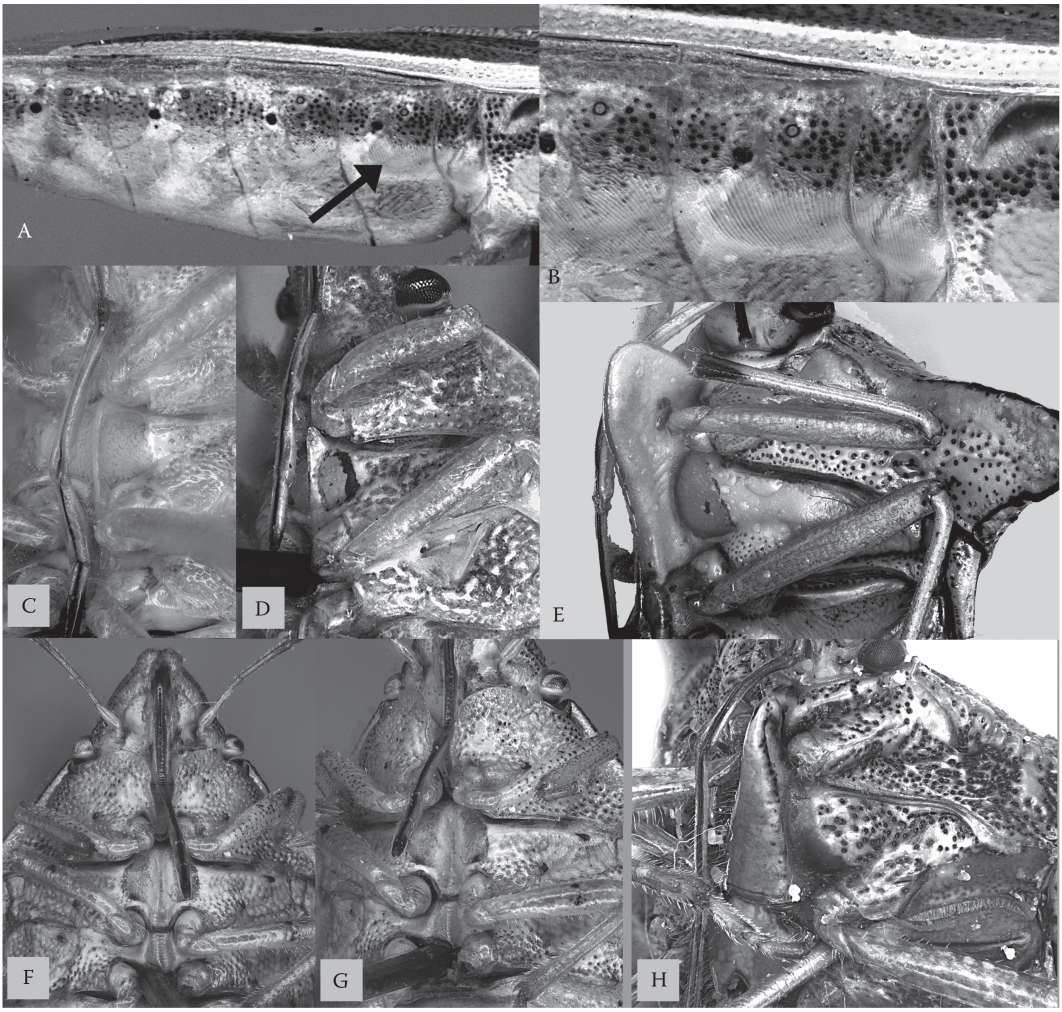

FIGURE 2.7 A, *Mecidea major*, abdomen, lateral view; B, *Mecidea major*, detail of abdominal segments II, III and IV, lateral view; C, *Thyanta acuminata*, thorax, ventrolateral view; D, *Piezodorus guildiniii*, thorax, ventrolateral view; E, *Rhynchocoris humeralis*, thorax, ventrolateral view; F, *Aelia acuminata*, head and thorax, ventral view; G, *Aelia acuminata*, thorax, ventrolateral view; H, *Evoplitus humeralis*, thorax, ventrolateral view.

