



ARTÍCULO ORIGINAL

CLASSIFICATION OF HARPACTORINAE, ASSASSIN BUGS (HEMIPTERA: HETEROPTERA: REDUVIIDAE)

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Abstract

A brief synopsis on the classification of the Harpactorinae is presented. The two tribes found in the Neotropical region are discussed and future directions for research are highlighted.

Introduction

Reduviidae, or assassin bugs, have more than 6.000 described species, and is one of the three most speciose families of Hemiptera (Forero 2008), and the second largest of Heteroptera, exhibiting a range of life histories (Schuh and Slater 1995, Weirauch and Schuh 2011). Species in this family are mostly predatory, although species of Triatominae are hematophagous, in which some are important vectors of Chagas disease in Latin America (Lent & Wygodzinsky 1979). Although generally polyphagous, some of the predatory groups show affinities for particular prey, such as ants in Holoptilinae (Jacobson 1911, Miller 1953, Poinar 1991), termites in *Salyavata* (Salyavatinae) (McMahan 1982, 1983), or millipedes in Ectrichodiinae (Miller 1953, Carpintero and Maldonado 1996).

The morphological diversity exhibited by Reduviidae is also reflected in the number of subfamilies so far proposed, which ranges from 21 to 32 (Maldonado 1990, Putshkov and Putshkov 1985). Recent phylogenetic analysis of the family might help to clarify and stabilize several of the classification issues (Weirauch 2008).

Of all Reduviidae subfamilies, Harpactorinae is by far the largest in terms of numbers of species described, with more than 2,000 species described (Maldonado 1990, Putshkov and Putshkov 1985, 1988). Species of Harpactorinae are largely predatory, feeding on a variety of arthropods (Ambrose 2000, Ishikawa et al. 2007, Miller 1953, Read 1927), but a rare case of phytophagy has been reported (Bérenger and Pluot-Sigwalt 1997). Some species have the potential (Ambrose 2002, Ambrose et al. 2009), or have already become successful agents in biological control programs (Grundy and Maelzer 2003, Grundy 2007). Despite its predatory habits, Harpactorinae are also usually closely associated with plants (Bérenger and Pluot-Sigwalt 1997), using them either as a preferred place to capture prey, as oviposition substrate, or as a source of exogenous resin (Bérenger and Pluot-Sigwalt 1997, Choe and Rust 2007, Forero et al. 2011).

Harpactorinae is monophyletic (Weirauch 2008, Weirauch and Munro 2008), and is supported by the following morphological synapomorphies: quadrate cell on the forewing, reduction of the vermiform gland on the bursa copulatrix of the female genitalia, absence of the dorsal connexival suture, and by absence of the metathoracic scent gland and its opening (Weirauch 2008).

In this paper, I briefly review the history of classifications proposed for Harpactorinae and provide an overview on the current taxonomy of the two tribes found in the Neotropical region.

Classification of Harpactorinae

Given its large size, it is not surprising that many classification schemes have been proposed for species of this subfamily. Harpactorinae was first recognized as a group by Amyot and Serville (1843), calling them “Harpactorides”. The group was composed of several genera, including the genus *Harpactor* Laporte. They also recognized three other generic groupings now included within Harpactorinae, the “Saccodérides” (including what is now *Notocyrtus* Burmeister among others), the “Zelides” (including *Zelus* Fabricius among other genera), and the “Apiomerides” (*Apiomerus* Hahn and related genera). Amyot and Serville (1843) distinguished them all from the “Harpactorides” mainly by the body shape, and head and pronotum structure.

Dohrn (1859a) considered the higher groupings of Amyot and Serville (1843) mostly wrong, basically for being too heterogeneous. He circumscribed the Harpactorinae to those genera with “serrate” claws, which were lacking in all the other genera. This character actually is a synapomorphy for a subordinate group within Harpactorinae that include what are now referred as Diaspidiini, Tegeini, and Harpactorini (Weirauch 2008). Dohrn’s (1859a) new conception of Harpactorinae included both the Saccodérides and Zelides groups of Amyot and Serville (1843), as well as the genus *Lophocephala* Laporte, placed by Amyot & Serville in a non related group (Conorhinides). Dohrn (1859a) kept as a separate group the “Apiomeridae”. In the same year, Dohrn (1859b) published a catalog of Hemiptera, and formalized some of his groupings. He named

five groups under his “Harpactorina”: Lophocephalidae (only *Lophocephala*), Sycanidae (*Eulyes* Amyot and Serville, *Sycanus* Amyot and Serville, and *Yolinus* Amyot and Serville), Saccoderidae, Haematocharidae (only *Haematochares* Stål) and Harpactoridae (many genera, including *Harpactor*). In the same catalog (Dohrn 1859b) placed the Apiomeridae under his “Reduvina”, including not only *Apiomerus* and other Neotropical genera, but also the Asian *Ectinoderus*.

