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Artículo de Revisión

# The systematics of the Hemiptera

## Sistemática de Hemiptera

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**Abstract:** The Order Hemiptera comprises four main clades: Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha and Heteroptera. In this article the main phylogenetic hypotheses for Hemiptera and its subgroups are reviewed. Important references regarding catalogs and identification aids are provided for the major groups, making emphasis in recent on-line tools.

**Key words:** Catalogs. Diversity. Heteroptera. Phylogeny. On-line taxonomic tools. Taxonomy.

**Resumen:** El Orden Hemiptera comprende cuatro clados: Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha y Heteroptera. En este artículo se revisan las principales hipótesis filogenéticas para Hemiptera y sus subgrupos. También se brindan referencias importantes para la identificación de los grupos principales, haciendo énfasis en herramientas recientes disponibles en la web.

**Palabras clave:** Catálogos. Diversidad. Filogenia. Heteroptera. Herramientas taxonómicas en línea. Taxonomía.

### Introduction

Hemiptera is the fifth largest group of insects after Coleoptera, Diptera, Hymenoptera, and Lepidoptera (Schuh and Slater 1995; Grimaldi and Engel 2005; Cameron *et al.* 2006), and the most diversified group of non-endopterygote insects (Kristensen 1991), with approximately 82.000 described species (Arnett 2000). Their feeding habits range from phytophagy to predation, including ectoparasitism and hematophagy. Many of them are important pest species to cultivated crops and some are important vectors of human diseases.

This review deals with the phylogenetic systematic hypotheses for Hemiptera. Throughout the text, common phylogenetic terminology is used in cladistics that the non-familiarized reader may find confusing. The reader shall refer to general references for an explanation of those terms and the logic behind it (e.g., Hennig 1966; Kitching *et al*. 1998; Schuh 2000; Albert 2005).

The number of described species within Hemiptera is not exactly known. It is considered to have roughly 82.000 described species (Slater 1982; Hodkinson and Casson 1991; Arnett 2000), a number that must be seen as conservative. For instance, an estimate of the total world fauna using Asian tropical rain forest samples lies between 184.000 and 193.000 species (Hodkinson and Casson 1991). In some diversified groups, as Cicadellidae, the proportion of undescribed tropical taxa may be as high as 90% (Dietrich and Wallner 2002). Of the total described species, merely three families account for most of the diversity: Cicadellidae, with approximately 22.000 species (Auchenorrhyncha) (Metcalf 1962a, 1962b, 1962c, 1962d, 1963a, 1963b, 1963c, 1963d, 1964a, 1965a, 1965b, 1966a, 1966b, 1966c, 1966d, 1967, 1968; Oman *et al*. 1990; McKamey 2001), and Miridae and Reduviidae (Heteroptera), with more than 10.000 and 6.000, respectively (Schuh 1995; Maldonado 1990).

### Characters defining Hemiptera

Hemiptera has long been recognized as a monophyletic group (Hennig 1969; Carver *et al.* 1991). It can be recognized by the particular structure of the mouthparts: the mandibles and maxillary laciniae are modified into concentric stylets, the mandibular enclosing the maxillary ones, both forming the food and salivary channels; the multisegmented sheetlike labium is covering the mandibular and maxillary stylets; and the maxillary and labial palpi are always absent (Weber 1930; Hennig 1969, 1981; Cobben 1978; Kristensen 1991).

### Paraphyly of Homoptera

There was a long-standing tradition to treat the Homoptera and Heteroptera as separate groups usually having each the rank of order or as suborders within Hemiptera (e.g., Brues *et al.* 1954; Borror and White 1970; Borror *et al.* 1981). The former approach was common in North American entomology, in which Hemiptera included Heteroptera only, thus restricting the concept for Hemiptera (Schuh and Slater 1995).

Morphological evidence, nonetheless, pointed out that Homoptera was probably paraphyletic (e.g., Goodchild 1966; Schlee 1969d; Bourgoin 1986a, 1986b, 1993; Sweet 1996), or at least that evidence of its monophyly was not documented (Schlee 1969d). Some of the alleged characters supporting "Homoptera" mentioned were: enlarged foramen in the head, large sutures defining the mandibular plate, forewing larger than hindwing, reduced tarsomeres, and simple sperm (Bou-

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dreaux 1979; Hamilton 1981). Nonetheless, some of these characters are not synapomorphies (e.g., forewing –hindwing character), or may be based on reductions, which are difficult to homologize (e.g., number of tarsomeres).

Hennig (1969, 1981) doubted the monophyly of Homoptera, stating that the characters used for distinguish it from Heteroptera were symplesiomorphies. He recognized three groups within Hemiptera: Sternorrhyncha, Auchenorrhyncha, and Heteropterodea (as "Heteropteroidea"), the latter clade formed by Coleorrhyncha + Heteroptera (Schlee 1969d). The paraphyly of Homoptera was further corroborated with 18S rDNA sequence analyses (Wheeler *et al*. 1993; Campbell *et al*. 1994, 1995; Sorensen *et al.* 1995; von Dohlen and Moran 1995).

Even though evidence is compelling towards a paraphyletic "Homoptera", and that this has been adequately communicated to a more general audience (e.g., Carver *et al*. 1991; Kristensen 1991; Gullan 2001; Fagua 2005), it is still frequent to see references to "Homoptera" in areas such as Integrated Pest Management (e.g., Pedigo 1996), or in general entomological textbooks (e.g., Arnett 2000), practice that should be avoided.

## Phylogenetic hypotheses

### 1. Paraneoptera

Paraneoptera is the group of Neoptera that includes Thysanoptera, Psocodea ("Phthiraptera" + "Psocoptera" [Lyal 1985; Yoshizawa and Johnson 2006]), and Hemiptera (Kristensen 1991; Wheeler *et al.* 2001). Kristensen (1991) listed for this clade the following putative synapomorphies: maxillary lacinia elongate and slender, detached from stipes; postclypeus enlarged; reduced number of tarsomeres (three or less); cerci absent; at most six Malpighian tubules; abdominal ganglia fused in one mass; gonangulum in the females fused with tergum nine (Scudder 1961); and sperm acrosome without perforatorium (Jamieson *et al.* 1999). Yoshizawa and Saigusa (2001) proposed nine additional synapomorphies from the front wing axillary sclerites for the group.

Some authors have included Zoraptera in Paraneoptera based on morphological characters (Hennig 1969, 1981; Kristensen 1981; Wheeler *et al.* 2001; Beutel and Weide 2005), in which the inclusive group of Psocodea + Thysanoptera + Hemiptera is denominated Acercaria, due to the absence of cerci (Börner 1904). The inclusion of Zoraptera in Paraneoptera, nonetheless, is highly controversial (Hennig 1969, 1981; Yoshizawa 2007), and has not always been followed (e.g., Kristensen 1991; Grimaldi and Engel 2005). The putative synapomorphies of Zoraptera + Acercaria are all reductions (number of Malpighian tubules, number of tarsomeres, and fusion of abdominal ganglia) (Hennig 1969, 1981; Kristensen 1981; but see Hünefeld 2007), and thus, difficult to homologize. Potential synapomorphies have been proposed for Zoraptera + Acercaria based on head capsule characters (Beutel and Weide 2005), and on genitalic characters both for Zoraptera + Psocoptera, and for Zoraptera + Hemiptera (Hünefeld 2007), but have not been tested in a phylogenetic analysis. Nonetheless, some authors had rejected the inclusion of Zoraptera in Paraneoptera, based on phylogenetic analyses of 18S rDNA sequences, which place Zoraptera closely related to Dictyoptera (Wheeler *et al.* 2001; Yoshizawa and Johnson 2005), and on wing base morphology (Yoshizawa 2007). These evidences support the hypothesis that Zoraptera is not a member of the Paraneoptera.

Relationships among members of Paraneoptera (in the restricted sense of Kristensen 1991) are still unclear. Some phylogenetic hypotheses show a polytomy among Psocodea, Thysanoptera, and Hemiptera (e.g., Kristensen 1991; Beutel and Gorb 2001). In other instances Hemiptera is the sister group of Thysanoptera + Psocodea (e.g., Whiting *et al.* 1997; Gorb and Beutel 2001; Wheeler *et al.* 2001; Willmann 2004), or the sister group of Thysanoptera (e.g., Hennig 1969, 1981; Kristensen 1981; Whiting *et al.* 1997; Wheeler *et al.* 2001; Yoshizawa and Saigusa 2001; Cranston and Gullan 2003). The latter clade, Hemiptera + Thysanoptera, is named Condylognatha (Börner 1904), and is supported by a few synapomorphies (Kristensen 1981), namely the modification of the mandibles and maxillary laciniae into stylets (Hennig 1969, 1981; Heming 1980), specialized sclerotized rings between antennal flagellomeres (Seeger 1975), and the particular conformation of the axillary sclerites of the forewing (Yoshizawa and Saigusa 2001). The character of the flagellomeres rings should be further evaluated since it was found only in Thysanoptera and in Pentatomidae (Heteroptera) (Seeger 1975).

