The 270 Million Year History of Auchenorrhyncha (Homoptera)

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Abstract

The four main stages of the Auchenorrhyncha history as documented in the fossil record are briefly outlined.

Key words: Auchenorrhyncha, fossil.

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Introductory remarks

Auchenorrhyncha (from Greek *auchen*, neck, and *rhynchos*, nose) usually ranked as the suborder of Homoptera (or of the larger order Hemiptera) comprise the planthoppers, leafhoppers, treehoppers, spittlebugs and singing cicadas. There are no common name for the whole group, and referring to all of them as just hoppers would be better, because the earliest Auchenorrhyncha were small, plant- or leafhopper-like, jumping creatures, whereas the large, non-jumping, cicada- or even moth-like forms appeared repeatedly in several hopper lineages.

Fig. 1: A disc-shaped nymph of primitive homopteran (?Archescytinidae), Upper Permian of Southern Siberia. Such short-legged creatures either lived in confined spaces of gymnosperm reproductive organs or clung tightly to the plant surface.

Except for cicadas, Auchenorrhyncha are unfamiliar to non-entomologist, but nevertheless very abundant and diverse (Cicadellidae estimated as the tenth largest family: HAMILTON 1984). It was no less so in the times of dinosaurs and before, when hoppers subdominated in many paleoentomofaunas. Fossil insects better known as attractive inclusions in amber more often (exclusively so before the Cretaceous) exist as compressions in the lake or lagoon sediments, and the stiff hoppers' forewings are almost as readily preserved as, and easier 42classified than, the beetle elytra. The hopper compression fossils were first described by BRODIE (1845) from the Mesozoic of England. Several years later the first Tertiary hoppers from the Baltic amber were named by GERMAR (GERMAR & BERENDT 1856). Permian Auchenorrhyncha were first reported by HANDLIRSCH (1904) from Russia.

The Auchenorrhyncha (and Hemiptera as a whole) is quite an old insect group. It is much younger than the dragonfly or cockroach lineages, of nearly the same age as the Coleoptera, and much older than the Diptera or Hymenoptera. The fossil record reveals taxonomic patterns fitting the traditional systematics rather than cladistics, confirming that the ancestral (paraphyletic, „mother") taxa are no less natural than their holophyletic („daughter") derivatives (see RASNITSYN 1996). The fact that paraphyletic Auchenorrhyncha are ancestral to Coleorrhyncha and to Heteroptera is not sufficient to discard this taxon.

Most Homoptera are plant suckers on the seed plants, and the same life mode is reconstructed for the basal Homoptera and Auchenorrhyncha. Heteroptera originated as littoral (and then aquatic) zoophages, and some groups of true bugs returned to phytophagy later on (in contrast to Coleorrhyncha which remained terrestrial and phytophagous for their entire history). So it is not surprising that the stages of homopteran history coincide with floral rather than faunal ones.

The following account is based mainly on previous papers of the author (POPOV & SHCHERBAKOV 1996; SHCHERBAKOV 1996, 2000; SHCHERBAKOV & POPOV in press; see the references herein).

Permian

The Permian period, concluding the Paleozoic era, was the time of marked climatic zonality not unlike the present-day one. Paleophytic flora characteristic of the preceding Carboniferous was gradually replaced with the Mesophytic one, and in parallel to that the earliest plant-sucking pterygotes, large to giant palaeodictyopteroids were superseded by initially small homopterans. The stem Homoptera, Paleorrhyncha (archescytinids) appeared and flourished in the Early Permian. About the mid-Permian they gave rise to two sternorrhynchan lineages and to Auchenorrhyncha.

The earliest hoppers known lived ca. 270 Ma (million years ago). By that time Cicadomorpha (represented with Prosbolopseidae and Ingruidae, both Prosboloidea) had already separated from Fulgoromorpha (Coleoscytoidea), the common ancestors of these lineages remaining unknown. All hoppers of that time were small, with the postclypeus (housing the muscles of cibarial pump) swollen but not hypertrophied, and the rostrum long, implying they fed on the phloem of stems or reproductive organs of their host plants. Unlike most living hoppers and similar to psyllids, their nymphs were disc-shaped, non-jumping, cryptic creatures (Fig. 1).

During the Late Permian the diversity of Auchenorrhyncha increased almost exponentially, peaking at some 15 families by the end-Permian. True Fulgoroidea (Surijokocixiidae) and three more extinct cicadomorph superfamilies (Pereborioidea, Palaeontinoidea, Scytinopteroidea) appeared. Pereborioids, namely Ignotalidae, reached the size maximal for the group (Fig. 2; wingspan up to 230 mm, nearly same as in living *Pomponia*). These, still silent cicadas contrasted to the tiny ingruid hoppers (some only 3 mm long). Palaeontinoids emerged later and began to flourish already in the Mesozoic.