Stål (1859a), based on the presence or absence of a tubercle in the mesopleura, pointed out that these two groupings might correspond to what Amyot and Serville (1843) called “Harpactorides” and “Zelides”. Stål (1859c) actually use the name “Hezida” for those with a tubercle (*Heza*, *Arilus*, *Isocondylus*, and related genera), and relegated those without a tubercle under his omnibus “Reduviida” (including *Harpactor*, *Zelus* and related genera). In his later, and probably most influential works, Stål (1872, 1874) dropped the name “Hezida”, favoring a more inclusive “Reduviida”, but still used the tubercle on the mesopleura as an important character to separate a number of Harpactorini genera in his keys.

Stål (1859c) proposed Apiomerinae as a subfamily within Reduviidae, but did not mention which genera should be included, probably following Amyot & Serville (1843) for this. Later on, Stål (1866) proposed Ectinoderinae as a subfamily to include *Ectinoderus* Westwood, *Amulius* Stål, and *Diaspidius* Westwood, separating those genera from his Apiomerinae. Nonetheless, Apiomerinae was later again treated by some authors to include ectinoderines (e.g., Distant 1904).

Stål (1859b) proposed the “Dicrotelida” to accommodate *Nyllius* Stål and *Dicrotelus* Erichson. It was not mentioned in the literature until much later (see below). Stål (1862) suggested the Bactrodinae (as “Bactrodida”) to accommodate the Neotropical genus *Bactrodes* Stål. He mentioned that it was close to the Saicinae (“Saicidis”). The affinities of this group remained unexplored until Davis (1969) analysis.

Distant (1904) used Amyot and Serville name “Harpactorides” over Stål’s “Reduviida” for the Harpactorinae. He proposed (Distant 1904) a number of generic groupings within this subfamily that are equivalent to tribal level ranking: Rhapsidosomaria, Harpactoraria, Vesbiaria, Velinaria, Sycanaria, Yolinaria, Euagorasaria, Panthousaria, Coranusaria, Pristhesancusaria, and Polididusaria. His groupings were based mostly on fauna from the Indian subcontinent, although for Rhapsidosomaria he noticed that some African genera might group with *Rhapsidosoma* Amyot and Serville. Jeannel (1919) elevated to tribal level the “Rhapsidosomaria” of Distant. Most of Distant’s (1904) names have remained unused since their publication, although were consistently used by Hsiao and Ren (1981).

Villiers (1948) proposed Tegeinae as a subfamily, including only in this subfamily the genus *Phonolibes* Stål. He indicated the similarity in forewing venation of this group with the Harpactorinae. Miller (1952) later proposed Phonolibinae, as a separate subfamily from Tegeinae, to include *Phonolibes* and *Lophocephala*. He also redefined the Tegeinae to include only *Tegea* Stål. In the same

paper he described Perissorhynchinae to accommodate his new genus *Perissorhynchus* Miller. He discussed the relationships of Phonolibinae, Tegeinae, and Perissorhynchinae and regarded them as different groupings within Reduviidae. China and Miller (1959), without comment, synonymized Perissorhynchinae under the Phonolibinae.

Miller (1959) proposed the Diaspidiinae to include *Cleontes* Stål, *Rodhainiella* Schouteden, and *Diaspidius*. He discussed some of the characters that differentiate these genera from Apiomerinae, restricting the concept of Apiomerini to include only Neotropical genera, and that of Ectinoderini for *Ectinoderus* and *Amulius*.

Davis (1969), in a seminal paper, studied a group of eight subfamilies that he generically named the “harpactoroids”: Harpactorinae, Rhaphidosominae, Tegeinae, Phonolibinae, Apiomerinae, Diaspidiinae, Ectinoderinae, and Bactrodinae and analyzed several morphological traits present in these groups, compared them to other Reduviidae subfamilies, and proposed a redefined Harpactorinae, in which he included as tribes the redefined groups formerly ranked as subfamilies, Harpactorini, Rhaphidosomini, Apiomerini, Tegeini (including phonolibines), Diaspidiini, and Ectinoderini. He still considered Bactrodinae as a separate subfamily because of the number of different characters compared to his Harpactorinae, but yet related to it. Davis (1969) was the first to use tribal level ranking within Harpactorinae. He redefined previously recognized groups,