No phylogenetic hypotheses have been proposed yet for Paraneoptera using molecular characters with a comprehensive taxon sampling. Crespi *et al.* (1996) analyzed 18S rDNA sequences of Thysanoptera with some Hemiptera as outgroups which resulted in a monophyletic Thysanoptera, but in a combined analysis with COI sequences it produced a polytomy of the two suborders of Thysanoptera with Hemiptera. Morris and Mound (2003) in an analysis with an extended Thysanoptera taxon sampling, with some Hemiptera and Psocodea as outgroup species, found a monophyletic Thysanoptera but a paraphyletic Hemiptera with respect to Psocodea. Johnson *et al.* (2004) while studying the relationships of Psocodea using 18S DNA, found moderate support for the Condylognatha, but again, with an extremely limited taxon sampling for Hemiptera and Thysanoptera.

In those phylogenetic analyses of Hexapoda including paraneopteran representatives, usually the taxon sample is small (e.g., Whiting *et al.* 1997) or some groups are missing completely (e.g., Thysanoptera: Kjer 2004), rendering the conclusions of paraneopteran relationships inadequate. When representatives of all the three major clades are included, the results are either an unresolved polytomy (Kjer *et al.* 2006) or unlikely poly- or paraphyletic groups (e.g., Hemiptera paraphyletic respect to Thysanoptera: Whiting *et al.* 1997; Paraneoptera and Hemiptera polyphyletic: Wheeler *et al*. 2001; Paraneoptera paraphyletic with Psocodea as basal-most Neoptera and Polyneoptera as sister group of Heteropterodea + Auchenorrhyncha: Whiting 2002; Psocodea paraphyletic respect to Thysanoptera: Kjer *et al.* 2006). The relationships among members of Paraneoptera are an open field of research.

### 2. Hemiptera

Hemiptera is an ancient lineage with fossils known since the Early Permian (Kukalová-Peck 1991; Shcherbakov and Popov 2002). Hemiptera is a monophyletic group, based on the unique structure of the mouthparts (see above), which consist of a labium enclosing the maxillary and mandibulary stylets (Kristensen 1991). Yoshizawa and Saigusa (2001) proposed another potential synapomorphy, the fork of the anterior axillary fold-line of the forewing, a character that is independent from that one of the mouthparts, which reinforces the monophyly of Hemiptera.

As discussed above, Hemiptera was traditionally divided in two groups: "Homoptera" and Heteroptera. Compelling evidence, nonetheless, suggest that Hemiptera is composed of three main clades: Sternorrhyncha, Auchenorrhyncha, and Heteropterodea, in which Sternorrhyncha is the sister group of Auchenorrhyncha + Heteropterodea (e.g., Hennig 1969, 1981; Kristensen 1975; Wootton and Betts 1986; Carver *et al*. 1991; Wheeler *et al*. 1993). Of these, only the monophyly of Auchenorrhyncha is still debatable (see below). Zrzavý (1990) termed the clade Auchenorrhyncha + Heteropterodea as Euhemiptera.

Shcherbakov and Popov (2002) proposed an alternative classification for Hemiptera, mostly following Börner (1904), in which they recognized five suborders and an "ancestral" group, the Archescytinoidea. In their view, the Auchenorrhyncha (as Cicadina) is paraphyletic, and the extant hemipterans that represent the sister group of the Heteropterodea (as Peloridiina + Cimicina) are the Cicadomorpha. They presented a phylogram depicting relationships among these groups (Shcherbakov and Popov 2002: see their fig. 179), which despite a list of characters supposedly supporting the nodes, can hardly be viewed as a phylogenetic hypothesis. However, Bourgoin and Campbell (2002), based on unpublished molecular data sets (18S rDNA), also argue that Auchenorrhyncha is paraphyletic, and that the sister group of Heteropterodea is Cicadomorpha, similar to the proposal of Shcherbakov and Popov (2002).

Yang (2004) proposed a scheme of relationships within Hemiptera based on morphological characters that differ from that presented by Wheeler *et al*. (1993), mainly in that Psylloidea is the sister group of Heteropterodea, Sternorrhyncha and Cicadomorpha are paraphyletic, and in the internal relationships of the Heteroptera infraorders (Leptopodomorpha, Cimicomorpha, and Pentatomomorpha are in a polytomy, Enicocephalomorpha is the sister group of this clade, and the remaining infraorders forms a basal group in an unresolved polytomy). Nonetheless, several flaws in the analysis, such as choosing *a priori* a "functional" outgroup (within Hemiptera) and not stating how the analysis was done, prevent his discussion of relationships being useful.

Sorensen *et al*. (1995) proposed unnecessary new names for clades already named (e.g., in Wheeler *et al*. 1993), in part, because Auchenorrhyncha was found to be paraphyletic respect to Heteroptera, and also because they wanted to recognize what they considered suborders of Hemiptera. They proposed: Clypeorrhyncha (for extant Cicadomorpha), Archaeorrhyncha (for Fulgoromorpha), Peloridiomorpha (for Coleorrhyncha [Peloridiidae]), Neohemiptera (for Fulgoromorpha + Heteropterodea), and Prosorrhyncha (for Heteropterodea) (Table 1). Nonetheless, these names may lead to confusion, in particular if Auchenorrhyncha is not paraphyletic (see below for discussion). Even more, the names Cicadomorpha, Fulgoromorpha, and Heteropterodea, independently of the outcome of the phylogenetic relationships within Hemiptera, convey a clear meaning already used in Hemiptera literature. Bourgoin and Campbell (2002) argue in favor of dropping the names proposed by Sorensen *et al*. (1995). Because the ICZN (1999) do not regulate the application of names above family rank, it depends on the researchers to favor the use of certain names.

Vibrational communication is diverse in Hemiptera, with species producing sound in terrestrial as well as aquatic ecosystems, being substrate communication common (Crocroft and Rodríguez 2005). There may be stridulation, tymbal, and percussional vibration (Claridge 1985; Hoy and Robert 1996; Gogala 2006; Hoch *et al.* 2006; Soulier-Perkins *et al*. 2007). It has been suggested that a tymbal-like communication is synapomorphic for Auchenorrhyncha + Coleorrhyncha + Heteroptera (Hoch *et al.* 2006).

## 3. Sternorrhyncha

Sternorrhyncha is a monophyletic group (Schlee 1969c; von Dohlen and Moran 1995), which includes four main groups: Psylloidea, Aleyrodoidea, Aphidoidea, and Coccoidea (e.g., Schlee 1969b; Carver *et al.* 1991; von Dohlen and Moran 1995; Bourgoin and Campbell 2002).

Goodchild (1966) based on the alimentary tract morphology regarded Aphidoidea as the sister group of Coccoidea + (Psylloidea + Aleyrodoidea). Schlee (1969a, 1969b) based on external morphology and male genitalic characters considered two sister groups within Sternorrhyncha: Psylloidea + Aleyrodoidea (Psylliformes), and Aphidoidea + Coccoidea (Aphidiformes). In some analyses Psylloidea is considered the sister group to the rest of Sternorrhyncha (e.g. Campbell *et al*. 1994, 1995). Despite these competing hypotheses, no modern comprehensive phylogenetic analysis is available for the group (but see review of previous phylogenetic hypotheses in Schlee 1969b).

The following subgroups of Sternorrhyncha are presented in alphabetical order because no consensus has been achieved about their phylogenetic relationships.

**3a. Aleyrodoidea.** The Aleyrodoidea, or whiteflies (Figs. 1A, B, C), includes 1.556 valid species in Aleyrodidae, the only included family, which is subdivided into three subfamilies: Aleurodicinae, Aleyrodinae, and the controversial Udamoselinae (Mound and Halsey 1978; Martin and Mound 2007). Manzari and Quicke (2006) analyzed the phylogenetic relationships of the large and widespread Aleyrodinae, which contains most of the economically important pest species (Byrne and Bellows 1991; Martin and Mould 2007). Their analyses based on pupal case characters (Manzari and Quicke 2006) found that only 45% of the genera with multiple representatives were monophyletic, and that most of the tribes and economically important genera (e.g., *Bemisia* and *Trialeurodes*) are not monophyletic. They did not propose any new taxonomic scheme at the tribal level arguing that the data set used is not enough to provide adequate resolution.