Remarkably, scytinopteroids share two characters with Heteroptera (costal fracture and perfect 'knob' device for fixing forewing base on mesopleuron), apparently allowing their elytrized forewings to fit the body closely for subelytral air storage (like in nepomorph bugs). These hoppers (in some localities buried in mass together with waterside horsetails) presumably dwelt the rush-like nearshore vegetation and were more amphibiotic than any other homopterans. Most of the Late Permian homopterofaunas are dominated by either Scytinopteridae (Fig. 3) or Prosbolidae (Fig. 4), therefore the latter family probably inhabited biotopes more remote from the water.

Scytinopteridae retaining the head structure and body construction of their prosboloid relatives (Ingruidae) stand nearest to the heteropteran origin. However, true bugs had not appeared before the Triassic. The only Late Permian bug-like forms were basal Coleorrhyncha (Progonocimicidae), likewise derivable from ingruids. The fossils show that superficial similarity between true bugs and coleorrhynchans is due to parallel evolution with retention of nymphal characters at the adult stage, presumably induced by emigration from three-dimensional habitat (foliage) to two-dimensional one (tree bark or littoral ground) with subsequent reduction of jumping abilities.

Homoptera were first recorded in equatorial belt. By the latest Permian they reached the high paleolatitudes (ca. 65°), their faunas differentiated according to zonal biomes, and some primitive groups persisted only in refugia with favourable climate.

Fig. 2:
Forewing of Ignotalidae, terminal Permian or basal Triassic of Eastern Siberia (length of preserved part 47 mm).

Fig. 3:
***Anomoscyta reducta* (Scytinopteridae), Late Permian of Russian North (length 9 mm). Fully three-dimensional preservation quite rare for the insects buried in the bottom sediments allows to study the head and body structure in more detail than usual.**

Triassic

The greatest biotic crisis in the Phanerozoic was associated with catastrophic volcanism at the Permian/Triassic boundary (ca. 250 Ma) causing rapid changes in the sea level and global temperature, anoxia, acid rain, harmful ultraviolet radiation etc. (ERWIN 1994). Climatic zonality was reduced and biogeographic patterns disrupted. Some plants and insects migrated polarwards, e.g. *Rhipiscytina* (Ignotalidae) described from the terminal Permian of China (tropic zone) is recorded in the basal Triassic of Tunguska Basin (high latitudes).

Fig. 4:
Forewing of *Sojanoneura edemskii* (Prosbolidae), Late Permian of Russian North (length 16 mm).

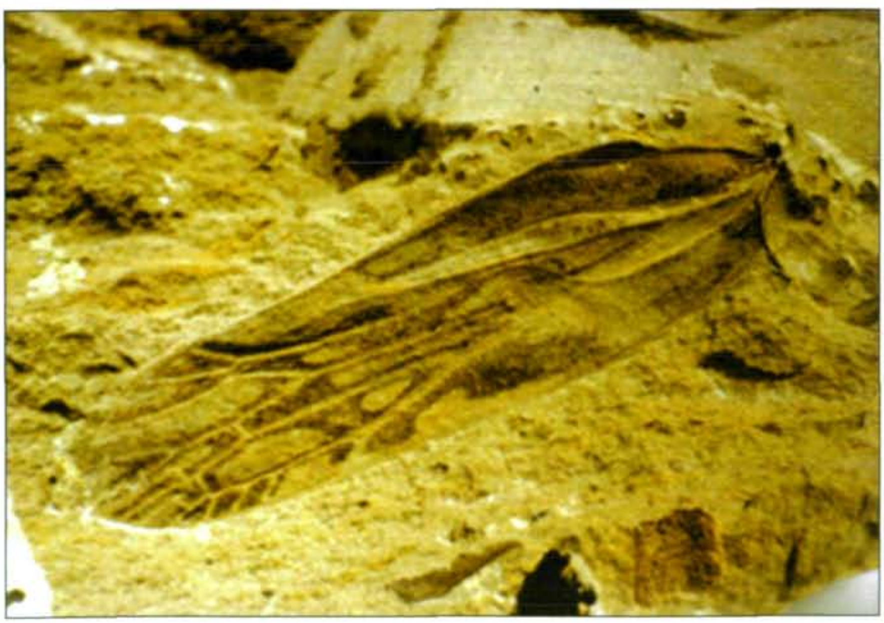

Fig. 5:
Forewing of Hylicellidae with distinctive colour pattern, Middle or Late Triassic of Kyrgyzstan.

Harsh climate resulted in decline of arboreal and peat-forming plants (the latter did not recover for ten million years), and in degradation of terrestrial habitats. Large and specialized forms suffered more than small generalists. Nearly half of the Auchenorrhyncha families went extinct (more than during subsequent crises), and no new ones appeared until the Middle Triassic. Scytinopteroids survived the crisis better than the other hopper lineages, probably due to their association with waterside vegetation.

