Progress in the Phylogeny of the Delphacidae using Molecular and Morphological Tools

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The principle phylogenetic hypothesis for the higher taxa of the Delphacidae is that of Asche (1985, 1990), who proposed 6 subfamilies based on a cladistic morphological analyses (Figure 1). Asche's (1985, 1990) hypothesis has a comb-like structure, with the primitive delphacids (the "Protodelphacida") combined into a paraphyletic subfamily, the Asiracinae, with two proposed tribes, the Ugyopini and the Asiracini. The advanced Delphacidae (the "Eudelphacida") consist of the subfamilies Kelisiinae, Stenocraninae, Plesiodelphacinae and Delphacinae; the latter with tribes Saccharosydnini, Tropidocephalini, and Delphacini. The very large tribe Delphacini includes 75% of delphacid species (1,569 of 2,084 species), and several previously recognized taxonomic groupings (e.g., Stirominae, Achorotilinae, Chlorioninae, Megamelinae, Alohini) dissolved by Asche (1985) because of a lack of synapomprphies. No phylogenetic hypothesis for the Delphacini has been proposed. The Vizcayinae form a "phylogenetic link" between the Protodelphacida and the Eudelphacida (Asche 1990).

Emeljanov (1996) proposed a modification of Asche's (1985, 1990) hypothesis based on features of the immatures. Emeljanov (1996) raised the Ugypini to subfamily status with three tribes (Ugypini, Neopunani, and Eodelphacini), the Asiracini to subfamily status with four paraphyletic tribes (Asiracini, Idiosystatini, Tetrasteirini, and Platysystatini), and subsumed the subfamilies of Eudelphacida plus Vizcayinae as tribes within the Delphacinae (i.e., 7 tribes, Vizcayini, Kelisiini, Stencranini, Plesiodelphacini, Saccharosydnini, Tropidocephalini, and Delphacini) with the same branching sequence proposed by Asche (1985, 1990).

Here we present results of phylogenetic analyses using morphological and molecular data for 49 genera and 86 species, including 3 genera and 4 species of cixiids as outgroups, presented both independently and combined (Table 1). Taxonomic sampling includes all of Asche's (1985, 1990) higher taxa, except for Vizcayinae; and 35 genera and 67 species of Delphacini are included to investigate the relationships among genera of this tribe. The morphological data consists of 139 parsimony informative characters. The molecular dataset consists of 1533 bp of 18s and 1653 bp of 28s ribosomal DNA. All analyses are maximum parsimony as implemented by PAUP* ver 4.0 beta.

Table 1. Taxon Sampling		
Taxon	**# genera**	**# species**
Outgroup: Cixiidae	3	4
Delphacidae		
Ugypinae:		
Ugyopini s.s.	1	1
Neopunanini	1	1
Asiracinae:		
Asiracini s.s.	2	2
Vizcayinae	0	0
Kelisiinae	2	2
Stenocraninae	2	6
Plesiodelphacinae	1	1
Delphacinae:		
Saccharosydnini	1	1
Tropidocephalini	1	1
Delphacini	35	67
Totals	49	86

All of the present analyses suggest that the Protodelphacida are a monophyletic lineage, and that the Plesiodelphacidae are much more primitive than previously suspected. The morphological analysis places the Plesiodelphacidae as the first branch following the Protodelphacida, whereas the molecular and combined analyses place the Plesiodelphacidae *within* the Protodelphacida (Figure 2). The placement of Plesiodelphacidae requires further investigation. The molecular and combined analyses suggest that the Kelisiinae and Stenocraninae are sister groups. Bootstrap analyses suggest strong support for most clades, except relationships among the tribes of Delphacinae were equivocal.

Analyses for the Delphacini consistently suggest relationships among certain genera, however, relationships among clades within the Delphacini varies considerably between analyses. Although some analyses generate few trees (less than 20), bootstrap analyses suggest little support in several positions along the spine of the tree. Analyses are hampered in the current data sets by homeoplasy in the morphological dataset and insufficient variation within the sequenced portions of the 18s and 28s ribosomal genes. Additional data will be required to clarify relationships among the Delphacini.