**3b. Aphidoidea.** Aphidoidea has three families, Phylloxeridae, Adelgidae, and Aphididae, commonly called aphids (Figs. 1D, E), with some 4.500 described species (Remaudière and Remaudière 1997; Blackman and Eastop 2006). Some authors prefer to give them rank of superfamilies (e.g., Shcherbakov and Popov 2002).

Heie (1987) proposed a scheme of relationships for the Phylloxeridae and Aphididae based on morphology of extant and extinct taxa. Von Dohlen and Moran (2000) proposed a phylogenetic scheme for Aphididae using 12S and 16S mtDNA. They found little support and structure at deeper nodes, only recovering recognized tribes but not subfamilies. Martínez-Torres *et al*. (2001), also using a mitochondrial gene, found similar results. Ortiz-Rivas *et al*. (2004) analyzed the relationships of Aphididae based on a single nuclear gene (long wavelength opsin) and the topologies of their analyses were better resolved than in previous analysis. They identified three main clades, with Aphidinae and Lachninae always monophyletic. The relationships within Aphidinae were examined by von Dohlen *et al*. (2006) with three genes: leucine tRNA, COII mtDNA, and EF1α.

**3c. Coccoidea.** The group has about 7300 described species (Miller and Ben-Dov 2006), and the 20 or more families (Figs. 1F, G) are usually divided into two groups: Archaeococcoidea and Neococcoidea (Koteja 1974; Miller and Kosztarab 1979; Gullan and Kosztarab 1997). Gullan and Cook (2007) review the phylogeny and classification of the coccoids in detail.

Miller (1984), Miller and Hodgson (1997), and Foldi (1997) proposed phylogenetic hypothesis based in morphological characters for the group. Nonetheless, their analyses had either a small taxon sampling or poor nodal support that renders the results non-conclusive.

Cook *et al*. (2002) assessed the phylogeny of the Coccoidea using rDNA sequences of the small subunit. They found that the neococcoids are a monophyletic group and that Pseudococcidae is the sister group to the rest of them. Eriococcidae was retrieved as a paraphyletic group in their analyses, corroborating previous views based on morphology (Cox and Williams 1987). The monophyly and relationships of the archaeococcoids are in doubt (Gullan and Cook 2007).

Two out of three of the largest families of Coccoidea have been assessed for phylogenetic relationships. Downie and Gullan (2004) assessed the phylogeny of the Pseudococcidae using DNA sequences of EF1α, 28S and 18S. They found that the three major clades of the analysis correspond to the subfamilies Pseudococcinae, Phenacoccinae and Rhizoecinae, with Sphaerococcinae as polyphyletic. Recently, Hardy *et al*. (2008) reassessed the relationships of the Pseudococcidae, using an expanded taxon sampling and adding morphological data. They recognized two main clades to which they apply the names Phenacoccinae and Pseudococcinae, including in the former the Rhizoecini.

Morse and Normark (2006) studied the phylogenetic relationships of Diaspididae using EF1α and 28S rDNA sequences. Most of the traditional groups recognized in classifications were broadly recovered, although none of them was strictly monophyletic. The remaining family, Coccidae, has never been subject of a comprehensive phylogenetic analysis. Qin and Gullan (1995) evaluated the relationships of one of the subfamilies, Ceroplastinae (Coccidae), finding that most of the genera were not monophyletic, and that most of the species should be grouped into the genus *Ceroplastes*.

**3d. Psylloidea.** Psylloidea (Fig. 1H) has more than 3000 described species (Hodkinson and Casson 1991; Hollis 2004; Burckhardt 2005). The classification of this group of sap-sucking insects has been extremely artificial (Burckhardt and Lauterer 1989). White and Hodkinson (1985) first proposed a phylogenetic scheme of the Psylloidea using mostly nymphal characters. In their phylogenetic analysis they regard Psyllidae as the sister group of all other psylloids. Of the eight families recognized by them, two, Aphalaridae and Spodyliaspididae, were accepted in their classification as paraphyletic following an "evolutionary" approach (White and Hodkinson 1985: 264). Ouvrard (2002) reassessed the relationships of the Psylloidea using morphological characters of the adult thorax and 18S rRNA sequences. His results differ from those of White and Hodkinson (1985), although it is difficult to compare and interpret them because Ouvrard did not present a list of characters, matrix, or list of species used in his analysis. Nonetheless, he concluded that Aphalaridae and Psyllidae are paraphyletic.

Recently, Ouvrard *et al*. (2008) identified potential morphological synapomorphies for Psylloidea in relation to the wing base structure: absence of subalare, a median notal wing process, and of the anterior arm of the third axillary sclerite; no articulation with the second axillary sclerite; a weakly-sclerotized third axillary sclerite; and presence of a two-horned basalare. Hodkinson (1989) provided a review of the faunal elements present in the Neotropical region.

## 4. Auchenorrhyncha

Auchenorrhyncha has been traditionally divided in two main groups, Cicadomorpha and Fulgoromorpha (e.g., Hennig 1969, 1981; Carver *et al.* 1991). Nonetheless, it has been extensively debated if Auchenorrhyncha is a monophyletic group or not. Goodchild (1966) based on the morphology and histology of the digestive tract considered Auchenorrhyncha as paraphyletic because he considered two groups: Fulgoromorpha + Heteroptera and Cicadomorpha + Sternorrhyncha, with the Coleorrhyncha in a polytomy with both. Hamilton (1981) regarded Auchenorrhyncha paraphyletic because he considered Fulgoromorpha as sister group to Cicadomorpha + Aphiformes, although he also considered Homoptera as monophyletic. Wootton and Betts (1986) using characters of wing morphology also doubted the monophyly of Auchenorrhyncha. Bourgoin proposed that Auchenorrhyncha is paraphyletic, based on head morphology (Bourgoin 1986a, 1986b), and on male (Bourgoin and Huang 1990) and female genitalia (Bourgoin 1993), because Fulgoromorpha is apparently more related to Heteropterodea than to Cicadomorpha. Nonetheless, the particular aristate antennae (e.g., Grimaldi and Engel 2005) and evidence from the fore wing base sclerites (Yoshizawa and Saigusa 2001), suggest that Auchenorrhyncha is in fact monophyletic.

Much of the recent evidence for the paraphyly of Auchenorrhyncha come from molecular sets alone. Campbell *et al*. (1995) using 18S rDNA sequences found a polytomy among Fulgoromorpha, Cicadomorpha, and Heteropterodea when using the full dataset (their fig. 3). When using a restricted data set (homoplasious sites removed), either Fulgoromorpha or Cicadomorpha become sister groups of Heteropterodea (Campbell *et al.* 1995, their fig. 4), but when Peloridiidae was removed from this restricted data set, Fulgoromorpha become the sister group of Heteroptera. Sorensen *et al*. (1995) also using 18S rDNA found that Auchenorrhyncha is not monophyletic. Despite their small dataset, they found that Auchenorrhyncha is either paraphyletic or polyphyletic respect to Heteroptera. Bourgoin *et al*. (1997) in an analysis of the Fulgoromorpha found that this group is the sister group to Heteroptera, rendering Auchenorrhyncha paraphyletic. They also found that Cicadomorpha was not monophyletic if Psyllidae was included as part of the outgroup, showing that their analysis is sensitive to taxon sampling. Ouvrard *et al*. (2000) found a polytomy among Fulgoromorpha, Cicadomorpha, and Heteropterodea, similar to the results of Campbell *et al*. (1995). Urban and Cryan (2007) using an extended data set of four genes and 83 species of Fulgoromorpha found a monophyletic Auchenorrhyncha, which was the sister group of Heteroptera.

**4a. Cicadomorpha.** Within this group three superfamilies are recognized: Cercopoidea (spittlebugs or froghoppers) (Figs.


**Figure 1.** Habitus illustrations of different groups of Hemiptera (not at the same scale). **A.** *Trialeurodes vaporariorum* (Westwood) (Aleyrodidae). **B.** *Bemisia argentifolii* Bellows & Perring (Aleyrodidae). **C.** *Aleurodicus dugesii* Cockerell (Aleyrodidae). **D.** *Adelges cooleyi* (Gillette) (Adelgidae). **E.** *Aphis nerii* Fonscolombe (Aphididae). **F.** *Pseudococcus longispinus* (Targioni-Tozzetti) (Pseudococcidae). **G.** *Aspidaspis arctostaphyli* Cockerell & Robbins (Diaspididae). **H.** *Russelliana solanicola* Tuthill (Psyllidae). Peru. Lateral and dorsal views. **I.** *Sphenorhina melanoptera* (Germar) (Cercopidae). Ecuador. **J.** *Prosapia bicincta* (Say) (Cercopidae). Panama. **K.** Cicadidae. Panama. Recently molted adult and exuviae. **L.** *Cladonota* sp. (Membracidae). Panama. **M.** *Heteronotus* sp. (Membracidae). Peru. **N.** *Ferrariana trivittata* (Signoret) (Cicadellidae). Panama. **O.** *Platygonia spatulata* (Signoret) (Cicadellidae). Panama. **P.** *Proconia* sp. (Cicadellidae). Ecuador.