Some evolutionary novelties are first recorded by the earliest Triassic. The oldest evidence of the insect acoustical communication is the stridulator in prosboloid Dysmorphoptilidae (strigil on forewing underside, plectrum at hind knee); an alarm signal was obviously emitted during escape leap in these cryptic creatures, often having their forewings bizarrely shaped. Some ignotalids with coarsely serrate forewing margin could have been perfectly camouflaged among the foliage of large-leaved gymnosperms.

Since the Middle Triassic the rich homopterofaunas come back to the record. Scytinopteroidea had diversified and gave rise to Heteroptera (initially represented by Nepomorpha). Palaeontinoids became the large cicadas and gradually ousted the last pereborioids. An anti-predator colour pattern, a pair of 'bird eyes' on the forewings, is found in one Triassic dunstaniid. Planthoppers still constituted a minor element of the fauna.

Along with derived scytinopteroids, the core of Triassic fauna was formed by Hylicelloidea (Fig. 5) which descended from Prosbolidae. They had a huge swollen postclypeus indicative of the xylem-feeding, and modified forelegs of some adult hylicellids infer that their nymphs were subterraneous. This group is ancestral to all three modern cicadomorph lineages, Cicadoidea, Cercopoidea and Membracoidea s.l. (all four united as Clypeata). If cryptobiotic non-jumping nymph and xylem-feeding are primary for clypeates (retained in cicadas, Cercopidae, and few primitive leafhoppers), then phloem-feeding and free-living, adult-like nymph in treehoppers and most leafhoppers are the later acquisitions.

Late Mesophytic (Jurassic to mid-Cretaceous)

From the beginning of Jurassic (ca. 205 Ma) the fauna became more similar to the present-day one. Several important extant groups appeared. Superfamilies Cercopoidea (spittlebugs) and Membracoidea (leaf- and treehoppers) were represented by the extinct Procercopidae and leafhopper-like Karajassidae, respectively, both retaining a median ocellus and complete hindwing venation reduced in parallel in their descendants. Cicadoid Tettigarctidae s.l. first recorded in the terminal Triassic is the oldest living Auchenorrhyncha family. In the Mesozoic it was diverse and widespread, in contrast to its present-day relict range in the mountains of Tasmania and Australia. Another modern family of pre-Cretaceous age (since the Late Jurassic) is Cixiidae; more primitive planthoppers fairly common in Early Jurassic faunas belong to related Fulgoridiidae. Among Triassic survivors only Hylicellidae were still abundant.

Palaeontinidae very common in the Jurassic and Early Cretaceous were robust, moth-like, hairy (like living *Tettigarcta*), and probably crepuscular as well, with clinging legs, extremely long rostrum reaching the end of abdomen, and often with disruptive, cryptic wing pattern of dark bands (Fig. 6). They have nearly the same distribution as, and probably fed on, ginkgoalean gymnosperms. Such long rostra were commonplace in Mesozoic Auchenorrhyncha (e.g. Fulgoridiidae) indicating that they were more often associated with arboreal plants than nowadays. Distractive colour pattern (dark „false eye" spots near the forewing apices) attracting predator's attention to the rear end of prey instead of its head seems to be more common in Jurassic than in recent planthoppers.

Around the Jurassic/Cretaceous boundary (ca. 140 Ma) homopterofaunas changed, possibly due to rise of precursors of the flowering plants. Auchenorrhyncha were less affected than plantlice (all the families originating from the Cretaceous onwards survived until now): true leafhoppers (Cicadellidae) and the first mycetophagous planthoppers (Achilidae) appeared in the Early Cretaceous, whereas several groups which flourished in the Triassic and Jurassic (Dysmorphoptilidae, Dunstaniidae, Fulgoridiidae) went extinct.

Cicadellidae and Dictyopharidae (first recorded in the Late Cretaceous) are the oldest modern families with free-living, jumping, adult-like nymphs (several such nymphs are found in the Early Cretaceous); the earlier groups presumably had their nymphs soil-dwelling or cryptic on the host plant. Until the mid-Cretaceous most fulgoroids were represented by Cixiidae and their allies (very diverse e.g. in the Early Cretaceous of Brazil: HAMILTON 1990), and probably lived in the soil or rotten wood at the nymphal stage.