for instance the Rhaphidosomini is a modification of the “Rhaphidosomaria” of Distant (1904), and the Tegeini is a redefined group that includes the Tegeinae of Villiers (1948) and the Phonolibinae of Miller (1952). Davis (1969) acknowledged that his redefined Harpactorini was the most generalized group, which in his view lacked any synapomorphies. He also suggested that probably additional tribes should be separated from this tribe, implying that it might not be monophyletic. Despite his important observations, Davis failed to mention or discuss the dicrotelines. Dicrotelini as a tribe was used before Davis’s (1969) paper by Miller (1954), who expanded Stål’s (1859b) concept on the group to include additional genera. Dicrotelini has been subsequently used by several authors (Hsiao and Ren 1981, Malipatil 1988, Cai 1995, Tomokuni and Cai 2002), but its relationships with other members of the Harpactorinae remain uncertain. The classification of the Harpactorinae of Davis (1969) has been widely accepted (Schuh and Slater 1995, Weirauch 2008), and therefore is the one used for the discussion of the Neotropical tribes below.

Villiers (1982) proposed the tribe Rhinocorini (sic) for those genera without a tubercle on the mesopleura. Later, he used Harpactorini (Villiers 1983) for all the remaining genera with such a tubercle. Thus, the Rhinocorini of Villiers is equivalent to Stål’s (1859c) “Reduviida” and his Harpactorini to Stål’s (1859c) “Hezida”.

In an unpublished catalog of Reduviidae, Putshkov and Putshkov (1985) listed all tribal names (mostly following Davis 1969) as synonyms under Harpactorinae.

Similarly, Maldonado (1990) discussed the classification of Harpactorinae and the problems with applying tribal names to some genera. Unlike Putshkov and Putshkov (1985), Maldonado (1990) regarded Harpactorinae in a somewhat restricted sense, including not only the Harpactorini, but also the Dicrotelini, Tegeini, and Rhaphidosomini. He segregated the Diaspidiini, Ectinoderini, and Apiomerini, ranking them as subfamilies. Both catalogs regard Bactrodinae as a separate subfamily (Putshkov and Putshkov 1985, Maldonado 1990).

A morphological phylogenetic analysis of Reduviidae (Weirauch 2008) gave support to Davis (1969) idea of having an inclusive Harpactorinae with several tribes. Weirauch (2008) found support for a monophyletic Harpactorinae, as well as for the tribes Apiomerini and Harpactorini. Ectinoderini, Diaspidiini and Tegeini had one representative each, so their monophyly could not be tested. More recently, Weirauch and Munro (2009) using molecular characters recovered a monophyletic Harpactorinae, but Harpactorini was rendered paraphyletic with the inclusion of one species of Rhaphidosomini sister to *Coranus*.

Future phylogenetic analysis of Harpactorinae in which critical taxa are included, such as Dicrotelini, and more species of Diaspidiini, Ectinoderini, and Rhaphidosomini, should test the monophyly of Harpactorinae, whether or not Harpactorini is paraphyletic with respect to other proposed tribes such as Rhaphidosomini and Dicrotelini, and the placement of Bactrodinae. More importantly, a much denser taxon

sampling of Harpactorini is needed in order to test the ideas exposed above with respect to its suprageneric classification.

Harpactorinae in the Neotropical region

In the Neotropical region two tribes of Harpactorinae are known (following Davis 1969): Apiomerini and Harpactorini (Davis 1969, Maldonado 1990, Putshkov and Putshkov 1985, 1988) (see table 1).

Apiomerini. This is a relatively small group with 12 extant genera (Maldonado 1990, Gil-Santana et al. 2002, 2003, Bérenger 2006) and one fossil genus described from Dominican Amber (Maldonado et al. 1993). Apiomerini have about 150 species, of which most belong to the large genus *Apiomerus* Hahn. Many of the genera are monotypic (e.g., *Beharus* Amyot and Serville, *Ponerobia* Amyot & Serville, *Calliclopius* Stål) or have very few species (e.g., *Agriocleptes* Stål). Only *Heniartes* Spinola is moderate in size, with 31 described species (Forero and Gil-Santana 2003, Gil-Santana and Forero 2010, Wygodzinsky 1947a). Species of Apiomerini are known from the United States south to Argentina, but most of the diversity is concentrated in tropical South America (Gil-Santana et al. 2003). Gil-Santana et al. (2003) provided a synopsis of the genera of Apiomerini, and a key to separate the genera.