1I, J), Cicadoidea (Fig. 1K), and Membracoidea (leafhoppers and treehoppers) (Figs. 1L, M, N, O, P), with approximately 35.000 described species (Cryan 2005; Dietrich 2005).

The monophyly of Cicadomorpha has never been doubted based on morphological characters; nonetheless, all possible relationships have been proposed among its superfamilies: Membracoidea has been proposed the sister group of Cercopoidea + Cicadoidea (Campbell *et al*. 1995; Ouvrard *et al*. 2000; Bourgoin and Campbell 2002); Cercopoidea as sister group of Membracoidea + Cicadoidea (Evans 1963; Hamilton 1999); and Cicadoidea as sister group of Membracoidea + Cercopoidea (Hamilton 1981; Sorensen *et al*. 1995; von Dohlen and Moran 1995). More recently, Cryan (2005) criticized previous analyses among the superfamilies arguing both poor taxon and data sampling. He proposed a phylogeny of Cicadomorpha based on three nuclear gene sequences. He found that including all data sets is better than analyzing individual gene data sets, and that 18S is a relatively poor molecular marker for recovering the relationships among superfamilies. Although some morphological evidence apparently placed Membracoidea as a derived taxon (e.g., Hamilton 1981), independent character analysis supports Membracoidea as a basal Cicadomorpha group, for instance, Liang and Fletcher (2002) with antennal characters, and Rakitov (2002) with structural characters of brochosomes, proteinaceous particles secreted by glandular regions of the Malpighian tubules of almost all cicadellids.

Membracoidea currently includes the extant families Aetalionidae, Cicadellidae, Melizoderidae, Membracidae, and Myerslopiidae (Hamilton 1999; Dietrich 2005).

Dietrich and Deitz (1993) analyzed the relationships of the Membracoidea using morphological characters, focusing mostly in non-cicadellid taxa (Aetalionidae and Membracidae). In their analysis Cicadellidae is monophyletic and the sister group of (Melizoderidae + (Aetalionidae + Membracidae)). Dietrich and Deitz (1993) listed as synapomorphies for Cicadellidae: the mesonotum exposed posteriorly, the labium not reaching the metathoracic coxae, m-cu1 crossvein present, metatibia with distinct long setae, tarsomere I of hind leg without cucullate setae, sternum IX and subgenital plate not fused, and abdominal tergum with divided acanthae; all of which are homoplastic characters in their analysis.

Hamilton (1999) presented a phylogeny of the extinct and extant families of Membracoidea, and placed Myerslopiidae as the sister group of the remaining families. In Dietrich *et al*. (2001b) analysis Myerslopiidae grouped with Cicadoidea taxa, whereas in Cryan's (2005) Myerslopiidae was recovered as the sister group to all remaining Membracoidea. Hamilton (1999) also considered Ulopidae as a separate group from Cicadellidae, and placed Cicadellidae as sister group of (Ulopidae + (Aetalionidae + Membracidae)), rendering Cicadellidae paraphyletic with respect to Membracidae. This scheme was first supported by Dietrich *et al*. (2001b) based on the analysis of 28S rDNA sequences, where the clade including Ulopinae and Megophthalminae appears as more closely related to Aetalionidae + Membracidae; and posteriorly by Cryan (2005).

Within Membracoidea, the Membracidae has received much attention on its suprageneric classification with recent phylogenetic analysis at the subfamily level using morphological characters (Dietrich and Deitz 1993; Dietrich *et al*. 2001a), molecular ones (Cryan *et al*. 2000), or in combined analysis (Cryan *et al.* 2004). The relationships within subfamilies, tribes, or genera have also been assessed for a number of taxa (e.g., Aconophorini: Dietrich and Deitz, 1991; Centrotinae: Wallace and Deitz 2004, 2005; Darnini: Roy *et al*. 2007; Membracinae: Lin *et al.* 2004; Microcentrini: Cryan *et al*. 2003; Nicomiinae: Albertson and Dietrich 2005).

The speciose family Cicadellidae, commonly called leafhoppers and sharpshooters (Membracoidea), has more than 22.000 described species worldwide and 5.000 species in the Neotropical region (Freytag and Sharkey 2002), and Cicadellidae has about 36 subfamilies worldwide (Oman *et al*. 1990; Dietrich 2004). Phylogenetic hypotheses based on morphology were first proposed by Ross (1957), then by Hamilton (1983) and Dietrich (1999). Dietrich *et al*. (2001b) was the first attempt to recover the phylogeny of most cicadellid subfamilies and tribes using 28S rDNA sequences, and found that most of them were not monophyletic. Within Cicadellidae some groups had been subject of analyses (e.g., Evacanthinae: Dietrich 2004; Cicadellinae: Takiya *et al*. 2006; Deltocephalinae: Zahniser and Dietrich 2008).

The phylogenetic relationships within Cicadoidea have rarely been addressed at the family level, except in a few instances, with characters used in traditional classifications (e.g., Chou *et al.* 1997). Recently, Moulds (2005) proposed a phylogenetic hypothesis for the Cicadoidea with an extended morphological data set in which he recognized two families, Tettigarctidae and Cicadidae, the latter with three subfamilies. The only higher phylogenetic proposal for Cercopoidea is that of Cryan (2005). He shows that Machaerotidae + Clastopteridae is the sister group of Cercopidae + Aphrophoridae. Cryan's (2005) analysis supports a monophyletic Cercopidae, and although it shows a monophyletic Aphrophoridae, he doubts of its monophyly based on additional unpublished data. Interestingly, the recently described family Epypigidae (Hamilton 2001), was found nested within the Aphrophoridae.

**4b. Fulgoromorpha.** This group, often referred as Fulgoroidea in the literature, and commonly named planthoppers (Figs. 2A, B, C), has more than 9.000 described species, and about 20 families (O'Brien and Wilson 1985).

Several hypotheses of relationships have been proposed for this group based on morphological characters, all of which support a monophyletic Fulgoromorpha (Muir 1923; Asche 1987; Emeljanov 1990; Bourgoin 1993; Chen and Yang 1995). In all but one of these hypotheses the Tettigometridae is considered the sister group to the rest of the fulgoroids, with various levels of resolution and clade composition for the remaining taxa (reviewed by Urban and Cryan 2007). Only Bourgoin (1993) considered the Tettigometridae as a derived taxon using morphological characters.

Bourgoin *et al.* (1997) assessed the relationships of a small sample of fulgoromorph taxa, targeting in particular the position of Tettigometridae. They found that Fulgoromorpha is a monophyletic clade and that the relictual Tettigometridae is not basal as previously thought. Yeh *et al*. (1998) analyzed a restricted set of Fulgoromorpha with partial sequences of 16S rDNA. Yeh *et al.* (2005) expanded their dataset of 16S sequence data and analyzed the fulgoroids with neighbor joining algorithms. They obtained similar results to that of Bourgoin *et al.* (1997) in placing Cixiidae and Delphacidae as the most basal groups, and in having the Tettigometridae in a derived position. Yeh and Yang (1999) using 28S rDNA sequences analyzed the relationships of some fulgoromorphs. They reached similar conclusions to Yeh *et al.* (2005). More recently,

