

Fossils *versus* Molecules and Cladistics: Controversies over the Hemiptera Phylogeny

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Ten years ago grouping Heteroptera (+Coleorrhyncha) together with Auchenorrhyncha as Euhemiptera, their sister relationships with Sternorrhyncha, and therefore paraphyly of Homoptera have been inferred from the 18S rDNA (Campbell et al. 1994, 1995; Sorensen et al. 1995; von Dohlen and Moran 1995). There is nothing new under the moon: morphological synapomorphies of Heteropterodea and Auchenorrhyncha have been listed by Emeljanov (1987), their common ancestry has been traced by Popov (1980), and they have been united as Hemelytrata (=Euhemiptera) and opposed to Hymenelytrata (sternorrhynchans and thrips) within Hemiptera by Fallen (1829). So the only novelty was a cladistic claim to abandon paraphyletic Homoptera. However, paraphyletic taxa are inherent in the Linnean classification (Brummitt 2003), so taxonomists and paleontologists will continue to use such concepts as Reptilia, Blattodea or Homoptera. When tracing phylogeny through the fossil record we arrange taxonomic clusters in branched chains of ancestry, rank these clusters according to the hierarchy of hiatuses between them, and accept all non-polyphyletic taxa as natural (Rasnitsyn 1996); holophyly and paraphyly are merely two stages in evolution of a taxon: all paraphyletic taxa had once been holophyletic, and all holophyletic taxa are potentially paraphyletic. Even taxa that do not have any diagnostic characters in common may fall into the same cluster if we find all the intermediate steps between them: ‘The characters do not make the genus; but the genus gives the characters’ (Linnaeus 1751).

For the basal branching of Hemiptera, molecular cladograms differ from morphology- and fossil-based phylogeny (Shcherbakov and Popov 2002). The lineage Psocida (Permopsocina)→Lophioneurina→Thysanoptera is traceable back along with the Hemiptera lineage into the earliest Permian (285 Myr ago), both descending from Paleozoic Hypoperlina. Fossils indicate that Thysanoptera and Hemiptera developed sucking mouthparts in parallel, contrary to their grouping as Condylognatha based on putative synapomorphies (Börner 1904) and 18S rDNA (Johnson et al. 2004).

The Psyllina lineage (Psyllomorpha and their offshoot Aleyrodomorpha, known since the Jurassic – Shcherbakov 2000) and Aphidina lineage (extinct Pincombeomorpha and their descendants Aphidomorpha and Coccoomorpha, both since the Triassic) separated before the mid-Permian (270 Myr) from Permian Paleorrhyncha (=Archescytinina), the stem hemipterans ancestral also to Hemelytrata and showing apomorphies of neither major lineage of the order. Extant Sternorrhyncha are diphyletic, but the transition from Paleorrhyncha to Hemelytrata is not as gradual as those from Paleorrhyncha to Psyllomorpha and to Pincombeomorpha, so one may include Paleorrhyncha in Sternorrhyncha s.l., which thus become paraphyletic with respect to Hemelytrata (Popov 1980). On the contrary, the 18S rDNA points to holophyletic Sternorrhyncha, usually with the topology Psyllomorpha+(Aleyrodomorpha+Aphidina) (Campbell et al. 1994, Aleshin et al. 1995), or a trichotomy in a later analysis (Ouvrard et al. 2000). However, not a single sound morphological synapomorphy of whiteflies with Aphidina has been found, whereas the opposition of Aphidina to Psyllina is well substantiated (Börner 1904, Schlee 1969). Psyllids show deviations from normal 18S rDNA sequence in places of insertions characteristic of the remaining Sternorrhyncha, hinting that these insertions had once been present, but later became lost (Aleshin et al. 1995). Long branch attraction (see e.g. Maddison 2004) may explain association of unusually long 18S rDNA sequences of whiteflies and Aphidina (Shcherbakov 2000).