14(13) Green in color when alive, and keeping the green color after death (note that some species have seasonal or semi-permanent yellowish or brownish forms, but the typical form is green); worldwide (**Figures 2.12E; 2.22I-L; 2.30K, L**).. Nezarini

14' Coloration variable, but if predominately green, this green fades to yellow after death.... 15

15(14) Usually small to medium in size; usually tans, browns and/or blacks, sometimes with pale marks; head relatively broad, usually semi-circular; abdominal spine may be relatively long, but usually terete, slender; ostiolar rugae elongate, reaching near to lateral margin of metapleuron, apex acute, attached to metapleuron; worldwide (except Europe) (**Figures 2.22C-E; 2.30H**) .... Menidini

15' Usually medium to large in size; color variable, but if tan, brown, or black, then head is not so broad and/or semicircular; abdominal spine usually large, robust; ostiolar rugae variable.... 16

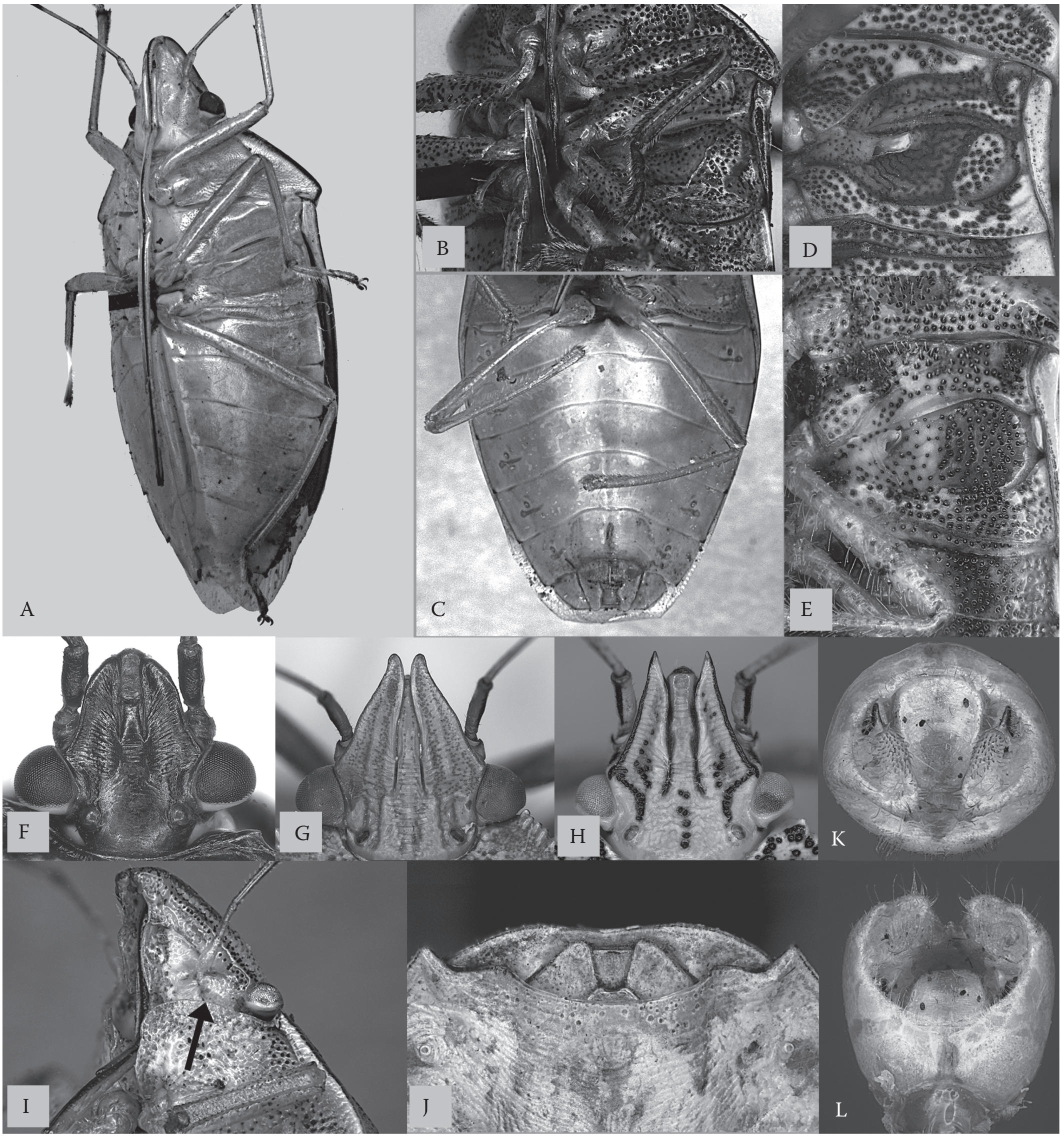

FIGURE 2.8 A, *Bathycoelia* sp., ventrolateral view; B, *Menida violacea*, thorax and anterior abdominal segments, ventrolateral view; C, *Chinavia viridans,* abdomen, ventral view; D, *Tibraca limbativentris*, evaporatorium, ventral view; E, *Eysarcoris aeneus*, evaporatorium, ventral view; F, *Catacanthus incarnatus*, head, dorsal view; G, *Loxa viridis*, head, dorsal view; H, *Arvelius albopunctatus*, head, dorsal view; I, *Aelia acuminata*, head and anterior part of thorax, ventrolateral view; J, *Odmalea concolor*, female genital plates, ventral view; K, *Odmalea concolor*, pygophore, posterior view; L, *Odmalea concolor*, pygophore, dorsal view.