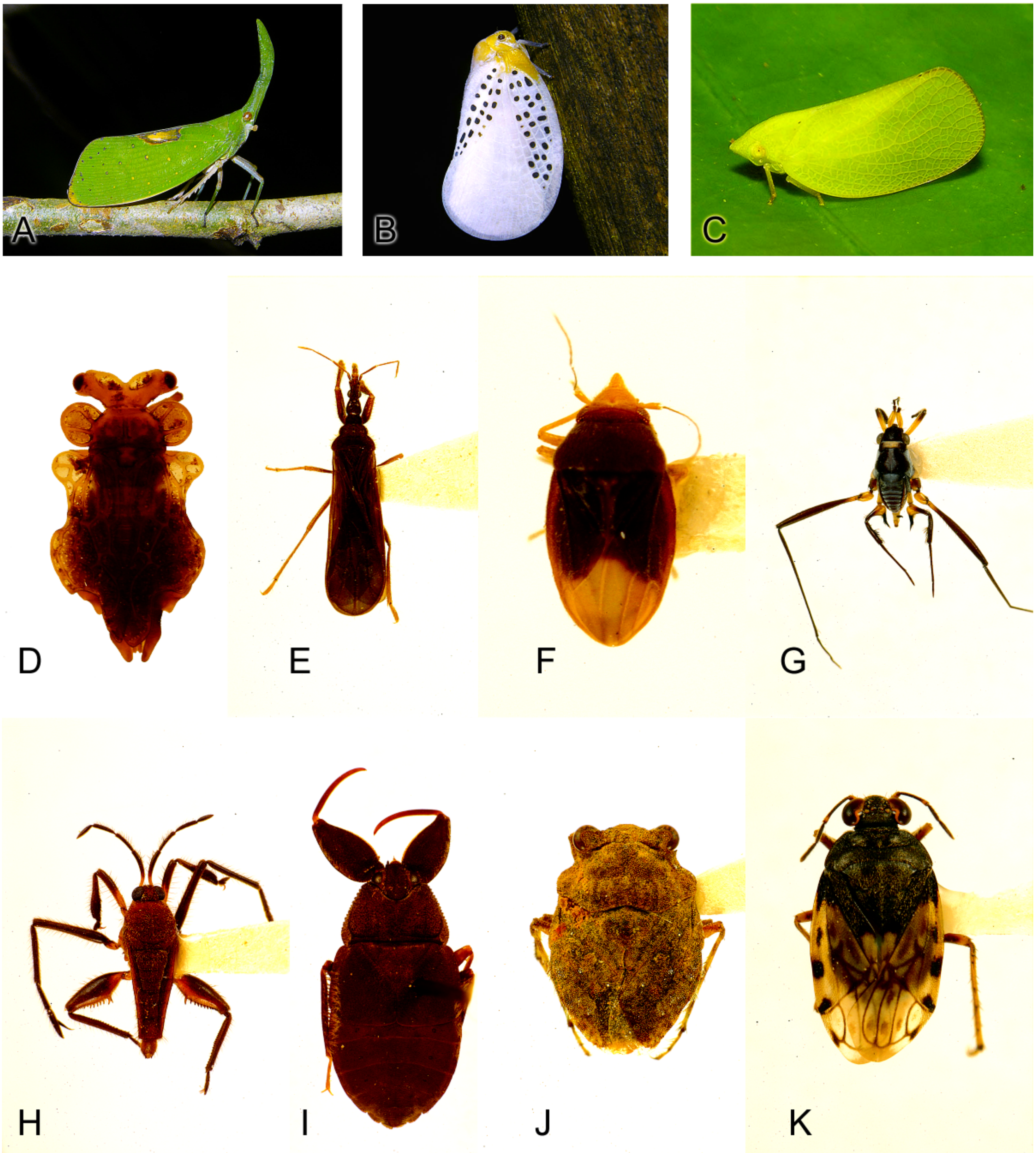


**Figure 2.** Habitus illustrations of different groups of Hemiptera (not at the same scale). **A.** *Pyrops* sp. (Fulgoridae). Borneo. **B.** Flatidae. Peru. **C.** *Acanalonia* sp. (Acanaloniidae). Panama. **D.** *Peloridora kuscheli* China (Peloridiidae). Chile. **E.** *Systelloderes* sp. (Enicocephalidae). Costa Rica. **F.** *Nannocoris* sp. (Schizopteridae). Ecuador. **G.** *Rheumatobates crassifemur schroederi* Hungerford (Gerridae). Brazil. **H.** *Rhagovelia* sp. (Veliidae). Colombia. **I.** *Cryphocricos latus* Usinger (Naucoridae). Costa Rica. **J.** *Gelastocoris* sp. (Gelastocoridae). Costa Rica. **K.** *Saldula pallipes* (Fab.) (Saldidae). USA.

Urban and Cryan (2007) assessed the phylogenetic relationships of 71 species of Fulgoromorpha and nine outgroup species, with 18S, 28S, Histone 3, and *Wingless* nucleotide sequences. They obtained Cixiidae and Delphacidae as the sister group of the rest. Many of the families were recovered as monophyletic, but some were poly- or paraphyletic, mostly in agreement with previous morphological hypotheses.

**5. Heteropterodea**

Heteropterodea is the clade containing Coleorrhyncha + Heteroptera (Schlee 1969d; Hennig 1969, 1981; Kristensen 1975). Zrzavý (1992) changed the term coined by Schlee (1969d), Heteropteroidea, to Heteropterodea, to avoid confusion with a superfamily rank. Heteropterodea is supported by the following synapomorphies: four antennal segments, body with a flattened dorsal area to receive the wings (Hennig 1969, 1981), anal veins of forewing fused forming a Y-shaped vein (Wootton 1965), last antennal segments larger than proximal ones, abdominal tergites flat with sharp connexivum, abdominal spiracles directed ventrad, anal cone forming a single, exposed element (Schlee 1969d), and wing coupling mechanism of heteropterous type (China 1962). This clade is further supported by a few 18S rDNA characters (Wheeler *et al.* 1993).

**6. Coleorrhyncha**

Coleorrhyncha is a small group of Hemiptera that comprises 13 extant genera and 25 species in the only extant family Peloridiidae (Fig. 2D) (China 1962; Evans 1981). The distribution is restricted to the Southern Hemisphere and is considered relictual, being found in Eastern Australia, New Caledonia, New Zealand, Chile and Argentina (Patagonia) (Evans 1981; Estévez and de Remes-Lenicov 1989; Burckhardt and Agosti 1991; Burckhardt and Cekalovic 2002). Extant species are associated with *Nothofagus* forests, and little is known about their biology, except that they live on mosses (Hacker 1932; Evans 1981), and are found on lichens, hepatics, and sphagnum bogs (Evans 1981). The South American fauna includes three monotypic genera, *Pantinia*, *Peloridium*, and *Kuscheloides*, as well as *Peloridora* with three species (China 1962; Evans 1981), although some undescribed taxa may still exist (e.g., Burckhardt and Agosti 1991).

Coleorrhyncha was traditionally included as a member of the "Homoptera" (e.g., Myers and China 1929; China 1962; Evans 1963), but it is now considered the sister group of Heteroptera due to compelling morphological and molecular evidence (Schlee 1969d; Hennig 1969, 1981; Wheeler *et al.* 1993; Sweet 1996; Ouvrard *et al.* 2000). Peloridiidae has been considered a monophyletic group because of its particular morphology (e.g., Evans 1963). Surprisingly, Ouvrard *et al.* (2000) found a paraphyletic Peloridiidae in some analysis with 18S rRNA, but recovered it as monophyletic after eliminating all homoplasious sites.

Popov and Shcherbakov (1996) revised the fossil Peloridiidae and proposed a scheme of relationships among the extant members. Despite presenting a "matrix" of characters and a tree, these certainly do not represent a cladistic analysis of relationships (see also Schuh 1997).

**7. Heteroptera**

Heteroptera is defined by the following putative synapomorphies: presence of gula, presence of metathoracic scent apparatus, abdominal dorsal scent glands (functional in nymphs), and strong reduction of the tentorium (Carayon 1971; Cobben 1978; Hennig 1969, 1981; Kristensen 1975). Although metathoracic scent glands are not easy to observe in Enicocephalomorpha, there is evidence for its presence (Carayon 1962, 1971; Cobben 1978). The presence of a frenum, which helps to attach the posterior claval margin of the forewing to the lateral margin of the scutellum, is also a potential synapomorphy for Heteroptera (Štys 1998). An open rhabdom structure in the ommatidia of Heteroptera is considered a synapomorphy for Heteroptera, in contrast to the fused rhabdoms in Auchenorrhyncha and Coleorrhyncha (Fischer *et al.* 2000). The absence of the tegula in the forewing is another potential synapomorphy for Heteroptera (Yoshizawa and Saigusa 2001).

Latreille (1810) was the first to recognize Heteroptera as it is conceived nowadays. Dufour (1833) first recognized major groups within Heteroptera. He based his scheme on the habitat occupied by the bugs: Geocorises (terrestrial bugs), Hydrocorises (water bugs), and Amphibicorises (superficial water bugs). Dufour's (1833) classification remained in use until the mid-20th century (e.g., China and Miller 1959). Reuter (1910) proposed a phylogenetic scheme for Heteroptera based on external morphological characters. Štys and Kerzhner (1975) and Schuh (1986) provided a review of the historical proposals of classification among Heteroptera groups that were not based on cladistic methodology.

