

Chapter 19

Leaf-Footed Bugs (Coreidae)

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Abstract The family Coreidae is distributed worldwide, but these phytophagous bugs are most abundant in the tropics and subtropics. In the Neotropical region, all of the subfamilies and 16 tribes are represented. In tropical ecosystems, these bugs feed on herbs and shrubs in open areas of forests as well as at the forest edge. Some species are spectacularly colored, and unusual expansions of antennae, humeral angles, femora, or tibiae occur in many groups. Some of them move lazily even when disturbed and hardly fly to escape; others are extremely nimble, fast flying away when disturbed. They are frequently encountered in crops, representing important pests in several commodities. No one common name is universally accepted for the family, and none of the frequently used names (e.g., squash bug, leatherbug, leaf-footed bug, Randwanzen) are collectively appropriate for all members of the family.

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19.1 Introduction

The family was established by Leach (1815), but Stål (1867, 1870) was the first author to propose a suprageneric structure to Coreidae. Surprisingly not much has been done at this level since then, and much of the suprageneric organization is still the same. The most comprehensive work at this level since Stål was presented by Schaefer (1964, 1965). For many years, the literature on Coreidae was fragmentary; keys are still lacking for several important groups. During the last few decades, Brailovsky and coworkers have revised or contributed to the knowledge of several Neotropical genera of Coreidae (see throughout the chapter). Only recently, a print catalog for the Neotropical Coreidae (Packauskas 2010) and an online catalog for Coreoidea of the world (CoreoideaSF Team 2015) were compiled. These recent revisions and catalogs will allow future works on Coreidae, especially on relationships among taxa.

19.2 General Characteristics and Diagnosis

Coreids are usually heavy-bodied insects, elongate or elliptical in shape. Species of the genus *Thasus* are bulky insects reaching 30–40 mm, and species of *Vilga* are delicate 6–10 mm bugs. Many have the hind femora enlarged, with spines and tubercles; hind tibiae curved, with spines or leaflike expansions; and third and fourth antennal segments dilated or tumid (Plate 19.1). Most of the species have dull colors like brown, gray, and yellow, but some have bright colors like red, green, orange, or sometimes a metallic coloring. Head smaller than pronotum; antennae with four segments and inserted above a line drawn through the eye; membrane of forewing with several veins; femora of hind legs frequently incrassate; hind tibiae terete or slightly to strongly dilated; abdominal spiracles ventral; 3 trichobothria on abdominal segments III–VI, 2 on segment VII; nymphal dorsal abdominal scent gland openings between terga 4/5 and 5/6; genital plates flattened; spermatheca only with proximal pump flange; eggs with pseudoperculum except in Pseudophloeinae.

19.3 General Biology and Ecology

Coreids are plant feeders; hosts include gymnosperms and angiosperms and monocots and dicots. However, dicots are far more common as hosts than monocots, and few coreid species are exclusive feeders on gymnosperms (Schaefer and Mitchell 1983). Opportunistic feeding on fecal matter, carrion, and insect eggs has been reported (Adler and Wheeler 1984; Menezes-Netto et al. 2012) but is never the primary source of nutrients. Plant preference spans a wide spectrum from specialization on a single genus to extreme polyphagy; reported host plants of one African



Leptoglossus zonatus
PHOTO: W.O. Ree, Jr.



Pachylis sp.
PHOTO: José A.M. Fernandes



Pachylis sp.
PHOTO: José A.M. Fernandes



Holhymenia sp.
PHOTO: José A.M. Fernandes



Eubule farinosa.
PHOTO: José A.M. Fernandes



Crinocerus sanctus
PHOTO: Arthur Anker



Spartocera sp.
PHOTO: Andreas Kay



Spartocera sp.
PHOTO: Andreas Kay

Plate 19.1 Field images of Coreidae

mictine species, *Anoplocnemis curvipes* (F.), represent >30 plant families. Legumes are the primary host plants of Pseudophloeinae and several tribes of Coreinae (Acanthocerini, Mictini, Nematopodini); this may be a primitive trait of Coreoidea (Schaefer and Mitchell 1983). Some genera or tribes may be characterized by their host plant preferences (e.g., *Chelinidea* spp. on Cactaceae), but most cannot; a single genus (e.g., *Leptoglossus* Guerin) may include polyphagous species and those with highly restricted feeding habits (Mitchell 2006).

Most coreids are winged, but members of the Australian tribe Agriopocorini are usually wingless (Schuh and Slater 1995), and the single described species of Barreratalpini is brachypterous (Packauskas 1994). Both macropterous and brachypterous forms are known in the Neotropical pseudophloeine *Vilga mexicana* Distant (Dolling 1977). At least one coreid has been described as migratory (Aldrich et al. 1982), but most movement involves shorter distances. Coreids move seasonally among host plants and between hosts and overwintering areas in temperate regions, occasionally becoming a problem in houses. Dispersal may occur in the nymphal stage, but in polyphagous species such as *L. phyllopus*, most movement occurs when recently molted winged adults disperse from deteriorating nymphal hosts (Mitchell 2006). Vast geographic range expansion has occurred through commercial movement of plants. For example, the conifer-feeding *Leptoglossus occidentalis* Heidemann, formerly restricted to western North America, spread eastward as far as Ontario and Connecticut and then, following accidental introductions, has spread through most of Europe, most recently being reported from Turkey (Hizal 2012) and parts of Asia, most recently Korea (Ahn et al. 2013). The Neotropical *Leptoglossus zonatus* (Dallas), long known as a highly polyphagous crop pest in Central and South America and Mexico, has also expanded its range recently, moving across the southern United States from Texas to Florida, becoming a problem in satsuma oranges and other citrus (Xiao and Fadamiro 2010).

A number of coreids are economic pests; grain legumes, tree nuts, rice, fruits, and garden vegetables are among the crops attacked. Several species pose problems in forest management (conifers and eucalypts). Only a small proportion of coreid species damage crops, but those few can cause serious losses (Mitchell 2000). Worldwide, legume feeders are likely the most important economically, especially in combination with alydids and pentatomids. Pests in the Neotropics include *Anasa* spp. on cucurbits, *Spartocera* spp. on Solanaceae and tobacco, *Phthiacnemia picta* (Drury) on tomatoes and *Leptoglossus* spp. on a variety of crops. Direct damage to grains and developing seeds within pods and seed heads is most common; pod abortion or reduced seed production may result from feeding damage. Fruits may become malformed, pithy, or corky, or develop blotches, spots, depressed areas or lesions. Wilting due to vascular damage can also result in losses, and the role of coreids and other Heteroptera in transmission of diseases is only recently becoming appreciated (Mitchell 2004). No coreids are known to transmit viruses or phytoplasmas, but 13 species are associated with fungal pathogens (Mitchell 2004) and 30 species representing 17 primarily Neotropical genera harbor trypanosomatids (adapted from Camargo and Wallace 1994 and Godoi

et al. 2002). A survey of Amazonian Heteroptera showed coreids to far outnumber other families in frequency of trypanosomatid infection; >80 % of Coreidae were infected, many with the plant parasite *Phytomonas*, compared with <10 % of other phytophagous families examined (Godoi et al. 2002). *Phthiacnemis picta* not only harbor phytomonads but have been shown to acquire and infect tomatoes with these flagellates (Jankevicius et al. 1989; Fiorini et al. 1993). *Leptoglossus zonatus* (Dallas) can transmit a trypanosomatid to corn kernels (Jankevicius et al. 1993). In the United States, transmission by *Anasa tristis* De Geer of the fastidious phloem-colonizing bacterium causing cucurbit yellow vine disease has recently been documented and extensively studied (Bruton et al. 2003). Although a few coreid species have been investigated as potential biocontrol agents (Mitchell 2000), none have been successfully adopted, either due to failure to disperse or insufficient host specificity.

Natural enemies of coreids include parasitic tachinid flies; several species of egg parasitoids in the families Encyrtidae, Eurytomidae, and Platygastriidae; and both vertebrate and invertebrate predators, particularly reduviids, spiders, and ants. Guarding of eggs by females has been reported for one species (Hemmingsen 1947). Scent glands, present in both adults and nymphs, provide effective protection from some predators. Blackbirds feeding on *Coreus marginatus* (L.) and various pentatomid species will wipe bugs along on the ground, or hit them repeatedly against the ground, to avoid consuming the defensive secretions (Schlee 1992). Adult scent glands are located ventrally on the metathorax, whereas nymphal scent glands are on the dorsum of the abdomen. Compounds produced by these glands differ between juveniles and adults. Chemical composition of the scent fluid was reviewed by Aldrich (1988).

19.3.1 Eggs and Oviposition

Egg shapes vary among coreid species. Ovoid or elliptical eggs are most common, but hemicylindrical, cuboidal, globular, and oblong eggs are known (Cobben 1968; Moulet 1995). The portion attached to the substrate may be flattened, producing an egg that is triangular in cross-section (e.g., *Acanthocephala terminalis* (Dallas), Yonke and Medler 1969b). However, in pseudophloeines, the side of the egg facing the substrate is convex (Cobben 1968). The hemicylindrical eggs of *Leptoglossus*, *Phthia s.l.*, and *Narnia* (as well as several Old World genera) are laid in long chains, end to end (Amaral 1981a; Mitchell and Mitchell 1986; Mitchell 2000), but other types may be oviposited singly, in small groups, adjacent rows, large clusters, or even atop one another as in the Old World pseudophloeine, *Ceraleptus gracilicornis* H.-S. (Cobben 1968). Most eggs are laid on host plants, generally on the undersides of leaves, but the egg chains of *Leptoglossus phyllopus* (L.) may be placed along virtually any linear surface—host or non-host, living or nonliving (Mitchell and Mitchell 1986). Females of *Phyllomorpha laciniata* (Villers) may choose to place eggs on leaves of the host plant or on the backs of males. Such oviposition blocks

wing movement so that individuals carrying eggs cannot fly and are subject to higher predation (Reguera and Gomendio 1999). Paternal care was found to be higher in a population subjected to heavy egg parasitism; eggs laid on males suffered less parasitism than those laid on plants (Gomendio et al. 2008).

Cobben (1968) provides detailed descriptions of the eggs of several species. A pseudopericulum is present in most Coreinae in the shape of a round cap, but not in Pseudophloeinae. In the latter subfamily, the extensive eclosion fracture may entirely separate the two halves of the eggshell. The number and placement of aeromicropyles also varies, from just a few to 60 in the species studied. They are most commonly arranged in a ring which crosses or more rarely coincides with the circular pseudopericulum. The chorion may be up to 100 μm thick, and the egg burster is triangular with a sclerotized ridge (Cobben 1968).

Eggs are cemented to the substrate by the female, and it has been suggested that trypanosomatid cysts may survive in this material, thereby providing a source of infection (Camargo and Wallace 1994). However, *Burkholderia* bacterial symbionts are not acquired from the eggs in *Thasus neocalifornicus* Brailovsky & Barrera and must be acquired de novo, presumably from the soil, by the early instars (Olivier-Espejel et al. 2011).

19.3.2 Nymph Feeding and Development

Five stadia occur between hatching and adult emergence. First instars often remain in the vicinity of the egg mass and appear to need only a source of water for successful molt to the second stadium (Cook and Neal 1999). Probing into plant tissue may occur, but the tissue selected is always vegetative (tendrils, leaves, terminal buds) (Rodrigues et al. 2007a; Wheeler and Miller 1990). Under laboratory conditions, survivorship of first instars provided with only a water wick was equivalent to that of first instars provided green bean and sunflower seed, and only the bean was used by the nymphs when food was provided (Mitchell 1980a).

Second through fifth instars require a nutrient source and feed similarly to the adults in most cases, although the shorter stylets may prevent access to deeper plant tissues. Younger instars are generally gregarious; research with *Phthia picta* (Amaral 1981a) has shown that grouped nymphs develop faster than isolated nymphs. Experimental studies of nymphal social groupings in the cactus bug *Chelinidea vittiger aequoris* McAtee (Miller et al. 2012) indicate that females reared alone are less likely to forage socially as adults than nymphs reared in a group; no similar effect of nymphal environment on adult behavior was found for males. Aggregation of juvenile bugs has been attributed to a number of factors, including both abiotic (humidity) and biotic (protection from predation) (Panizzi 2004a). Coreid nymphs are often highly visible—brightly colored with flattened hind tibiae and/or antennal segments—and all have dorsal abdominal scent glands. Aposematic feeding aggregations of nymphs of a Costa Rican coreid species responded to disturbance by

pulsating, spraying anal fluid, and releasing scent fluid (Aldrich and Blum 1978). The various secretions of the dorsal abdominal glands function in defense against natural enemies as repellents, deterrents, and/or toxins (Noge et al. 2012) and as an alarm pheromone. Nymphs will also respond to the alarm pheromones of adults in *L. zonatus* (Leal et al. 1994), but not in *T. neocalifornicus* (Prudic et al. 2008). Interestingly, the chemistry of coreid nymphal secretions differs from that of pentatomids, in that aldehyde chains are shorter and little or no *n*-tridecane is present. The short chain keto-aldehyde of coreids (4-oxo-(E)-2-hexenal) is potent against ants, whereas the longer chain compounds of pentatomid nymphs are less potent but are synergized by *n*-tridecane (Eliyahu et al. 2012).

19.3.3 Adult Feeding and Reproduction

Coreids feed on a range of plant parts, including vegetative tissue, phloem, buds, fruits, developing seeds, and mature seeds (Mitchell 2000). Such preferences are often specific at the tribal level; bugs are either associated with vegetative and vascular tissue or with reproductive plant parts. Kumar (1966) separated Australian coreids into those that fed exclusively on sap or those that fed on sap and fruit, and this early observation has held for other groups studied subsequently (Schaefer and Mitchell 1983). Like all Pentatomomorpha, coreids produce two types of saliva, gelling saliva to line the path of the stylets, producing a salivary sheath, and watery saliva containing enzymes (Miles 1972; Cobben 1978). The mode of feeding in several species of Australian coreids has been described as an “osmotic pump.” In this process, a short salivary sheath extends into parenchyma associated with vascular tissue. Sucrase in the watery saliva induces phloem unloading and discharge of parenchyma cell contents into the spaces between cells, and nutrients are thereby obtained from the extracellular spaces without direct penetration of the membranes of individual cells. The resulting effect on the plant may be a necrotic lesion or wilting of shoots beyond the feeding site (Miles and Taylor 1994). This feeding mode has been associated with species from Amorhini, Mictini, and Dasynini but may be more widespread within the family. True phloem feeding—similar to that of aphids, in which stylets penetrate phloem sieve elements—is assumed for the very few coreid species (*Hygia cliens* Dolling, *Notobitus affinis* (Dallas), and *Cloesmus* sp.) in which ant-tending for honeydew has been observed (Maschwitz et al. 1987). No coreids feed exclusively from xylem, but hydration from xylem certainly occurs. Stylet sheaths terminating in xylem are reported for *Leptoglossus phyllopus* (L.), which feeds primarily on developing seeds (Mitchell 2006), and wilting of squash leaves has been attributed to xylem blockage by the gelling saliva of *A. tristis* (Neal 1993).

The number of generations per year varies with latitude and as a function of crop cycles, host plant phenology, and host plant specificity. In temperate zones, the overwintering stage is usually the adult. Adults are long-lived; mark-release-recapture

studies indicate maximal lifespan of over 50 days (Mitchell 2006). Courtship and mating have been described for several species and involve antennation, touching with the legs, or other body contact prior to copulation (Eberhard 1998; Miller 2011; Tatarski and Spence 2013). Both males and females may mate multiple times. Duration of mating varies within and between species but may be as long as 6–7 h (McLain et al. 1993; Tatarski and Spence 2013). Mating often occurs on fruits, and feeding by one or both partners during copulation is common. The most frequent mating position is end to end, with the male facing the opposite direction from the female. Copulatory success appears to correlate with size of male (McLain et al. 1993; Tatarski and Spence 2013).

In several coreid tribes, a pronounced sexual dimorphism occurs in the size and armament of the hind femur, although the expression of this trait may vary within and across populations (Miller and Emlen 2010). This trait has been linked to male-male combat and territoriality or female defense polygyny in at least 8 species (Fujisaki 1980, 1981; Mitchell 1980b; Aldrich et al. 1982; Miyatake 1995, 1997; Eberhard 1998; Miller and Emlen 2010; Miller 2013). However, large mixed gender aggregations occur in other species (Mitchell 1980b; Solomon and Froeschner 1981), and male-specific attractant compounds have been identified for several species (Miller 2005). These species-specific volatile compounds are released from epidermal cells, ventral abdominal glands, or the lateral lobe of the metathoracic scent gland, depending on species (Aldrich et al. 1982, 1993; Soldi et al. 2012), and may serve in short-range communication, as attractants for females only or as aggregation pheromones.