Apiomerus, being the largest, has the most problems taxonomically. Champion (1899) treated the Central American species and provided schemes of the external male genitalia for many species. Later Costa Lima and collaborators (Costa Lima et al. 1951, 1952, Costa

Lima and Mendes 1952) described many South American taxa. Costa Lima's work was close to a revision, but still many problems subsist, in particular regarding the correct application of names and the documentation for species. These problems make close to impossible to identify any of the species of *Apiomerus* with confidence. Nonetheless, a revision of the *crassipes* and *spissipes* groups has been finished, and is close to submission (Berniker et al. in prep), and a monograph for the whole genus is now being prepared (Forero and Weirauch, in prep.).

Harpactorini. Stål (1872) provided the only known key to separate the genera of Harpactorini of the Neotropical region.

This key is now badly dated. Many genera have been renamed, a few others have been redefined, and many more have been described since its publication. All these makes very difficult to identify them without all the pertinent literature and a good reference collection.

In the Neotropical region, 51 genera of Harpactorini are found (Bérenger 2003, 2007, Carvalho et al. 2001, Forero et al. 2004, Gil-Santana and Forero 2009, Maldonado 1990, 1992, Maldonado and Farr 1977). *Fitchia* Stål, 1859 is endemic to the Nearctic region and is not found in the Neotropical region. All other genera of Harpactorini from the Nearctic region are shared with the Neotropics.

Table 1. Checklist of the Neotropical genera of Harpactorinae.

HARPACTORINI	APIOMERINI
<i>Acanthischium</i> Amyot & Serville, 1843	<i>Agriocleptes</i> Stål, 1866
<i>Acholla</i> Stål, 1862	<i>Agriocoris</i> Stål, 1866
<i>Ambastus</i> Stål, 1872	<i>Amaurocopius</i> , 1868
<i>Amphibolus venator</i> (Klug, 1830) *	<i>Apicrenus</i> Maldonado, Santiago-Blay & Poinar, 1993 †
<i>Arilus</i> Hahn, 1831	<i>Apiomerus</i> Hahn, 1831
<i>Aristathlus</i> Bergroth, 1831	<i>Beharus</i> Amyot & Serville, 1831
<i>Atopozelus</i> Elkins, 1954	<i>Calliclopius</i> Stål, 1868
<i>Atrachelus</i> Amyot & Serville, 1843	<i>Foucartus</i> Bérenger, 2006
<i>Carmenula</i> Maldonado, 1992	<i>Heniarthes</i> Spinola, 1840
<i>Castolus</i> Stål, 1858	<i>Manicocoris</i> Stål, 1866
<i>Cidoria</i> Amyot & Serville, 1843	<i>Micrauchenus</i> Amyot & Serville, 1843
<i>Coilopus</i> Elkins, 1969	<i>Ponerobia</i> Amyot & Serville, 1843



<i>Corcia</i> Stål, 1859	<i>Sphodrolestes</i> Stål, 1866
<i>Cosmoclopius</i> Stål, 1866	
<i>Debilis</i> Stål, 1859	
<i>Diarthrotarsus</i> Bergroth, 1905	
<i>Doldina</i> Stål, 1859	
<i>Ecelenodalus</i> Elkins & Wygodzinsky, 1957	
<i>Erbessus</i> Stål, 1872	
<i>Graptocleptes</i> Stål, 1866	
<i>Harpactor</i> Laporte, 1833	
<i>Harpactorella</i> Wygodzinsky, 1947	
<i>Heza</i> Amyot & Serville, 1843	
<i>Hiranetis</i> Spinola, 1837	
<i>Iquitozelus</i> Bérenger, 2003	
<i>Ischnoclopius</i> Stål, 1868	
<i>Isocondylus</i> Amyot & Serville, 1843	
<i>Lindus</i> Stål, 1860	
<i>Loboplusius</i> Bergroth, 1909	
<i>Marjoriana</i> Bérenger, 2007	
<i>Montina</i> Amyot & Serville, 1843	
<i>Mucrolicter</i> Elkins, 1962	
<i>Myocoris</i> Burmeister, 1835	
<i>Neotropiconyttus</i> Kirkaldy, 1909	
<i>Nesocastolus</i> Bruner & Barber, 1937	
<i>Notocyrthus</i> Burmeister, 1835	
<i>Orbella</i> Maldonado, 1987	
<i>Pirnonota</i> Stål, 1859	
<i>Ploeogaster</i> Amyot & Serville, 1843	

<i>Pselliopus</i> Bergroth, 1905	
<i>Pyrrhosphodrus</i> Stål, 1866	
<i>Repipta</i> Stål, 1859	
<i>Ricolla</i> Stål, 1859	
<i>Rocconota</i> Stål, 1859	
<i>Sava</i> Amyot & Serville, 1843	
<i>Sindala</i> Stål, 1861	
<i>Sinea</i> Amyot & Serville, 1843	
<i>Sosius</i> Champion, 1899	
<i>Thysanuchus</i> Bergroth, 1918	
<i>Xystonyttus</i> Kirkaldy, 1909	
<i>Zelus</i> Fabricius, 1803	

* This species has been introduced from the Old World (Forero et al. 2004).

