

## On Permian and Mesozoic Fulgoroidea

Dmitry E. Shcherbakov

Paleontological Institute RAS, Moscow. E-mail: lab@palaeoentomolog.ru

All higher fulgoroids (with 2nd metatarsal pecten reduced or lost) and most extant families of lower fulgoroids (with the pecten complete) are first recorded in the Cenozoic (last 65 Myr): Delphacidae, Kinnaridae, Derbidae, Fulgoridae, Tropiduchidae, Nogodinidae, Issidae, Flatidae, Lophopidae, Ricaniidae, and possibly Tettigometridae.

In the mid-Late Cretaceous (Santonian, ca. 80 Myr) amber from Taimyr, the oldest member of Dictyopharidae+Fulgoridae lineage is found, *Netutela*, closely related to extant *Cladodiptera* (Emeljanov, A.F. 1983. *Paleontol. Zh.*, 17(3): 77–82). These genera, now in Dictyopharidae, are similar to primitive Fulgoridae (Emeljanov, A.F. 1979. *Tr. Zool. Inst. Akad. Nauk SSSR*, 82: 3–22) in the *cup-pcu* crossvein present. *Netutela* retains a fold at nodus, the character usual e.g. in achilids.

Dictyopharidae and Cicadellidae are the oldest extant auchenorrhynchous families having free-living, adult-like nymphs with long hind legs (such nymphs are known since the Early Cretaceous). The earlier groups of Auchenorrhyncha presumably had the nymphs cryptobiotic (e.g. in soil or under bark) or flat, clinging to the host plant like psyllid ones. Until mid-Cretaceous, nearly all fulgoroids were cixiid-like, and their nymphs probably lived in soil or rotten wood (Shcherbakov, D.E. & Yu.A. Popov. 2002. In: *History of Insects*, Kluwer: 143–157).

From the later Early Cretaceous (Aptian, ca. 110 Myr) of Brazil a family Lalacidae was described (Hamilton, K.G.A. 1990. *Bull. Am. Mus. Nat. Hist.*, 195: 82–122), hardly distinguishable from Cixiidae, except for the metatibial apical pecten often more primitive than in any living fulgoroid. Cixiids and achilids have hind leg spinulation variable (metatarsal pectens either both 1st and 2nd with few asetigerous spines, or 2nd setigerous, or both with numerous setigerous spines), but metatibial pecten always with few asetigerous spines (Emeljanov, A.F. 1987. *Tr. Vses. Entomol. Obshch.*, 69: 19–109). Lalacids extend this morphoserries down (towards ancestral homopterans): their metatibial pecten is also variable, from that with numerous setigerous spines to that with few asetigerous spines as in cixiids. This group may be treated as a subfamily of Cixiidae in the broadest sense, the more so that compression

fossils rarely allow us to determine whether the spines were setigerous. Only one lalacid genus (*Ancorale*) had polymerized venation.

In the earliest Cretaceous (ca. 130 Myr), first Achilidae are recorded. These mycetophagous planthoppers, tree-dwelling and therefore so common in the Baltic amber, in the Cretaceous were small, with venation like in Plectoderini.

In the Late Jurassic (ca. 150 Myr) of Asia, the earliest fulgoroids attributable to Cixiidae are found, having five-keeled mesonotum and rudimentary extravenal pterostigma.

Most of Jurassic planthoppers are referable to Fulgoridiidae, quite abundant e.g. in the Liassic of Germany (ca. 180 Myr). Though their hind leg spinulation is not known in detail, presumably most if not all extinct fulgoroid families had the metatibial pecten setigerous. Fulgoridiidae held wings steeply tectiform and differ from Cixiidae s.l. in the *CuA* forking more proximal in the forewing. *Fulgoridium* had an extremely long rostrum (almost up to the end of abdomen, as in cixiid *Mnemosyne*) and five-keeled mesonotum (median and submedian keels obsolete); the rostrum was of normal length in some other genera. Fulgoridiids show a transition to Cixiidae, but it seems reasonable to keep them as a full family. Few Jurassic planthoppers deviate from fulgoridiid plan, e.g. *Eofulgoridium* with wide precostal area bearing numerous crossveins.

The oldest known planthoppers are from the mid-Late Permian (ca. 265 Myr) and belong to the genera *Scytocixius* (Martynov, A.V. 1937. *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 7(2): 1–91) and *Surijokocixius* (Becker-Migdisova, E.E. 1961. *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 85: 286–293), originally assigned to Cixiidae, but now in a separate family, presumably comprising most if not all pre-Jurassic fulgoroids. Surijokocixiidae were small planthoppers with wings held shallowly tectiform. Forewings usually coriaceous with membrane smooth, costal area broad, precostal carina wide, *C* slightly angulate near base, *R* and *CuA* deeply forked, *M* at least twice forked, *cup-pcu* absent, *Pcu+Al* joining claval commissure. In the type genus, in hindwings *R*, *M* and *CuA* once forked each, corypha transverse rectangular with median keel, pronotum with a pair of lateral keels, mesonotum two-keeled (lateral keels arched mediad). Triassic fulgoroids sometimes show also faint median and submedian keels, some others had crossveins in precostal area or reticulate distal venation.

Therefore, the basic difference between planthoppers and other, cicadomorphous Auchenorrhyncha (Hansen, H.J. 1890. *Entomol. Tidskr.*, 11: 19–76) is traceable back up to the Late Permian or, if little known Permian Coleoscytoidea were indeed ancestral to Fulgoroidea, even up to the earliest

record of Auchenorrhyncha in the latest Early Permian (ca. 280 Myr). Cicadomorpha were quite common and diversified in the Permian and Triassic; they underwent two radiations at the family level and above (five superfamilies and many families extinct, including lineages ancestral to Coleorrhyncha and Heteroptera), and three extant superfamilies of this infraorder are first recorded near the Triassic/Jurassic boundary (ca. 210 Myr). On the contrary, pre-Jurassic Fulgoromorpha were not numerous and little diversified, and Late Permian planthoppers are already cixiid-like, similar to living ones enough to be included in Fulgoroidea, the oldest extant hemipteran superfamily. Such cixiid-like forms retaining evolutionary plasticity of the hind leg spinulation constitute the stem of fulgoroid family tree, and Cixiidae itself changed little during last 150 Myr.

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## ABSTRACTS



RUSSIAN ACADEMY OF SCIENCES  
DEPARTMENT OF BIOLOGICAL SCIENCES  
ST. PETERSBURG SCIENTIFIC CENTRE  
ZOOLOGICAL INSTITUTE

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