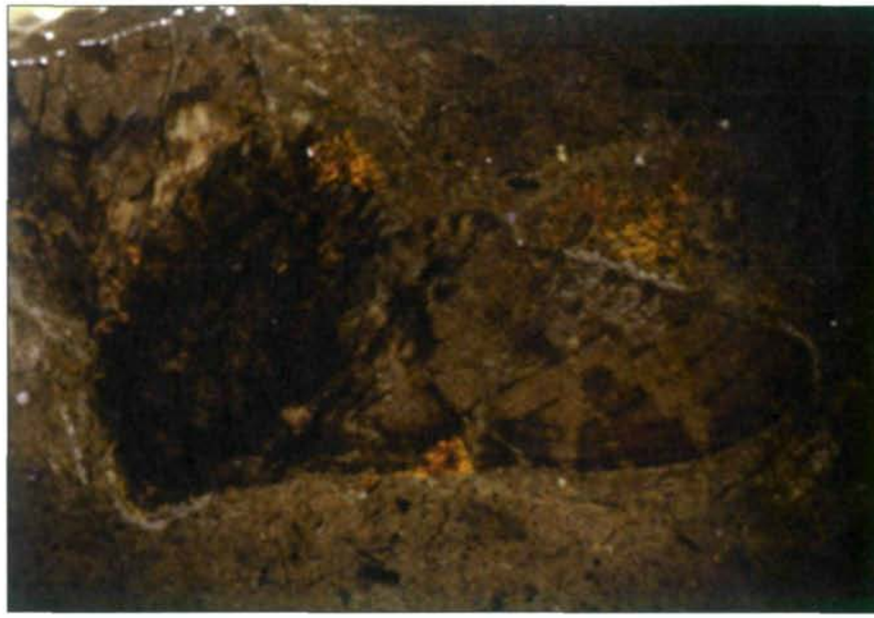

Fig. 6:
***Pseudocossus* sp. (Palaeontinidae), Late Jurassic of Kazakhstan (forewing length 28 mm). Note the long hairs all over the body and very long rostrum.**

Cenophytic

About the mid-Cretaceous (ca. 100 Ma), remaining Mesozoic families died out (Palaeontinidae, Hylicellidae, Procercopidae, Karajassidae). The extant spittlebug families (Aphrophoridae and Cercopidae), and the planthopper family Dictyopharidae entered the record. The Late Cretaceous fauna is quite similar to the Cenozoic one, both containing only the modern Auchenorrhyncha families. Hoppers are not very common in the Cretaceous ambers.

In contrast to dinosaurs and some marine animals, there was no extinction at the family level in Auchenorrhyncha at the Creta-

Fig. 7:
A spittlebug (Aphrophoridae), Early Oligocene of Russian Far East.

Fig. 8:
Members of mycetophagous family Achilidae are more common in the Late Eocene Baltic amber than the other planthoppers.

Fig. 9:
The rarest find - first instar nymph of singing cicada (Cicadidae) entrapped into the resin when travelling down the trunk of amber pine from the site of eclosion to the ground (Baltic amber, Late Eocene).

ceous/Paleogene boundary (65 Ma). In the Paleogene the number of living families further increased: Cicadidae recorded since the Paleocene, Delphacidae since the Eocene, cercopoid Clastopteridae and membracoid Aetalionidae since the Oligocene. Higher planthoppers came into existence, represented by Ricaniidae, Tropiduchidae, Issidae and Flatidae. Another mycetophagous planthopper family, Derbidae has the earliest record in the Baltic amber. The earliest record of Fulgoridae from the Eocene (some 35 Ma: LUTZ 1988, Abb. 103) is attributable to the primitive modern genus *Dichoptera*. Some compression fossil assemblages of that period were dominated by planthoppers, and the others by spittlebugs (Fig. 7); presumably they originated from the warmer and the cooler climate, respectively. Leafhoppers (especially their nymphs) are more abundant than planthoppers (Fig. 8) in the Baltic amber, spittlebugs being quite rare and cicadas exceptionally so (Fig. 9).

The Dominican and Mexican ambers dated near the Paleogene/Neogene boundary (ca. 23 Ma) yielded abundant planthoppers, including the earliest records of Kinnaridae and Nogodinidae, as well as the oldest treehoppers belonging to a primitive subfamily of Membracidae. Treehoppers are surprisingly young derivatives of leafhoppers and seemingly diversified during the Neogene in the modern tropics and subtropics. The oldest living hemipteran species known is the familiar *Cicadella viridis* recorded since the Middle Miocene (some 15 Ma: BEKKER-MIGDISOVA 1967).

Zusammenfassung

Zikaden sind eine sehr alte Insektengruppe; erste Fossilfunde liegen bereits aus dem Perm vor. Aus dem späten Perm sind 15 Familien bekannt, die Hälfte davon starb allerdings am Ende dieses Erdzeitalters wieder aus. Aus der Trias stammen die ersten Belege für akustische Kommunikation. Ab der mittleren Trias nahm die Vielfalt der Hemipteren deutlich zu, die ersten Wanzen traten auf. Aus der Jura stammen die ältesten Nachweise zweier rezenter Familien, der Cixiidae und der Tettigarchidae.

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