References:

Asche, M. 1985. Zur Phylogenie der Delphacidae Leach, 1815 (Homoptera: Cicadina: Fulgoromorpha). Marburger Entomologische Publikationen 2(1), volume 1 pp. 1-398, volume 2 pp. 399-910.

Asche, M. 1990. Vizcayinae, a new subfamily of Delphacidae with revision of *Vizcaya* Muir (Homoptera: Fulgoroidea) - a significant phylogenetic link. Bishop Museum Occasional Papers 30: 154-187.

Emeljanov, A. F. 1996. On the question of the classification and phylogeny of the Delphacidae (Homoptera, Cicadina), with reference to larval characters. Entomological Review 75(9):134-150 (translation of Entomologicheskoye Obozreniye 1995 74(4):780-794 from Russian).
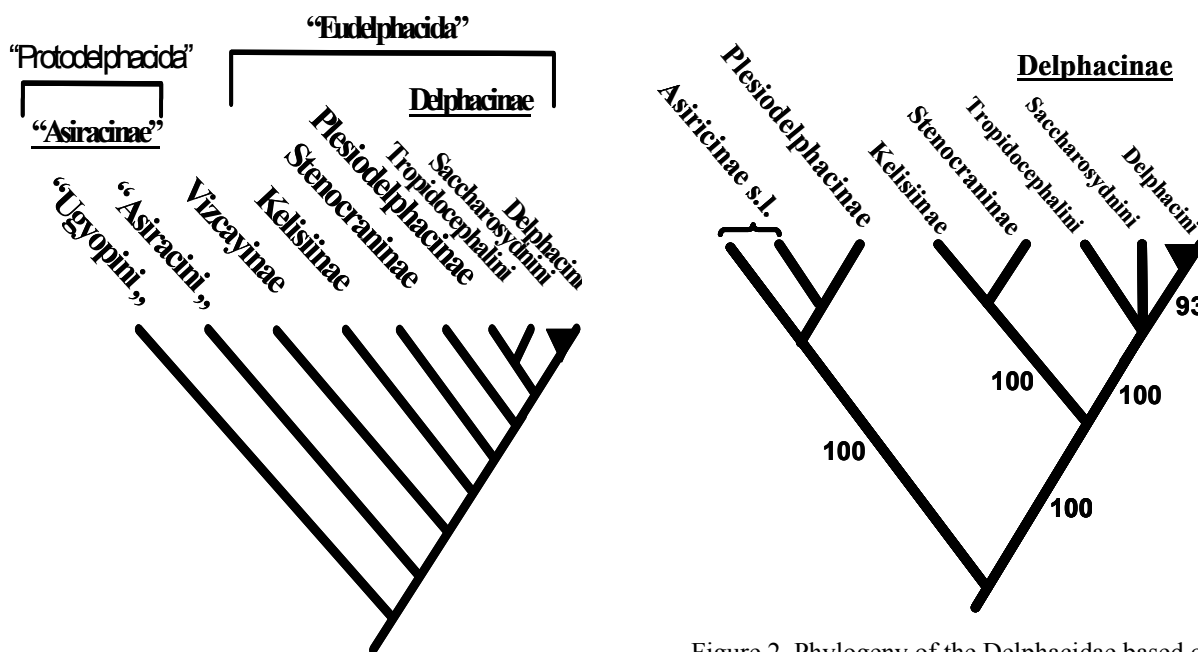
Figure 1. Phylogeny of the Delphacidae according to Asche (1985, 1990)

Figure 2. Phylogeny of the Delphacidae based on combined molecular and morphological analyses (1 tree, CI = 0.819, RI = 0.771). Numbers on branches are bootstrap values based on 100 replicates.