16(15) Usually tans, browns, and/or blacks in color, occasionally with metallic green, if green in life, does not fade to yellow after death; worldwide (**Figures 2.23A-H; 2.31C-H**)............ ....Pentatomini (part)

16’ Usually yellowish-green fading to yellow after death (exception South African *Flaminia* [**Figure 2.21F**] which is black with red and white markings).. 17

17(16) Scutellum usually large, spatulate, apex broadly rounded; Old World (**Figures 2.21F, 2.29L**)..Eurysaspini

17’ Scutellum subtriangular in shape, apex narrowly rounded; worldwide (**Figures 2.23K, 2.31J**) .... Piezodorini

18(12) Relatively large and colorful, marked with reds, yellows, oranges, and sometimes metallic blues or greens; dorsal surface of head often nearly impunctate, but with oblique transverse ridges or wrinkles (**Figure 2.8F**); worldwide (except Europe) (**Figures 2.20I, J; 2.29C, D**) .... Catacanthini (part)

18’ Small to medium sized, if larger, then usually not colorfully marked, if colorfully marked, then dorsal surface of head usually distinctly punctate 19

19(18) Ostiolar rugae relatively short, often auriculate in form (**Figure 2.9F**), if more spout-like, still not reaching beyond middle of metapleuron (**Figure 2.9D**) 20

19’ Ostiolar rugae relatively long, reaching beyond middle of metapleuron, usually acute or acuminate apically, curving anteriad laterally (**Figures 2.9B, C**) 29