19.4 Classification and Diversity

Although distributed worldwide, coreids are most abundant in the tropics. A recent catalog of New World Coreidae (Packauskas 2010) lists 158 genera that contain species with distribution records from the Neotropical region. All three subfamilies—Coreinae, Meropachyinae, and Pseudophloeinae—are represented in this region. A detailed study of the species richness of the coreoid fauna of relict pluvial subtropical forest in southern Brazil revealed 20 species of Coreidae present, with one species, *Cebrenis supina* Brailovsky, dominating beat-sheet collections (Barcellos et al. 2008). A number of economically important species have been extensively studied, but for the majority of Neotropical species, unfortunately little or nothing is known about their biology. Here we present keys to the subfamilies and the tribes of Coreinae of the Neotropical region; in addition, we present information on the biology of these groups, insofar as it is known. Species of major economic importance, and others that have been studied in depth, are treated separately in Sect. 19.5.

Key to subfamilies of the Neotropical Region Coreidae (adapted from Packauskas 1994).

1. Tibiae not sulcate on outer surface; metathoracic scent gland orifices with a single large or two nearly fused auricles; meso- and metasterna sulcate; posterior coxae contiguous or nearly so; all species less than 12 mm long.....Pseudophloeinae
- Tibiae clearly or slightly sulcate on outer surface; other characteristics different from above; length variable.....2
2. Metathoracic scent gland orifices deep between coxae; hind coxae far separate; hind femora strongly clavate and curved; hind tibiae with an apical tooth or spine.....Meropachyinae
- Scent gland lateral to coxae; hind coxae not so separate; hind femora not or rarely strongly clavate and usually straight; hind tibiae unarmed at apex.....Coreinae

19.4.1 *Pseudophloeinae* Stål (Plate 19.2)

Pseudophloeinae species are known to feed on legumes (Fabaceae) that grow in open woodlands or grasslands with scattered trees; apparently dense forests are not occupied by most of the species (Dolling 1986).

Pseudophloeinae is composed of two tribes: Clavigrallini and *Pseudophloeini*. The former apparently is monophyletic and the latter paraphyletic according to Dolling (1986). *Pseudophloeinae* is represented in the New World by three genera: *Coriomeris* Westwood, *Ceraleptus* Costa, and *Vilga* Stål, all belonging to *Pseudophloeini*. The first two genera are Holarctic in distribution, but one species of *Coriomeris* is found in the mountainous areas of Oaxaca, Mexico. Only *Vilga* Stål is registered to the Neotropical region.

Packauskas (1994) in the key to subfamilies of the New World Coreidae characterized *Pseudophloeinae* by the tibiae not sulcate; metathoracic scent gland orifices with a single large or two nearly fused auricles; meso- and metasternum sulcate; males with a bilobed genital capsule opening filled by the clearly visible parameres. Dolling (1986, 1987) and Schuh and Slater (1995) presented a more complete diagnosis for *Pseudophloeinae* including: antennae inserted at sides of head; antennifers with porrect or deflexed process at outer apical angles; rostrum at rest reaching metasternum; posterior coxae separated by about the width of a coxa or less; femora moderately to strongly clavate; posterior femora typically with two or more large subapical spines beneath on anterior side with some smaller spines, tubercles, or granules between them and a terminal series of about four spines diminishing in length toward apex of femur; tibiae without apical spines; membrane of hemelytron with a compound vein near base almost parallel with apical margin of corium; posterolateral angle of sternite VII almost always and of sternites III–VI commonly produced into teeth or spines; female paratergite VIII without functional spiracle; first valvula of ovipositor without peg-like setae; spermatheca with bulb lunate and duct devoid of prominent flange; egg not operculate or pseudoperculate, opening by a transverse eclosion rent. *Pseudophloeines* are easy to recognize because they do not

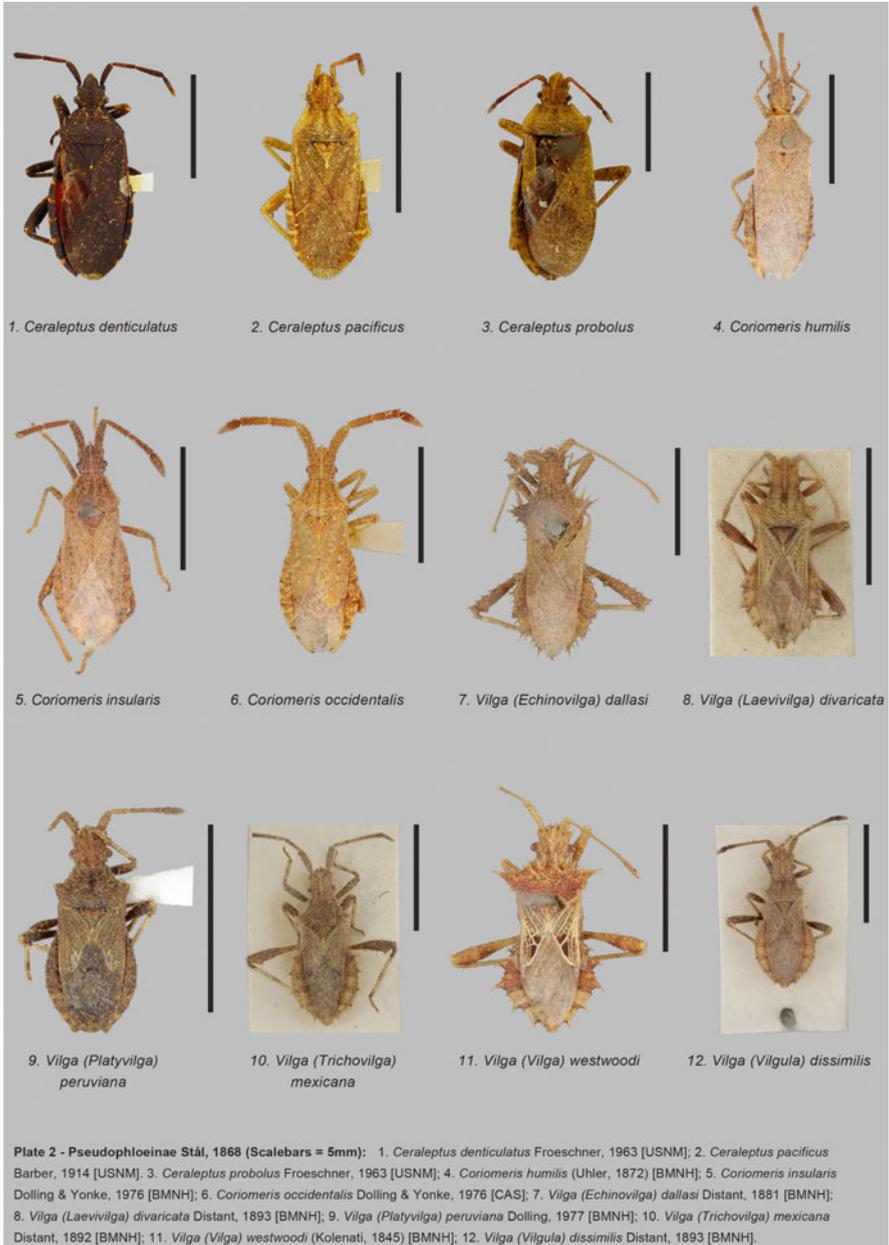


Plate 19.2 Coreinae plate—Pseudophloeinae

have the dorsal surface of the tibiae sulcate; a tribe of Coreinae—Hydarini—also lack these sulci, but do not occur in the Neotropical region. All remaining Coreinae taxa present tibiae sulcate.

The genus *Vilga* is composed of 14 species divided into 6 subgenera (Dolling 1977). This genus has a striking feature, probably apomorphic, grouping all species and not presented in any other genera of the subfamily—the freely projecting lobe on the seventh tergum of the male. This taxon is also characterized by the absence of an antevannal vein (“glochis”) in the hind wing, a feature used by Stål (1870) to characterize Pseudophloeinae. Dolling (1977) noted that this absence can be a plesiomorphic state shared with the Old World *Hoplolomia* Stål and *Risbecocoris* Izzard. This genus was revised and keyed by Dolling (1977); he also included in his key a pair of couplets to separate *Vilga* from *Ceraleptus* and *Coriomerus*. No host plants are known for this genus, but legumes are likely based on the feeding habits of other Pseudophloeini. One species, *Vilga mexicana* Distant, is unusual in having both macropterous and brachypterous forms (Dolling 1977).

19.4.2 *Meropachyinae* Stål (Plate 19.3)

Meropachyinae has a striking characteristic that is the hind tibiae with an apical spine or tooth used in keys to separate *Meropachyinae* from other subfamilies. Other characteristics used are the small head and narrow thorax; metathoracic scent gland opening deep between coxae, opening anteriorly; projections of peritreme fused; evaporatorium moderate and without ridges; veins of the forewing arising from a vein close to corial border; widely separated hind coxae; hind femur curved and strongly incrassate; second through fifth abdominal sterna fused in both sexes; plus several characteristics from male and female genitalia.

This subfamily has a history of name changes that started with Stål (1867) erecting it under *Meropachydida* afterwards changed to *Merocorina* (Stål 1870). Further authors used both names to designate the same group of genera; thus, *Meropachyinae* was indicated as the correct name for the subfamily by Schaefer (1964) followed by Froeschner (1981), Henry and Froeschner (1988), Schuh and Slater (1995), and Brailovsky (1998a, 1999a) among others. *Merocorinae* was used by Van Duzee (1916), Torre-Bueno (1941) and Kormilev (1954). Packauskas (1994) explained that *Meropachyinae* should be used rather than *Meropachyinae*, and more recently Brailovsky (2009a) and CoreoideaSF Team (2015) also use this name.

Kormilev (1954) revised *Meropachyinae* and proposed three tribes: *Merocorini* Stål, *Meropachyini* Stål, and *Spathophorini* Kormilev. After that, only keys and lists of regional fauna were presented till Brailovsky (1998a) started a series of works dealing with the entire subfamily. Additional keys to the tribes may be found in Packauskas (1994). The subfamily currently includes 27 genera, most of them monotypic, comprising about 60 species (CoreoideaSF Team 2015).

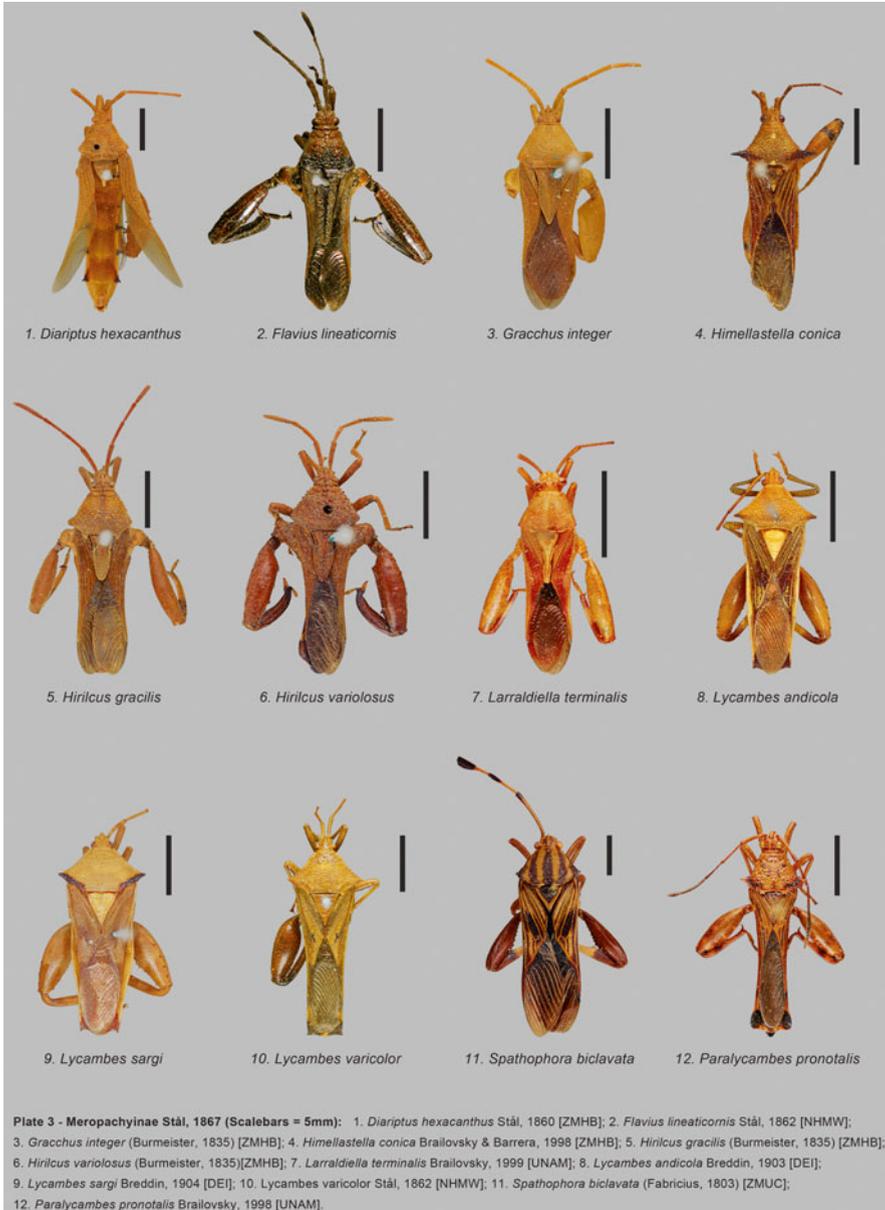


Plate 19.3 Meropachyinae plate

Merocorini Stål

This tribe can be identified by the small size of the species; scutellum triangular, short, not surpassing base of claval commissure, the apex of scutellum elevated as a small knob and not hiding claval commissure; abdominal spiracles circular and located almost on the anterior third of each sternite (Kormilev 1954). Only one genus is currently included—*Merocoris* Perty—divided in two subgenera. The nominal subgenus has five species spread from Argentina to Central Part of Brazil; this group can be recognized by the scutellar disk with a high conical tubercle. The subgenus *Corynocoris* Mayr has three species, but one is registered only to North America, the other two distributed in Central America and Great Antilles; this group can be recognized by the scutellar disk almost flat. Brailovsky and Barrera (2009a) described a new species from Brazilian Cerrado areas collected on grassland, and presented a key to subgenera and species of *Merocoris*. Other *Merocoris* spp. are reported to feed on milkworts (*Polygala* sp.) (Schaefer and Mitchell 1983).

Meropachyini Stål

This tribe is easily recognized by the elongate scutellum extending beyond the distal end of the clavus; hind acetabulae laterally projected, visible in dorsal view; posterior tibiae broadly curved distally. The hind coxae widely separated looking like thoracic appendages, and the hind coxae strongly incrassate and long produce a unique facies remarkable among coreids.

This tribe contains 18 genera so far with 30 species chiefly South American and only a few species registered to Central America. Brailovsky (1999a) started the study with Meropachyini describing several genera and presenting a key to the known genera. Further contributions (Brailovsky and Barrera 2001; Brailovsky and Luna 2000; Brailovsky 2009a) included several new genera and species plus an updated key. The large old genera—*Hirilcus* Stål, *Marichisme* Kirkaldy, *Meropachys* Burmeister, and *Peranthus* Stål—are still to be revised. Little is known of the biology of this group. A key to genera can be found in Brailovsky (1999a, 2009a) and Brailovsky and Barrera (2001).

Spathophorini Kormilev

Spathophorini is a tribe recognizable by the triangular scutellum, flat, shorter than clavus; hind femora not attaining the apex of the abdomen; antennal segment IV usually slender; and abdominal spiracles elliptical and positioned between the anterior and middle third of the segment. This tribe is quite neglected because after Kormilev (1954), not much was added to it, except works by Brailovsky (1998a,

2000, 2008) and Brailovsky and Barrera (1998a). *Lycambes varicolor* Stål is reported to feed on *Lonchocarpus guatemalensis* and *L. cruentus* (Peredo 1999). A key to genera can be found in Brailovsky (1998a, 2000, 2008).

19.4.3 *Coreinae Leach*

Most of the coreids are included here. Extremely diverse in shape, color, and size; distance from eye to ocellus smaller than that between ocelli; anterolateral opening of the metathoracic scent gland well developed, peritreme with developed projections, auricle usually occupying half of the size of evaporatorium; corial margins straight or slightly sinuate; membranal veins of forewing arising from a transverse vein very close, or touching, corial margin; abdominal terga 1–2 and 3–7 fused; genital capsule of male without lateral prolongations; articulation of female genital plates usually membranous; gonangulum usually flat and folded.