Evolutionary patterns of the Achilidae and their allies (Hemiptera: Fulgoromorpha)

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Fulgoromorpha is a group of Hemiptera that differentiated very early from the common hemipteran ancestors, i.e. Archescytinoidea, known and widely distributed during the Permian. A descendant of Archescytinidae was the earliest Fulgoromorpha — Coleoscytoidea, known from the Permian. Coleoscytoidea were small hoppers, with the frontoclypeus swollen, but not hypertrophied and long rostrum, implying they feed on the phloem or other plant tissues high in nitrogen: buds, seeds, fruits, meristems, etc. of gymnosperms. Coleoscytoidea did not survive the biotic crisis at the Permian Triassic boundary. Their descendants, Surijokocixiidae, are present from Upper Permian through the Triassic, but were a minor element of the fauna. Surijokocixiidae, extinct at end of the Triassic, had been replaced in the Jurassic by Fulgoridiidae, a highly differentiated taxon, believed to be ancestral to all extant Fulgoroidea families. Fulgoridiidae have been common in the Jurassic strata, with over 130 species described in several genera from Western Europe and China (Szwedo *et al*. 2004). Representatives of this family have a characteristic habitus and tegmen venation similar to Cixiidae, recorded since the Late Jurassic/Early Cretaceous. Fulgoridiidae had very long rostra, indicating that they were more often associated with arboreal gymnosperms, sucking from trunks and thick branches, than were extant planthoppers. Their clypeus was not hypertrophied, suggesting phloem-feeding for Fulgoridiidae. Another feature of Fulgoridiidae was distracting color patterns, with dark 'false eye' spots near the apex of tegmen or disruptive, cryptic

patterns with dark spots on tegmina. Nymphs of Fulgoridiidae are not known, but it seems reasonable to assume that they were cryptic, flattened, biscuit-like creatures with short legs, small frontoclypeus and long rostrum. They might have fed on phloem of rather thick stems or in bark cavities (Shcherbakov & Popov 2002, Bourgoin & Campbell 2002). Late Fulgoridiidae or their descendants, lacking the filter chamber of co-existing plant sucking lineages (Sternorrhyncha, Cicadomorpha) probably found fine roots and/or fungal hyphae with relatively nutritious cells that were easily attacked and that had relatively high soluble nitrogen content. Particular types of mutualistic relationships between plant roots and fungi, e.g. ectomycorrhizal, ericoid and orchid mycorrhizae, originated in the Jurassic or Cretaceous and evolved during the rapid angiosperm radiation in the Cretaceous (Brundrett 2002). Sorensen *et al.* (1995) suggested that early Fulgoromorpha initially evolved to feed on roots and fungal hyphae in subterranean/semisubterranean (duff) niches, much as many of their immatures do now. However, this supposition may be restricted only to Fulgoroidea. It is quite evident that the Jurassic/Cretaceous border and Cretaceous period were important times for origination and diversification of main lineages of extant Fulgoromorpha, but fossil data from this period are very scarce (Szwedo *et al.* 2004). Planthopper families recorded from Lower Cretaceous contain more "basal" groups: Cixiidae, Achilidae, probable Derbidae and Fulgoridae, as well as the extinct family Lalacidae, restricted in distribution to Brazil. It is noteworthy that in the Cretaceous some important features appeared: free living nymphs, adult-like and able to jump, in contrast to sessile forms from earlier periods (Shcherbakov & Popov 2002).
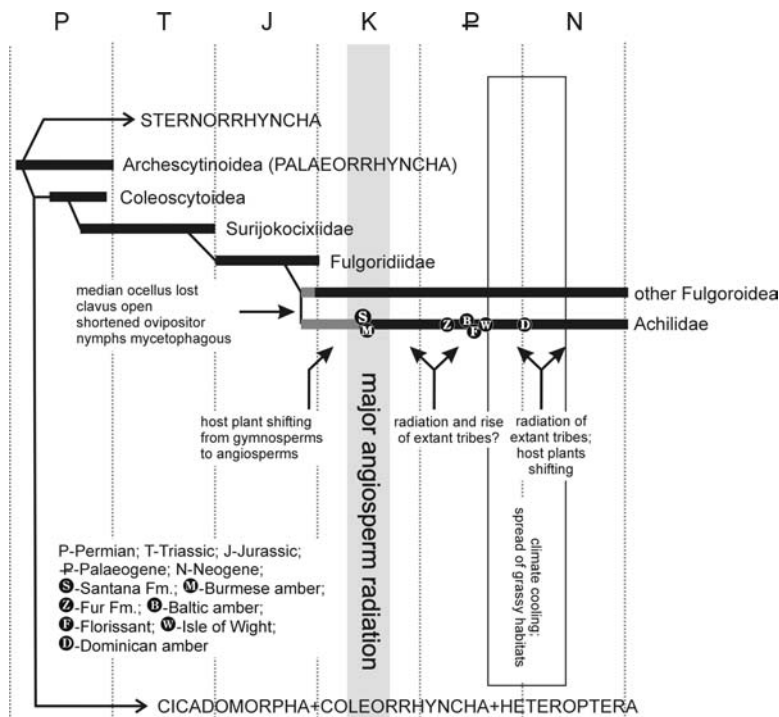

