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Paradise Lost? – Cretaceous and Palaeogene diversification of planthoppers and leafhoppers

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Abstract

History of the evolutionary changes of the Fulgoromorpha and Cicadomorpha (Hemiptera) in the Cretaceous and Palaeogene is shortly presented. Rapid differentiation and extinction of the groups is related to Mid-Cretaceous biotic events. Early Palaeogene is believed to be the time of dispersal of numerous groups, while Eocene greenhouse time as the period of differentiation and dispersal of descendants of both lineages, including extinct groups. Oligocene cooling and further Miocene biotic changes as the times of origination of recent faunas are discussed in brief.

Key words: Fulgoromorpha, Cicadomorpha, Cretaceous, Palaeogene, faunistic turnover.

Introduction

Fulgoromorpha and Cicadomorpha are ancient lineages of the Hemiptera, known since the Permian. The fossil record and diversity of the ancient Fulgoromorpha have not been very high. Cicadomorpha appears more diversified since their beginnings. Roots of most of the recent groups of Fulgoromorpha and Cicadomorpha could be placed in the Jurassic, or even as far as in Triassic (Shcherbakov and Popov, 2002; Szwedo *et al*., 2004). In the Jurassic the first Fulgoroidea – Fulgoridiidae appeared. The oldest Membracoidea are dated as Uppermost Triassic/Lowermost Jurassic, while Tettigarctidae: Cicadoprosbolinae are dated back to Upper Permian. A few lineages of Fulgoromorpha as Coleoscytoidea, Surijokocixioidea became extinct. It is also true for lineages of Cicadomorpha: Prosboloidea, Pereborioidea, Palaeontinoidea, Hylicelloidea, Dysmorphoptiloidea.

Fulgoromorpha and Cicadomorpha in the Early Cretaceous

Faunistic changes at the Jurassic/Cretaceous boundary were the most conspicuous ones since the beginning of Jurassic and were probably caused by expansion of proangiosperms (Ponomarenko, 1998). The earliest section of the Cretaceous is not well represented in respect to known diversity of planthoppers, leafhoppers and their relatives. The list of taxa placed in the Jurassic family Fulgoridiidae is long, however most of them needs reexamination and redescription. Fulgoridiidae seems to be paraphyletic unit, however it is ancestral to lineages of Fulgoroidea, both extinct and extant. There are a few records of Fulgoroidea from the Lowermost Cretaceous deposits of China, these represent Lalacidae, supposed Cixiidae are listed from deposits of similar age in Russia and UK (Shcherbakov and Popov, 2002; Szwedo *et al*., 2004). Record of Cicadomorpha is richer, it differs from those in Jurassic by dominance of Cicadellidae and relatives among smaller hoppers, while Procercopidae retain dominance in some Early Cretaceous faunas.

Mid-Cretaceous turnover

The mid-Cretaceous is generally referred to as a greenhouse period characterized by exceptionally warm climates. Mid-Cretaceous is regarded as a period of environmental change and biotic crisis (Rasnitsyn, 1988). Angiosperms were more frequent and abundant at lower latitudes in a dry (sub)tropical zone, at that time mainly tropical Gondwanaland, though gymnospermous forests prevailed in wetter climates in the higher latitudes of northern Laurasia and southern Gondwanaland (Scotese, 1997/2003; Anderson *et al*., 1999). By the mid-Cretaceous, some of the extant Fulgoromorpha families present in the fossil record are: Achilidae, probable Derbidae, Cixiidae, Fulgoridae. This period is also characteristic of presence of extinct families: Lalacidae, Neazoniidae, Mimarachnidae and Perforissidae not described families from Spanish, Lebanese and Jordanian ambers, Crato Formation in Brazil and Bon Tsagaan in Mongolia. Until the mid-Cretaceous nearly all fulgoroids were "cixiid-like", with nymphs probably living in the soil or rotten wood as well. Some new kinds of mycorrhizal relationships of plants and fungi are recorded for the first time. Mycetophagous nymphs of Achilidae, Cixiidae and Neazoniidae could use these resources. The first free living nymphs appeared in this time (Lalacidae). In this time some of the remaining Mesozoic families of Cicadomorpha became extinct: Palaeontinidae, Hylicellidae, Procercopidae, Karajassidae. Extant Aphrophoridae and Cercopidae (Cercopoidea) have appeared that time. Cicadellidae, are present in this time, and supposed ancestors of Ulopidae+ lineage and Myerslopiidae.