These are the most common and striking coreids both in the field and in collections. This is by far the largest subfamily, with a mostly tropical worldwide distribution. This is also the subfamily in which discussions about taxonomical levels of certain groups are concentrated. Neotropical tribes are not much affected by such discussions; thus, they will not be treated here (see Schuh and Slater 1995 for more on suprageneric changes). Hydarini was raised by Ahmad (1970) to subfamily level, but recent works (i.e., Schuh and Slater 1995; Brailovsky 2010a) have considered this taxon as a tribe, which is the position followed here. Coreinae comprises 32 tribes, but Neotropical fauna comprises only 11 tribes, presented below. Several authors worked with Coreinae, but the subfamily still needs a phylogenetic analysis to raise hypotheses about relationships among genera. Packauskas (1994) presented a key to the Neotropical tribes, which is a keystone to understanding Coreinae.

Key of Coreinae (adapted from Packauskas 1994). Packauskas used Coreini to refer to the set of genera we are considering under Hypselonotini according to the Coreoidea catalog (CoreoideaSF Team 2015).

1. Tylus projecting conspicuously beyond juga as a distinct knob
or strongly compressed plate; juga strongly deflex.....2
- Tylus not or only vaguely projecting beyond juga; juga variable.....3
2. Tylus projected as a distinct knob; ventral surface of the body
with several small black spots; hind femur of the males not
or slightly incrassate.....Placoscelini
- Tylus well projected as a strongly compressed plate; ventral surface
of the body with ventral color greatly variable but not as above;
hind femur of the males greatly incrassate.....Acanthocephalini

3. With the combination of hind femora spinose or tuberculate; strongly incrassate in males; head not over half as long as pronotum and not extending past antenniferous tubercles or very slightly so; antenniferous tubercles occupying most of anterior head width, space between them rarely wider than one tubercle.....4
 – Not with this combination of characters.....5
4. Metathoracic scent gland with a single fused auricle (sometimes bilobed); ocellar tubercles large; usually with a spine present on antenniferous tubercles; parameres membranous.....Acanthocerini
 – Metathoracic scent gland with two completely separated auricles (area between them depressed); ocellar tubercles small; antenniferous tubercles never armed; parameres sclerotized.....Nematopodini
5. Head porrect; juga and tylus extended forward beyond antenniferous tubercles; bucculae never reaching midlength of head; all femora spinose below, rostrum almost reaching or extending onto abdomen.....Anisoscelini
 – Not with this combination of characters.....6
6. Juga extended and exceeding or equal to tylus in length.....7
 – Juga deflexed or at least not exceeding nor equal to tylus in length.....8
7. Head shorter than pronotum; antennae terete; brachypterous.....Barreratalpini
 – Head equal in length to pronotum; antennae triangular in cross-section; macropterous.....Chelinideini
8. Distance between hind coxae equal to distance from coxa to lateral margin; antenniferous tubercles prominent, subcontiguous above deflexed tylus and juga.....Spartocerini
 – Distance between hind coxae much narrower than distance from coxa to lateral margin, if distances nearly equal then head elevated between antenniferous tubercles; tylus and juga variable.....9
9. Third antennal segment expanded, other segments terete; tylus and juga deflexed; not filling space between antenniferous tubercles; all femora armed distally.....Chariesterini
 – Third antennal segment never expanded, if appearing expanded, then other segments also appearing expanded; tylus and juga usually extended anteriorly between antenniferous tubercles; femora rarely armed.....10
10. Spiracles situated twice as far from posterior border of middle abdominal segments (III–VI) as from anterior border.....Discogastrini
 – Spiracles equidistant from anterior and posterior borders of middle abdominal segments (III–VI).....11
11. Fourth antennal segment flattened; third antennal segment over twice as long as second.....Hydarini
 – Fourth antennal segment not flattened; third antennal segment usually shorter than second, never twice as long as second.....Hypselonotini

Acanthocephalini Stål (Plate 19.4)

This tribe groups species with medium to large size and interesting color patterns that are found in well-preserved forest. The tribe was established by Stål (1870) as Acanthocephalina, but no description was given. Schaefer (1964) also did not present a description of the tribe but mentioned the striking spinelike tylus. The most significant features of this tribe are the tylus, which projects conspicuously beyond the juga as a distinct acute plate, juga deflexed, abdominal spiracles close to anterior margin of the sternum, hind femur of males greatly incrassate, all femora of both sexes spinose ventrally, and hind tibia slightly or strongly expanded in both sexes (Packauskas 1994; Brailovsky 1997a). Several genera were described and revised or new species added in the last decades mainly by Brailovsky and coauthors (Brailovsky 1991, 1999b; Brailovsky and Barrera 1999, 2005). The largest genus *Acanthocephala*—one of the most common and conspicuous—still needs revision; Brailovsky (2006b) reviews the Mexican species, and McPherson et al. (2011) treats the species of America north of Mexico. No key to the entire tribe has been published so far.

This tribe is distributed across the Americas, but the largest number of species is found in the North and Central parts of South America, especially Peru and Ecuador; only a few are distributed across Central America and Nearctic region. Acanthocephalini includes 15 genera: *Acanthocephala* Laporte (27 species, three of them invading Nearctic region and three exclusively Nearctic), *Cervantistellus* Brailovsky & Barrera (two), *Cleotopetalops* Brailovsky (three), *Ctenomelyntus* Breddin (five), *Empedocles* Stål (two), *Ichilocoris* Brailovsky & Barrera (two), *Laminiceps* Costa (18), *Leptopetalops* Breddin (two), *Lucullia* Stål (one), *Meluchopetalops* Breddin (two), *Petalops* Amyot & Serville (12), *Placophyllopus* Blöte (one), *Salapia* Stål (17), *Stenometaopodus* Breddin (five), and *Thymetus* Stål (two) (CoreoideaSF Team 2015).

The natural history and behavior of *Acanthocephala* spp. have been studied in depth by several authors. The incrassate hind femora of males are used as a weapon in aggressive encounters in two species. Eberhard (1998) provides a detailed description of feeding, aggression, and mating behavior in *Acanthocephala declivis guatemalensis* [which may be *Acanthocephala alata* Burmeister; see McPherson et al. (2011) and Brailovsky (2006a, b) and similar aggressive behavior occurs in *A. femorata* (Mitchell 1980b)]. The trunks and branches of *Cordia* sp. (Boraginaceae) trees were the feeding site for *A. declivis*, whereas *A. femorata* males defended territories on the stalks of cultivated sunflower. McPherson et al. (2011) provide host plant records for two species whose distribution extends into the Neotropics: *Acanthocephala femorata* (F.) and *Acanthocephala declivis* (Say). Vegetative plant parts (stems, shoots, and branches) appear to be the preferred sites for species in this genus, but more information is needed regarding other genera before a generalization may be made regarding the tribe.

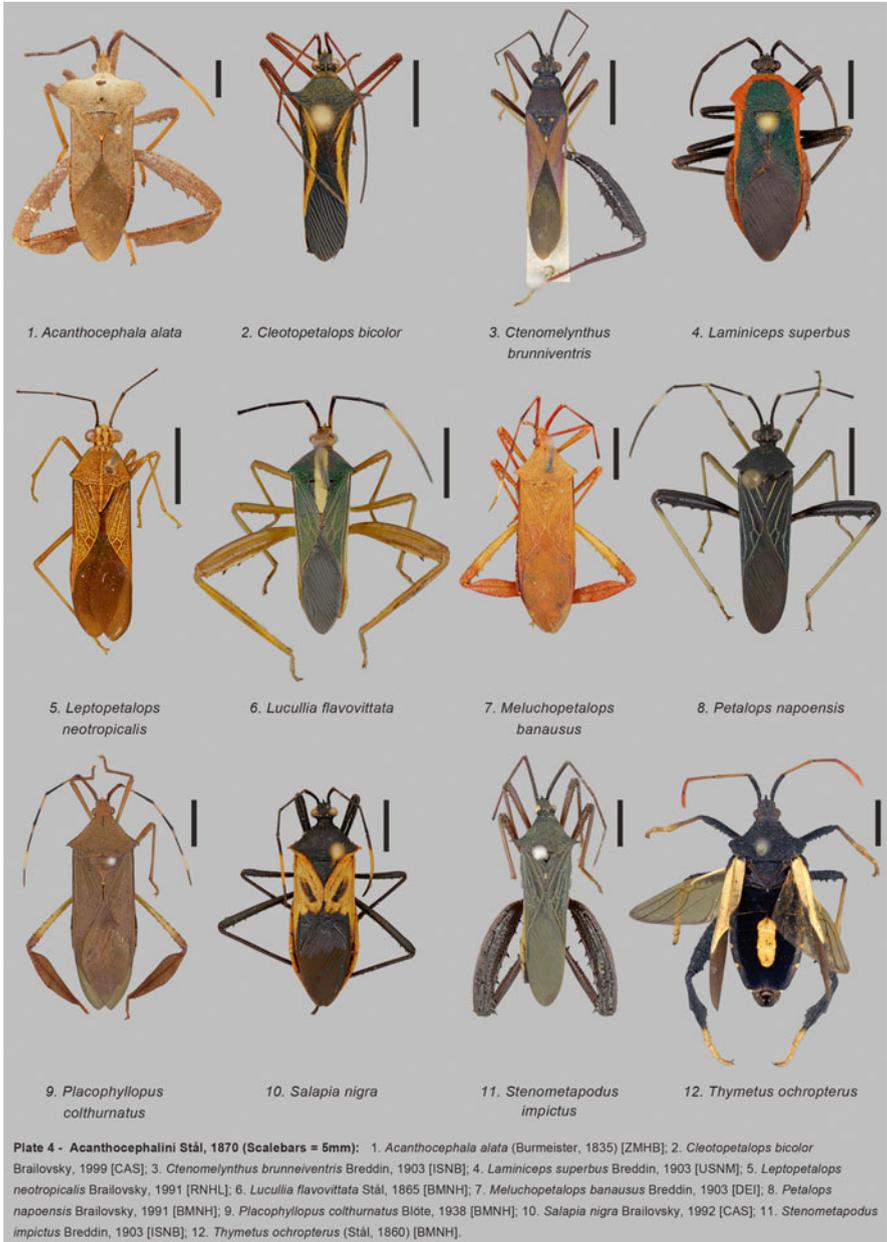


Plate 19.4 Coreinae plate—Acanthocephalini

Acanthocerini Bergroth (Plate 19.5)

Species belonging to this tribe can be found in open areas on herbs, shrubs, and small trees but also in crops. Bugs belonging to Acanthocerini have the head subquadrate; ocelli placed on prominent tubercles; blunt tylus slightly exceeding the jugae; antenniferous tubercles often armed laterally with a spine; antennal segment four robust; metathoracic scent gland opening placed almost ventrally, with a single, sometimes double, fused auricle; femora incrassate especially in males, sometimes armed subapically on ventral surface; hind tibiae lacking foliaceous expansions; spermatheca with the bulb elongate; parameres membranous (O'Shea 1980a; Packauskas 1994). This tribe has received little attention since O'Shea (1980a) for a group with species easy to find and catch, very common in collections, and with a certain economic importance. Brailovsky (1987a, 1988a) and Brailovsky and Barrera (2003a) described new genera and added important information to identify some genera.

Acanthocerini includes 17 genera (most of them with very few species) and 50 species: *Acanthocerus* Palisot de Beauvois (three species), *Athaumastus* Mayr (8), *Beutelspachoris* Brailovsky (two), *Camptischium* Amyot & Serville (three), *Crinocerus* Burmeister (one), *Dersagrena*, Kirkaldy (three); *Elachisme* Kirkaldy (one), *Euthochtha* Mayr (one), *Golema* Amyot & Serville (two), *Lybindus* Stål (four), *Machtima* Amyot & Serville (three), *Moronopelios* Brailovsky (two), *Rondoneva* Brailovsky & Barrera (one), *Sagotylus* Mayr (one), *Schaeferocoris* O'Shea (one), *Thlastocoris* Mayr (two), and *Zoreva* Amyot & Serville (12) (CoreoideaSF Team 2015). This group is basically South American, but genera like *Acanthocerus* and *Euthochtha* have a North American and Antillean distribution, and *Sagotylus* can be found in the northern part of the Neotropical region and United States.

The natural history of *Athaumastus haematicus* (Stål) has been described in Brazil (Merti 1940, cited in O'Shea 1980a); Schaefer and Mitchell (1983), Schaefer and O'Shea (1979), and Bosq (1937) also give host plant records for this minor crop pest. On pineapple, *Lybindus dichrous* Stål adults and nymphs cluster on the peduncle of the fruit and suck plant juices; plants without fruits are not attacked (Mariconi 1953). Other minor economic pests include *Thlastocoris laetus* Mayr on pineapple; *Machtima crucigera* (F.) and *Euthochtha galeator* (F.) on flowers; *Dersagrena flaviventris* (Berg) on cotton; *Camptischium clavipes* (F.) on castor bean, ice cream bean, and the medicinal plant, guaco; and *Sagotylus confluens* (Say) on cowpea (Mead 2014; Mitchell 2000; Schaefer and O'Shea 1979, and references therein). The immature stages of *E. galeator* in North America were described by Yonke and Medler (1969a), and combat between males of this species was noted by Mitchell (1980b). *Crinocerus sanctus* (F.), a major pest of cowpea in Brazil, is treated below (section "*Crinocerus Burmeister*"). A key to the genera of Acanthocerini can be found in O'Shea (1980a).

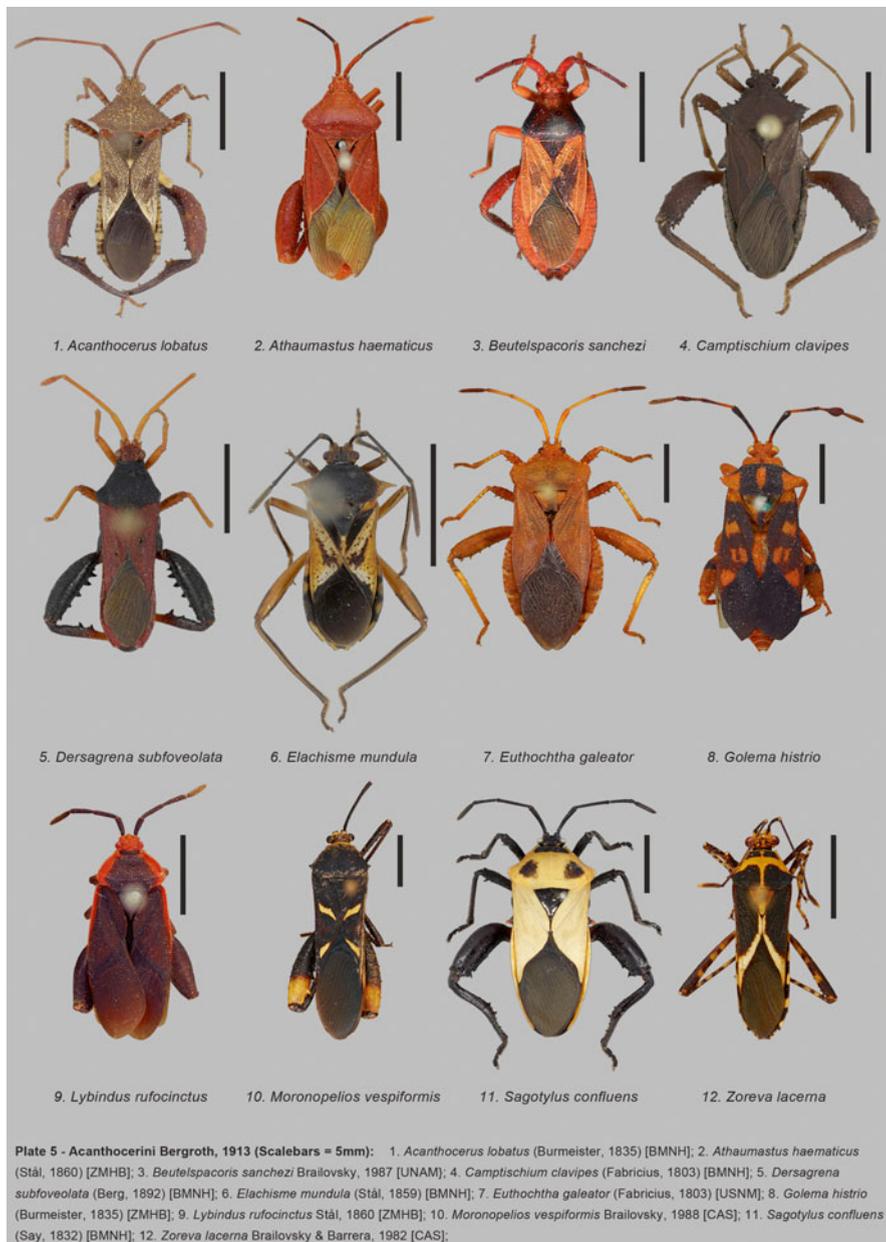


Plate 19.5 Coreinae plate—Acanthocerini

Anisoscelini Laporte (Plate 19.6)

Since Stål (1868), several authors have used erroneously the name Anisocelidini to designate this tribe. Species belonging to Anisoscelini are very characteristic because of the foliaceous expansion of the hind tibiae, bright colors, and abundance in agricultural and urban environments. Body elongate and narrow, ratio of body length to width greater or equal to three, less than four. Head usually longer than scutellum. Head usually correct; tylus and mandibular plates never deflexed; both usually extend beyond antenniferous tubercles. Distance between antenniferous tubercles greater than width of one tubercle. Antennal segment IV never the shortest and longer than segment III. Antennal segment I usually longer than head. Bucculae short extending or not to the level of anterior margin of the eye. Rostrum extending to at least metacoxae, usually onto abdomen. Pronotum steeply declivent; with distinct collar, punctate, occasionally rugose, never tuberculate; humeral angles acute to obtusely angled; posterior angles obtuse to rounded; callar region raised. Usually lacking metapleural supracoxal spine. Metapleural scent gland opening separated, with two auricles; anterior auricle larger. Abdomen rarely wider than thorax. Spiracle of abdominal segment IV closer to lateral edge of segment than to anterior or posterior edge. Abdominal segments never spined posterolaterally. Connexivum VI separated from dorsum or slightly fused at apex; connexivum VII fused to dorsal plate. Scutellum longer than wide or subequal, rarely wider than long. All femora spined below, at least distally. Hind femora rarely incrassate or spined above.