Fig. 1. Scheme of events affecting evolution of Achilidae

The family Achilidae is one of these old families, lying near the basal stock of recent Fulgoromorpha (Fig. 1), but with unresolved taxonomic problems. Numerous fossil taxa ascribed to Achilidae have been described, but some of them with limited validity and a need for revision (Szwedo *et al.* 2004). The first trace of Achilidae is known from the Lower Cretaceous strata of Santana Formation of the Araripe Plateau in North-Eastern Brazil. These fossils have more primitive venation than in extant genera, resembling that of primitive Derbidae. A very long rostrum, extending beyond the hind coxae near the apex of hind femorae, is another feature of these achilids. In Lower Cretaceous amber of Myanmar (Burma), few inclusions have been identified as Achilidae, but only a few of them are preserved in a more or less complete state that would permit further analyses. Only a single species, *Niryasaburnia burmitina* (Cockerell, 1917), is formally described. None of Lower Cretaceous Achildae can be placed among recently recognized tribes of Achilidae (Szwedo 2004). The Palaeocene record of Achilidae seems to be relatively rich both in imprints and in fossil resins. From the Uppermost Paleocene/Lower Eocene strata of Fur Formation from Denmark, a limited number of undescribed Achilidae have been reported. A number of taxa ascribed to Achilidae are known from the Middle Eocene Baltic amber. Baltic amber inclusions of Achilidae are relatively rich and represent most recently recognized tribes, as well as a tribe known only from this period and area. The little known taxon *Elidiptera regularis* Scudder, 1890 comes from Eocene deposits of Florissant, Colorado, U.S.A. Eocene/Oligocene deposits of the Gurnet Bay (Isle of Wight) in England contains *Hooleya indecisa* Cockerell, 1922, originally placed in Derbidae, but transferred to Achilidae. The recent genus *Synecdoche* L. O'Brien was identified in Oligocene/Miocene amber of Dominican Republic, dated 20–15 Mya, and a few specimens are recorded.

Although the data are scarce, some hypotheses could be proposed for the evolution of the Achilidae. It could be hypothesized that ancestral Achilidae lacked a median ocellus, had fused transverse carinae at vertex/frons border, retained a very long rostrum, evolved short pronota, with a shifted and anteriorly elevated disc, fused veins on costal margin, a few branches of longitudinal veins, with more terminals of RA and RP in marginal portion, two-branched CuA, open truncate clavus with veins Pcu+ A_1 entering apex, hind leg tarosomeres basal and middle one with subapical setae and/or platellae, and shortened ovipositor of raking type. Fossil nymphs of Achilidae are not known, but