Leston *et al.* (1954) recognized monophyletic groups within the terrestrial Heteroptera (= Geocorises) of Dufour (1833), proposing and listing the characters defining Cimicomorpha and Pentatomomorpha. They typified these suprageneric names based on genera. Štys and Kerzhner (1975) recognized seven infraorders within Heteroptera, and standardized their names. They followed Leston *et al.* (1954) in applying the -morpha suffix to their infraordinal names.

Schuh (1979) first proposed a phylogenetic scheme for the infraorders of Heteroptera reanalyzing the data of adults and nymphs presented by Cobben (1978). Schuh (1979) considered Enicocephalomorpha as the sister group of the remaining Heteroptera, with Leptopodomorpha + Nepomorpha as the sister group of Cimicomorpha + Pentatomomorpha. Zrzavý (1992) regarded Enicocephalomorpha the sister group of Dipsocoromorpha + Gerromorpha, together forming a basal heteropteran clade, but presented the relationships among Nepomorpha, Leptopodomorpha, and Cimicomorpha + Pentatomomorpha as unresolved. Wheeler *et al.* (1993) used 18S rDNA sequences and morphological characters to resolve the relationships of the Heteroptera infraorders. Their results mostly agree with Schuh's (1979) scheme. They only disagree in the position of Leptopodomorpha, which they consider the sister group of Cimicomorpha + Pentatomomorpha.

Cimicomorpha and Pentatomomorpha are considered sister groups (Schuh 1979; Wheeler *et al.* 1993). Beside the characters mentioned by Schuh (1979) and Wheeler *et al.* (1993), they also share a V-pattern in the rhabdomeres of the ommatidia, further supporting their relationship (Fischer *et al.* 2000).

Schuh (1986) summarized the phylogenetic hypotheses available at that time for all Heteroptera infraorders. The following sections update the information provided by him.

**7a. Enicocephalomorpha.** This relatively small group of true bugs contains approximately 450 described species (Schuh and Slater 1995). Enicocephalomorpha contains two families: Aenictopecheidae and Enicocephalidae (Štys 1989). This


**Figure 3.** Habitus illustrations of different groups of Hemiptera (not at the same scale). **A.** *Diactor* sp. (Coreidae). Panama. **B.** *Dinidor* sp. (Dinidoridae). Ecuador. **C.** *Edessa rufomarginata* (DeGeer) (Pentatomidae). Panama. **D.** *Lygaeus* sp. (Lygaeidae). Peru. **E.** *Harpactor* sp. (Reduviidae). Peru. **F.** *Zelurus* sp. (Reduviidae). Peru. **G.** *Agriocoris flavipes* (Fab.) (Reduviidae). Ecuador. **H.** *Zanchius* sp. (Miridae). Nepal. **I.** *Zanchius* sp. (Miridae). Nepal. **J.** *Pseudoloxops* sp. (Miridae). Nepal.

monophyletic clade was at one point considered part of the Reduviidae (Cimicomorpha) (e.g., Usinger 1943), but is now considered the sister group of the remaining Heteroptera (e.g., Schuh 1979; Wheeler *et al*. 1993).

Wygodzinsky and Schmidt (1991) provided a preliminary phylogenetic scheme of the New World taxa. They placed Aenictopecheidae (as subfamily) as sister group to the remaining taxa. No comprehensive cladistic phylogenetic analysis has been carried out on this group of Heteroptera.

**7b. Dipsocoromorpha.** Five families (Fig. 2F) are included in the most recent classification of the infraorder (e.g., Schuh and Slater 1995). Štys (1985) termed Euheteroptera the clade containing Dipsocoromorpha + (Gerromorpha + (Nepomorpha + (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha)))). The monophyly of this infraorder was proposed by Štys (1983) based on the structure of the male genitalia and legs. Nonetheless, these characters are homoplastic within the infraorder (see Wheeler *et al*. 1993). Despite abundant morphological documentation (e.g., McAtee and Malloch 1925; Hill 1987; Rédei 2007; Štys 1970; Wygodzinsky 1950), no modern phylogenetic analysis is available for this rarely collected group of true bugs.

**7c. Gerromorpha.** There are approximately 1900 described species in this group (Figs. 2G, H) (Andersen and Weir 2004b). Species of this infraorder inhabits the surface of marine or freshwater systems, belonging to this clade the only true marine insect, the genus *Halobates* (Andersen and Weir 1994, 1999). The single most important reference for the Gerromorpha, or semiaquatic bugs, is that of Andersen (1982), in which he reviewed the biology, the morphology, and phylogeny of the group. An update for the phylogenetic hypotheses of the infraorder was provided by Spence and Andersen (1994), as well as a review of their ecology and behavior. Štys (1985) termed Neoheteroptera the clade containing Gerromorpha + (Nepomorpha + (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha))).

Beside the characters listed as synapomorphic for Gerromorpha (Andersen 1982; Wheeler *et al*. 1993; Schuh

**Table 1.** Equivalences of terms for the higher categories of Hemiptera. Synonyms in parentheses are terms created by Sorensen *et al.* (1995). See text for details.

| **Major groups** | **Subordinate groups** |
|---|---|
| Sternorrhyncha | Aleyrodoidea |
| | Aphidoidea |
| | Coccoidea |
| | Psylloidea |
| Auchenorrhyncha | Cicadomorpha (= Clypeorrhyncha) |
| | Fulgoromorpha (= Archaeorrhyncha) |
| Heteropterodea (= Prosorrhyncha) | |
| Coleorrhyncha (= Peloridiomorpha) | Peloridiidae |
| Heteroptera | Enicocephalomorpha |
| | Dipsocoromorpha |
| | Leptopodomorpha |
| | Gerromorpha |
| | Nepomorpha |
| | Cimicomorpha |
| | Pentatomomorpha |

and Slater 1995), it can de added that the eyes dorsally have the ommatidia with a rhabdom pattern of R7 and R8 in tandem (Fischer *et al*. 2000). Andersen (1998) reviewed fossil species of Gerromorpha, and mapped them on his previous phylogeny of the group (Andersen 1982), in which he placed the extinct subfamily Electrobatinae (Gerridae).

Muraji and Tachikawa (2000) analyzed the relationships among the families of Gerroidea (Gerridae, Hermatobatidae, and Veliidae), including 30 species of the superfamily and two other species of Gerromorpha as outgroups, using 16S rDNA and 28S rDNA. Sequence data were analyzed with parsimony and neighbor-joining algorithms. They recovered a monophyletic Gerroidea, and some other clades within the superfamily already supported by morphological characters.

Andersen and Weir (2004b) reanalyzed the relationships of Gerromorpha using 56 morphological characters with a numerical cladistic approach. The topology presented is mostly similar to that of Andersen (1982), except that the relationships of the Veliidae subfamilies Rhagoveliinae, Perittopinae, and Veliinae are unresolved, as well as most of the subfamilies of Gerridae. They also presented arguments for the monophyly of Veliidae and discussed the inclusion of *Ocellovelia* in this family.

Damgaard *et al.* (2005) reanalyzed the relationships of Gerromorpha using the same two gene regions of Muraji and Tachikawa (2000), but with an expanded taxon sampling, and adding morphological characters from Andersen (1982). They assessed the effects of alignment and taxon sampling in their analysis, showing that there is little node stability with different parameters. They recovered as monophyletic the superfamily Gerroidea, and Gerridae, but Veliidae as paraphyletic. They also found support for the Halobatinae (Gerridae) which had ambiguous morphological support, and that *Ocellovelia* was placed as sister group of "Veliidae" + Gerridae only with molecular characters. Recent systematic work has focused on the relationships within families (e.g., Andersen 1999), subfamilies (e.g., Andersen 1995, 2000), and genera, in particular within Gerridae (e.g., Damgaard *et al*. 2000a, 2000b; Damgaard and Sperling 2001; Damgaard and Cognato 2005).

**7d. Nepomorpha.** This infraorder contains about 2000 species in eleven families (Figs. 2I, J) (Štys and Jansson 1988; Hebsgaard *et al*. 2004). The group corresponds to the Hydrocorisae of Dufour (1833). Štys (1985) termed Panheteroptera the clade containing Nepomorpha + (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha)).