This tribe is one of the largest in the Neotropics and the subject of recent revisions: taxonomic and nomenclatural changes led *Leptoscelini* to be considered part of Anisoscelini; important revisions affected *Leptoglossus* and *Phthia*, genera that contain several species quite common in human-altered environments and causing damage to a number of crops; other studies revealed several new genera and species (Packauskas 1994, 2008; Packauskas and Schaefer 2001; Allen 1969; Osuna 1984; Gibson and Holdridge 1918; Brailovsky 1989, 1990a, 1990b, 1996, 1997b, 2001a; Brailovsky and Barrera 1994, 1998b; Brailovsky and Sánchez 1983a).

Anisocelini comprises 27 genera: *Anisoscelis* Latreille (11 species); *Baldus* Stål (one); *Bellamynacoris* Brailovsky (two); *Belonomus* Uhler (one); *Chondrocer*a Laporte (two); *Coribergia* Casini (one); *Dalmatomammurius* Brailovsky (six); *Diactor* Perty (two); *Holhymenia* Lepeletier & Serville (eight); *Kalinckascelis* Brailovsky (one); *Leptoglossus* Guérin-Méneville (57); *Leptopelios* Brailovsky (one); *Leptoscelis* Laporte (25); *Leptostellana* Brailovsky (one); *Malvana* Stål (three); *Malvanaoides* Brailovsky (five); *Narnia* Stål (seven, mostly Nearctic with four species invading northern boundaries of Neotropical region); *Onoremia* Brailovsky (one); *Phthia* Stål (four); *Phthiacnemia* Brailovsky (one); *Phthiadema* Brailovsky (three); *Phthiarella* Brailovsky, 2009 (4); *Plurentis* Stål, 1860 (2); *Rhytidophthia* Brailovsky, 2009 (1); *Sephinoides* Brailovsky (two); *Tarpeius* Stål (two); and *Ugnius* Stål (two) (CoreoideaSF Team 2015). Most of the species belonging to this tribe are found in tropical areas, but a few are found in North America (e.g., species of *Leptoglossus*). Osuna (1984) made several changes,

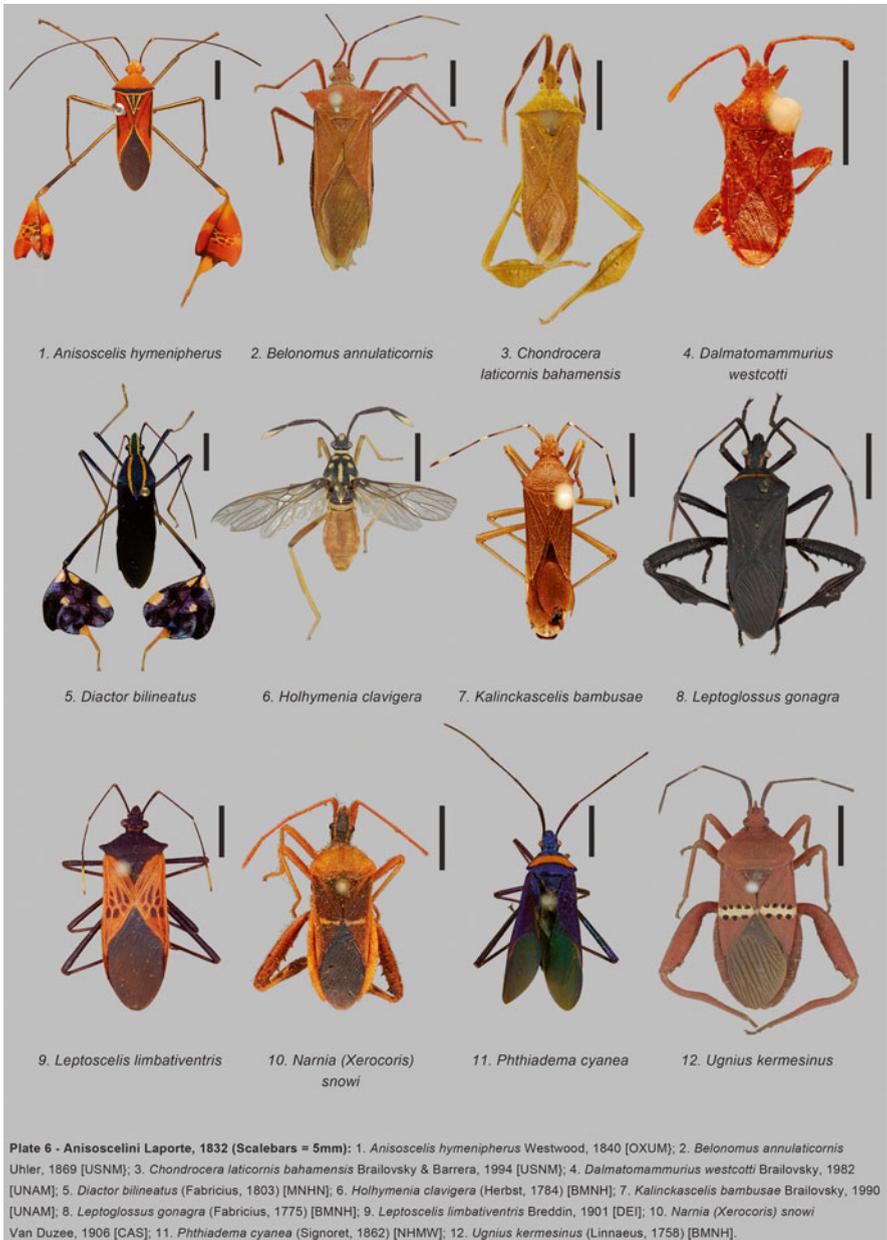


Plate 19.6 Coreinae plate—Anisocelini

especially splitting *Leptoglossus* into several genera, but this arrangement was not recognized by other authors, and these genera were given only species-group status by Packauskas and Schaefer (2001). Brailovsky and coauthors contributed new species and genera, mainly in the former tribe Leptoscelini (i.e., Brailovsky 1990b, 1993, 1997b, 2001a, b, 2009b; Brailovsky and Barrera 1994, 1998b, 2004, 2011, 2013; Brailovsky and Sánchez 1983a). Despite the visibility of the tribe, no comprehensive key to the genera is presented in the literature.

Anisosceline biology has been studied more extensively than that of most other tribes, partly due to the economic importance of a few species but also because of their very noticeable physical and behavioral traits, including the large and often colorful tibial foliations, flattened antennal segments, and territorial defense involving the spined incrassate femora. Perhaps the most striking of all anisoscelids are the two species of *Diactor*, with their broad, spotted tibial foliations and bright orange or yellow stripes on the metallic green body. Antennal expansions are found in nymphs of many species, but appear in the adult stage as well in *Holhymenia*, *Tarpeius*, and *Chondrocera laticornis* Laporte (Brailovsky and Barrera 1994). Not all species have incrassate femora, nor is the enlargement as impressive as in, for example, Nematopodini, but male combat has been noted in species of *Leptoglossus*, *Narnia*, and *Leptoscelis* (Miyatake 1997; Miller 2011, 2013; Miller and Emlen 2010). The natural history, ecology, and behavior of *Leptoscelis tricolor* Westwood on inflorescences of *Heliconia* spp. have been particularly well-studied. Both female choice and male combat operate in this species. Males defend territories on flower spikes, and femur width varies among locations and between *Heliconia* species within a location. Furthermore, the scaling relationship between body size and femur width varies; for a given body size, femur width differs across populations (Miller and Emlen 2010). Females may accept or reject courting males and usually feed during the mating, while males stroke the female's abdomen and perform other courtship behaviors. Natal host plant species and seasonal quality of the host affect female fecundity and male courtship behavior (Miller 2008).

No strong association with a particular host plant family is evident for the tribe as a whole. Feeding preference ranges from highly polyphagous [e.g., *Leptoglossus zonatus* (Dallas)] to specialization on a single genus or family. As mentioned above, *L. tricolor* specializes on *Heliconia* species. All *Narnia* spp. plus two species of *Leptoglossus* are specialists on cactus. Species in several genera (*Holhymenia*, *Anisoscelis*, *Diactor*) feed exclusively on Passifloraceae; anisoscelines constitute the second most important group of pests on cultivated passion fruit in the Lake Maracaibo region of Venezuela (Aguiar-Menezes et al. 2002). The latter authors provide information on the life history of *Diactor bilineatus* (F.).

Most if not all anisoscelines seem to be associated with reproductive plant parts. Feeding on vascular tissue (primarily xylem) and nectar is reported, but xylem represents a source of hydration (Rodrigues et al. 2007a; Mitchell 2006). Nymphs are usually observed on buds or fruits. When two species of oligophagous anisoscelines were offered a mixed diet of *Passiflora* spp., food preference (species and tissue) changed with instar (Rodrigues et al. 2007b). Polyphagous species [e.g., *Leptoglossus phyllopus* (L.)] may move generationally among host plants, tracking plant reproductive structures (Mitchell 2006).

Host plant records for various species are given by Brailovsky and Sánchez (1983a) and Schaefer and Mitchell (1983). Species and genera of major importance, including targets of ecological and behavioral research as well as serious economic pests, are treated separately in Sect. 19.5.2 (*Anisoscelis*, *Holhymenia*, *Leptoglossus* *Narnia*, and *Phthia* s.l.).

Barreratalpini Brailovsky (Plate 19.7)

This tribe can be recognized by body brown, medium size, dorsoventrally flattened; head longer than wide, shorter than pronotum; mandibular plates longer than tylus but not contiguous in front of it; antennae terete, first antennal segment strong, fourth the shortest; brachypterous; ventral surface of the femora with two short distal spines; tibiae terete; abdomen enlarged; connexival angles not developed.

This tribe was proposed by Brailovsky (1988b) for the new genus and species—*Barreratalpa bambusii*—collected on bamboo in Mexico. After the initial description, only Packauskas (1994) mentioned this tribe. Brailovsky (1988b) provides a short but useful discussion justifying the separation of the new tribe from others.

Chariesterini Stål (Plate 19.7)

This small tribe is formed by four genera and 24 species, most living in Central America and the northern part of South America. No formal description has been made, but species can be identified by the small size; body narrow with lateral margins almost parallel; third antennal segment expanded, other segments terete; tylus and juga deflexed not filling space between antenniferous tubercles; all femora armed distally; distance between hind coxae much narrower than distance from coxa to lateral margin, hind tibiae never expanded. The single species of *Chariesterus* registered to Brazil—*C. armatus*—can be collected on Euphorbiaceae (*Euphorbia* spp.). The Caribbean species *Chariesterus gracilicornis* (Stål) is reported from amaranth and cucurbits in addition to euphorbs (Schaefer and Mitchell 1983). The two most comprehensive works are the revision of *Chariesterus* by Ruckes (1955) and the description of *Ruckesius* by Yonke (1972) that also presented a key to the genera.

Chelinideini Blatchley (Plate 19.7)

Species of Chelinideini belong to a single genus—*Chelinidea* Uhler. They are known as cactus bugs because they live on these plants causing damage to certain species. Hamlin (1924) revised *Chelinidea* Uhler and gave a more comprehensive description of the genus. Herring (1980) revised *Chelinidea* again adding new species, a key to the species, and new information about distribution, biology, and host plants. They can be recognized by the body short somewhat broader, oval. Head as

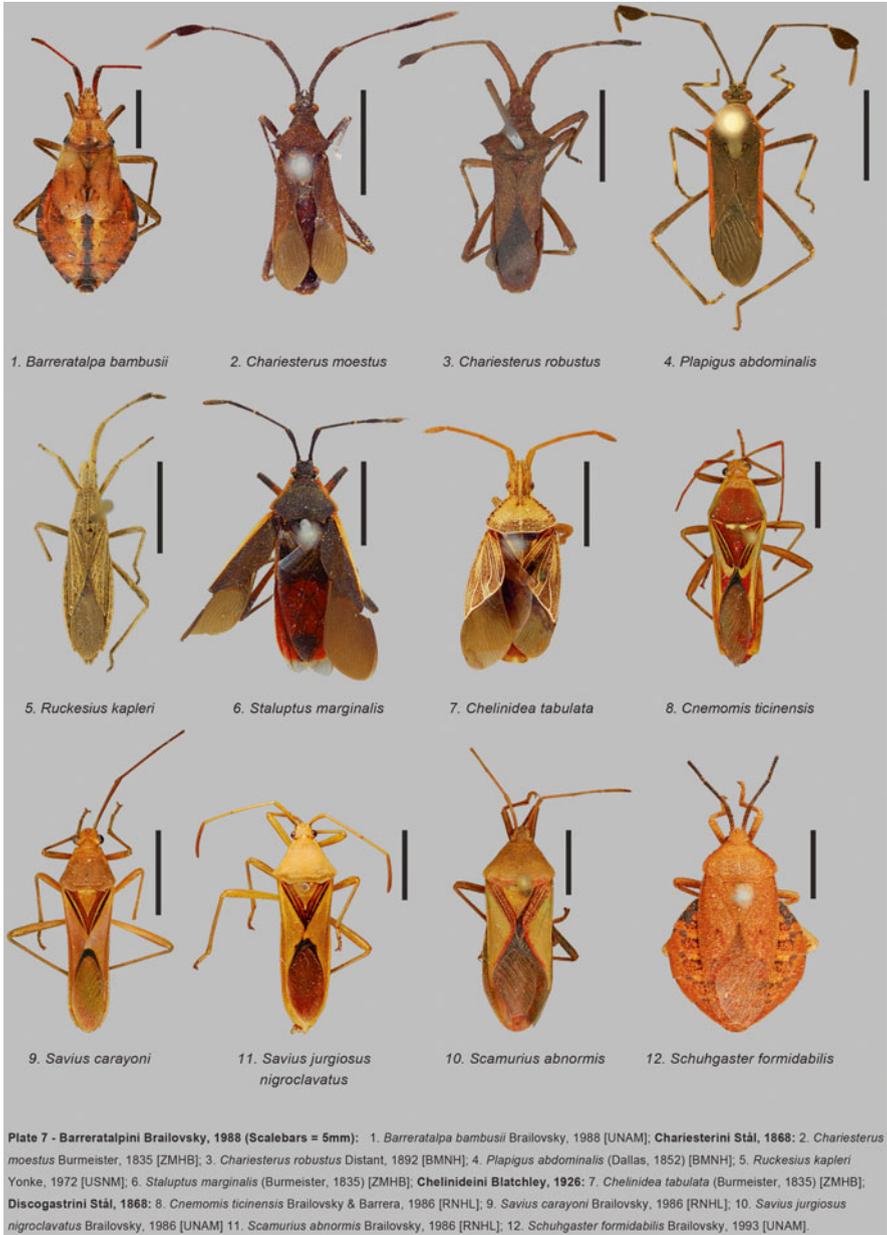


Plate 19.7 Coreinae plate—Barreratalpini-Chariesterini-Chelinideini-Discogastrini

long as pronotum. Tylus appearing conical from above. Jugs acutely pointed and level with or surpassing tylus. Eyes small, subcircular, and closer to base of the head than to antennal tubercle. First three antennal segments prismatic; basal segment flattened and crested on inner edge; second and third subequal; distal rounded and tapered toward either extremity. Bucculae about one-third length of the basal segment of rostrum. Rostrum just attaining the abdomen; first segment slightly longer than the head; second subequal to first; third the shortest and fourth two-thirds the length of the second. Pronotum nearly twice as long as wide; anterior margin forming a narrow collar; anterolateral margin entire straight to slightly rounded; humeral angles rounded to obtuse and not developed. Sterna sulcated to receive the rostrum. Connexivum bent upward and distinctly dilated. Posterior femora enlarged and armed with two rows of teeth on under surface; anterior and middle femora armed with smaller and fewer teeth on under surface (adapted from Hamlin 1924).