mycetophagy was postulated for immatures, which is in concordance with raking type of ovipositor. Rotten wood seems to have been used as nymphal habitats by the common ancestor of Achilidae and Derbidae, because in these two closely related families, extant nymphs are mycetophagous and feed under bark, in cavities of rotting wood, or in litter. It appears that soil-dwelling and mycetophagous nymphs have been the source of separation of Achilidae+Derbidae lineage. The ancestral lineage of achilids may have lived in gymnosperm woods, which diversified during the Late Jurassic and Early Cretaceous. Angiosperm radiation seriously affected various groups of insects, and it is probable that some Achilidae shifted from a gymnosperm hosts to woody angiosperms, perhaps during Lower Cretaceous/Upper Cretaceous floristic events. It seems that both groups – gymnosperm-associated and angiosperm-associated Achilidae - survived the late Cretaceous events and extinctions. Some of the plant families known as hosts of Achilidae underwent adaptive radiations during the Eocene and it could be supposed that also some achilids diversified with these host plants, while others, strongly related to conifers became extinct. Terminal Eocene events and climatic cooling in the Early Oligocene (Prothero 1994) also probably strongly affected Achilidae. It seems that accelerated evolution and maybe also host-plant shifting could be related to climatic changes, as well as spread of open communities dominated by grasses and dicotylodones herbs during the Miocene. Switching to new host plants in many cases influenced the speciation rate in phytophagous insects (Farrell 1998, von Dohlen & Moran 2001), and such a situation could also have taken place within Achilidae. It seems that accelerated evolution and maybe also host-plant shifting could be related to climatic changes, as well as the spread of open communities dominated by grasses and dicotylodones herbs during the Miocene. Extant taxa of Achilidae are trophically related to rather old plant families of gymnosperms, dicotyledons, monocotyledons, a few, namely Plectoderini, within Poaceae.

Acknowledgements

References

Bourgoin, Th., and B.C. Campbell 2002. Inferring a Phylogeny for Hemiptera: Falling into the 'Autapomorphic Trap'. pp. 67–82. *In* W. Holzinger, (ed.), Zikaden – Leafhoppers, Planthoppers and Cicadas (Insecta: Hemiptera: Auchenorrhyncha). Denisia 04, Linz, Austria.

Brundrett, M.C. 2002. Coevolution of roots and mycorrhizas of land plants. New Phytologist 154: 275–304.

Farrell, B.D. 1998. "Inordinate fondness" explained: why are there so many beetles? Science 281: 555–559.

Prothero, D.R. 1994. The Eocene–Oligocene Transition. Paradise Lost. Columbia University Press, New York, U.S.A.

Shcherbakov, D.E., and Yu. A. Popov 2002. 2.2.1.2.5. Superorder Cimicidea Laicharting, 1781 Order Hemiptera Linné, 1758. The Bugs, Cicadas, Plantlice, Scale Insects, etc. (= Cimicida Laicharting, 1781, = Homoptera Leach, 1815 + Heteroptera Latreille, 1810). pp. 143–157. *In* A.P. Rasnitsyn and D.L.J. Quicke, (eds.), History of Insects. Kluwer Academic Publishers, Dordrecht / Boston / London.

Sorensen, J.T., Campbell, B.C., Gill, R.J., and J.D. Steffen-Campbell 1995. Non–monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: eco–evolutionary and cladistic implications within pre–Heteropterodea Hemiptera (s.l.) and a proposal for new monophyletic sub-orders. Pan-Pacific Entomologist 71(1): 31–60.

Szwedo, J. 2004. *Niryasaburnia* gen. nov. for '*Liburnia*' *burmitina* Cockerell, 1917 from Burmese amber (Hemiptera, Fulgoromorpha: Achilidae). Journal of Systematic Palaeontology 2(2): 105–107.

Szwedo, J., Bourgoin, Th., and F. Lefebvre 2004. Fossil planthoppers of the World (Hemiptera: Fulgoromorpha). An annotated catalogue with notes on Hemiptera classification. Studio 1, Warszawa, Poland.

von Dohlen, C.D., and N.A. Moran 2000. Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. Biological Journal of Linnean Society 71: 689–717.