

EVOLUTIONARY AFFILIATIONS AMONG HEMIPTERAN (*S. L.*) SUBORDERS; PARAPHYLY OF HOMOPTERA AND NON-MONOPHYLY OF AUCHENORRHYNCHA

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Classification of higher taxonomic levels within Hemiptera (*sensu lato*) have been debated since Linnaeus established the orders Hemiptera (for true bugs) and Homoptera in 1758. Fabricius merged the orders as Ryngota in 1775; later modified to Rhynchota by Burmeister in 1835. Latreille proposed Heteroptera and Homoptera as sections of Hemiptera (*s. l.*); largely accepted to date with exception of the USA, where Hemiptera and Homoptera are still recognized as distinct insect orders (see Henry & Froeschner, 1988; Schuh, 1995).

Disagreement on higher level (suborder) hemipteran classification is largely a reflection of uncertainty with regard to evolutionary affiliations. Post-Darwinian interpretations of phylogenetic affiliations of major hemipteran lineages based on morphology of extant and fossil specimens have been multifarious and contradictory. Heteroptera, often with Coleorrhyncha, has customarily been placed as sister to other Hemiptera. Two major "homopteran" infraorders, Cicadomorpha and Fulgoromorpha, have been generally seen as monophyletic and placed in the suborder Auchenorrhyncha. Other proposals based on morphology, both external and internal, have placed fulgoromorphs and heteropterans as sister groups (Goodchild, 1966; Bourgoïn, 1993). Hamilton (1990), based on a fossil, placed sternorrhynchan whiteflies and fulgoromorphs as sister groups. Paleontomological interpretations by Shcherbekov (1993) render Cicadomorpha para- or polyphyletic. Numerous other morphologically-based studies increasingly support a consensus that Homoptera is not monophyletic and that monophyly of Auchenorrhyncha is uncertain (see: Sorensen *et al.*, 1995; Campbell *et al.*, 1995; and Schaefer, 1996).

Recent studies based on molecular phylogenetic analysis of nucleotide sequences of the gene 18S rDNA, encoding 18S rRNA, infer Sternorrhyncha is sister to all other Hemiptera (Euhemiptera *sensu* Zrzavy), rendering Homoptera paraphyletic, and that Heteroptera is a relatively distal lineage (Wheeler *et al.*, 1993; Sorensen *et al.*, 1995; Campbell *et al.*, 1995; von Dohlen & Moran, 1995). The latter three studies also found little or no support for a monophyletic Auchenorrhyncha. In the studies by Campbell *et al.* (1995) and Sorensen *et al.* (1995) complete or almost complete sequences of the gene were used in the analysis. Complete sequences enabled determination of numbers and positions of synapomorphic sites on the gene which supported basal topology of the hemipteran phylogenetic tree (Fig. 1). Clades for Sternorrhyncha, Euhemiptera, Fulgoromorpha, Cicadomorpha, Heteropteroidea and Heteroptera were all supported by one or more synapomorphic sites when aligned with all insect 18S rDNA sequences published or available from GenBank (>70). There is no synapomorphic site supporting Auchenorrhyncha. However, one site supports a sister relationship between Heteropteroidea and Fulgoromorpha (Neohemiptera *sensu* Sorensen *et al.*).

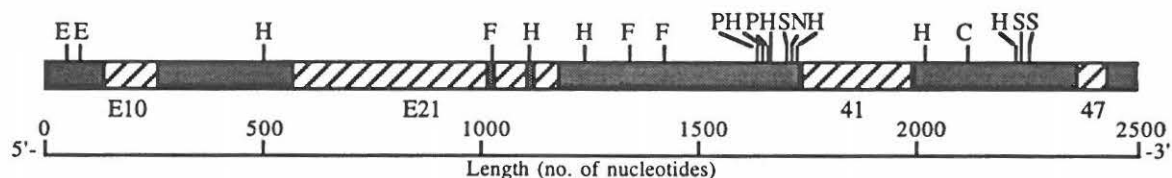


Fig. 1: Distribution of synapomorphic sites on 18S rDNA supporting basal affiliations of major hemipteran (*s. l.*) lineages. Hatched regions correspond to variable helices of synonymous 18S rRNA as defined by Kwon *et al.* (1991). C= Cicadomorpha, E= Euhemiptera, F= Fulgoromorpha, H= Heteroptera, N= Neohemiptera, P= Peloridiidae + Heteroptera (Heteropteroidea *sensu* Zrzavy), S= Sternorrhyncha. These synapomorphic sites are interpreted from alignment of >70 insect 18S rDNA sequences available from the literature and GenBank.

The molecular-based inferred paraphyly of Homoptera, distal placement of Heteroptera, and absence of support for Auchenorrhyncha essentially reflect the relatively recent morphological literature, including debates on lack of support for Auchenorrhyncha (see authors in Schaefer, 1996). The molecular results should certainly stimulate a reassessment of the current classification of higher groups of Hemiptera.

To deal with paraphyly of Homoptera and absence of a monophyletic Auchenorrhyncha, Sorensen *et al.* (1995) proposed four, new suborder names for Hemiptera (Fig. 2). To avoid confusion of “-morpha” suffices, used informally for Cicadomorpha and Fulgoromorpha, with infraorders of Heteroptera (*e.g.*, Enicocephalomorpha, Pentatomomorpha, *etc.*), now a distal clade in hemipteran phylogeny, a “-rrhyncha” suffix is used for conformity. Sternorrhyncha is retained with new suborder names as follows: Clypeorrhyncha (Gr. “shield-nose”) for extant, monophyletic cicadomorphs; Archaeorrhyncha (Gr. “ancient-nose”) to include both fossil and extant fulgoromorphs; Prosorrhyncha (Gr. “front-” or “forward nose”) to replace Heteropterodea.

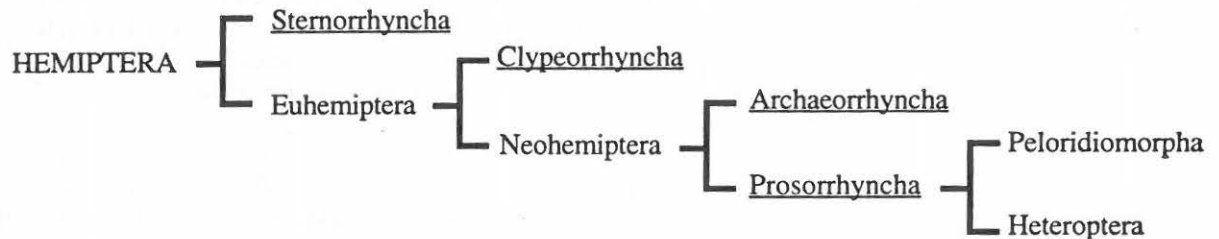


Fig. 2: Phylogenetically based hierarchic nomenclature for major taxonomic groups of Hemiptera (*s. l.*). Proposed new suborder names are underlined. Euhemiptera and Peloridiomorpha are node names previously proposed by Zrzavy.

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