The genus *Chelinidea* Uhler is formed by five species found in Nearctic region but also reaching or crossing Neotropical northern boundaries. Only *C. tabulata* (Burmeister) has a larger distribution in the Neotropical region, reaching Venezuela. *Chelinidea staffilei* and *C. tabulata* nymphs were studied and described by Brailovsky et al. (1994). Several species, including *C. tabulata*, have been considered as biological control agents for cacti (*Opuntia* spp.) but have either failed to disperse or were never released due to the potential to damage other plants (Mitchell 2000 and references therein).

Discogastrini Stål (Plate 19.7)

Species belonging to this tribe are usually medium in size; elongate; light green to green. Head is square and shorter than pronotum. Tylus longer than mandibular plates but not projected in a spine, both usually anteriorly extended between antenniferous tubercles. Rostrum short not reaching mesosternum. Pronotal disk rough and transversely sulcate. Pronotal angles rounded or subacute but never developed. Evaporatorium slightly developed and sulcate. Femora and tibiae terete. Spiracles on anterior third of each abdominal segment. Spine of the sternite VII bifid.

This tribe is formed by eight genera [*Cnemomis* Stål (eight species), *Coryzoplatus* Spinola (two), *Discogaster* Burmeister (five), *Karnaviexallis* Brailovsky (one), *Lupanthus* Stål (two), *Savius* Stål (nine), *Scamurius* Stål (11), and *Schuhgaster* Brailovsky (one)]. Most of the species are found in South America with only a few specimens living in the northern part of the Neotropical region. Only *Cnemomis* and *Scamurius* were revised (Brailovsky and Barrera 1986a; Brailovsky 1987b), but Brailovsky added valuable information to four other genera (Brailovsky 1986a, b, c; Brailovsky and Barrera 2003b) and described two others (Brailovsky 1984, 1993). Information on biology is limited; *Savius jurgiosus jurgiosus* Stål was reported from leaves and pods of *Prosopis laevigata* and leaves of *Ziziphus pedunculata* (Brailovsky et al. 1995) and from *Buddleja sessiliflora* (Brailovsky 1986b) in Mexico; immatures of this subspecies are described by Brailovsky et al. (1995). *Savius* sp. was also reported from the petioles and shoots of Texas ebony, *Ebenopsis*

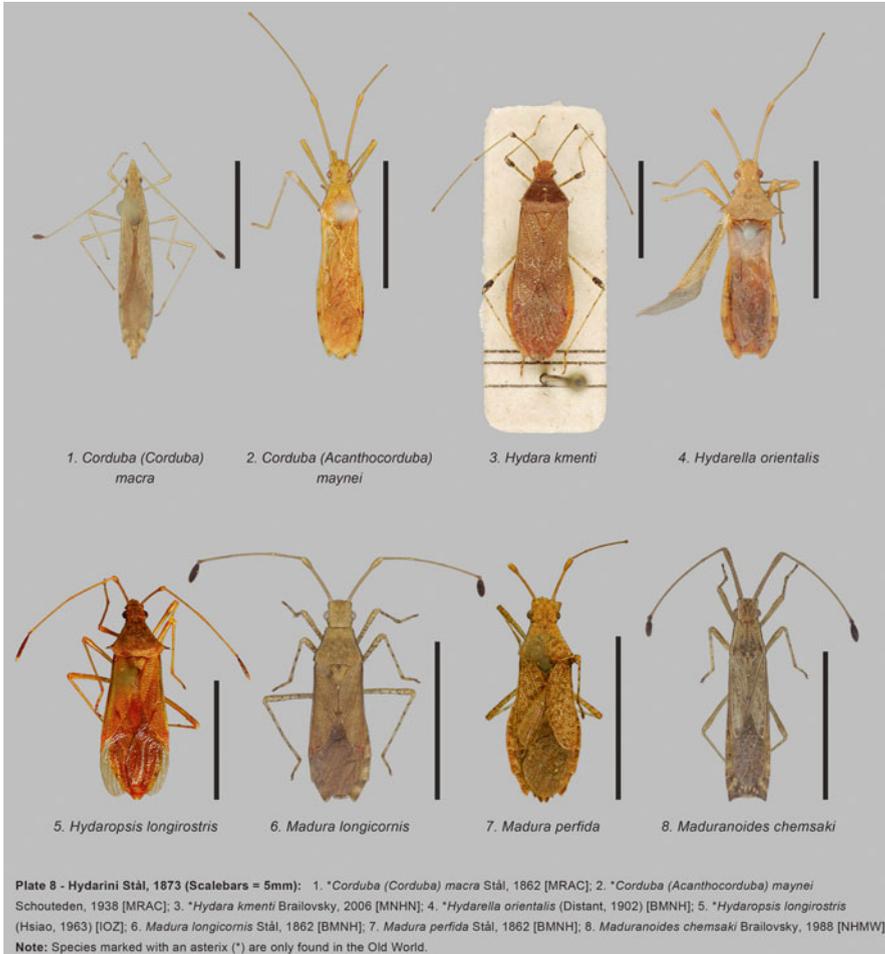


Plate 19.8 Coreinae plate—Hydarini

ebano (Berl.) Barneby & Grimes (as *Pithecellobium*) in southern Texas (Schaefer and Mitchell 1983). A key to the genera included in Discogastrini can be found in Brailovsky (1984, 1993).

Hydarini Stål (Plate 19.8)

This tribe was always considered quite apart from other taxa (Stål 1873; Schaefer 1964) and Ahmad (1970) raised this taxon to subfamily level, but later authors (with the exception of (CoreoideaSF Team 2015) are still considering Hydarini as a tribe. The tribe is characterized by the lack of a dorsal tibial sulcus; paramere with

a subdistal projection; broad direct articulation of the first valvifer and valvula; and lack of a spermathecal bulb. Head squared to rectangular and rough; first antennal segment slightly swollen distally; antennal segment III more than twice as long as segment II, and antennal segment IV short and flattened; spur of the third metathoracic axillary sclerite well developed; the anterior and posterior lobes of metathoracic peritreme completely separated; evaporatorium without ridges; connexivum ending at sixth tergite; trichobothria of third sternum level with spiracles; anterior spur of the seventh sternum double; trichobothria of fourth sternum anterior to spiracle; all femora slightly swollen anteriorly; and the hind tibiae not expanded.

This small tribe is formed by nine genera and 23 species; most of the genera and species are found in Africa and Asia. The Neotropical fauna is composed of *Hydarellamixia* (one species), *Hydascelis* (one), *Madura* (three), and *Maduranoides* (one). These species are distributed from Argentina to the United States. Brailovsky (1988c, 2010a) provides the necessary information to identify genera. *Madura perfida* Stål is reported from grasses and dry corn (references in Brailovsky and Rivera 1979) and from *Annona cherimola* Mill. (Peña and Bennett 1995). A key to the genera known from Neotropical region can be found in Brailovsky (2010a).

Hypselonotini Bergroth (Plates 19.9 and 19.10)

This tribe was first mentioned by Bergroth (1913) as Hypselonotaria, which was also used by Blöte (1935). No description or diagnosis for the tribe was given by Bergroth or Blöte, so a study of the relationships among these genera is badly needed and a careful evaluation of the separation between Hypselonotini and Coreini considered. Several genera belonging to this tribe were the subject of recent revisions, and when mentioned, Coreini is considered as the valid tribe for them (Brailovsky 1983a, 1985, 1988d, 1988e, 1989, 1990c, 1992a, 1995a; Brailovsky and Cadena 1992; Brailovsky and Garcia 1987; Brailovsky and Melendez 1989; Whitehead 1974). Species belonging to this tribe are distributed across the Americas, including Chile, with a considerable number living in subtropical areas. No key for the genera of the tribe is known.

This tribe comprises 34 genera and 352 species: *Acanonicus* Westwood (three species), *Acidomeria* Stål (11), *Althos* Kirkaldy (24), *Anasa* Amyot & Serville (76), *Arioge* Stål (one), *Astygiton* Berg (one), *Catorhintha* Stål (32), *Cebrenis* Stål (25), *Cebreniscella* Brailovsky (two), *Cebrenistella* Brailovsky (three), *Cimolus* Stål (four), *Collatia* Stål (five), *Daphnasa* Brailovsky (four), *Eldarca* Signoret (two), *Encedonia* Stål (two), *Hypselonotus* Hahn (12), *Microbasis* Dallas (one), *Namacus* Amyot & Serville (four), *Nirovecus* Stål (three), *Nisoscolopocerus* Barber (two), *Paryphes* Burmeister (28), *Petersitocoris* Brailovsky (one), *Petersitocoroides* Brailovsky (four), *Rochrosoma* Reed (one), *Scolopocerus* Uhler (four), *Sethenira* Spinola (five), *Sphictyrtus* Stål (20), *Stenoprasia* Horváth (five), *Stiroptus* Stål (one), *Sundarus* Amyot & Serville (31), *Vazquezitocoris* Brailovsky (14), *Viklundocoris* Brailovsky (one), *Villasitocoris* Brailovsky (1), and *Zicca* Amyot & Serville (19) (CoreoideaSF Team 2015).

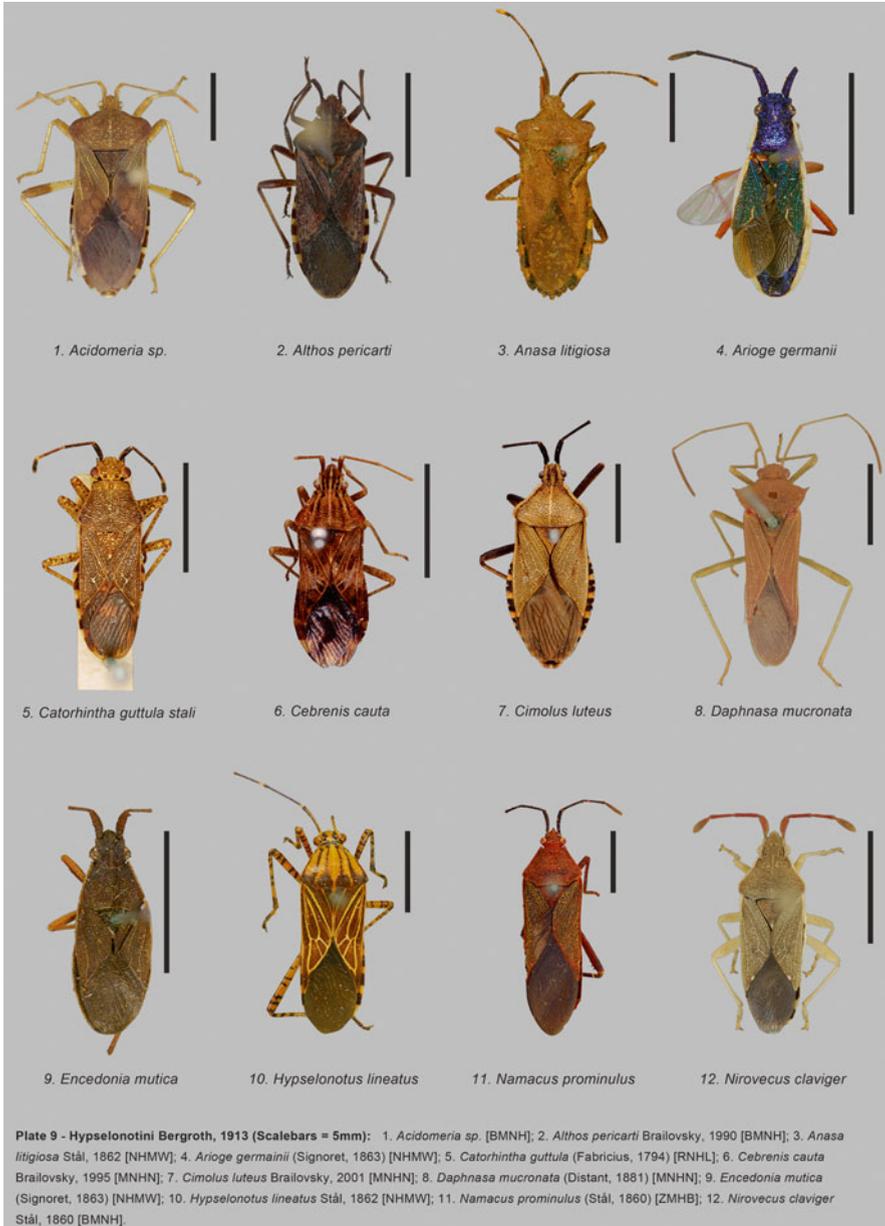


Plate 19.9 Coreinae plate—Hypselonotini

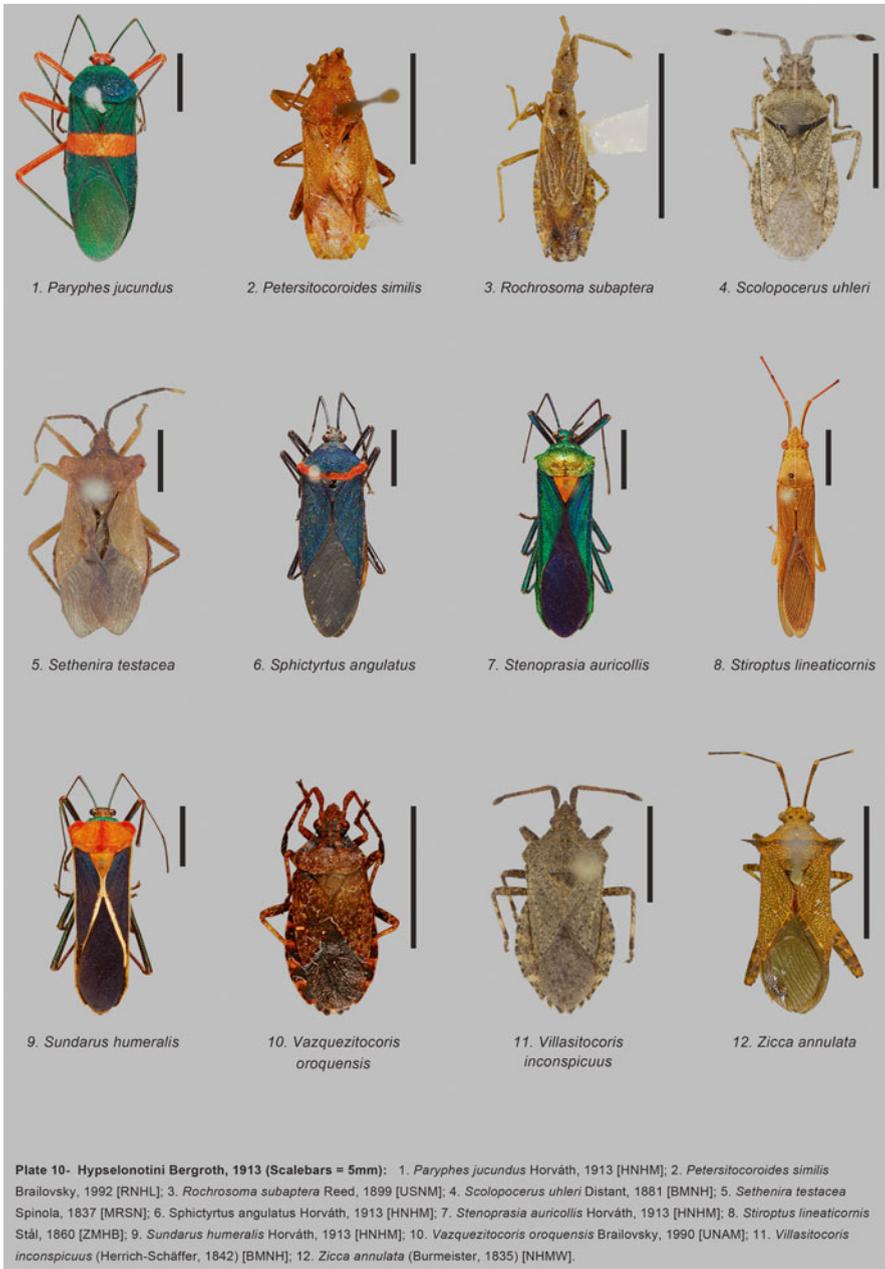


Plate 19.10 Coreinae plate—Hypeslonotini 2

Many *Anasa* spp. feed on cucurbits, and these bugs are by far the most economically important in the tribe; *Anasa tristis* (De Geer) and congeners are treated separately in section “*Anasa* Amyot & Serville”. But the Hypselonotini is not linked strongly to Cucurbitaceae; *Paryphes blandus* Horváth feeds on the leaves of a cucurbit vine (Young 1980), but other species of Hypselonotini have been reported from a variety of crops. Adults of *Hypselonotus lineatus* Stål were noted to feed in large numbers on the flowers of physic nut, *Jatropha curcas* L. (Euphorbiaceae), in addition to their usual breeding host, *Waltheria indica* L. (Sterculiaceae) in Nicaragua (Grimm and Maes 1997; Grimm and Führer 1998), and both nymphs and adults of *H. fulvus* (De Geer) (as *H. lanceolatus* Horváth) were observed to pierce the fruits of arazá (*Eugenia stipitata* McVaugh, Myrtaceae) in Peru (Couturier et al. 1996). The latter species also feeds on the euphorb *Julocroton argenteus* (L.) in open pastures in Costa Rica (Solomon and Froeschner 1981) and comes to flowering cotton in Trinidad although mainly found on another malvaceous plant, *Malachra capitata* L. (Urich 1916). Whitehead (1974) provides host plant collection records for several other *Hypselonotus* species. In southern Brazil, *H. interruptus* Hahn was recorded from three native tree species: *Casearia sylvestris* (Flacourtiaceae), *Campomanesia xanthocarpa* Berg (Myrtaceae), and *Myrciaria rivularis* Cambessedes (Myrtaceae) (Thum and Costa 1997). In this same survey, *Zicca nigropunctata* (De Geer) (as *Z. nigropunctulata*) was found on *Patagonula americana* L. (Boraginaceae). *Sphictyrtus chrysis* (Lichtenstein) is reported to feed on *Annona muricata* L. in Venezuela (Peña and Bennett 1995) and is associated with cashew in Brazil (Bleicher and Melo 1996). Known host plants of *Cebrenis supina* are in Asteraceae (*Neurolaena lobata* (L.) R. B. R., *Mikania scandens* (L.) Willd, and *Verbesina* sp.) (Brailovsky 1995, cited in Barcellos et al. 2008). Schaefer and Mitchell (1983) present additional host records and speculated that the food plant preferences of Coreini (s.l.) might aid in determining relationships among genera.