Wheeler *et al.* (1993) presented molecular evidence for a monophyletic Nepomorpha, rejecting a basal position within Heteroptera as argued by some authors (e.g., Reuter 1910; Mahner 1993). The relationships within the clade, nonetheless, were unresolved probably due to the limited taxon sampling. Mahner (1993) provided a phylogenetic analysis for Nepomorpha and all the subordinate groups. His scheme is similar to that of Rieger (1976) in the placement of Nepoidea [i.e., (Nepidae + Belostomatidae), see Schuh and Slater 1995: 110] as sister group to the remaining Nepomorpha, and in having as the most derived clade the Notonectoidea [i.e., (Notonectidae + (Helotrephidae + Pleidae))]. Mahner's (1993) scheme differs from Rieger's (1976) in the position of Corixidae, which is considered the sister group of (Ochteroidea + (Naucoroidea + Notonectoidea)); whereas in Rieger's scheme the position of the Ochteroidea and Corixidae are inverted [i.e., (Ochteroidea + (Corixidae + ("Naucoroidea" + Notonectoidea)))]. In addition, Rieger (1976) data suggest a paraphyletic Naucoroidea, whereas Mahner (1993) treat this superfamily as monophyletic, but without placing the Potamocoridae in his analysis.

Hebsgaard *et al.* (2004) proposed a phylogenetic hypothesis for the Nepomorpha using both molecular (16S and 28S rDNA) and morphological characters. They found support for the monophyly of all Nepomorpha families, and superfamilies except Naucoroidea (i.e., Naucoridae, Aphelocheiridae, and Potamocoridae). Their analysis place Nepoidea as the most basal group, and Corixidae as sister group remaining Nepomorpha, similar to the proposal of Mahner (1993).

**7e. Leptopodomorpha.** This infraorder contains four families (Fig. 2K) and about 300 described species, nearly all of them in Saldidae (Schuh *et al*. 1987). Schuh and Slater (1995) listed the synapomorphies for the infraorder. An additional synapomorphy for Leptopodomorpha is the shape of the rhabdom resembling a "5" pattern on a dice (Fischer *et al.* 2000).

Schuh (1986) reviewed the phylogenetic proposals and classification scheme for the infraorder. In the cladistic analysis of Schuh and Polhemus (1980) the relationship of the higher groups is ((Saldidae + Aepophilidae) + (Omaniidae + Leptopodidae)). Polhemus (1985) presented a cladistic analysis of the Leptopodomorpha, based on his PhD dissertation data, in which the relationships of the higher groups are (Leptopodidae + (Omaniidae + (Saldidae + Aepophilidae))), differing from that of Schuh and Polhemus (1980) in the position of the Omaniidae. Polhemus (1985) presented in addition phylogenetic hypotheses for the subfamilies and tribes of Saldidae, for the genera of Saldini, and for the genera of the large Saldoidini. No more recent hypotheses with additional morphological or molecular characters has been proposed.

**7f. Pentatomomorpha.** This infraorder contains about 15.000 described species (Figs. 3A, B, C, D) (Henry 1997, Schuh and Slater 1995). Leston *et al*. (1954) first recognized Pentatomomorpha as a monophyletic group. It included those groups with abdominal trichobothria, the Trichophora of Tullgren (1918), plus Aradoidea (Aradidae + Termitaphididae). Although Sweet (1996) has given infraordinal status to Aradoidea, ranking it differently does not modify its placement as the sister group of the remaining Pentatomomorpha, as argued by Henry (1997). Sweet (2006) has even further suggested that the position of the Aradoidea may lay outside the Leptopodomorpha, Cimicomorpha, and Pentatomomorpha, which clearly contradicts the available morphological and molecular evidence (e.g., Wheeler *et al*. 1993; Grazia *et al*. in press).

Henry (1997) assessed the relationships of the infraorder in a morphological cladistic analysis. He included 53 taxa, using families, subfamilies, and tribes –in particular of the Lygaeoidea (*sensu* Schuh and Slater 1995)– as terminals using a *ground plan* approach. He chose Aradoidea as the outgroup for his analyses. He also included the Pentatomoidea as a single terminal taxon in the analysis providing evidence for its monophyly, but showing the difficult position of Thaumastellidae, usually included in this group. Henry's main interest was to elucidate the relationships among the Lygaeoidea and to test the monophyly of this group, while looking for a sister group relationship for the Berytidae. In his analyses Pentatomoidea is the sister group of the remaining Pentatomomorpha, i.e., ((Coreoidea + Pyrrhocoroidea) + (Idiostoloidea + Lygaeoidea *sensu stricto*)). He found that Lygaeoidea is paraphyletic with respect to the Berytidae, Colobathristidae, and Piesmatidae, which were nested within Lygaeidae *sensu lato* (e.g., Schuh and Slater 1995). Henry raised several of the previous subfamilies and tribes of the Lygaeidae (*sensu lato*) to family status proposing a new classification for Pentatomomorpha reflecting the phylogenetic pattern found.

Li *et al*. (2005) analyzed the relationships of Pentatomomorpha groups using partial 18S and COI gene sequences. About half of the terminal taxa used in their analysis had sequences from GenBank produced by Wheeler and Schuh. They used parsimony, maximum likelihood, and distance methods to analyze the data. Sequence data were aligned using the default parameters of Clustal and "by eye", and variable regions excluded from the analyses. As results, they found support for a monophyletic Pentatomomorpha and Trichophora in all analyses. Other groups, nonetheless, are in disagreement with previous morphological hypotheses. In the combined parsimony analysis, Lygaeoidea (*sensu* Henry 1997) is paraphyletic with respect to Berytidae and Piesmatidae, the latter two nested within a paraphyletic Pyrrhocoroidea. Having a paraphyletic Lygaeoidea may not be surprising because of the limited taxon sampling within the superfamily, in which only four out of 15 groups (as in Henry 1997) were included. The Coreoidea was found paraphyletic in this combined parsimony analysis. Pentatomoidea was as well paraphyletic because one of the species of Pentatomidae was the sister group of the remaining Pentatomomorpha species less the Aradoidea. In the maximum likelihood combined analysis, the Pentatomoidea was monophyletic. All of the other groups, nonetheless, in this analysis were recovered again as poly- or paraphyletic, with a more scrambled topology compared to that of the parsimony analysis. Despite these surprising findings, Li *et al*. (2005) failed to adequately discuss their results in light of previous morphological hypotheses (e.g., Henry 1997).

More recently, Grazia *et al*. (in press) analyzed the relationships within Pentatomoidea. They employed 135 terminals, using 57 morphological characters, and sequence data from 18S rDNA, 16S rDNA, 28S rDNA, and COI gene regions. They found that Urostylidae *sensu lato* is not monophyletic, and that Urostylidae *sensu stricto* is the sister group of the remaining Pentatomoidea, whereas Saileriolinae should be elevated to family status and placed as the sister group of the remaining Pentatomoidea less Urostylidae *sensu stricto*. Cydnidae is monophyletic only in the morphological analysis, but in the molecular and combined ones it is paraphyletic, in particular because of Corimelaenidae and Thaumastellidae. Parastrachiinae, formerly considered a family different from the Cydnidae (e.g., Sweet and Schaefer 2002), forms a monophyletic group with Corimelaenidae. Pentatomidae is a strongly supported monophyletic group, and based on morphology it also includes Aphylinae and Crytocorinae, sometimes treated as families distinct from Pentatomidae (e.g., Schuh and Slater 1995; Packauskas and Schaefer 1998). The expanded scutellum that occurs in many pentatomoid groups is probably a convergent feature as suggested by their analyses. Clearly, as the authors point out, a broader taxon sampling of Pentatomoidea, and additional and more complete data sets will help clarify the status of several equivocal taxa, in particular of the Cydnidae.

**7g. Cimicomorpha.** After Leston *et al*. (1954) proposed the infraorder, only a few phylogenetic schemes were presented for the groups included. Schuh (1986) reviewed and discussed the schemes of relationships within Cimicomorpha proposed by Kerzhner (1981) and Schuh (1979). He also presented the cladogram of an unpublished analysis of Cimicoidea relationships (see Schuh 1986: 79). Schuh's (1979) analysis differs mainly from that of Kerzhner (1981) in the placement of the Reduvioidea, which Schuh considered to be the sister group to the remaining Cimicomorpha, contrary to Kerzhner's assertion of being a derived clade.

Schuh and Štys (1991) analyzed for the first time the relationships within Cimicomorpha using cladistic methods. They provided a historical review of the terminal taxa used and arguments for the monophyly of each. Schuh and Štys

(1991) used in their analysis a *ground plan* approach for certain characters, and families as terminal taxa instead of species. Their analysis shows that Reduvioidea (i.e., Reduviidae + Pachynomidae) is the sister group to the remaining Cimicomorpha, agreeing with the hypothesis of Schuh (1979), and that Velocipedidae is the sister group of ((Microphysidae + (Joppeicidae + Miroidea)) + (Naboidea + Cimicoidea)).