20(19) Occurs in the New World 21

20’ Occurs in the Old World 24

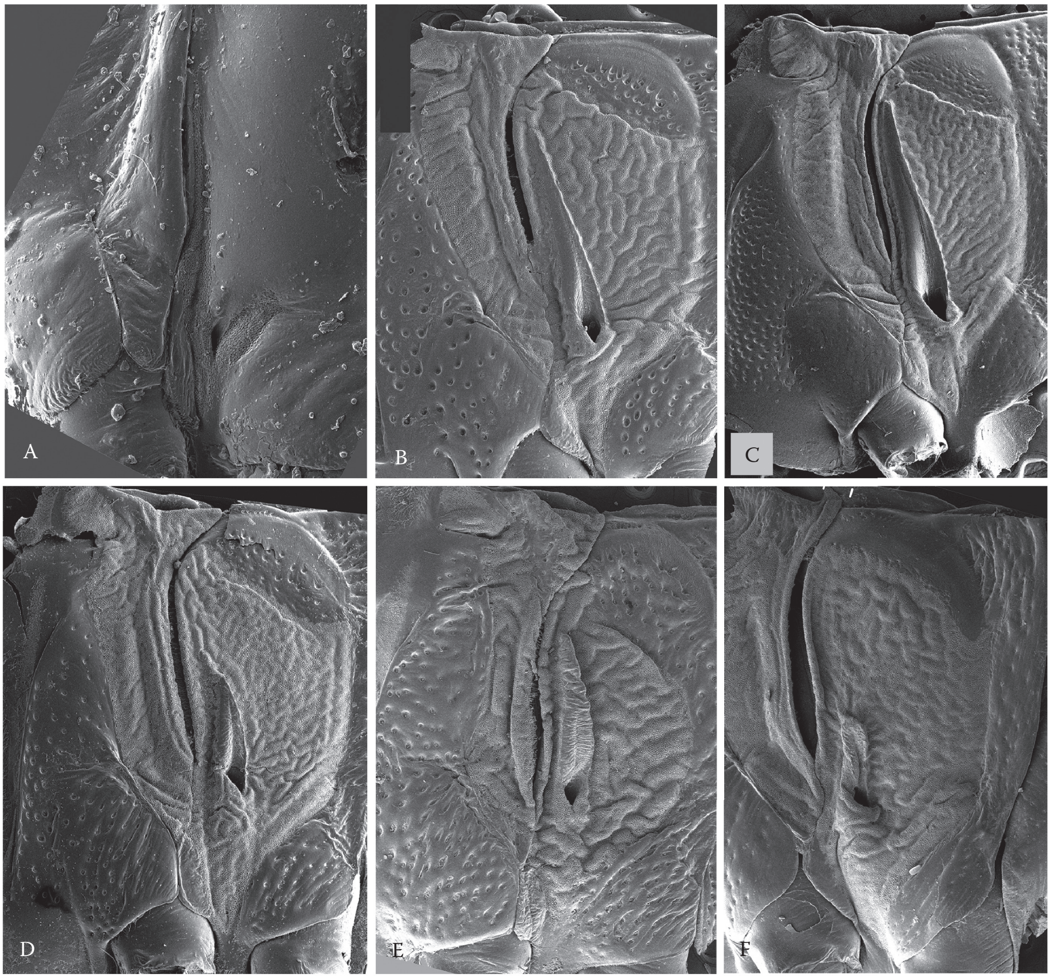

FIGURE 2.9 Evaporatoria, ventral view. A, *Murgantia histrionica*; B, *Acrosternum millierei*; C, *Bathycoelia horvathi*; D, *Palomena prasina*; E, *Carpocoris purpureipennis*; F, *Pentatoma rufipes.*

21(20) Yellowish-green in life (*Rhyncholepta* may be reddish brown with yellowish-green areas), usually fading to yellow after death; dorsal surface of head relatively flat, often subtriangular in shape (**Figures 2.8G, H**; **2.20K, L; 2.21A; 2.29F**) .... Chlorocorini

21’ Color variable, but usually not yellowish-green in life fading to yellow after death; characters of head variable, but usually not with the combination of flat dorsal surface and subtriangular shape 22

22(21) Black to grayish-black, dorsal surface coarsely punctate, roughened; juga somewhat foliaceous or at least dentate near apex; North and Central America (**Figure 2.21K**)........ Halyini (part)

22’ Color variable; puncturing and dorsal surface variable, but usually with coloration not black to grayish-black with dorsal surface roughened; juga not foliaceuos nor dentate near apex 23

23(22) Dorsal surface covered with elongate hairs; veins in wing membrane marked with fuscous or black; rostrum usually elongate, reaching onto base of abdomen or more; one introduced species occurring in southern North America and the West Indies (**Figures 2.19B; 2.28E**)........ Agonoscelidini (part)

23’ Dorsal surface usually not covered with elongate hairs, if elongate hairs present, then veins in wing membrane are not marked with color; length of rostrum variable, but usually reaching at most onto base of abdomen (**Figures 2.12A, I; 2.19J-L; 2.20A-H; 2.29A, B**) ....Carpocorini (part)

24(20) Small to medium in size; scutellum enlarged, spatulate in shape; ostiolar rugae short, usually auriculate (**Figures 2.8E; 2.30A**)........ Eysarcorini (part)

24’ Size variable, but if small then scutellum not usually enlarged; ostiolar rugae variable..... 25

25(24) Usually medium to large in size, gray to grayish-black mottled; head often with long preocular portion, narrowed, slender, lateral margins sometimes foliaceous or dentate (**Figures 2.21J, L; 2.22A, B; 2.30B, C**)........ Halyini (part)

25’ Size variable but usually small to medium, color variable; head shape variable, but usually not as above 26

26(25) Body shape somewhat elongate, slender, narrowing posteriorly; humeral angles usually prominent, rounded or often spinose; female genital plates sharply produced posteriorly as an ovipositor; Africa to India (**Figure 2.30E**)........ Lestonocorini

26’ Body shape variable, but if somewhat elongate-slender, narrowing posteriorly, then female genital plates typically pentatomid, not produced posteriorly as an ovipositor 27

27(26) Body often covered with elongate hairs; head tends to be elongate, slender; rostrum usually elongate, usually reaching onto base of abdomen or more; Africa, India, Southeast Asia to Australia (**Figures 2.19B, 2.28E**) .... Agonoscelidini (part)

27’ Body usually not covered with elongate hairs, if elongate hairs present, head not particularly elongate and slender; length of rostrum variable, but usually reaching at most onto base of abdomen........ 28

28(27) Ostiolar rugae short, usually auriculate (**Figures 2.8E; 2.21G-I; 2.30A**).... Eysarcorini (part)

28’ Ostiolar rugae longer, usually spout-like (**Figures 2.9E; 2.12A; 2.19J, L; 2.29A**) .... Carpocorini (part)

29(19) Uniformly light brown to dark brown in color; juga longer than and meeting anterior to tylus, head distinctly triangular in shape; China, Southeast Asia, Madagascar (**Figure 2.28F**) .... Amyntorini

29’ Coloration variable but if brown, usually with pale markings; juga and tylus usually subequal in length, if juga longer than tylus, then head not distinctly triangular in shape ... 30

30(29) General coloration green to dark green, often with some pale or dark markings, sometimes with bright orange or reddish markings; ostiolar rugae elongate, often reaching to near lateral margin of metapleuron, apex acute, attached to metapleuron; worldwide (**Figures 2.19D, E; 2.28G, H**)........ Antestiini