Nematopodini Amyot & Serville (Plate 19.11)

This is the tribe of the bulky bugs; here is found the second largest group of bugs—*Thasus* and *Pachylis* (Plate 19.11). Species large to very large, head subquadrate; tylus projecting slightly beyond juga; antenniferous tubercles unarmed, occupying most of anterior head, ocellar tubercles small; metathoracic scent gland opening placed almost ventrally, peritreme with two completely separated lobes and area between them depressed; femora incrassate, posterior femora markedly incrassate especially in male and armed ventrally, anterior femora distally armed with two ventral spines; tibiae sometimes dilated; abdominal venter unarmed; paramere heavily sclerotized (O’Shea 1980b; Packauskas 1994).

Nematopodini and Acanthocerini were part of the Mictini until O’Shea and Schaefer (1978) reinstated them, separating the Neotropical species of the first two

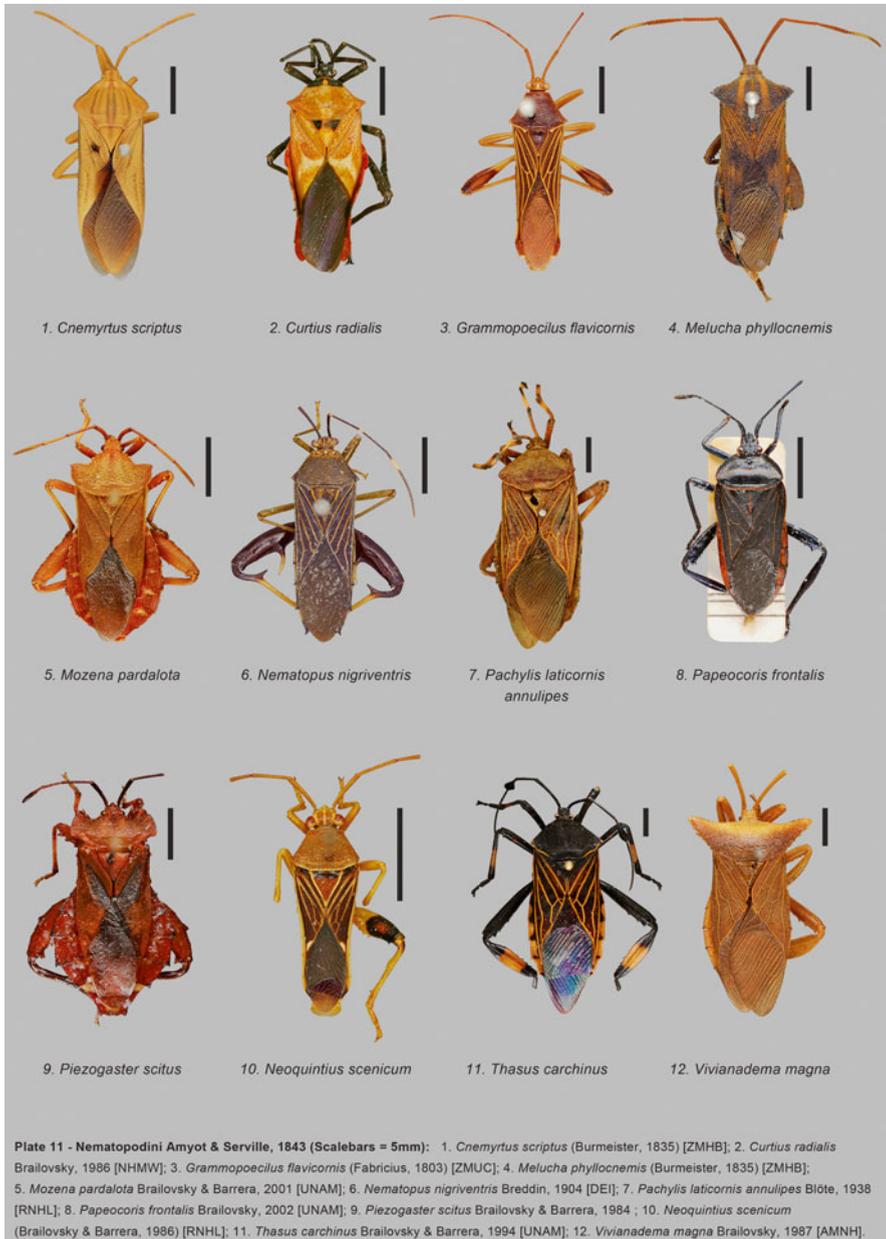


Plate 19.11 Coreinae plate—Nematopodini

mentioned tribes and keeping the Old World species in Mictini. Nematopodini comprises 22 genera and 161 species distributed across the Americas, but only 8 genera are represented in Central America and only *Mozena* is predominantly distributed in the northern part of the Neotropical region and the United States. Genera belonging to Nematopodini are: *Cnemyrtus* Stål (two species), *Curtius* Stål (four), *Grammopocilus* Stål (two), *Himella* Dallas (three), *Melucha* Amyot & Serville (11), *Meluchamixia* Brailovsky (one), *Mozena* Amyot & Serville (31), *Nectoquintius* Brailovsky & Barrera (one), *Nematopus* Berthold (31), *Neoquintius* Brailovsky & Barrera (six), *Ouranion* Kirkaldy (three), *Pachylis* Le Peletier & Serville (10), *Papeocoris* Brailovsky (three), *Piezogaster* Amyot & Serville (33), *Quintius* Stål (three), *Saguntus* Stål (two), *Stentoquintius* Brailovsky & Barrera (two), *Thasopsis* O'Shea (two), *Thasus* Stål (eight), *Tovarocoris* Brailovsky (one), *Vivianadema* Brailovsky (one), and *Wilcoxina* O'Shea (one) (CoreoideaSF Team 2015). Keys to the genera of Nematopodini and additional notes can be found in O'Shea (1980b), Brailovsky (1987a, 1995b), and Brailovsky and Barrera (1986b, 2002, 2009b).

The strong association between Nematopodini and Fabaceae was noted by Schaefer and O'Shea (1979) and is clearly apparent from the known host records; mesquite and acacia are the most frequently reported hosts. All *Mozena* spp. are associated with legumes (*Acacia*, *Prosopis*, *Schrankia*), as are *Thasus* (*Prosopis*), *Pachylis laticornis* (F.) (*Pithecellobium*), *P. hector* Stål (*Mimosa*, *Prosopis*), and *Piezogaster odiosus* (Stål) (*Pachyrrhizus*) (Schaefer and O'Shea 1979; Schaefer and Mitchell 1983; Brailovsky et al. 1995), although *P. laticornis* has also been reported from banana (Musaceae) (Schaefer and O'Shea 1979). Also clear from host records and behavioral observations is a preference for vegetative structures, especially new growth and young shoots, although pods may also be used (Schaefer and Mitchell 1983). Aggregation behaviors of *P. laticornis* (as *Thasus acutangulus*) in Costa Rica are described by Aldrich and Blum (1978), but little is known of the biology of other Neotropical species other than host plant records. Nymphal descriptions and host plant associations for several species in Mexico are given by Brailovsky et al. (1995) and components of the scent fluid have been identified for nymphs of one Mexican species (Noge et al. 2012). The biology of the North American species, *Thasus neocalifornicus* Brailovsky & Barrera, has been thoroughly investigated, including the chemistry of the scent glands (Prudic et al. 2008) and the gut biota (Olivier-Espejel et al. 2011). *Mozena obtusa* Uhler has been extensively studied in Texas as a potential biological control agent for mesquite in Australia and South Africa (Cuda and DeLoach 1998).

Placoscelini Stål (Plate 19.12)

This tribe was proposed by Schaefer (1968) as Stenoscelideini, but only Packauskas (2006) presented a more complete description and the synapomorphies that support this taxon (mostly from the internal genitalia). Brailovsky and Barrera (2012) presented a diagnosis of the tribe and a key for the genera, both reproduced below. Dolling in the Coreoidea Species File (CoreoideaSF Team 2015) commented that

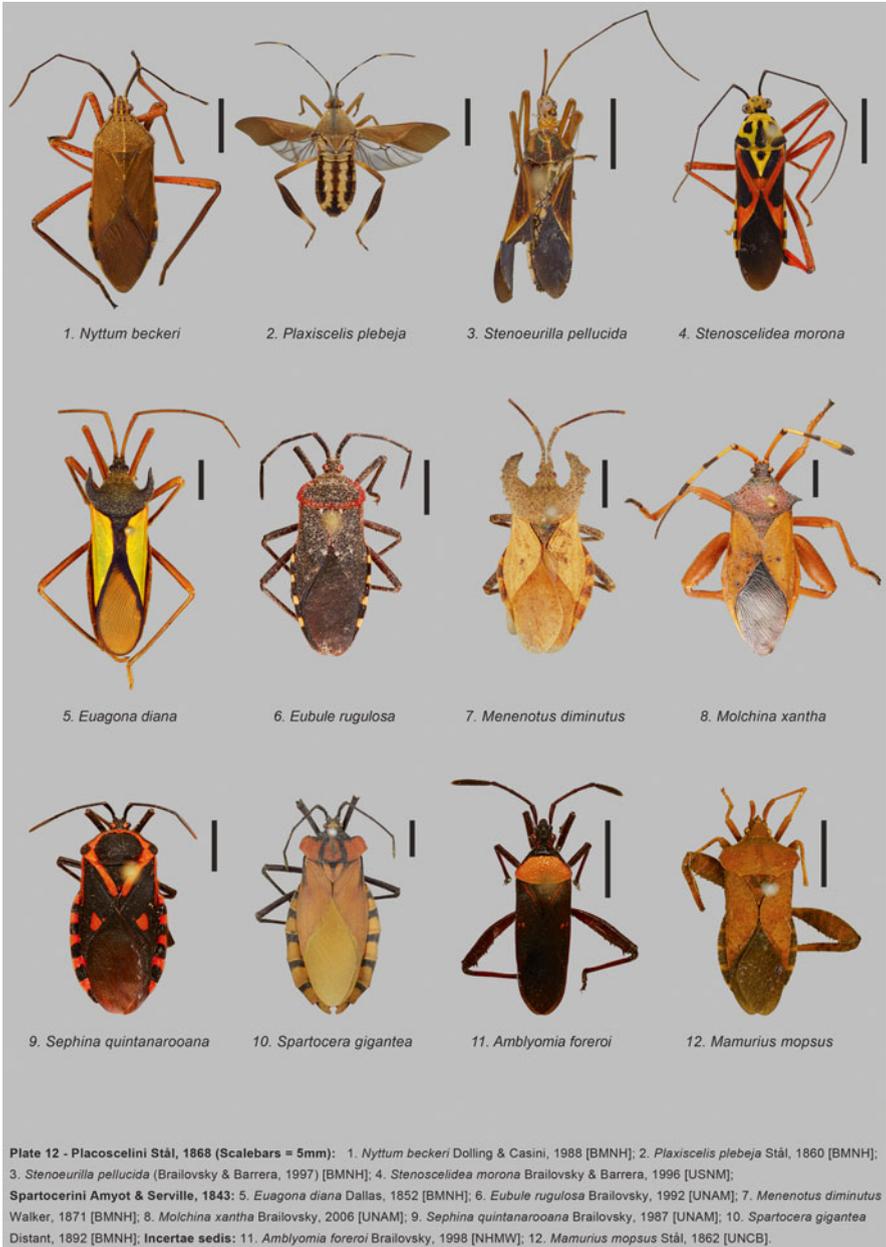


Plate 19.12 Coreinae plate—Placoscelini Spartocerini

Placoscelini Stål (as Placoscelida) has priority over Stenoscelideini Schaefer, because *Plaxiscelis* Spinola (= *Placoscelis* Agassiz) is included in this tribe. Head with postclypeal sulcus single or double (with internal ridge); clypeus raised as a short tubercle above deflexed juga; distance between antenniferous tubercles slightly less than width of one tubercle; antennal segment I longer than maximal length of head; antennal segment IV the longest and never longer than II and III together; rostrum reaching posterior margin of mesosternum or anterior third of metasternum; rostral segment III the shortest. Pronotum slightly declivent, bilobate; callar region slightly raised; collar present; humeral angles obtusely rounded or with a tiny spinous projection; metathoracic scent gland peritreme in form of two separate auricles with distinct bridge between them. Macropterous, hemelytra extending beyond apex of last abdominal segment. Connexival segments raised above terga; posterior angle unarmed, never spined postero-apically; abdominal spiracles circular.

This tribe comprises only four genera: *Nyttum* Spinola (10 species), *Plaxiscelis* Spinola (eight), *Stenoaurilla* Brailovsky & Barrera (eight), and *Stenoscelidea* Westwood (13) (CoreoideaSF Team 2015). These taxa are composed of species found basically in South America and previously placed in Acanthocephalini, except those belonging to *Stenoaurilla*. *Stenoaurilla aenescens* (Stål) (as *Stenoscelidea*) was reported by Solomon and Froeschner (1981) to feed on *Lonchocarpus costaricensis* Pittier. A key can be found in Brailovsky and Barrera (2012).

Spartocerini Amyot & Serville (Plate 19.12)

This tribe was called erroneously Corecorini by several authors that followed van Duzee (1916) considering *Corecoris* Hahn as the valid name instead of *Spartocera* Laporte. Specimens small to large with body robust. Head rectangular and declivent. Antenniferous tubercles close together, unarmed and projected beyond tylus. Antennae short with segments stout. Rostrum short just surpassing procoxae. Pronotum steeply declivent with anterior margin tuberculate or crenulate. Metacoxae separate from each other by the same distance of the metacoxa to the lateral margin. Posterior wing with cubital vein strongly curved anteriorly and hamus reaching the base of the wing. Spur of the third alar sclerite not developed. Trichobothria of the third abdominal segment located before the spiracle. Inner laterotergites of the connexivum fused.

This tribe is exclusively Neotropical and represented by six genera: *Euagona* Dallas (three species), *Eubule* Stål (13), *Menenotus* Laporte (two), *Molchina* Amyot & Serville (six), *Sephina* Amyot & Serville (24), and *Spartocera* Laporte (18). No key for all genera has been produced, and information is spread out in the literature. Only *Euagona* was revised recently (Brailovsky 2010b), but other genera were treated to some extent—*Eubule* (Brailovsky 1992b), *Sephina* (Brailovsky 1983b, 1987a, 2001b; Brailovsky and Sánchez 1983b), and *Molchina* (Brailovsky 2006a, key to the species) (CoreoideaSF Team 2015). Two species of *Sephina* are reported

to feed on *Metastelma* spp. (Apocynaceae). *Eubule sculpta* (Perty) is reported from *Morrenia* sp. (Apocynaceae) but also from a cucurbit host (Schaefer and Mitchell 1983). The brightly colored bull's horn bugs, *Euagona* spp., exhibit an unusual trait, in that the dorsal coloration of the abdomen of nymphs appears to resemble that of the wings of the adults (W.R. Dolling, pers. comm.). Only one genus in this tribe is of major economic importance: *Spartocera* spp. are covered in detail in section "*Spartocera Laporte*".