Schuh *et al*. (in press) reanalyzed the relationships of Cimicomorpha with new characters. The taxon sampling comprised 92 taxa and eight outgroups, using species instead of composite taxa (vs. Schuh and Štys 1991). They prepared a morphological matrix of 73 characters coded for all taxa, and sequence data from 16S rDNA, 18S rDNA, 28S rDNA, and COI, coded for 83 taxa. They also included morphological and sequence data for the recently described family Curaliidae from the Eastern United States (Schuh *et al.* 2008). Their results support a monophyletic Geocorisae (i.e., Pentatomomorpha + Cimicomorpha), but not a monophyletic Cimicomorpha (including Thaumastocoridae) in all analyses. The Thaumastocoridae was found to be polyphyletic when added the molecular data, with the Thaumastocorinae placed as the sister group of Pentatomomorpha, and the Xylastodorinae nested within Cimicomorpha, although their placements are ambiguous. They found that Reduvioidea is monophyletic and nested within Cimicomorpha. Schuh *et al*. (in press) modified the concept of Cimiciformes to include Joppeicidae, Microphysidae, Velocipedidae, and Curaliidae, the first two thus removed from Miriformes of Schuh and Štys (1991). The monophyly of Cimiciformes is supported with several morphological and molecular data. The new circumscription of the Miriformes includes Miridae and Tingidae only (=Miroidea), because the monophyly of Thaumastocoridae was found to be ambiguous (see also Schuh *et al*. 2006).

The two largest groups within Cimicomorpha, Miridae and Reduviidae have been subject of cladistic analyses. Schuh (1974, 1976) proposed different phylogenetic hypotheses of relationship for the Miridae, which were discussed by Schuh (1986). Schuh *et al*. (in press) found a monophyletic Miridae, but with the suprageneric relationships in little agreement with previous morphological hypotheses. Extensive taxon sampling, and additional morphological and molecular characters, may help resolve these incongruences. No other recent attempt of elucidating the higher relationships of the Miridae has been carried out.

Recently, Weirauch (2008) for the first time presented a comprehensive morphological cladistic analysis of Reduviidae using 162 characters and 75 ingroup taxa. She found that Reduviidae is monophyletic, and that Pachynomidae is its sister group, confirming previous views (Schuh 1979; Schuh and Štys 1991). She also found that Hammacerinae is the sister group of the remaining Reduviidae; and the monophyly of the Phymatinae complex, which occupies a basal position, and comprises Centrocneminae, Elasmodeminae, Holoptilinae, and Phymatinae, with Phimophorinae probably included in this clade (not included in her analysis). Other findings show that the Harpactorinae exhibit a relatively basal position; that the Ectrichodiinae + Tribelocephalinae forms a monophyletic group; that Salyavatinae is paraphyletic with respect to Sphaeridopinae and together they form a monophyletic group; the Reduviinae is clearly paraphyletic, and the Triatominae is monophyletic, with some of these "Reduviinae" as sister groups. Future phylogenetic work including molecular markers may test some of the hypotheses presented by Weirauch.

## Economic importance

Most of the groups of Hemiptera are phytophagous. Vast literature exists for groups containing pest species (e.g., aphids, coccoids, psyllids), not restricted to management but also treating their complex life cycles. A review of this literature is beyond of the scope of the paper and thus the reader shall refer to particular references or to some of the general references indicated below.

Many species of Fulgoromorpha and Cicadomorpha are considered pests of cultivated crops. Dietrich (2005) and Wilson (2005) provide keys to economically important groups and provide useful literature.

Schaefer and Panizzi (2000) reviewed the economic importance, both of beneficial and pest species, of several groups of Heteroptera. Most of the economically important groups fall in the group of phytophagous species attacking cultivated crops, although one, Triatominae (Reduviidae), has species that are important vectors of Chagas' disease (Lent and Wygodzinsky 1979).

## Catalogs and identification aids

Far from being complete, this section provides basic references for catalogs and or identification aids, in particular for the Neotropical Region. One general book of entomology, "Insects of Australia" (CSIRO 1991), has useful identification keys that cover South American taxa.

### Identification aids

Hodgson (1994) provided a review of the genera of the Coccidae of the world with illustrations of key characters. Williams and Granara de Willink (1992) provided a synopsis for the Pseudococcidae of Central and South America.

Wilson (2005) provided keys to the economic important species of Fulgoromorpha of the Southeastern United States, with important references on the taxonomy and biology on the group as a whole. Deitz and Dietrich (1993) provided a key to the families of Membracoidea. Deitz (1975) provided keys to the subfamilies of Membracidae. Dietrich (2005) provided an illustrated key to the Cicadomorpha families, and to the subfamilies and tribes of Cicadellidae (except tribes of Deltocephalinae).

Schuh and Slater (1995) is an indispensable source of information for the classification, biology, and faunistics of Heteroptera in general, with keys to subfamilies or tribes of all groups. Comprehensive regional treatments for water bugs have been published for some tropical areas (e.g., Andersen and Weir 2004a). In the Neotropical region, nonetheless, scattered publications provide help to identify regional faunas (e.g., Nieser 1975; Pereira *et al.* 2007). In most cases original literature must be consulted for identification purposes.

### Printed catalogs and lists

Ben-Dov (1993) provided a catalog of Coccidae, Ben-Dov (1994) of Pseudococcidae and Putonidae, Miller and Gimpel (2000) of Eriococcidae, Ben-Dov and German (2003) of Diaspididae, Ben-Dov (2005) of Margarodidae, Miller *et al*. (2005) and Ben-Dov (2006) for several other Coccoidea families. Kondo (2001) provided a list of the Coccoidea of Colombia.

Funkhouser (1927) catalog of the Membracidae, Aetalionidae, and Melizoderidae, was complemented with the additions of Metcalf and Wade (1963, 1965a, 1965b), and McKamey (1998). Metcalf's catalog for the Homoptera (Fulgoromorpha, Cicadoidea, and Membracoidea) is the starting point for much of the literature in Auchenorrhyncha (Metcalf 1932, 1936, 1943, 1945, 1946, 1947a, 1947b, 1954a-c, 1955a, 1955b, 1956, 1957, 1958, 1960a, 1960b, 1961, 1962a-f, 1963a-g, 1964a, 1964b, 1965a, 1965b, 1966a-d, 1967, 1968). Duffels and van der Laan (1985) and Oman *et al.* (1990) updated to the catalogs of Cicadoidea and Cicadellidae, respectively. A checklist with illustrations of the types of Cercopidae species of the New World was published by Carvalho and Webb (2005). Freytag and Sharkey (2002) provided a preliminary list of Cicadellidae from Colombia.

Stonedahl and Dolling (1991) provided a list of catalogs, monographs, and other literature relevant to identification purposes of different groups of Heteroptera. References not included in Stonedahl and Dolling (1991) include: Andersen (1995), for a checklist of the Gerrinae of the World; an update of the catalog of the Miridae (Schuh 1995); the update of the lygaeoid catalog (Slater and O'Donell 1995); the Heteroptera catalog of Australia (Cassis and Gross 1995, 2002); the multivolume catalog of the Heteroptera of the Palearctic Region (Aukema and Rieger 1995, 1996, 1999, 2001, 2006); and the annotated checklist of the Heteroptera of Panama (Froeschner 1999).

## Online catalogs and keys

Although printed catalogs are an indispensable source of information, the information contained is rapidly outdated, and they are more useful if available in digital format, for instance, in mapping taxa distribution in real-time from relational databases, or in showing the most current classification for a group. Furthermore, catalogs can link species and higher taxa to their respective digital publications if available (e.g., Schuh 2006). Many catalogs are already available, for instance, Coccoidea (Sternorrhyncha) (Miller and Ben-Dov 2006); Fulgoromorpha (Bourgoin 2007), Cercopoidea (Soulier-Perkins 2007), (Auchenorrhyncha), and Miridae (Heteroptera) (Schuh 2006). In addition, some regional checklists may provide further assistance in the identification of specimens, for instance, of Neotropical Cicadellidae (Freytag and Gaiani 2002), and the Cicadellinae of Colombia (Vargas-Rojas *et al*. 2006).

In addition, digital keys are now available via the Internet, which can display not only text information, but also color images. Another advantage of some of these keys is that they can be interactive and character based, unlike dichotomous, traditional keys. Identification keys are available for several groups of Hemiptera. For instance, families of Coccoidea (Miller *et al*. 2004); tribes of Cicadellidae (Dmitriev 2006), the genera of Erythroneurini (Dmitriev and Dietrich 2006) and Proconiini (Takiya and Dmitriev 2007); the Deltocephalinae related tribes (Zahniser 2007); families of Heteroptera of Australia (Cassis *et al*. 2002); and the genera of Pentatomidae (Cassis *et al.* 2003) and Tingidae of Australia (Cassis and Bulbert 2004).

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