Late Cretaceous and Early Palaeogene

Fossil record of the latest Cretaceous and the earliest Palaeogene is scarce, however it could be assumed that it was the period of diversification and migration of extant lineages of Fulgoromorpha and Cicadomorpha. The first Dictyopharidae appeared in Taimyr amber, Nogodinidae and/or Ricaniidae are recorded in the Arkhara locality in Siberia and Nogodinidae in Palaeocene of Argentina, Tropiduchidae and Cixiidae(?) are

found in the Orapa locality in Botswana. Cicadomorpha are represented by Cicadellidae in the Canadian amber, Fox Hills in Colorado, U.S.A., Scotland, and in Orapa deposits in southern Hemisphere. The supposed Cicadidae appeared in the Orapa deposits, as well as Cercopoidea are present there. In overall appearance, the Late Cretaceous fauna seems similar to the Palaeogene one.

PETM and Eocene greenhouse world

The number of the still living families was further increasing. During the Palaeocene and Eocene fulgoroids are often dominating in the fossil assemblages. Ricaniidae, Nogodinidae, Issidae, Achilidae and Cixiidae are numerous in Fur Fm. deposits of Denmark. Fulgoridae, Lophopidae and Eurybrachidae are recorded in the Messel Maar, Germany. Baltic amber record is rich in Cixiidae and Achilidae; Delphacidae, Derbidae, Dictyopharidae, Nogodinidae, Tropiduchidae, Issidae are recorded both in ambers and from impressions in sedimentary rocks of northern hemisphere. Another "short-recorded cixiid-like" family (under description) is discovered in the Lowermost Eocene Oise amber of France. Record of Cicadomorpha in the northern hemisphere is relatively rich, while scarce in the southern lands. It is represented i.e. by Tettigarctidae, recently restricted to Australia and Tasmania, but present in France and Scotland, Cercopidae and Aphrophoridae in Greenland and Epipygidae in the Baltic amber, Cicadellidae were widespread and diversified, including extinct groups as Nastlopiinae or Protodikraneurini, as well as recent as Bathysmatophorini and Mileewinae. It could be supposed that during Palaeocene-Eocene Thermal Maximum numerous lineages of fulgoroids and cicadomorphs became widespread throughout the world.

Eocene/Oligocene transition and Late Oligocene cooling

Eocene/Oligocene transition is related to cooling and drying of global climate. However, Fulgoroidea are still numerous in Isle of Wight deposits of UK and in Florissant deposits of U.S.A. Groups present in recent fauna in wet, tropical and subtropical zone are known from much more northern localities. Cixiidae: Bothriocerinae and Mnemosynini, Lophopidae, Tropiduchidae: Jantaritambini, Dictyopharidae: Netutelini (the latter known from the Baltic amber and Taimyr amber respectively) are recorded in Isle of Wight deposits, as well as Cicadidae, Cercopidae, Aphrophoridae and Cicadellidae: Mileewinae and Typhlocybinae. Some other Cicadomorpha, e.g. Clastopteridae appear for the first time in North American deposits and dominate in some other fossil sites. In South America, a few Cicadellidae and supposed Aetalionidae are recorded from the Oligocene Tremembé Fm. in Brazil.

Late Oligocene and Miocene – origin of modern faunas

The environmental changes started in the Oligocene, was continuing in the Miocene. Modern grassland vegetation types are first recorded from the Oligocene, as a result of increased aridity (Bredenkamp *et al*. 2002). This influenced strongly numerous groups, particularly grass-feeding lineages among Delphacidae and Cicadellidae. In both Fulgoroidea and Cicadomorpha lineages the extant genera appear in the fossil record dated as Miocene, e.g. Derbidae, Dictyopharidae and Cicadellidae in deposits of Stavropol' in Russia, Radoboj in Croatia, Cixiidae, Cicadellidae and Cercopoidea in Oeningen and Rott in Germany, and the most famous Dominican and Mexican ambers, with inclusions of modern Cixiidae, Delphacidae, Derbidae, Achilidae, Fulgoridae, Issidae, Cicadellidae, Membracidae, Aetalionidae, etc.

Conclusion

We are still far from the full knowledge on the diversity of modern faunas. It must be remembered then, that the recent faunas are rooted in the past, with relics and exiles from the past paradises, as well as modern forms. These resulted of origination, migration, diversification and extinction – evolutionary processes, which took place, take place and will take place.

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