Incertae sedis (Plate 19.12) Two genera of Neotropical Coreidae were considered *Incertae sedis* by CoreoideaSF Team(2015). The genus *Amblyomia* Stål is composed by three species revised by Brailovsky (1998b) and considered in Leptoscelidini. Species are known from Mexico and Colombia and apparently feed on bromeliads. Packauskas (2008) removed *Amblyomia* from this tribe and considered it *Incertae sedis* based on an uncoiled vesica and absence of a posttylar sulcus.

The genus *Mamurius* Stål is composed by two northern Neotropical species resembling a small *Piezogaster* (Nematopodini). Some diagnostic characteristics were mentioned by Brailovsky (1982) comparing this genus to *Dalmatomammurius*. O'Shea (1979) considered *Mamurius* out of Nematopodini due to the small size, tylus much projected anteriorly and genitalia not similar to those of the nematopodines.

19.5 Main Species

Here we discuss some genera of major importance for which the biology, ecology, behavior, natural enemies, and/or pest status were not covered in detail in Sect. 19.4. Information on many of these economically important species was summarized in Mitchell (2000); rather than repeat information already available in the literature, we refer the reader to *Heteroptera of Economic Importance* (Schaefer and Panizzi 2000) and focus here primarily on more recent research and updates to our knowledge.

19.5.1 *Acanthocerini* Bergroth

Crinocerus Burmeister

The single species in this genus, *Crinocerus sanctus* (F.) (Plate 19.1), has a quite recognizable dorsal pattern described by O'Shea (1980a) as "a light brown St. Andrew's cross on a darker brown background." Aspects of the life history and photographs of immature stages and adults are provided by Amaral (1986). Photographs of an adult male, illustrating the incrassate femora, declivent pronotum, and distinctive markings, may also be found in Pall and Coscarón (2013).

These bugs have a wide host range, including leaves, green stems, and nuts of cashew (Bleicher and Melo 1996); oranges, limes, cotton, and leaves and fruit of guava (Amaral 1986); and new shoots and green fruit of acerola (*Malpighia* spp.) (Soglia et al. 1998). On the latter host, wilting of shoots and deformation of fruit are reported. However, *C. sanctus* is most commonly a pest of legumes, including *Canavalia ensiformis*, guandu bean, *Dolichos* sp., and particularly cowpea, on which bugs cause serious losses, feeding on stems, new foliage, and pods. (Bosq 1937; Amaral 1986; Daoust et al. 1985). In northern Brazil (Pará, Amazonas, Acre), this species is considered a principal pest of cowpea, forming part of a pod-sucking bug complex that includes the pentatomid *Piezodorus guildinii* (Westwood) (Daoust et al. 1985). Laboratory rearing studies using cowpea plus acerola or guandu bean leaves plus cowpea have shown nymphal development to range from 56 days at 27 ± 2 °C (Soglia et al. 1998) to 58.41 ± 1.25 days at 22 ± 2 °C (Amaral 1986).

19.5.2 *Anisoscelini* Laporte

Anisoscelis Latreille

Bugs in this genus feed on *Passiflora* spp.; flower buds and fruits of cultivated passion fruit damaged by feeding may wither or drop from the vine (Polaszek and Kolberg 2008). *Anisoscelis foliaceus* (F.) has been the most extensively studied, particularly in southern Brazil where it overlaps and shares host plants with *Holhymenia clavigera* Herbst (Rodrigues and Moreira 2005). Eggs are ovoid, golden initially but later turning brown; nymphs are green in the early instars, darkening to ochre in the fifth instar. The expansion of the hind tibia becomes visible in third instars and continues to enlarge during development. Eggs and juveniles of both species were described and compared (Rodrigues and Moreira 2005) and were found to be remarkably similar through the fourth instar except in size and tibial foliation; *H. clavigera* are larger and lack the broad, leaflike expansions characteristic of *Anisoscelini*. Rearing experiments showed the wild host, *P. suberosa*, to be optimal for growth and development compared with cultivated passion fruit, *P. edulis*. A mix of vegetative and reproductive structures is used, and plant part preference changes over the course of development (Rodrigues et al. 2007b, 2008). Detailed histological studies of feeding sites showed mainly penetration to xylem in mature leaves, whereas several sites within the fruit were targeted, including pericarp, aril (pulp), endosperm, and embryo (Rodrigues et al. 2007a). *Anisoscelis flavolineatus* Blanchard is listed as a pest of cultivated passion fruit in Columbia (Urueta-Sandino 1975), but the genus is not mentioned for Venezuela (Aguiar-Menezes et al. 2002). Only low densities of *A. foliaceus* were found on cultivated passion vines in southeastern Brazil (Caetano et al. 2000, cited in Rodrigues et al. 2007b). Egg parasitoids of *A. foliaceus* include *Gryon chrysolauum* Walker and *G. vitripenne* Masner (Polaszek and Kolberg 2008).

***Holhymenia* Lepelletier & Serville**

These unusual-looking bugs, with black and white markings and clear wings, are thought to be Batesian mimics of ichneumonid wasps (Rodrigues and Moreira 2005) (Plate 19.1). Two very similar species, *Holhymenia histrio* (F.) and *H. clavigera* (Plate 19.6, #6), cause extensive damage to cultivated passion fruit by feeding on stems, floral buds, and fruits. Feeding and consequent damage by *Holhymenia* spp. resembles that of *A. foliaceus*; xylem is probed on leaves, but feeding occurs on pericarp, aril, and seeds. First instars fed on tendrils of *P. edulis* and terminal buds and leaves of the native host, *P. suberosa*; fruit was preferred by later instars. Adults preferred green fruits over purple fruits (Rodrigues et al. 2007a, 2008). The egg and immatures of *H. clavigera* were described in detail by Rodrigues and Moreira (2005) and closely resemble those of *A. foliaceus* until the fifth instar, when the foliated antennal segments of *H. clavigera* develop a brown margin and the legs are strikingly banded. Two platygastriid parasitoids have been reared from eggs of *H. rubiginosus* Breddin: *G. chrysolauum* and *G. vitripenne* (Polaszek and Kolberg 2008).

***Leptoglossus* Guérin-Ménéville**

Primarily Neotropical with some Nearctic species, this large genus includes some of the more damaging and most extensively studied of the coreid economic pests. The majority of species are primarily found in South America (Allen 1969), but two species have achieved considerably wider distribution. The range of *Leptoglossus gonagra* (F.) extends well beyond the Neotropics, to Africa, Asia, and Australia. The North American conifer pest, *L. occidentalis* Heidemann, recently invaded Europe, Turkey, and East Asia; it represents a potential threat to commercial seed orchards and European alpine forest ecosystems (Lesieur et al. 2014). In the Neotropics, however, the most damaging species is unquestionably the highly polyphagous *L. zonatus* (Dallas), distributed from Argentina north to the southern United States.

Leptoglossus spp. are characterized by an elongate body shape, head porrect, humeral angles of the pronotum slightly to greatly expanded, hind femora slightly incrassate in males, and hind tibiae foliated, although the shape of the inner and outer dilations varies among species. Sexual dimorphism of the tibial dilations has been reported for a few species (Schaefer et al. 2008). A transverse fascia may be present on the corium; its color varies from bright white to pale, and shape varies in width and in the appearance of the margin: straight or zigzag (Allen 1969). Presently, 61 species are placed in the genus (CoreoideaSF Team 2015), although information on biology is available for relatively few species, primarily those with economic importance or unusual feeding habits.

Some species are host specific at the genus level; others are highly polyphagous, but there appear to be no evolutionary patterns of relatedness among the preferred host plants. Two species are associated with Amazonian palms, *L. hesperus*

Brailovsky in Brazil and *L. lonchooides* Allen in Peru (Couturier et al. 1991; Brailovsky and Couturier 2003). In North America, two species breed exclusively on mistletoe, and two are associated with conifers (Schaefer and Mitchell 1983). The conifer-feeding species are related to one another and to a more broadly feeding species that includes gymnosperms in the diet; together they constitute the *corculus* group of Allen (1969) and belong to the *zonatus* group of Packauskas and Schaefer (2001). Similarly, the mistletoe feeders are closely related (Allen 1969). However, the three specialists on Magnoliaceae (*L. katiae* Schaefer & Packauskas, *L. fulvicornis* (Westwood), and *L. dilaticollis* Guérin) are divided between two species groups (Schaefer et al. 2008). Similarly, the various cactus feeders (*L. subauratus* Distant, *L. dentatus* Berg, and *L. cinctus* Herrich-Schäffer) are divided among three species groups (Packauskas and Schaefer 2001); thus, host plant relationships do not always reflect taxonomic relationships.

The more generalist feeders, pests on a variety of crops, are primarily in the *zonatus* group. Species with exceptionally broad host plant ranges include *L. phyllopus* (L.) (Mitchell 2006), *L. zonatus* (Dallas) (Fernandes and Grazia 1992), *L. stigma* (Herbst) (Amaral and Cajueiro 1977), and *L. gonagra* (F.) (Mitchell 2000). Other Neotropical species mentioned as being crop pests are *L. conspersus* Stål on tomato and passion fruit (Urueta-Sandino 1975; Mitchell 2000); *L. balteatus* (L.) on guava, loofah, oranges, tomatoes, and legumes (Barber and Bruner 1947; Schaefer and Mitchell 1983); *L. chilensis* (Spinola) on various fruits; and *L. cinctus* on various fruits in addition to cacti (Faúndez and Carvajal 2011; Schaefer and Mitchell 1983). The latter species has the distinction of being the only coreid ever reported to bite a human, presumably to acquire fluids (Faúndez and Carvajal 2011). Allen (1969) notes that damage to guava, cashew, lychee, and annatto attributed to *L. stigma* probably refers to the very similar *L. concolor* (Walker).

Several species of *Leptoglossus* are known to transmit or facilitate the transmission of plant diseases, including fungal pathogens and fruit-inhabiting trypanosomatids. Two fungal diseases of pistachio, botryosphaeria panicle and shoot blight and stigmatomycosis, are transmitted by *L. clypealis* Heidemann in North America. Among the Neotropical species, *L. gonagra* transmits citrus diseases, *L. zonatus* transmits stigmatomycosis from pomegranate to citrus, and puncture wounds on fruit caused by *L. stigma* facilitate the entry of fungi. *Phytomonas* spp. are carried internally (salivary glands, alimentary canal) in *L. gonagra*, *L. ingens* (Mayr), and *L. stigma* (Mitchell 2004 and references therein). The ability of *L. zonatus* to harbor and transmit *Phytomonas mcgheeii* to corn seeds has been studied experimentally; this species is considered a potential trypanosomatid vector because trypanosomes from bug salivary glands could infect corn in laboratory studies (Jankevicius et al. 1993).

Mitchell (2000) reviews the biology, life history, and distribution of *L. stigma*. This species, similar to *L. concolor* (Walker) but with a more steeply declivent pronotum and smooth pronotal calli, ranges from Mexico through South America east of the Andes, as far south as Paraguay and Brazil (Allen 1969; Packauskas 2010). An irregular fascia is usually, but not always, present on the corium. Food plants include pumpkin, guava, starfruit, cashew, oranges, mango, pomegranate, and

tangerine. Adults attack the fruits and buds of guava (Amaral and Cajueiro 1977 and references therein). The development and behavior of *L. stigma* (as *Veneza stigma*) was observed and documented in the laboratory (Amaral and Cajueiro 1977). Nymphs could be reared on a diet of guava, pumpkin, and chayote, although mortality was high. Durations of the egg stage and nymphal stadia were determined and adult reproductive behavior described.

The distribution of *L. phyllopus* extends from the United States south through much of Central America, but it has only been considered to be of economic importance in the United States. These bugs have a broad, straight transverse fascia on the corium and bicolored hind wings (Allen 1969). The natural history, seasonal dispersal, host plant preference, feeding behavior, and tissue preference were examined by Mitchell (2006), using mark-release-recapture, field censuses, laboratory rearing experiments, and histological techniques. Stylets penetrated to xylem on vegetative tissue and to developing seeds and xylem on pods of green bean and tomato fruit. Nymphs developed equally well on reproductive structures from plants from different families, but could not survive on vegetative tissue alone. In the field, host-switching occurred frequently; teneral adults moved from the nymphal host to another plant species shortly after emergence, suggesting that the observed polyphagy is sequential rather than concurrent and the ability to develop on a variety of plants allows versatility in locating hosts in the appropriate reproductive condition.

Allen (1969) confirmed the synonymy of *L. membranaceus* (F.) with *L. australis* (F.). Baranowski and Slater (1986) then synonymized the Eastern Hemisphere *L. australis* with the Neotropical *L. gonagra* s.s., thereby expanding the range of this species nearly worldwide. There is great variability in tibial dilations and humeral angles, but the orange-red to yellow lunate transverse fascia on the pronotal disk and the variegated antennae are quite recognizable in this species (Plate 19.6, #8) (Allen 1969; Baranowski and Slater 1986). Mitchell (2000) summarized the Eastern Hemisphere literature under *australis* and that of the Western Hemisphere under *gonagra*. In the Neotropics, *L. gonagra* damages citrus throughout its range, with damage reported in Florida, Puerto Rico, Argentina, and Brazil; however, this insect is highly polyphagous, and other crops attacked include pumpkin, chayote, loofah, cucumber, bitter melon, watermelon, guava, araçá, passion fruit, papaya, mango, pomegranate, tobacco, physic nut, and corn. However, breeding hosts are more limited; bitter melon, loofah, watermelon, and citron support nymphal populations (Mitchell 2000). Damage to citrus fruit has been described in detail: fruit drop, necrotic spots and lesions, dried, damaged, and bitter pulp, and secondary fungal infections are characteristic of *L. gonagra* infestations (Calza et al. 1964; Albrigo and Bullock 1977).

Extensive studies of the biology of *L. gonagra*, including egg stage duration and hatching success, nymphal development on leaves and fruit of pumpkin, and adult reproductive cycle were conducted in the lab under varying conditions of temperature and humidity (Amaral and Storti 1976). High mortality occurred during the second stadium on both pumpkin and bitter melon, the wild host. Duration of the total life cycle was 80.7 ± 1.12 days. Development times (in days) were 8.2 for eggs and 3.6, 13.9, 10.3, 11.2, and 15.4 for the five nymphal instars, respectively.

Nymphal development and growth under controlled laboratory conditions were compared among five species of *Passiflora* (Caetano and Boiça 2000). Nymphs could not complete development on fruits alone. When provided branches, buds, flowers, and fruits, nymphs failed to complete development on *P. nitida* and showed the lowest adult weight on *P. giberti*. *P. laurifolia* was judged to be the most susceptible species, based on development time, adult weight, and longevity.

The literature on *L. zonatus* has grown substantially in recent years, due to increased interest in its economic importance on a variety of crops in South America and its spread across the southern United States. This species is typically characterized by two large whitish-yellow spots on the pronotal disk and a wide irregular fascia across the corium (Plate 19.1), but the fascia may vary in width or be missing entirely (Allen 1969). The eggs and immatures are described and illustrated by Fernandes and Grazia (1992), with observations on adult behavior. Mitchell (2000) summarizes older information in the literature on biology, host plants, economic damage, and control.

In the southern United States, satsuma mandarin oranges are damaged directly by bug feeding and indirectly by transmission of the yeast, *Nematospora coryli*; *L. zonatus* is considered to be a key pest (Henne et al. 2003; Xiao and Fadamiro 2010). The latter authors evaluate damage to satsumas (2010) and provide developmental data for nymphs and adult life history and reproductive parameters (2009). Preferences were tested between ripened and unripened fruit and among tomato, satsumas, kumquats, lemons, and peach; tomato was highly preferred, but *L. zonatus* can survive and develop on a diet entirely composed of satsuma fruit. Fruit maturity did not affect preference (Xiao and Fadamiro 2009). Among the wild hosts in the United States is Chinese tallow, an invasive euphorb (Johnson and Allain 1998).