The basic divergence of Hemelytrata is between Fulgoromorpha and Cicadomorpha (s.l.). Fulgoroidea are known since the mid-Late Permian (260 Myr), and their presumed ancestors, Coleoscytoidea, appeared before the mid-Permian (270 Myr), concurrent with the earliest Cicadomorpha (Prosboloidea: Prosbolopseidae and Ingridae). Cicadomorphans diversified rapidly during the Late Permian. Hylcelloidea, the common ancestors of the three living superfamilies, evolved from Prosboloidea by the Middle Triassic (240 Myr). Coleorrhyncha, traceable back via Progonocimicidae to the latest Permian (255 Myr), are derivable from Ingridae; this lineage evolved in parallel to true bugs, acquiring some superficial similarities but retaining basic differences (Popov and Shcherbakov 1991, 1996). Heteroptera, appearing much later, in the Middle Triassic, share the costal fracture and forewing-thoracic coupling device with, and doubtless descended from, a superfamily of primitive Cicadomorpha, Scytinopteroidea, which, like Coleorrhyncha, is derivable from Ingridae. Ingridids form a base of the Heteropterodea clade, but are deep within the Prosboloidea grade, remaining typical primitive Cicadomorpha and showing no heteropterodean traits, except for a presumed shift of the forewing coupling lobe onto the stem of the Y-vein. Fossils show Cicadomorpha s.l. and Auchenorrhyncha paraphyletic with respect to Coleorrhyncha and Heteroptera (Popov and Shcherbakov 1991, Shcherbakov 1996).

Fulgoromorpha have been united with Heteropterodea as Neohemiptera (making Auchenorrhyncha paraphyletic) based on the 18S rDNA (Sorensen et al. 1995), the same having been suggested earlier on account of anatomical evidence (Goodchild 1966). Support of this grouping became equivocal when Coleorrhyncha were included in 18S rDNA analyses (Campbell et al. 1995, Ouvrard et al. 2000), and subsequent studies suggested a closer relationship of Heteropterodea to Cicadomorpha (Bourgoin and Campbell 2002, Johnson et al. 2004). Putative morphological

synapomorphies of Neohemiptera are either symplesiomorphies, or synapomorphies of Hemelytrata (Y-vein in clavus, transformed to imitate two free veins in extant Cicadomorpha s.str.), or homoplasies not shared by Coleorrhyncha. Mesonotal carinae of Fulgoroidea and some Progonocimicidae and Corixidae represent one more symplesiomorphic trait in 'Neohemiptera'.

Virtually all Triassic Heteroptera are Nepomorpha; these shore or water dwellers are the most hopper-like among bugs (including shorter antennae); other infraorders appeared by the earliest Jurassic (200 Myr), except for enicocephalids known since the Cretaceous (120 Myr). Primitive nepomorphans and leptopodoids were united with homopterans as Hypostomophora and opposed to remaining bugs (Prostomophora) by Spinola (1850). Contrary to cladistic analyses of the morphology (Schuh 1979) and 18S rDNA (Wheeler et al. 1993) showing Enicocephalomorpha as the most basal branch, fossils help us to reconsider character polarity and point to nepomorphans as the most primitive bugs (Handlirsch 1906–1908), to other bug lineages as their descendants, and to enicocephalids as derivatives of Dipsocoromorpha.

Topologies of molecular trees, especially basal branching, are sensitive to choice of outgroup, taxon sampling, alignment parameters, and method of tree reconstruction (Jenner 2004). Using neighbor-joining analysis of 18S rDNA sequences from GenBank, aligned with ClustalW, we obtained trees looking quite reasonable from the paleontological point of view in one or more aspects, such as Aphidina opposed to Psyllina, Coleorrhyncha grouped with Cicadomorpha, Nepomorpha basal to other bugs, etc. Demise of 'Neohemiptera' with molecular methods make us optimistic about remaining controversies, stemming from earlier 18S rDNA analyses of few species. Indeed, comprehensive rDNA analyses of broader sets of taxa agree with fossils and morphology in: (1) placing Cixiidae and/or other cixiid-like families as the most basal branch, and Tettigometridae near the tip, of Fulgoroidea (Shcherbakov 1996, Bourgoïn et al. 1997, Yeh et al. 1998); (2) grouping Cicadoidea with Cercopoidea, Clastopteridae with Machaerotidae, and placing Myerslopiidae at the base of Membracoidea (Shcherbakov 1981; Emeljanov 1987; Hamilton 1999, 2001; Cryan 2004); (3) showing Cicadellidae paraphyletic with respect to Membracidae+Aetalionidae, and Stegaspidae as basal among treehoppers (Hamilton 1971, 1983; Shcherbakov 1992; Dietrich et al. 2001; Cryan et al. 2004); (4) showing archaeococcids paraphyletic with respect to neococcids (Koteja 1996, Cook et al. 2002).

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