† This is a fossil genus (Maldonado et al. 2003).

The following genera have been described after the publication of Stål's key (1872): *Atopozelus* (Elkins 1954a), *Carmenula* (Maldonado 1992), *Coilopus* (Elkins 1969), *Ecelenodalus* (Elkins and Wygodzinsky 1957), *Harpactorella* (Wygodzinsky 1947b), *Iquitozelus* (Bérenger 2003), *Marjoriana* (Bérenger 2007), *Mucrolicter* (Elkins 1962), and *Orbella* (Maldonado 1987).

Of all genera of Harpactorini in the Neotropical region, just a few have been either revised taxonomically or redescribed, whereas others have been treated in just a synoptic way, *Aristathlus* Bergroth (Forero et al. 2009), *Atopozelus* Elkins (Hart 1972b), *Atrachelus* Amyot and Serville (Elkins 1954b), *Castolus* Stål (Maldonado 1976b), *Diarthrotarsus*

Bergroth (Wygodzinsky 1948), *Doldina* Stål (Hussey and Elkins 1955), *Erbessus* Stål (Wygodzinsky 1947b), *Harpactor* Laporte (Wygodzinsky 1947b), *Heza* Amyot and Serville (Maldonado 1976a, 1983), *Ischnoclopius* Stål (Hart 1975), *Nesocastolus* (Maldonado 1993), *Notocyrtus* Burmeister (Carvalho and Costa 1992, 1993), *Sosius* Champion (Maldonado and Carpintero 1993), and *Sava* Amyot and Serville (Coscarón et al. 1999). Hart (1986, 1987) treated the speciose genus *Zelus* Fabricius for North America and the West Indies, but more than 20 new species remain unpublished (Hart 1972a).

Some genera have been treated partially, dealing either with species from a particular geographic area

(e.g., the Mexican species of *Pselliopus* [Brailovsky and Barrera 2004, Brailovsky et al. 2007]), or dealing with a particular group of species (e.g., *Cosmoclopius* [Melo and Coscarón 2002]). But at least is a beginning for a full taxonomic revision.

In many cases genera are not well studied, and even sometimes only the original description is known with no reference to an illustration of its habitus or morphological details. Some of these taxa are badly known because they might be really rare in nature (e.g., *Cidoría*), and therefore in collections, or because the habitats they occur have not yet being targeted by collectors. A few genera have never been mentioned again in the literature, for instance *Loboplusius* Bergroth and *Thysanuchus* Bergroth. Some have never been illustrated, and in a few even the type has been either lost or misplaced (Jansson & Coscarón 1989), complicating the identification of the taxa. Taxonomic revisions are important because they provide a more thorough view on the taxa. For instance, *Notocyrtoides* Carvalho, Costa and Gil-Santana which was described as close to *Notocyrtus* (Carvalho et al. 2001), was later found to be a synonym of *Coilopus* (Gil-Santana and Forero 2009).

Even for those genera which have been revised, many species might still be undescribed. For instance, *Notocyrtus* was revised by Carvalho and Costa (1992, 1993), but still a number of new species have been added afterwards: *N. ricciae* (Gil-Santana and Costa 2001), *N. tibanae* (Costa and Gil-Santana 2001), and *N. costai* (Gil-Santana and Forero 2009).

One of the great challenges is that many of the genera lack good diagnostic characters. Therefore, taxonomic revisions are needed in many cases to provide good documentation of characters. After taxonomic revisions are provided, it still remains the question of the relationships of these taxa with other Harpactorinae of other geographic regions. For instance, we do not know yet if some of the Neotropical taxa are more related to other taxa of the same region or to other regions such as Africa or Asia. Most generic concepts in Harpactorinae are geographically biased, making it difficult to predict when a given genus is a natural group or not.

Future research in Harpactorini has to focus on taxonomic revisions, not only to provide names for new taxa, but also to document characters that allow phylogenetic analysis of the species, and let assess their relationships with other members of the subfamily. A strong emphasis should be put on detailed documentation of male and female genitalia, to make easy future comparisons.

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