Development of *L. zonatus* and the reproductive parameters of adults have also been studied on sorghum and corn (Matrangolo and Waquil 1994) and on corn, soybean, and green bean (Panizzi 1989). Corn seeds were far preferable for rearing than pods of either legume, and this insect is abundant in corn fields in Brazil (de Souza and Amaral 1999a; Panizzi 2004b). An African tree widely planted in greenbelts, *Spathodea campanulata* Beauv (Bignoniaceae), supports adults and nymphs and may serve as an alternate host (de Souza and Amaral 1999a). The entire life cycle can also be completed on physic nut; instar duration data, nymphal measurements, and reproductive parameters have been determined for this host plant (Grimm and Somarriba 1999). *L. zonatus* is the second most common heteropteran on this crop in Nicaragua (Grimm and Maes 1997) and also occurs on physic nut in Mexico (Tepole-García et al. 2012). Damage to pomegranate (Raga et al. 1995) and guava (Pires et al. 2013) has also been described, and occurrence of this insect on *Annona* spp. (Peña and Bennett 1995), *Malpighia emarginata* Sessé & Moc, *Morus nigra* L., and *Mangifera indica* L. (Pires et al. 2013) has been recorded.

Omnivory has also been observed in *L. zonatus*; egg masses of fall armyworm, *Spodoptera frugiperda*, were consumed by adults in maize fields in Brazil (Menezes-Netto et al. 2012). *L. zonatus* has also been observed to orient

toward and land on humans and on plastic cylinders hung from poles in corn fields, possibly representing either territorial or recognition behavior (Panizzi 2004b). Natural enemies include *Trichopoda pennipes* F. and egg parasitoids including *Gryon* sp. (de Souza and Amaral 1999b). Control using entomopathogens (*Beauveria bassiana* (Bals.) Vuil. and *Metarhizium anisopliae* (Metsch.) Sorok) appears promising in laboratory and field trials and was more effective than treatment with neem seed (Grimm and Guharay 1998).

***Narnia* Stål**

Narnia spp. inhabit primarily the desert areas of North America; however, the distribution of *N. femorata* Stål extends to Guatemala (Brailovsky 1975). Various cacti are hosts for *Narnia* spp., including *Opuntia* spp. (Brailovsky 1975), but unlike the cactus pad specialists in Chelinideini, these bugs preferentially feed on fruits. Brailovsky et al. (1994) provide detailed descriptions of the egg, nymphal stadia, and life cycle of *N. femorata* in Mexico. Eggs are laid on the spines and pads, and the life cycle is dependent on the fruiting and flowering cycle of the host. First instars are gregarious, but do not feed; late instars disperse. Recent behavioral studies of *Narnia femorata* Stål have added substantially to our understanding of coreid feeding and mating. Adults reared exclusively on pads survive, but development is delayed and body size is smaller compared with individuals with access to fruits (Nageon de Lestang and Miller 2009). In the presence of cactus fruit, females prefer the odor of males who developed on fruit although no preference is exhibited in the absence of fruit odors (Addesso et al. 2014). Both male-male competition and female choice operate in this species; enlarged femora in males are used in combat (Miller 2013) to defend territories on cactus, but male body size and leg area only strongly affect the outcome of male-male competition in the presence of females (Procter et al. 2012).

***Phthia* Stål**

The genus *Phthia* Stål was recently revised by Brailovsky (2009c) with the erection of four new genera. Of the 13 species originally in *Phthia* s.l., *Phthia picta* (Drury) has been placed alone in the genus *Phthiacnemis* Brailovsky, while *P. lunata* (F.) remains, along with three other species, in *Phthia* s.s. Three additional species were placed in *Phthiadema* Brailovsky, four in *Phthiarella* Brailovsky, and one in *Rhytidophthia* Brailovsky. Brailovsky (2009c) provides a key to genera, which may be distinguished from one another by the development of the humeral angles and the extent of metallic iridescence on the head, clavus, and corium. Although all are Neotropical, only the widely distributed *P. picta* has received any mention in the economic literature; this species may be distinguished by the dull, non-metallic body surface and the truncate (non-acute) humeral angles. A narrow orange-red transverse band may be present on the posterior portion of the

pronotum (see illustration in Brailovsky 2009c), and other orange markings may be variably present (Baranowski and Slater 1986), but unlike *Phthia s.s.*, no yellow transverse fasciae occur on the anterior lobe or on the corium (Brailovsky 2009c). Literature records for this species may be found under *Dallacoris* Osuna in addition to *Phthia* and *Phthiacnemia*.

Host plant records are available for *P. picta*, *P. lunata*, and *Rhytidophthia splendens* (Valdés). The latter, endemic to Cuba, was collected from *Taonabo* (= *Ternstroemia parviflora* Krug & Urban (Theaceae) (Barber and Bruner 1946). *P. lunata* is reported from Cucurbitaceae (*Citrullus* and *Cucurbita*) (Maes and Goellner-Scheiding 1993). Published host plant records for *P. picta* are summarized by Schaefer and Mitchell (1983), Baranowski and Slater (1986), and Mitchell (2000). Serantes (1973) lists the known hosts in Argentina. *Solanum nigrum* L. is the common wild breeding host in Florida, and occurrence on tomato has been reported throughout the range of *P. picta*, from the Caribbean to Argentina (Baranowski and Slater 1986; Serantes 1973). However, the species is not always considered an economically important pest (Mitchell 2000), and despite the common names, “chinche de tomate” and “percevejo do tomate,” it is not restricted to Solanaceae. This species is in fact highly polyphagous, feeding on cultivated cucurbits and legumes in addition to tomato and eggplant; plants from 11 families are reported as feeding or breeding hosts (Schaefer and Mitchell 1983). Feeding punctures cause direct damage resulting in deformed fruit; indirect damage includes entry pathways for fungal pathogens (Amaral 1980) and transmission of a trypanosomatid of tomatoes, *Phytomonas serpens* (Gibbs) (Jankevicius et al. 1989; Freymuller et al. 1990; Fiorini et al. 1993). Flagellates of *P. serpens* were found in the digestive tract of field-collected insects and appear in hemocoel and salivary glands 1 week following acquisition in the laboratory. Transmission in both directions (from *P. picta* to tomato fruit and from tomato fruit to insect) was documented. The nature of the relationship between tomato and *P. serpens* is not known with certainty; fruit-dwelling trypanosomatids may not actually be pathogenic although phloem-inhabiting trypanosomatids, also transmitted by bugs, cause serious disease and economic losses (e.g., hartrot of coconut transmitted by *Lincus lobuliger* Breddin (Sgrillo et al. 2005).

The eggs of *P. picta*, like those of *Leptoglossus* and *Narnia*, are hemicylindrical and laid in a single row, end to end. The juvenile stages are described by Serantes (1973) with illustrations of the egg and first and fifth instars. Detailed measurements, descriptions, and illustrations of all five instars are provided by da Silva et al. (2001). Younger instars, brightly colored and gregarious, develop faster when reared in aggregations (Amaral 1981a). Life history and behavioral observations are given by Serantes (1973) for Argentine populations and Amaral (1980, 1981a, b) for Brazil and reviewed by Mitchell (2000) and da Silva and Carvalho (2001). More recent studies of development under controlled laboratory conditions (da Silva and Carvalho 2001) showed total nymphal development time to be 34.39 ± 0.67 days on tomato at 26 ± 1 °C, 70 ± 10 % RH, and 14: [L:D] photoperiod, with 56 % mortality.

For females, the pre-oviposition period was 62.83 ± 9.86 days, with 9.37 ± 1.48 days between egg batches. Data are also provided on clutch size, adult longevity, and development time for eggs and each instar.

19.5.3 *Hypselonotini* Bergroth

Anasa Amyot & Serville

This large genus comprises 76 species (CoreoideaSF Team 2015) with distributions ranging from Canada to northern Argentina and Uruguay (Brailovsky 1985; Packauskas 2010), although the majority of species are Neotropical. These medium-sized bugs are elongate-oval, with the pronotum strongly declivent; the connexivum widely exposed; the antennae, femora, and tibiae slender; and the beak extending at least to the middle coxae (Blatchley 1926). Although several species have been noted as injurious to cucurbit crops, only *Anasa tristis* (De Geer) is currently considered a serious economic pest. Reports of other *Anasa* spp. feeding on cultivated cucurbits include *A. trilineata* Stål in Venezuela; *A. incompta* Brailovsky in Colombia; *A. costalis* Stål, *A. litigiosa* Stål, *A. maculipes* Stål, *A. ruficornis* Stål, and *A. uhleri* Stål in Mexico; and *A. guttifera* Berg in Argentina (Brailovsky 1985; Brailovsky et al. 1994). The widely distributed *A. scorbutica* (F.) is reported from loofah, squash, gourds, maize, tomato, and physic nut in various parts of its range (Mitchell 2000 and references therein), but cucurbits are the only hosts on which breeding was noted (Barber and Bruner 1947). *A. andresii* (Guérin-Méneville), distributed from the southern United States and the Caribbean to Colombia and Ecuador (Packauskas 2010), is reported from cucurbits, including *C. pepo* (L.) and *C. ficifolia* Bouché, cotton, tomatoes, and bromeliads (Brailovsky 1985) and was described in Cuba to be “at times a pest on squash” (Barber and Bruner 1947). On squash, these bugs cluster on the leaf underside, causing wilting and death, and may also feed on fruits (Mitchell 2000 and references therein). Interestingly, a number of *Anasa* spp. have been collected from bromeliads: *A. litigiosa* (Plate 19.9, #3) occurs on *Tillandsia* in addition to wild and cultivated cucurbits (Brailovsky 1985), and *A. costalis* has been reported from both *C. pepo* and two species of *Tillandsia* (Brailovsky 1985; Brailovsky et al. 1994), whereas *A. capaneodes* Stål and *A. impictipes* Stål may be more strictly associated with *Tillandsia* spp. (Brailovsky 1985). Brailovsky (1985) compiled a thorough list of all known host plants and habitats for *Anasa* spp., adding more Mexican host plants subsequently (Brailovsky et al. 1994). Of the 17 species for which host plants are known, 13 feed on cucurbits (although not always exclusively), with stem, leaf, and fruit all mentioned as feeding sites. With the exception of *A. tristis* and two strictly North American species (*A. armigera* (Say) and *A. repetita* Heidemann), virtually nothing is known of the natural history of *Anasa* species (Brailovsky 1985).

The notorious “squash bug,” *A. tristis*, occurs from Canada to Brazil and is a pest of squash and pumpkin in the United States and Mexico. A vast amount of research has been dedicated to understanding the biology of *A. tristis*, the damage it causes, and potential control methods. Mitchell (2000) reviewed this primarily North American literature, including life cycle, behavior, feeding and oviposition preferences, histological studies of feeding damage, insecticidal control methods, cultural controls, natural enemies, and tritrophic interactions. More recent studies have revealed that, in addition to direct damage to vascular tissues, the squash bug transmits a phloem-colonizing bacterium, *Serratia marcescens* Bizio, the causative agent of cucurbit yellow vine disease (Bruton et al. 2003). This disease was first described in 1988 in Texas and Oklahoma and subsequently spread eastward in the United States. The pathogen can be acquired in the nymphal stage and transmitted after the bug reaches adulthood; transmission appears to be propagative rather than non-circulative. No bacteria are found in the cibarium, suggesting that the likely location for retention of the bacterium is the hemocoel (Wayadande et al. 2005). Overwintering infected adults can transmit *S. marcescens* to cucurbit crops the following spring (Pair et al. 2004). The pathway of transmission from insect to phloem sieve tube cells is not yet understood (Wayadande et al. 2005; Maskey 2010); wilting caused by *A. tristis* has been attributed to xylem blockage (Neal 1993), but stylets do penetrate to the phloem tissue. However, the diameter of the stylets is too large to permit direct insertion into phloem sieve tube elements in the manner of aphid or leafhopper feeding (A. Wayadande, personal communication), and despite several studies of squash bug feeding using electrical penetration graphing (Bonjour et al. 1991; Cook and Neal 1999; Maskey 2010), the mode of feeding and the mode of pathogen transmission in *A. tristis* remain uncertain (Maskey 2010). Nonetheless, the economic importance of the squash bug, and possibly other *Anasa* spp. as well, has increased with the recognition of its vector competence.

19.5.4 *Spartocerini* Amyot & Serville

Spartocera Laporte (Plate 19.1)

Much of the older literature on this group, especially the species of economic importance, was published under the synonym *Corecoris* Hahn. These bugs are characteristically large and ovoid, with a broad abdomen and prominent connexivum. Of the 18 species distributed from the southern United States through South America, six have been noted as injurious to crops. In the United States, *Spartocera diffusa* (Say) damages potato; Chittenden (1927) provides nymphal descriptions and information on natural history and host plants. A preference for solanaceous crops also characterizes the Neotropical species, but sweet potato (*Ipomoea batatas* (L.), Convolvulaceae) is also attacked. *Solanum nigrum* L. is reported as a wild host for several pest species, including *S. diffusa*, *Spartocera brevicornis* (Stål), *Spartocera batatas* (F.), and *Spartocera fusca* (Thunberg) (Chittenden 1927; Bosq

1937; Costa Lima 1940; Halbert 2003). Little is known of the natural history of species that pose no economic threat, with one exception. *Spartocera lativentris* Stål feeds on the leaves and stems of *Solanum sisymbriifolium* L., with two generations per year in southern Brazil. No feeding on fruits was observed, and first instars were not observed to feed (Becker and Prato 1982). These authors also provide detailed information on the eggs of this species, including a description, oviposition sites, egg clusters, female reproductive organs, and egg mortality, hatching success, and parasitism.

Spartocera batatas (F.) feeds on sweet potato in Jamaica, Cuba, Puerto Rico, and other Caribbean islands; it is currently considered to reach minor pest status only in Puerto Rico. One infestation in Florida has also been reported (Halbert 2003 and references therein). Adults are parasitized by the tachinid fly, *Trichopoda pennipes* (F.) in the Caribbean and in Brazil (Amaral and Vieira 1978). Both *S. brevicornis* and *S. fusca* are associated with various cultivated solanaceous crops; tobacco and tomato, respectively, are mentioned by Costa Lima (1940) for Brazil. However, *S. fusca* has been noted elsewhere in its broad range to feed on a variety of hosts including *Capsicum annuum* (chili peppers) and *Physalis* sp. and has been collected from citrus. In Florida, it breeds on *Solanum americanum* P. Mill (Blatchley 1926; Brailovsky and Sánchez 1983b; Baranowski and Slater 1986). *Spartocera granulata* Stål is also registered in Brazil as a pest of cultivated solanaceous crops (Becker and Prato 1982).

By far the most damaging species in the genus, and the best studied, is *Spartocera dentiventris* Berg, a pest of tobacco in Brazil. Feeding causes the tobacco leaves to twist and wilt, causing economic losses. Detailed information on the biology of this species is provided by Caldas et al. (1998, 1999, 2000) including a description of the immatures, reproductive biology, longevity of adults, and cage studies of life history in tobacco. Mark-release-recapture in tobacco fields (Jesus et al. 2002) documented the population dynamics of the bug over the tobacco growing season, showing an aggregated pattern of distribution and predation by the reduviid *Cosmoclopius nigroannulatus* Stål on the second generation of nymphs Canto-Silva & Romanowski (2003). This assassin bug shows a type II functional response when feeding on first instar *S. dentiventris* (da Rocha and Redaelli 2004). Reported parasitoids of both *S. dentiventris* and *S. lativentris* include the eurytomid wasp *Neorileya ashmeadi* Crawford and the platygastriid *Gryon gallardoi* (Brèthes) (Becker and Prato 1982; Santos et al. 2001). Extensive studies have been conducted on the behavior of *G. gallardoi* as a potential biological control agent for *S. dentiventris* (da Rocha et al. 2007, 2008).

19.6 Concluding Remarks

Two recently compiled catalogs (Packauskas 2010; CoreoideaSF Team 2015) provide an invaluable resource for continued and expanded study of the Neotropical Coreidae. Catalogs of the North American fauna (e.g., Baranowski and Slater 1986; Henry and Froeschner 1988) have been available for some time, but only recently

has information on the entire New World Coreidae become easily accessible. As Packauskas (2010) noted, studies of New World coreids, and especially the Neotropical genera, languished for over 100 years. The higher classification of the Coreoidea has received attention (e.g., Schaefer 1964) and Stål's (1867) key to New World subfamilies and tribes has been updated (Packauskas 1994), but no modern comprehensive key to genera exists. The voluminous contributions of Brailovsky and his collaborators (see References for an appreciation of the extent of these works) include keys to genera for five Neotropical tribes discussed herein; papers by Yonke (1972) and O'Shea (1980a, b) provide information and keys for another three tribes. However, keys are lacking for some of the largest Neotropical coreid tribes and those with the most economically damaging members (e.g., Hypselonotini). Furthermore, keys to species exist for fewer than half the described genera in most tribes (see listings in Packauskas 1994). The Coreidae of the Neotropical region form an impressive and complex assemblage, with striking, often bizarre, characters and spectacular coloration. It is hoped that the advent of the newly launched Coreoidea Species File Online (CoreoideaSF Team 2015) will stimulate further, much needed, work on these elegant bugs.

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